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par

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# Evolution de la biodiversité des trilobites du Dévonien d’Afrique du Nord : richesse taxonomique, disparité morphologique et impact de l’environnement

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Thèse dirigée par

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## RÉSUMÉ :

L'effet des changements environnementaux sur la biodiversité actuelle est une préoccupation majeure. Comprendre l'impact de ces changements sur la biodiversité passée est une des clés pour pouvoir appréhender les bouleversements actuels et futurs. Les trilobites, ont connu de nombreux changements favorables à leur diversification ainsi que de nombreuses crises les amenant proche de l'extinction. Leurs fossiles abondent en Afrique du Nord, ce qui en fait une région idéale pour les étudier. L'objectif de cette thèse a été d'estimer les variations de la biodiversité des trilobites de cette région et d'en identifier leurs origines et conséquences à partir de bases de données compilant l'ensemble des occurrences issues de la littérature. Le premier aspect de la biodiversité étudié a été celui de la richesse taxonomique. A l'aide de différents indices de diversité, on a évalué les grandes tendances globales puis les variations régionales. Alors que la diversité générique était faible au début du Dévonien, une régression marine a ensuite conduit à une importante diversification, visible à l'échelle globale : la diversification Praguienne. Les trilobites atteignirent un pic de diversité à l'Emsien, mais par la suite, une succession de changements abrupts du niveau marin associés à de l'anoxie les ont affectés sévèrement. Entre l'Eifelien et le Givétien, les trilobites ont perdu plus de 90% de leur diversité générique. Celle-ci devient encore plus faible au Frasnien et deux ordres disparurent. Après l'extinction de masse du Kellwasser à la limite Frasnien-Famennien, une légère récupération eut lieu impliquant uniquement les ordres Proetida et Phacopida. Le deuxième aspect a été d'étudier la disparité morphologique avec l'aide de points homologues et d'analyses Procruste. Cette étude de la variabilité morphologique a montré les mêmes tendances que celle de la diversité avec un nombre important d'innovations au Dévonien inférieur. Parmi les nouveautés on a noté le développement d'épines. Si les premiers événements biotiques n'ont conduit qu'à une faible perte de morphologies, la plupart des formes ont disparu au Givétien. Les formes les plus touchées sont celles apparues au Praguien et à l'Emsien alors que les formes héritées du Silurien vont se maintenir tout au long du Dévonien. La versatilité de ces formes vis-à-vis des changements d'environnements ou de mode de vie les a aidés à survivre, les ordres caractérisés par ces morphologies ont pu ainsi résister aux différentes crises écologiques. La transition Frasnien-Famennien a marqué le développement des trilobites à vision réduite en réponses aux événements environnementaux. La diversité et la disparité des trilobites d'Afrique du Nord sont donc relativement couplées. Une attention particulière a été donnée aux phacopidés, une famille emblématique du Dévonien qui y atteindra son apogée avant de disparaitre à la fin de la période. Les variations géographiques ont aussi joué un rôle important dans la biodiversité des trilobites avec d'importants échanges fauniques qui ont caractérisé les environnements homogènes du Dévonien inférieur. A contrario, les disparités géographiques et les événements tectoniques du Dévonien moyen et supérieur ont empêché les migrations et les échanges fauniques et ont accéléré le déclin des trilobites. En conclusion, cette étude régionale a montré que les changements environnementaux ont eu des effets importants sur la biodiversité mais que ces effets ont pu être positifs ou négatifs. Un même type de changement peut aboutir à des conséquences différentes en termes de diversité et de disparité car plusieurs phénomènes peuvent intervenir en même temps et l'estimation de leur impact mutuel reste primordial.

**Mots-clés :** Trilobites, Dévonien, Afrique du Nord, Extinction, Changements environnementaux, Diversité, Disparité morphologique

## ABSTRACT:

The effect of environmental changes on current biodiversity is a major concern. Understanding the impact of these changes on past biodiversity is one of the keys to interpret current and future upheavals. The trilobites have undergone many changes favourable to their diversification as well as many crises leading them close to extinction. Their fossils abound in North Africa, which make it an ideal region to study them. The objective of this thesis was to estimate the variations in the biodiversity of trilobites in this region and to identify their origins and consequences from databases compiling all the occurrences of the literature. The first aspect of biodiversity studied was the taxonomic richness. Using different diversity indices, we assessed the major global trends and then regional variations. While generic diversity was low at the beginning of the Devonian, a subsequent marine regression led to an important diversification, observable at a global : the Pragian diversification. Trilobites reached a peak of diversity in the Emsian, but subsequently a succession of abrupt sea level changes associated with anoxia events severely affected them. Between the Eifelian and the Givetian, trilobites have lost more than 90% of their generic diversity. Generic diversity still decreased in the Frasnien and two orders disappeared. After the Kellwasser mass extinction at the Frasnian-Famennian boundary, a slight recovery occurred involving only the Proetida and Phacopida orders. The second aspect was to study the morphological disparity by using landmarks. This study of morphological variability showed the same trends as that of diversity with a significant number of innovations in the Lower Devonian. Among the novelties, there was the development of spiness. While the first biotic events only led to a slight loss of morphology, most forms disappeared in the Givetian. The most affected shapes are those that appeared in the Pragian and Emsian, while the forms inherited from the Silurian persisted throughout the Devonian. The versatility of these forms toward environmental or lifestyle changes helped them to survive, as the orders characterized by these morphologies were thus able to withstand various ecological crises. The Frasnien-Famennien transition marked the development of reduced vision trilobites in response to environmental events. The diversity and disparity of North African trilobites are therefore relatively coupled. Particular attention was given to phacopids, an emblematic Devonian family which reached its peak there before disappearing at the end of the period. Geographic variations also played an important role in the biodiversity of trilobites with important faunal exchanges that characterized the homogeneous environments of the Early Devonian. Conversely, the geographic disparities and tectonic events of the Middle and Late Devonian prevented migration and wildlife exchanges and accelerated the decline of trilobites. In conclusion, this regional study showed that environmental changes had significant effects on biodiversity but that these effects could be positive or negative. The same type of change can lead to different consequences in terms of diversity and disparity because several phenomena occurred at the same time and it is essential to estimate their combined effect.

**Keywords:** Trilobites, Devonian, North Africa, extinction, environmental changes, diversity, morphological disparity

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# SOMMAIRE

# INTRODUCTION

## 1. Evolution en temps profond

Depuis l’apparition de la vie il y a plus de 3,5 milliards d’années (Nutman et al., 2016 ; Dodd et al., 2017), la biodiversité a beaucoup changé. Les changements sont de différentes natures avec des variations de forme, d’abondance, d’écologie, de métabolisme et bien d’autres (Bambach et al., 2002 ; McNamara, 2008 ; Alroy, 2010 ; Klug et al., 2010). Comprendre ces modifications et expliquer la disparition de certaines espèces au cours des temps géologiques est devenue une préoccupation scientifique et sociétale majeure (Bellard et al., 2012 ; Jones et Cheung, 2015 ; Briggs, 2017 ; Worm et Lotze, 2021). L’étude de ces changements de biodiversité peut être abordée selon deux échelles évolutives complémentaires : la macroévolution et la microévolution (Erwin, 2010 ; Li et al., 2018). La microévolution concerne tout ce qui se passe à l’échelle intra-spécifique, notamment les changements génétiques au sein des populations (Hendry et Kinnison, 2001) alors que la macroévolution se réfère aux changements supra-spécifiques (Hautmann, 2020). Ainsi, si les biologistes tentent de comprendre les extinctions actuelles et leurs conséquences potentielles, les paléontologues contribuent à cet effort en analysant l'évolution de la biodiversité dans le temps profond. Un objectif essentiel en macroévolution est de mieux connaître les événements de la biodiversité telles que les phases d'extinction et de radiation (Sepkoski, 1984 ; Jablonski, 1994 ; Kirchner et Weil, 2000 ; Bambach et al., 2004 ; Erwin, 2008). Ces événements sont souvent consécutifs à des changements paléoenvironmentaux et leurs études permettent notamment de comprendre les modalités (mode et rythme) d'évolution (Eldredge et Gould, 1972). C’est dans ce cadre d’évolution de la biodiversité en temps profonds que s’inscrit cette thèse.

### 1.1. Evolution et paléobiodiversité

L’étude de la biodiversité passée - la paléobiodiversité - et son évolution au cours du temps se base surtout sur le registre fossile (Benton et Harper, 2021). L’enregistrement des données fossiles a fortement augmenté depuis l’explosion cambrienne avec le développement d’organismes biominéralisés plus facilement préservables (Briggs, 2015). La préservation des fossiles n’est d’ailleurs pas homogène ni dans le temps, ni dans l’espace (Holland, 2016). De plus, de nombreux organismes sont composés majoritairement - voire complètement - de tissus mous et restent difficilement conservés au cours des temps géologiques (Briggs, 1995 ; Klompmaker et al., 2017 ; Purnell et al., 2018). Ils sont surtout connus grâce aux sites à conservation exceptionnelle, les Lagerstätten, dont l'un des plus connus est celui de Burgess (Morris 1979 ; Gaines 2014). Ce problème de préservation s'ajoute à d'autres biais d'échantillonnages comme l'effort d'échantillonnage (Tarver et al., 2007). Ces biais compliquent le travail des paléontologues, l'étude de la paléobiodiversité se basant sur l'abondance et les caractéristiques des fossiles.

Les savants ont cherché à comprendre ce qu'étaient ces fossiles et pourquoi il y avait de tels changements de forme dès l'Antiquité. Les doctrines telles que l'établissement des modalités évolutives, l'identification des processus mis en jeu et l'évaluation de l'impact de l'environnement se sont basées sur les études de la forme des organismes (Simpson, 1953 ; Eldredge et Gould, 1972 ; Hunter, 1998 ; Gayon, 2000 ; Gerber et al., 2008). Les premières véritables théories de l'évolution n'ont été établies qu'au XIX$^{\text{ème}}$ siècle par Jean-Baptiste Lamarck puis Charles Darwin. Charles Darwin met en avant la sélection naturelle comme mécanisme de l'évolution (Darwin, 1859 ; Greenberger, 2005). Il explique que l'élimination des individus les moins adaptés à la survie permet aux espèces de se perfectionner. Au XX$^{\text{ème}}$ siècle, la théorie a évolué avec le courant Néo-Darwiniste emmené notamment par Ernst Mayr, Theodosius Dobzhansky et George G. Simpson. Ces scientifiques ont établi la Théorie Synthétique de l'Evolution (TSE, Huxley, 1942), attribuant les changements évolutifs aux mutations génétiques aléatoires adoptées ou non par la sélection naturelle. La sélection naturelle est donc le moteur de l'évolution, l'adaptation à l'environnement est le seul critère d'évolution à partir de mutations (Gould, 1984). Les espèces doivent alors évoluer en permanence pour survivre dans un environnement sans cesse changeant : c'est la théorie de la Reine Rouge (Van Valen, 1973). La question de l'impact de l'environnement sur la biodiversité est donc primordiale. Cependant, lors des dernières décennies, les avancées réalisées en biologie et en paléontologie ont montré que la Théorie Synthétique de l'Evolution était trop simpliste (Alberch, 1982 ; Smith, 1992 ; Lenski et Mittler, 1993). Les Néo-Darwinistes ont situé l'évolution au niveau des populations et ont négligé les mécanismes au niveau de l'individu et en particulier au niveau de l'ontogénèse (Depew et Weber, 1989). Cette phase développementale a pourtant un rôle majeur dans les mécanismes de l'évolution (Alberch, 1980 ; Minelli, 2003 ; Klingenberg, 2010) et a été intégrée dans la théorie actuelle connue sous le nom d' « Evo-Dévo ». L'environnement reste cependant un acteur majeur de l'évolution même si selon certaines théories, la sélection des mutations reste très limitée : c'est le neutralisme (Kimura 1983). La sélection naturelle agit donc en fait plutôt comme un filtre à partir d'une évolution dirigée par les contraintes développementales et la dérive génétique. L'évolution se fait donc au niveau de l'individu, mais se manifeste à différents niveaux taxonomiques.

Les variations spatiale et temporelle de l'environnement sont donc en partie source de divergence écologique, amenant à des espèces différentes avec des morphologies et des écologies différentes (Erwin, 1993, 2015 ; Dumont et al., 2012). La spéciation est notamment une composante primordiale des changements de paléobiodiversité, les espèces étant des lignées de métapopulations évoluant séparément (De Queiroz, 2007). Il est donc important de quantifier les morphologies (i.e., la disparité morphologique) et la biodiversité au cours du temps pour comprendre les adaptations et ainsi interpréter les processus de diversification.

### 1.2. Paléobiodiversité, crises biotiques et phases de récupération post-crise

Bien que les écosystèmes précambriens sont de mieux en mieux identifiés (Buatois et Mángano, 2016 ; Darroch et al., 2018), les études de paléobiodiversité se focalisent surtout sur le Phanérozoïque (Raup et Sepkoski, 1982 ; Alroy et al., 2008 ; Fan et al., 2020). La diversité a rapidement augmenté au Cambrien avant de fluctuer pendant les 500 millions d'années qui suivirent. Les clades phanérozoïques connaissent généralement un pic de diversité assez tôt dans leur histoire évolutive (Hughes et al., 2013). Ce type de clade est appelé « *Bottom Heavy Clade* » (Gould et al., 1987). En plus des changements quantitatifs, le paysage biologique a changé avec le renouvellement des faunes et des flores au cours du temps (Sepkoski, 1981 ; Alroy, 2010 ; Capel et al., 2021). La biodiversité est notamment dirigée par les changements environnementaux aussi bien à long qu'à court terme (Roberts et Mannion, 2019).

Au cours du Phanérozoïque, des phases d'extinctions brutales sont venues perturber la biodiversité avec la disparition de nombreux clades (Raup et Sepkoski, 1982 ; Bambach, 2006) et une modification considérable de la biosphère (Jablonski, 2005). Ces crises biotiques sont causées par des perturbations plus ou moins brutales de l'environnement à grande échelle (Hallam, 1998 ; Bond et Grasby, 2017). Parmi les causes des extinctions de masse on retrouve le volcanisme (Wignall, 2001 ; Bergquist, 2017), la chute d'astéroïdes (Schulte, 2010), les changements climatiques (Song et al., 2021), les variations eustatiques associées à des événements anoxiques (House, 2002), les paramètres orbitaux (De Vleeschouwer et al., 2017), tous ces facteurs pouvant être étroitement liés. Cinq extinctions ont notamment eu un impact considérable sur la paléobiodiversité : ce sont les cinq extinctions de masses (Raup et Sepkoski, 1982). Elles ont eu lieu à la fin de l'Ordovicien, à la fin du Dévonien, à la limite Permien-Trias, à la limite Trias-Jurassique et à la limite Crétacé-Paléogène (Fig. 1) et ont toutes conduit à la disparition de plus de 75% des espèces (Jablonski, 1994), la plus sévère étant celle survenant à la fin du Permien (Erwin, 1990). D'autres crises ayant eu un moindre impact ont aussi eu lieu au cours du Phanérozoïque (Walliser, 1996 ; House, 2002 ; Bambach, 2006). Outre les extinctions brutales que constituent les crises biologiques, la biodiversité est en renouvellement sans-cesse avec des apparitions et des disparitions continuent d'espèces (Hartvigsen, 2013). Ce bruit de fond est majoritairement dû à des facteurs biotiques tels que la compétition et la prédation (Hartvigsen, 2013). Les taux d'apparitions augmentent en périodes de faible diversité, après les extinctions, et au contraire, les taux d'extinctions augmentent en périodes de forte diversité (Alroy, 2008). Les extinctions ayant conduit à la disparition de nombreux taxons, les survivants peuvent coloniser de nouvelles niches laissées vacantes et ainsi se diversifier : c'est l'hypothèse de l'éco-espace vide, ou « *empty ecospace* » (Erwin, 1993, 2001). Ces nouvelles opportunités peuvent conduire à la diversification écologique et morphologique des taxons, c'est une radiation adaptative (Erwin, 2015 ; Jablonski, 2017 ; Stroud et Losos, 2016). Ce phénomène est en partie le moteur des récupérations post-crises, périodes plus ou moins longues où la biodiversité redémarre (Jablonski, 1994, 2005). Cependant, certains clades ayant échappé à une extinction ne connaissent pas de récupération et restent longtemps appauvris avant de disparaitre, ce sont les « *Dead Walking Clade* » (Jablonski, 2002 ; Barnes et al., 2021).

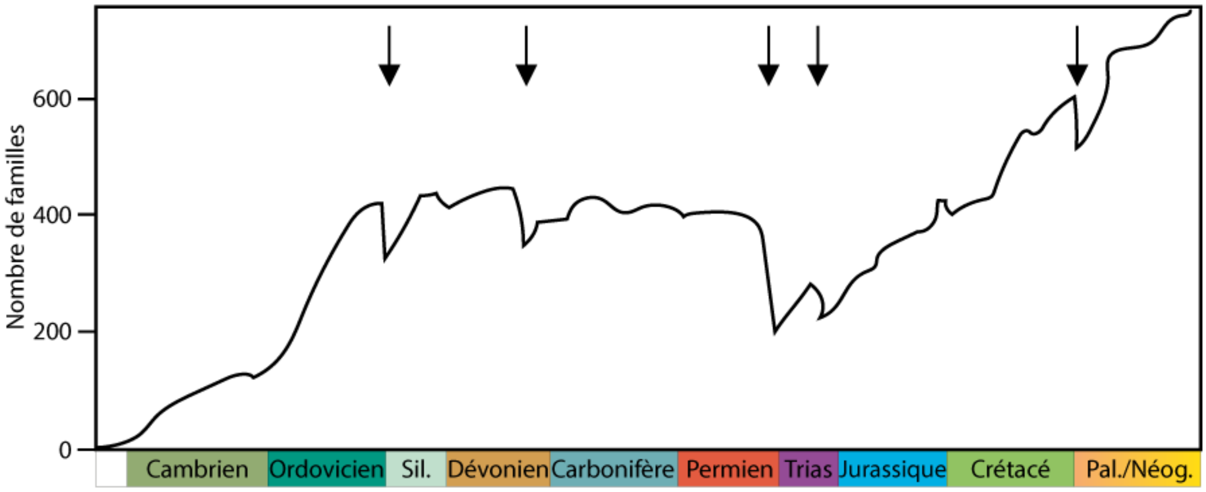


***Figure 1 :*** *Evolution de la diversité des organismes marins au cours du Phanérozoïque et position des cinq extinctions de masse (modifié d'après Raup et Sepkoski, 1982). Abréviations : Sil. : Silurien ; Pal. : Paléogène ; Néog. : Néogène*

### 1.3. Macroévolution et disparité

Lors des dernières décennies, de nombreuses études ont montré l'intérêt d'analyser la disparité morphologique des clades (Roy & Foote, 1997 ; Neige, 2003 ; Adams et al., 2004, 2009), la macroévolution reposant principalement sur l'étude de la forme des organismes. En quantifiant la diversité de formes dans différents contextes, cette métrique est largement complémentaire de la diversité taxonomique, longtemps considérée comme la métrique standard de l'étude de la biodiversité et de ses fluctuations (Sepkoski, 1978 ; Hallam et Wignall, 1997). L'approche morphologique n'est pas nécessairement corrélée avec l'approche taxonomique. Leur confrontation dans le temps (Roy et Foote, 1997) et dans l'espace (Neige, 2003) est une source importante de compréhension des fluctuations de la biodiversité à grande échelle, en termes de patrons et de processus.

La disparité morphologique s'est accrue dès le Paléozoïque inférieur et a continué à s'étendre ensuite (Foote, 1993 ; Deline et al., 2018). En effet, les clades se diversifient morphologiquement généralement assez rapidement au cours de leur histoire évolutive (Hughes et al., 2013), bien qu'une augmentation tardive de disparité morphologique puisse se produire (Hopkins et Smith, 2015). Disparité morphologique et diversité peuvent être couplées bien que ce ne soit pas automatique (Foote, 1993). Ainsi, au-delà de l'aspect quantitatif, les crises biologiques impliquent des modifications morphologiques avec des changements de taille (Harries et Knorr, 2009), de la perte de morphologies (Korn et al., 2013 ; Puttick et al., 2020 ; Cole et Hopkins, 2021) et des innovations (Friedman, 2010 ; Schoenemann, 2018 ; Lowery et Fraas, 2019) en lien avec les changements environnementaux. Une perte de morphologie peut mettre en évidence la sélectivité des extinctions, ce qui n'est pas systématiquement le cas (Peters, 2008 ; Janevski et Baumiller, 2009 ; Korn et al., 2013 ; Payne et al., 2016 ; Cole et Hopkins, 2021). Les innovations peuvent être la conséquence d'une adaptation à un nouveau biotope suite aux changements environnementaux (Schoenemann, 2018 ; Feist, 2019).

### 1.4. Paléobiodiversité et paléobiogéographie

La diversité des organismes évolue au cours du temps mais aussi dans l'espace. Une composante importante de son estimation est donc la biogéographie, qui est l'étude de la distribution géographique des êtres vivants. Elle a pour objectif d'identifier les facteurs biotiques et abiotiques responsables de la répartition des espèces. La biogéographie est en fait subdivisée en deux aspects : la biogéographie écologique qui analyse l'interaction fonctionnelle des organismes avec l'environnement et la biogéographie historique qui étudie l'héritage historique (Cecca et Zaragüeta, 2015). Des provinces biogéographiques (Udvardy, 1975 ;

Costello et al., 2017) ou paléobiogéographiques (Boucot et al., 1969 ; Dowding et Ebach, 2019) ont ainsi pu être identifiées. Les espèces ne réagissent pas toutes de la même façon face aux hétérogénéités environnementales de la planète, certaines étant cosmopolites avec un fort pouvoir de migration et de dispersion tandis que d'autres sont plus endémiques, restreintes à un environnement particulier (Fattorini, 2017 ; Eller et al., 2017). Les changements environnementaux impactent différemment les espèces suivant leur faculté de dispersion (Pacifici et al., 2015 ; Button et al., 2017).

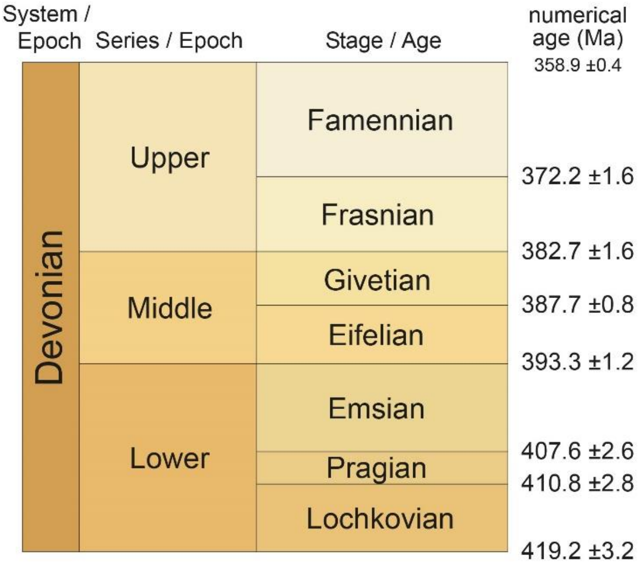
### 1.5. Modèle d'étude

Ce travail a pour objectif de contribuer à la compréhension des facteurs de régulation biotiques et abiotiques de la diversité. Il s'agit de comprendre comment s'articulent les diversités taxonomique et morphologique au cours des temps géologiques. Le but étant de comprendre comment certains changements écologiques ont pu avoir des conséquences positives sur la diversité alors que d'autres ont au contraire eu des répercussions néfastes. De plus, un même type de changement environnemental a-t-il toujours eu les mêmes conséquences ? Si non, comment l'expliquer ? Quels sont les effets des changements environnementaux sur la biosphère ? Comment la biodiversité redémarre-t-elle après une extinction ? Pour répondre à ces questions, le modèle du passé choisi doit être restreint dans le temps et l'espace. Il doit aussi se baser sur un support permettant de quantifier ces changements. C'est dans ce contexte que les **trilobites du Dévonien d'Afrique du Nord** ont été choisis comme modèle d'étude.

## 2. Le Dévonien, période clé de l'histoire de la vie

### 2.1. La période Dévonienne

Afin d'analyser quantitativement la biodiversité passée et ses réponses face aux changements environnementaux, il est nécessaire de travailler sur une échelle contrainte temporellement. Le Dévonien est l'une de ces périodes clés qui a été grandement étudiée. C'est la quatrième période géologique du Paléozoïque après le Cambrien, l'Ordovicien et le Silurien. Il s'étend de -419 à -359 millions d'années et est subdivisé en trois époques (tableau 1). Le Dévonien représente une période clé de l'histoire de la vie pour l'Ere Paléozoïque puisqu'il comporte l'une des cinq grandes crises biologiques du Phanérozoïque : la crise Frasnien–Famennien. C'est une période caractérisée par de profonds changements environnementaux, climatiques et écologiques qui se répercutent sur la biosphère. C'est une période idéale pour étudier l'impact de l'environnement sur la biodiversité ainsi que la capacité de réaction des organismes.



| System / Epoch | Series / Epoch | Stage / Age | numerical age (Ma) |
|---|---|---|---|
| | | | 358.9 ±0.4 |
| Devonian | Upper | Famennian | 372.2 ±1.6 |
| | | Frasnian | 382.7 ±1.6 |
| | Middle | Givetian | 387.7 ±0.8 |
| | | Eifelian | 393.3 ±1.2 |
| | Lower | Emsian | 407.6 ±2.6 |
| | | Pragian | 410.8 ±2.8 |
| | | Lochkovian | 419.2 ±3.2 |

***Tableau 1 :*** *Divisions stratigraphiques internationales du Dévonien (modifié d'après Cohen et al., 2013 ; v. 03/2020).*

## 2.2. Contexte paléogéographique et paléoenvironnemental

Au Dévonien inférieur, il existe trois principaux continents : le Gondwana, la Laurentia, la Siberia-Kazakstania (Fig. 2). La plupart des surfaces continentales sont situées dans l'hémisphère sud et entourées par un immense océan : la Panthalassa (Scotese et al., 2021). Entre ces continents se situent deux océans plus petits : l'Océan Rhéique et la Paléothétys. Le Gondwana tend à remonter vers le nord au Dévonien (Scotese et al., 2021). L'orogénèse Calédonienne à l'origine de la Laurentia s'est terminée au Silurien mais témoigne de la dynamique d'unification des continents, afin de former le futur supercontinent la Pangée au Carbonifère (Stampfli et al., 2013 ; Scotese et al., 2021). Toutefois, le continent Cathaysia (Chine du Sud et Chine du Nord) se sépare du Gondwana au Dévonien inférieur (Scotese et al., 2021). Au Dévonien supérieur, l'océan Rhéique qui sépare la Laurentia et le Gondwana se ferme (Scotese et al., 2021). L'orogénèse Varisque se met alors en place en Europe et en Afrique du Nord (Franke et al., 2017, 2021) et l'orogénèse Acadienne en Amérique du Nord (Hatcher, 2010). De son côté, la Paléothétys s'agrandit et des zones de rifting affectent la Laurussia et la Siberia produisant une forte activité volcanique (Golonka, 2020).

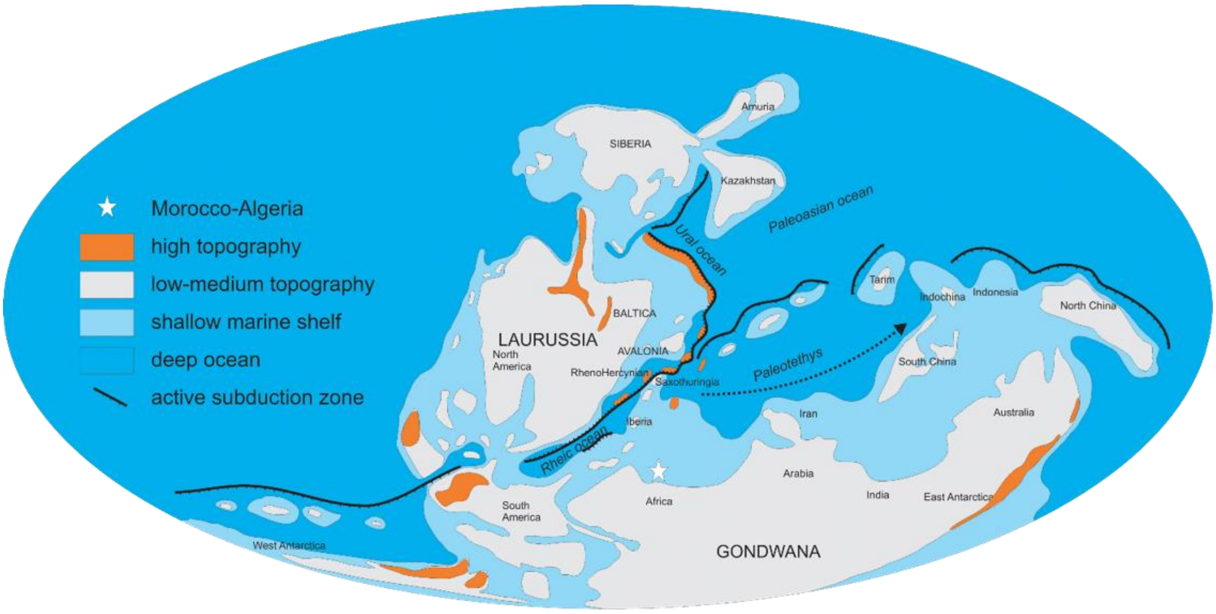


***Figure 2 :*** *Paléogéographie du Dévonien Moyen et position du Maroc et de l'Algérie (modifié d'après Golonka et Gaweda, 2012).*

Les progrès de la science permettent de reconstituer de mieux en mieux les variations environnementales passées. Un des moyens pour arriver à ces reconstitutions est l'utilisation de proxies isotopiques comme le $\delta^{13}C$, indicateur du cycle du carbone, le $\delta^{18}O$, indicateur des paléotempératures, et le rapport $^{87}Sr/^{86}Sr$, indicateur de l'expansion crustale et/ou de l'altération des silicates continentaux (Jones et al., 1994 ; Capo et al., 1998 ; Joachimski et al., 2009). D'autres paramètres environnementaux sont reconstitués à partir des données stratigraphiques et biologiques entre autres. Cela a notamment permis d'obtenir pour le Paléozoïque des données concernant l'indice de fragmentation continentale (Zaffos et al., 2017), la pression partielle en $CO_2$ ($pCO_2$, Foster et al., 2017), la paléotempérature marine et atmosphérique (Scotese et al., 2021) ou encore le niveau marin (Haq et Schutter, 2008). Cocks (2007) a contribué à mieux connaître les environnements passés en identifiant les périodes de glaciations et Hay et al. (2006) en estimant la masse sédimentaire des continents et océans.

Avec toutes ces informations compilées, le climat et la paléogéographie du Dévonien ont pu ainsi être reconstruits. Le climat était chaud au Lochkovien et le niveau marin était élevé. Mais, dès le Praguien, une phase régressive commenca, associée à une baisse des températures (Fig. 3). Cette tendance continua à l'Emsien où les températures atteignirent des valeurs relativement basses, malgré un bref réchauffement à l'Emsien inférieur (Scotese et al., 2021). Entre l'Emsien et le Givétien, le climat était le plus froid du Dévonien avec des températures moyennes de 18,7°C (Scotese et al., 2021), ce refroidissement restant néanmoins modéré (Boucot et al., 2013). Le climat commenca à se réchauffer au Givétien tandis qu'une phase transgressive à

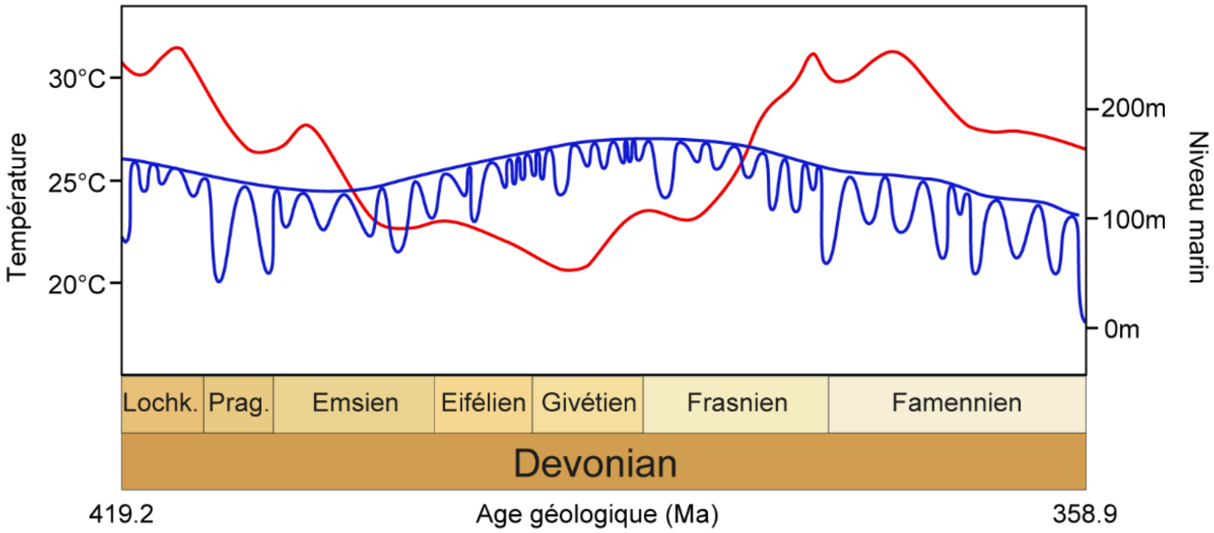


***Figure 3 :*** *Variations du niveau marin d'après Haq et Schutter (2008) et paléotempérature d'après Joachimski et al. (2009) au cours du Dévonien. Age d'après Cohen et al. (2013, v. 03/2020).*

long-terme se mit en place (Haq et Schutter, 2008). L'augmentation des températures conduisit au développement de nombreux récifs (Copper et Scotese, 2003 ; Joachimski et al., 2009). Au Dévonien supérieur, les températures étaitent élevées tout comme le niveau marin, notamment au Frasnien (Johnson et al., 1985 ; Haq et Schutter, 2008 ; Joachimski et al., 2009). Cette époque a également été marquée par un volcanisme effusif intense, en lien avec la tectonique Eovarisque, qui a été un acteur de la crise du Frasnien–Famennien (Racki, 2020). L'eau de mer est devenue alors anormalement riche en $^{87}Sr/^{86}Sr$ (Zhang et al., 2020). Une importante et rapide transgression suivie d'une régression globale accompagna ces changements (Johnson et al., 1985 ; Bond et Wignall, 2008). A la fin du Famennien, le niveau marin et les températures diminuèrent, menant jusqu'à une potentielle glaciation (Joachimski et al., 2009 ; Kaiser et al., 2015). Tout au long du Dévonien, la pression partielle en $CO_2$ atmosphérique diminua (Witkowski et al., 2018). Cette baisse était probablement due au développement de la végétation continentale augmentant l'altération des silicates et donc l'apport de nutriments, et à l'augmentation de l'enfouissement du carbone résultant de l'augmentation de la productivité primaire (Algeo et Scheckler, 1998 ; Simon et al., 2007). La tectonique et le volcanisme en résultant ont également pu amener à l'altération des silicates et donc au refroidissement du climat (Macdonald et al., 2019 ; Racki, 2020).

### 2.3. Evolution de la biodiversité Siluro-Dévonienne

L’étude des proxies environnementaux liés à l’évolution paléogéographique et celle du registre fossile ont montré que la première extinction de masse causée par les changements climatiques à la fin de l’Ordovicien (Bond et Grasby, 2020 ; Liao et Sun, 2020) a eu des conséquences cataclysmiques avec la disparition de 85% des espèces (Sheehan, 2001). Cependant, après une telle extinction, les océans n’ont pas été dépeuplés pour autant et de nombreux clades siluriens ont remplacé ceux qui n’ont pas survécu à la crise (Jin et Copper, 2010 ; Melchin et al., 2011 ; Copper et Jin, 2012). Malgré quelques crises écologiques mineures provoquées par des changements environnementaux (Calner, 2008), le Silurien est réputé comme une période relativement stable. En revanche, la période suivante, le Dévonien, est caractérisé par des changements majeurs à la fois en termes de biodiversité et d’environnement. En effet, il y a eu des phases importantes de diversification, dont le développement de certains clades qui changeront le visage de la Terre et des océans à tout jamais, mais aussi des extinctions majeures. Une régression majeure à la transition Lochkovien–Praguien a permis la mise en place de vastes mers épicontinentales peu profondes ayant favorisé la prolifération de faunes benthiques au Dévonien inférieur (Chlupáč, 1994 ; Morzadec, 2001). Le Dévonien étant une période plus chaude que les précédentes (Tinn et al. 2020), le développement de vastes récifs a été facilité au Dévonien moyen et au Frasnien (Copper et Scotese, 2003 ; Copper, 2011). Cependant, les faunes benthiques ne sont pas les seules à connaître une diversification significative à cette époque puisque les océans ont connu à cette période la Révolution Nectonique Dévonienne (The Devonian Nekton Revolution, Klug et al., 2010). Alors que la plupart des espèces étaient benthiques, démersales ou planctoniques auparavant, de nombreux clades nectoniques se sont développés dont les poissons et les céphalopodes. Toutes les espèces nectoniques ne se sont pas diversifiées en même temps puisque les Dacryoconaridés (tentaculites) ou les Ostréostracés (poissons sans mâchoire) se sont développés dès le Praguien alors que les Nauliloïdes, les Ammonoïdes, les Placodermes (poissons à mâchoire) et les Elasmobranches (poissons cartilagineux) se sont diversifiés dans la seconde moitié du Dévonien (Klug et al., 2010). Sur terre aussi, la vie connait une diversification importante avec le développement des plantes. Si les traces des premières plantes terrestres remontent à l’Ordovicien (Servais et al., 2019), elles ont colonisé de manière importante les continents au Dévonien grâce notamment au développement des plantes vasculaires (Capel et al., 2021).

Le Dévonien n’est cependant pas seulement une période de prolifération de la vie, puisqu’à partir du Dévonien moyen, de nombreux clades vont connaitre une perte de diversité à cause d'événements environnementaux répétés (Walliser, 1996 ; House, 2002 ; Becker et al., 2016). Ces événements brutaux correspondent généralement à une phase transgressive rapide associée

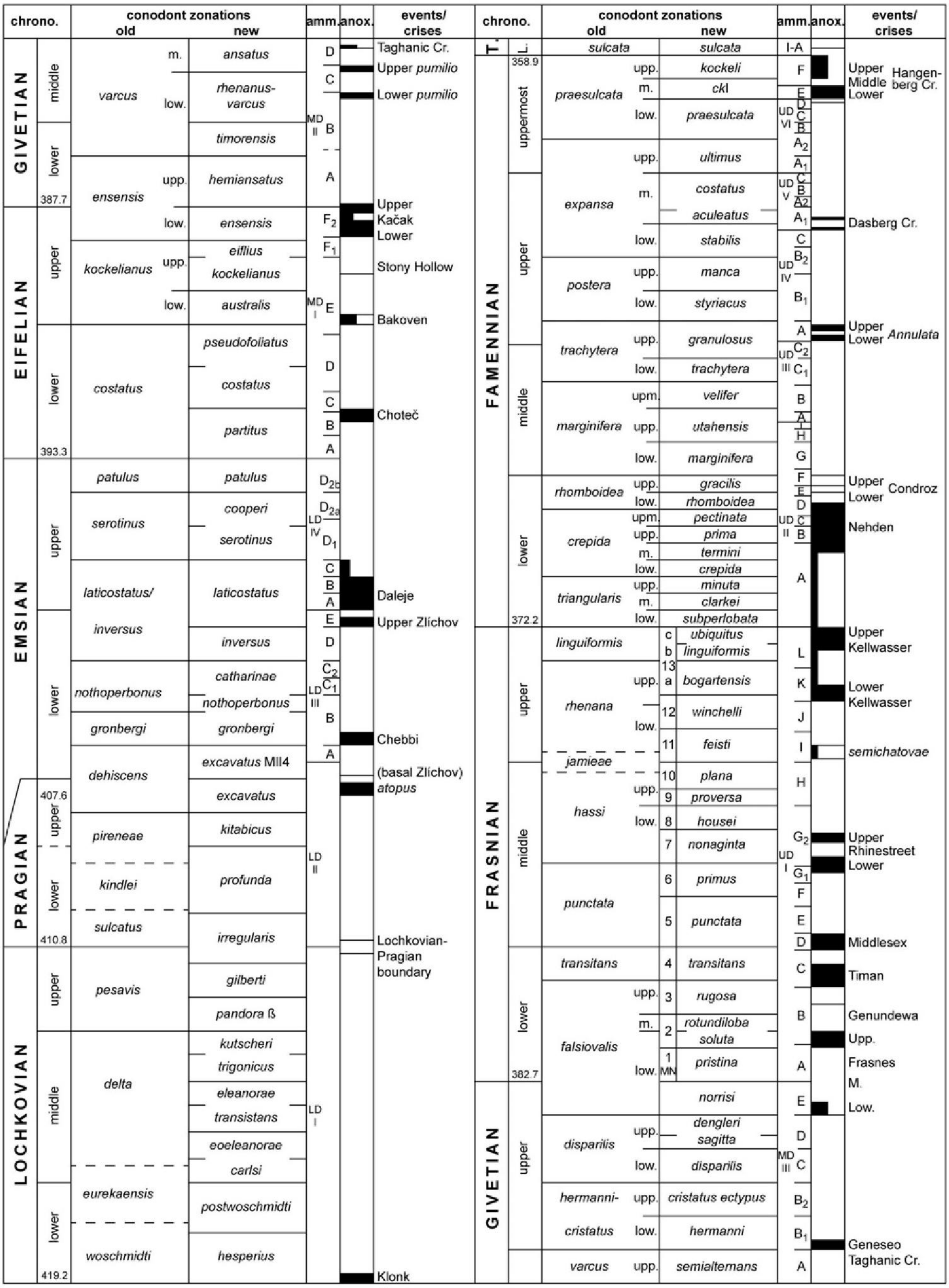


***Figure 4 :*** *Succession des événements globaux et des crises au Dévonien (Becker et al., 2016).*

à des événements d'anoxie/dysoxie au niveau du fond marin (Fig. 4). Ils peuvent se produire en plusieurs pulses. Le premier d'entre eux est l'évènement Basal Choteč au début de l'Eifelian, suivi de l'évènement Kačak à la fin de l'Eifelien, et de l'évènement Taghanic à la fin du Givétien moyen. Ces événements ont conduit à divers changements fauniques et extinctions à l'échelle planétaire. Ils ont principalement affecté les faunes benthiques mais l'évènement Taghanic a également été létal pour les organismes nectoniques comme les ammonoïdes (Walliser, 1996). Le début du Dévonien supérieur n'est pas non plus épargné par des événements qui vont affecter la biodiversité. L'évènement Frasnes est dû à un approfondissement marin à la base du Frasnien et a principalement affecté les faunes récifales (Walliser, 1996). A la transition Frasnien–Famennien, l'évènement Kellwasser, une crise majeure en deux phases distinctes a eu un impact conséquent sur la biodiversité dévonienne tel que Raup et Sepkoski (1982) l'ont considérée comme l'une des cinq crises majeures ayant frappé la Terre au Paléozoïque. D'autres événements mineurs ont été reportés au Dévonien supérieur (le Condroz, l'Annulata et le Dasberg) mais sans réellement bouleverser les écosystèmes. En revanche, la transition entre le Dévonien et le Carbonifère est marquée par une nouvelle crise biologique de grande ampleur, c'est l'évènement Hangenberg (Kaiser et al., 2015).

## 3. Les trilobites, groupe majeur du Paléozoïque

### 3.1. Taxonomie et écologie des trilobites

Pour comprendre l'impact des changements globaux sur la biodiversité au Dévonien, il est nécessaire de travailler sur un clade bien représenté dans le registre fossile. Les trilobites, groupe emblématique du Paléozoïque offrent cette perspective de comprendre ces variations de diversité et de forme. Ces animaux sont apparus lors de l'explosion cambrienne parmi de nombreuses autres faunes (Foote, 1991 ; Shu, 2008 ; Paterson et al., 2019) et disparaissent au Permien (Lerosey-Aubril et Feist, 2012). Ce sont des arthropodes (Harrington et al., 1959 ; Fortey, 2001). Les arthropodes sont un clade majeur dans l'histoire de la biodiversité et ont l'avantage d'abonder dans le registre fossile (Edgecombe et Legg 2013). Comme tous les arthropodes, les trilobites sont segmentés. Ils sont composés, comme leur nom l'indique, de trois lobes longitudinaux. Leur corps est aussi décomposé en trois tagmes : céphalon, thorax et pygidium (Harrington et al. 1959 ; Fig. 5). Ces segments sont recouverts d'un exosquelette de calcite faiblement magnésienne qui protège leurs parties molles (Wilmot et Fallick, 1989;

Whittington et al., 1997). La croissance discontinue des trilobites impose des mues successives lors du processus d'exuviation (Daley et Drage, 2016).

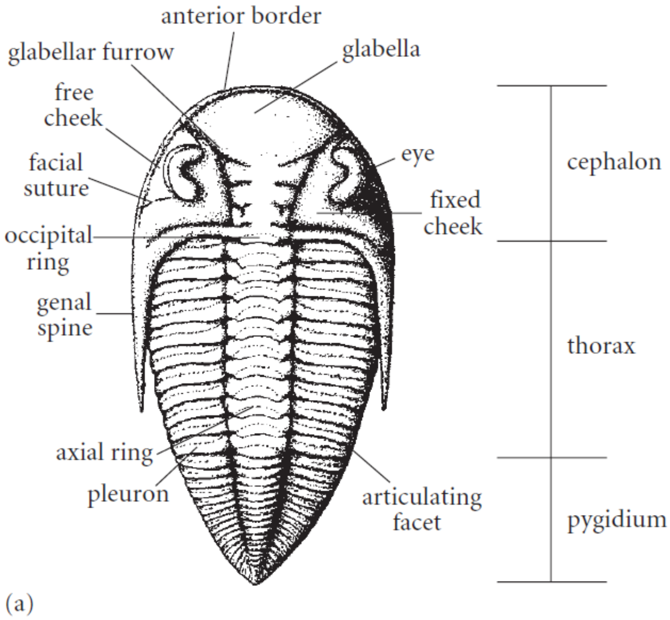


***Figure 5 :*** *Principaux traits de la morphologie des trilobites (d'après Benton et Harper, 2009).*

La taxonomie de la classe des Trilobites a beaucoup évolué au cours du temps et reste encore aujourd'hui source de débat et d'incertitudes (Paterson, 2020). La dernière classification complète est celle de Adrain (2011) mais depuis d'autres analyses à plus haut niveau taxonomique ont apporté des modifications. Un nouvel ordre a été extrait des Asaphida : les Trinucleida (Bignon et al., 2020). *A contrario*, Aulacopleurida, qui avait été érigé au rang d'ordre par Adrain (2011), serait plutôt une super-famille de Proetida (Lamsdell et Selden, 2014). Au total, à ce jour, il y a onze ordres de trilobites, tous apparus au Paléozoïque inférieur (Fig. 6). Les ordres les plus anciens apparus au Cambrien sont les ordres Redliichida, Olenida, Eodiscida et Corynexochida. Six ordres sont présents au Dévonien et seul l'ordre Proetida a survécu jusqu'au Permien (Lerosey-Aubril et Feist, 2012).

Les trilobites ont connu un succès évolutif notamment grâce à leur faculté à s'adapter et à proliférer dans de nombreuses niches écologiques. En effet, ces arthropodes ont intégré le benthos comme le pélagos lors de leur histoire. Parmi les trilobites benthiques, certains ont adopté un mode de vie épibenthique tandis que d'autres ont opté pour un mode de vie plutôt endobenthique (Whittington et al., 1997). Au niveau de la nutrition Fortey et Owens (1999) ont identifié différentes stratégies alimentaires, regroupées en quatre catégories. Certains étaient prédateurs et/ou charognards, d'autres étaient plutôt détritivores, d'autres filtreurs et enfin, certains trilobites étaient suspensivores. Seules les trois premières habitudes alimentaires étaient encore présentes au Dévonien. Fortey et Owens (1999) notèrent d'ailleurs que le régime alimentaire pouvait changer au cours de l'ontogénèse, le stade larvaire impliquant probablement

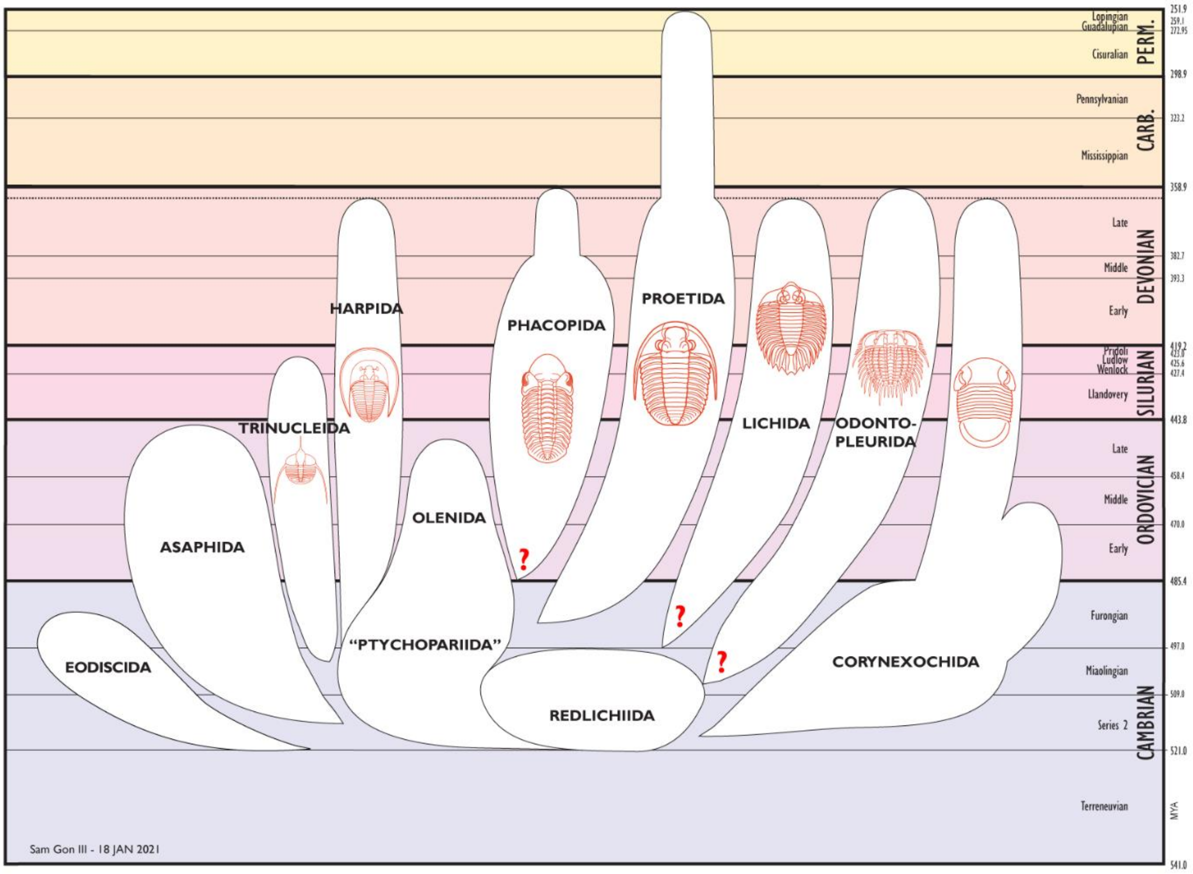


***Figure 6** : Représentation schématique de l'histoire evolutive des oerdres de trilobites au cours du Paléozoïque. Modifié de Gon, S.M. (https://www.trilobites.info).*

un mode de nutrition différent à l'instar de nombreux arthropodes actuels (Fryer, 1988). Les trilobites ont également montré une facilité d'adaptation à coloniser le milieu marin à différentes profondeurs. En effet, ils étaient benthiques ou nectoniques et on les retrouvait des environnements peu profonds jusqu'au-delà de la zone d'action des vagues de tempête, dans des environnements de pente et de bassin (Thomas, 1979 ; Adrain et al., 2004). Les trilobites sont également trouvés dans des dépôts sédimentaires de différentes natures lithologiques : ils pouvaient aussi bien apprécier les environnements silicoclastiques que les environnements carbonatés (Hopkins, 2014). Certains trilobites se développaient même dans les environnements récifaux (Ludvigsen, 1987). Par contre, au niveau des familles ou sous-familles, la nature des sédiments a une importance, comme par exemple les astéropyginés qui proliféraient dans les environnements clastiques (Morzadec, 1992).

La diversité des milieux colonisés, des comportements se traduit également par une diversité de taille et de forme. Ainsi, les trilobites étaient diversifiés au niveau de la taille. La plus grande espèce de trilobite connue est *Isotelus rex* Rudkin et al., 2003 qui vivait à l'Ordovicien et mesurait plus de 70 cm (Rudkin et al., 2003) alors que les plus petits n'excédaient pas 1 mm (Clarkson et Ahlberg, 2002). Deux périodes particulières sont notamment connues pour la présence de formes géantes, favorisées par un climat avantageux pour le développement des trilobites : ce sont l'Ordovicien et le Dévonien inférieur (Klug et al., 2014).

Au cours de leur histoire évolutive, de nombreux cas de réduction des yeux pouvant aller jusqu'à la cécité ont été répertoriés, et tout particulièrement dans des lignées indépendantes du Dévonien supérieur (Feist et Clarkson, 1989 ; Feist, 1995 ; Crônier et Feist, 2000 ; Crônier et Courville, 2003 ; Lerosey-Aubril et Feist, 2012 ; Schoenemann, 2018 ; Feist, 2019). Cette évolution a été interprétée comme une adaptation à une vie marine à plus grande profondeur dans une période de haut niveau marin ; cependant, une réduction des yeux peut également correspondre à un mode de vie endobenthique (Clarkson, 1967 ; Feist et al., 2009). Ces changements polyphylétiques soulignent que des changements de vision constituent une adaptation à des changements environnementaux. Les trilobites ont aussi développé des épines au cours de leur histoire évolutive. Ces épines pouvaient aller de simples épines génales comme chez *Dalejeproetus owensi* (Johnson et Fortey, 2012) à de longues épines sur tout le corps comme chez *Kettneraspis prescheri* (Van Viersen et Heising, 2015). Les épines pouvaient présenter des intérêts variés pour les trilobites que ce soit pour leur défense ou leur mode de vie (Knell et Fortey, 2005). L'enroulement des trilobites constitue également une phase importante chez les trilobites puisqu'il leur permet notamment de se protéger contre des prédateurs (Clarkson et Henry, 1973). Il existe différents modes d'enroulement qui jouent sur leur morphologie (Oudot et al., 2019 ; Suárez et Esteve, 2021).

### 3.2. Les trilobites : groupe clé en macroévolution

Depuis que Walch (1771) a érigé l'ordre Trilobita au XVIIIème, les trilobites ont été à la base de nombreuses recherches scientifiques. Les trilobites présentent en effet plusieurs avantages pour les paléontologues. Ils sont plus fréquemment préservés dans les dépôts sédimentaires au cours des temps géologiques que la plupart des organismes grâce à leur exosquelette (Pérez-Huerta et al., 2018). Leur état de conservation est d'ailleurs souvent bon, avec des caractères morphologiques bien visibles. Un autre avantage est que les fossiles de trilobites sont retrouvés en grand nombre, notamment grâce au fait que de nombreuses mues sont aussi conservées dans le registre fossile. De plus, les traits morphologiques de l'exosquelette des trilobites peuvent être quantifiés à partir de la morphométrie géométrique. Cela permet la quantification possible des caractères morphologiques et la création d'un espace morphologique. Puisque les trilobites présentent un grand nombre de caractéristiques, de formes et de milieux de vie, ils présentent un fort potentiel pour toutes études en macroévolution. Pour ces raisons pratiques, les trilobites ont été très utilisés en paléontologie et ils ont été à la base de grandes avancées sur les modalités macroévolutives, notamment dans l'interprétation des changements de forme en termes évolutif et adaptatif. Eldredge et Gould (1972) s'en sont notamment servis dans le développement du modèle des équilibres ponctués. Foote (1989, 1990, 1991, 1993) a utilisé les trilobites pour améliorer les études sur la disparité morphologique. Foote a ainsi développé des indices de disparité morphologique basés sur l'analyse des espaces moprhologiques à partir de l'étude des trilobites (Foote, 1989, 1990). Leur analyse morphologique a aussi permis de connaître plus en détails les dynamiques de diversification des clades (Foote, 1991, 1993). L'étude du taux d'évolution des trilobites a apporté des informations sur le timing de l'Explosion cambrienne, qui a probablement débuté vers la transition Ediacarien–Cambrien, avant la multiplication des fossiles (Paterson et al., 2019). De nombreuses études détaillées sur les stades ontogéniques des trilobites ont également été réalisés, les stades juvéniles étant relativement bien conservés dans le registre fossile et les séries ontogéniques bien identifiées (Crônier et Feist, 1997 ; Crônier et al., 1999 ; Kim et al., 2002 ; Crônier et al. 2005 ; Lerosey-Aubril et Feist, 2005 ; Webster, 2007 ; Cederström et al., 2009 ; Crônier, 2010 ; Hopkins, 2020 parmi d'autres). Par conséquent, des études récentes sur l'ontogénèse (Hughes et al., 2017 ; Lerosey-Aubril et Laibl, 2021) et la modularité/intégration (Webster et Zelditch, 2011 ; Gerber et Hopkins, 2011 ; Oudot et al., 2019) ont pris comme support les trilobites. Ils permettent ainsi de mieux comprendre le rôle du développement dans l'évolution. Fort de leur grande abondance dans les sédiments paléozoïques, les trilobites ont également servi de support pour identifier l'influence des différents biais d'échantillonnage en macroévolution (Tarver et al., 2007).

## 4. L'Afrique du Nord, région hospitalière du Paléozoïque

Afin d'analyser quantitativement la biodiversité passée et ses réponses face aux changements environnementaux, il est nécessaire également de travailler sur une échelle contrainte spatialement. L'Afrique du Nord étant une région connue pour ses riches contenus fossilifères, elle constitue une région idéale pour examiner la paléobiodiversité. Cela est particulièrement le cas pour les fossiles paléozoïques qui sont retrouvés en grande quantité dans diverses régions du Maroc et de l'Algérie. Si les dépôts ordoviciens des Fezouata sont les plus réputés pour la qualité exceptionnelle de leurs fossiles (Van Roy et al., 2015), les gisements du Silurien et du Dévonien sont aussi nombreux et pertinents pour leur richesse. En plus des trilobites, les sédiments de cette période abondent d'ammonoïdes (Klug, 2002 ; Allaire, 2017 ; Becker et al., 2019), de poissons (Derycke, 2015), de crustacés (Maillet et al., 2013 ; Jobbins et al., 2020) et bien d'autres organismes (Klug et al., 2008, 2018 ; Frey et al., 2014). Ces fossiles sont en partie exploités à des fins commerciales par les locaux afin d'être vendus à des collectionneurs, mais ils sont également utilisés et analysés par les scientifiques depuis plus d'un siècle. Les premiers travaux sur les trilobites ont été réalisés par des pionniers scientifiques français et allemand (Lecointre, 1926 ; Richter et Richter, 1943 ; Termier et Termier, 1950 ; Le Maître, 1952). De nombreuses études vont suivre dans les années 60 et 70 avant une perte d'intérêt à partir du milieu des années 80. Cependant, durant ces 20 dernières années, les paléontologues se sont de nouveau intéressés aux trilobites d'Afrique du Nord avec les travaux récents de Crônier et al. (2018a, 2018b), Chatterton et al. (2019), Feist (2019) et Van Viersen et Lerouge (2019, 2021) notamment. La plupart des travaux publiés concernent la taxonomie et la systématique avec la description de nouvelles espèces et genres. Ces études sont d'ailleurs réalisées à l'échelle locale, seuls les travaux taxonomiques de Alberti (1969, 1970) ont porté sur une échelle régionale.

La richesse en fossiles en Afrique du Nord du Silurien au Dévonien s'explique par la présence de nombreux dépôts sédimentaires où les conditions d'affleureuments sont excellentes (Fig. 7). Il y a 400 millions d'années, cette région était particulièrement hospitalière pour les faunes marines. Le Maroc et l'Algérie étaient situés sur la plate-forme du craton saharien dans la partie nord-ouest du Gondwana (Wendt et al., 1984 ; Wendt, 2021). Cette région était située à des latitudes subtropicales (Scotese et al., 2021). Au Dévonien moyen le Maroc était même situé aux latitudes subtropicales chaudes (Scotese et al. 2021). Aujourd'hui, ces terrains dévoniens affleurent largement en Algérie et au Maroc, on peut les regrouper en huit bassins distincts : la Meseta centrale, le massif du Rehamna, le Tafilalt, le Maïder, le bassin du Tindouf, la vallée du Draa, la Kabylie, le bassin de Béchar et l'Ougarta (Fig. 7). Au Dévonien inférieur, l'Anti-Atlas était une plateforme avec un environnement relativement homogène (Kaufmann, 1998 ; Lubeseder et al., 2010). La phase extensive de l'orogénèse Hercynienne (ou varisque) conduisa à des phases de subsidence dans l'Anti-Atlas menant à une accumulation conséquente de sédiments (Ouanaimi et Lazreq, 2008). Sous l'action de l'orogénèse Varisque l'Anti-Atlas et la zone adjacente de l'Ougarta se sont transformés en une succession de plateformes et bassins au Dévonien moyen (Wendt et al., 1984 ; Kaufmann, 1998 ; Wendt, 2021). Cette différentiation s'est poursuivie au Dévonien supérieur.

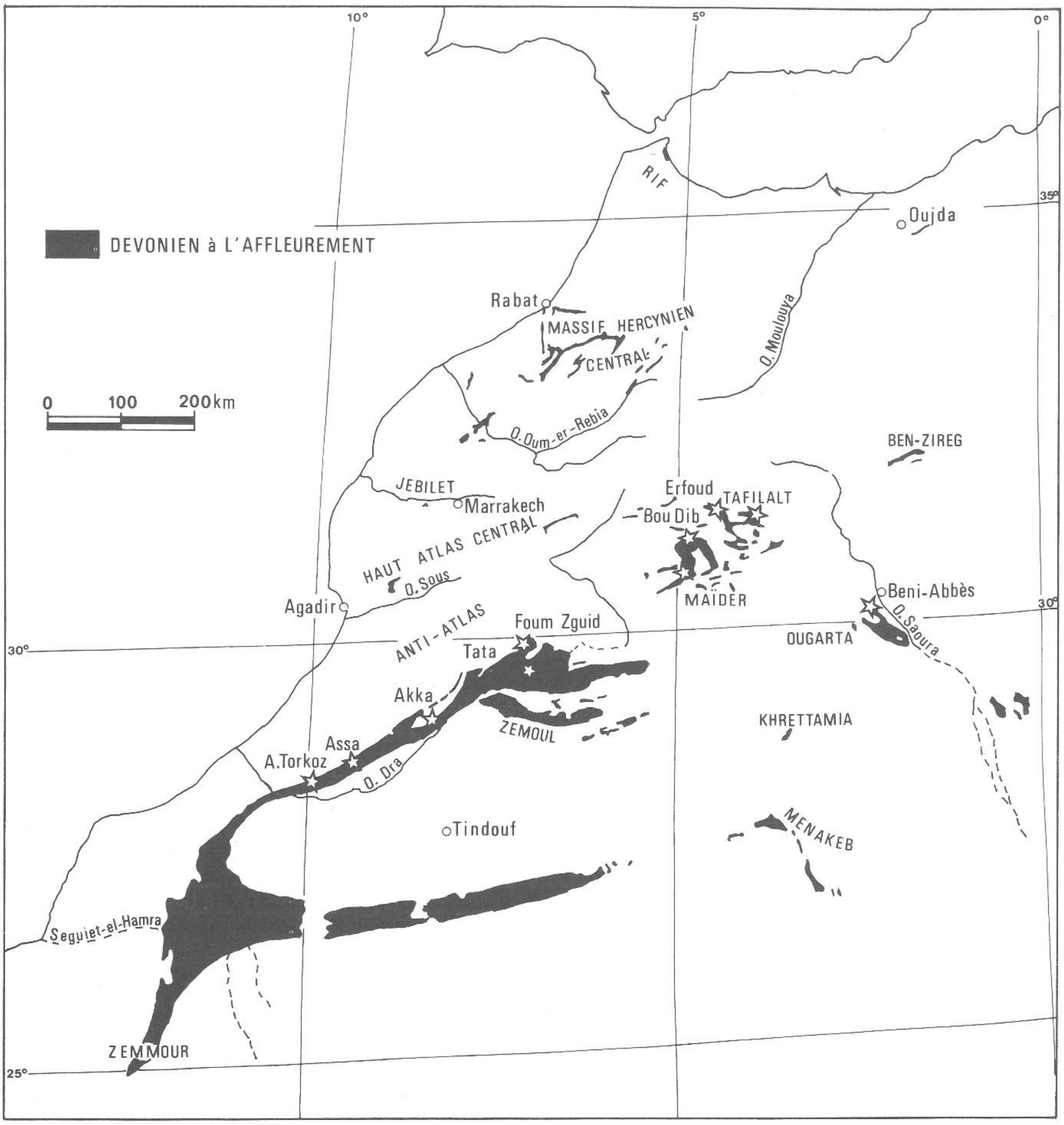


***Figure 7 :*** *Principaux affleurements dévoniens du Nord-ouest d'Afrique du Nord (Hollard, 1968).*

## 5. Objectifs de la thèse

Afin de se focaliser sur la paléobiodiversité en temps profond et ses variations spatio-temporelles, trois axes majeurs ont été développés au cours de cette thèse, à savoir un axe concernant la diversité taxonomique, un axe concernant la disparité morphologique, et un axe concernant les dynamiques spatiales. Ces axes ont été considérés à l'échelle globale (chapitre 1) et à l'échelle régionale (chapitre 2).

### Chapitre 1. Dynamique des trilobites du Silurien au Permien à l’échelle mondiale

Il s’agit ici d’étudier les tendances globales concernant la distribution et les changements de faunes depuis le Silurien jusqu’au Permien afin de mieux comprendre le contexte dans lequel se placent les trilobites du Dévonien d’Afrique du Nord. L’article 1 « Post-Ordovician trilobite diversity and macroevolutionary history » discute des évolutions fauniques à l’échelle globale qui ont suivi la première extinction de masse qui a lourdement affecté les trilobites. Le but est de quantifier la diversité mondiale mais également de voir comment se sont effectués les renouvellements de faunes au cours de la seconde partie du Paléozoïque. L’influence des nombreux changements environnementaux et écologiques globaux pourrait ainsi être identifiée. Afin de mieux caractériser les faunes de trilobites, il est également nécessaire de caractériser les tendances morphologiques et leurs variations au cours du temps. Pour cela, avant de pouvoir concrétiser une étude à l’ensemble des taxons du Dévonien à l’échelle globale, une première étude (article 2 « Morphological disparity of phacopids ») s’est focalisée sur une famille emblématique du Dévonien : les phacopidés. Cette famille probablement apparue à la fin de l’Ordovicien s’est développée jusqu’au milieu du Dévonien avant de décliner et de disparaître à la toute fin du Dévonien. Cette dynamique de diversité est typique de nombreuses familles post-ordoviciennes et est intéressante à étudier au niveau de la morphologie pour identifier des innovations et la sélectivité ou non des extinctions.

### Chapitre 2. Biodiversité et Disparité des trilobites du Dévonien d'Afrique du Nord

Il s’agit ici d’étudier la biodiversité des trilobites présents au Maroc et en Algérie. Ce chapitre est constitué de trois articles : un sur la diversité taxonomique (article 3 « Trilobite biodiversity trends in the Devonian of North Africa »), un sur la disparité morphologique (article 4 « Morphological disparity trends of Devonian trilobites from North Africa ») et le troisième comparant les deux dynamiques diversité *vs*. disparité (article 5 « No decoupling between taxonomic diversity and morphological disparity in the trilobites from the Devonian of North Africa? »). L’article 3 (Bault et al., 2021) discute des tendances de diversité au niveau de l’Afrique du Nord. Il repose sur une base de données recensant la centaine de publications portant sur les trilobites d’Afrique du Nord, et permettant ainsi de faire un état des lieux de tout ce qui est connu sur les trilobites nord-africains. La diversité peut être mesurée à différents niveaux taxonomique aussi bien au niveau des ordres qu’au niveau des espèces. Des tendances différentes peuvent caractériser ces différents niveaux taxonomiques. Ce « zoom » réalisé à l’échelle régionale offre l’opportunité de mieux comprendre les interactions environnement-diversité. La région d’étude est également connue pour ses affleurements riches en ammonoïdes coexistant sur la même période avec les trilobites. Cet article offre ainsi l’opportunité de comparer une faune nectonique et une faune benthique d’une même région. L’intérêt est d’autant plus grand que les ammonoïdes sont susceptibles d’avoir été des prédateurs de trilobites. La plupart des articles publiés et utilisés pour la construction de la base de données sont des travaux de systématique, offrant ainsi de très nombreuses illustrations des spécimens figurés. Cela permet de rajouter une composante à la richesse taxonomique : la disparité morphologique. C’est l’objet de l’article 4 (Bault et al., accepté avec modifications) basé sur le même jeu de données. Les études morphologiques sont complémentaires de celles de la diversité. L’utilisation de photos implique des études en 2D uniquement, mais cela n’est pas problématique chez les trilobites, leur morphologie ne nécessitant pas forcément la 3D. Ce travail a permis de faire l’état des lieux des formes des trilobites du Dévonien et d’identifier leurs principales variations. Les innovations et les pertes de morphologies des trilobites d’Afrique du Nord ont ainsi pu être identifiées et rattachées aux événements écologiques. L’article 5, quant à lui, se focalise sur la comparaison entre la richesse taxonomique et la disparité morphologiques, ces deux métriques pouvant être couplées ou non. Evaluer leurs dynamiques apporteraient des indications précieuses sur les modalités évolutives des trilobites du Dévonien.

La biodiversité ne change pas qu’au cours du temps mais aussi dans l’espace. L’article 6 (« The influence of palaeogeography and tectonic events on trilobite distributions in Morocco and north-western Algeria », Bault et al., accepté avec modifications) discute de la diversité paléogéographique qui peut être source de diversité taxonomique et morphologique. Le Maroc et l’Algérie concentrent un grand nombre de bassins caractérisés par des environnements différents qui ont été bien décrits. Cette paléogéomorphologie en bassins et plate-formes résulte d’une tectonique régionale, la région ayant été le siège de l’orogénèse varisque. Cette connaissance du secteur étudié a ainsi offert l’opportunité d’appréhender l’impact de la paléogéographie régionale sur la biodiversité et la distribution des trilobites. En identifiant des associations de trilobites, on peut mettre en évidence leurs affinités du point de vue environnemental et temporel. Des voies de migrations et des barrières géographiques peuvent également être identifiées.

# **Chapitre 1.** Dynamique des trilobites du Silurien au Permien à l'échelle mondiale

Les dynamiques biologiques et environnementales globales ont un effet majeur sur les écosystèmes régionaux. Comprendre les tendances globales permet de connaitre le cadre dans lequel les trilobites du Dévonien d'Afrique du Nord se situent et les enjeux. L'objectif est d'identifier l'effet de l'environnement et les changements de population d'abord au niveau taxonomique (article 1) puis au niveau morphologique (article 2).

## 1.1. Diversité et histoire macroévolutive des trilobites Post-Ordoviciens

Article 1: Post-Ordovician trilobite diversity and macroevolutionary history

Pour être soumis à Earth-Science Reviews.

# Post-Ordovician trilobite diversity and macroevolutionary history

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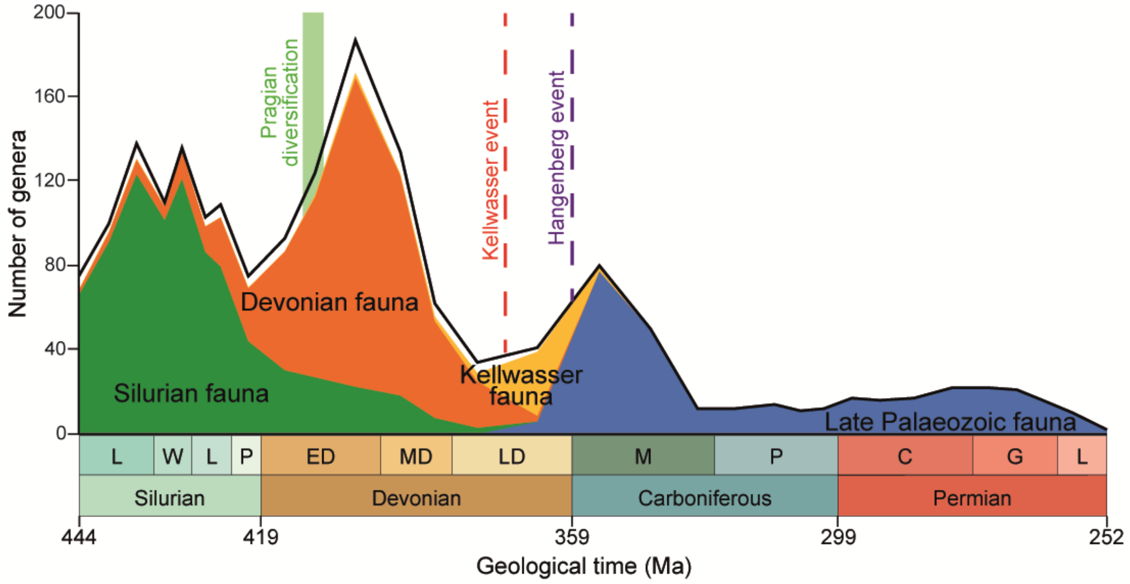


## Abstract

Trilobites were the successful clade of marine invertebrates during the Palaeozoic as highlighted by Sepkoski's evolutionary faunas. Since the Cambrian they were very abundant, widespread and highly diversified, but they were severely affected by the Late Ordovician extinction event. Our study investigates the evolutionary trends of trilobites after this crisis, especially by evaluating how their diversity recovered and structured itself in evolutionary faunas, as well as the how environments influenced these trilobite faunas. Using occurrences from the Paleobiology Database, we estimated the post-Ordovician paleobiodiversity of trilobites by coverage rarefaction (SQS) and identified the trilobite evolutionary faunas by means of a factor analysis. During the Silurian, the trilobite taxonomic richness was relatively high and did not undergo important changes; this Silurian Fauna was dominated by the families that appeared in the Ordovician and survived the end-Ordovician extinction. Next, a Devonian Fauna established, progressively since the end of the Silurian, by the diversification of other families and subfamilies, especially in the early Devonian, which records the highest post-Ordovician peak of diversity, probably favoured by the spreading of epicontinental shallow seas. Abrupt sea-level changes and anoxic events during the Middle Devonian strongly reduced the trilobite diversity and brought both Silurian and Devonian faunas close to their disappearance. Then, during the Late Devonian, trilobite diversity was low and dominated by phacopids and proetids. Finally, the Hangenberg event (end-Devonian) affected all existing trilobite clades and the following Tournaisian diversification was the onset of the Late Palaeozoic Fauna, constituted by phillipsiids and brachymetopids. Despite an important diversity decrease in the Visean–Serpukhovian (early Carboniferous), this fauna was the only one to persist until the doom of trilobites at the end of the Permian.

**Keywords:**

Trilobites, Palaeozoic, factor analysis, evolutionary fauna, extinction, environmental events, diversity

## 1. Introduction

Trilobites appeared at the beginning of the Cambrian at the same time as several other metazoan clades (Fortey et al., 1996, 1997; Paterson et al., 2019). They became quickly abundant in the Early Palaeozoic with a maximum diversity between the Late Cambrian and the Late Ordovician (Foote, 1993; Westrop and Aldrain, 1998). In addition to this diversification, the first trilobites showed an increase of morphological disparity until a maximum disparity during the Ordovician (Foote, 1991, 1993; Webster, 2007). These arthropods also developed a wide range of feeding habits (Fortey and Owens, 1999) and various palaeoecological adaptations (Fortey, 2004, 2014, Hopkins, 2014), highlighting their capacity for adaptation and their presence in all fully marine habitats, and even brackish habitats by the Early Ordovician (Mángano et al., 2021; Serra et al., 2021). These ecological adaptations contributed to a resilience against the Palaeozoic extreme environmental changes and thus, the trilobites survived two of the five biggest mass extinction events, i.e., the Late Ordovician and the Late Devonian mass extinctions (Raup and Sepkoski, 1982; Raup, 1986; Bambach et al., 2004). However, about 250 million years ago, the trilobites became extinct at the end of the Permian (Owens, 2003; Lerosey-Aubril and Feist, 2012).

The Early Palaeozoic faunas and their evolutionary trends have been well studied in the literature. Originally, Adrain et al. (2004) identified three evolutionary faunas from the Ordovician to the Early Silurian, which are characterized by different families showing a similar pattern of diversity. These faunas were identified according to geographical/environmental features such as the latitude or the marine habitats (Adrain et al., 2000, 2004). However, trilobite evolutionary faunas from the Silurian to the Permian remained undefined, although important compositional changes occurred. In the Silurian, although considered relatively stable from an environmental point of view (Calner, 2008; Melchin et al., 2021), environmental changes did take place with temperature variations and transgressive events associated with anoxia. These environmental conditions were favourable for trilobites, which recover from the Late Ordovician mass extinction and become diverse (Adrain et al., 2000). The Early Devonian led to a diversity peak (Chlupáč, 1994; Adrain, 2008; Alroy, 2010b) followed by a sharp decrease in the Middle and Late Devonian, to the extent that only one order survived in the Carboniferous (Feist, 1991; Lerosey-Aubril and Feist, 2012). The Early Devonian represents the only important period of diversification after the Late Ordovician. This period was characterized by several environmental changes, including the displacement of Gondwana towards lower latitudes leading to the increase of carbonate deposits (Scotese and McKerrow, 1990; Scotese, 2021) and important temperature variations (Scotese et al., 2021). Repeated and rapid sea-level changes and anoxic/hypoxic events also affected the planet at this time (House, 1985, 2002; Johnson et al., 1985), leading to the Kellwasser events (Buggisch, 1991; Bond and Wignall, 2008; Carmichael et al., 2019). The Late Palaeozoic was also a period of important ecological changes with the proliferation of nektonic organisms during the Devonian Nekton Revolution (Klug et al., 2010), the colonisation of land by vascular plants (Gerrienne et al., 2016; Capel et al., 2021) and the invasion of the continents by animals (Selden, 2016; Van Straalen, 2021). Because trilobites within changing ecosystems have not responded in the same way to environmental changes over this period, it is important to identify which taxa had similar behaviour in order to identify the causes influencing trilobite richness, their diversifications and their declines.

## 2. Material and methods

### 2.1. Dataset

Trilobite occurrences were downloaded from the Paleobiology Database (PBDB, www.paleobiodb.org) on May 21st 2021. Data on diversity data were collected as follows: (1) selection of all the trilobite genera (column “accepted_name” from the “taxa” record) present in each stage from the Silurian to the Permian; (2) subgenera not treated as genera and not taken into account; (3) number of occurrences per stage for each genus counted. In total, 570 genera in 23 families and six orders from the Silurian to the Permian were used. This dataset comprising 13802 occurrences extracted from the “Occurrences” was used for rarefaction methods. In order to better understand the relationship between the environment and the location with the taxonomy, we collected data on habitat affinities and palaeolocation from PBDB. For each occurrence for which some additional data were available, we collected lithological data from the “lithology1” and “lithology2” fields, the environmental data from the “environment” field and latitudinal data from the “paleolat” field. In total 9045 occurrences (66%) record lithological data, 5064 occurrences (66%) environmental data, and 9356 occurrences (68%) latitudinal data. Lithological data were simplified in three categories (Fig. SUPPL. A): siliciclastic (i.e., lithology1 = any clastic lithology AND lithology2 = any clastic lithology or NA), carbonate (i.e., lithology1 = any carbonate lithology AND lithology2 = any carbonate lithology or NA) and mixed (i.e., lithology1 = any carbonate lithology AND lithology2 = any clastic lithology (or *vice versa*). Bathymetrical data were spread in four categories, i.e., shallow, inner platform, outer platform and slope/basin, and latitudinal data in three categories, i.e., low, middle and high latitudes (Fig. SUPPL. A). We followed the International Chronostratigraphic Chart (Cohen et al., 2013) as the geochronological framework.

## 2.2. Dataset

Trilobite systematics and phylogenetic relationships remain unclear, especially between major post-Cambrian trilobite clades and their Cambrian ancestors (Paterson, 2020). The latest studies carried out at the class level were those of Fortey (1997) and Adrain (2011). For more robust analyses, some studies have focused on smaller subsets such as the recent analyses on Asteropygines (Bignon and Crônier, 2014), Calmoniids (Abe and Lieberman, 2009), Phacopids (McKellar and Chatterton, 2009), or the recent redefinition of the order Trinucleida (Bignon et al., 2020). We have chosen to carry out our analyses based on the taxonomic framework described by Adrain (2011) with some updates. First, we follow Bignon et al (2020) in the newly erected order Trinucleida separately from Asaphida. Second, although Adrain (2011) created the order Aulacopleurida distinctly from Proetida, the monophyly of the order Proetida, including the superfamily Aulacopleuroidea as one of the three super-families with Proetoidea and Bathyuroidea, has been regularly questioned (Lamsdell and Selden, 2015). Consequently, we considered Aulacopleuroidea as a super-family of Proetida, not as an order. We followed Adrain (2013) in considering, within the order Proetida, the family Phillipsiidae as a subfamily of Proetidae.

Eleven orders are recognized within trilobites across their evolutionary history (Fig. 1). All of them appeared in the Cambrian-Ordovician. Eodiscida, Ptychopariida, Asaphida, Olenida and Redlichiida disappeared before the Silurian; Trinucleida in the Silurian; and Harpetida, Odontopleurida, Lichida and Corynexochida in the Middle Devonian. If only Phacopida and Proetida survived to the Kellwasser events, Phacopida disappeared with the Hangenberg event at the Devonian-Carboniferous boundary (Feist, 1991; Chlupáč, 1994; Lerosey-Aubril and Feist, 2012).

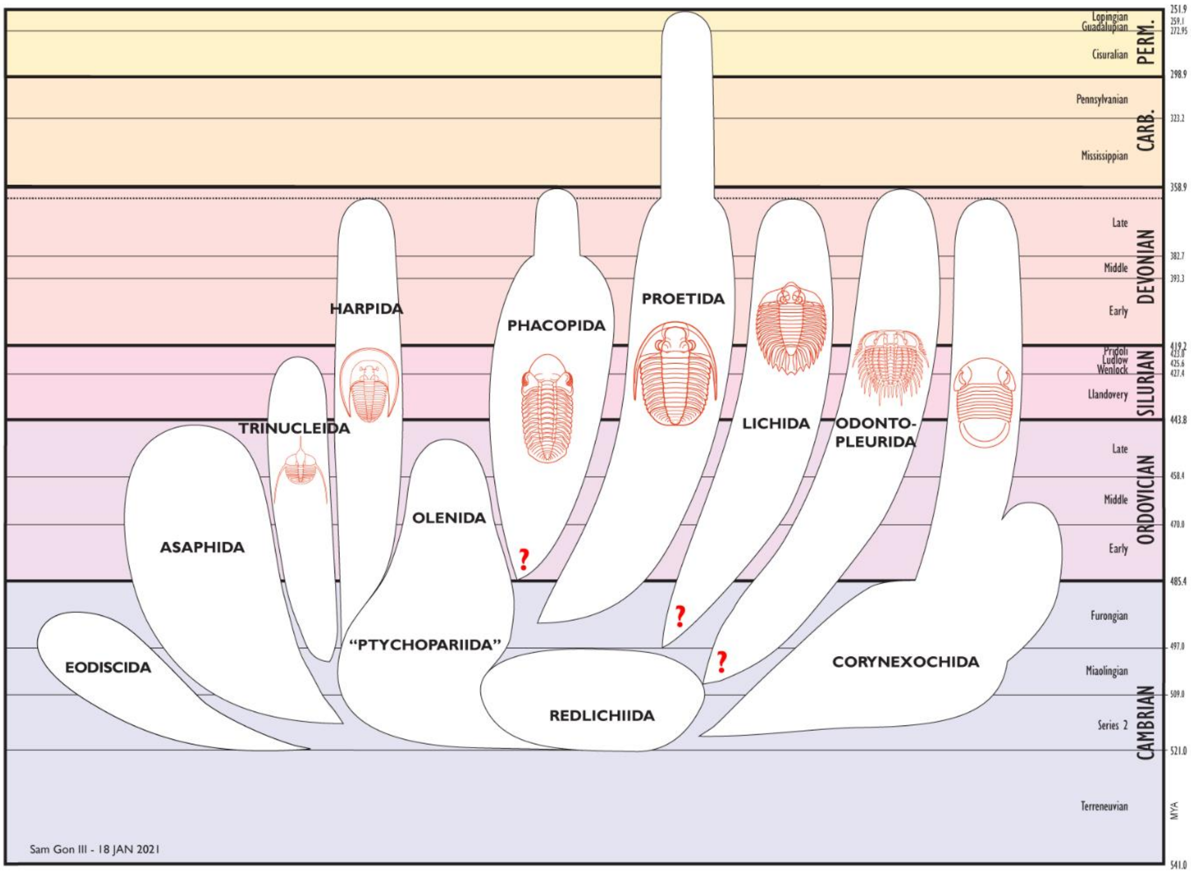


***Figure 1**. Schematic representation of the evolutionary history of the trilobite orders through time. The y-axis approximates a log to permit the more detailed illustration of the Cambrian and Ordovician diversifications. Horizontal distance between orders should not be interpreted as phenetic difference no more than the diagram implies maximal phenetic variance in the early part of the Cambrian. Modified from Gon, S.M. (https://www.trilobites.info).*

Within the orders that crossed the Ordovician-Silurian boundary, some families disappeared (Adrain, 2013). Consequently, post-Ordovician trilobites were spread into the 22 families used for this work. Within the family Proetidae, as there are many subfamilies with different diversity dynamics and temporal distribution, we used them as clades for our analyses, represented by Cornuproetinae, Crassiproetinae, Cyrtosymbolinae, Dechenellinae, Drevermanniinae, Eodrevermanniinae, Mirabolinae, Proetinae and Warburgellinae.

As the taxonomic assignments in the PBDB are not systematically updated, a revision of the taxonomy has been carried out. Some subfamilies have been reassigned to families. Tropidocoryphidae has been considered as a distinct family comprising Eremiproetinae, as in recent studies (Helling and Schöllmann, 2018; Feist and Belka, 2018), although this subfamily has sometimes been assigned to Proetidae. We considered that the Scutelluidae are different from the exclusively Ordovician Styginidae (Holloway, 2007). Therefore, the trilobites assigned to the Styginidae in the database were transferred to the Scutelluidae.

In the same way, some genera have been reassigned to families and subfamilies. Some issues of junior synonyms were also solved. Reassignments were made using the statements of Jell and Adrain (2002) and subsequent updating. The following proetid genera *Constantina* Cisne, 1970, *Ormistonia* Maksimova, 1978, *Pseudoproetus* Poulsen, 1934 and *Schaderthalaspis* Alberti, 1983 not assigned to a subfamily were not used in the Factor Analysis. A database with updated taxonomy is given in Appendix A.

## 2.3. Diversity

Attempts to reconstruct  taxonomic richness face several biases (Smith, 2001; Alroy, 2010b) but the development of modern methods have helped palaeontologists to estimate diversity in the fossil record using resampling methods (Alroy, 2010a, Close et al., 2018). Here, trilobite diversity is estimated at genus level from the Silurian to the Permian using two different methods. First, we calculated the Range-Through diversity including single-interval taxa (RT), which is the raw count of actually documented taxa per stage plus interpolated discontinuous taxon ranges (Foote, 2000). Indeed, some genera had an irregular presence through time with virtual absence between two stages of occurrences due to the incompleteness of PBDB. As we are working at the global , we corrected this issue by assuming presence in all stages between the first and last appearance. For this estimation, and given that many trilobite genera have short longevities, we chose to include singletons. Second, we performed a Shareholder Quorum

Subsampling (SQS) diversity (Alroy, 2009). This is a subsampling method that aims to overcome uneven sampling between intervals. We further estimated net change rates corresponding to the difference in logged diversity between successive intervals. Net changes highlight periods of gain and loss of genera.

Diversity indices are computed with the package ‘epaleo’ (v. 0.8.41; Monnet, unpub.) using R statistical environment (v. 3.6.2; R Core Team 2019; https://cran.r-project.org/).

### 2.4. Factor Analysis

Factor Analysis (FA), a multivariate statistical method, was used to describe Phanerozoic evolutionary faunas (Sepkoski, 1981) and was further been applied for more specific analyses of faunas or floras (Figueirido et al., 2012; Cleal and Cas-Miñana, 2014; Morales et al., 2015; Capel et al., 2021). To assess the inter-sample relationships in trilobites, we performed a Q-mode factor analysis (Mulaik 1972). This method allows decreasing space dimensionality in the original database to a smaller number of variables known as factors. We implemented Sepkoski’s (1981) approach to the raw-normalized diversity of Silurian-Permian trilobites, consisting of the number of genera in each family or subfamily per stage. We obtained factors (orthogonal vectors) with their associated eigenvalues (factor loadings) and the percentage of explained total variance. The importance of each family or subfamily to each factor is indicated by its score. The composition of each fauna is therefore defined as the group of families or subfamilies that record the highest scores in each factor. A varimax rotation (Kaiser, 1958) was used to clarify the relationship among factors and to maximize the sum of the variances of the squared correlations between variables, i.e., families and subfamilies, and factors to avoid nonsense associations determined by raw eigenvectors. Hence, this rotation clearly segregates the variables onto different factors. The selection of the number of factors used can be done in different ways. Sepkoski (1981) chose to select the factors located before the slope break of the successive factor eigenvalues plotted logarithmically. As our data do not show a break, we chose the number of factors explaining 95% of the variance, i.e., four factors.

Because a family or subfamily could record high scores in more than one single factor, we also performed a Hierarchical Cluster Analysis (HCA). We used the UPGMA linkage method (Sokal and Michener, 1958) and the Morisita’s similarity index (Morisita, 1959), which is insensitive to the sample size. This clustering method linked families and subfamilies according to their temporal distribution.

Alroy (2010c) suggested to study the different faunas on the basis of changes in diversity and not just on taxonomic richness. For this analysis we used the logarithmic transformation of taxonomic richness [Log(N+1)], because differences in counts of the logged data are equivalent to net turnover rates (Foote, 2000; Alroy, 2000). Since FA could not be used with this type of data due to the presence of zeros, we used a PCoA of an Euclidean distance matrix of log ratios without undefined values in order to highlight the correlation between the faunas (Alroy, 2010c). FA, HCA and PCoA were carried out using the software PAST version 3.14 (Hammer et al., 2001).

### 2.5. Environmental impact

The latitudinal distribution of trilobites played a major role in their survival in the first half of the Palaeozoic (Westrop and Ludvigsen, 1987). A preferential extinction among families living in high latitudes affected Late Ordovician communities, while families living in lower latitudes survived and radiated into the Silurian (Adrain et al., 2004). We estimated the latitudinal distribution of families and subfamilies through time as well as the distribution of each fauna. We divided each hemisphere in three latitudinal bins: 0-30°, 30-60° and 60-90°.

Several sea-level changes occurred between the Silurian and Permian (Walliser, 1996; House, 2002; Calner, 2008; Haq and Schutter, 2008) and affected the benthic fauna, including trilobites. Moreover, it has been shown that bathymetry played a major role in replacement patterns (Jablonski and Bottjer, 1991; Adrain et al., 2004). In order to understand the impact of such events, we analysed the evolution of trilobite diversity at different bathymetry: shallow, inner shelf, outer shelf and slope/basin. The latter two are relatively deep environments, while shallow and inner shelf are rather shallow. Bathymetrical distributions for each factor were also estimated.

Type of sedimentation had an impact on the Palaeozoic benthic fauna (Balseiro and Powell, 2020). Substrate type has also shown to be important for macroevolutionary dynamics of origination and extinction (Foote, 2006; Kiessling et al., 2010), and faunal replacements (Tomašových, 2006; Miller and Connoly, 2001). Climate change and environmental events such as sea-level changes or perturbations of the carbon cycle also affected the biodiversity through time (Walliser, 1996; House, 2002). Thus, we compared the temporal trends in diversity for trilobite families and for described faunas (=factors) between siliciclastic and carbonate environments.

We also studied the relationship between trilobite total diversity with different environmental proxies estimated for the Palaeozoic from the literature. Because most trilobites lived along continental margins, changes in coastal length related to the collision of continents and the opening of new oceans (Scotese and McKerrow, 1990; Scotese, 2021) may have influenced their diversity. A fragmentation index estimated by Zaffos et al. (2017) was used as proxy for the amount of continental coastal environments available. Different isotope ratios were used as environmental proxies (Veizer et al., 1999). We used $^{87}Sr/^{86}Sr$ ratio (McArthur et al., 2012) as a proxy for seafloor spreading and/or continental weathering (Jones et al., 1994; Capo et al., 1998); $\delta^{18}O_{apatite}$ (Veizer and Prokoph, 2015) as a proxy for temperature change and $\delta^{13}C$ (Saltzman and Thomas, 2012) as a proxy for the global carbon cycle variation linked to changes in primary production and climate variations. We also compared total diversity and diversity of each fauna to $pCO_2$ (Foster et al., 2017) and the mean tropical sea-surface temperatures (Song et al., 2019; mean values from Scotese et al., 2021). We further used the Palaeozoic sea-level estimated by Haq and Schutter (2008) to identify faunal changes linked to the extent of continental flooding. The volume of sediments on the continental margins and ocean basins (Hay et al., 2006) was also analysed. Finally, we performed pairwise correlation tests of detrended values of these environmental proxies with detrended raw diversity values (McKinney, 1990; Alroy, 2000) in order to identify if some proxies could explain some trends in diversity. For detrending of time series we used the generalized differencing approach using the gen.diff() function for R (Lloyd, 2008). Correlations were done for the whole dataset together and for each fauna individually. Pairwise correlation tests were performed using Spearman's r as correlation index. As multiple comparisons were done between each diversity series and the eight environmental series, we used the False Discovery Rate approach (Benjamini and Hochberg, 1995) to reduce the risk of detecting false correlations. Analyses were carried out in the R statistical environment (v. 3.6.2; R Core Team 2019; https://cran.r-project.org/).

## 3. Results

### 3.1. Diversity

Both Range-through (RT) and Shareholder Quorum Subsampling (SQS) diversities (Fig. 2) show similar trends except for the Mississippian, where the diversity peak lasted until the Visean according to SQS, in agreement with Lerosey-Aubril and Feist (2012). Trilobite diversity increased in the Llandovery and remained high in the Wenlock despite slight variation in richness. A decrease in diversity occurred in the Ludlow-Pridoli before a sharp diversification in the Early Devonian to reach a maximum richness for the studied period with more than 180 genera referenced in the Emsian (Fig. 2). The Middle Devonian events appear to have the strongest impact, with SQS subsampling suggesting a very low Givetian diversity (Fig. 2). A sharp decline affected Middle Devonian trilobites with the loss of 80% of the number of genera before a period of low diversity in the Late Devonian. A final peak in diversity was documented in the Tournaisian but after another important decline, the trilobite diversity remained low until the end of the Permian despite a slight increase of diversity in the Middle Permian (Fig. 2).

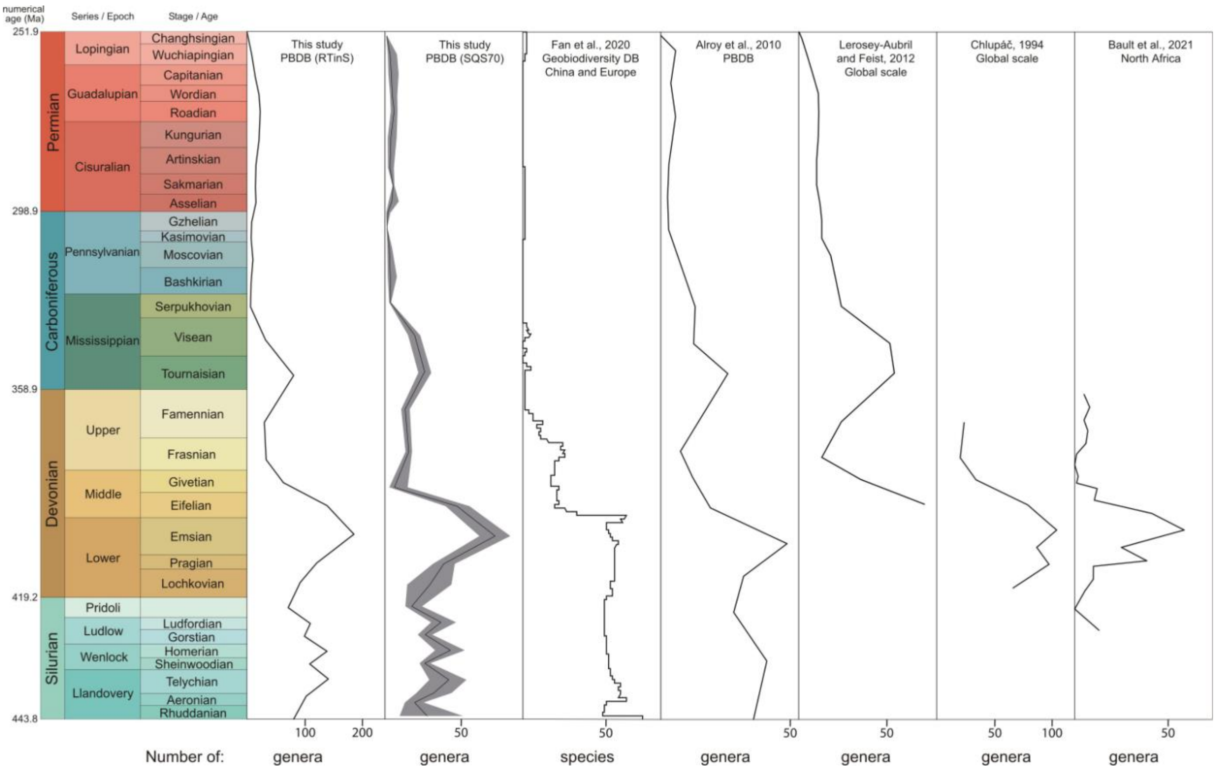


***Figure 2**. Diversity dynamics of trilobites from the Silurian to the Permian. Taxonomic richness from the PBDB estimated as Range-through diversity including single-interval taxa (RT) and the Shareholder Quorum Subsampling (SQS) diversity, estimation for a quorum of 70. Other curves correspond to the diversity estimated by Fan et al. (2020), Alroy et al. (2010c), Lerosey-Aubril and Feist (2012), Chlupáč (1994) and Bault et al. (2021) at regional or global . Diversity is estimated for each stage at the generic level except for Fan et al. (2020) who used the species level. Age from* Cohen et al. (2013, updated).

Positive net diversity changes were registered four times between the Silurian and Permian, namely the Early Silurian, the Early Devonian, the Mississippian and the Cisuralian. Four periods of negative turnover occurred: in the Late Silurian, the Middle Devonian, the Visean and at the end of the Permian (Fig. 3). Peaks of both maximum positive and negative net changes occurred both in the Devonian with a gain of 28 genera in the Pragian and a loss of 44 genera in the Eifelian respectively.

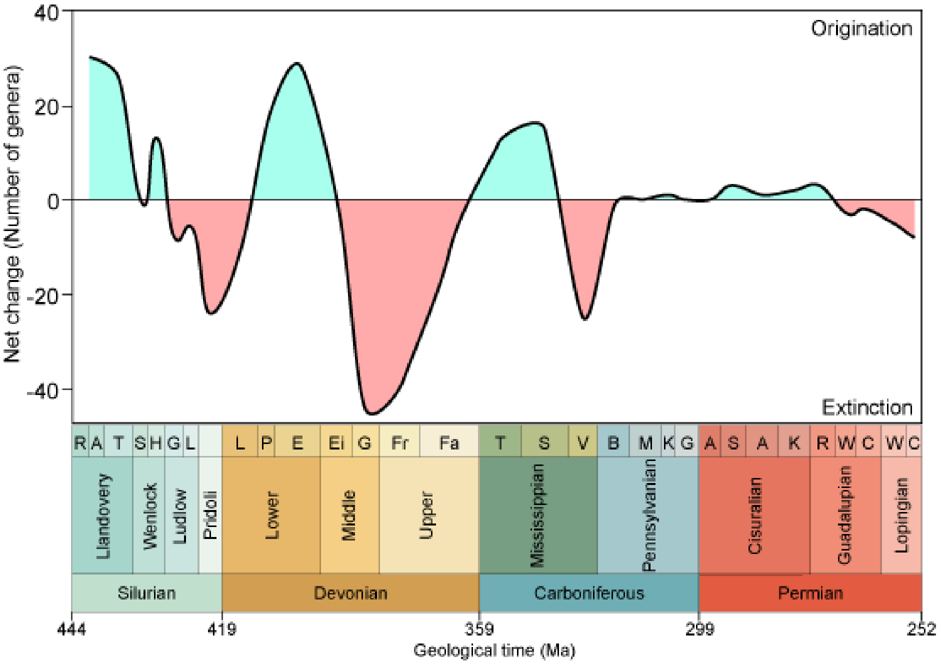


***Figure 3.*** *Net change of trilobites between the Silurian and the Permian. Net change per stage correspond to the number of origination of genera minus the number of extinction of genera. Positive net change indicates a period of origination and negative values indicate period of extinction. Age from Cohen et al. (2013, updated).*

## 3.2. Trilobite faunas

We defined trilobite faunas following a factor analysis, where each selected factor represents a single fauna (Sepkoski, 1981; Figueirido et al., 2012). Four factors accounting for the 97% of the variance of the trilobite diversity were selected (Fig. SUPPL. B). The first factor explains 52% of the total variance, the second 35% while factors 3 and 4 are less important with respectively 7% and 3% of the explained variance. These four trilobite faunas developed from the Silurian to Permian (Fig. 4). Each fauna dominated a period before giving another fauna diversified. The Silurian Fauna lasted from the Rhuddanian to Famennian, but was dominant only until the Pridoli (Factor 2 of FA, Fig. SUPPL. C; Fig. 4). The Devonian Fauna was present during the same period but became important only from the Lochkovian to the Givetian (Factor 3 of FA, Fig. SUPPL. C; Fig. 4). The Kellwasser Fauna was present only for short period, from the Eifelian to the Tournaisian, and became important only in the Late Devonian particularly in the Famennian (Factor 4 of FA, Fig. SUPPL. C; Fig. 4). Finally, a Late Palaeozoic Fauna emerged in the Famennian, became dominant in the Tournaisian and lasted until the end of the Permian (Factor 1 of FA, Fig. SUPPL. C; Fig. 4).

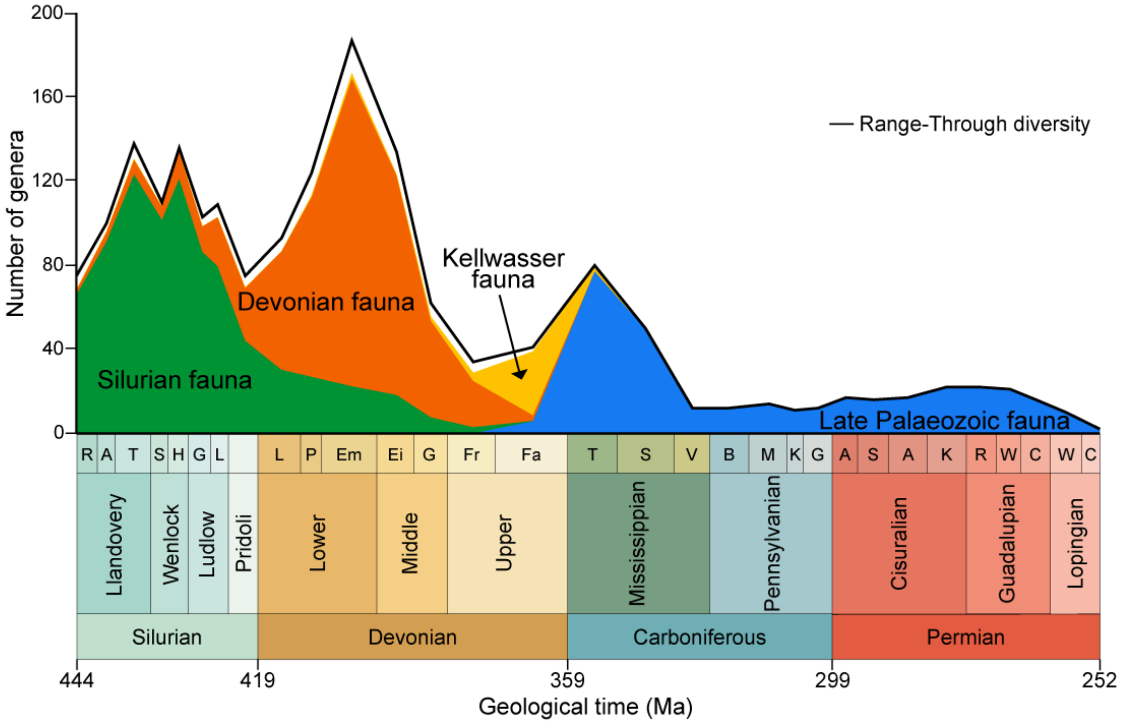
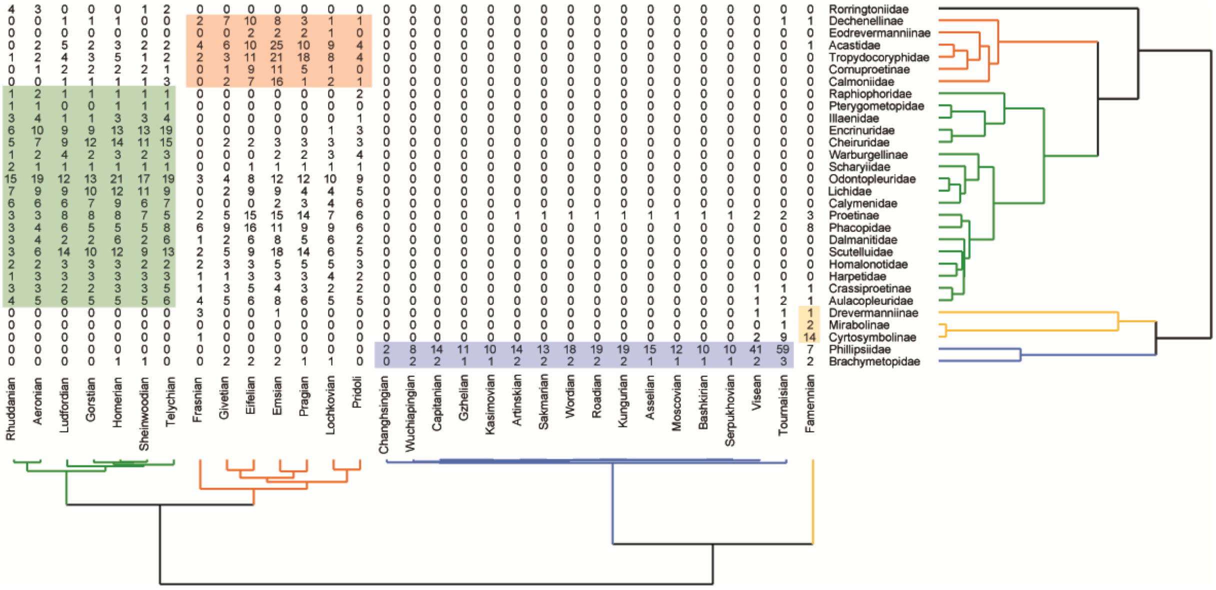


***Figure 4**. Diversity of each of the four trilobite evolutionary faunas from the Silurian to the Permian. Evolutionary faunas estimated with Sepkoski (1981)'s method. Black line represents the Range through diversity and the white part corresponds to the part of the diversity not explained by the model. Age from Cohen et al. (2013, updated).*



| Rhuddanian | Aeronian | Ludfordian | Gorstian | Homerian | Sheinwoodian | Telychian | Frasnian | Givetian | Eifelian | Emsian | Pragian | Lochkovian | Pridoli | Changhsingian | Wuchiapingian | Capitanian | Gzhelian | Kasimovian | Artinskian | Sakmarian | Wordian | Roadian | Kungurian | Asselian | Moscovian | Bashkirian | Serpukhovian | Visean | Tournaisian | Famennian | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 4 | 3 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | Rorringtoniidae |
| 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 7 | 10 | 8 | 3 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | Dechenellinae |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | Eodrevermanniinae |
| 0 | 2 | 5 | 2 | 3 | 2 | 2 | 4 | 6 | 10 | 25 | 10 | 9 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | Acastidae |
| 1 | 2 | 4 | 3 | 5 | 1 | 2 | 2 | 3 | 11 | 21 | 18 | 8 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | Tropydocoryphidae |
| 0 | 1 | 2 | 2 | 2 | 2 | 1 | 0 | 1 | 9 | 11 | 5 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | Cornuproetinae |
| 0 | 0 | 1 | 1 | 1 | 1 | 3 | 0 | 2 | 7 | 16 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | Calmoniidae |
| 1 | 2 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | Raphiophoridae |
| 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | Pterygometopidae |
| 3 | 4 | 1 | 1 | 3 | 3 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | Illaenidae |
| 6 | 10 | 9 | 9 | 13 | 13 | 19 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | Encrinuridae |
| 5 | 7 | 9 | 12 | 14 | 11 | 15 | 0 | 2 | 2 | 3 | 3 | 3 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | Cheiruridae |
| 1 | 2 | 4 | 2 | 3 | 2 | 3 | 0 | 0 | 0 | 2 | 2 | 3 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | Warburgellinae |
| 2 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | Scharyiidae |
| 15 | 19 | 12 | 13 | 21 | 17 | 19 | 3 | 4 | 8 | 12 | 12 | 10 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | Odontopleuridae |
| 7 | 9 | 9 | 10 | 12 | 11 | 9 | 0 | 2 | 9 | 9 | 4 | 4 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | Lichidae |
| 6 | 6 | 6 | 7 | 9 | 6 | 7 | 0 | 0 | 0 | 2 | 3 | 4 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | Calymenidae |
| 3 | 3 | 8 | 8 | 8 | 7 | 5 | 2 | 5 | 15 | 15 | 14 | 7 | 6 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 3 | Proetinae |
| 3 | 4 | 6 | 5 | 5 | 5 | 8 | 6 | 9 | 16 | 11 | 9 | 9 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | Phacopidae |
| 3 | 4 | 2 | 2 | 6 | 2 | 6 | 1 | 2 | 6 | 8 | 5 | 6 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | Dalmanitidae |
| 3 | 6 | 14 | 10 | 12 | 9 | 13 | 2 | 5 | 9 | 18 | 14 | 6 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | Scutelluidae |
| 2 | 2 | 3 | 3 | 3 | 2 | 2 | 2 | 3 | 3 | 5 | 5 | 5 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | Homalonotidae |
| 1 | 3 | 3 | 3 | 3 | 3 | 3 | 1 | 1 | 3 | 3 | 3 | 4 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | Harpetidae |
| 3 | 3 | 2 | 2 | 3 | 3 | 5 | 1 | 3 | 5 | 4 | 3 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | Crassiproetinae |
| 4 | 5 | 6 | 5 | 5 | 5 | 6 | 4 | 5 | 6 | 8 | 6 | 5 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | Aulacopleuridae |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | Drevermanniinae |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | Mirabolinae |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 9 | 14 | Cyrtosymbolinae |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 8 | 14 | 11 | 10 | 14 | 13 | 18 | 19 | 19 | 15 | 12 | 10 | 10 | 41 | 59 | 7 | Phillipsiidae |
| 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 2 | 2 | 1 | 1 | 0 | 0 | 2 | 2 | 1 | 1 | 2 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 2 | 3 | 2 | Brachymetopidae |

***Figure 5**. Hierarchical Cluster Analysis of the Post Ordovician trilobite families and subfamilies according their temporal distribution. Method used is UPGMA (Sokal and Michener, 1958) and the similarity index is Morisita's (Morisita, 1959).*

| Scores | Factor 1 | Factor 2 | Factor 3 | Factor 4 |
|---|---|---|---|---|
| >2 | Phillipsiidae (5.5)<br>81% | Odontopleuridae (3.2)<br>Encrinuridae (2.4)<br>Cheiruridae (2.1)<br>40% | Acastidae (2.5)<br>Tropydocoryphidae (2.3)<br>Phacopidae (2.2)<br>33% | Cyrtosymbolinae (4.4)<br>Phacopidae (2.6)<br>46% |
| >1 | | Lichidae (1.8)<br>Calymenidae (1.5)<br>Scutelluidae (1.3)<br>64% | Proetinae (1.9)<br>Dechenellinae (1.4)<br>Scutelluidae (1.4)<br>Encrinuridae (1.1)<br>Aulacopleuridae (1.1)<br>65% | Tropydocoryphidae (1.2)<br>49% |
| >0,5 | Brachymetopidae (0.6)<br>89% | Aulacopleuridae (0.7)<br>Illaenidae (0.6)<br>Proetinae (0.6)<br>Warburgellinae (0.5)<br>77% | Calmoniidae (0.9)<br>Cornuproetinae (0.8)<br>Homalonotidae (0.8)<br>Dalmanitidae (0.7)<br>81% | Scutelluidae (0.8)<br>Drevermanniinae (0.7)<br>Mirabolinae (0.6)<br>Cornuproetinae (0.6)<br>Calmoniidae (0.6)<br>Aulacopleuridae (0.5)<br>79% |

***Table 1**. Factor scores of the four evolutionary faunas. Family and subfamilies with a score higher than 0.5 are noted and distributed in to classes (>0.5, >1 and >2).*

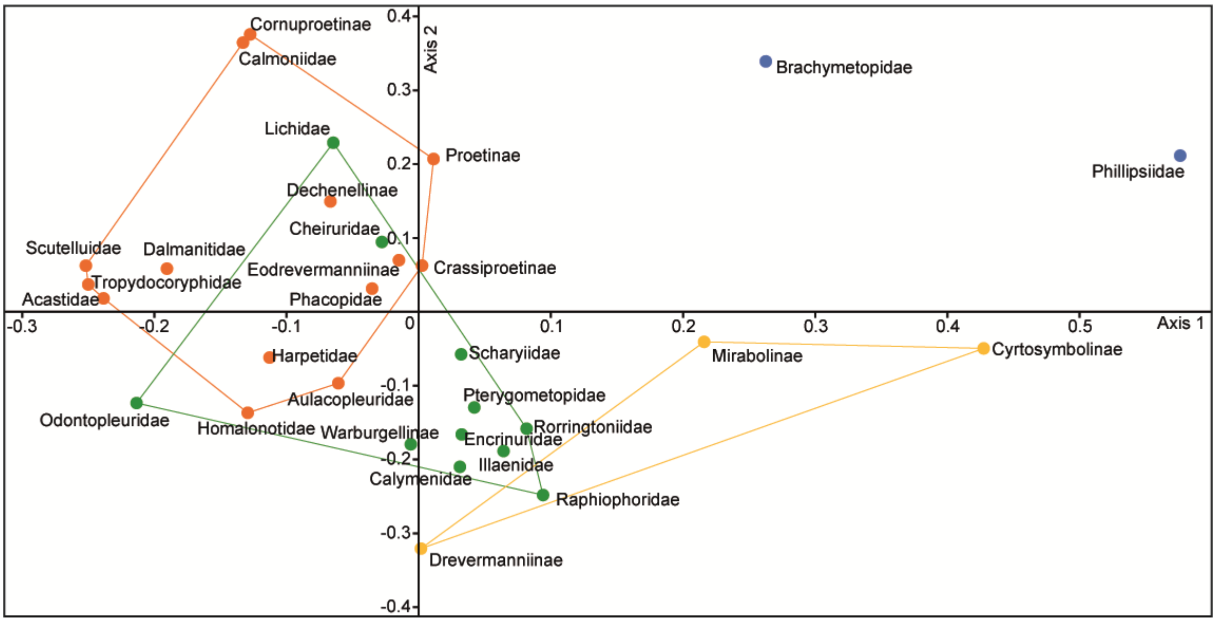


***Figure 6**. PCoA of a Euclidean distance between trilobite families and subfamilies according to their net change through time. Faunas defined by the factor analysis. Method from Alroy (2010c).*

All families and subfamilies were distributed into different faunas according to their scores in each of the four factors (Table 1). The Silurian Fauna was dominated by cheirurids, Encrinurids and Odontopleurids, while the main components of the Devonian Fauna were tropydocoriphids, acastids and phacopids. Phacopids and cyrtosymbolines were the main members of the Kellwasser Fauna and finally the Late Palaeozoic Fauna was dominated by phillipsiids. A few families, however, had equivalent scores in more than one factor. Scutelluids, pterygometopids, harpetids and crassiproetines were components of the Silurian and Devonian faunas. Similarly, phacopids were distributed between the Kellwasser and the Devonian faunas but represented a higher proportion of the Kellwasser Fauna (Fig. SUPPL. D). HCA helped to classify them into the fauna with which they were most related (Fig. 5).

PCoA shows that families and subfamilies were relatively equally distributed either based on their total diversity or change in diversity (Fig. 6). Cyrtosymbolinae, Mirabolinae, Brachymetopidae and Phillipsiidae show the highest PCoA1 values while the last two stand out with higher PCoA2 values (Fig. 6). PCoA groups families and subfamilies belonging to the Silurian and Devonian Faunas defined by the factor analysis. However, there is a relatively good separation between most families in the ordination belonging to the Silurian fauna which scattered along positive PCoA1 and negative PCoA2 values and most families from the Devonian Fauna which have negative PCoA1 and positive PCoA2 scores (Fig. 6). The only differences were that Drevermanniinae were closer to the Silurian Fauna and Phacopidae, Lichidae, Odontopleuridae and Cheiruridae closer to the Devonian Fauna.

Based on the abundance and turnover analyses, we could associate each family or subfamily with the fauna with which it had more affinity. The Silurian Fauna was composed of 11 families and subfamilies, i.e., Calymenidae, Cheiruridae, Encrinuridae, Illaenidae, Lichidae, Odontopleuridae, Pterygometopidae, Raphiophoridae, Rorringtoniidae, Scharyiidae, and Warburgellinae (Fig. 7). This fauna reached its maximum of diversity in the Silurian before a long decline until the end Devonian. The Devonian Fauna was composed of eight families and five subfamilies, i.e., Acastidae, Aulacopleuridae, Calmoniidae, Cornuproetinae, Crassiproetinae, Dalmanitidae, Dechenellinae, Eodrevermanniinae, Harpetidae, Homalonotidae, Proetinae, Scutelluidae and Tropydocoryphidae (Fig. 7). Most of these clades already existed in the Silurian but the diversity peak of this fauna was in the Early Devonian. The Kellwasser Fauna was composed of Cyrtosymbolinae, Drevermanniinae, Mirabolinae and Phacopidae, with a combined diversity increasing from the Silurian to the Late Devonian before a steep decline. The components of the Late Palaeozoic Fauna were Phillipsiidae and Brachymetopidae, which diversified mainly in the Early Carboniferous and survived until the end of the Permian (Fig. 7).

Different faunas coexisted at the same time, but one of them was generally dominant, except in the Pridoli-Lochkovian. The three main peaks in diversity from the Silurian to Permian can be explained by the emergence of one new fauna each time (Fig. 4). The Kellwasser Fauna, on the other hand, dominated during a period of reduced diversity is not related to a diversification event. Once a fauna lost its dominance it never regained it again. The decline of faunas was not similar for different faunas. While the Silurian Fauna progressively declined through more than

60 million years, the Devonian and Kellwasser faunas disappeared abruptly in less than 20 million years. After a rapid and significant loss of diversity in the Mississippian, the Late Palaeozoic Fauna survived for nearly 150 million years before becoming extinct.

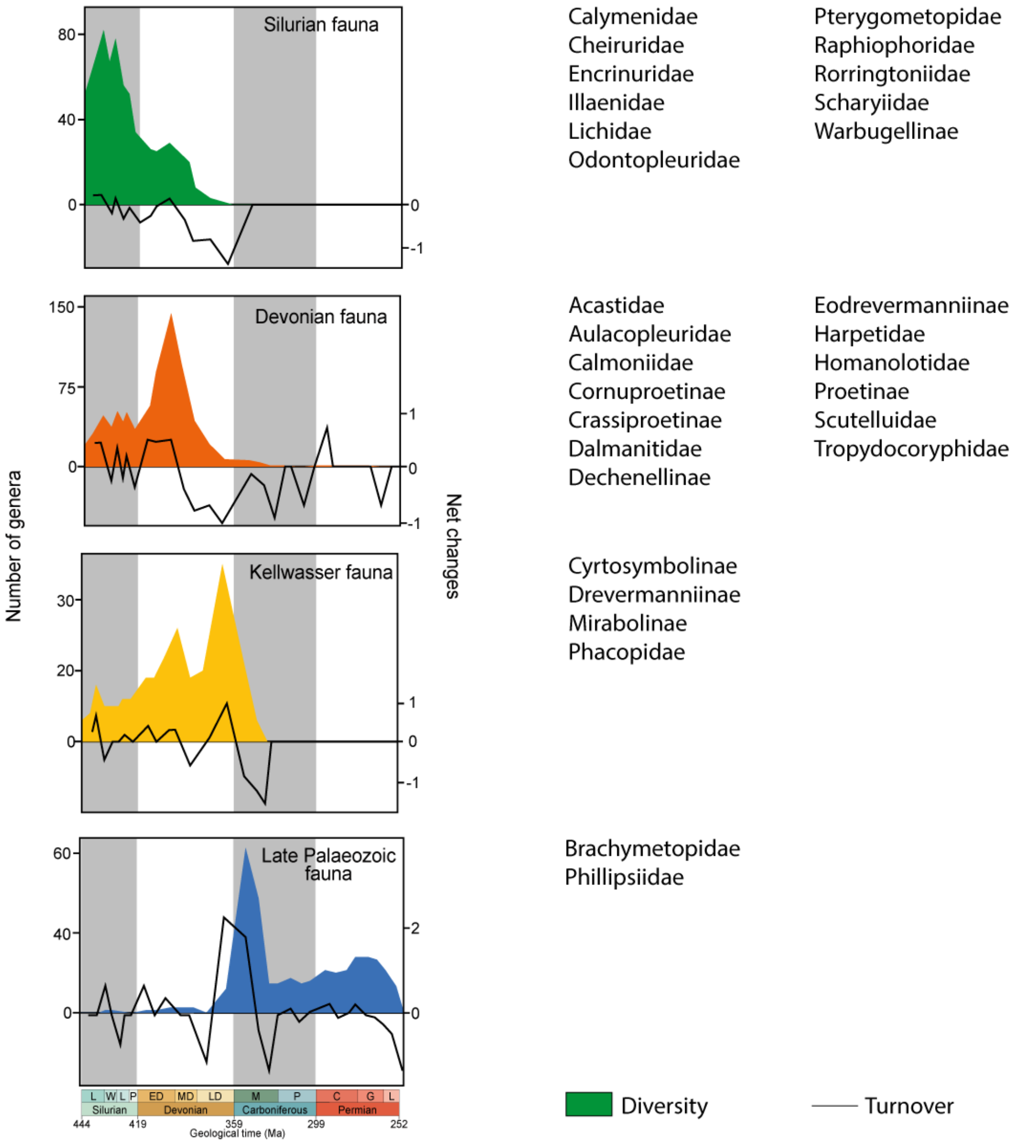


***Figure 7***. *Detail of the composition of each trilobite evolutionary fauna. Diversity of faunas corresponds to the sum of the Range-through diversity of all the family and subfamily components. Black lines correspond to the net change (logged) for each fauna. Age from Cohen et al. (2013, updated).*

### 3.3. Latitude

Most trilobite genera lived at low latitudes from the Rhuddanian to the Givetian (Fig. 8A). For the same period, the proportion of trilobites living/dwelling beyond 60° latitude increased until the end of the Silurian, although it remained largely minor. High latitude habitats were progressively depopulated by trilobites before being abandoned in the Frasnian. High latitude data from the Givetian to the Cisuralian should be taken with caution because there are no collections at all from these areas at this time; it could be a sampling bias. Frasnian corresponds to the only period when diversity became more important in the middle latitudes (Fig. 8A). The trend has been reversed since the Famennian with increasing numbers of trilobites dwelling at low latitudes (Fig. 8A). It is difficult to analyse post Mississippian data because they are based on the presence of only a few genera, leading to considerable uncertainty, but most trilobites appeared to live at low latitudes. However, some trilobites seemed to invade the high latitudes again in the Permian.

The latitudinal distribution of each fauna somewhat mirrors latitudinal trends for all trilobites (Fig. 8B). Small differences are found Kellwasser Fauna, which records a large proportion of genera at high latitudes during the Silurian (Fig. 8B). The Devonian Devonian Fauna shows a greater proportion of diversity at high latitudes (above 60° latitude), probably related to the diversification of Calmoniids (Abe and Lieberman, 2009). Interestingly, genera belonging to the Devonian Fauna that survived after the Late Devonian crisis, were constrained to low latitude habitats. The Late Palaeozoic Fauna developed initially at mid latitudes, and only later diversified in high and low latitude environments. Unfortunately, the low abundance of this fauna prevents any definitive interpretation. In the Carboniferous and Permian only the Late Palaeozoic Fauna was present beyond 30° latitude (Fig. 8B).

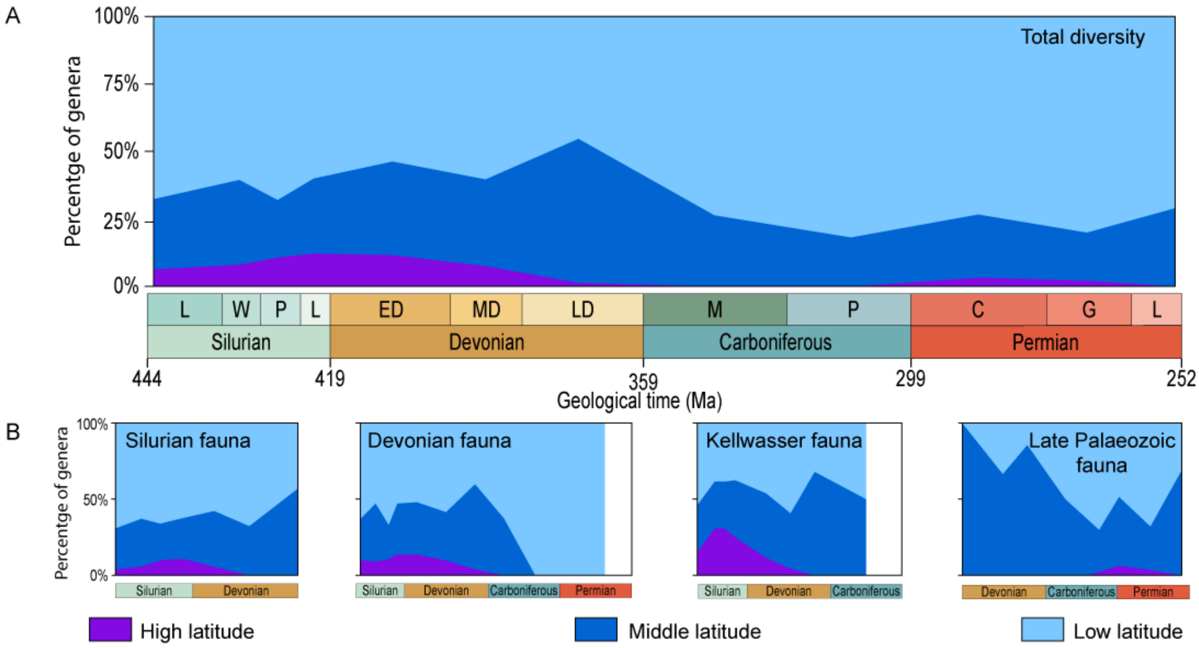


***Figure 8****. Latitudinal repartition through time of trilobites for the total diversity and for the four evolutionary faunas. Repartition is expressed in the percentage of genera. Age from Cohen et al. (2013, updated).*

## 3.4. Bathymetry

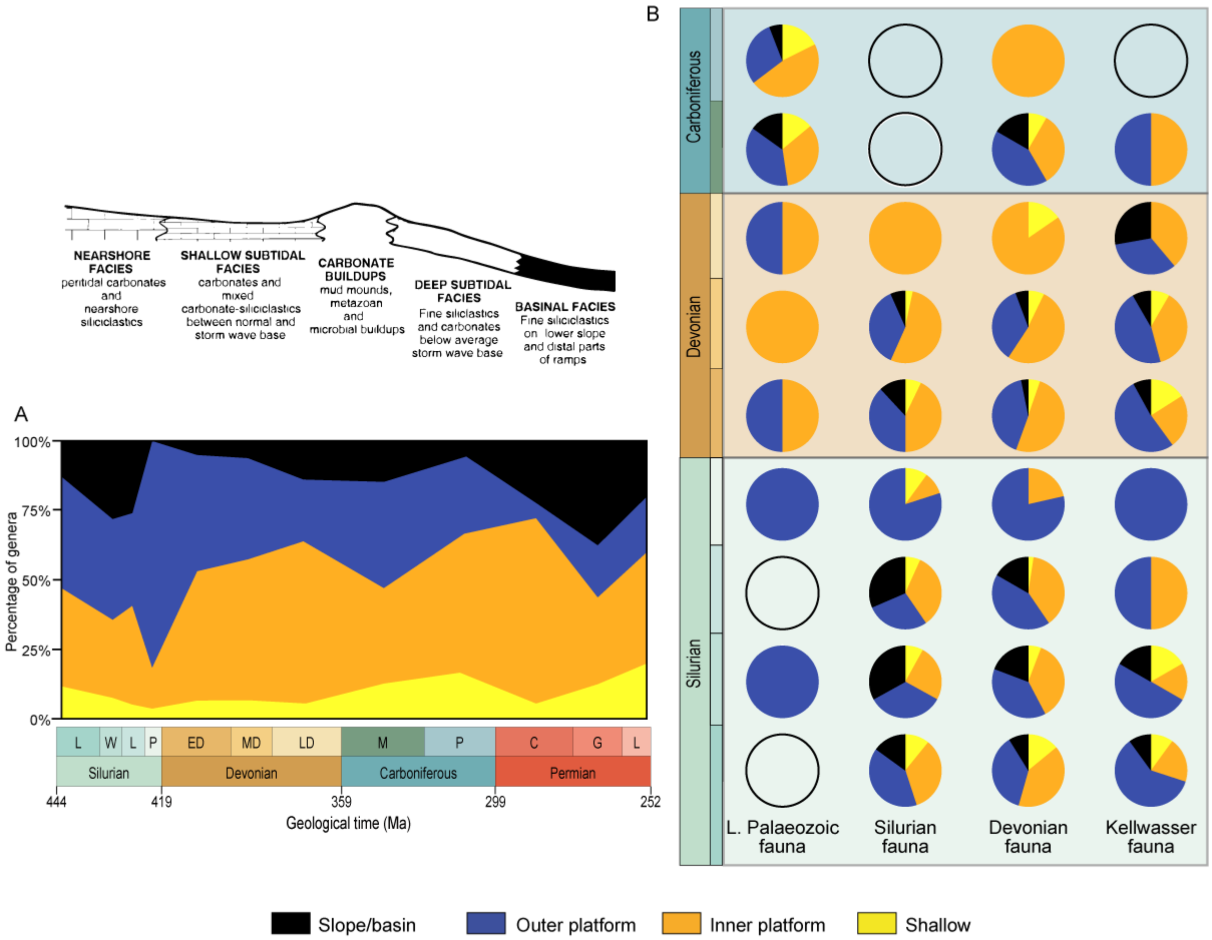


***Figure 9***. *Lithological repartition through time of trilobites (A) for the total diversity and (B) for the four evolutionary faunas. Diversity corresponds to the number of genera. Age from Cohen et al. (2013, updated).*

The bathymetrical distribution of trilobites changed over time (Fig. 9B). Trilobites living in deep water (i.e., Outer Platform and Slope/Basin facies) were an important part of the Silurian period before losing their importance in the Devonian. During this Period, trilobites developed preferentially in shallower environments (i.e., Shallow and Inner platform) but the Late Devonian corresponded to an increase in trilobites living in basinal environments (Fig. 9B). The importance of deep-water trilobites continued to increase in the Mississippian, but later they became rarer, excepted in the Guadalupian (Fig. 9B).

Most faunas showed similar bathymetric trends from the Silurian to the Middle Devonian. The Late Paleozoic Fauna, however, seems to have diversified in outer platform environments during this interval (Fig. 9C). Interestingly, during the Late Devonian only the Kellwasser

Fauna was present in the deep-water facies (Fig. 9C). It was not until the Carboniferous that the Late Paleozoic fauna accessed to shallow and deep-water environments, therefore dominating the whole bathymetric gradient.

### 3.5. Depositional environment

In the analysed dataset, most trilobites inhabited carbonate environments in all studied intervals (Fig. 10A). Diversity was almost equivalent between uniquely carbonate and siliciclastic or mixed environments during the Silurian. Nethertheless, trilobites with a carbonate affinity became particularly important from the Middle Devonian (Fig. 10A, Fig. SUPPL. E). Beyond this trend, the number of trilobites shows that diversification and extinction events occurred in any type of environments (Fig. 10A). After the Serpuhkovian crises few trilobites lived in siliciclastic environments (Fig. 10A).

The Silurian Fauna did not show a preference for either lithology throughout its history. Both the Devonian and Kellwasser faunas, however, showed no evident preference during the Silurian but occurred primarily in carbonates in the Devonian. With the exception of the Pennsylvanian, the Late Palaeozoic Fauna was preferentially recorded in carbonate environments (Fig. 10A).

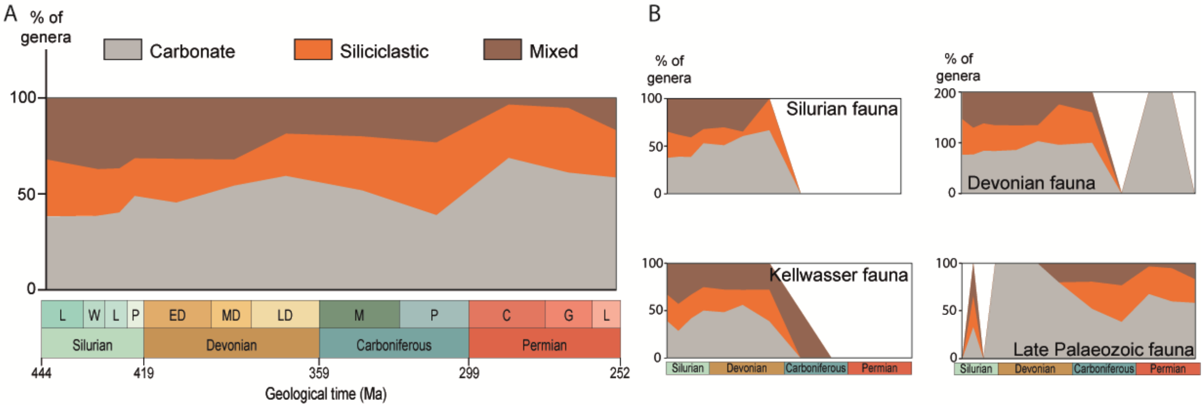


***Figure 10**. Environmental repartition through time of trilobites (A) for the total diversity and (B) for the four evolutionary faunas. Repartition is expressed in the percentage of genera. Age from Cohen et al. (2013, updated).*

### 3.6. Correlation with environmental proxies

Total trilobite diversity and evolutionary faunas were not correlated to any proxy (Table 2). Changes of a single proxy could not explain diversity dynamics.

| | Total | | Silurian | | Devonian | | Kellwasser | | Carboniferous | |
|---|---|---|---|---|---|---|---|---|---|---|
| | p | rho | p | rho | p | rho | p | rho | p | rho |
| **dSr** | 0.95 | -0.04 | 0.95 | -0.08 | 0.60 | -0.29 | 0.57 | 0.70 | 0.84 | 0.11 |
| **Sea-level** | 0.83 | 0.12 | 0.54 | 0.38 | 0.72 | 0.21 | 1 | 0 | 0.43 | 0.33 |
| **d13C** | 0.95 | 0.02 | 0.95 | -0.06 | 0.54 | -0.33 | 0.43 | 0.80 | 0.43 | 0.33 |
| **Sedimentation** | 0.43 | 0.31 | 0.43 | 0.48 | 0.43 | 0.42 | 0.83 | -0.40 | 0.69 | -0.20 |
| **Fragmentation** | 0.95 | 0.05 | 0.86 | -0.13 | 0.95 | 0.03 | 0.43 | 0.90 | 0.43 | 0.44 |
| **Temperature** | 0.83 | 0.11 | 0.64 | -0.30 | 0.83 | -0.15 | 0.43 | 0.80 | 0.66 | 0.21 |

***Table 2****. Results of the pairwise correlation tests of detrended (first differences) values of these environmental proxies with detrended raw diversity. Diversity at the global and by evolutionary faunas were compared to environmental proxies. Pairwise correlation tests were performed using Spearman's r as correlation index and p values were corrected because of multi correlation tests.*

## 4. Evolutionary faunas

### 4.1. Late Ordovician mass extinction and the early Silurian recovery

The Late Ordovician extinction event resulted in the disappearance of about 60% of genera and 25% of families (Sepkoski, 1996). It was probably a consequence of an important glaciation and a subsequent sea-level fall (Sheehan, 2001; Harper et al., 2014). Although trilobites were highly diverse in the Early Palaeozoic, this extinction strongly affected them, particularly the Cambrian faunas (Owen et al., 1991; Sheehan, 2001). All the families that successfully crossed the Ordovician-Silurian boundary without significant losses originated in the Ordovician (Owen et al., 1991; Adrain et al., 1998; Sheehan, 2001). Calymenids, cheirurids, encrinurids, illaenids, lichids, odontopleurids, pterygometopids, raphiophorids, rorringtoniids, scharyiids and warburgellines survived Late Ordovician events (Sepkoski, 1996; Sheehan, 2001; Harper et al., 2014) and have proliferated in many places since the Llandovery (Figs. 4, 7). These families and subfamilies were components of the Silurian Fauna, which is a subset of the Whiterock Fauna, as Adrain et al. (1998) already underscored (Adrain et al., 2000, 2004). The families and subfamilies of the Silurian Fauna were not the only ones to live in Silurian waters and some families and subfamilies of the Devonian Fauna were already present, such as acastids, scutellids, aulacopleurids and proetines (Fig. 7). The recovery was quick, the diversity of the Early Silurian trilobites was similar to that of the Cambrian and Ordovician at local (i.e., alpha diversity), despite a decrease in provincialism and β diversity (Adrain et al., 2000; Chatterton and Ludvigsen, 2004).

Polar areas were devoid of trilobites in the Rhuddanian (Fig. 4) because the Late Ordovician extinction strongly affected high latitude trilobites (Adrain et al., 2004). Consequently, the Early Silurian radiation occurred preferentially at low latitudes (Adrain et al., 1998). Similarly, many Silurian trilobites lived in shallow environments (Thomas and Narbonne, 1979; Siveter, 1995; Mikulic and Kluessendorf, 1999; Chatterton and Ludvigsen, 2004; Stocker et al., 2019; Wendruff et al., 2020; Yuan et al., 2020) because the Hirnantian extinction had a lesser impact on shallow water communities than on deep-water ones (Adrain et al., 2000).

## 4.2. Silurian

No important trilobite diversity changes occurred in the Silurian due to the relative climate stability in terms of environmental changes (Tinn et al., 2020). Nonetheless, Silurian trilobites were subject to minor taxonomic changes at low taxonomic ranks linked to environmental variations. The earliest events happened locally in the early Llandovery of the Northwestern Canada (Chatterton et al., 1990). This minor extinction affected the global diversity anyhow (Fig. 2). The first important event occurred at the Llandovery-Wenlock boundary and is known as the Ireviken event (Jeppsson, 1987; Munnecke et al., 2003). During this event, there was a sea-level fall associated with a positive excursion of $\delta^{13}C$ linked to anoxia and dysoxia. These environmental changes affected different biota as conodonts, corals, ostracods for example (Aldridge et al., 1993). 50 % of the trilobites of Gotland disappeared (Ramsköld, 1985). Although the Ireviken event was mainly spotted in Scandinavia, it occurred elsewhere in the world (Calner, 2008; Molloy and Simpson, 2012; Noble et al., 2012). It corresponded to the most important period of extinctions and migrations for Silurian trilobites of Northwestern Canada (Chatterton et al., 1990) and central USA (Mikulic and Kluessendorf, 1999). The global diversity was affected by this event (Fig. 2). In the early Ludlow, another important facies shift associated with positive excursion of $\delta^{13}C$ and sea-level drop occurred. It was the Mulde event, which led to diversity decrease. However, this event had a stronger impact on pelagic fauna as graptolites than on the benthic biota, which were mainly characterized by faunal changes (Calner, 2008). Therefore, trilobites were not strongly affected by this event and were found in the sediments deposited during this event (Jarochowska et al., 2014; Spiridonov et al., 2017). In addition, trilobites took advantage of the new conditions as odontopleurids arrived in Poland and in Scandinavia just after this event (Porębska et al., 2004; Calner et al., 2006).

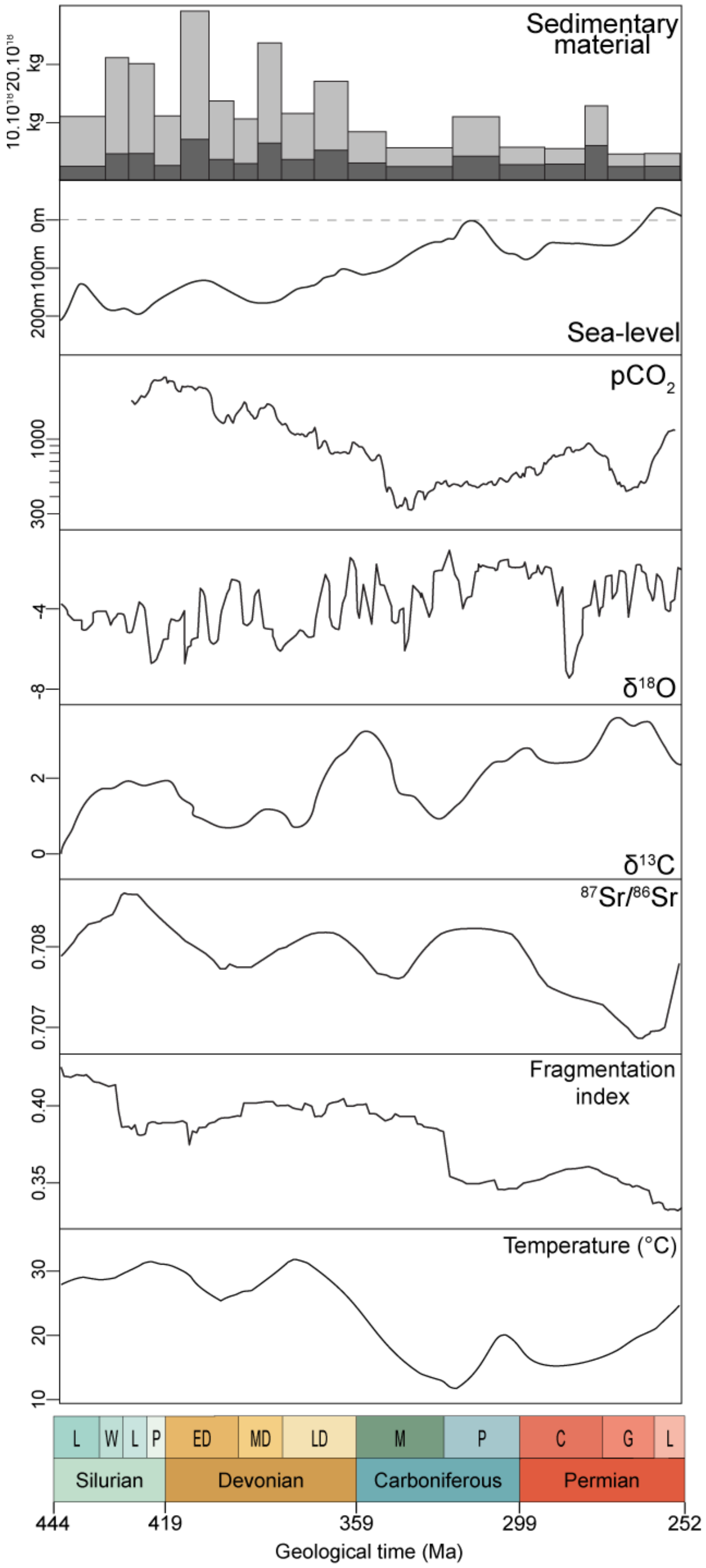


***Figure 11**. Trends of multiple environmental proxies. Existing (dark grey) and reconstructed (light grey) mass of continental and oceanic sediments from Hay et al. (2006). Sea-level from Haq and Schutter (2008); pCO$_2$ from Foster et al. (2017); $\delta^{18}$Oapatite from Veizer and Prokoph (2015); $\delta^{13}$C from Saltzman and Thomas (2012); $^{87}$Sr/$^{86}$Sr ratio from McArthur et al. (2012); Fragmentation index from Zaffos et al. (2017) and mean tropical sea-surface temperatures (Song et al., 2019, mean values from Scotese et al., 2021). Age from Cohen et al. (2013, updated).*

No important environmental affinity occurred during this relatively stable period. Since the Aeronian, trilobites started to develop beyond 60° latitude in Gondwana and Baltica, with several families restricted to high latitudes (Adrain et al., 1998). During the whole Silurian, high latitudinal trilobites were thus well-represented (Fig. 9). Latitudinal distribution partly explains the important proportion of Silurian trilobites in both mixed and silicilastic environments. Indeed, polar trilobites proliferated preferentially in siliciclastic environment whereas fauna living in carbonate deposits proliferated at low latitudes (Cocks and Fortey, 1990). Moreover, the Silurian was a period of large deposits of sedimentary material with a high $^{87}$Sr/$^{86}$Sr ratio (Fig. 11), indicating a period of important erosion and weathering (Capo et al., 1998). Colder and humid episodes occurring in the Silurian (e.g., P-episodes postulated by Jeppsson, 1990) increased weathering and erosion; the products of these weathering and erosion flowed into the oceans and led to more clastic deposits. The Silurian was also the last period of important erosion and sedimentation due to limited land plant cover (Hay et al., 2006), before the development of vascular plants in the Devonian (Pawlik et al., 2020). Consequently, there were large terrigenous inputs to the continental margins, which explains why many trilobites diversified in siliciclastic environments. Nevertheless, carbonate environments were also appreciated by Silurian trilobites (Mikulic and Kluessendorf, 1999; Chatterton and Ludvigsen, 2004; Hughes and Thomas, 2011; Wendruff et al., 2020; Fig. 10). Silurian trilobites were all benthic contrary to the Ordovician ones (Thomas and Lane, 1984), the substrate type had a strong effect on benthic communities (Henderson and Dann, 2010; Hopkins, 2014). Silurian trilobites also developed in relatively deep environments until the Ludlow (Fig. 9). Aulacopleurids were the first groups to diversify in high depth (Fortey and Owens, 1975). They were followed by many families until deep environments concentrate a relevant proportion of the total diversity (Storey et al., 2016). Trilobite proliferation in deep environment coincided with the Silurian long-term transgression until the Wenlock (Haq and Schutter, 2008). Differentiated trilobites biofacies could be recognized along the whole bathymetric profile, proliferating in various facies (Thomas, 1979; Mikulic and Kluessendorf, 1999; Chatterton and Ludvigsen, 2004) both carbonate and clastic (Fig. 10).

A third relatively important event struck the Silurian: the Lau event in the Ludfordian. This event had the most important impact on Silurian trilobites (Fig. 2) and corresponded to the beginning of the decline of the Silurian Fauna (Fig. 4). The Lau event was mostly spotted in central and Northern Europe (Lehnert et al., 2003; Antoshkina, 2018) and was characterized by a sea-level fall before a transgression and a perturbation in the carbon cycle as in the Ireviken and Mulde events (Calner, 2008; Munnecke et al., 2010; Bowman et al., 2019). Trilobites were affected by this event as were many other groups like acritarchs, chitinozoans, polychaetes, tentaculids and ostracods in Scandinavia but also in Canada, in Poland and in Britain (Jeppsson and Aldridge, 2000 and references therein; Eriksson et al., 2009). At the same time, a decrease of trilobite diversity occurred in North Africa even if the Lau event has not yet been recorded in this region (Bault et al., 2021). Decrease of diversity also concerned trilobites of Uzbekistan and Tajikistan between Ludlow and Pridoli (Ivanova et al., 2009) and in the Prague basin, there were trilobite extinctions in the Kozlowskii zone, just after the Lau event (Manda and Kříž, 2006). However, the impact of this event on trilobites concerned mainly taxonomic changes and trilobites were among the fauna participating to the recovery in the Prague basin (Lehnert et al., 2003; Manda and Frýda, 2014). Long-term sea-level drop began also in the Ludlow (Haq and Schutter, 2008). The effects associated with environmental changes (i.e., sea-level fall and carbon isotope disruption) particularly affected shallow environments and fauna at low latitudes (Calner, 2008). Thereby, Pridoli trilobites were mainly found in deep environments at higher latitudes. In addition, Calner (2008) highlighted important changes in carbonate platforms after the Lau event, explaining why trilobites living in carbonate environment were affected. Within the Silurian Fauna, Raphiophoridae and Encrinuridae disappeared shortly after the Pridoli (Chlupáč, 1994). The decline of the Silurian Fauna also corresponded to a reduction of continental margins, as suggested by a decrease of the fragmentation index (Fig. 11), partly due to the closure of the Iapetus Ocean and the collision of Baltica and Laurentia (Roberts, 2003; Scotese, 2021). As many Silurian trilobites lived along the coasts of these two continents (Cocks and Fortey, 1990; Adrain et al., 1998, 2000), these two palaeogeographical changes may have played a role in the weakening of the Silurian Fauna. Moreover, although the Silurian began with an icehouse climate with glaciations events (Calner, 2008; Munnecke et al., 2010; Trotter et al., 2016; Cuervo et al., 2018), a progressive warming of the oscillating climate occurred (Azmy et al., 1999; Gambacorta et al., 2019) to reach high temperatures in the Late Silurian and Lochkovian (Joachimski et al., 2009). Thus, the drop of the Silurian Fauna occurred when the climate no longer resembled to the one during its peak.

In parallel with the gradual decline of the Silurian Fauna, a gradual increase in the Devonian Fauna occurred since the Ludfordian (Fig. 4). The passage from one fauna to the other constituted a temporally diffuse turnover, the Devonian Fauna having a strong positive diversification from the Ludlow while the Silurian Fauna did not rebound after the Pridoli decline (Fig. 4). As for trilobites, a progressive faunal turnover occurred for decapods, another marine arthropod clade, in response to sea-level fluctuations and explosive radiations (Schweitzer and Feldmann, 2015). Schweitzer and Feldmann (2015) suggested a potential competition between decapods to explain such faunal turnover. This hypothesis could explain the Silurian-Devonian faunal transition among trilobites.

### 4.3. Early Devonian

The Devonian Period was characterized by vast continental seas with many carbonate environments (Tinn et al., 2020) and a climate that continued to warm (Torsvik and Cocks, 2013). The transition between the Silurian and the Devonian did not show important taxonomical changes and only low extinction rates (Chlupáč, 1994). Many families diversified in the Lochkovian suchas acastids, which lived in shallow siliciclastic environment (Morzadec, 1992; Chlupáč, 1994). Proetids, scutelluids and dalmanitids also diversified in this stage (Chlupáč, 1994), although they already existed in the Silurian. These families belonged to the Devonian Fauna, which become the dominant fauna. Diversity increased in the Pragian (Fig. 2). The global regressive event at the Lochkovian-Pragian boundary possibly led to this diversification (Chlupáč and Kukal, 1986; Chlupáč, 1994) with the increase in speciation rates by vicariance (Abe and Liebermann, 2009). This diversification was registered worldwide with the increase of diversity in the Pragian of North Africa (Bault et al., 2021), Czech Republic (Chlupáč et al., 1985) and Falklands Islands (Carvalho, 2006) for instance. Subsequently, trilobites diversified more in shallower environments (Fig. 9) in this period of global sea-level lowstand (Haq and Schutter, 2008), while the Silurian Fauna shallowed little preference for these shallow environments. Therefore, such changes accelerating the decline of the Silurian Fauna to the benefit of the Devonian Fauna. At the Pragian-Emsian transition, a transgression known as the Basal Zlichov Event occurred (Johnson et al., 1985; House, 2002), leading to a decrease of provincialism (Chlupáč, 1994). After this event, the early Emsian coincided with a slightly less diverse period. The following Daleje event corresponded to a worldwide sea-level rise and sedimentological changes (House, 1985, 2002; Chlupáč and Kukal, 1986) influencing trilobites (Chlupáč, 1994). After the transgression, blind and reduced-eyes trilobites developed as well as offshore trilobites, but shallower fauna remained highly diverse (Fig. 8). This led to a peak of low taxonomic rank richness in the late Emsian (Fig. 2, Chlupáč, 1994; Bault et al., 2021). It was particularly the time of the adaptive radiation of calmoniids (Eldredge and Branisa, 1980; Eldredge and Cracraft, 1980) and Chlupáč (1994) also noticed the increasing diversity during the Early Devonian of proetids, homanolotids, aulacopleurids, dalmanitids, scutelluids, acastids (asteropygines) and harpetids. Taxa of the Devonian Fauna were thus the main taxa responsible for the Early Devonian diversification. Phacopids, which are major taxa of the Kellwasser Fauna, also participated in the diversification of the Devonian (Fig. 6) with a maximum diversity in the Middle Devonian (Chlupáč, 1975; Crônier et al., 2011). The Emsian also showed higher diversity in different places like Ardennes (Crônier and Van Viersen, 2007), Colombia (Morzadec et al., 2015) or Morocco (Crônier et al., 2018), although it was not the case everywhere (Khaldi et al., 2016; Van Viersen and Taghon, 2020). The high diversity reached in the Early Devonian was the maximum post-Ordovician diversity (Adrain, 2008).

Carbonate and reef environments were widespread throughout the Devonian, favoured by the greenhouse climate and the presence of large epicontinental seas (Copper and Scotese, 2003; Joachimski et al., 2009; Copper, 2011; Tinn et al., 2020). Consequently, since the Early Devonian trilobites proliferated more in these carbonate environments (Chlupáč, 1994) relative to siliciclastic environments (Fig. 10). This interval also records the highest diversity in high latitude regions, with the flattest latitudinal diversity gradient. This pattern is probably related to the greenhouse climate (Cocks, 2007; Joachimski et al., 2009), as it is known that greenhouse intervals record rather flat latitudinal biodiversity gradients (Mannion et al., 2014). The Devonian Fauna diversification also occurred at high latitudes, notably with the development of calmoniids in the cold waters of the Malvinokaffric Realm (Carvalho and Ponciano, 2015). A diversification occurring at different latitudes characterized the trilobites because the Whiterock fauna originated at different place during its Ordovician radiation (Adrain et al., 2004). Such a biogeographic macroevolutionary pattern, however, is not the most frequent one, as highest origination rates occur frequently in the tropics (Jablonski, 1993; Brown, 2013).

Simultaneously to the Early Devonian diversification of the Devonian Fauna, a slowdown in the decline of the Silurian Fauna is observed between the Lochkovian and Eifelian (Fig. 4), during a period of diversification (Chlupáč, 1994), but without an increase in diversity. Between the Lochkovian and Eifelian, cheirurids, lichids and odontopleurids proliferated (Chlupáč, 1994).

### 4.4. Middle Devonian

No important changes in trilobite fauna characterized the transition to the Middle Devonian (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012) but the Middle Devonian events affected trilobite diversity negatively (Fig. 2). It was the onset of the decline of the Devonian Fauna while the Silurian Fauna fall accelerated (Fig. 7). A first event (i.e., the basal Choteč event), corresponding to a deepening associated to anoxia and dysoxia (House, 2002), occurred in the early Eifelian. These environmental changes affected the trilobites at the global with migrations and extinctions despite a stable rate of diversification (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012). Trilobite families did not react in the same way because at the opposite of the decline of many families, Lichidae, Acastidae and Proetidae showed important innovations (Lerosey-Aubril and Feist, 2012). Transgression and anoxia could be more important at the regional as in North Africa (Klug et al., 2000; Ouali Mehadji et al., 2004), leading to a sharper decline of trilobites (Bault et al., 2021). At the opposite, the sea-level rise offered new shallow carbonate areas where trilobites proliferated (Fig. 10) and diversity increased (Crônier and Van Viersen, 2007; Bignon et al., 2008). The following Kačak event and its oxygen-depleted conditions also influenced Devonian Fauna (House, 1985, 2002; Walliser, 1996) including trilobites with extinctions and migrations (Feist, 1991; Morzadec, 1992; Chlupáč, 1994). However, Eifelian events were not the most devastating Middle Devonian events. The middle Givetian Taghanic event is associated with an important sea-level rise that killed many taxa, particularly ammonoids (House, 1985, 2002; Walliser, 1996). Trilobites were severely affected by this event, particularly those living in shallow environments. Lichids, cheirurids and calmoniids as well as some proetid and aulacopleurids subfamilies went extinct (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012), whereas deep-water clades survived (Feist, 1991).

The decrease in the diversity in deep-water environments (Fig. 9) and high latitude (Fig. 8) was gradual. It was a consequence of a long-term effect (Haq and Schutter et al., 2008) and the succession of rapid sea-level transgressions. The decline in high latitudes was possibly linked to the progressive climate cooling in the Early and Middle Devonian (Joachimski et al., 2009; Scotese et al., 2021) affecting cold-water taxa. A cooler climate is associated with a steeper latitudinal gradient, possibly related to a decrease in high latitude diversity (Mannion et al., 2014). Furthermore, northward migration of Gondwana (Scotese and McKerrow, 1990; Scotese, 2021) must also have resulted in a decrease in high latitude coastlines. No lithological selectivity happened with the Middle Devonian events because both carbonate and clastic environments were involved in the decline (Fig. 6). Therefore, the disappearance of the Devonian Fauna corresponded to the decline of the trilobites rather than a faunal replacement, as it was the case for the Silurian Fauna.

### 4.5. Late Devonian

After the Taghanic event, no important changes affected trilobites which reached the late Frasnian without drastic changes (Fig. 2). The generic diversity remained low with few originations (Feist, 1991; Chlupáč, 1994; Lerosey-Aubril and Feist, 2012). Absent in the

Givetian, the Kellwasser Fauna replaced the Devonian Fauna in the Late Devonian (Fig. 4). The Kellwasser Fauna, primarily phacopids and cyrtosymbolines, began to become highly diverse in the Frasnian (Fig. 4) with the adaptive radiation of phacopids present in shallow neritic to outer shelf habitats (Feist, 1991). The only event occurring in this period was the Frasnes event which affected both pelagic and benthic organisms (Walliser, 1996). This event only had a low impact on trilobites (Lerosey-Aubril and Feist, 2012). On the other hand, the Upper Kellwasser event occurring at the end of the Frasnian was one of the five mass extinctions (Raup and Sepkoski 1982; McGhee et al., 2013). This event was characterised by sea-level changes with a transgression followed by a regression and an important episode of anoxia (House, 2002; Bond and Wignall, 2008; Carmichael et al., 2019; Lu et al., 2021). The impact on the biota was important and many clades were severely affected (Buggish, 1991). This event had a strong effect on both low and high taxonomic levels of trilobites. Indeed, three of the five orders still living in the Frasnian disappeared: Corynexochida, Harpetida and Odontopleurida (Lerosey-Aubril and Feist, 2012). These orders were already impoverished in genera after being severely affected by the Taghanic event and the disappearance of their last genera at the end of the Frasnian led them to their extinction (McNamara and Feist, 2006; Feist and McNamara, 2007; McNamara et al., 2009). Subsequently, the Silurian Fauna disappeared with the Frasnian-Famennian crisis and the extinction of Odontopleuridae (Feist, 1991; Feist and McNamara, 2007).

Only two orders survived to the Kellwasser events, i.e., Phacopida and Proetida, but many of their families and subfamilies vanished: Asteropyginae, Cornuproetinae and Tropidocoryphinae (Chlupáč, 1994). After the Kellwasser biocrisis, the first trilobite to recover worldwide was the phacopid *Pulvinocephalus* in the early *triangularis* zone (Feist, 2019). Then, drevermanniines and cyrtosymbolines appeared in the *crepida* zone of the early Famennian (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012). However, trilobite diversity remained low until the late-early Famennian when the recovery really happened, giving a Famennian taxonomic richness similar to the Frasnian one (Fig. 2).

These trilobites took advantage of the Late Devonian environmental changes and invaded shallow and deep environments globally (Brauckmann et al., 1992; Lerosey-Aubril and Feist, 2005; Feist et al., 2003, 2009; Crônier et al., 2013). The Kellwasser Fauna became the dominant fauna in the Famennian. It was the only fauna that diversified in a context of a global decrease in diversity and with a short existence. This evolutionary fauna could be characterized as an opportunistic (Levinton, 1970) or crisis fauna.

Although the Kellwasser event severely affected offshore communities, recovery largely occurred in deep environments (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012). Temperature and bathymetry seemed to be two key parameters in the evolutionary fauna change although none of the fauna were strongly correlated with these parameters (Table 1). Indeed, the Silurian and the Kellwasser faunas that succeeded each other are faunas with different bathymetry affinities. In addition, they evolved in a different global temperature context. Temperature started to increase in the Frasnian (Fig. 11), to reach Lochkovian values, i.e., before the diversification of the Devonian Fauna. The affinity of the Kellwasser Fauna for warm waters seems to explain why the recovery occurred in a carbonate environment first and not in high latitudes (Figs. 8, 10). The higher faunal diversity at middle latitudes was related to a lower latitudinal gradient during greenhouse periods (Mannion et al., 2014). During its origins in the Silurian, the Kellwasser Fauna was mainly composed of high latitude genera in contrast to its Late Devonian distribution. A greater intensity of Middle and Late Devonian events in the tropics could lead to the migration of extratropical genera toward low latitudes. Indeed, reef communities representing complex ecosystems were strongly affected by the Frasnian-Famennian extinction event, resulting in greater consequences at low and middle latitudes (Buggish, 1991; McGhee, 1996; Walliser, 1996; Gong, 2002; Bond et al., 2013; Barash, 2017, Huang et al., 2018). Another explanation for the displacement of the Kellwasser Fauna towards lower latitudes could be related to the ecology of extratropical Silurian phacopids. Some of them were adapted to relatively deep environments near the storm wave base (Holloway, 1980; Sánchez et al., 1991; Rustán et al., 2011b; Fig. 9). Thus, after the deepening linked to the Devonian events, they could invade other places deserted by previous evolutionary faunas.

In addition to the taxonomic changes, important morphological changes affected trilobites around the Frasnian-Famennian boundary. Eyes reduction and blindness occurred in different taxa and in different parts of the globe (Feist, 1991, 2019; Crônier et al., 2004; McNamara and Feist, 2008, 2016; Lerosey-Aubril and Feist, 2012; Schoenemann, 2018) and were related to deepening and turbidity causing decrease of light (Feist et al., 2009). This common explanation is not enough in few cases and a propensity to an endobenthic behaviour were suggested for reduced-eyes and blind trilobites (Feist and Clarkson, 1989; McNamara and Feist, 2016). A size reduction could also affect trilobites (Feist and McNamara, 2016). The first Famennian trilobites were the phacopids *Pulvinocephalus* (*Cryphopsides*) and *Nephranops* appeared in the early Famennian in the *triangularis* zone in deep offshore environment (Feist, 2019). This reflected the post-Kellwasser trend of trilobites to move toward deeper habitats (Chlupáč, 1994; Feist et al., 2009; Lerosey-Aubril and Feist, 2012; Bault et al., 2021) as slope or basins (Fig. 8).

Nonetheless, many trilobites still occurred in shallow environment (Fig. 8; Crônier et al., 2020). Subsequently, other anoxic/hypoxic events and sea-level changes happened, i.e., Condroz and Annulata events (Walliser, 1996; House, 2002), with a low impact on trilobites. A second diversification occurred in the late Famennian during the Dasberg event among both Proetida and Phacopida (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012), following a transgressive event implying diversification in nektic fauna such as Gonioclymeniina (House, 2002). Near the Devonian/Carboniferous boundary, another important biotic turnover linked to anoxia/dysoxia and sea-level fall occurred (Walliser, 1996; House, 2002; Kaiser et al., 2016; Zhang et al., 2020). Trilobites were strongly affected by this event (Fig. 2), with the disappearance of the order Phacopida as well as blind and reduced-eyes Proetida trilobites (Lerosey-Aubril and Feist, 2012). The Hangenberg event was lethal for both shallow and deep water trilobites (Chlupáč, 1994), but it had a stronger impact on deeper trilobites and consequently, survivors mostly lived in shallower areas (Feist and Petersen, 1995). Important faunal changes coincided with this event (Brauckmann et al., 1992). The Kellwasser Fauna almost disappeared with the Hangenberg event at the end of the Devonian, resulting in the extinction of phacopids (Lerosey-Aubril and Feist, 2012) and the decline of cyrtosymbolines, so that this subfamily was considered extinct for a long time (Feist, 1991). Climate cooling and glaciation at the Devonian-Carboniferous boundary (Isaacson et al., 2008; Kaizer et al., 2016) affected more severely a fauna accustomed to warmer temperatures.

### 4.6. Carboniferous and Permian

The early Carboniferous recovery was achieved with the survival of two families, namely Brachymetopidae and Phillipsiidae, which characterized the Late Palaeozoic Fauna (Figs. 4, 7). While the brachymetopids already existed in the Devonian, the phillipsiids emerged and diversified in the Tournaisian (Owens, 1990; Lerosey-Aubril and Feist, 2012; Vanderlaan and Ebach, 2015), and were largely responsible for the peak in diversity of the latest trilobite evolutionary fauna. The diversification of this fauna was very rapid after the Late Devonian extinction events and could be considered as a recovery fauna. Tournaisian diversity recovered to the higher taxonomic richness values since the Eifelian (Fig. 2). This rise of diversity was not homogeneous at the global and trilobite diversity remained low in China (Fan et al., 2020). This diversity peak was mainly due to the great radiation of phillipsiids whereas the other families remained low diversified (Owens, 1990). With this diversification, trilobite and especially phillipsiids occupied various environment from reef to outer platform (Fig. 8; Owens, 1990). There were no differential trends in bathymetric repartition because no long-term sea-level changes affected the Famennian-Tournaisian transition (Haq and Schutter, 2008). Tournaisian diversification coincided with a higher $^{87}Sr/^{86}Sr$ ratio (Fig. 11), indicating a possible increase in continental supply due to erosion. As a result, trilobites invaded the siliciclastic environments whereas they previously preferred shelf carbonate environments (Owens, 1990; Lerosey-Aubril and Feist, 2012; Fig. 10). While the Late Palaeozoic Fauna was restricted to the mid-latitudes in the Devonian, it invaded the low latitudes deserted by other trilobite evolutionary faunas in the Carboniferous. The high latitudes remained deserted in a context of low temperatures (Scotese et al., 2021).

Contrary to pelagic clades, Trilobites survived anoxia and sea-level changes of the Mid-Tournaisian event (Walliser, 1996). Subsequently, the decline of phillipsiids corresponded to the decline of the Late Palaeozoic Fauna in the Visean and Serpukhovian (Fig. 2) in all depositional environments and at all depths. Then, trilobite diversity stagnated while other benthic faunas could strongly diversify in the second part of the Carboniferous (Shi et al., 2021). As this fauna never reached a similar taxonomic richness again and remained essentially undiversified for the next tens of millions of years, it could be considered as a ‘dead clade walking’ (Jablonski, 2002; Barnes et al., 2021). From the Serpukhovian, the fauna developed preferentially in low latitudes due to the establishment of a progressive icehouse climate (Cocks, 2007; Shi et al., 2010; Fig. 8). Since the Mississippian, only a small proportion of trilobites were found in deep-water facies due to the decline of phillipsiids in basinal environments (Fig. 8; Owens, 1990). The Mid-Carboniferous events (Saunders and Ramsbottom, 1986; Walliser, 1996) led to the extinction of many benthic and pelagic taxa. However, the trilobite diversity was already low at this time and no significant changes happened (Lerosey-Aubril and Feist, 2012). Then, the beginning of the Pennsylvanian was characterised by another period of origination and a rise of diversity, but not in the same magnitude as the Tournaisian (Fig. 2). Trilobites followed a global trend resulting in the diversification of numerous clades at this period, boosted by the closure of the Rheic ocean and advantageous environmental changes (Shi et al., 2021). A higher proportion of trilobites lived in siliciclastic environments than in carbonate environments. This was a consequence of the cooling of the Late Palaeozoic Ice Age, which had an impact on the carbonate factory (Balseiro and Powell, 2020). With this cooling, tropical faunas slightly decline (Fig. 9). Powell (2005) noticed that brachiopods from low latitudes were the most affected too, suggesting that tropical taxa disappeared because they had a narrower latitudinal distribution. At the end of the Pennsylvanian another diversity decrease occurred (Lerosey-Aubril and Feist, 2012). Trilobites did not show important diversity changes in the end of the Carboniferous and the beginning of the Permian (Lerosey-Aubril and Feist, 2012) during a period characterized by important glaciation and low marine invertebrate diversity (Alroy et al., 2008). Since the Asselian, the Late Palaeozoic Fauna developed again preferentially in carbonate environments (Fig. 10). With the climate warming, trilobite diversity slightly rose in the Sakmarian-Artinskian (Lerosey-Aubril and Feist, 2012). The reappearance of the high latitude fauna in this warmer phase during a period of glaciation is notable (Cocks, 2007; Haig et al., 2014, 2017). Then, another decrease linked to very low origination rates because of unfavourable environment (Lerosey-Aubril and Feist, 2012). The Late Palaeozoic Fauna disappeared at the Permian-Triassic boundary sealing the fate of the trilobites (Lerosey-Aubril and Feist, 2012; Song et al., 2013).

## 5. Ecological changes

The Devonian was a key period in the Palaeozoic history with important changes in both marine and terrestrial ecosystems. On the continents, land plants diversified and invaded continental environments (Cleal and Cas-Miñana, 2014; Pawlik et al., 2020; Dahl and Arens, 2020). Land plants are suspected to be a major driver of environmental changes occurring from the Devonian to the Permian. In the Late Devonian, vascular plants developed on lands with the consequence of increased burial of organic carbon in marine sediments and the enhancement of the silicate weathering (Algeo and Scheckler, 1998, 2010; Pawlik et al., 2020; Dahl and Arens, 2020). These upheavals dropped the atmospheric $CO_2$ levels and positive $\delta^{13}C$ shift in marine carbonates (Fig. 11) leading to climate cooling (Algeo and Scheckler, 1998; Algeo et al., 2001), although effect of land plants was not the only mechanism evoked for weathering (Goddéris et al., 2017; Racki et al., 2018; McDonald et al., 2019). However, recent studies argued that land plants hampered weathering (D'Antonio et al., 2020) leaving the land plant effect an ongoing debate. Diversification of vascular plants affected marine environments with the supply of nutrient fluxes and plant litter in epicontinental seas leading to increase of primary productivity and thus, eutrophication and anoxia (Algeo and Scheckler, 1998; Zhang et al., 2020; Lu et al., 2021). Trilobites and particularly those of the Devonian Fauna were affected by anoxic events. In addition to these changes, diversification of vascular land plants could lead to a late Famennian glaciation and especially the Carboniferous-Permian glaciation (Algeo and Scheckler, 1998). Environmental changes induced by continental plants affected trilobites in the same way as changes in marine ecosystems did, particularly the Kellwasser Fauna, which appreciated warm climate. Therefore, changes in ecosystems in the second part of the Palaeozoic challenged trilobites, which never regain their former diversity despite the Tournaisian diversification.

In parallel to the plant terrestrialization, the Devonian Nekton Revolution (Klug et al., 2010) occurred in the oceans with the diversification of many nektic animals, although the nekton was diversified prior to the Devonian (Whalen and Briggs, 2018). Development of such fauna could influence trilobite diversity in two different ways. Nektic organisms could be new predators for trilobites or new concurrent for food resource. Concerning predation, Palaeozoic trophic links remains largely unknown (Brett and Walker, 2002) but some assumptions are made on the possible predators. Besides, the number of durophagous predators sharply increased in the Devonian (Signor and Brett, 1984; Brett, 2003). In parallel, trilobite ecdysis was different from other arthropods and implied longer intermoult periods, enhancing their vulnerability to predators (Brandt, 2002). Babcock (2003) envisaged different trilobite predators appearing progressively in the Palaeozoic seas: phyllocarids, eurypterids, malacostracans, jawless and jawed fishes, cephalopods, some echinoderms, and even other trilobites. There was a rise of predator diversity from the Middle Devonian with the diversification of nautiloids, placoderms, elasmobranches and Sarcopterigii/Actinopterygii (Klug et al., 2010) contemporary to the decrease of the Devonian Fauna. Ammonoids appeared in the Emsian while nautiloids developed (Klug et al., 2010). Nautiloids were suspected to hunt trilobites since the Early Palaeozoic (Brett and Walker, 2002; Brett, 2003; Bicknell et al., 2019), their increasing diversity could mean increasing predation on trilobites. Concerning ammonoids, their potential predation on trilobites remained uncertain, particularly because there is no evidence that ammonoids had jaws and radula in the Palaeozoic (Nixon, 1996; Tanabe et al., 2015). Despite the lack of strong evidence, jawed fishes were able to eat chitinous arthropods and shelly benthic organisms (Mark-Kurik, 1995; Brett and Walker, 2002). Consequently, frequency of healed bite marks and peeling on trilobite exoskeletons increased since the Devonian (Brett, 2003). Crustaceans, asteroids and gastropods could also have predator/scavenging behaviour (Gale, 1987; Brett and Walker, 2002). Marine predators could also play a major role in the Mississippian trilobite dynamic, particularly regarding the Visean-Serpukhovian extinction in the absence of important environmental events. Camerate crinoids showed the same diversity trends as trilobites with a Tournaisian diversification followed by a strong decline in the Visean (Sallan et al., 2011). After the Late Devonian extinctions, the predators were scarce and benthic prey including trilobites and crinoids could diversify. Subsequently, predators and especially durophagous fishes proliferated, strongly affecting their prey diversity. Consequently, camerate crinoids dropped (Sallan et al., 2011) and a similar pattern could occur with trilobites, explaining the short Tournaisian recovery.

In response to increasing predation, trilobites adopted different strategies. In the Devonian, many trilobites tended to develop spines, which were supposed to be helpful against predators. Spines functioned as defensive structures to protect trilobites or to camouflage oneself (Kloc, 1992, 1993, 1997; Pates and Bicknell, 2019). However, spines were inefficient against predators with large jaws, which developed from the Late Devonian and in the Mississippian (Brett, 2003; Sallan et al., 2011). Another way to escape from predation could be size changes. A size reduction of prey could occur, as it was the case for crinoids (Waters and Maples, 1991; Brett, 2003). Indeed, it seems that the larger trilobites were more attacked than the others (Bicknell et al., 2019). Conversely, predation is avoided by achieving larger body too. An enlargement could be done with the development of spines (Johnsen et al., 2013) without a strong increase in biomass. Cryptic behaviour as infaunal moulting could also be considered as defensive behaviour (Rustán et al., 2011a; Rustán and Balseiro, 2016). Moreover, many Kellwasser Fauna genera were characterized by eyes reduction, which could be interpreted as endobenthic behaviour (Feist and Clarkson, 1989; McNamara and Feist, 2016). Consequently, changes in predation affected trilobite faunas, taxa with infaunal moulting and small size abilities were thus better equipped to cope with increasing predation.

From the Silurian to the Permian, the nektic fauna and benthic trilobites were decoupled, as the nekton diversity was low in the Early Devonian, the Devonian Nekton Revolution persisted throughout the Devonian environmental events and the Mississippian showed opposite trends between nekton and benthos (Klug et al., 2010; Sallan et al., 2011; Whalen and Briggs, 2018). This decoupling was not only due to predation but also to different reaction facing Devonian environmental events as it was suggested for North Africa (Ebbighausen et al., 2011; Bault et al., 2021). Indeed, similar benthic fauna showed the same variation as trilobites, like brachiopods (Carlson, 2016).

An increase in resource competition with the appearance of new clades could affect trilobites, similarly as in other communities, by impeding diversification (Bailey et al., 2013) leading to extinctions (Smith and DeSantis, 2020), or the opposite, inducing adaptive radiation (Meyer and Kassen, 2007; Bailey et al., 2013). In trilobites, resource competition could partly explain the Early Devonian diversification. Indeed, a strong resource competition in a dense population or with new ecological opportunities could favoured inter and intraspecific diversification (Rainey and Travisano, 1998; Bailey et al., 2013; Aristide and Morlon, 2019). Conversely, the arrival of new competitors with the same food niche could lead to the decline or demise of a taxon (Smith and DeSantis, 2020). With the diversification of predators (Klug et al., 2010), the predator/scavenger trilobites saw the arrival of new competitors in the Devonian. The predator/scavenger behaviour concerned trilobites from the four evolutionary faunas and especially Corynexochida, Lichida, Odontopleuridae, Calymenoidea, Phacopina and secondarly conterminant Proetida, Fortey and Owens, 1999). However, the trilobite clades that persisted in the Late Palaeozoic were probably all predators or scavengers (Fortey and Owens, 1999), so the competition was potentially enhanced for the particle feeding (e.g., aulacopleurids) and the filter (e.g., harpetids, raphiophorids) trilobites. Thus, resource competition could explain the low diversity of trilobites from the Middle Devonian and the inability of radiating afterwards, except for the moderate Tournaisian peak. Phases of low resources accentuated the competition effects on the demise of taxa (Vakulenko et al., 2018). Consequently, the extinction of potential prey because of the Devonian events, which affected several taxa (Buggish, 1991; Walliser, 1996; House, 2002), and the decrease of nutrient supply in the Middle and Late Devonian (Large et al., 2015) could participate in the decline of trilobites in the late Palaeozoic.

It is complicated to know whether predation, resource competition or asymmetrical effect of Devonian events, but faunal changes occurring in the Devonian-Permian clearly affected trilobites.

## 6. Conclusion

On the basis of abundance and faunal turnover over time, we identified four evolutionary faunas characterizing trilobites from the Silurian to the Permian:

1. The Silurian Fauna was inherited from the Ordovician fauna that survived the Hirnantian extinction events and was dominant until the Pridoli. This evolutionary fauna was dominated by Cheiruridae, Encrinuridae and Odontopleuridae but several other families and subfamilies developed in this diverse fauna. The Silurian trilobites developed more at high latitudes and in a siliciclastic environment than later faunas. This evolutionary fauna progressively lost its dominance with the Devonian environmental changes, although it may have survived until the Frasnian-Famennian boundary.
2. Another evolutionary fauna has progressively dominated the trilobite community since the Pridoli, represented mainly by Acastidae and Tropydocoryphidae. This is the Devonian Fauna, whose members already existed at the beginning of the Silurian. This evolutionary fauna developed mainly in the Devonian with the environmental changes, i.e., a greenhouse

environment, an increasing carbonate environment and drowned epicontinental seas. The development of this fauna led to an important diversification of trilobites to the highest post-Ordovician taxonomic richness. However, the Devonian Fauna was challenged by environmental and ecological changes. Several Middle Devonian events affected the trilobites, leading to a sharp decline in diversity and the disappearance of the Devonian Fauna at the end of the Frasnian.

3. The Kellwasser Fauna had the shortest life span, only in the Late Devonian and Tournaisian. This is the only evolutionary fauna that is characterized by low diversity, as the Middle Devonian environmental changes decimated the ancient evolutionary faunas. Dominated by Phacopidae and Cyrtosymbolinae, this evolutionary fauna invaded both shallow and deep environments. The taxa of this fauna are characterized by important morphological changes such as the eye-reduction. At that time, trilobites appreciated warm and carbonate environments. The gradual cooling that began in the Famennian and the Hangenberg event at the Devonian-Carboniferous boundary led to the disappearance of this evolutionary fauna.

4. Only the order Proetida developed in the Late Palaeozoic Fauna, dominated by Phillipsiidae. Although trilobites were able to recover in the Tournaisian, a further decline in the late Mississippian left them poorly diversified despite their survival until the Permian-Triassic crisis.

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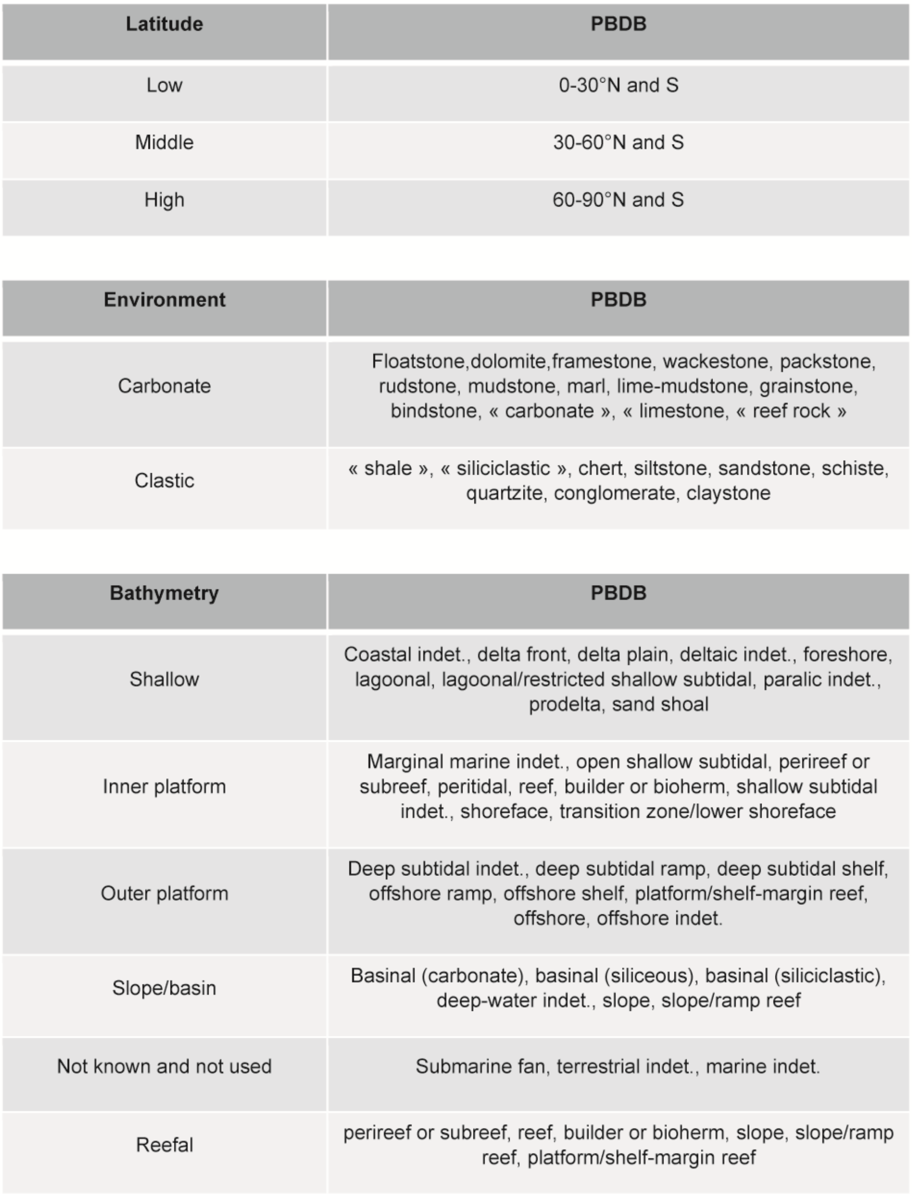
## Supplementary figures

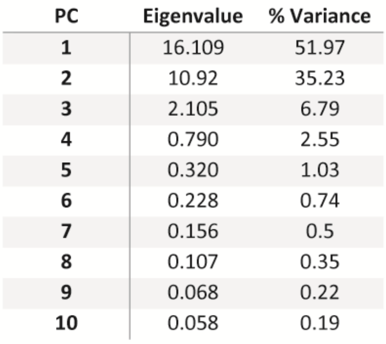


| Latitude | PBDB |
|---|---|
| Low | 0-30°N and S |
| Middle | 30-60°N and S |
| High | 60-90°N and S |

| Environment | PBDB |
|---|---|
| Carbonate | Floatstone,dolomite,framestone, wackestone, packstone, rudstone, mudstone, marl, lime-mudstone, grainstone, bindstone, « carbonate », « limestone, « reef rock » |
| Clastic | « shale », « siliciclastic », chert, siltstone, sandstone, schiste, quartzite, conglomerate, claystone |

| Bathymetry | PBDB |
|---|---|
| Shallow | Coastal indet., delta front, delta plain, deltaic indet., foreshore, lagoonal, lagoonal/restricted shallow subtidal, paralic indet., prodelta, sand shoal |
| Inner platform | Marginal marine indet., open shallow subtidal, perireef or subreef, peritidal, reef, builder or bioherm, shallow subtidal indet., shoreface, transition zone/lower shoreface |
| Outer platform | Deep subtidal indet., deep subtidal ramp, deep subtidal shelf, offshore ramp, offshore shelf, platform/shelf-margin reef, offshore, offshore indet. |
| Slope/basin | Basinal (carbonate), basinal (siliceous), basinal (siliciclastic), deep-water indet., slope, slope/ramp reef |
| Not known and not used | Submarine fan, terrestrial indet., marine indet. |
| Reefal | perireef or subreef, reef, builder or bioherm, slope, slope/ramp reef, platform/shelf-margin reef |

***Figure SUPPL. A.*** *Table of the attribution of each PBDB category to latitudinal, environmental and bathymetrical categories used in this article.*



| PC | Eigenvalue | % Variance |
|---|---|---|
| **1** | 16.109 | 51.97 |
| **2** | 10.92 | 35.23 |
| **3** | 2.105 | 6.79 |
| **4** | 0.790 | 2.55 |
| **5** | 0.320 | 1.03 |
| **6** | 0.228 | 0.74 |
| **7** | 0.156 | 0.5 |
| **8** | 0.107 | 0.35 |
| **9** | 0.068 | 0.22 |
| **10** | 0.058 | 0.19 |

***Figure SUPPL. B.*** *Eigenvalues for the first ten eigenvectors given by the CABFAC factor analysis of trilobite family and subfamily diversity from the Silurian to the Permian.*

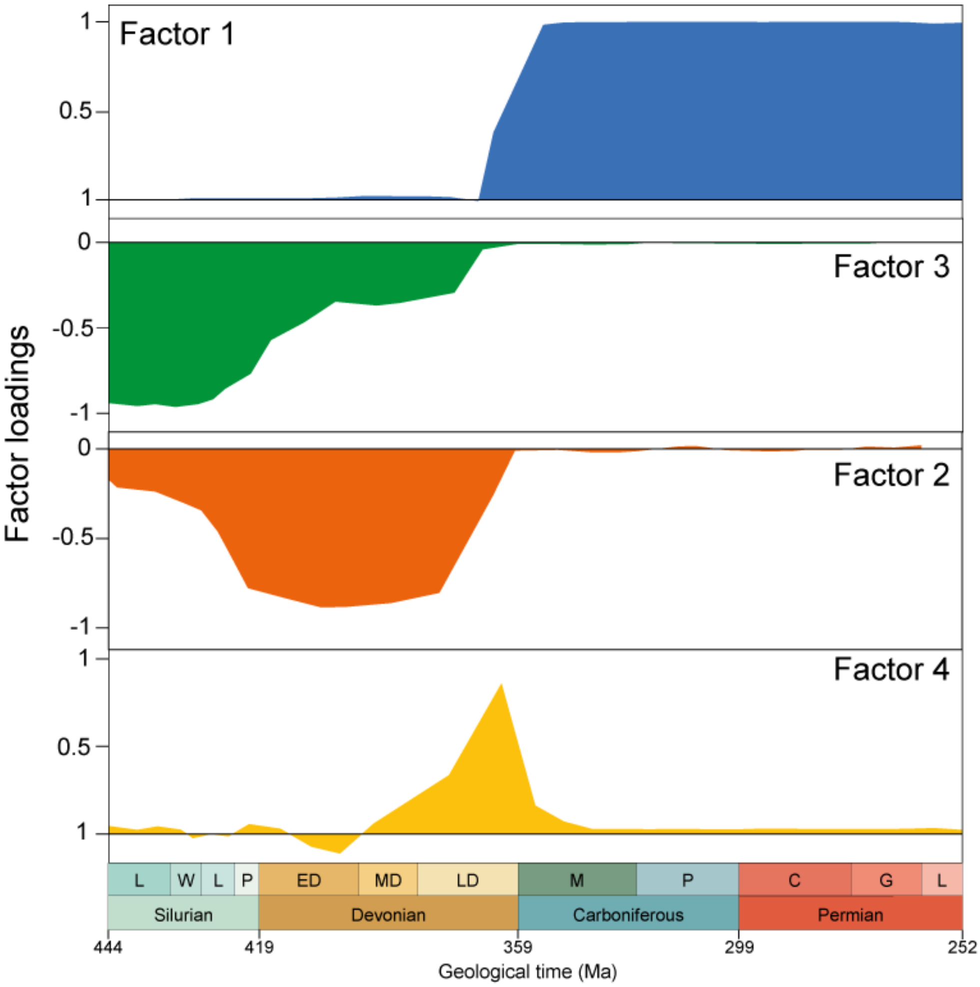


***Figure SUPPL. C.*** *Factor loadings of the first four factors generated by the CABFAC factor analysis. Age from Cohen et al. (2013, updated).*

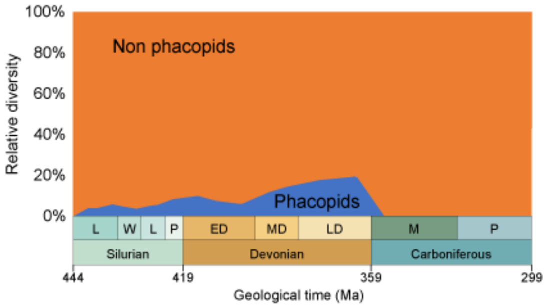


***Figure SUPPL. D.*** *Percentage of phacopids from the Silurian to the Carboniferous. Age from Cohen et al. (2013, updated).*

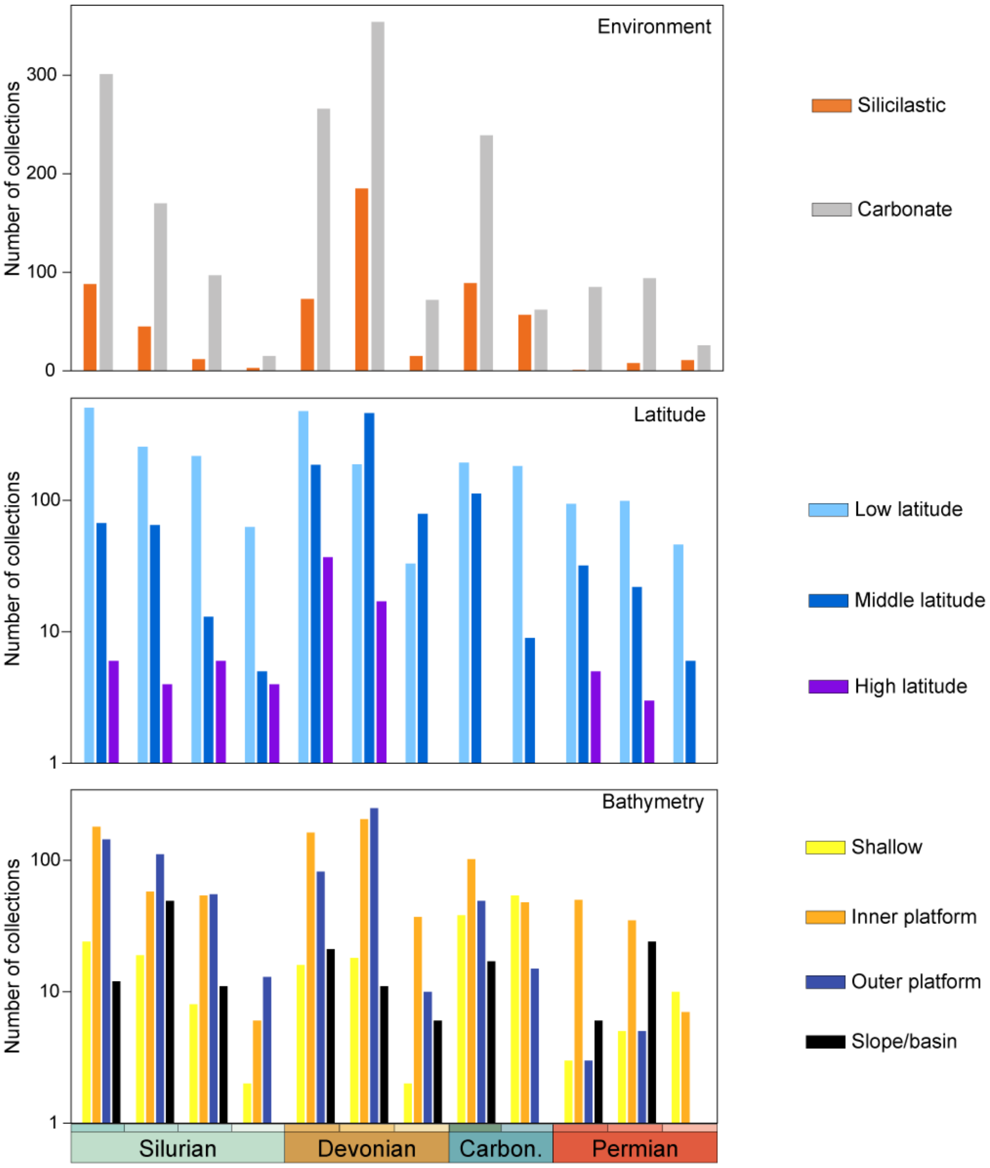


***Figure SUPPL. E.*** *Number of collection recorded in the PBDB for each environmental category.*

## 1.2. Disparité morphologique des phacopidés

### Article 2 : Morphological disparity of phacopids

Pour être soumis à Lethaia

# MORPHOLOGICAL DISPARITY OF PHACOPIDS

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## Abstract:

Phacopidae was a successful family of the Silurian-Devonian period. Their morphologies were analysed by using Procrustes analyses and morphometric disparity indices. Results showed some morphological variations between the genera and through time. Phacopids differ from each other by the position of the facial suture linked to the visual complex size, the shape of the genal angle and the elongation of both cephalon and pygidium. The morphological disparity of the cephalon was high since the Silurian contrary to that of the pygidium. Subsequently, the morphological disparity increased in the Early Devonian with the development of narrow cephala and triangular pygidia. The peak of morphological disparity was reached in the Emsian for both cephala and pygidia, more than 50 Myr after the phacopid origination. This late diversification was favoured by the appearance of new environmental opportunities. Strong decrease of morphological disparity occurred in the Middle Devonian, caused by sea-level changes and anoxic events. Although the diversity increased until the Eifelian, taxonomic richness declined strongly in the Givetian. These extinction phases were non-random affecting particularly blind morphologies. Despite morphological changes in the Frasnian with a progressive eye reduction, the morphological disparity remained low. An important recovery occurred in the Famennian with the important increase of both diversity and morphological disparity. A Famennian trend toward reduced-eyes and blindness was confirmed and the pygidia became more elongated. Once again, environmental changes led to the morphological dynamics. However, the last Devonian event caused the final extinction of phacopids.

## Keywords:

Trilobites, Palaeozoic, phacopids, morphological disparity, diversity, diversification, extinction

## 1. Introduction:

Phacopidae is a typical family of the Siluro-Devonian epicontinental platforms, and an important component of the marine benthos, represented worldwide, especially in Europe and North Africa. This family originates at the end of the Ordovician (Campbell 1967, Adrain 2013), probably derived from the Pterygometopidae family (Ludvigsen & Chatterton 1982). The first phacopid was *Sambremeusaspis* Lespérance in Lespérance and Sheehan 1988, the most primitive member of the whole family (Ramsköld and Werdelin 1991). After this genus all phacopid genera developed, firstly a few in the Silurian, then several in the Devonian, to reach its highest diversity in the Middle Devonian (Crônier et al. 2011). While the Phacopidae was one of the rare trilobite families to survive the Frasnian-Famennian extinction, they vanished at the end of the Devonian with the Hangenberg event (Chlupáč 1994; Lerosey-Aubril & Feist 2012). Throughout their long evolutionary history, phacopids underwent several environmental changes (Walliser 1996; House 2002; Calner 2008; Qie et al. 2019) including the second of five mass extinctions described by Raup & Sepkoski (1982), i.e., the Kellwasser events (Buggisch 1991; Carmichael et al. 2019). These events positively influenced their diversity as for example the Pragian regression which led to the Pragian diversification of phacopids as well as many other trilobite clades (Chlupáč 1994), or negatively such as for example the Late Devonian events which led to the extinction of many genera (Feist 1991).

In this Epoch, this family, by its great diversity in genera and species (McKellar and Chatterton 2009; Crônier and François 2014), occupied numerous habitats of the epicontinental platforms from the shallow depths to beyond the photic zone, and they showed strong bathymetrical and palaeogeographical affinities (Crônier & François 2014). Their morphology but also their behaviour were affected by environmental changes and particularly at the Frasnian-Famennian boundary with the development of blind forms living in deeper-water environment and/or endobenthic (Feist et al. 2009).

Phacopidae firstly described by Hawle & Corda (1847) are characterised by a glabella broadening markedly forward with lateral glabellar furrows S2 and S3 obsolescent, and S1 often transglabellar leading to an 'intercalating ring', genal angles rounded without genal spines, and a visual complex often well-developed. The phacopid pygidium is well rounded, semicircular or shorter, without lateral or marginal spines (Harrington et al. 1959). The morphological diversity among Phacopidae is expressed especially in the shape of both the vincular furrow and visual complex and in the course of the facial suture (Fig. 1). Systematic clusters are based primarily on these characters (Crônier et al. 2011). Chlupač (1977) identifies two sub-families, i.e., Phacopidellinae Delo, 1935 characterised by a cephalic doublure without a vincular furrow and Phacopinae Reed, 1905 characterised by a cephalic doublure with a deep and continuous vincular furrow. McKellar & Chatterton (2009) proposed a distribution of genera and sub-genera in tribes based on the work of Flick & Struve (1984), Haas (1998) and Struve (1970, 1972, 1976, 1982, 1989, 1990, 1992, 1995). This distribution is in disagreement with the previous work of Chlupač (1977): numerous members belonging to Phacopidellinae or Phacopinae are in the same tribe. Moreover, all taxa belonging to this family, listed in the exhaustive list of Jell & Adrain (2003), have not been taken into consideration.

Environmental changes are reflected in the variations of the exoskeleton of trilobites and their evolutionary history, which is essentially adaptive. Trilobites seem to represent a potential to analyze trends and evolutionary processes (Foote 1989, 1990, 1991a, 1993, Gerber & Hopkins 2011, Webster & Zelditch 2011). Some analyses focused at the family or the subfamily level, such as the analysis of Pterocephaliidae (Hopkins 2013) but not in Phacopidae.

Therefore, the present study aims to investigate the morphological evolution of all phacopids from their origination in the Silurian to the end of Devonian, by analysing their cephalic and pygidial shapes at the genus level. Here, the morphological disparity is investigated for the first time at the global  and using the stage as temporal .

## 2. Material and methods:

### 2.1. Datasets

To explore the morphology of the Phacopidae family, we have compiled two datasets respectively to investigate the two main structures in the trilobites, i.e., the cephalon and the pygidium (Whittington et al. 1997), and, we have selected most of genera confirmed by Jell & Adrain (2002). Updates since this publication were taken into account such as the replacement for *Cultrops* Struve, 1995 to *Struvephacops* (Ghobadi Pour 2015) as well as the description of new genera: *Morocops* (Basse, 2006), *Enigmapyge* (Feist et al. 2016), *Magreanops* (VanViersen & Vanherle 2018) and *Feistops* (Crônier et al. 2020). The Late Devonian *Phacops* Emmrich, 1839 being significantly different from previous ones (Crônier et al., 2011), we separated them into a distinct genus named: *Phacops sensu lato*. Moreover, the Pterygometopidae *Calyptaulax* Cooper, 1930 was also included. The Pterygometopidae family is considered as the sister group of the Phacopidae family (Ludvigsen & Chatterton 1982) and one of its genera, i.e., *Calyptaulax* was used as outgroup in cladistics to study the relationships within phacopids (McKellar & Chatterton 2009; Oudot et al. 2019). Nevertheless, some poorly known and badly illustrated genera were excluded (*Somatrikelon* McMurtrie, 1819 without illustration in both datasets; *Enygmapyge* Feist et al., 2016 without cephalon in ‘cephalon’ dataset; *Adastocephalum* Mitchell, 1919, *Afrops* Alberti, 1983, *Burtonops* Struve, 1990, *Cryphops* Richter & Richter, 1926, *Portlockia* McCoy, 1846, *Spinicryphops* Crônier and Feist, 2000, *Struvephacops* Ghobadi Pour, 2015, *Tangbailaspis* Xiang & Zhang, 1983 in Zhang 1983, and *Zaplaops* Baldis & Blasco, 1976 in Baldis et al. 1976 without pygidium in ‘pygidium’ dataset). For each genus, a representative specimen was selected, most often the holotype of the type species, unless the illustrations were insufficient. Because of the lack of illustration, the species of six genera were not the same between cephalon and pygidium: *Nephranomma* Erben, 1952, *Pedinopariops* Struve, 1970, *Prokops* Chlupáč, 1971, *Struveaspis* Alberti, 1966, *Teichertops* Struve, 1992 and *Weyerites* Crônier & Feist, 2000. 72 cephala and 63 pygidia representing different genera were analyzed, all at a holaspid stage (Appendix A). For each genus, the stage of the first apparearance and the last appearance are noted.

For the assessment, two components that can influence the shape distribution have been tested: the specimen selected and the measurement error. In order to evaluate the impact of the selected species representing the genus, we analysed 10 specimens representing 10 different species for the genus *Morocops*. Furthermore, one randomly selected cephalon was also digitized 10 times to identify the part of variation attributed to measurements (Bartlett & Frost 2008). To compare the variation between the different subgroups (i.e. measurement error, inter-specific variability and inter-generic variability), we measured the variance of the distance to the centroid size of each subgroups.

## 2.2. Landmarks and geometric morphometrics

To describe the 2D morphology of cephala and pygidia, we used a morphometric approach based on homologous points, i.e., landmarks (Bookstein 1991; Rohlf & Marcus 1993; Adams et al. 2004; Mitteroecker & Gunz 2009; Zelditch et al. 2012). This method is regularly used on trilobites for macroevolutionary topics (Gerber & Hopkins 2011, Webster & Zelditch 2011; Oudot et al. 2019; Bault et al. 2021, submitted). The *x*- and *y*- coordinates of 13 landmarks and 4 semi-landmark curves of 30 points on the cephalon and 8 landmarks and one semi-landmark curve of 24 points on the pygidium were digitized (Fig. 1) using the software TPSDig 2.32 (Rohlf 2006, 2015). For the cephalon, the semi-landmark curves represent respectively the glabella shape, the facial suture shape and the cephalic outline (Fig. 1). For the pygidium, the semi-landmark curve represents the pygidial outline (Fig. 1). The landmark 2D coordinates were exported in the standard TPS file format (Rohlf 2012). For all configurations of landmarks, a generalized Procrustes analysis (GPA) was performed to remove effects of size, position and orientation in order to minimize the distances between each landmark of configurations (Gower 1975; Rohlf & Slice 1990; Bookstein 1991; O'Higgins 2000; Zelditch et al. 2012). All configurations of landmarks were d to unit centroid size. The centroid size is the square root of the sum of squared distances between the centroid and each landmark of the configuration (Dryden & Mardia 1998). Thereby the d configurations are then superimposed, i.e., translated and rotated. Then, we projected the superimposed configurations to a linear tangent space at the full Procrustes mean (Rohlf 1999; Kendall 1984). The superimposed configurations constitute a data set corresponding to Procrustes residuals, i.e., *x*-, and *y*-coordinates of each landmark of configurations superimposed on a reference configuration, and describing only the shape of each landmark configuration.

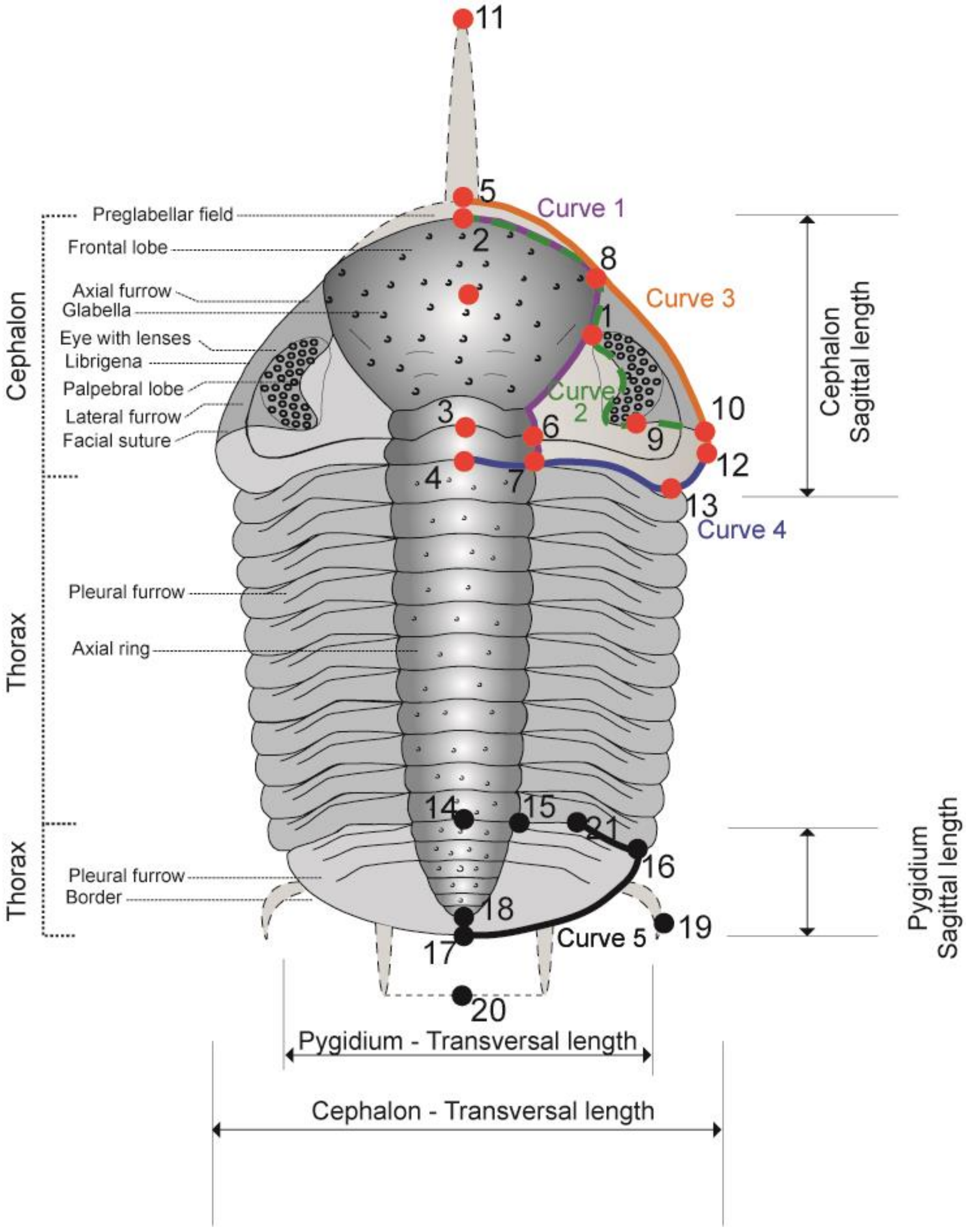

***Figure 1.*** *Thirteen landmarks and four semi-landmark curves of 30 points defined on the cephalon and 8 landmarks and one semi-landmark curve of 24 points on the pygidium.*

A principal component analysis (PCA; Ringnér 2008; Abdi & Williams 2010) was performed on the variance-covariance matrix of Procrustes residual coordinates to identify the major trend of the morphological variation. Each specimen was represented by eigenvalues in a morphospace, positioned along Principal Components (PCs, eigenvectors) ordered by shape variance explained. Series of virtual shapes were reconstructed to illustrate the largest shape changes for PC1 and PC2. Empirical morphospace were established for each stage from the Late Ordovician to the end of the Famennian (Adrain 2013; Lerosey-Aubril & Feist 2012). Because of the low number of genera before the Devonian, the Silurian is considered as a unique time bin.

Additionally, in order to identify morphological changes related to eye-reduction or blindness in the cephalon but also in the pygidium, blind and occulated genera were illustrated separately in PCA.

Morphological analyses have been computed with the software R (v. 3.6.2; R Core Team 2019; https://cran.r-project.org/) and the packages ‘geomorph’ (v. 3.2.1; Adams & Otárola-Castillo 2013) and ‘epaleo’ (v. 0.8.41; Monnet, unpub.).

### 2.3. Morphological disparity indices

To quantify accurately the morphological disparity changes through time based on the obtained morphospaces, disparity indices were used: the sum of range (SoR), the sum of variance (SoV) and Nearest Neighbour Distance (NND) (Foote 1991b; Ciampaglio et al. 2001; Wills 2001; Guillerme et al. 2020); disparity indices already used in trilobites (Foote 1990, 1993; Hopkins 2013). Disparity indices have been estimated for the Silurian as a whole and for each stage of the Devonian. Morphological indices have been performed with the package ‘epaleo’ (v. 0.8.41; Monnet, unpub.) on the software R (v. 3.6.2; R Core Team 2019; https://cran.r-project.org/).

Two indices were used to estimate the size of the morphospace, i.e., the Sum of Range (SoR), corresponding to the total range of morphologies, and the Sum of Variance (SoV) corresponding to the average dissimilarity between morphologies. The overall first-order Nearest Neighbour Distance (NND) is the shortest Euclidean distance between two points of the morphospace and characterises the density of the morphospace. The mean values per stage for PC1 and PC2 were computed to identify potential morphospace displacement.

Finally, the confidence intervals on the obtained disparity values were obtained with a bootstrap approach, by randomly resampling with individual points in the morphospace and calculating SoR, SoV and NND again (Foote 1993). This was iterated 1000 times, creating a distribution from which 2.5 and 97.5 percentile values were used as lower and upper confidence intervals.

## 3. Results:

### 3.1. Global morphospace

The measurement errors and the interspecific variation tests indicated a smaller (one order of magnitude) variation than the inter-generic variation analysed thereafter, although some variations existed.

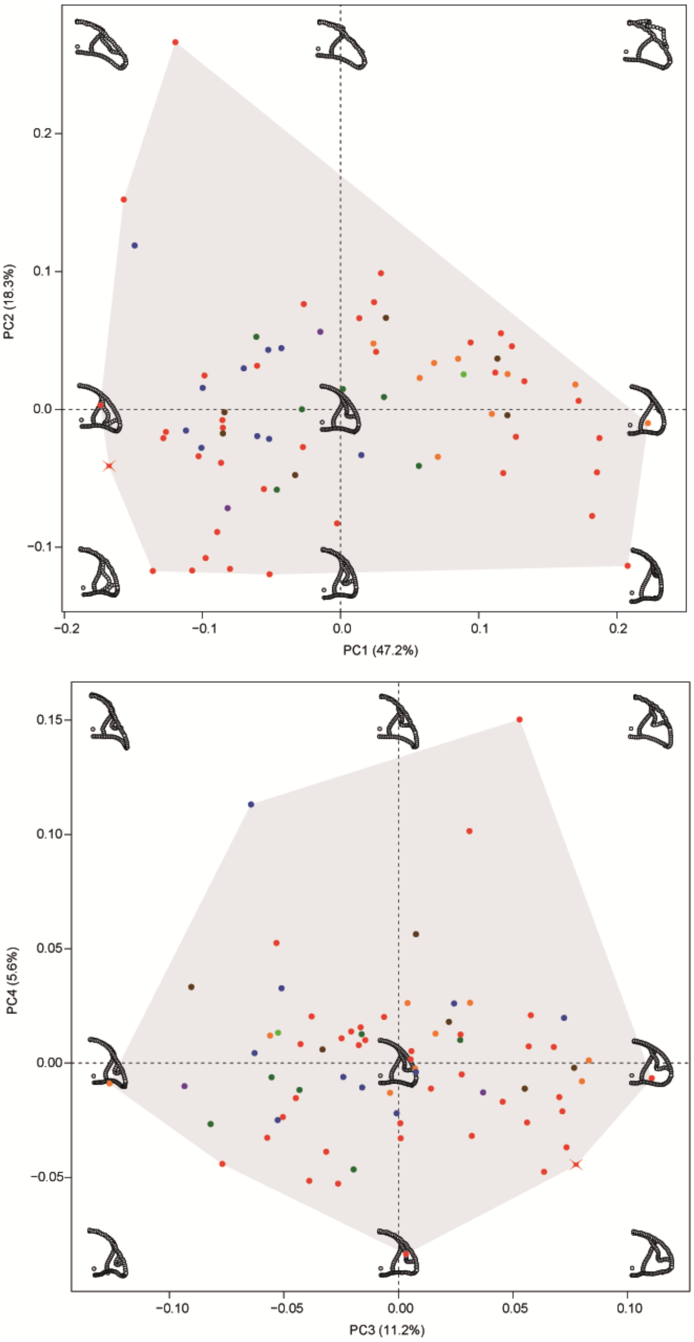

***Figure 2.*** *Global morphospace for phacopid cephalon computed by performing a PCA based on Procrustes residuals. (A) The first two axes PC1 and PC2 explain 66% of the variance; (B) the PC3 and PC4 axes explain 17% of the variance. Tribes according to McKellar & Chatterton (2009): Ananaspini Haas, 1998 (Brown); Cordapeltini Struve, 1989 (Dark green); Cryphopini Struve, 1989 (Orange); Geesopini Flick & Struve, 1984 (Blue); Phacopini Flick & Struve, 1984 (Light green); Reedopini Struve, 1989 (Purple) and Incertae sedis (Red). The pterygometopid Calyptaulax is represented by a red cross. Virtual shapes were reconstructed by doing the back transformation from the considered PC scores, and then reshaped to landmark data.*

*Cephalon shape*. The total variance among occulated cephala was explain by 71 principal components (PC's). The four first axes (Fig. 2) explain 82% of the total shape variance as following: PC1 (47%), PC2 (18%), PC3 (11%) and PC4 (6%). The first axis PC1 (Fig. 2) depicts changes in the position of the facial suture and the visual complex. The higher PC1, the more the suture is close to the lateral margin and more the visual complex is reduced. The second axis PC2 (Fig. 2) depicts changes associated with the width/length ratio: narrow (transversal) cephala in negative values to elongated (tr.) cephala in positive values. The distribution of genera is relatively fairly homogeneous in the morphospace with the exception of three outliers characterised by low PC1 and high PC2 values: *Illaenula* Chlupáč, 1977, *Teichertops* and *Zaplaops*; and no taxa for high PC1 and high PC2 values. The pterygometopid *Calyptaulax* has the lowest PC1 values but is not distinct from phacopids with an average PC2 value. The global morphospace (Fig. 2) forms a triangle reflecting the influence of the three cephalic parameters (width/length ratio, facial suture and visual complex location). The bottom-left part of the morphospace corresponds to narrow cephala with a more developed visual complex, the bottom-right part to narrow cephala with a more reduced visual complex, and the top-left part to elongated cephala. The shape of the genal angle is depicted by PC1 and PC2. The more PC1 is low and PC2 high, the more the genal angle is curved, and conversely, with high PC1 values, the genal angle is rounded.

Along the PC3 axis (Fig. 2), the cephalic variations are associated with the genal angle shape and the cheek proportion: cephala with an elongated genal angle and larger cheeks relative to the cephalic shield in negative values and cephala with rounded genal angle and smaller cheeks relative to the cephalic shield in positive values. Along the PC4 axis (Fig. 2), the cephalic variations are associated with genal spines (high PC4 values) or their absence (low PC4 values). The distribution of genera is relatively fairly homogeneous in the morphospace with the exception of three outliers characterised by high PC4 values: *Acernaspis*, *Babinops* Feist & Becker, 1997 and *Drotops* Struve, 1990.

*Pygidium shape*. The total variance among pygidia was explained by 60 PC. The four first axes (Fig. 3) explain 91% of the total shape variance as following: PC1 (60%) PC2 (18%), PC3 (9%) and PC4 (4%). The first axis PC1 (Fig. 3) depicts changes in the pleural field proportion and the lateral border angle. The lower PC1, the more the pleural field is important and the lateral border angle acute. The second axis PC2 (Fig. 3) depicts changes associated with the position of the greatest width: backward in negative values to forward in positive values. A higher PC2 value indicates a higher width/length ratio. The distribution of genera is relatively fairly homogeneous in the morphospace (Fig. 3). *Calyptaulax* has the highest PC1 values but is not distinct from phacopids with an average PC2 value.

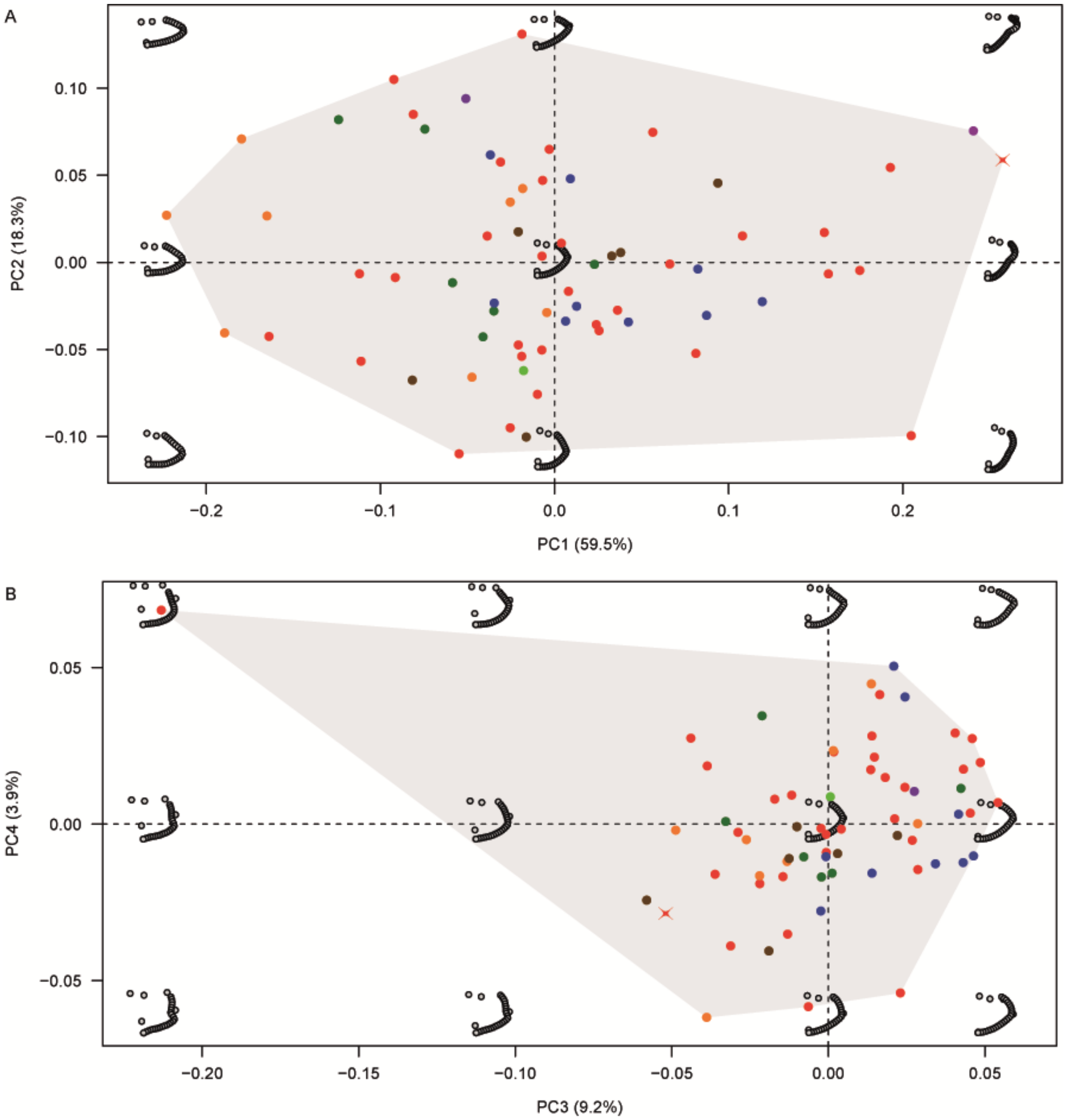

***Figure 3.*** *Global morphopace for phacopid pygidium computed by performing a PCA based on Procrustes residuals. (A) The first two axes PC1 and PC2 explain 78% of the variance; B) the PC3 and PC4 axes explain 13% of the variance. Tribes sensu McKellar & Chatterton (2009): Ananaspini Haas, 1998 (Brown); Cordapeltini Struve, 1989 (Dark green); Cryphopini Struve, 1989 (Orange); Geesopini Flick & Struve, 1984 (Blue); Phacopini Flick & Struve, 1984 (Light green); Reedopini Struve, 1989 (Purple) and Incertae sedis (Red). The pterygometopid Calyptaulax is represented by a red cross. Virtual shapes were reconstructed by doing the back transformation from the considered PC scores, and then reshaped to landmark data.*

Along the PC3 axis (Fig. 3), the pygidial variations are associated with the position of the rachis relative to the pygidial posterior border: rachis more (high PC3 values) or less (low PC3 values) close to the posterior border of the pygidium. Along the PC4 axis (Fig. 3), the pygidial variations are associated with the lateral outline. All genera are clustered in the mophospace in high PC3 values except *Enigmapyge* characterised by high PC4 and low PC3 values: with a short (sag.) rachis and a maximum pygidial width located backward with a linear lateral border (Fig. 3).

*Tribes*. The Phacopid tribes were widespread in the morphospace and there were mingled each other. Nevertheless, some trends exist, Cryphopini being restricted in the positive PC1 values of the cephalon (Fig. 2) and negative PC1 values of the pygidium (Fig. 3). Conversely, Geesopini occupies negative PC1 values of the cephalon and positive PC1 values of the pygidium.

## 3.2. Global morphospace with blind taxa

Absence of eyes strongly affected the shape of phacopids cephala (p=0.001, r²=0.09). Most of blind and reduced-eyed trilobites are gathered in the highest PC1 values, while the occulated trilobites are gathered in the lowest PC1 values (Fig. 4). However, some blinds genera are characterised by lower PC1 values comparable to eyed trilobites. Nevertheless, these blind taxa correspond to shape with a facial suture close to the antero-lateral margin. Trilobites with eyes

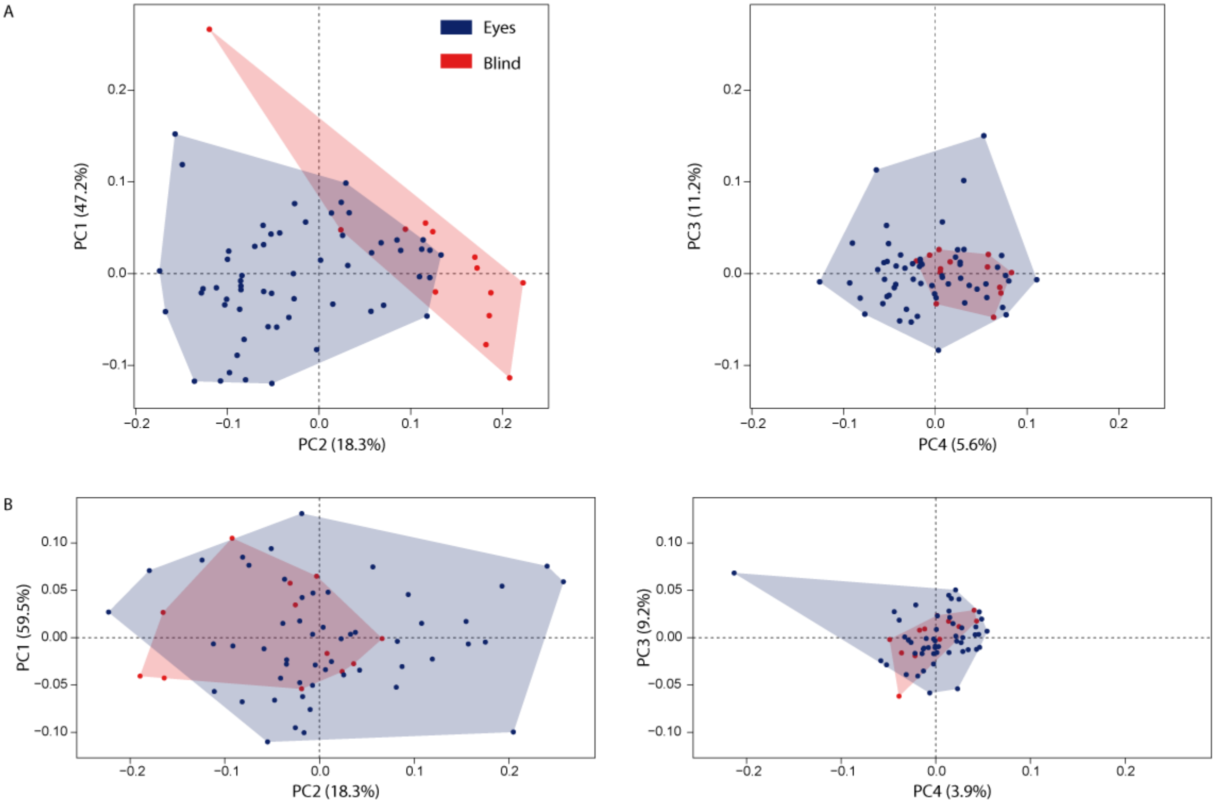

***Figure 4.*** *Location of: cephala (A) and pygidia (B) according visual abilities of phacopids in the global morphospace defined according to the four first principal component axes performed on Procrustes residuals.*

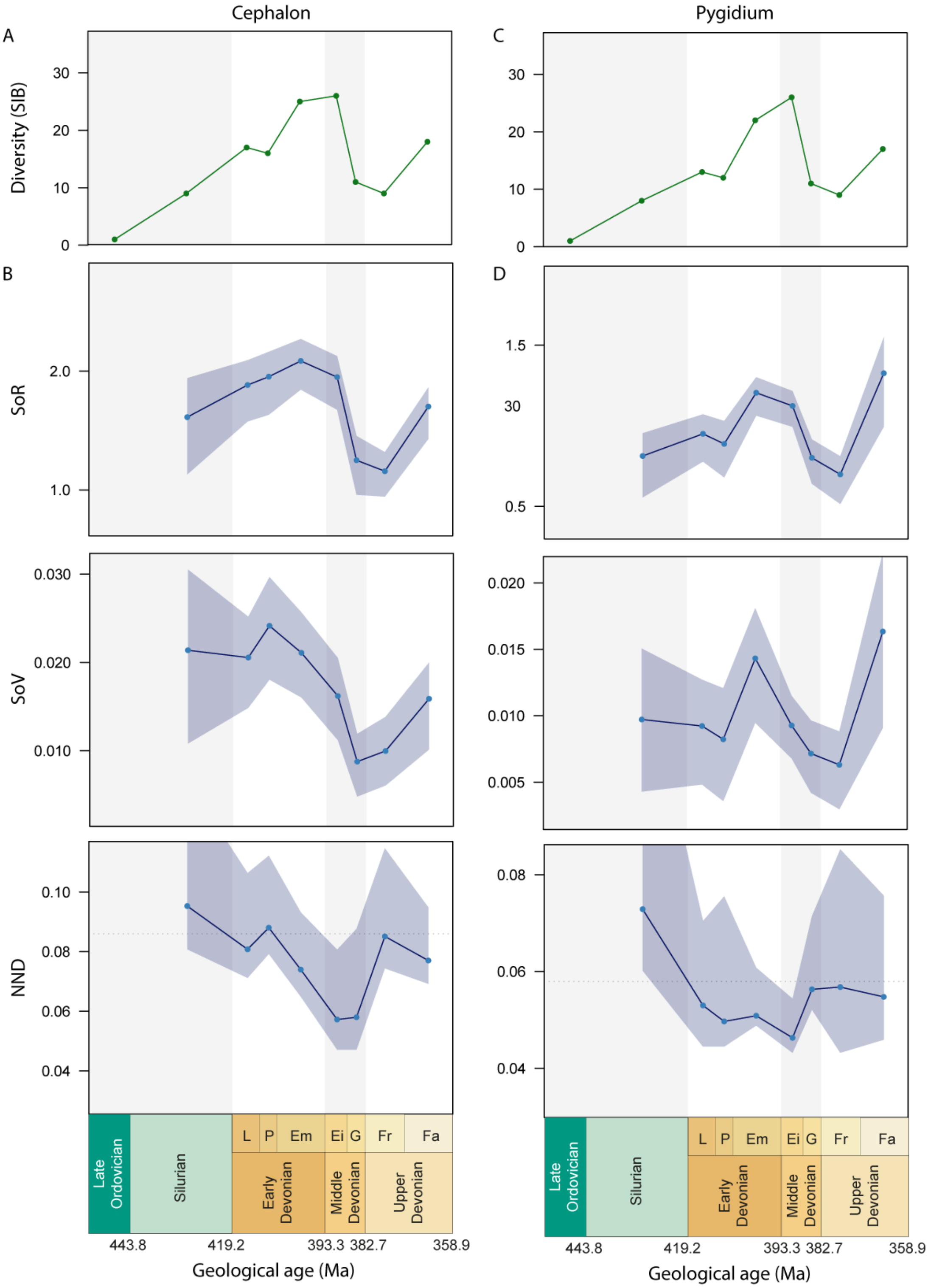

***Figure 5****. Fluctuations of the morphological disparity and taxonomic diversity of phacopids through time, respectively based on the cephalon and the pygidium. (A) Cephalon: taxonomic richness; (B) Cephalon: morphological disparity. (C) Pygidium: taxonomic richness; (D): Pygidium: morphological disparity. SoV: Sum of Range SoV: Sum of variance, NDD: Nearest-Neighbour Distance Solid lines correspond to mean values from 1000 bootstrap replicates and shaded areas represent 95% confidence intervals. See text for the explanations of the indices. Ages from Cohen et al. 2013, updated.*

or not are distributed along PC2 except for *Illaenula*, characterised by the highest PC2 values. Only *Nephranops* Richter & Richter, 1926 and *Pulvinocephalus* Feist, 2019 were included in the area of sighted trilobites. Blind taxa are distributed along PC3 and PC4: blind trilobites being restricted to positive PC3 values and average PC4 values.

The blindness observed in cephala did not imply a different morphology of pygidia ($p=0.112$, $r^2=0.03$). However, the pygidia associated with blind cephala are all gathered in the part of PC1 with the lowest values (Fig. 4). This indicates that blind phacopids did not display or a rounded lateral border either a large pleural field. The type of vision had no effect on PC2, PC3 and PC4.

### 3.3. Diversity, disparity indices and morphospaces through time

*Diversity*. Phacopids were poorly diversified in the Silurian but their taxonomic richness increased almost continuously until the Eifelian (Fig. 5). Only a slight decreased occurred in the Pragian. In the Givetian, the diversity decreased strongly from 26 to 11 genera. This decline continued in the Frasnian before a substantial increase in the Famennian. No phacopids survived in the Carboniferous.

*Disparity*. Bootstrapped confidence intervals indicate a relative robustness of the morphological disparity indices through time (Fig. 5). However, evolutionary interpretations of poorly diversified time bins (i.e., Silurian to Emsian) should be made with caution. This is particularly the case with the NND for both cephala and pygidia, but also with the SoV for pygidia.

Cephalon. From the Late Ordovician to the Pragian, the morphospace occupation moved toward higher PC1 values, while the average PC2 values did not change through the Silurian and the Devonian (Fig. 6). The Late Ordovician pterygometopid *Calyptaulax* is characterised by a glabella with a hypertrophic frontal lobe anteriorly with well-developed S3 and a subtriangular pygidium. In the morphospace, *Calyptaulax* is located on one extremity of the morphospace, with one of the lowest PC1 value (Fig. 7). In the Silurian, the phacopid shapes appeared (Fig. 7) with the appearance of more rounded cephala and a facial suture closer to the anterolateral border such as in *Denckmannites* Wedekind, 1914 and *Orygmatos* Sandford, 2000. The morphospace enlarged progressively in the Early Devonian with new morphologies in the Pragian: cephala characterised by a narrow (tr.) cephalic shield associated with antero-lateral facial sutures. The appearance of *Afrops* at the right edge (i.e. high PC1 values) of the morphospace illustrated this trend. In the Emsian, the morphospace is almost entirely occupied except the top-left part of all phacopid distribution (Fig. 7). Thus, the morphological disparity increased (see SoR, Fig. 5). In the same time, the NND and the SoV tend to decrease (Fig. 5).

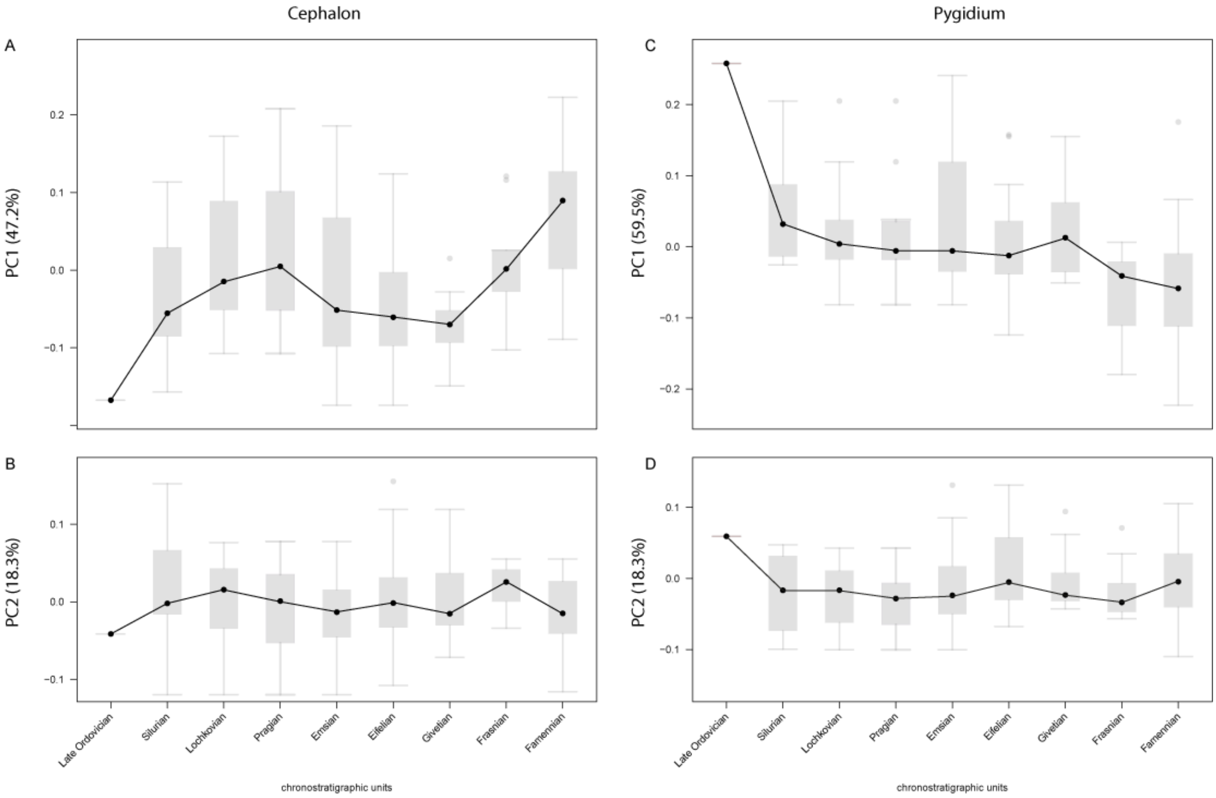

***Figure 6.*** *Location of the morphospace occupation on PC1 and PC2 through time. (A and B) Average values of PC1 and PC2 on the cephalon. (C and D) Average values of PC1 and PC2 on the pygidium.*

During the Middle Devonian, the morphospace occupation moved to opposite values, i.e., lower PC1 values; no real displacement on PC2 (Fig. 6). The morphological disparity strongly decreased (see SoR and SoV, Fig. 5). This collapse of the occupied part of the morphospace was only reduced in the Eifelian (Fig. 5, 7). Firstly, shapes with a facial suture located close to the lateral border, such as *Altaesajania* Maksimova, 1978a and *Angulophacops* Maksimova, 1978b are no longer present and disappeared at the Emsian-Eifelian boundary. Conversely, no new genera appeared. The Eifelian was also characterised by the lowest NND despite the presence of two outliers *Illaenula* and *Teichertops*. These outliers were located in the top-left part of all phacopid distribution during the Eifelian (Fig. 7). Subsequently, the morphospace collapsed in the Givetian (Fig. 7) because of the extinction of genera, such as *Nandanaspis* Zhang & Yin in Yin & Li, 1978, *Eocryphops* Richter & Richter, 1931, *Plagiolaria* Kegel, 1952 and *Reedops* Richter & Richter, 1925. Their morphology implied a facial suture near the antero-lateral border and a rounded genal angle. Subsequently, *Geesops* Struve, 1982 and *Nyterops* Struve, 1972 disappeared at the end Givetian and they are characterised by a cephalon with acute genal angles and a posterior section of the facial suture close to the posterior border (Fig. 7). The occupied part of the morphospace is limited to the bottom-left part of all phacopids distribution (Fig. 7).

Finally, during the Upper Devonian, the morphospace occupation shifted again to higher PC1 values to reach the highest values with more elongated pygidial shapes (Fig. 6); once again there is no real displacement on PC2 (Fig. 6). The morphological disparity increased (see SoR and SoV, Fig. 5). Nevertheless, the morphospace occupation remain reduced in the Frasnian but with a displacement of the occupied part of the morphospace. The morphological disparity was minimal (see SoR, Fig. 5), while SoV and NDD remain almost unchanged (Fig. 5). This displacement is due to the successive origination of *Acuticryphops* Crônier & Feist, 2000 and *Trimerocephaloides* Feist et al., 2009 in the Frasnian, which spread in the middle-

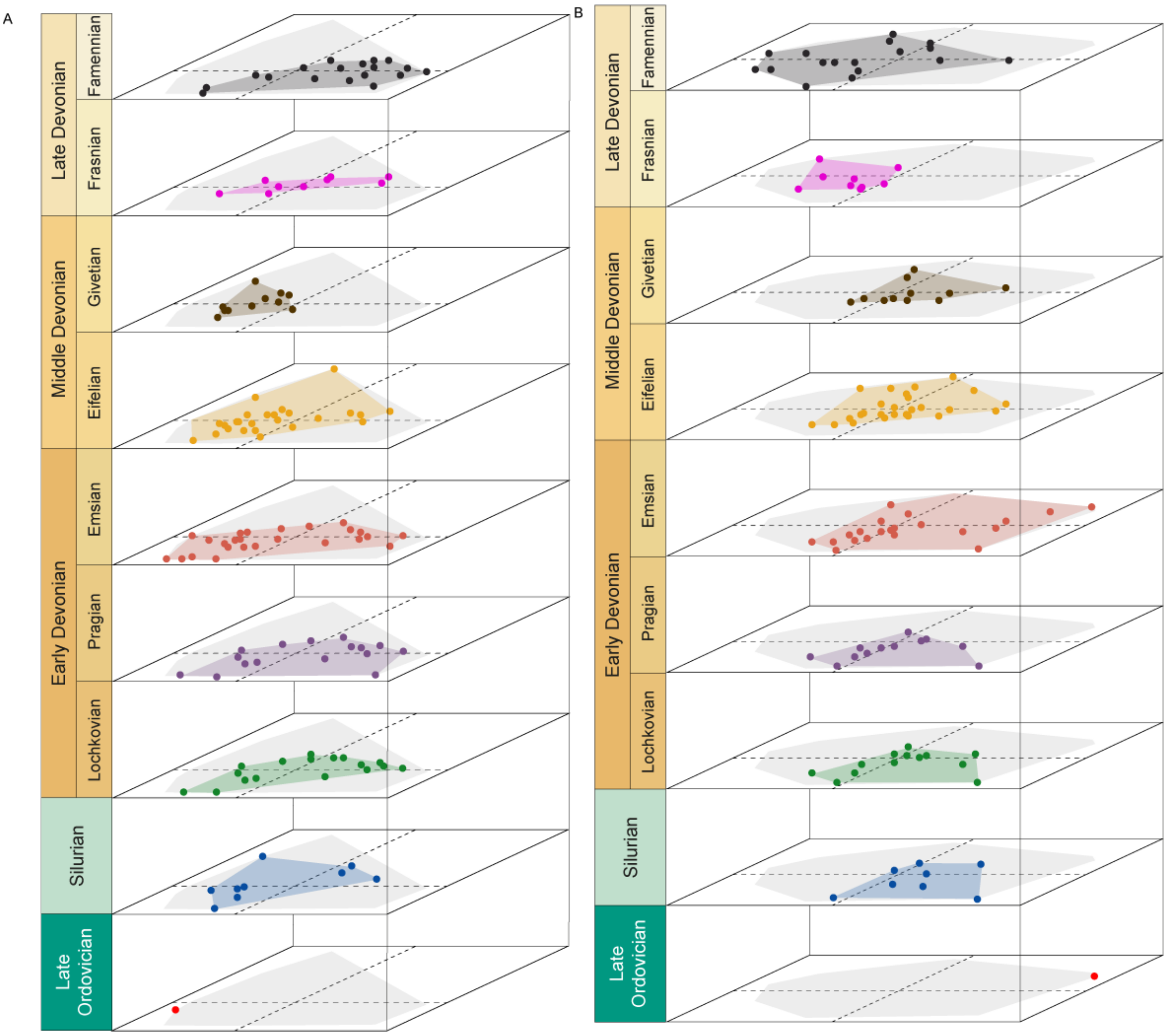

***Figure 7.*** *Morphological occupation of the (A) cephalon and (B) the pygidium through time (PCA based on Procrustes residuals). Ages from Cohen et al.2013.*

right part of the morphospace with their antero-lateral facial sutures and a narrow cephalon with rounded genal angles (Fig. 7). New genera appeared in the Famennian, such as *Dianops* Richter & Richter, 1923, *Ductina* Richter & Richter, 1931, *Struveops* Crônier & Feist, 2000 and *Trimerocephalus* McCoy, 1849. They contributed to refill partially the morphospace (Fig.7). These taxa exhibit the facial suture closest to the lateral margin border, a small (tr.) cheek and a rounded genal angle. In the Famennian, the morphological disparity strongly increased (see SoR, Fig. 5), SoV still increased, and NND decreased slightly (Fig. 5).

Pygidium. From the Late Ordovician to the Silurian, the morphospace occupation moved toward lower PC1 and PC2 values to stay stable until the Emsian (Fig. 6). *Calyptaulax* by its a subtriangular pygidium is located, on one end of the morphospace, as for the cephalon (Fig. 7). In the Silurian, the phacopid shapes appeared (Fig. 7) with the appearance of more enlarged (tr.) pygidia with a larger pleural field. This morphospace occupation (mainly the bottom-middle right part) persisted until the Pragian. Thus, the morphological disparity remained almost stable, except a decrease of the NND (Fig.5). In the Emsian, the morphological disparity increased (see SoR and SoV), while NDD remained almost stable (Fig. 5). Consequently, some innovations occurred with the origination of *Austerops* McKellar & Chatterton, 2009, *Rhinophacops* Kaneko, 1990 and *Toxophacops* Zhou & Campbell, 1990 for instance. It corresponds to their triangular pygidial shape and weakly curved posterior border. The morphospace became filled and almost occupied except the extreme left part of morphospace (Fig. 7).

During the Middle Devonian, the morphospace occupation shifted slightly to opposite values, i.e., higher PC1 values; no real displacement on PC2 (Fig. 6). The morphological disparity decreased (see both SoR and SoV, Fig. 5); and NND tends to increase (Fig. 5). The occupied part of the morphospace was relatively expanded in the Eifelian, with the disappearance of taxa in the top-right and the bottom-right parts of the morphospace (Fig. 7). *Echinophacops* Zhou, 1983 and *Rhinophacops* were no longer present and disappeared at the Emsian-Eifelian boundary; they are characterised by narrow (tr.) pygidia with small pleural fields (Fig. 7). Subsequently, the morphospace collapsed in the Givetian (Fig. 7) because of the extinction of *Morocops*, *Signatops* Přibyl & Vaněk, 1971 and *Viaphacops* Maksimova, 1972 in the left part of the morphospace. Therefore, the occupied part of the morphospace was limited to the left part of all phacopids distribution (Fig. 7).

Finally, during the Upper Devonian, the morphospace occupation shifted again to reach the lowest PC1 values (Fig. 6) whereas there is no real displacement on PC2 once again (Fig. 6). In the same time, the morphological disparity increased (Fig. 5) although the morphospace occupation remained reduced in the Frasnian. Only a displacement of the occupied part of the morphospace to the left occurred (Fig. 7). As for the cephala, the morphological disparity is minimal (see SoR and SoV (Fig. 5), while NDD remained almost unchanged (Fig. 5). This displacement is due to the appearance of genera characterised by an elongated (tr.) pygidium, such as *Acuticryphops*, *Chlupacops* Feist et al., 2016 and *Phacops s.l.*. In the Famennian, new genera appeared such as *Dianops* Richter & Richter, 1923, *Trifoliops* Crônier, 2003, *Trimerocephalus* McCoy, 1849 and *Weyerite*s for instance and contributed to refill partially the morphospace (Fig. 7). All taxa exhibit an elongated (tr.) pygidium. The morphological disparity strongly increased to reach highest values (see both SoR and SoV, Fig. 5), SoV still increased, and NND decreased slightly (Fig. 5).

## 4. Discussion:

### 4.1. Morphological disparity – cephalon *vs*. pygidium shapes

Phacopids did not exhibit a large morphological variation. This absence of strong difference among phacopid genera and tribes explains the difficulties encountered by the scientists to determine their systematic structure (McKellar & Chatterton 2009). Only one genus differs strongly from the others: *Echinophacops* is the only phacopid, which developed prominent spines on the cephalon (Zhou 1983). This genus occurred with ammonoids, conodonts, brachiopods, gastropods and corals (Hua-Zhang & Cook 2003) in the Lower Devonian from calcareous sandstones of the Zhusileng representative of subtidal environments (Zhou & Campbell 1990). In this kind of environment, spinose asteropygines, another Phacopida subfamily, proliferated also at the same time (Morzadec 1992, 2001). Other phacopids co-occurred with *Echinophacops* in the same horizon (i.e. *Rhinophacops* and *Toxophacops*), and *Zhusilengops* Zhou & Campbell, 1990 and *Atopophacops* Zhou & Campbell, 1990 above the Zhusileng (Zhou & Campbell 1990). Contrary to *Echinophacops*, these genera did not have spines. Nevertheless, an intermediate morphology existed between taxa with long spines (i.e., *Echinophacops mirabilis* Zhou, 1983) and taxa without spines: *Rhinophacops schlizoma* Zhou, 1983.

Among phacopids, very few have a very differentiated morphology like *Enigmapyge* from the Famennian of Algeria (Feist et al. 2016). Although incompletely preserved, its cephalon shows all the characteristics of a phacopid. Nonetheless, its pygidium is unusual among this family with a large pygidial margin and a short (sag.) pygidial axis ending at a considerable distance from the posterior edge (Feist et al. 2016). The morphology of the cephalon of

*Teichertops* and *Zaplaops* was also uncommon. These two genera are represented by very few specimens in the literature and a deformation of the landmarked fossils is possible. The specimen of *Teichertops* was found in black marls (Struve 1970) where distortions are susceptible to happen (Webster & Hughes 1999). The ordinary shape of the pygidium of *Teichertops* tends to confirm this assumption although the cephalon and the pygidium of a same taxon show different distribution in a morphospace (Bault et al. 2021, submitted). For its part, *Zaplaops* could be a junior synonym of *Ananaspis* Campbell, 1967 (Holloway & Rustán 2012), which is not an outlier. This latter genus is characterised by an elongated cephalon as in *Zaplaops* (negative PC1 value) but without a downward genal field (average PC2 value), probably a consequence of a deformation. *Acernaspis*, *Adrisiops*, *Babinops*, *Drotops* and *Viaphacop*s are the five genera differentiated by an elongated genal angle. Genal spines could develop from this configuration, as it is the case for *Babinops* (Feist & Becker 1997), *Viaphacops* (Eldredge 1973) and *Drotops armatus* (Struve 1995). Usually, phacopids had a genal spine during the early stages of their development, but these spines then reduced (Crônier & Courville 2003). Contrary to the Early Devonian tendency among Trilobita (Bault et al. 2021, submitted), this development of genal spines among phacopids was not a temporal trend because trilobites with genal spines existed throughout the evolutionary history of phacopids. Only the presence of the strongly spinose *Echinophacops* coincided with the Early and Middle Devonian trends in spiny marine faunas (Brett 2003). The presence of such genal spines could be linked to the ecology of trilobites for stabilization on soft substrates (Brett 2003).

Except the few taxa described above, most phacopid genera showed slight differences between them. The main variation concerns the position of the facial suture. That corresponds to a line of weakness facilitating the moulting process (Daley & Drage 2016; Drage 2019). This allows the separation between the cranidium and the free cheeks during the ecdysis (Drage 2019). Among trilobites, the phacopids have a proparian suture, the posterior section of which intersects the lateral cephalic margins in front of the genal angles (Harrington et al. 1959). The position of this facial suture constituted a trade-off between the ability to moult and a resistance to burrowing loads (Esteve et al. 2021). However, among phacopids, the size of the visual complex influences the location of the facial suture. Blindness or reduced-eyes implie a facial suture situated close to the lateral margin. Indeed, the reduction and ‘migration’ of the visual complex caused the displacement of the associated dorsal facial sutures (Feist 1995). Consequently, the facial sutures of blind taxa are located on the anterolateral margins related to a macroevolutionary paedomorphic process (Feist 1995;

Crônier & Courville 2003; Crônier 2013). This ‘migration’ occurred although the facial sutures became brittle in such position (Esteve et al. 2021). In addition to the facial suture displacement with the visual complex reduction, blind trilobites have a less curved genal angle, except *Illaenula*. A marginal facial suture and weakly arched genal angles characterised blind trilobites but also some sighted genera. There were reduced-eye trilobites such as *Eocryphops* (Holloway 2005), that showed the suture displacement described by Feist (1995). Concerning the pygidium, blind trilobites did not imply a new morphology as it was the case for the head. Nevertheless, the morphology of blind phacopids was limited to a particular shape of pygidium: those with high width/length ratios.

The second most important morphological variation in phacopids concerned the curvature of the genal angle and the cheek width. A vaulted cephalon also found in other clades was supposed to prevent the trilobite from sinking into mud (Richter 1920; Feist & Clarkson 1989). The phacopids with the most vaulted cephalon lived in a muddy environment like *Echidnops taphomimus* (Rustán & Balseiro 2016), *Illaenula struvei* (Basse & Müller 2000), *Nephranomma sweeti* (Sandford 2003), *Orygmatos yanyeani* (Sandford 2000), *Teichertops soetenicus* (Struve 1970) and *Zaplaops zaplensis* (Baldis et al. 1976). However, some trilobites with a vaulted cephalon occurred in limestone deposits, such as *Lochkovella misera* (Chlupáč 1977). Consequently, the type of substrate is not the only factor influencing the shape of the cephalon. The shape of the glabella also changed with the shape change of the cephalon. If the phacopids are characterized by a similar shape of glabella, narrower (tr.) at the base and wider (tr.) at the front, the glabella is even wider at its front with a less curved genal angle for vaulted cephalon, The base/frontal part width ratios are partly due to the predatory/scavenger habit of phacopids, a forwardly expanding glabella allowing ingestion of higher volumes (Fortey & Owens 1999). This pattern contrasts with the morphological changes observed during the ontogeny for which the maximal width of the glabella/minimal width of the glabella ratio increases while the genal spines reduce (Crônier & Fortey 2006; Crônier 2007).

The elongation of the pygidium was also a major variation in phacopids. Some genera had an elongated pygidium with a width/length ratio greater than 2 (e.g., *Trifoliops*) while others had a ratio less than 1 such as *Enygmapyge* (Feist et al. 2016). It is noticeable that the genera with the most elongated pygidium are not the same as those with the largest cephalon. There is a decoupling at the level of innovations between cephala and pygidia. The pygidium shape was probably less suitable for stabilizing the organism on the seafloor. The morphology of organisms being the result of trade-offs between different tasks (Shoval et al. 2012; Ou et al.

2020), the pygidial organization was dedicated to other functions. For example, the enrolment influenced both cephalon and pygidium morphology, but it had probably a stronger effect on the pygidium, which was dedicated to fewer tasks (Oudot et al. 2019; Suárez & Esteve 2021). The length of the pygidial axis also changes between different phacopids. However, except *Enigmapyge* discussed above, only a short (sag.) postaxial area characterised the phacopid family.

### 4.2. Evolutionary history

The shape of *Calyptaulax* is positioned at the edge of phacopid morphologies but is not completely different, being close to the shape of the first phacopid *Acernaspis* (Chlupáč 1975). The assumption that Pterygometopidae is a sister taxa of phacopids seems relevant (Ludvigsen & Chatterton 1982). Similarities between ontogenetic trajectories of this genus and some phacopids (Jacobs & Carlucci 2019) reinforce this hypothesis. *Calyptaulax* had a facial suture (and therefore the eyes) near to the posterior border furrow and a vaulted cephalon (Clarkson & Tripp 1982). From these ancestral character states, phacopids developed from the Silurian onwards leading to an increase of the morphological disparity. Although the first phacopids *Acernaspis* exhibited a general morphology similar to *Calyptaulax*, the facial suture of phacopids are relatively close to the lateral margin in the Silurian. This was particularly the case for *Denckmannites*, *Lochkovella* and *Orygmatos*, the first reduced-eye phacopids (Chlupáč 1977; Sandford 2000; Crônier & Courville 2003). An eye reduction in trilobites could be linked to the migration and an adaptation to deeper environments (Feist et al. 2009; Feist 2019). While *Acernaspis* lived in shallow environments (Owen & Harper 2008), *Denckmannites*, *Lochkovella* and *Orygmatos* lived in a relatively deep environment. The observed morphological change seems to be related to the invasion of this environmental niche. However, *Calyptaulax* has proliferated in a deep environment (Owen & Parkes 2000; Carlucci & Westrop 2012), indicating that this large-eyed morphology is not inconsistent with the habitat of a basin environment. On its side, the pygidium of phacopids has lengthened compared to its ancestral morphology.

The morphological disparity curves, respectively corresponding to the cephalon and to the pygidium shapes, are partly uncorrelated. The constant increase of the morphological disparity from the Silurian until the Emsian observed in the cephalon is more irregular in the pygidium. Indeed, the pygidial disparity decreased in the Pragian. The diversity increase in the Lochkovian was associated with only a slight extension of the morphospace. This period was more favourable to the origination of novelties in other trilobite families, such as proetids, scutelluids and dalmanitids than in phacopids (Chlupáč 1994). No important innovations occurred, the new morphologies remained close to those of the Silurian. Thus, the origination of new species brought morphologies close to those already existing.

During the Pragian-Emsian diversification, the taxonomic richness of phacopids increased, like many trilobite families (Feist 1991; Chlupáč 1994; Bault et al. 2021). This boost of diversity was linked to the increase in morphological disparity for both cephala and pygidia. Again, no important novelties characterised the development of new phacopids. Only the blind genus *Afrops* exhibits a new cephalon morphology with a small cephalic shield without a genal angle (Alberti 1983). For pygidia, the main innovation involved the triangular shape as in *Rhinophacops schizoloma* (Kaneko 1990) or the elongated (tr.) pygidium as in *Morocops granulops* (Chatterton et al. 2006). Nevertheless, the Emsian was the age of the maximum disparity for the cephala and was only exceeded in the Famennian for the pygidia. This morphological disparity peak occurred earlier than the maximum diversity, which followed in the Eifelian (Crônier & Courville 2003). Decoupling between morphological disparity and taxonomic diversity is common in the fossil record (Foote 1993) but it was often linked to extinctions (Bapst 2012; Hopkins 2013; Wan et al. 2021). Although Foote (1993) noted that the peak of morphological disparity occurred usually after the peak of diversity, especially for trilobites, it was the opposite in phacopids.

Another feature of the morphological diversification of this family is that its peak was reached in the late part of its evolutionary history. This was the opposite of the common trend among Palaeozoic clades, which often have a maximum of disparity early in their evolutionary history (Hughes et al. 2013). Hopkins & Smith (2015) argued evolutionary dynamics changed through time and were not necessarily higher in the first period of their existence. New ecological opportunities such as the Devonian ones could generate an increase of the evolutionary rate and thus, a disparity rise. On the other hand, the decrease of morphological disparity in the Eifelian was caused either by a loss of ecological habitats (Valentine 1995; Oyston 2015) or by an increase of developmental constraint (Gould 1991; Oyston 2015).

An important extinction phase occurred in the Givetian with a strong decrease of both diversity and morphological disparity. The sea-level changes and the anoxia of the Middle Devonian events (Walliser 1996; House 2002) affected all the trilobites (Chlupáč 1994; Lerosey-Aubril & Feist 2012). The phacopids did not escape these environmental events and lost more than 60% of their genera. The mid-Givetian Taghanic event was the most devastating for them (Crônier & Courville 2003). This was a non-random extinction because it caused a collapse of the morphospace size (Ciampaglio et al. 2001). On the contrary, the density of the morphospace was not disturbed by these events, implying a marginal or lateral extinction (Korn et al. 2013). Interestingly, a lateral extinction affected the cephalon, and the morphospace shifted during the Middle Devonian, while the pygidium underwent a rather marginal extinction with no change in the morphospace range. The Taghanic extinction event led to the disappearance of genera with a cephalon characterised by an anterolateral facial suture. Consequently, during the end-Givetian all phacopids only had large eyes. Nevertheless, reduced-eyed taxa still occurred in other families such as Tropidocoryphidae (Feist 2003). At the same time, two of the largest genera of the family appeared, it was *Drotops* and *Hypsipariops* Struve, 1982 (Struve 1995). The Early and the Middle Devonian were the time of giant organisms including trilobites (Klug et al., 2014). This trend was hardly explained by single environmental parameters, although a latitudinal influence cannot be excluded (Klug et al., 2014). *Drotops* and *Hypsipariops* lived in the mid-latitudes of Morocco (Struve, 1995), exactly the range of gigantism occurrences.

In the Frasnian, morphological disparity remained low, probably the lowest in phacopid history. However, this stagnation of morphological disparity was accompanied by important morphological changes. For cephala, morphospace occupancy shifted to the area indicating the acquisition of an anterolateral facial suture, underlying the Late Devonian trend toward blindness (Feist 1995; 2019; Crônier & Courville 2003). This trend was also noticed in other families (Feist & Clarkson 1989; Lerosey-Aubril & Feist 2012; Schoenemann 2018). As for the Silurian, the existence of blind phacopids was associated with a life in deeper environments (Feist et al. 2009; Feist 2019). The successive transgressions and the long-term sea-level rise in the second part of the Devonian forced the trilobites to adapt to these new environments (Lerosey-Aubril & Feist 2012; Crônier & François 2014). Whatever the water depth, an endobenthic behaviour or a turbid environment with low luminosity implied also an eye-reduction (Feist et al. 2009). Concomitantly to the progressive modification of the eye and the displacement of the facial suture on the cephalon, the pygidium changed to a more elongated shape in phacopids. The morphological innovations still developed in the same direction in the Famennian. The combination of lateral facial sutures and elongated pygidium contributed to increase the morphological disparity, particularly for the pygidium. Subsequently to the disastrous Kellwasser events at the Frasnian-Famennian boundary (Buggisch 1991; Bond and Wignall 2008), trilobites recovered and invaded various habitats and areas (Crônier and François 2014). As the result of this dispersal, morphological disparity increased, as was the case with the appearance of new niches in the Pragian. Some phacopids recolonized shallower environments and developed large eyes, such as *Omegops* (Crônier and François 2014).

The evolutionary history of phacopids stopped at the end of the Devonian with the disappearance of the whole order Phacopida (Lerosey-Aubril & Feist 2012). Their extinction was the consequence of the Hangenberg event consisting of sea-level changes, carbon cycle perturbation and temperature oscillations (Kaiser et al. 2016). All phacopids vanished regardless of their shapes, but the predominance of reduced-eyed and blind taxa inhabiting more distal environments probably doomed them. Indeed, this event was devastating for non-occulated and reduced-eyed trilobites, including Proetida (Lerosey-Aubril & Feist 2012).

## 5. Conclusion:

Phacopidae originated at the end of the Ordovician and diversified since the Silurian. They had a morphology close to their sister taxon Pterygometopidae, with a glabella broadening forward and a proparian facial suture. Some genera had an unusual morphology but most of them had rather a similar shape with minor morphological changes. The main morphological variations among phacopids were the position of the facial suture, the shape of the genal angle and the elongation of both cephalon and pygidium. For cephala, most morphologies already existed in the Silurian but the morphological diversity increased in the Devonian. Innovations and novelties were particularly favoured by the colonisation of new habitats offered by the environmental changes in the Pragian. The maximum of morphological disparity occurred in the Eifelian, late in the evolutionary history of the phacopids. Their diversity peak occurred later, in the Eifelian. At this time, morphological disparity had already started to decrease. The Middle Devonian events strongly affected the phacopids, leading to a decrease of more than half of the morphological and taxonomical diversity in the Givetian. These extinctions were non-random, particularly affecting trilobites with reduced-eyes. Although morphological disparity remained low in the Frasnian, some morphological changes occurred. The facial suture migrated toward the anterolateral margins related to the eye-reduction and blindness and the pygidium elongated laterally. Eye reduction was achieved during environmental changes, especially sea-level changes. These trends continued in the Famennian, during which a recovery caused an increase in both diversity and morphological disparity. However, the Hangenberg event at the Devonian-Carboniferous boundary led to the disappearance of this representative family in trilobites during the Devonian.

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## Supplemental figures

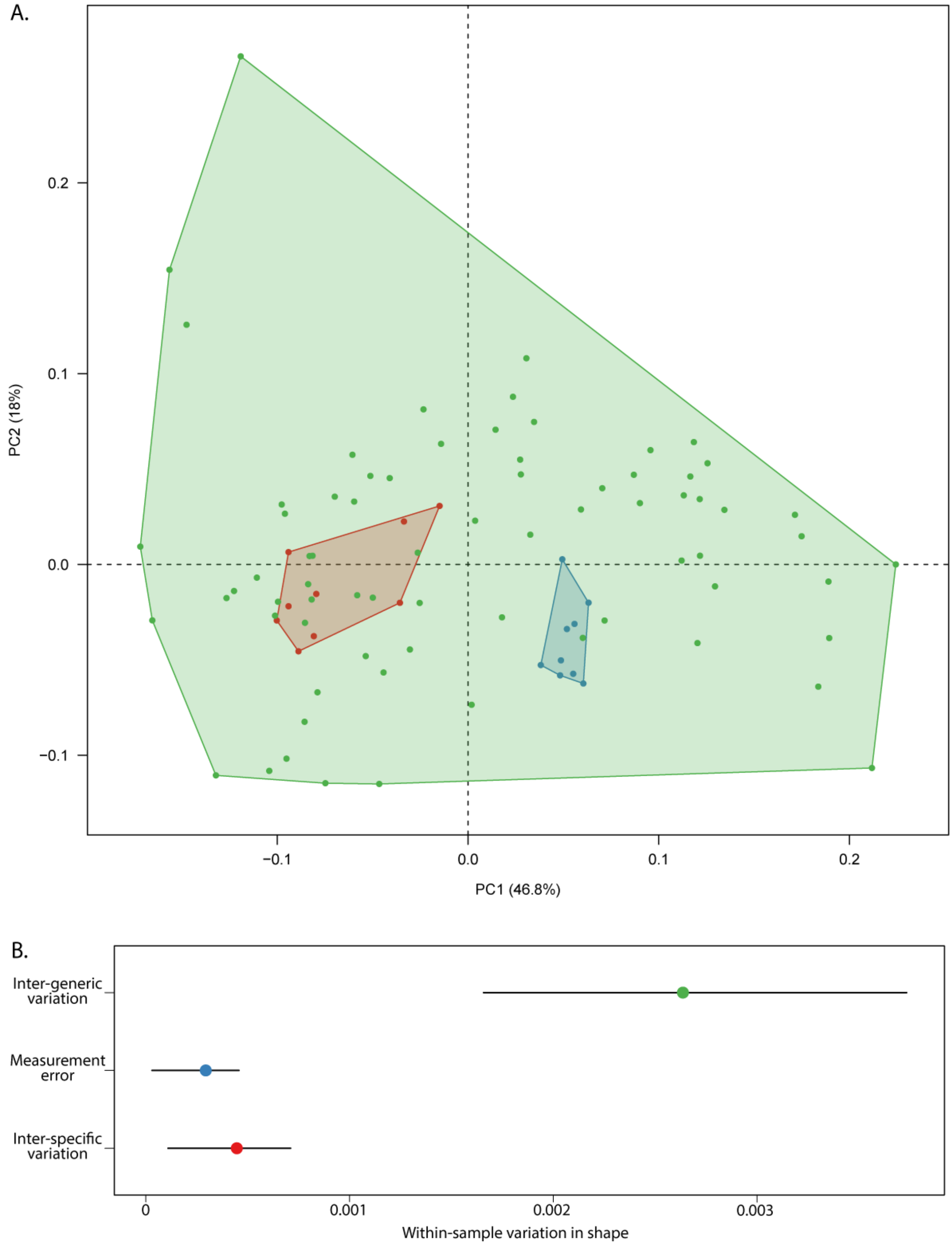

***Figure S1:*** *Evoluation of the measurement process bias (blue) and the intra-generic variation (red). (A) phacopid cephala morphospace and (B) phacopid pygidia are distributed along PC1 and PC2.*

# Chapitre 2. Diversité et la Disparité des trilobites du Dévonien d'Afrique du Nord

Les changements environnementaux et les faunes ne sont pas homogènes à l'échelle planétaire, c'est pourquoi un focus au niveau régional est nécessaire afin de mieux comprendre les relations entre les faunes et avec l'environnement. L'objectif est de comprendre les effets de l'environnement et d'identifier les périodes de diversification et d'extinction, à la fois en terme de diversité taxonomique (article 3) qu'en terme de disparité morphologique (article 4). La comparaison de ces deux métriques et l'identification d'un éventuel couplage permet également de mieux comprendre les phases de diversification et d'extinction (article 5). Enfin, dans l'optique d'analyser la composante spatiale de la biodiversité et le rôle de la géographie, une étude de la paléobiogéographie des trilobites du Maroc a été réalisée (article 6).

## 2.1. Tendances de la biodiversité des trilobites du Dévonien d'Afrique du Nord

Article 3 : Trilobite biodiversity trends in the Devonian of North Africa

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# Trilobite biodiversity trends in the Devonian of North Africa

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ABSTRACT

Taking advantage of the exceptional record of Devonian trilobites in North Africa, a new dataset was compiled in order to reveal their long-term evolutionary history leading to their extinction. This dataset comprises 1171 trilobite occurrences from 168 different localities, within 22 consecutive and discrete chronostratigraphic intervals (substage temporal scale), representing 556 species, 179 genera, and 15 families scattered among nine North African basins. The reconstructed palaeobiodiversity trajectories by means of various biodiversity estimators of taxonomic richness are consistent and highlight a progressive and continuous diversification throughout the Early Devonian to reach a maximum of diversity at the end of the Emsian. Most families encountered in North Africa contribute to this increase of diversity. This regional diversification shows the same trends as the global one. Thereafter, the trilobite diversity began to decline due to extinction rates higher than origination rates during the Eifelian (Middle Devonian). From the middle Givetian to the late Frasnian, the trilobite diversity remained low. After this major decline, and the Frasnian events, a faunal change occurred, especially in phacopid and proetid trilobites, which were the only two families crossing the Frasnian/Famennian boundary. Indeed, the Kellwasser Event impacted an already impoverished diversity leading to a major faunal renewal associated with quick taxonomic changes at the genus level. A larger proportion of deeper water and reduced-eye/blind trilobites who acted as opportunists characterized the Famennian recovery. Finally, these palaeobiodiversity trends are compared to those of ammonoids from the same area.

## 1. Introduction

During the Cambrian Explosion, trilobites diversified rapidly at a low taxonomic level to become a dominant macrobenthic fauna thanks to several novelties (Clarkson, 1975; Clarkson et al., 2006; Hughes, 2007; Esteve et al., 2018), which evolved during the 'Great Ordovician Biodiversification Event' (GOBE; Harper, 2006; Servais et al., 2010; Harper et al., 2015). They invaded both nektic and benthic zones (Fortey, 1985), shallow and deep waters (Fortey, 1975) and were present at many different latitudes (Cocks and Fortey, 1990; Adrain, 2013).

Whereas the diversity of trilobites have been well-studied and documented during the GOBE (Westrop and Adrain, 1998; Adrain et al., 2004; Adrain, 2013), much less attention has been accorded to their late evolutionary history; a period marked by important environmental changes, i.e., important temperature variations (Joachimski et al., 2009) and palaeogeographic changes causing volcanism (Ziegler et al., 1979). Only a few works (Feist, 1991; Lerosey-Aubril and Feist, 2012) focused on the diversity of Devonian trilobites and on the related events, which led to their decline from the Middle Devonian. Chlupáč (1994) identified general trends in diversity for the Devonian as a whole.

The 'Devonian Nekton Revolution' (Klug et al., 2010) was an important event, which led to another major diversification of trilobites, especially during the Early Devonian. At the beginning of the Devonian, five orders and nearly eighteen families were present worldwide (Crônier and van Viersen, 2007). They experienced a great diversification during the sea-level rise of the basal Pragian Event (House, 2002) and the related climate warming (Vacek, 2011). This sea-level rise probably contributed to the widening of shallow marine carbonate realms favourable for the development of trilobite communities (Chlupáč, 1994; Crônier and van Viersen, 2007; Khaldi et al., 2016), and led to the maintenance of family-level diversity, which persisted with some minor changes until the early Eifelian. Their subsequent diversity decreased dramatically and high taxonomic levels disappeared due to a series of biological events (they were strongly affected by the Kacák and Taghanic events in the late Eifelian and the middle Givetian, respectively; Chlupáč, 1994; Lerosey-Aubril and Feist, 2012). These biotic events were associated with major rises in sea level and led to more widespread extinctions (Chlupáč, 1994; Crônier and van Viersen, 2007;

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McKellar and Chatterton, 2009).

Devonian trilobites are especially well represented and diverse in North Africa (Fig. 1). Originally part of a regionally continuous Gondwana passive margin, the North African platform experienced an increase of epeirogenic activity during Devonian times, reflecting the initial collision between Gondwana and Euramerica and the progressive creation of Pangaea (Boote et al., 1998). During this episode, intracratonic basins were created, such as the Tindouf, Maider and Tafilalt basins of Morocco, and the Ougarta Basin of Algeria. In these basins, carbonate production led to carbonate-dominated facies and brought favourable conditions for the settlement and the development of trilobites (McKellar and Chatterton, 2009). Devonian outcrops are mainly composed of limestones with shale intercalations and correspond to a temperate platform environment of the Rheic Ocean. This platform was progressively flooded until the Givetian, which corresponds to the maximal transgression before the latest Devonian regression (Conrad et al., 1986; Hollard, 1967).

In this context, we focused our investigations on biodiversity analyses of trilobite data gathered from this emblematic North African area, i.e., Morocco and Algeria, famous for their exceptional record of Silurian and Devonian trilobites, both qualitatively and quantitatively (Errami et al., 2015; Bonino and Kier, 2010). The aim of this study is to better understand the impact of the biological events occurring through the Devonian on macrobenthic organisms. Although the Silurian and Devonian trilobites from North Africa have been widely documented since the pioneer works of Richter and Richter (1943), Termier and Termier (1950), Alberti (1964, 1966a, 1966b, 1966c, 1967a, 1967b, 1969, 1970a, 1970b, 1981a, 1981b, 1982, 1983), and the subsequent studies of Morzadec (1997, 2001), Chatterton et al. (2006), McKellar and Chatterton (2009), Gibb and Chatterton (2010), van Viersen and Prescher (2011, 2014), van Viersen and Heising (2015), van Viersen et al. (2017), Johnson and Fortey (2012), Feist and Chatterton (2015), Feist et al. (2016), Khaldi et al. (2016), van Viersen and Holland (2016), Feist and Belka (2018), and Crônier et al. (2013, 2018a, 2018b), among others; but no analysis based on a substantial occurrence database has been performed at a regional scale for this area.

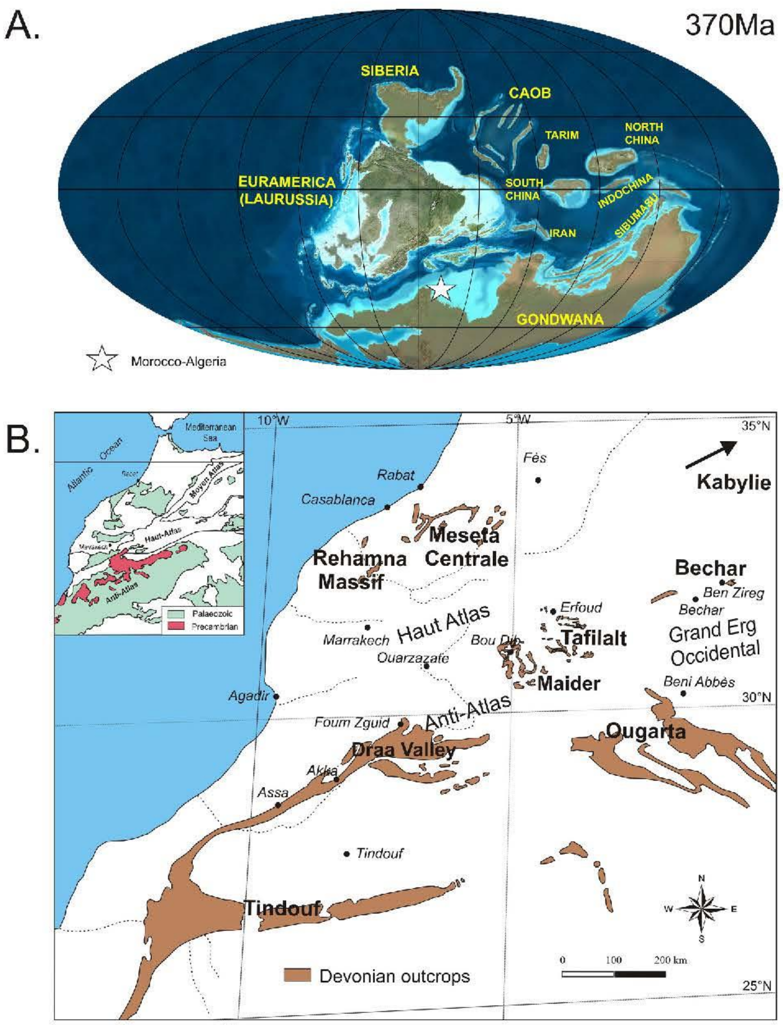

**Fig. 1.** (A) Location of Morocco and Algeria (white star) on a palinspastic map (modified from Blakey (2016), with continent positions and shapes for the Late Devonian modified from the tectonic data of Hara et al. (2010), Metcalfe (2011), and Xiao et al. (2010). (B) Geographical location of studied area with the nine studied basins (in bold; modified from Hollard, 1968).

A new dataset of trilobite occurrences is used and modern biodiversity metrics are applied to quantify the biodiversity fluctuations characterizing the evolution of trilobites throughout the Silurian and the Devonian, and to better document the Devonian extinction events in North Africa. Our investigations focus on the representative trilobite-bearing areas of Morocco and Algeria (North Africa) and on the taxonomic component of biodiversity (taxonomic richness, composition, and similarities), at the substage temporal scale. To understand their fluctuations in time and space, their distribution patterns are assessed thanks to diversity curves and by considering the palaeogeographic and palaeoenvironmental context.

## 2. Data

### 2.1. Occurrences

To analyse accurately the fluctuations in biodiversity, a dataset has been compiled to list all occurrences of Silurian and Devonian trilobites documented in Morocco, Algeria, Mauritania and Libya from the available literature (Appendix A). Only studies published after 1943 have been included, because the former publications either present an outdated taxonomy in need of revision, and/or a poor temporal resolution. This selection represents 98 publications (Appendix B) which cover the end of the Silurian and the Devonian from North Africa (Fig. Suppl. A). Our dataset contains all identified taxa at the species rank in a revised taxonomy and temporal framework, and is as much representative as possible of the current state of research concerning the knowledge of the Silurian and the Devonian trilobites from North Africa. All in all, this dataset (Appendix A) comprises 4324 trilobite specimens, i.e., 1171 trilobite bed-occurrences in total from 168 different localities, within 22 consecutive and discrete chronostratigraphic intervals from the Homerian to the Famennian. Only the highest number of either cephala/cranidia, pygidia or complete exoskeletons per occurrence was kept to avoid duplicates. This number represents 556 species, 179 genera, and 15 families scattered among nine North African basins (Fig. Suppl. B). For each trilobite bed-occurrence, the dataset also contains the following information: source study (reference), location (locality, basin, country), stratigraphic position at different resolutions (stage and substage; their numerical ages are derived from the ICS International Chronostratigraphic Chart v2016/10; Cohen et al., 2013; updated), abundance, taxonomic information including the classification, taxonomic qualifiers (such as '?', 'cf.' and 'aff.') if relevant for genus and/or species, authorship, and original identification if it has been revised. In order to create a taxonomic framework reflecting the current state of research with as much consistency as possible, we relied on the identification and age-assignment in the original studies or subsequent published revisions and considered the intending synonymies. Without intention to validate or revise the taxonomy, the names used follow the last usage. Throughout our data compilation, genera and species were considered, but only the diversity fluctuations at the generic level are presented and discussed herein. The diversity changes at the specific level are presented in a supplemental figure (Fig. Suppl. F). The stratigraphic intervals or bins used in the database corresponds to the last three Silurian series and to the 18 Devonian substages. The duration of a substage varies from 1.6 Myr (lower and upper Pragian) to 8.6 Myr (lower Emsian) for a total duration of 68.5 ±0.5 Myr.

### 2.2. Trilobite vision and palaeoenvironments

In order to highlight the potential environmental/ecological affinities or morphological adaptation of trilobites, two additional sets of information are recorded in the dataset. First, we considered the visual system of studied trilobites, which can be inferred directly from the eyes preserved as calcite lenses on a visual surface (Clarkson et al., 2006). Each taxon has been assigned to one of the three categories: blind, reduced-eye, or well-developed-eye. The diagnostic features related to the eye size or to the number of lenses were considered to establish these categories.

Second, we considered the marine environment of studied trilobites, for which associations are well-known to reflect relatively precise palaeoenvironmental indicators of different depths across shelves (Fortey, 1975; Speyer and Brett, 1986; Turvey, 2005; Crônier and van Viersen, 2007; Crônier and François, 2014). Four major environments can be recognized along a bathymetric profile: (1) the shoreface environment characterized by shallow, proximal and agitated deposits including trilobites as fragmented exoskeletons in sandstones; (2) the inner shelf environment characterized by mudstones intercalated with sandstones including trilobites as disarticulated and fragmented exoskeletons and/or as coquinas; (3) the middle shelf environment characterized by relatively deep deposits including moderately to highly diverse assemblages with trilobites with well-developed eyes, clumped or dispersed sclerites commonly articulated in mudstones; and (4) the outer shelf environment located below the effective storm wave-base including rare trilobites, as articulated exoskeletons, often blind or with reduced-eyes, in shales. Consequently, according to its depositional environment and to the observed faunal assemblages, each genus has been assigned to only one of these four categories. Trilobites considered to have habitat specificity are found almost exclusively in their specific environment.

Blind or reduced-eye trilobites often indicate a dark and relatively deep environment, i.e., outer shelf/external platform, near or below the photic zone (Clarkson, 1967; Feist, 1991). By contrast, trilobites with well-developed eyes often indicate a shallow (i.e., inner platform) or a mid-depth (i.e., middle shelf) environment. For example, it has been demonstrated that Late Devonian phacopid trilobites, in the context of a deepening ocean, were subject to such evolutionary changes, i.e., a gradual reduction of the visual complex leading to blindness (Crônier and Courville, 2003; Crônier et al., 2004, 2011; Crônier and François, 2014). Only, the state of preservation and/or the nature of sediments and the associated fauna allow us to determine roughly the palaeoenvironmental/palaeoecological position along a bathymetric profile.

## 3. Methods (biodiversity metrics)

The estimation of palaeobiodiversity and its variation through geological time is a major issue in macroevolution. Major biases (rock/fossil preservation, facies/ecology, sampling, …) affect taxonomic richness reconstruction (Foote, 2000; Smith, 2001). For Morocco in particular, the biases concern also the issues due to the trade of valuable trilobites. Throughout the past decades, some beds that yield complete, articulated and well-preserved trilobites have often been the focus of investigations (e.g. Chatterton et al., 2006; van Viersen and Holland, 2016; among others). Even if major biases exist, the last decades have seen substantial progress in the knowledge of the Phanerozoic biodiversity (Sepkoski Jr. et al., 1981; Benton, 1993; Alroy et al., 2008; Fan et al., 2020), notably thanks to the use of resampling methods (Alroy, 2010a; Chao et al., 2012, 2014; Close et al., 2018).

Palaeobiodiversity can be measured in different ways and for any taxonomic rank. To produce reliable biodiversity trajectories through time close to the true diversity of coexisting taxa at a given time (i.e., 'standing diversity', Cooper, 2004), taxonomic approaches based on the count of distinct names for a given taxonomic rank (species, genera, families) and known as 'taxonomic richness' indices were used. Taxonomic richness indices were calculated by computing traditional incidence-based binning approaches, as well as modern occurrence-based resampling methods.

Classical binning approaches estimate taxonomic richness according to different biostratigraphic categories (e.g., single-interval, ranging through, originating, and disappearing; see Foote, 2000) based on the synthetic incidence (i.e., binary presence) range of the taxa considered in a moving "window" covering three time bins (for additional details and discussion, see Foote, 2000; Alroy, 2010b; Nowak et al., 2015): the sampled-in-bin diversity (SIB), which is the raw count of actually documented taxa; the range-through diversity (RT), which includes or excludes single-interval taxa, but interpolates discontinuous taxon ranges; the normalized diversity (NORM), which weights differently the various biostratigraphic categories; the boundary-crosser diversity (BC), which focuses at the chronostratigraphic limits and not within these time bins; and the single-interval diversity (SGL). All these traditional metrics can be biased by various effects such as heterogeneous sampling, but they are still useful in highlighting peculiarities in the dataset. Cooper (2004) evaluated the normalized diversity as a good approximation of the mean standing diversity. Additionally, the recent stochastic uniform-time-bin diversity (UTB) of Gibert and Escarguel (2017) has been applied: this approach is a back-transformation into a virtually continuous-time averaged time series of the time-discretized dataset constructed from the fossil record; the period of time under study was split into 2 Myr time bins, and each specimen was assigned multiple times at random to one of the bins between its maximum and minimum age brackets. This method has been shown to provide more accurate estimates of standing diversity than binning approaches, even when the origination and extinction are biased towards coinciding with the boundaries of bins (Gibert and Escarguel, 2017). Finally, origination and extinction rates are calculated based on range-through diversity excluding single-interval taxa. More precise and accurate methods of calculating origination/extinction rates such as the gap fillers method (Alroy, 2014, 2015) cannot be applied to our dataset because of the high proportion of taxa documented in less than four time intervals.

Although taxonomic richness is an intuitive measure of biodiversity, it is an elusive quantity to measure properly, because as more individuals are sampled, more species will be recorded (the so-called sampling intensity/effort problem) (Simpson, 1949; Bunge and Fitzpatrick, 1993; Gotelli and Colwell, 2001; Chao et al., 2014). Therefore, because the robustness of estimated curves of taxonomic richness depend on sample size, modern biodiversity metrics based on the resampling of abundance and/or collection data were also performed in this study: size-based rarefaction (CR) and coverage-based rarefaction (SQS), which are two interpolation methods, and richness estimated using a Poisson sampling model (TRiPS), which is an extrapolation approach (see Close et al., 2018). First, the conventional size-based rarefaction estimates taxonomic richness by repeated random downsampling of data to a user-defined sample size (Sanders, 1968; Hurlbert, 1971; Foote, 1992; Shimadzu, 2018) to enable comparison of the time intervals considered at equal sampling effort. Second, the coverage-based rarefaction (shareholder quorum subsampling, SQS; Alroy, 2010a-b, Alroy, 2013) repeatedly randomly draws taxa from compiled in-bin occurrence lists, until a summed proportion of these taxa relative occurrence frequency reaches a certain 'quorum' to finally sum the taxa sampled. Coverage, as a measure of sampling quality, is defined as the proportion of the frequency distribution of taxa within a sample. In this study, diversity was estimated at various levels of coverage at intervals of 0.1 and by including dominant and single-interval taxa. Coverage-based rarefaction has been shown by both simulation studies and empirical data to be a robust method of correcting for preservation and sampling heterogeneity (Alroy, 2010a-b; Chao and Jost, 2012; Close et al., 2018). Finally, TRiPS (Starrfelt and Liow, 2016) aims to estimate true richness by modelling per-interval sampling rates (inferred by maximum likelihood using observed taxon occurrence frequencies and interval durations) for extinct lineages as a homogeneous Poisson process.

Additional insights on the biodiversity of the Devonian trilobite fauna from North Africa were completed by investigating their evenness component (Smith and Wilson, 1996; Tuomisto, 2012; Kvålseth, 2015). Taxonomic evenness ('equitability') refers to how equal in numbers (relative abundance) each taxon in a (space/time) bin is, and is typically derived by rescaling a diversity measure to the interval from 0 to 1. Two measures of evenness are here computed: the Simpson index of dominance (D; Simpson, 1949) and the Pielou's equitability (E; Pielou, 1966) derived from the Shannon–Wiener index (Shannon and Weaver, 1949). Low values of dominance indicate taxa rather evenly represented, and conversely the index will be close to 1 if there is a single very dominant taxon. Inversely, values of equitability close to 0 reflect an overabundant taxon, while high values indicate almost equally distributed taxa.

In this work, the various biodiversity indices and methods were computed with the scientific environment R (version 3.5.2; R Core Team, 2019) using the package 'epaleo' (version 0.8.27; Monnet C., unpublished, University of Lille; for applications using this package, see e.g., Tétard et al., 2017; Shen et al., 2020), and with the software PAST (version 3.24; Hammer et al., 2001).

## 4. Results

### 4.1. Genus richness

The reconstructed biodiversity curves of the trilobite genera from North Africa during the Silurian and the Devonian substages are illustrated in Fig. 2 and Suppl. C and D, for both raw binning and collection resampling methods. As indicated by the various biodiversity estimates and notably the coverage-based rarefaction (SQS), the generic richness shows important fluctuations during the Silurian and the Devonian in North Africa (Fig. 2). The local diversity was characterised by low to moderate values from the Ludlow to the Lochkovian, followed by peaks of highest diversity in the second part of the Early Devonian and at the beginning of the Middle Devonian, i.e., from the Pragian to the Eifelian. This period constituted a plateau of high diversity. During this period, the diversity still fluctuated with a decrease of diversity in the early Emsian before the major peak at the late Emsian. After this high diversity period, the generic richness strongly decreased until the middle Givetian and stayed low until the late Frasnian. After a small diversification phase observed at the end of the Frasnian, there was a moderate decrease of diversity in the early Famennian, then, another small diversification phase occurred in the late Famennian (Fig. 2). However, the Late Devonian diversity remained low compared to the Early Devonian plateau.

The taxonomic richness evaluated by the boundary-crosser diversity (BC) shows similar trends to the SQS, such as the initial protracted increase of diversity from the Ludlow to the early Eifelian (Fig. 2). The major difference is the absence of a diversity decrease in the early Emsian. Next, a huge decrease took place and the diversity reached low values during the middle Givetian, and stayed relatively low until the end of the Famennian. The range-through diversity excluding single-interval taxa (RTexS) shows as the boundary crosser diversity, a continuous Early Devonian diversification from the Lochkovian to the Emsian (Fig. 2). This period is followed by a relatively regular decrease of the diversity until the early Famennian. No increase was spotted in the late Frasnian contrary to the SQS method. Then, an increase happened in the middle and late Famennian as shown by the SQS curve. The sampled-in-bin diversity (SIB) and the uniform-time-bin diversity (UTB) show the same trends as the SQS diversity (Figs. 2, Suppl. C and D). This method also suggests a slight increase of the generic richness throughout the Frasnian. Most discrepancies observed between these various biodiversity estimates were due to episodic increases of single-interval taxa (e.g., late Pragian, late Emsian, late Frasnian and early Famennian; Fig. Suppl. D) or to increases of virtual ranges (e.g., early Emsian), depending on the importance given to these parameters by each index.

The size-based rarefaction (CR, Fig. Suppl. E2) analysis shows that some substages are under-sampled and require a higher number of individuals to achieve robust diversity estimates. Therefore, additional studies and fieldworks are required to complete the knowledge of trilobites especially for the early Lochkovian, the Givetian and the Frasnian. Nevertheless, the size-based rarefaction analysis confirms the trends observed with the other indices: a high diversity from the late Pragian to the late Emsian followed by a decrease during the Eifelian.

### 4.2. *Origination and extinction*

With regard to taxonomic changes, i.e., extinctions ($E_{RT}$) and originations ($O_{RT}$) (Fig. 3), the observed evolutionary pattern shows a global increase of the number of originations with moderately high values from the late Lochkovian to the late Emsian, interrupted by two major decreases occurring during the early Pragian and the early Emsian. Then, the number of originations decreased drastically during the Eifelian and the early Givetian. Thereafter, a small peak of originations occurred during the early and the middle Famennian (Fig. 3).

Concerning extinctions, the evolutionary pattern shows a major increase during the Early Devonian, with a maximum reached in the early Eifelian. This peak of extinction followed the high origination period observed during the Early Devonian. During the Middle and Late Devonian, four other moderate extinction peaks occurred (early and late Givetian, late Frasnian and late Famennian; Fig. 3).

### 4.3. *Evenness and dominance*

In North Africa, the dominance was generally low (less than 0.3) during the Early and Middle Devonian (Fig. 4). Only the Ludlow, the early Lochkovian and the late Givetian were characterized by a dominance above 0.4, and the middle Givetian was characterized by a dominant taxon (D = 1) in a very depauperate assemblage (Fig. 4). Throughout this period, a relatively high evenness (more than 0.4) is recorded except for the Emsian. The transition from the late Frasnian to the late Famennian was characterized by a sharp decrease of evenness (from 0.82 to 0.23) and a distinct increase of dominance (from 0.23 to 0.72). After these important changes, the evenness increased gradually during the Famennian to reach high values, and conversely, the dominance decreased until the late Famennian before a slight increase at the end of the Devonian.

### 4.4. *Richness per family*

Six orders of trilobites (Trinucleida, Lichida, Harpetida, Corynexochida, Proetida, Phacopida) are documented in North Africa from the Ludlow to the latest Famennian (Fig. 5). Trinucleida (see Bignon et al., 2020) did not reach the Devonian, Corynexochida disappeared in the Middle Devonian, and Lichida and Harpetida did not cross the Frasnian/Famennian Boundary. Only Proetida and Phacopida were present until the Famennian.

Sixteen families are documented in North Africa during the studied period (Fig. 5). The Raphiophoridae (Trinucleida) were only present during the end of the Silurian. Among Phacopida, Calmoniidae, Calymenidae, Cheiruridae, Dalmanitidae and Homalonotidae did not cross the Early Devonian. During the maximum diversity period characterizing the late Emsian, 12 families coexisted in North Africa. After the major decrease of the diversity observed during the Eifelian, the middle Givetian records the presence of only one family (Proetidae). In comparison to the Emsian and Eifelian stages, the Frasnian is relatively poor in both phacopids and proetids. The odontopleurids and the harpetids were present until the late Frasnian, where they are both represented by only one genus. Then, only two families managed to survive the Kellwasser Crisis, proetids and phacopids, which experienced a new diversification in the Famennian.

### 4.5. *Vision of trilobites and palaeoenvironments*

The variations of the relative genus diversity according to the visual capabilities (blind, reduced-eye or well-developed-eye taxa) and to the living environment (shoreface, inner shelf, middle shelf, outer shelf) are reported in Fig. 6. Three time intervals were marked by peaks of presence of reduced-eye and blind taxa: the Pragian, the late Emsian and the Famennian (Fig. 6A). Compared to the total taxonomic richness, the early Famennian was characterized by the greatest proportion of

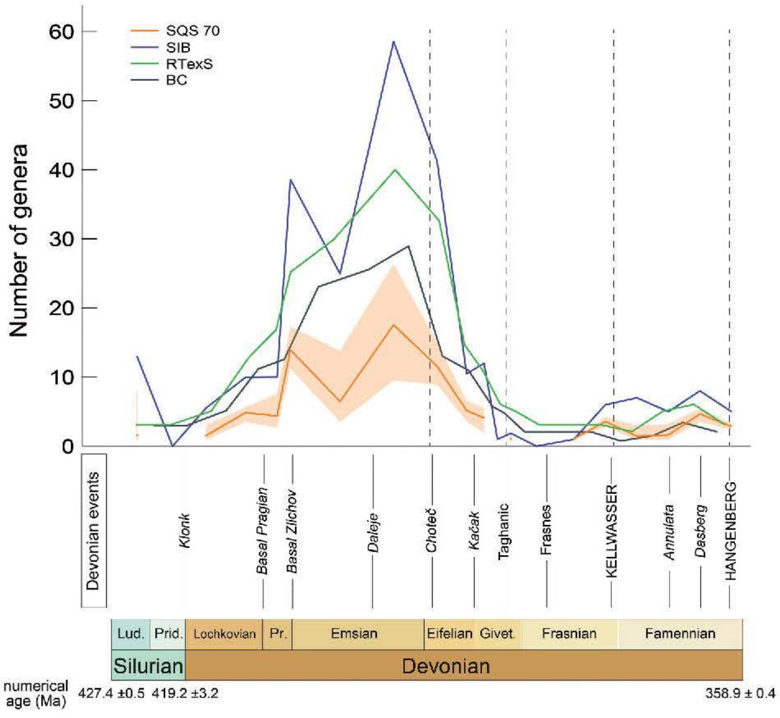

**Fig. 2.** Diversity dynamics of trilobites from North Africa during the Silurian and the Devonian. See text for the definition of indices. Diversity values, i.e., taxonomic richness at the generic level per substages. Shareholder Quorum Subsampling (SQS) diversity, estimation for a quorum of 70; Sampled-in-bin index (SIB), total count of taxa from a given stratigraphic interval; Range-through diversity excluding single-interval taxa (RTexS), which estimates diversity from counting everything that is known to occur in an interval plus everything that is inferred to be present; Boundary-Crosser diversity (BC), count of all taxa present in two successive intervals. Stratigraphic position of the extinction events according to Becker et al. (2016b); first-order events in capital, second-order events in bold and third-order events in italic. Ages from Cohen et al. (2013, updated).

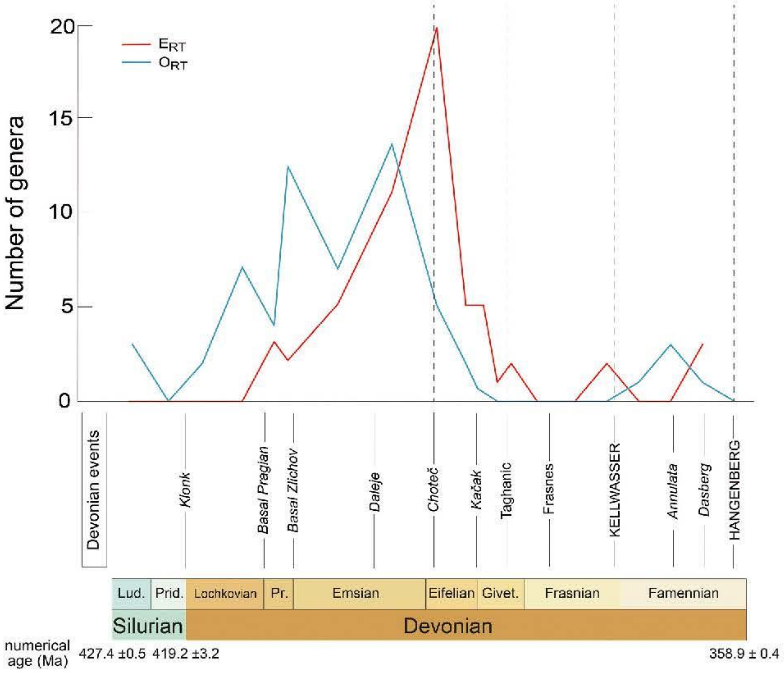

**Fig. 3.** Fluctuations of the number of extinctions ($E_{RT}$) and originations ($O_{RT}$) of trilobites from North Africa during the Silurian and the Devonian, at the generic level. Stratigraphic position of the extinction events according to Becker et al. (2016b); first-order events in capital, second-order events in bold and third-order events in italic. Ages from Cohen et al. (2013, updated).

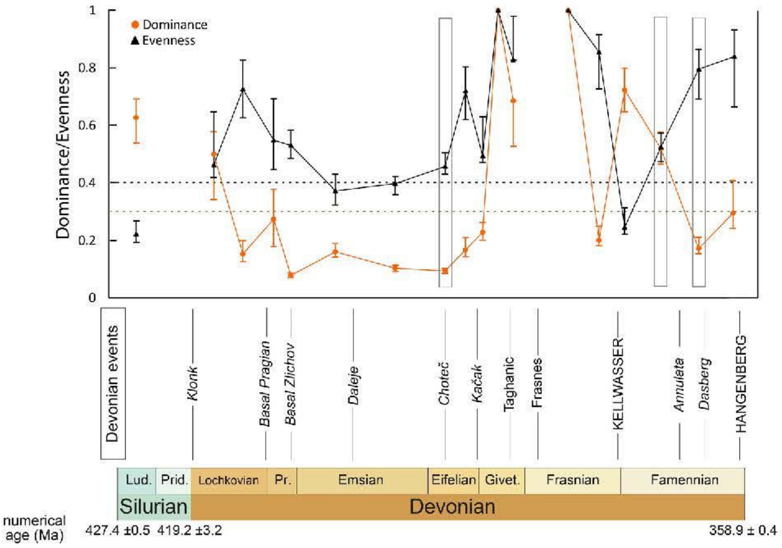

**Fig. 4.** Variations of two diversity indices (dominance and evenness) during the Silurian and the Devonian, computed for the trilobites from North Africa at the generic level. Stratigraphic position of the extinction events according to Becker et al. (2016b); first-order events in capital, second-order events in bold and third-order events in italic. Ages from Cohen et al. (2013, updated).

reduced-eye or blind taxa. The Pragian showed a relatively substantial number of reduced-eye and blind trilobites. The increase of trilobites with a reduced vision in the late Emsian corresponded to a global and regional diversity peak, whereas the two other peaks of reduced-eye taxa occurred in the Famennian were associated to low diversity values (Fig. 6A).

Regarding the depositional environments and faunal assemblages, trilobites encountered in shallow environments (shoreface) were present

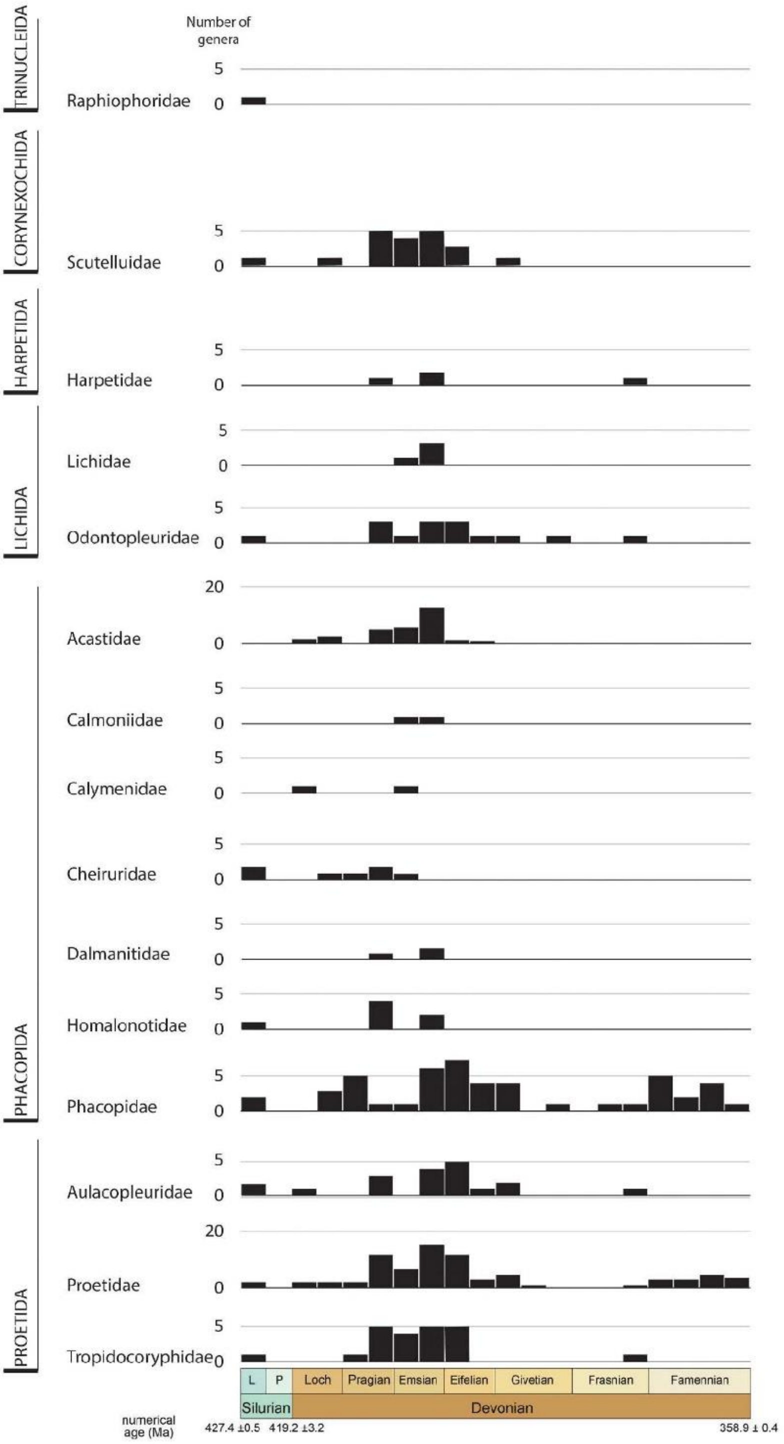

**Fig. 5.** Number of genera for each trilobite family during the Silurian and the Devonian in North Africa. Families are ordered by order. Ages from Cohen et al. (2013, updated).

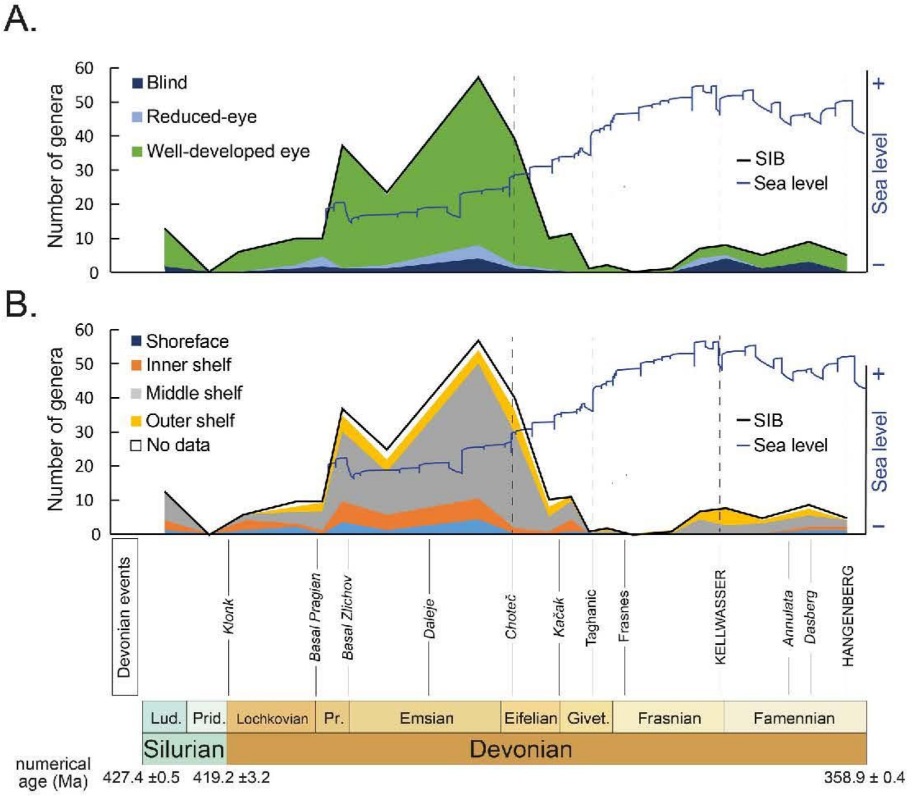

**Fig. 6.** Fluctuations of the relative genus diversity of trilobites from North Africa during the Silurian and the Devonian, according to (A) three visual capabilities (blind, reduced-eye or well-developed-eye taxa), and (B) four depositional environments, i.e., bathymetric depth (shoreface; upper offshore or inner shelf; median offshore or middle shelf; lower offshore or outer shelf located below effective storm wave-base environments; and not allocated or ubiquitous genera). Each genus is attributed to its main environment even if it could live in other environment. Sea level from Johnson et al. (1985). Stratigraphic position of the extinction events according to Becker et al. (2016b); first-order events in capital, second-order events in bold and third-order events in italic. Ages from Cohen et al. (2013, updated).

especially during medium to high diversity periods, i.e., during the entire Early Devonian, the early Givetian and the latest Famennian (Fig. 6B). In contrast, the trilobites encountered in deeper environments (outer shelf) were present throughout the Devonian but in higher proportion in the late Frasnian and the Famennian.

## 5. Discussion

The palaeobiodiversity trends of the North African trilobites reconstructed using various biodiversity indices are consistent and highlight significant diversity changes throughout the end of the Silurian and the Devonian. In summary (Fig. 2), North African trilobites were characterised by a low diversity, slightly increasing during the Lochkovian. A sharp increase was recorded during the Pragian, leading to a plateau of maximum diversity during the Emsian and the early Eifelian. An abrupt diversity decrease occurred subsequently during the late Eifelian, from which the diversity stayed low until the end of the Devonian, with only small changes observed.

### 5.1. *End of the Silurian and Lochkovian*

The comparison of the regional diversity with the global diversity patterns described in the literature shows marked similarities and differences. At the global scale, the trilobite diversity that is characterized by numerous genera that belongs to conservative and long-ranging genera, was documented from the Silurian to the Lochkovian with few changes due to only minor extinctions (Chlupáč, 1994). A decrease of diversity occurred in the Ludlow and the Pridoli in some places (e.g., Prague Basin; Manda and Frýda, 2014) and especially in North Africa. The Lau Event (Jeppsson and Aldridge, 2000) which took place during this interval with faunal changes concerning conodonts and graptolites among others, at the global scale. This event was not clearly identified in North Africa but could be associated to this decrease. No trilobites are found in the shale and black limestone deposits of the eastern Anti-Atlas because of the deep-water conditions, which are not favourable to the development of benthic fauna (Morzadec, 2001). Thus, in North Africa, a low trilobite diversity was documented from the Silurian to the Lochkovian. Only few trilobite taxa dominated these communities as shown by the high dominance index in the Ludlow and the Lochkovian (Fig 4).

### 5.2. *Pragian and Emsian*

At a global scale, the major regressive Basal Pragian Event (Chlupáč and Kukal, 1986) contributed to the widening of shallow marine environments with carbonate sedimentation favourable for trilobites, and led to an increase of the genus diversity (Chlupáč, 1994) associated with the proliferation of many benthic species on the continental shelves (Morzadec, 2001). There was a protracted diversification throughout the Early Devonian, with a diversity maximum recorded during the late Emsian. Meanwhile, the long-term gradual transgressive Daleje Event occurring at the beginning of the late Emsian (House, 1985; García-

Alcade, 1997; Becker et al., 2018) contributed to the installation of siliciclastic environments and led to strengthening the trilobite diversity increase. As a result of the preceding Daleje Event, offshore trilobites also proliferated worldwide, with numerous blind and reduced-eyes taxa (Chlupáč, 1994). The fauna composed of *Plagiolaria* associated with other small-eyed or blind trilobites (*Piriproetus*, *Leonaspis*) encountered in the Pragian, represents a specialized group of trilobites inhabiting a muddy and rather deep water environment (Chlupáč, 1977, 1983). Hence, the generic richness reached its maximum level (Adrain, 2008).

In North Africa, the Pragian diversification is also documented (Hollard, 1967; Morzadec, 2001; Ouali Mehadji et al., 2011). However, whereas the peak of diversity was recorded in the early Pragian at the global scale (Chlupáč, 1994), the African regional diversity showed a peak rather in the late Pragian. This difference can be explained by the fact that most studies concerning Pragian trilobites from North Africa lack enough chronostratigraphic resolution to be included in our analysis. However, our study is the only one with a substage chronostratigraphic resolution, contrary to previous ones with a stage chronostratigraphic resolution. The increase of diversity is not explained by the proliferation of a few genera but corresponds to a general trend: the diversification (Fig. 6) is also observed at the family level (Fig. 5). The majority of Pragian genera persisted through the Emsian, both in North Africa (Fig. 2, see BC curve) and at the global scale, therefore, contributing to the richest interval, i.e., the Emsian (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012).

A decrease of diversity occurred in the early Emsian. However, the poor preservation of trilobites with no commercial opportunities limits their sampling and their subsequent analyses despite the notified presence of dalmanitids (odontochilines) for instance in the Draa valley (Becker et al., 2004). After this decrease of diversity, the transgressive

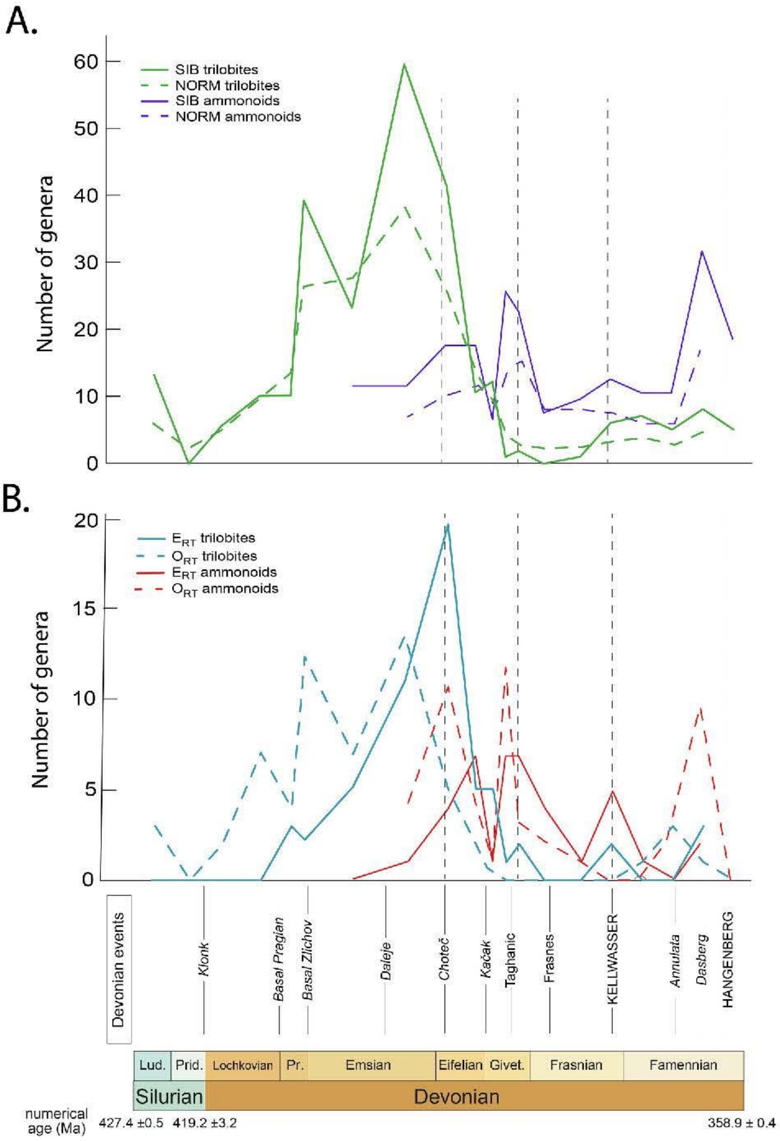

**Fig. 7.** Diversity dynamics of trilobites from North Africa and ammonoids from Morocco during the Silurian and the Devonian, at the generic level. See text for the definition of indices. Data for trilobites: this study; data for ammonoids from Allaire (2017, unpublished PhD). (A) Taxonomic richness: Sampled-in-Bin diversity (SIB) and normalized diversity (NORM). (B) Extinctions ($E_{RT}$) and Originations ($O_{RT}$).
Stratigraphic position of the extinction events according to Becker et al. (2016b); first-order events in capital, second-order events in bold and third-order events in italic. Ages from Cohen et al. (2013, updated).

Daleje Event led to an increase of the abundance of trilobites encountered in deeper environments in North Africa (Fig 6). Blind and reduced-eye trilobite genera were better adapted to live in this environment and become more numerous in the late Emsian (Fig 6). Additionally, trilobite taxa from shallow siliciclastic environments such as asteropygins were also well diversified in Morocco (Morzadec, 2001). All these diversification phases led to the Devonian peak of diversity recorded in the late Emsian (Fig. 2) in North Africa but also at the global scale (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012). The evenness decreased with the Early Devonian diversification to reach a minimum in the late Emsian, which corresponds to the substage with the highest diversity (Fig 4). This decrease shows that even if no genera dominate the community, some of them took advantage of the environment (e.g., proetids, acastids and phacopids; Fig 5).

In the context of the progressive colonization of the water column by predators during the 'Devonian Nekton Revolution' (Klug et al., 2010, 2017), potential connections especially with ammonoids can be evaluated. Indeed, the ammonoids which appeared during the early Emsian worldwide, were efficient nektic predators during the Devonian, as the jawed fishes (Klug et al., 2017). A comparison with the ammonoids from Morocco (data from Allaire, 2017, unpublished PhD; the same methods as those used in this study were performed to obtain these data) has been done in order to evaluate differences and similarities between trends. Evolutionary novelties within the trilobites may be a direct response of the development of passive morphological defences (as spinose skeletons) or active behavioural defences (as infaunal moulting or other cryptic behaviours) against durophagous predators such as nektic ammonoids. During the Devonian, the highly diverse Emsian and Eifelian trilobites from Morocco and from North America show a high frequency of spinose genera in several lineages (Brett and Walker, 2002). Such spinose skeletons may have had a selective advantage against durophagous predators (Brett and Walker, 2002). The ammonoids from Morocco showed a relatively low diversity during the Emsian, while the trilobites were characterized by a very high diversity (Fig. 7A). This trend suggests a nekton-benthos decoupling as proposed by Ebbighausen et al. (2011) for the Draa Valley in Morocco. These low diversity values represent the first step of the Nekton Revolution (Klug et al., 2010) which is underway and has not yet reached its acme. The subsequent increase of the ammonoid diversity (see following section) could be a consequence of the development of benthos such as trilobites in oxic zones.

### 5.3. *Eifelian and Givetian*

In contrast to the Silurian and Early Devonian, the diversity patterns observed during the Middle Devonian were somewhat different considering regional and global scales. Lerosey-Aubril and Feist (2012) noted a global diversity loss from the Eifelian to the Frasnian, but without an examination at a substage resolution. Trilobite faunas were rather diverse and locally abundant, and often distributed in geographically restricted biofacies. As underlined by Lerosey-Aubril and Feist (2012), this period was affected repeatedly by environmental disturbances generating large restructuration within marine ecosystems at a global scale (Walliser, 1996).

Although only a small faunal turnover occurred at the global scale during the Choteč Event (Barnes et al., 1996), a sharp decrease of the diversity occurred at the regional scale in North Africa in the early Eifelian. Indeed, a transgression occurred in the Western Sahara Platform (Ouali Mehadji et al., 2004) leading to biotic and abiotic changes. These changes were not favourable for trilobites and led to extinctions such as the genus *Paralejurus*, which disappeared both at the regional and global scales (Chlupáč, 1994). Additionally, this event strongly affected the Proetida with the regional extinction of some representatives of the Proetidae and Aulacopleuridae. Morzadec (2001) noted that because of the high sea level, trilobites living in shallow environments such as Asteropyginae remained scarce even if, at a global scale, they were able to adapt in deep environments (Bignon and Crônier, 2015). In North Africa, numerous taxa were impacted by this event; after the crisis, the diversity and the evenness remained relatively low and the dominance index suggests the presence of barely dominant taxa (Fig. 4).

The Choteč Event, which particularly affected trilobites in North Africa, did not affect all organisms in the same way. Indeed, as pelagic and nektic organisms, the ammonoids were less impacted by this transgressive event than the trilobites. The generic richness of the Moroccan ammonoids showed a progressive increase from the late Emsian to the late Eifelian; no drop down is recorded after the Choteč Event (Fig. 7A; Allaire, 2017, unpublished PhD).

The Kacák and Taghanic events (late Eifelian and middle Givetian, respectively) mark the end of the sharp decrease of the trilobite diversity already underway at all taxonomic ranks, and lead to a stepwise diversity drop (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012). The major transgressive Taghanic Event initiated in the middle Givetian led to a worldwide development of a deep-sea/pelagic cephalopod environment (Johnson, 1970; House, 1985) not favourable for trilobites; the disappearance of numerous families is observed (Calmoniidae, Cheiruridae, Lichidae) due to the disappearance of the near-shore neritic and perireefal environments. Only, a few taxa survived this worldwide deepening and successfully adapted to deeper and more homogeneous environmental conditions which characterise the late Givetian. The surviving faunas exhibited a pronounced reduction in generic and specific diversity concomitant with an increasing cosmopolitanism (Lerosey-Aubril and Feist, 2012).

At the regional scale, the Kacák Event was underlined by an increasing number of extinctions in trilobites. As the Choteč Event, the Kacák Event corresponds to a global eustatic rise combined to oxygenated-depleted conditions in benthic environments (Lerosey-Aubril and Feist, 2012) not favourable to trilobites (Fig. 6A). This deepening (House, 1985) affected the North African faunas (Bełka et al., 1999). The low trilobite diversity recorded after the Kacák Event corresponds to assemblages dominated by one genus (i.e., *Gerastos*).

For ammonoids, the early Givetian is poorly documented in the literature; only a few genera have been reported in Morocco. Consequently, the ammonoid diversity characterising the early Givetian is certainly underestimated (Fig. 7B) and so the impact of the Kacák Event is difficult to evaluate. Aboussalam and Becker (2011) noted a remarkable near absence of trilobites (and also brachiopods) in south-eastern Tafilalt in comparison to the similar reefal environments observed in Germany for the middle Givetian. Kaufmann (1998) highlighted that significant faunal and lithological changes affected the eastern Anti-Atlas from the early Eifelian to the early Givetian, and documented the replacement of benthic faunas (trilobites) by pelagic ones (ammonoids). Our results seem to confirm such patterns: for trilobites, the diversity continues to decrease dramatically, while for ammonoids, the diversity reaches high values and the number of originations significantly increases during the Givetian (Fig. 7B).

After the Choteč and Kacák events, the trilobite diversity remained very low in North Africa and the middle Givetian Taghanic Event (Johnson, 1970; House, 1985) impacted already impoverished trilobite faunas. Aboussalam and Becker (2011) noted that the Taghanic Event affected trilobites, in particular those of the Tafilalt basin and the Draa Valley; this extinction phase is immediately followed by a radiation in the Tafilalt basin only. They reported only the presence of phacopids and proetids in the Givetian of Morocco. Moreover, McKellar et al. (2012) reported an exceptional occurrence of *Pedinopariops (Hypsipariops)* in the Givetian coarsely siliciclastic facies from Libya. Such occurrence suggest a shift away from carbonate environment in which phacopids prospered during much of the Lower to early Middle Devonian.

For ammonoids, the Taghanic Event seems to have not sharply affected the communities: the late Givetian record high diversity values (Fig. 7A). However, when regarding the fluctuations at a higher time resolution (i.e., biozone temporal scale), the diversity recorded through the Taghanic interval is particularly low and the impact of the Taghanic

Event in ammonoids can be seen (Allaire, 2017, unpublished PhD). Thus, the Taghanic Event seems to have more impacted nektic organisms as ammonoids.

As it was demonstrated in the Ardenne Massif (Belgium) by Bignon and Crônier (2015) during the Middle Devonian, the trilobite biodiversity was more influenced by the global events than the local environmental changes. However, due to regional peculiarities, the global events may have different consequences at the local scale compared to the global scale.

### 5.4. *Frasnian*

At a global scale, the trilobite diversity was low during the early Frasnian and the Frasnes Event (*sensu* House, 1985), called also the *Manticoceras* Event (*sensu* Walliser, 1985), was marked by few extinctions of trilobites, and showed the appearance of two subfamilies, the Pteropariinae and Drevermanniinae (Feist, 1991).

During the late Frasnian, the pronounced eustatic deepening became maximal just before the upper Kellwasser event (Girard et al., 2005), leading to the development of pelagic and euxinic facies. The Kellwasser Event, leading to one of the five major extinctions (Raup, 1986; Raup and Sepkoski, 1982), was characterized by an eustatic instability and hypoxic/anoxic depositional conditions in the deeper outer-shelf environment, affecting especially benthic trilobites adapted to life in deep environments. In these offshore depositional environments beyond the light penetration limit, the visual complex regression leading to blindness in trilobites was an evolutionary trend observed in various independent lineages (phacopids and proetids). This evolutionary trend may result from an 'opportunistic' and adaptive strategy correlative with environmental constraints, insofar as it leads to a good match between organisms and their environment (Crônier, 1999; Crônier and Courville, 2003). However, such a link led them to a subsequent evolutionary impasse resulting in their extinction. Moreover, the late Frasnian *Acuticryphops* showed a morphological intra-specific drift inducing a variability of the visual complex (Crônier et al., 2004; Feist et al., 2009), which would be located at speciation boundaries. These disturbances that occurred during the development seem to be linked to environmental stress, which can be induced by the rapid sea-level fluctuations recorded at the end-Frasnian (Feist and Schindler, 1994). The Kellwasser Event led also to the extinction of almost all reefs and their associated trilobite faunas (Odontopleuridae), and to a significant decrease of diversity for other trilobite taxa (Chlupáč, 1994; Lerosey-Aubril and Feist, 2012). Otherwise, the late Frasnian trilobites from shallow/near-shore deposits remain poorly known (Lerosey-Aubril and Feist, 2012). Only few data are available; they concern the trilobite faunas from the Canning Basin in Australia (Feist et al., 2009), where well-oxygenated conditions prevailed throughout the Frasnian–Famennian transition (George and Chow, 2002).

In North Africa, only four trilobite orders (Fig. 5) were present during the Frasnian (Lichida represented by Odontopleuridae, Harpetida, Phacopida, and Proetida). For phacopids, among the seven genera known during the Frasnian at the global scale (Crônier et al., 2013; Crônier and François, 2014; van Viersen and Vanherle, 2018), only two were present in North Africa (*Chlupacops* originated in the middle Frasnian and *Acuticryphops* in the late Frasnian; Fig. 8). Phacopids were also rare elsewhere and only one genus (i.e., *Eldredgeops*) was reported so far in North America for example (Crônier and François, 2014). No Proetida were present during the early and the middle Frasnian (Fig. 8). The Drevermanniinae (*Palpebralia*) appeared in the late Frasnian at the same time as other genera (Fig. 8), implying an increase in diversity (Fig. 2). Additionally, the low dominance and the high evenness observed during the late Frasnian suggest a balanced ecosystem for benthic trilobite faunas for this period (Fig 4).

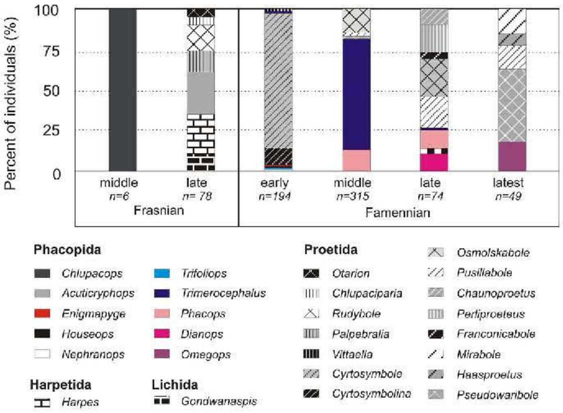

**Fig. 8.** Relative diversity of trilobite genera in percent of individuals, for the Late Devonian in North Africa.

Unlike trilobites, ammonoids experienced a severe extinction during the Frasnes Event, both in North Africa (Fig 7) and at the global scale (Walliser, 1996). The generic richness of the Moroccan ammonoids shows a sharp decrease around the Givetian–Frasnian boundary, and the values stayed low throughout the Frasnian. Although the ammonoids diversity shows low values during this stage, their diversity was significantly higher than the trilobite diversity (Fig. 7A). This difference reflects a global trend. In the Frasnian deposits, the trilobites as well as the majority of the benthic faunas remain scattered, the nektic and planktic faunas were more widespread (Wendt and Belka, 1991).

For the North African trilobites, the impact of the Late Devonian mass extinction remains elusive because the taxonomic richness is already low during the Frasnian (Fig. 2). Nevertheless, the coverage-based rarefaction and the boundary-crosser diversities show a small decrease during this event (Fig. 2). For the Moroccan ammonoids, an increasing number of extinctions was recorded and no origination has so far been reported (Fig. 7B; Allaire, 2017; unpublished PhD). However, this interval needs to be better documented to assess robust and precise conclusion concerning the impact of the Frasnian–Famennian biocrisis on the ammonoids from Morocco.

### 5.5. *Famennian*

The Famennian was punctuated by several global events (i.e., the Condroz–Enkeberg events in the early Famennian, the *annulata* event in the middle Famennian, and the Dasberg and Hangenberg events in the late Famennian), which impacted the trilobite diversity (Walliser, 1996; Lerosey-Aubril and Feist, 2012). Of the five orders present during the Frasnian (Corynexochida, Harpetida, Lichida, Phacopida, and Proetida), only the Phacopida and Proetida persisted into the Famennian (Feist, 1991; Chlupáč, 1994; Lerosey-Aubril and Feist, 2012) by surviving to the Kellwasser Event. The post-Kellwasser recovery was slow, and no trilobite was found in the first Famennian conodont zone (Lerosey-Aubril and Feist, 2012). The earliest Famennian trilobite encountered was a blind phacopid (*Nephranops*) from European offshore environments and in North Africa, the oculated phacopid (*Houseops*), earlier than the reappearance of proetids (Lerosey-Aubril and Feist, 2012). The recovery occurring during the early Famennian was due to the development of blind phacopids. At the global scale, they even have the highest origination rate (Feist, 2019). Apart from these blind phacopids, the other taxa present in the Famennian were mainly blind or small eyed, both in North Africa (Fig. 6) and at a global scale (Feist, 1991; Becker et al., 2016a); except in the Americas where no phacopid are reported (Chlupáč, 1975; Lerosey-Aubril and Feist, 2012; Crônier and François, 2014) and in the Central Asian Orogenic Belt where phacopids have well-developed eyes (Crônier et al., 2020). A new turnover occurred during the late Famennian (Crônier et al., 2013) and the late

Famennian Dasberg Event witnessed a major diversification of both phacopids and proetids at the global scale (Lerosey-Aubril and Feist, 2012). Phacopids originated and diversified in the deeper offshore environments and were mostly blind or reduced-eyed, reflecting the ultimate evolutionary step of the visual complex regression leading to blindness. On the shallow carbonate platforms, the phacopids *Omegops*, *Rabienops*, and *Phacops sensu lato* and the proetids *Pseudowaribole* and *Perliproetus*, which were oculate taxa, were widely distributed, exhibiting a high degree of cosmopolitanism (from eastern to western of the North Peri-Gondwanan margin), except in the Americas and in Australia (Lerosey-Aubril and Feist, 2012; Crônier et al., 2013; Crônier and François, 2014). The global Hangenberg Crisis which was caused by a complex pattern of palaeoenvironmental changes (Kaiser et al., 2015) seriously impacted the diversity of pelagic and hemipelagic environments (Walliser, 1996) including trilobites. The disappearance of Phacopida strongly impoverished and several genera of Proetida including all reduced-eyed and blind taxa suggests a significant eustatic lowering (Lerosey-Aubril and Feist, 2012). The reason why the widespread phacopids died out in the neritic environments whilst the associated brachymetopids managed to survive remains unexplained (Kaiser et al., 2015).

In North Africa, the very high dominance and the low evenness (Fig. 4) show that the Kellwasser Event had an impact on the trilobite community and a few opportunistic taxa such as Cyrtosymbolinae took advantage of the extinction event and became dominant during the early Famennian (Fig. 4). Thus, the post-Kellwasser recovery marked a new step for biodiversity and occurred during the middle Famennian leading to a new turnover. A relative increase in taxonomic richness is observed for trilobites, linked to increasing origination (Fig. 7). This pattern is also observed at the global scale in trilobites (Lerosey-Aubril and Feist, 2012) and largely results of the diversification of Cyrtosymbolinae fostered by the development of shallow outer-shelf in northern Gondwanan margins (Feist, 1991; Wendt, 1993). Proetida and Phacopida remained the only trilobite component in the Famennian (Fig. 5). For proetids, of the 11 genera present in North Africa, all were new and dominated by two Cyrtosymbolinae: *Cyrtosymbolina* and *Cyrtosymbole*, which represent 100% of the proetids and 95% of all the trilobites (Fig. 8). Apart from these well-developed eye proetids, other taxa present in the Famennian were mainly blind or small eyed taxa both in North Africa (Figs. 6, 8) and at a global scale (Feist, 1991; Becker et al., 2016a). For phacopids, of the eight genera present in North Africa, seven were new and dominated by the blind *Trimerocephalus* taxa until the middle Famennian; *Trimerocephalus* represented almost 70% of the phacopid generic diversity during the middle Famennian (Fig. 8). The development of blind and reduced-eye trilobites after the Frasnian–Famennian crisis partially explain the rise of the diversity during the Famennian. Another peak of blind trilobites occurred, after their diversity decrease in the middle Famennian. Two blind phacopid genera, i.e., *Dianops* and *Trifoliops*, occurred and persisted during the late Famennian (Fig. 8). No reduced-eyed phacopid taxa has so far been encountered in North Africa (but newly sampled in the Famennian of the Saoura Valley, a work in progress). From the middle to the latest Famennian in North Africa, the reappearance of trilobites inhabiting shallow habitats (*Omegops, Phacops, Pusillabole, Osmolskabole*) in northwest Gondwana is coherent with the wide distribution of well-developed-eyed phacopids and proetids in contemporaneous shallow shoal environments (Lerosey-Aubril and Feist, 2012; Crônier and François, 2014). *Omegops*, a well-developed-eyed taxon replaced another well-developed-eyed taxon, i.e., *'Phacops'*. *Phacops* known in the Early and Middle Devonian were different from those known in the Late Devonian such as *'Phacops' granulatus* widely distributed geographically all around the world (Crônier and François, 2014). In North Africa, this diversification initiated during the Dasberg Event (late Famennian) was followed by a decrease of the diversity which led to the lower values recorded during the latest Famennian (Fig. 2). The same pattern affected the ammonoids. Throughout the Famennian, the evenness increased and the dominance decreased and tended to reach the late Frasnian values, symbol of a balanced community. Finally, at the Devonian–Carboniferous boundary, the rise of the sea-level trapped the deep sea trilobites and for this reason, blind taxa and/or outer shelf trilobites almost disappeared. Phacopida died out without leaving any Carboniferous descendants.

## 6. Conclusions

Based on a substantial compilation of published data on North African trilobites during the end of the Silurian and throughout the Devonian, the taxonomic diversity of these organisms has been accurately estimated at the genus level.

The reconstructed regional diversity follows the patterns observed at a global scale, except an important diversification in the Early Devonian (from the Lochkovian to the Emsian) in North Africa. The sharp decrease of the trilobite diversity observed through the Middle Devonian at a global scale, occurred earlier in North Africa (Eifelian) than in other localities where this important decrease was generally recorded during the Givetian. In North Africa, the diversity remained very low in the Givetian and the early Frasnian before a slight increase in the late Frasnian. Then, the well-known Kellwasser Event (one of the big five mass extinction) at the Frasnian–Famennian boundary also affected the North African trilobites with a decrease in diversity which is associated to an increasing number of extinctions. Only two orders crossed this limit: Phacopida and Proetida. Then, the trilobites recovered in the early Famennian thanks to the development of opportunistic taxa. This recovery was accompanied by morphological and habits changes. Indeed, a high fraction of blind, reduced eyes and/or deep-water trilobite genera proliferated after the Kellwasser Crisis. Afterward, another increase of diversity occurred in the late Famennian, then, the diversity decreased again, at the end of the Devonian. This decrease in diversity is followed by the occurrence of the Hangenberg Event, which led to the disappearance of the Phacopida. All these diversity fluctuations through the Devonian seems to reflect the rapid reaction of trilobites facing abrupt sea level changes and hypoxic/anoxic events. This review concerning a famous region for its trilobites highlights a lack of data for the Lochkovian, Givetian and Frasnian stages, for which more studies will help to better estimate the regional diversity of North African trilobites.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2020.110208.

## Declaration of Competing Interest

For our manuscript entitled "Trilobite biodiversity trends in the Devonian of North Africa" by Bault, Allaire, Monnet and myself that we wish to submit for publication in the Palaeogeography, Palaeoclimatology, Palaeoecology, there is no conflict of interest.

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## Supplemental figures

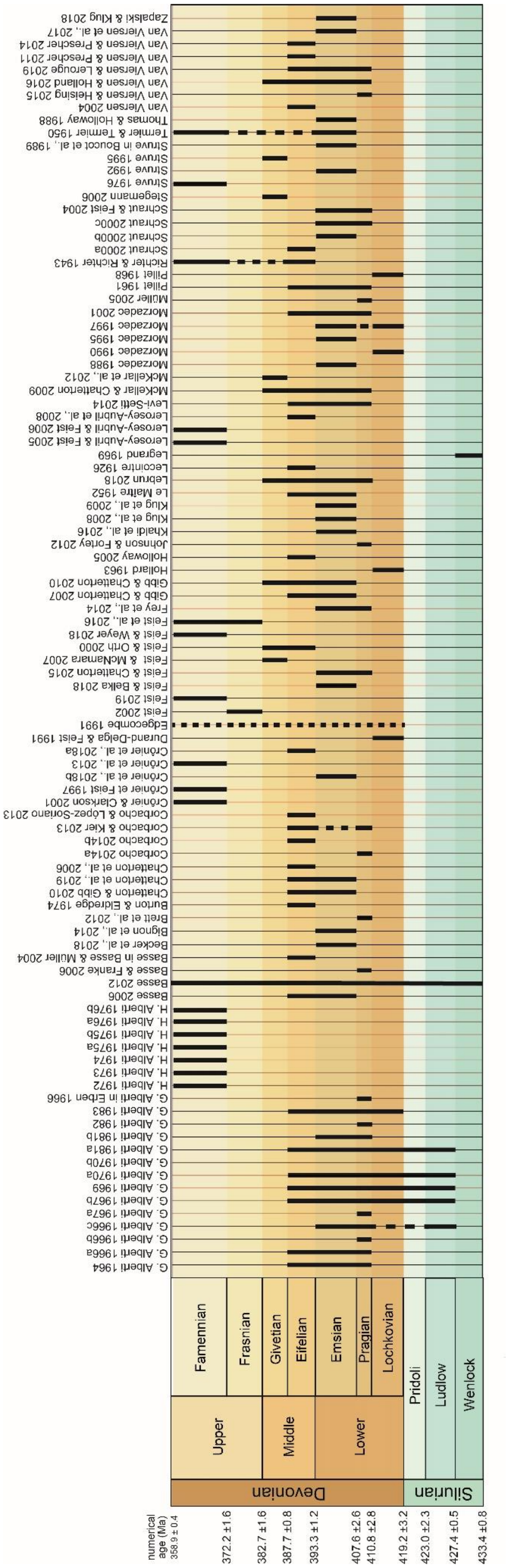

***Figure A.*** *Devonian stratigraphic scheme and stratigraphic ranges of source studies used for the diversity analyses. Ages from Cohen et al. (2013, updated).*

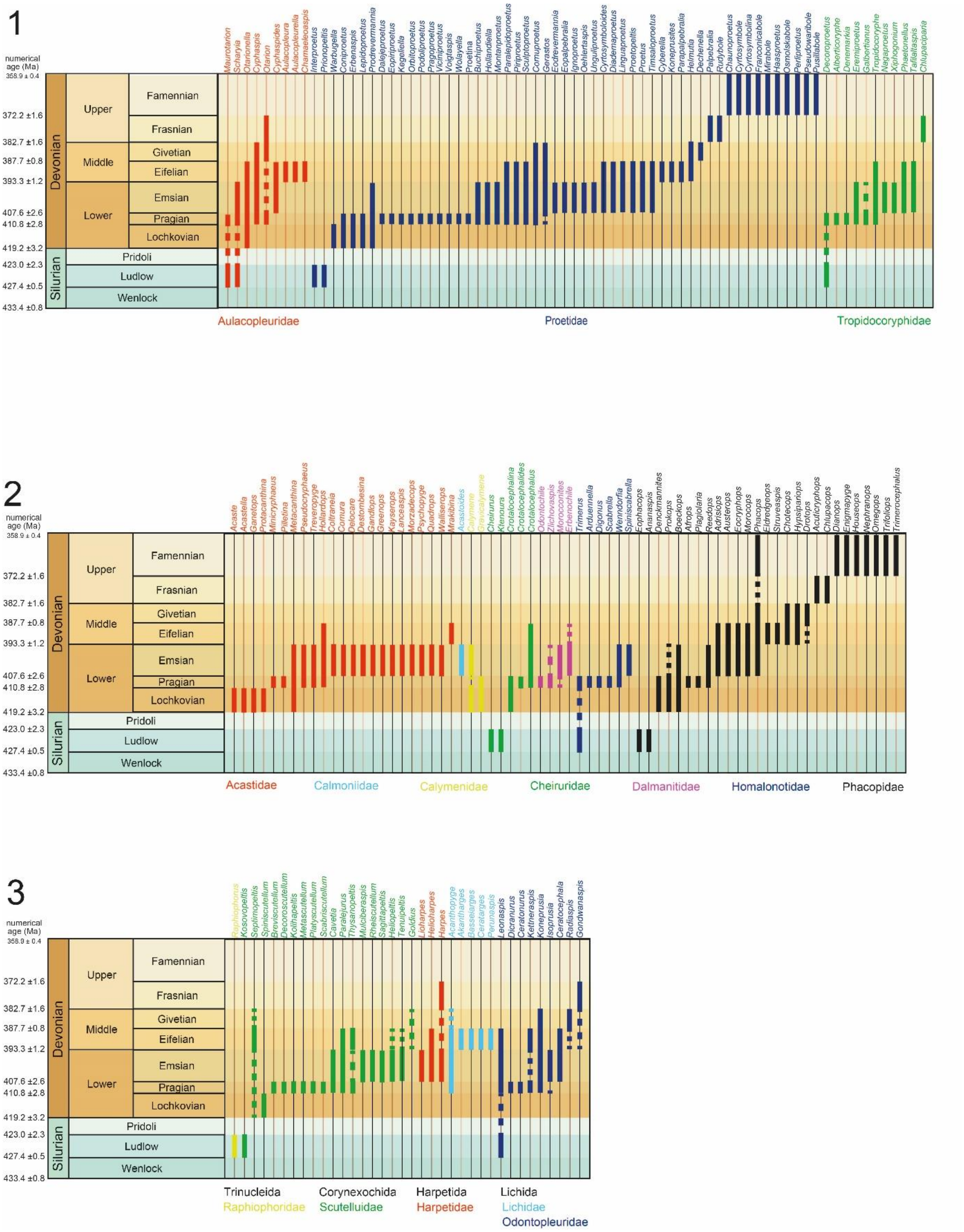

***Figure B***. *Synthetic occurrence range chart; genera are ordered by family. (1) Proetida. (2) Phacopida. (3) Other orders.*

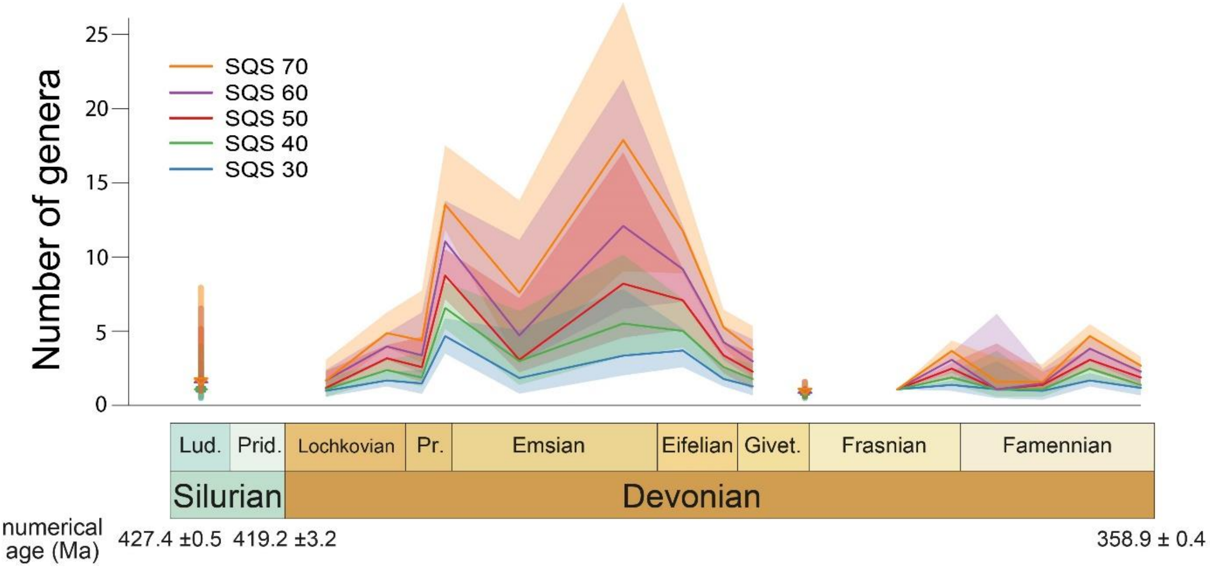

***Figure C.*** *Fluctuations of the Shareholder Quorum Subsampling (SQS) diversity of trilobites from North Africa during the Silurian and the Devonian, computed at the generic level (estimations for quorums of 30, 40, 50, 60 and 70). See text for the definition of indices. Ages from Cohen et al. (2013, updated).*

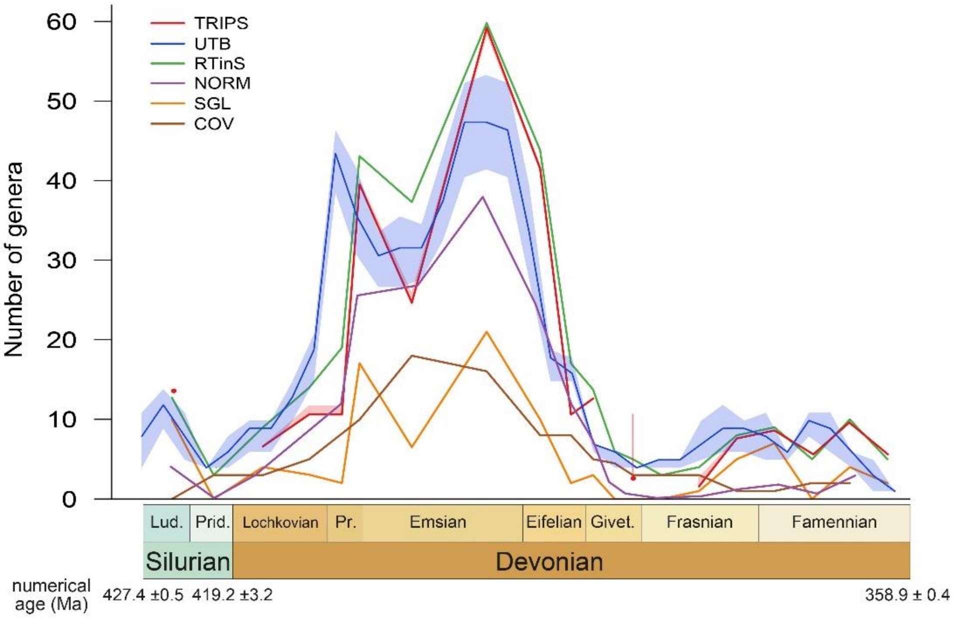

***Figure D.*** *Diversity dynamics of trilobites from North Africa during the Silurian and the Devonian. See text for the definition of indices. Diversity values, i.e., taxonomic richness at the generic level per substages. Poisson-based resampling diversity (TRiPS), computes the approach of 'true richness estimation using Poisson sampling' based on an abundance range chart and a time; Uniform time bin diversity (UTB), quantifies the length of uniform time bins to reconstruct time series by using the mean time interval duration; Range-through diversity including single-interval taxa (RTinS; aka. total diversity), estimates the diversity from counting everything that is known to occur in an interval plus everything that is inferred to be present; Normalized diversity (NORM), corresponds to the number of taxa ranging from the interval below to the interval above, plus half the number of taxa originating and/or becoming extinct within the interval, plus half of those present only to the interval itself; Single-interval diversity (SGL), corresponds to the number of single-interval taxa known from only one bin; Crossover diversity (COV), counts the number of taxa known before and after the considered stratigraphic interval. Ages from Cohen et al. (2013, updated).*

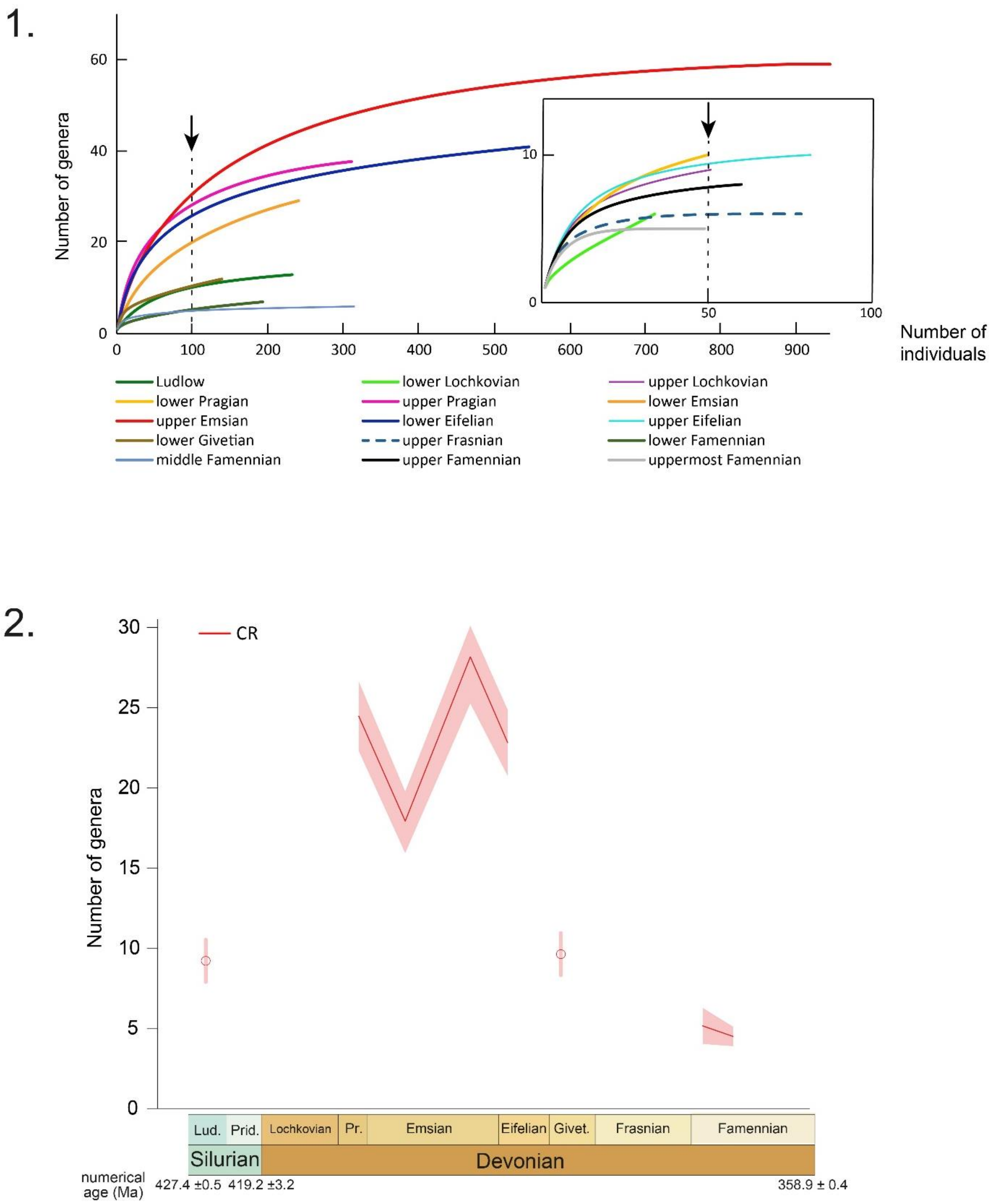

***Figure E**. Rarefaction methods. (1) Rarefaction curves per substages. Arrows indicate the comparative individual number for substages of same size (50 or 100). (2) Size-based rarefaction (CR). Ages from Cohen et al. (2013, updated).*

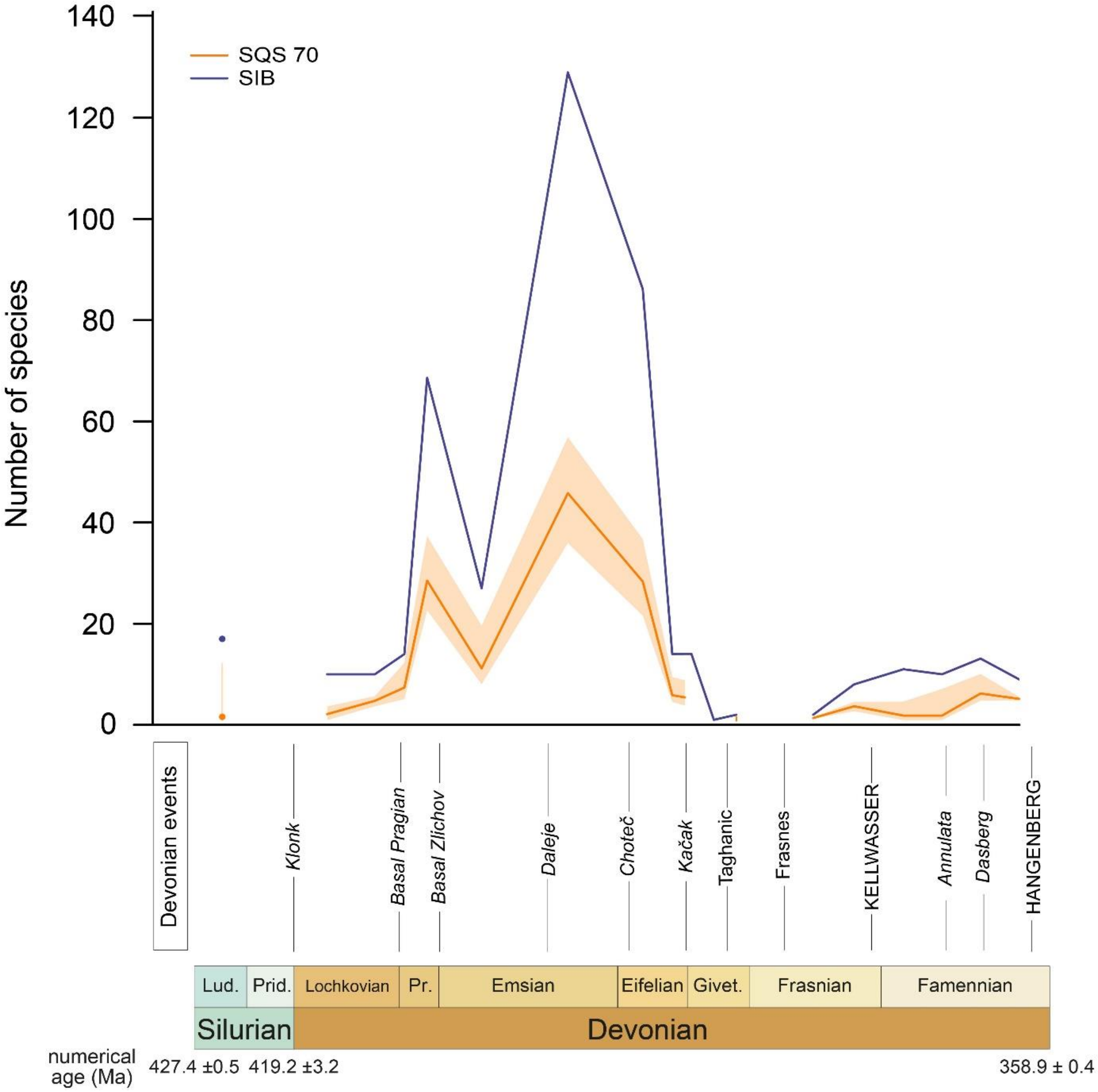

***Figure F***. *Diversity dynamics of trilobites from North Africa during the Silurian and the Devonian. See text for the definition of indices. Diversity values, i.e., taxonomic richness at the specific level per substages. Sampled-in-bin index (SIB), total count of taxa from a given stratigraphic interval; Normalized diversity (NORM), number of taxa ranging from the interval below to the interval above, plus half the number of taxa originating and/or becoming extinct within the interval, plus half of those present only to the interval itself. Stratigraphic position of the extinction events according to Becker et al. (2016b); first-order events in capital, second-order events in bold and third-order events in italic. Ages from Cohen et al. (2013, updated).*

## 2.2. Tendances de la disparité morphologique des trilobites du Dévonien d'Afrique du Nord

Article 4 : Morphological disparity trends of Devonian trilobites from North Africa

Article accepté avec revisions par Palaeontology

# MORPHOLOGICAL DISPARITY TRENDS OF DEVONIAN TRILOBITES FROM NORTH AFRICA

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## Abstract:

The Devonian was a time of drastic environmental changes that shaped the morphology of trilobites. This study aims to investigate their morphological evolution and to show the influence of some abiotic and biotic factors (bathymetry, feeding habits and visual abilities) on their shape. A dataset was compiled to investigate the shape of three structures (cephalon as a whole, cranidium and pygidium) of Devonian trilobites from North Africa, using a geometric morphometric approach. Based on empirical morphospaces, the morphological changes were quantified through the Devonian stages. The results reveal significant variation in the morphological disparity of the glabella shape, the facial suture location, the pygidial length and the presence of spines. In the Lochkovian, morphological disparity was low, but it subsequently increased in the Pragian with numerous innovations, and reached a maximum in the Emsian. If the morphospace occupancy persisted until the Eifelian, a severe loss of disparity occurred in the Givetian, a time known for important environmental changes. Disparity then remained low in the Late Devonian. The shapes inherited from the Silurian persisted throughout the Devonian whereas Pragian novelties were most affected by morphological losses. These persistent shapes were more versatile for environmental adaptation, helping those trilobites to survive environmental events. Similarly, the trilobite orders that survived Devonian events had a wide morphological spectrum and were better adapted to withstand environmental change.

**Key words:** Trilobites, North Africa, Devonian, Morphological disparity, Morphometrics, Evolution, environmental changes

## INTRODUCTION

Appearing as early as the Cambrian Explosion, trilobites diversified quickly to reach their maximum diversity at the end of the Cambrian (Westrop & Aldrain 1998) and then underwent an irregular decline until the end of the Permian (Sepkoski & Sheehan 1983; Foote 1993; Fan *et al*. 2020). Especially, the Devonian marked an important step of this decline. Despite an important diversity increase in the Early Devonian, a protracted decrease at all taxonomic ranks (family, genus, species) occurred during the Middle Devonian up to the disappearance of three of the five orders (i.e., Odontopleurida, Harpetida and Corynexochida using Adrain (2011) classification updated by Lamsdell & Selden (2015) concerning the superfamily Aulacopleuroidea) in the Late Devonian during the Kellwasser events (Feist 1991; Chlupáč 1994; Crônier & vanViersen 2007; Lerosey-Aubril & Feist 2012; Bault *et al*. 2021). In addition to these diversity losses, the visual abilities and the life environments were modified in trilobites, and especially after the Frasnian/Famennian boundary (Chlupáč 1994; Lerosey-Aubril & Feist 2012). Therefore, the Devonian is a critical period in the evolutionary history of trilobites. This interval of time is also well known to record major biotic and abiotic changes, such as the Devonian Nekton Revolution (Klug *et al.* 2010), the development of vascular land plants (Pawlik *et al.* 2020), exceptional sea-level highstands, widespread epicontinental shallow seas, greenhouse climates (Tinn *et al.* 2020) and several anoxic/hypoxic events and rapid sea level fluctuations (House 2002; Becker *et al.* 2016).

Another important morphological indicator of evolutionary success or failure is disparity, as measured by the occupancy of a morphospace (Foote 1997; Wills 2001; Erwin 2007, Minelli 2016, Guillerme *et al.* 2020). Success in diversity does not necessarily go together with success in disparity. Many taxa show high diversity with low disparity, while others are highly diverse but also exhibit high disparity (Minelli 2016). Taxonomic richness and morphological disparity are two complementary metrics, which can be decoupled (Foote 1991a, 1991b, 1993). Such decoupled changes in taxonomic diversity and morphological disparity can suggest different proxies for understanding the ecological effect of an extinction event for example (Wan *et al.* 2021). Morphological disparity of trilobites has been extensively documented in the Cambrian and the Ordovician (Foote 1991a; Smith & Lieberman 1999; Webster 2007; Hopkins 2013; Jacobs & Carlucci 2019). On the contrary, Devonian studies are rare and often dedicated to developmental and ontogenetic topics exploring the intrinsic factors of morphological changes (e.g. Crônier *et al.* 1998; Crônier 2013; Oudot *et al.* 2019). However, if biotic and abiotic factors are known to contribute to diversification, they also contributed to the morphological disparity (Crônier *et al.* 2004; Hopkins & Gerber 2017). Some relationships have been noticed or demonstrated between trilobite shapes and ecological affinities such as bathymetric conditions (Hopkins 2014), feeding habits (Fortey & Owens 1999) or life habits (Fortey 2014). Although the environmental influence on morphological disparity was rarely evaluated, Hopkins (2014) emphasized the effect of bathymetry, substrate and latitude on the trilobite shape for the entire Palaeozoic. As the result of these environmental effects, morphological disparity can be dependant of the geographical location of populations through time (Hopkins & Webster 2009; Abe & Liebermann 2012; Esteve *et al.* 2017). These recent studies have been done at the global or focusing on only one family. Nevertheless, for Devonian trilobites, no studies have been performed on the total richness available throughout a span time for a relatively well-constrained area.

During the Devonian, the environmental and ecological changes were particularly well exhibited in North Africa wherein trilobites were especially well represented and diverse (Lebrun 2018; Bault *et al*. 2021). This area is one of the richest in terms of Devonian trilobites with five orders and 15 families (Bault *et al*. 2021), corresponding to all known worldwide Devonian orders and the majority of families (Crônier & van Viersen 2007). In addition to its fossil record, this area is also particularly well known for its stratigraphy and its palaeoenvironmental context (Massa 1965; Hollard 1967; Wendt & Belka 1991; Becker *et al*. 2004; Abbache *et al*. 2019; among others). It allows establishing the relationship between the trilobites characterized by their shape and their habits and their palaeoenvironmental affinities. Moreover, the Devonian events were all spotted in this area (Kaufmann 1998).

In the context of a period of diversity changes (Bault *et al*. 2021), analysing the morphological changes through time for a relatively well-constrained area, helps to better understand the impact of the Devonian biological events on benthic faunas. We focused our investigations on the Devonian trilobites gathered from the North African area. To understand the fluctuations in time and space, the disparity patterns are assessed through morphological space in a stratigraphic and palaeoenvironmental framework. First, we investigated the evolution of the trilobite morphospace to identify the different morphotypes and to explore the presence of evolutionary key innovations in lineages for each stage. Then, we investigated how the morphological shape may be linked to different palaeoenvironmental and/or palaeoecological factors (such as bathymetry, feeding habits and visual ability) and detecting which factors contribute most to the observed patterns.

## MATERIAL AND METHODS

### *Trilobite data and frameworks*

We compiled a dataset to investigate the morphology of Silurian and Devonian trilobites from Morocco and Algeria (Fig. 1). This area was situated on the continental margin of the Gondwana at a latitude between 30° and 45°S (Scotese & Golonka 1992; Golonka 2002). It was a favourable place for the settlement of benthic communities such as trilobites (Morzadec 2001; McKellar & Chatterton 2009). All figures of specimens illustrated over the last 80 years with a sufficient quality have been exploited for shape analyses (Appendix S1). Morphology of trilobites is here quantified by focusing on their most important structures, i.e., cephala, cranidia and pygidia (Fig. 2). The cranidium is a subset of the cephalon, which is actually composed by

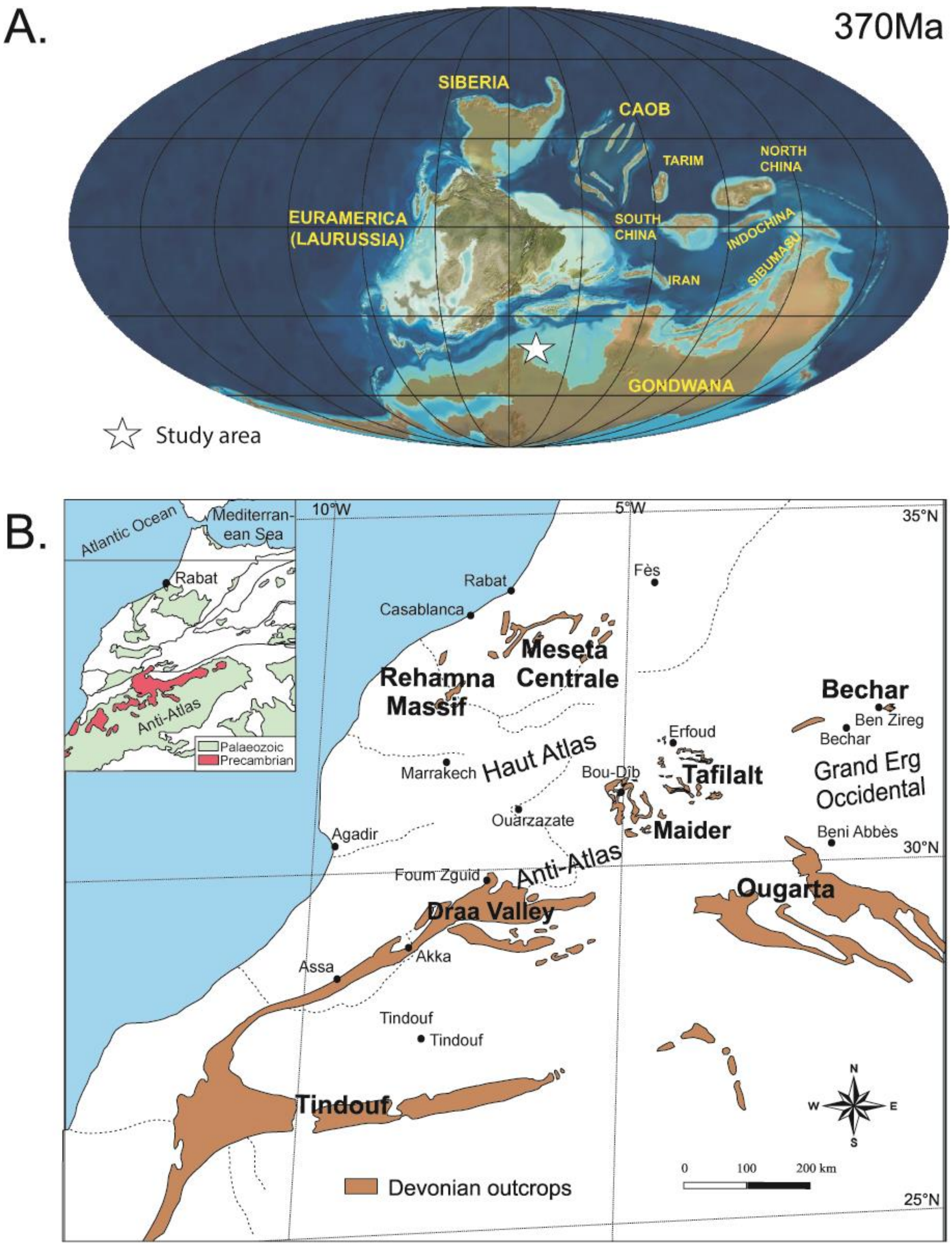


***Figure 1***. *(A) Location of Morocco and Algeria (white star) on a palinspastic map (modified from Blakey (2016), with continent positions and shapes for the Upper Devonian modified from the tectonic data of Hara et al. (2010), Metcalfe (2011), and Xiao et al. (2010). (B) Geographical location of studied area with the Devonian outcrops (in bold; modified from Hollard 1968).*

two modules: the cranidium (fixigena) and the free cheeks (librigena). For morphological analyses the cephalon is studied as a whole, including the cranidium landmarks.

A first dataset contains 328 complete cephala, 959 complete cranidia and 605 complete pygidia; each structure being studied independently. This dataset includes all well-preserved and illustrated specimens during the last 80 years from 65 publications (Appendix S2). Only dorsal views were used and the right-side from each structure was selected except if the left-side was more completed; mirror images were used to correspond to the right side. A second dataset contains 30 complete specimens of 30 different species for which both the cephalon and the pygidium were simultaneously preserved.

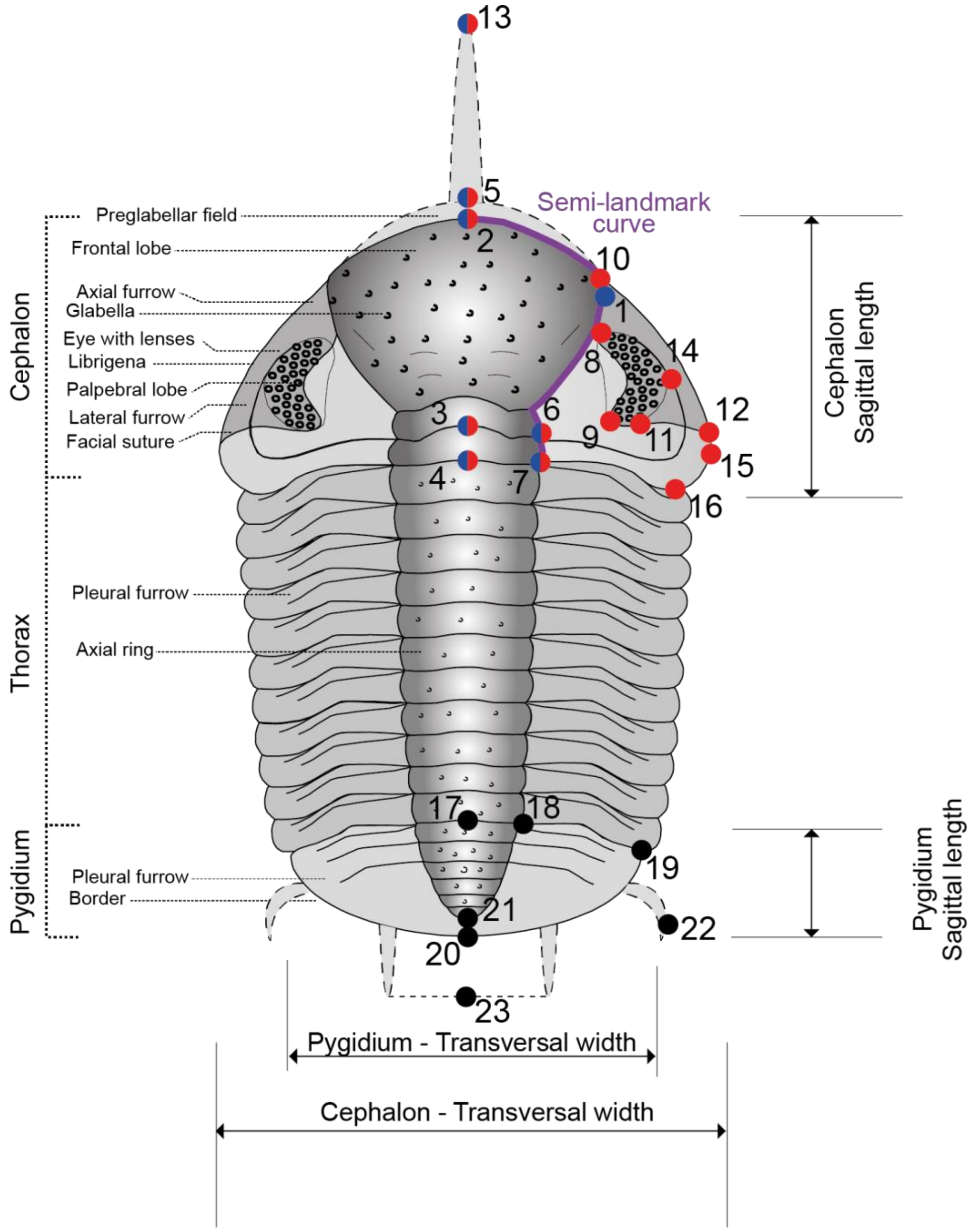


***Figure 2**. Complete chimeric exoskeleton of trilobite in dorsal view exhibiting eight landmarks for cephalon (in red), plus eight for cranidium (in blue), and seven for pygidium; and some linear measurements. Modified from Crônier (2013).*

For each specimen, taxonomy, age (stage) as well as ecological characteristics were also included in the dataset. Firstly, genera were classified by environmental affinities, i.e., by water depth conditions (Fortey 1975; Turvey 2005; Crônier & vanViersen 2007). Bathymetrical affinity for each genus was determined as the environment where it mainly occurred. Because these data were not available for each occurrence, we interpolated it with the data from other papers with the same stratigraphic context or from genera with the same affinity. Four categories are identified along the bathymetric profile: (1) the shoreface environment characterized by shallow and proximal conditions; (2) the upper offshore or inner shelf environment characterized by relatively shallow waters; (3) the median offshore or middle shelf environment characterized by relatively deep deposits; and (4) the lower offshore or outer shelf environment located below effective storm wave base. It is important to note that depth categories were based on sedimentological evidence and not from trilobite shapes to avoid analysis biases.

Secondly, genera were classified by their diet. We referred to Fortey and Owens (1999) to determine the feeding habits of genera based on hypostome features. Three diet categories are recognized in our database: 'Predator/Scavenger', which ingested small prey, 'Particle feeding', which fed on nutrients and 'Filter chamber', which brought sedimentary material into suspension before selecting out edible particles (Fortey & Owens 1999). It should be noted that the estimates of feeding habits are only assumptions and the evidence in the fossil record is rare. For instance, only two examples confirmed as particle feeders are known (Zhu *et al*. 2014; Gutiérrez-Marco *et al.* 2017). Feeding habits are still an ongoing debate and advances in biomechanics (Bicknell *et al*. 2018, 2021) will help refine the trilobite diets.

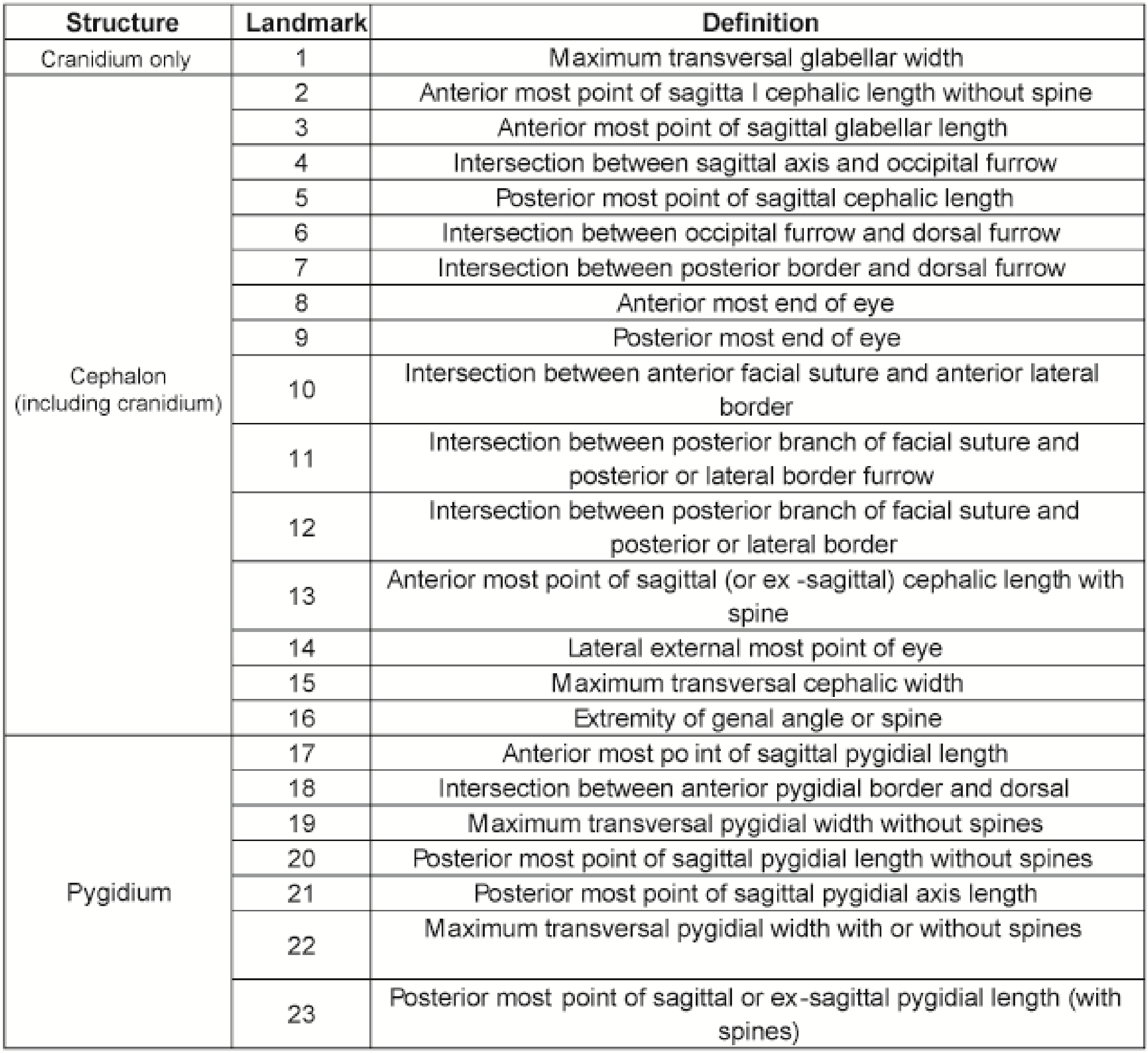
Third, genera were classified by their eyes, preserved as calcite lenses on a visual surface (Clarkson *et al.* 2006). Each taxon has been assigned to one of the three categories: blind, reduced-eye, or well-developed-eye. The diagnostic features related to the eye size or to the number of lenses were considered to establish these categories. In trilobites, the visual ability has often been linked to environment or life habits (Clarkson 1967; Feist 1991). For this last analysis, blind cephala were not considered because of the lack of three landmarks (i.e., landmarks 8, 9 and 14; Fig. 2).

### *Landmark data*

The 2D shape of studied trilobites is here quantified by a geometric morphometric approach, which is now a standard set of techniques for quantifying shape independently of size by using homologous points (landmarks) on the surface of a series of objects (Bookstein 1991; Rohlf &

Marcus 1993; Rohlf 1999; Adams *et al*. 2004, 2013; Mitteroecker & Gunz 2009; Zelditch *et al*. 2012). This method preserves the geometry of the landmark configurations throughout the analysis and thus permits representation of analytical results as actual shapes or forms. It is routinely used in biological and palaeontological studies.

The shape of cephala is here described by a set of 15 landmarks and one curve of 24 equally spaced semilandmarks between landmark 2 and landmark 7 (Fig. 2, Table 1). For cranidia (i.e., cephala without free cheeks), seven landmarks plus the semi-landmark curve have been digitized (Fig. 2, Table 1). Similarly, seven landmarks were digitized for pygidia (Fig. 2, Table 1). Landmarks were positioned in key locations to summarize the complexity of morphologies. The semi-landmarks were used as landmarks and were not transformed into a curve. Specimens with missing landmarks were excluded. The *x*- and *y*- coordinates of 2D landmarks and semilandmarks were digitized (Fig. 2) with TPSdig 2.32 (Rohlf 2010, 2015). The landmark 2D coordinates were then exported in the standard TPS file format (Rohlf 2012).



| Structure | Landmark | Definition |
|---|---|---|
| Cranidium only | 1 | Maximum transversal glabellar width |
| Cephalon (including cranidium) | 2 | Anterior most point of sagitta l cephalic length without spine |
| | 3 | Anterior most point of sagittal glabellar length |
| | 4 | Intersection between sagittal axis and occipital furrow |
| | 5 | Posterior most point of sagittal cephalic length |
| | 6 | Intersection between occipital furrow and dorsal furrow |
| | 7 | Intersection between posterior border and dorsal furrow |
| | 8 | Anterior most end of eye |
| | 9 | Posterior most end of eye |
| | 10 | Intersection between anterior facial suture and anterior lateral border |
| | 11 | Intersection between posterior branch of facial suture and posterior or lateral border furrow |
| | 12 | Intersection between posterior branch of facial suture and posterior or lateral border |
| | 13 | Anterior most point of sagittal (or ex -sagittal) cephalic length with spine |
| | 14 | Lateral external most point of eye |
| | 15 | Maximum transversal cephalic width |
| | 16 | Extremity of genal angle or spine |
| Pygidium | 17 | Anterior most po int of sagittal pygidial length |
| | 18 | Intersection between anterior pygidial border and dorsal |
| | 19 | Maximum transversal pygidial width without spines |
| | 20 | Posterior most point of sagittal pygidial length without spines |
| | 21 | Posterior most point of sagittal pygidial axis length |
| | 22 | Maximum transversal pygidial width with or without spines |
| | 23 | Posterior most point of sagittal or ex-sagittal pygidial length (with spines) |

***Table 1***. *Description of landmarks.*

Because we analysed specimens from different lineages, shapes can be different with extreme landmark locations and thus, geometric morphometric methods could not be applied (Zelditch *et al*. 2012). In our case this issue concerns only the cephala where landmarks 10, 11 and 12 can exhibit topological changes compared to relative position to other landmarks (Fig. 2, Table 1). The Pinocchio effect (Chapman 1990; Thulman 2019) can also affect landmarks 13 and 16 (Fig. 2, Table 1). In order to assess the impact of these issues, we removed them to see if the morphospace is affected by these *biases* or not. We also performed a correlation circle of landmarks to identify if some of them strongly affected the morphospace, emphasizing a topological issue rather than a morphological pattern. Our morphospaces are not determining by topological issues or a Pinocchio effect: the potential problematic landmarks (11, 12, 13, and 16) due to their extreme location among individuals did not influence the morphospace more than the other landmarks (Fig. S1).

### *Shape analyses*

Standardization of the landmark data (superimposition) to remove variability due to differences of size, placement, and orientation was performed by means of a generalized Procrustes analysis (GPA), which minimizes the sum of square distances between equivalent landmarks (Gower 1975; Rohlf & Slice 1990; Bookstein 1991; O'Higgins 2000; Zelditch *et al*. 2012). The superimposed landmarks are projected to a linear tangent space at the full Procrustes mean (Rohlf 1999; Kendall 1984).

For each of the three studied structures (i.e., cephala, cranidia and pygidia), we performed a principal components analysis (PCA; Ringnér 2008; Abdi & Williams 2010) to reduce the high-dimensionality of the superimposed landmarks to fewer variables (eigenvectors), along which the shape variation is maximal. Each specimen can be represented by relatively few variables and can be plotted in a PCA-space (morphospace) defined by principal component axes (PCs), which are ordered by decreasing percentage of the total shape variance. The morphospace is centred on the average shape (consensus) and where each point represents a specimen shape and its position reflects the relative shape similarities and differences between specimens. Finally, among the studied specimens, series of virtual shapes were reconstructed by doing a back transformation from the PC scores for PC1 and PC2 to illustrate the largest shape changes over the morphospace. Shape analyses have been computed with the R scientific environment (v. 3.6.2; R Core Team 2019; https://cran.r-project.org/) and the packages 'geomorph' (v. 3.2.1; Adams & Otárola-Castillo 2013) and 'epaleo' (v. 0.8.41; Monnet, unpub.), as well as the software PAST (version 3.24; Hammer *et al*. 2001). Figures from R outputs.

To identify some morphological clusters or morphotypes (Fig. S2), we performed a Hierarchical Cluster Analysis (HCA) with the package ‘epaleo’ on the Principal Component scores by using the Euclidean distance measure and Ward’s linkage algorithm. See Everitt *et al*. (2011) or Murtagh & Contreras (2012) for more details on methods.

*Morphospace analyses*

Morphospaces were established for the complete data set of all specimens independently for cephala, cranidia and pygidia. They were explored to evaluate the morphospace occupation first by the previously defined morphotypes, and then by the orders (using Adrain (2011) classification updated by Lamsdell & Selden (2015) concerning Proetida). Moreover, to investigate trilobite shape changes through time, individuals for each structure were categorized by stages on their respective morphospace. This allows visualizing how the different groups are distributed in the morphospace, to identify which morphotypes or orders are impacted by morphological changes and how, and to identify key morphologies among trilobites for a given stage for a successful diversification or disappearance.

Additionally, the morphospace was explored according to the inference of the potential influence on morphospace variation of three different factors related to life modes known to be changing with Devonian events: bathymetry, feeding habits and visual ability (Chlupáč 1994; Lerosey-Aubril & Feist 2012). Effect of eye reduction was investigated for all the structures, including those without eyes (i.e. cranidium and pygidium). This analysis was done by mapping each factor of each individual onto the morphospace. We computed a one-side nonparametric, permutational ANOVA on the PC axes to test statistically if a shape difference exists according to these three palaeoenvironmental and palaeoecological different factors (i.e., bathymetry, feeding habits and visual ability). Procrustes ANOVA with permutation procedures are performed using the Wilks’lambda test to quantify the amount of shape variation allocated to factors in a linear model and to estimate the probability of this variation for a null model (Collyer & Adams 2018). Statistical analyses based on PCA axes are advocated instead of original Procrustes coordinates because the scores of each axis are uncorrelated and the number of dimensions corresponds to the degree of freedom (Rohlf 1993; Polly 2017). Then, to assess how the shape is distributed according to these factors, we highlighted the different categories of our factors on PCA. Morphospace analyses have been also computed with R 3.6.2 and PAST 3.24.

## RESULTS

### *Global morphological space*

For cephala, the PCA yields 78 principal components (PCs), five of which explained 84.2% of the variance in shape of the studied trilobites: PC1, 48.7%; PC2, 15.2%; PC3, 11.6%; PC4, 4.6%; and PC5, 4.1%. The remaining components accounted for less than 4% each. The morphological interpretation of the shape changes associated with PC1 and PC2 is depicted by overlying reconstructed shapes at various locations of the morphospace (Fig. 3A). PC1 depicts the presence or absence of genal spines and a sagittal spine, the shape change of the glabella and the postero-lateral position (i.e., opistoparian, proparian or gonatoparian; Fig. 2) of the facial suture. Negative scores of PC1 show the presence of long genal or sagittal spines, a wide transversal (tr.) glabella at its base and an opistoparian facial suture with its terminal end to the posterior border (Fig. 3A). At the opposite, positive scores of PC1 show cephala without spines, a wide (tr.) glabella at the frontal lobe and a proparian facial suture with its terminal end to the lateral border. PC2 depicts the presence or absence of spines and the postero-lateral position of the facial suture too (Fig. 3A). However, the main shape change seems to be depicted by the shape of the occipital ring. High scores of PC2 show a wide (tr.) occipital ring, while low scores of PC2 show a narrow (tr.) occipital ring. PC3 contrasts two different morphologies with spines (Fig. S3A). Negative scores of PC3 show a long sagittal spine without a genal spine, while positive scores of PC3 show genal spines without a sagittal spine. Finally, positive scores of PC4 indicate a narrow (tr.) librigena, while negative scores show a wide (tr.) librigena.

The set of individuals are grouped into five morphotypes, along the first two principal component axes, with only few individuals between them (Fig. S2A, Fig. 3A). HCA shows five main morphologies corresponding to five main morphotypes (Fig. S2). The most common shapes are depicted by positive PC1 and null PC2 scores (Fig. 3A). These shapes assigned to Morphotype 1 (MCp1) correspond to cephala without sagittal and genal spines, with a wide frontal lobe (tr.) and a proparian facial suture (Fig. 3A). MCp1 spread to similar glabellar shape and facial suture position but with presence of genal spines, i.e., MCp3, and of a sagittal spine, i.e., MCp2, depicted by negative PC1 and PC2 scores. Other morphologies are depicted by slightly positive PC1 and PC2 scores (i.e., MCp5) to negative PC1 and positive PC2 scores (i.e., MCp4). These two morphotypes 4 and 5 correspond to cephala with a proparian or opistoparian facial suture, with a frontal lobe narrower (tr.) than in the other morphotypes, such as the basal part of the glabella is wider (tr.). The main difference between MCp4 and MCp5 is

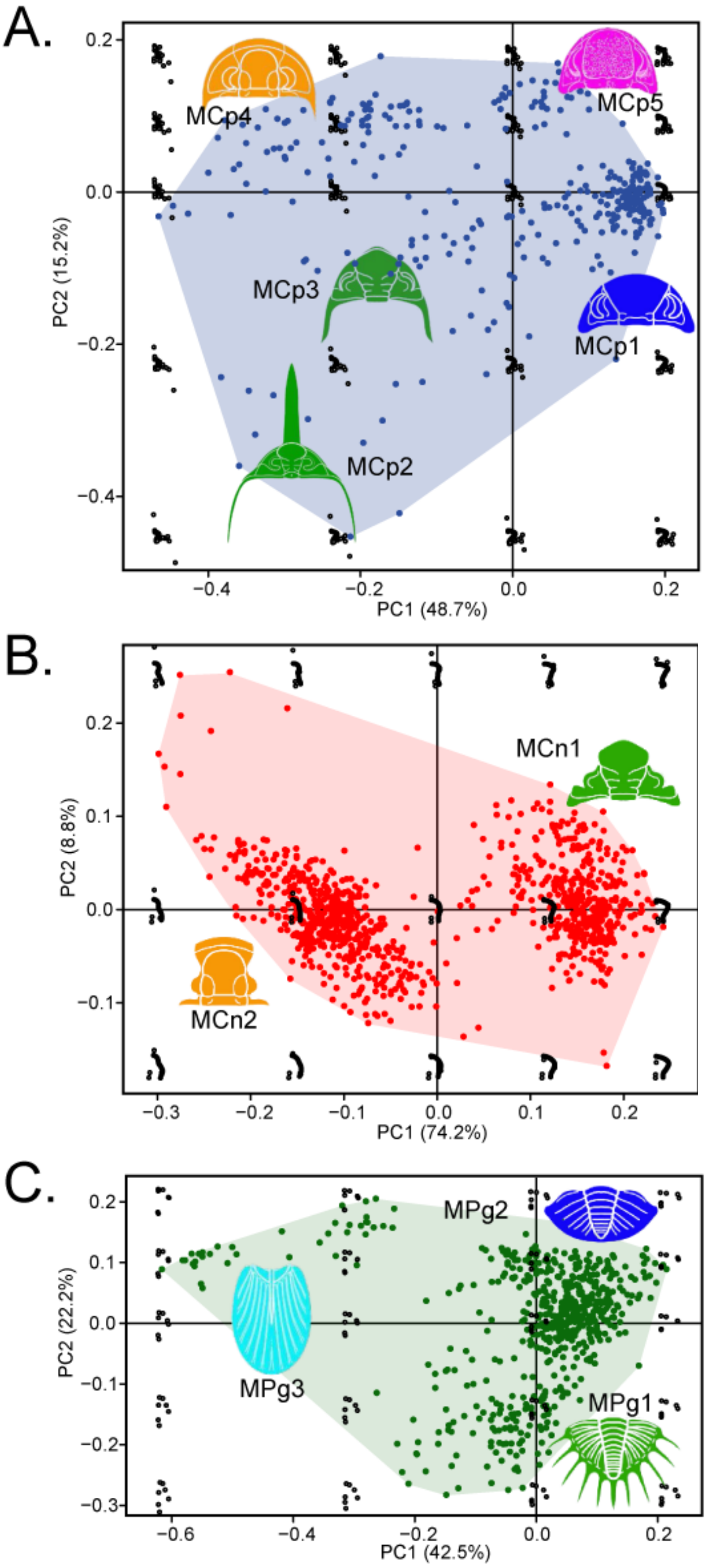


***Figure 3****. Location of: A, 328 cephala; B, 959 cranidia; and C, 605 pygidia from the Devonian of North Africa in the global morphospace defined according to the two first principal component axes performed on Procrustes residuals. Black dots represent the reconstructed virtual shape, see Fig. S8 for more details. Coloured representative morphotypes are displayed.*

the presence of genal spines in MCp4. For all types of glabella (i.e., wide or narrow frontal lobe (tr.), MCp1 and MCp5), cephala can exhibit spines but it requires narrower (tr.) glabellar furrows without an inflated frontal lobe (Morphotypes 2, 3 and 4).

For cranidia, the PCA yields 62 PCs, two of which explained 83% of the variance in shape of the studied trilobites: PC1, 74.2%; PC2, 8.8%. The remaining components accounted for less than 6% each. PC1 depicts the variation in glabellar shape. Positive PC1 scores depict individuals with a wide (tr.) frontal lobe compared to the glabellar base and without a preglabellar field anteriorly (Fig. 3B). Negative PC1 scores depict individuals with wide (tr.) preoccipital and occipital rings and with a preglabellar field (Fig. 3B). Rare intermediate shapes show a frontal lobe just slightly wider (tr.) than the glabellar base. Shapes with very narrow (tr.) or very wide (tr.) occipital and preoccipital rings do not exist. PC2 depicts the presence or absence of a preglabellar field and the width (tr.) of glabellar lobes.

The set of individuals are grouped into two morphotypes (MCn1 and MCn2; Fig. S2B), mainly along the first principal component axis PC1 (Fig. 3B). Positive PC1 and null PC2 scores depict a common shape (Fig. 3B). This shape assigned to MCn1 corresponds to cranidia with a wide (tr.) frontal lobe compared to the glabellar base and without a preglabellar field anteriorly (Fig. 3B). Negative PC1 and null PC2 scores depict another common shape (Fig. 3B). This shape assigned to MCn2 corresponds to cranidia with wide (tr.) preoccipital and occipital rings and with a preglabellar field (Fig. 3B).

For pygidia, the PCA yields 14 PCs, four of which explained 89.9% of the variance in shape of the studied trilobites: PC1, 42.5%; PC2, 22.2%; PC3, 14.2%, and PC4, 11.0%. The remaining components accounted for less than 5% each. PC1 (Fig. 3C) shows that the main shape change contrasts narrow (tr.) pygidia (negative scores) to wide (tr.) pygidia (positive scores). PC2 depicts the sagittal (sag.) length of the pygidial axis, PC3 depicts the presence of lateral and sagittal spines and PC4 depicts the curve of the pygidial border (Fig. S3B). Along PC3 and PC4, most of the shapes show individuals with no spines. Only a few individuals located in the negative PC3 scores have small pygidial spines. These pygidial spines are generally short and never longer (sag.) than the pygidium itself. Positive scores on PC4 indicate a maximal (tr.) length below the anterior most point of sagittal pygidial length and conversely negative scores indicate a maximal (tr.) length above the anterior most point of sagittal pygidial length (Fig. S3B). No pygidia are present in the area of the morphospace that depicts pygidia with a very narrow (tr.) and a long (sag.) pygidial axis (i.e., negative PC1 and PC2 scores).

The set of individuals are grouped into three morphotypes (Fig. S2C). The most common shapes assigned to MPg1 and MPg2 are depicted by rather null scores of PC1 (Fig. 3C). These shapes correspond to pygidia with a medium size and with either a long (i.e., MPg1) or a medium length of the pygidial axis (i.e., MPg2). MPg3 is depicted by negative PC1 and positive PC2 scores (Fig. 3C). The shapes associated with this cluster correspond to pygidia with a narrow (tr.) and a short (sag.) axis (i.e., MPg3).

### *Morphospace occupation by time*

The changes in occupancy/filling of the morphospaces (i.e., the morphological disparity) through time are illustrated in figure 4 for the three structures. For cephala, the morphological space was characterized by a reduced occupation from the Ludlow to the Lochkovian, followed by widespread occupation in the second part of the Early Devonian. During the Ludlow, the filling of morphological space was narrow (Fig. 4A) and was restricted to MCp1 and MCp5. The location of morphotypes through time is given in figure S4A. Then, morphological disparity remained reduced in the Lochkovian and restricted to only one cephalon assigned to a new morphotype (i.e., MCp4) in the early Lochkovian and three cephala to MCp1 in the late Lochkovian. After this low disparity period, the disparity in the Pragian covered almost all the morphospace, with the only exception of some cephala with sagittal spines i.e., MCp2 (Fig. 4A, Fig. S4A). This morphology appeared during the Emsian when the morphospace reached its maximal coverage.

The transition to the Middle Devonian (Fig. 4A, Fig. S4A) did not coincide with an important loss of morphological disparity for the cranidium and the pygidium but the cephalon was more affected with the disappearance of MCp2. Only cephala characterized by low PC2 scores disappeared. These cephala exhibit sagittal spines. However, morphotypes 2, 3 and 4 disappeared from North Africa in the late Eifelian (Fig. 4A, Fig. S4A). These morphotypes correspond to cephala with spines. Although MCp1 and MCp5 were maintained in the early Givetian, MCp1 disappeared in the middle Givetian and MCp5 in the late Givetian. In the Late Devonian, only MCp1 reappeared.

As for cephala, the morphospace occupation for cranidia was narrow from the Ludlow to the Lochkovian, but largely extended during the Pragian toward shapes with wide sagittal (sag.) preglabellar field and wide (tr.) occipital ring. The morphospace occupation remained constant during the Emsian and the Eifelian but collapsed during the Givetian (Fig. 4B, Fig. S4B ). This collapse concerned both density and expansion, with the disappearance of shapes with a wide (tr.) frontal lobe in both morphotypes. This disappearance led to a morphospace occupation comparable to the Lochkovian one. During the Frasnian, the morphological expansion increased to specimens with a wide (sag.) preglabellar field and a wide (tr.) occipital ring despite the decrease of specimen density. Finally, the morphospace collapsed again during the Famennian to achieve a similar morphospace occupation as the Lochkovian or the Givetian (Fig. 4B, Fig. S4B).

As for cephala and cranidia, the morphological space for pygidia was characterized by a broad occupation of shapes during the late Early Devonian (Fig. 4C, Fig. S4C). From the

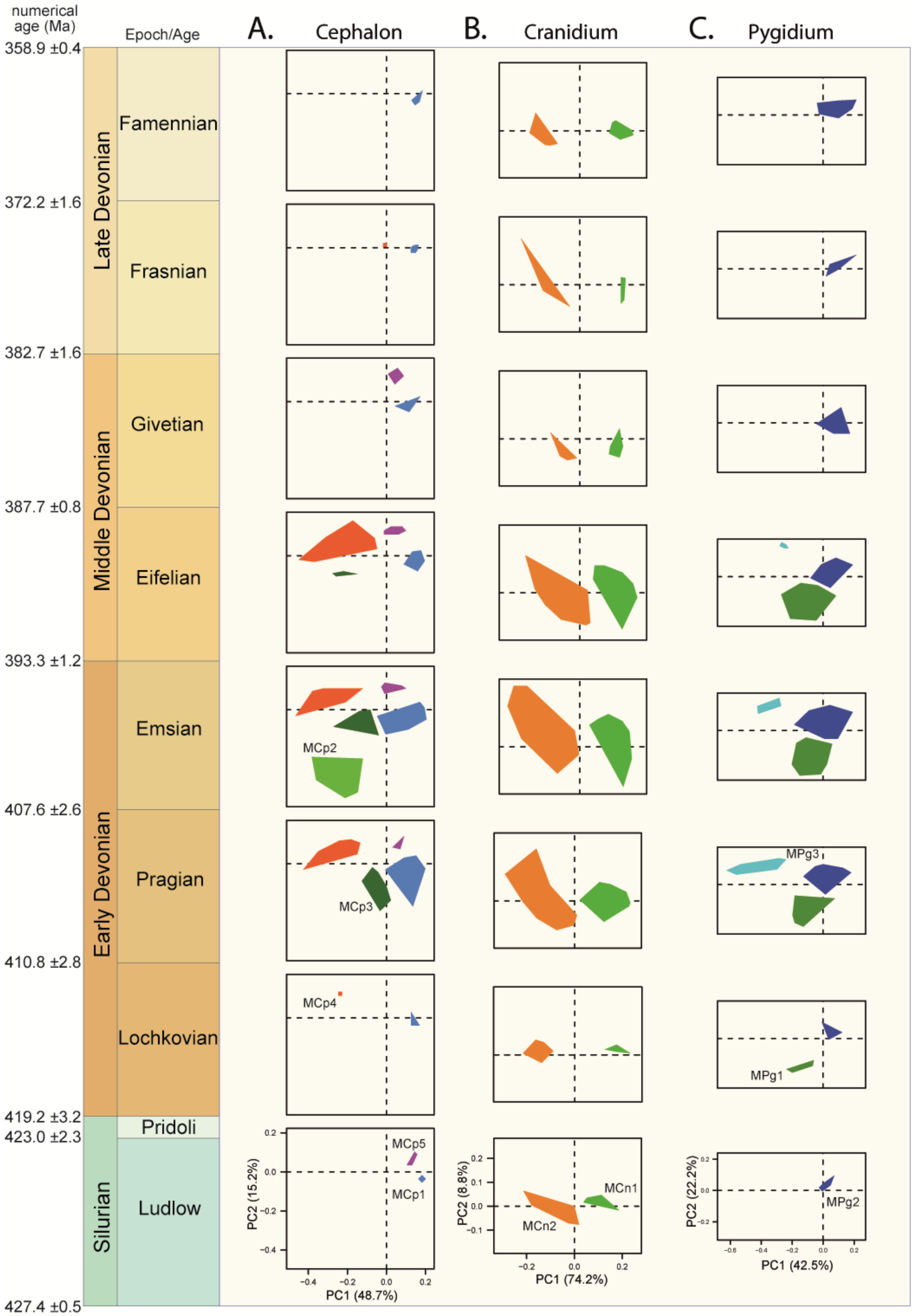


***Figure 4***. *Location of the morphotypes of: A, cephala; B, cranidia; and C, pygidia from the Devonian of North Africa in the global morphospace defined according to the two first principal component axes performed on Procrustes residuals, represented for each Devonian stage. Coloured morphotypes according to Figure 3. Ages from Cohen et al. (2013, updated with the version of 3/2020).*

Ludlow to the Lochkovian, the morphological space slightly increased by the appearance of MPg1 which is characterized by a long (sag.) pygidial axis (Fig. 4C, Fig. S4C). After this low disparity period, the morphological space reached a maximal occupation by maintaining the previous morphologies but also by developing a new one, i.e., MPg3 (negative PC1 scores) with narrow (tr.) pygidia from the Pragian to the Emsian (Fig. 4C, Fig. S4C). In this morphological space, MPg1 with a long (sag.) pygidial axis developed but without co-occurring with pygidia with a long (sag.) axis and a narrow (tr.) outline. Morphologies with spines and a curved pygidial border were also developed (negatives PC3 and PC4 scores). Narrowest (tr.) pygidia occurred only in the Pragian, never again.

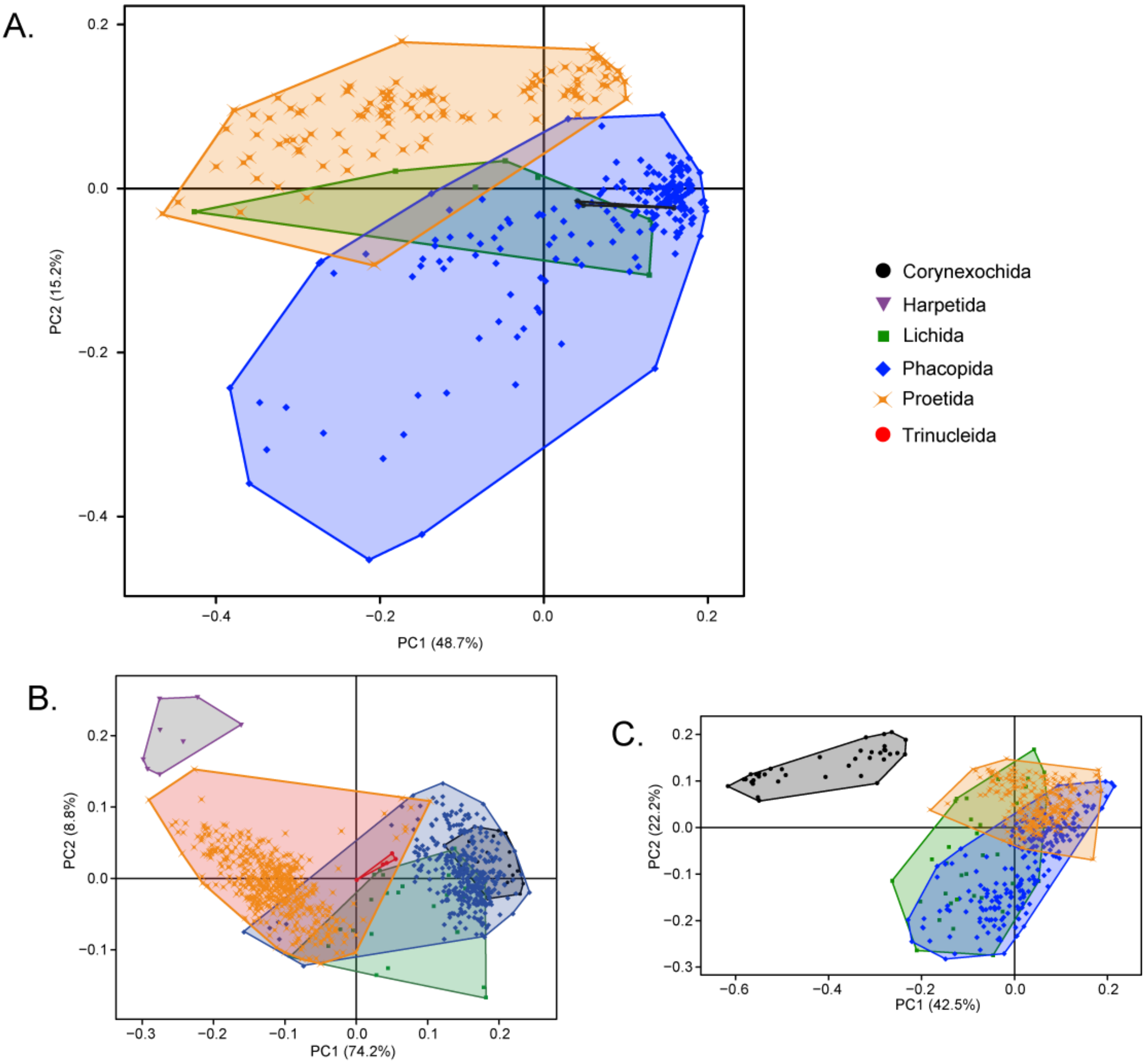


***Figure 5**. Location of: A, cephala; B, cranidia; and C, pygidia from the Devonian of North Africa in the global morphospace defined according to the two first principal component axes performed on Procrustes residuals for each order.*

The transition to the Middle Devonian did not coincide with a loss of morphological disparity; the three main morphotypes remain present (Fig. 4C, Fig. S4C). The reduction of the morphological space occurred during the late Eifelian. All the extreme shapes disappeared: narrow (MPg3) and wide (tr.) pygidia disappeared as well as long (MPg1) and short (sag.) pygidial axis and pygidia with a curved pygidial border (Fig. 4C, Fig. S4C). Although the pygidia with spines were maintained in the Eifelian, they disappeared in the Givetian with the collapse of the morphospace; only one pygidium morphotype is encountered, i.e., MPg2. A slight expansion of the morphological space occurred during the Frasnian but remained relatively restricted compared to the Early Devonian. Only wide (tr.) pygidia were present. During the Famennian, the morphological space was a little bit more widespread and not so scarce but remained in the same occupation ranges until the latest Famennian where a reduction of the morphological space occurred. Only MPg2 was maintained in the Late Devonian (Fig. 4C, Fig. S4C).

*Morphospace occupation by taxonomic orders*

For cephala, the morphospace shows a reduced overlap between Phacopida and Proetida, two orders that occupied respectively a vast area (Fig. 5A). Lichida appeared somewhat an intermediate Order (Fig. 5A). Corynexochida is the only Order with a restricted area (Fig. 5A). The main cephalic shape differences between these lineages are related to the position of the facial suture and the relative width (tr.) of the frontal lobe. Proetida were distinguished by an opistoparian facial suture and a wide (tr.) glabellar lobe equal to the frontal lobe (MCp4 and MCp5). Proetida have no sagittal spines and no or short genal spines (according to PC3 scores close to zero, Fig. Fig. S3A). At the opposite, Phacopida are distinguished by a wide (tr.) frontal lobe (according to positive scores of PC2) and mainly without spines assigned to morphotypes 1, 2 and 3 (according to positive scores of PC1). All of the Phacopida specimens have a proparian facial suture and no genal spines but some of them are characterized by the presence of sagittal spines. Corynexochida are distinguished by a prominent frontal lobe and no long (sag.) spines (MCp1). Finally, Lichida are characterized by a wide (tr.) frontal lobe as in Phacopida and an opistoparian facial suture as in Proetida. Like Proetida and Corynexochida, Lichida have no sagittal spines and no or short (sag.) genal spines (according to PC3 scores close to zero).

For cranidia, six orders are documented (Fig. 5B). The morphospace shows important overlap between Trinucleida, Phacopida, Proetida, Corynexochida, and Lichida (Fig. 5B). Phacopida and Proetida remain two orders that occupied respectively a vast area sharing a moderate overlap (Fig. 5B). Proetida are characterized mainly by MCn2 with a wide (tr.) preoccipital and occipital rings, while Phacopida are characterized mainly by MCn1. Corynexochida are characterized only by MCn1 with a wide (tr.) frontal lobe and no preglabellar field. Trinucleida are characterized by an intermediate morphology between wide (tr.) frontal lobe (i.e., MCn1) and wide (tr.) preoccipital and occipital rings (i.e., MCn2). Lichida is another order with a vast area but sharing an important overlap with Phacopida (Fig. 5B). As for cephala, Lichida are characterized by various morphologies corresponding to both MCn1 and Mcn2 excluding the morphologies with a preglabellar field. Harpetida is the only Order with an isolated area with no overlap. They are characterized by narrow (tr.) cranidia with a broad preglabellar field.

For pygidia, the morphospace shows a large overlap of most orders. However, Phacopida and Corynexochida are quite separate (Fig. 5C). The main pygidial shape differences between lineages are related to the width (tr.) of pygidia and the length of the pygidial axis. Proetida are distinguished by a wide (tr.) pygidium with a medium-size axis (MPg2). As for Proetida, Phacopida can have a wide (tr.) pygidium with a medium-size axis (MPg1). However, most of them have a wide (tr.) pygidium with a long (sag.) axis (MPg1). Corynexochida is the only order with a narrow (tr.) pygidia (MPg3) with a small axis. Lichida order is characterized by a relatively important shape variation despite its low number of specimens where the pygidial axis length or the pygidial (tr.) width seem to be not discriminant (MPg1, MPg2 and MPg3).

### *Morphospace occupation by bathymetry*

For cephala, cranidia and pygidia, all habitat groups related to the depth/bathymetry show a very large overlap (Fig. 6A-C). Nevertheless, the results of the ANOVA (Table 2) show significant p-values ($p<0.05$) suggesting a shape difference between all habitat groups according to bathymetry with some exceptions. These exceptions mainly concerned cephala from deep environments or with major difference in water depth affinities (i.e., shallow vs. middle shelf). These datasets (i.e., cephala, cranidia, pygidia) reveal a differentiation between bathymetry-related groups. For cephala, MCp1 and MCp4 were present at every bathymetric level, unlike other morphotypes (Fig. 6A). MCp2 gathers mainly trilobites that lived in the middle shelf. Some trilobites from shallow environments have also this morphotype but they are rare and this trend never concerns the extreme shapes with long (sag.) spines (according to the lowest PC2 scores). Almost all the trilobites that lived in the inner shelf correspond to MCp5. Two specimens from the middle shelf correspond to MCp5. MCp4 is dominated by trilobites from the middle shelf but trilobites with other bathymetrical affinities could also have this morphology. Finally, trilobites from shallow to middle shelf environments could have cephala attributed to MCp3, but are never encountered in the deep environment. All cranidium morphologies were present at different depths except cranidia with a large (sag.) preglabellar field (Fig. 6B). For pygidia, morphological differences related to bathymetry affinities affect only the MPg3 which was absent from shallow and deep environments. MPg1 and MPg2 encountered at every bathymetric depth were present in the deep environment (Fig. 6C).

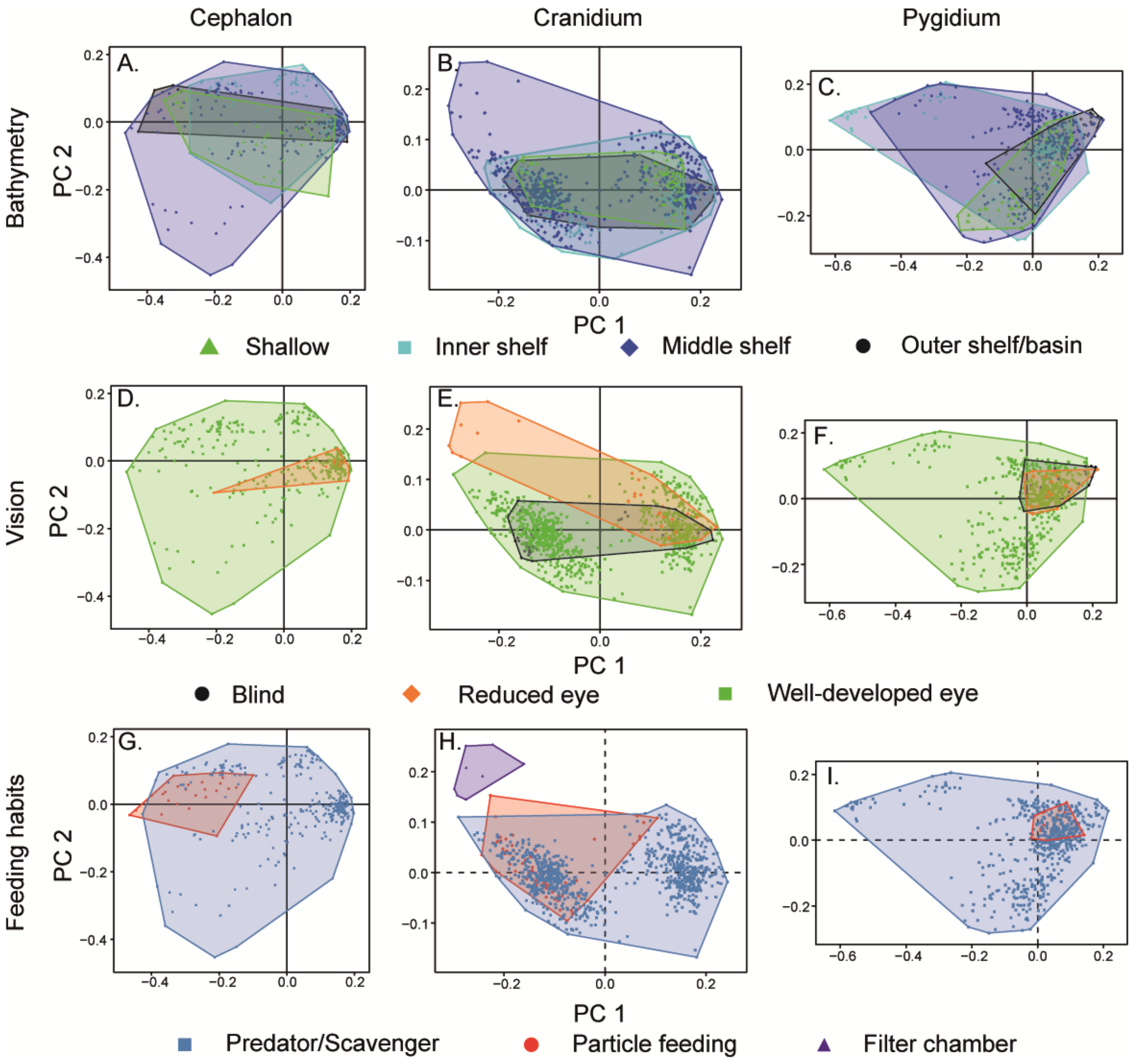
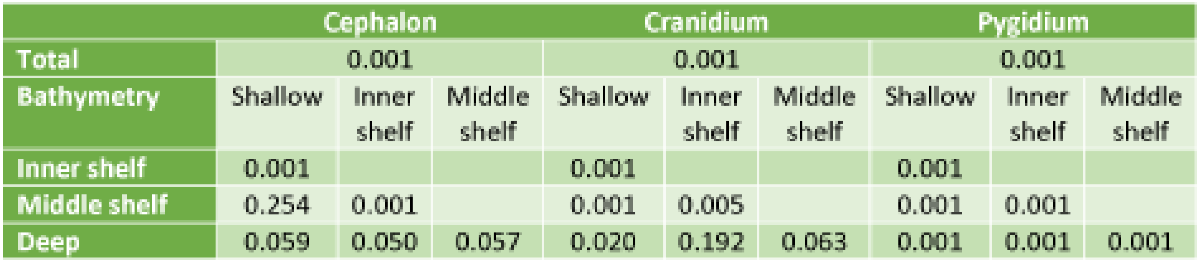
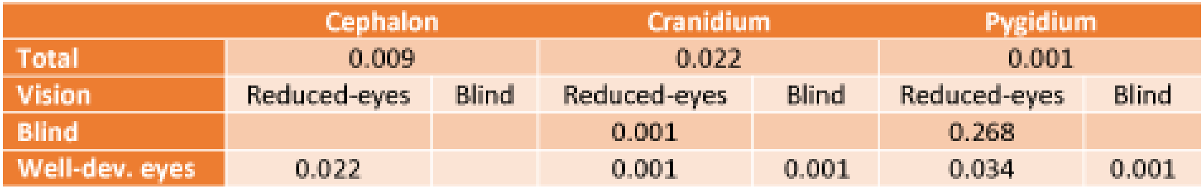


***Figure 6***. *Location of: A, D, G, cephala; B, E, H, cranidia; and C, F, I, pygidia from the Devonian of North Africa in the global morphospace defined according to the two first principal component axes performed on Procrustes residuals for three factors: (A-C) bathymetry; (D-F) visual abilities and (G-I) feeding habits. See supplementary figures S5, S6 and S7 for more details.*

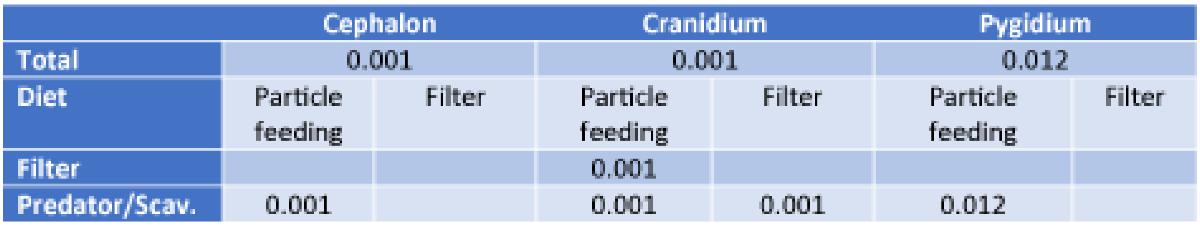
### *Morphospace occupation by vision*



| | Cephalon | | | Cranidium | | | Pygidium | | |
|---|---|---|---|---|---|---|---|---|---|
| **Total** | 0.001 | | | 0.001 | | | 0.001 | | |
| **Bathymetry** | Shallow | Inner shelf | Middle shelf | Shallow | Inner shelf | Middle shelf | Shallow | Inner shelf | Middle shelf |
| **Inner shelf** | 0.001 | | | 0.001 | | | 0.001 | | |
| **Middle shelf** | 0.254 | 0.001 | | 0.001 | 0.005 | | 0.001 | 0.001 | |
| **Deep** | 0.059 | 0.050 | 0.057 | 0.020 | 0.192 | 0.063 | 0.001 | 0.001 | 0.001 |



| | Cephalon | | Cranidium | | Pygidium | |
|---|---|---|---|---|---|---|
| **Total** | 0.009 | | 0.022 | | 0.001 | |
| **Vision** | Reduced-eyes | Blind | Reduced-eyes | Blind | Reduced-eyes | Blind |
| **Blind** | | | 0.001 | | 0.268 | |
| **Well-dev. eyes** | 0.022 | | 0.001 | 0.001 | 0.034 | 0.001 |



| | Cephalon | | Cranidium | | Pygidium | |
|---|---|---|---|---|---|---|
| **Total** | 0.001 | | 0.001 | | 0.012 | |
| **Diet** | Particle feeding | Filter | Particle feeding | Filter | Particle feeding | Filter |
| **Filter** | | | 0.001 | | | |
| **Predator/Scav.** | 0.001 | | 0.001 | 0.001 | 0.012 | |

***Table 2***. *p-values of the Procrustes ANOVA with permutation procedures to assess shape covariation according to bathymetry, visual abilities and feeding habits as factors.*

For cephala, cranidia and pygidia (Fig. 6D-F), the morphospace shows a widespread area for large-eyed trilobites, while reduced-eye trilobites show a more restricted area. Blind trilobites show a restricted area (Fig. 6E-F). Nevertheless, the results of the ANOVA (Table 2) show significant p-values ($p<0.05$), suggesting a shape difference between all vision groups according to visual abilities except between two compared groups of pygidia represented by reduced-eyed and blind taxa. These datasets (i.e., cephala, cranidia, pygidia) reveal a differentiation between visual abilities. For cephala, reduced-eyes trilobites are not represented in MCp2, MCp4 and MCp5 and they are characterized by shape without spines or with very small spines. For cranidia, both blind and reduced-eye trilobites are represented by both MCn1 and MCn2. However, for MCn2, reduced-eye trilobites did not constitute a subset of the large-eyed trilobites but had their own unique morphology with a wide (sag.) preglabellar field contrary to MCn1 for which they showed no new morphology (Fig. 6E). For pygidia, only MPg2 corresponds to blind or reduced-eyes trilobites, while all other morphotypes show large eyes.

### *Morphospace occupation by feeding habits*

For cephala as for cranidia and pygidia (Fig. 6G-I), the morphospace shows a widespread area for one group, i.e., predator/scavenger habits, while particle feeding and filter chamber habits show a restricted area. The results of the ANOVA (Table 2) show significant p-values ($p<0.001$) suggesting a shape difference between all diet groups according to feeding habits; only two compared groups of pygidia represented by particle feeding and predator/scavenger taxa show a p-value $p<0.05$. For cephala, particle-feeding trilobites were mainly restricted to MCp4 characterized by no genal spines except one specimen within MCp3 (Fig. 6G). In terms of morphology, predators and/or scavengers were distinguished from particle feeding trilobites, although these differences could be minor as for MCp4 where the facial suture was slightly different between both diet categories. For cranidia, particle-feeding trilobites were also characterized by narrow (tr.) frontal lobes occurring mainly in MCn2 (Fig. 6H). At the opposite, Predator/Scavenger trilobites occupied all the morphospace. The greatest number of cranidia allows having the repartition of filter chambers, which had very large preglabellar field and narrow (tr.) frontal lobes. For pygidia, particle-feeding trilobites show only MPg2 (Fig. 6I). They also have no spines occupying only the centre of the PC3-PC4 morphospace.

## DISCUSSION

### *Relationships between morphological spaces and proxies*

The maximum morphological disparity in trilobites with many different morphologies for both cephala and pygidia was documented in the Ordovician but remained important in the Devonian (Foote 1993; Webster 2007). During this Devonian time interval, and according to our results, the overall dispersion of taxa in the morphospace shows (1) cephala with spines or not, visual surfaces or not, proparian or opistoparian facial sutures, glabella with wide or narrow (tr.) anterior frontal lobes, and (2) pygidia with spines, wide or narrow (tr.) outlines and different lengths (sag.) of the pygidial axis. The type of sutures was already an important criterion to segregate the trilobite morphologies in the Early Palaeozoic (Foote 1991a) although their ecological or life-history-strategy significance is uncertain (Hopkins 2014). The position of facial sutures corresponded to a trade-off between burrowing and moulting and could be an advantage to develop an infaunal lifestyle (Esteve *et al.* 2021). The presence of spines is identified as a contributor to overall morphological variation for pygidia too, for which elongation (sag.) is a major axis of shape variation.

The three studied morphospaces are characterized by the presence of morphological clusters. The palaeoecology, measured here as the bathymetry and the diet factors, has only a weak effect on the trilobite morphology because different categories overlapped, and cannot explain such identified morphotypes (Fig. 6, Table 2). Hopkins (2014) already noticed a weak bathymetric influence on trilobite morphology except during the Ordovician and the Late Devonian when Proetida lived in shallow environments and Phacopida in deeper ones. The absence of real links between the trilobite morphologies and the water depth contrasts with the structure of the morphological disparity in ammonoids (Neige *et al.* 1997). As nektonic organisms, the ammonoids colonized the water column from the platform to the basin with typical morphologies related to the pressure, which is not the case for benthic trilobites found only on the sea floor of the platform.

The diet influenced on the shape of trilobites as it contributed to morphological variations in modern arthropods (Lunardi *et al.* 2017). The distinct glabellar shapes recognized in our analyses (Fig. 6) are already identified in previous studies and are interpreted as an indicator of feeding habits (Fortey & Owens 1999). The expanded glabella anteriorly with wide frontal lobes observed in our study was interpreted as predator feeding habits, which are associated with the ingestion of bulky food (Fortey & Owen 1999). However, some predator/scavenger taxa showed a glabellar shape with narrower anterior frontal lobes, a morphology attributed to particle feeding trilobites. Difference of feeding habits for a same dorsal morphology is explained by the fact that morphological changes in connection with diet mostly concerned especially the ventral structure, i.e., the hypostome (Fortey & Owens 1999). Filter chamber feeding trilobites needed a large cephalic shield to filter suspension particles in the water. Consequently, these trilobites presented the larger preglabellar field (Fig. 6). However, a large cephalic shield can also be used to avoid sinking into the mud (Richter 1920) and would not be related to feeding habits. Although pygidium shape did not play a role in trilobite feeding, particle feeding trilobites occupied only a small area of the morphospace.

The visual abilities, estimated here from the shape of the visual surfaces, have an important effect on the global trilobite morphology. Devonian trilobites with well-developed eyes occupied the global morphospace whereas blind and reduced-eye trilobites occupied only a small part of this morphospace (Fig. 6). Moreover, blind and reduced-eye trilobites occupied the same small part of the morphospace, except for taxa with narrow frontal lobes anteriorly (Fig. 6, Table 2). During the Devonian, paedomorphic evolutionary trends have been observed in Late Devonian taxa showing progressive eye reduction between closely related species that eventually leads to blindness (Feist & Clarkson 1989; Feist 1995; Crônier & Courville 2003; Schoenemann 2018). Such eye reduction implies morphological changes such as the enlargement of fixigenae observed among Proetida or the ’displacement’ of the facial suture towards the outer margins observed among Phacopida (Feist 1995; Crônier & Courville 2003). Consequently, Phacopida with reduced eyes are mainly confined to the part of the morphospace characterized by a suture closer to the lateral border (i.e., higher PC1 values, Fig. 6D).

In addition to diets and habitats, the trilobite morphologies are known to be influenced by their lifestyle, such as living in low-oxygen habitats (Fortey 2004) or the enrolment type (Suárez & Esteve 2021). In the same way, competition between species is also a driver of diversification recognized in arthropods (Eberle *et al*. 2014).

### *Morphological evolution through time*

The trilobite morphospace occupation evolved during the Devonian in North Africa. A minimum occupancy in the morphospace occurred at the beginning of the Early Devonian, inherited from the end of the Silurian (Fig. 4). Only one cephalic and pygidial morphotype and two cranidial morphotypes were encountered; the difference between cephala and cranidia being due to a lack of cephalic record. These morphologies were adapted to all depth/bathymetry and vision abilities but not to a particle feeding behaviour. Despite a reduced shape variability, trilobites were not restricted to any depth or type of vision. These morphologies coincided with the expansion of Phacopida disparity (Fig. 5A) and their dominance during the Lochkovian in North Africa (Bault *et al*. 2021).

During the Pragian, morphological disparity increased and new morphologies were explored, i.e., cephala with an opistoparian facial suture and a narrow (tr.) frontal lobe. These new morphologies are assigned to Proetida (Fig. 5A) which developed in North Africa (Bault *et al*. 2021) and exhibited their maximal dispersion at the global at this time (Foote 1993). Moreover, exoskeletons with spines proliferated, i.e., pygidia with spines developed as well as cephala with genal spines, which became more diverse and extended towards shapes with very long genal spines. Pygidia with a narrow (tr.) outline assigned to Corynexochida appeared too (Fig. 5C). Cephala with a wide preglabellar field appeared in both Proetida and Phacopida morphologies without a link to environmental depth (Fig. 6A-C) contrary to the Ordovician (Fortey & Wilmot 1991). Genal spines and a preglabellar field appeared at the same time in different lineages showing a common trajectory in morphospace through time. However, Phacopida explored morphologies with sagittal spines but not Proetida, suggesting that different causes could influence different lineages. The diversification of morphologies with the appearance of novelties in the Pragian coincided with new ecological opportunities due to the sea-level fall (Chlupáč 1994). The extension of the carbonate platform toward offshore environments offered new habitats leading to the morphospace expansion toward the middle shelf and to a trilobite radiation. Similarly, the predator/scavenger trilobites showed an increasing morphospace occupation possibly linked to a food partitioning and to an interspecific competition (Schluter 2000; Grant & Grant 2006). The increase of enrolment type in the Devonian was also a source of morphological disparity (Suárez & Esteve 2021). More generally, the diversification phases could be partly attributed to interspecies competition in arthropods (Eberle *et al.* 2014). The diversification of many clades in the Early Devonian (Alroy *et al.* 2008; Klug *et al.* 2010; Fan *et al.* 2020), may have an influence on the predator morphology with the arrival of new prey (Cattau *et al.* 2017). This advantageous feeding strategy could induce a radiation of predator/scavenger trilobites and at the opposite, particle feeding trilobites decreased maybe because of an increasing competition of more efficient organisms. Despite new morphologies explored in the Pragian, those already present during the Lochkovian remained the majority.

During the Emsian, all the main morphologies maintained with the maximum dispersion in the morphospace with the development of cephala with long genal spines and especially with a wide (tr.) frontal lobe (Fig. 3). Only shape losses regarding the narrowest (tr.) pygidia occurred. In trilobites, spinose exoskeletons were interpreted as passive morphological defences by some authors (Fortey 2004; Pates & Bicknell 2019). In a context of the Devonian Nekton Revolution (Klug *et al.* 2010), the emergence of morphologies with spines can be interpreted as a new answer to an increase of the predation. However, this hypothesis seems unlikely because some potential predators appeared only from the Emsian like ammonoids or chondrichtyans (Becker *et al.* 2019) or developed in the end of the Devonian like fishes (Derycke 2017). In addition, the morphologies with spines disappeared in the Middle Devonian and Frasnian, contrary to other shapes, which remained in the Famennian (Fig. 4). Nevertheless, these disappearances could be attributed to the inefficiency of spines against the large-jawed predators of the Late Devonian (Brett 2003). The diversification of morphologies in the Early Devonian could be partly related to novel feeding habits, i.e., particle feeding habits with the appearance of glabella with a short (sag.) preglabellar field (Fortey 2014). In addition, only exoskeletons with genal spines were attributed to this diet as well as in North Africa during the Devonian as in other areas and at other times (Fortey & Owens 1999). In their evolutionary history during the Early Devonian, trilobites explored morphospace with much of the subsequent variation in their cephalic features compared to their pygidial features. Accordingly, the pygidial characters display much overlap of taxonomic groups in the morphospace, while the cephalic characters show more distinct morphospace occupation at the order level.

The morphospace was maintained during the Eifelian with all the cephalic, cranidial and pygidial morphotypes despite environmental changes implying sea-level and oxic condition changes (Kaufmann 1998). Only the morphologies appeared during the Pragian were rarer, especially MCp2 for cephala and MPg3 for pygidia (Fig. 4).

The Givetian was characterized by an important loss of morphology. The disappearance of some orders, i.e., Lichida and Corynexochida (Bault *et al*. 2021) led respectively to the loss of exoskeletons (i.e., cephala and pydidia as well) with spines or the loss of cephala with a long (sag.) glabella and of pygidia with a long (sag.) axis. However, Corynexochida was known in the lower Givetian of North Africa (Feist & Orth 2000) but only represented by a single pygidium; thus, the loss of the cephalic morphology occurred later although it is not possible to observe this in the morphospace. Between the different lineages, a common pattern of disappearance seems to exist and in particular, for both Proetida and Phacopida, which showed that the most affected trilobites were those with morphologies with protuberance like spines and preglabellar field implying a common origin of disappearance. The Givetian is known to be a period marked by a series of anoxic/hypoxic events associated with sea-level rise (Kaufman 1996; House 2002; Becker *et al*. 2016) and to have an important impact on trilobite diversity (Feist 1991; Chlupáč 1994; Lerosey-Aubril & Feist 2012). The morphospace was reduced probably due to marginal or lateral extinctions (Foote 1991b; Korn *et al*. 2013). Morphologies with the lowest bathymetric extent such as the MCp2 and MCp3 for cephala and MPg3 for pygidia were the most impacted and they disappeared (Fig. 6A-C). Indeed, these morphologies have never been encountered in a deep environment, which could be a disadvantage in a context of rising sea level. In addition, the morphologies that remained were versatile and exhibited different vision abilities (Fig. 6). Accordingly, these morphologies were more adapted to environmental changes. The morphologies maintained during the Givetian corresponded to morphologies already present in the Ludlow and represent persistent morphologies.

The dispersion in the morphospace decreased in the Frasnian to reach only one morphotype for cephala (MCp1) and for pygidia (MPg2). Nevertheless, the absence of additional morphotypes (i.e., MCp3 and MCp4 without spines or short genal spines) for cephala in Proetida is due to the lack of sampled specimens in our dataset. Some Proetida were encountered in the upper Frasnian of North Africa (Feist 2002). The Frasnian is marked by the reappearance of morphologies with numerous spines. These morphologies occurred within the dark-grey hypoxic limestone levels of the Kellwasser deposits related to relative deep-sea conditions (Feist 2002). Trilobite morphologies did not show significant shape losses and seem to have been little affected by the Kellwasser Events that occurred at the Frasnian/Famennian boundary and was one of five major extinction events in the history of life on Earth (McGhee 1988, 1996; Racki 2005, 2020). The main shape change was the disappearance of morphologies with spines except genal spines in Cyrtosymbolinae (Proetida). Unfortunately, only the cranidia and the pygidia for the Famennian Proetida are available in North Africa and they are therefore not included in the cephalic morphospace. As for the Givetian and the Frasnian, only the versatile morphologies related to depth conditions and vision abilities were maintained during the Famennian. Only Proetida and Phacopida crossed the Frasnian-Famennian boundary both at the global and at the North Africa regional (Chlupáč 1994; Lerosey-Aubril & Feist 2012; Bault *et al*. 2021). These two orders are characterized by the maximal morphological variation in the Devonian morphospace in North Africa (Fig. 4). Such variability is known to be helpful to cope the environmental changes in other clades (Kolbe *et al*. 2011; González-Suárez & Revilla 2012; Huang *et al*. 2015; Austin & Dunlap 2019). Across all these events, from the Eifelian to the Famennian, there were progressive shape losses among trilobites but no extensive morphological innovation occurred after mass extinctions despite potential availability of the ecospace (Erwin 2015).

The notable extinction at the end of the Famennian, i.e., the Hangenberg event led to the demise of Phacopida whereas Proetida survived (Feist 1991; Lerosey-Aubril & Feist 2012; Bault *et al*. 2021). During this event, a severe but selective shape loss occurred which only affected Phacopida and their cephala. Such selective patterns were previously identified in other organisms such as ammonoids where the morphology of clymeniids was more affected than that of goniatitids (Korn *et al*. 2013). If Phacopida and Proetida showed different morphologies of cephala, they exhibited similar morphologies of pygidia, suggesting that the pygidia were the structures with the less extinction selectivity contrary to the cephala.

### *Morphospace divergence in the light of morphological constraints*

Location of cephala, cranidia and pygidia in the morphospaces showed a different relative distribution of specimens: for instance, Corynexochida and Phacopida that occupied the same part of the cranidium morphospace occupied distinct parts of the pygidium morphospace (Fig. 5B-C). This is explained by the relatively independence of the evolution of the studied structures known as tagmata (Hughes 2003) even if some covariations between these different structures exist due to enrolment (Oudot *et al*. 2019). Functional morphology, consequently functional modularity, explains why some orders showed overlapping morphologies for cephala or pygidia but different shapes for other structures. Modularity was implied in the developmental process of trilobites indicating a developmental constraint on the morphology.

Not all combination of characters were possible due to intrinsic constraints that channel the morphological evolution like physical or developmental constraints (Arnold 1992; Gould 2002; Gerber 2014; Briggs 2017). For trilobites from the Devonian of North Africa, it was not possible to develop a sagittal spine without genal spines in the cephalon (high PC1 and low PC2 scores; Fig. 3A). Ontogenetic studies underlined a progressive enlargement (tr.) of the glabella during the development, especially in Phacopida due to a change in the food niche (Crônier & Feist 1997; Crônier & Fortey 2006; Jacobs & Carlucci 2019). Thus, feeding constraints during development probably led to the absence of trilobites with a very narrow (tr.) glabella at an adult stage (high PC2 scores; Fig. 3B) in our dataset.

Some taxa exhibit intermediate morphologies between the morphotypes indicating that physical constraints did not hamper the existence of these morphologies (Fig. 3). The density distribution of morphologies in morphospace can reflect the positions of clusters with high-fitness interpreted as an ‘adaptive peak’, separated by ‘valleys’ with few morphologies, driven by competition, trophic specialization or behaviour (McGhee 2007; Polly 2017). The trade-offs between different tasks led to an adaptive landscape and therefore to phenotypic clusters (Shoval *et al*. 2012; Tendler *et al*. 2015). Thus, the overall dispersion of taxa was restricted to some areas of the morphospace with some empty areas and with a heterogeneous distribution for the Devonian time slice. This explains why some morphologies were absent during the Devonian such as a narrow (tr.) pygidium associated with a long (sag.) axis while such morphologies were present during the Cambrian, in the genus *Balcoracania* for example (Pocock 1970). Consequently, intrinsic factors alone cannot explain the absence of these morphologies and two other factors can be identified: the environmental conditions were not favourable to these morphologies or these morphological areas were simply never explored again after their disappearance. In the case of *Balcoracania*, this genus was found in very shallow environments, like lagoon or estuaries, during the Cambrian (Paterson *et al*. 2007) but trilobites deserted this environment during the Devonian of North Africa, suggesting an environmental explanation for the absence of a narrow (tr.) pygidium. The evolution of such parameters may be a trade-off between selection on factors such as function, ecology/environment, or development.

Our study shows some trends of covariation of different characteristics and the most obvious covariation concerns the cephalon, for which a common pattern of morphological changes occurred. For both Proetida and Phacopida, some arrangements of the cephalon were needed to develop spines: the glabellar shape became less curved with a narrow (tr.) frontal lobe (lower PC1 and PC2 scores, Fig. 3A). Morphological covariations are known in trilobites and were mainly due to physical and developmental constraints (Hughes 2003; Crônier & Feist 1997; Gerber & Hopkins 2011; Webster & Zelditch 2011; Oudot *et al*. 2019).

## CONCLUSION

In the Devonian, North African trilobites showed substantial morphological variation in their cephala, cranidia and pygidia. The morphological disparity concerned the width (tr.) of the glabella, the location of facial sutures, the elongation (sag.) of pygidia and the presence of spines. Both abiotic and biotic factors such as depth of water conditions, feeding habits and visual abilities seem to have only a weak effect on the global trilobite morphology. Trilobites with well-developed eyes occupied the global morphospace whereas blind and reduced-eye trilobites occupied only a small part of this morphospace.

North African trilobites experienced significant morphological fluctuations from the Early to the Late Devonian. During the Devonian, the trilobites exhibited cases/examples of convergence in the visual surfaces or and spines and, a development of ‘rare’ morphologies such as the very spiny shapes of the Pragian-Emsian. The morphological disparity was low at the end of the Silurian and the Lochkovian. The trilobites occupied a relatively small part of the morphospace. Subsequently, the disparity increased considerably in the Pragian with the appearance of several new morphologies. Then, the disparity reached a maximum in the Emsian. The trilobites occupied the global morphospace and exhibited additional new morphologies, although some areas of the morphospace remained empty because some morphologies did not develop in the Devonian. The morphological disparity maintained until the Eifelian, decreased considerably in the Givetian, and reached a minimum in the Late Devonian with a density more important for the Famennian than for the Frasnian. The trilobites developed no novelties anymore. This significant decrease in the morphological disparity occurred during a period characterized by numerous environmental events implying habitat changes with sea-level fluctuations and anoxic/hypoxic conditions. Some taxa (i.e., morphologies) were more resilient to these environmental changes and persisted during the Devonian because of their adaptation to different bathymetry and their visual ability. Similarly, Phacopida and Proetida survived most of the events thanks to their large morphospace occupation, and they were characterized by an evolutionary trend toward a progressive eye reduction leading to blindness.

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## SUPPLEMENTAL FIGURES

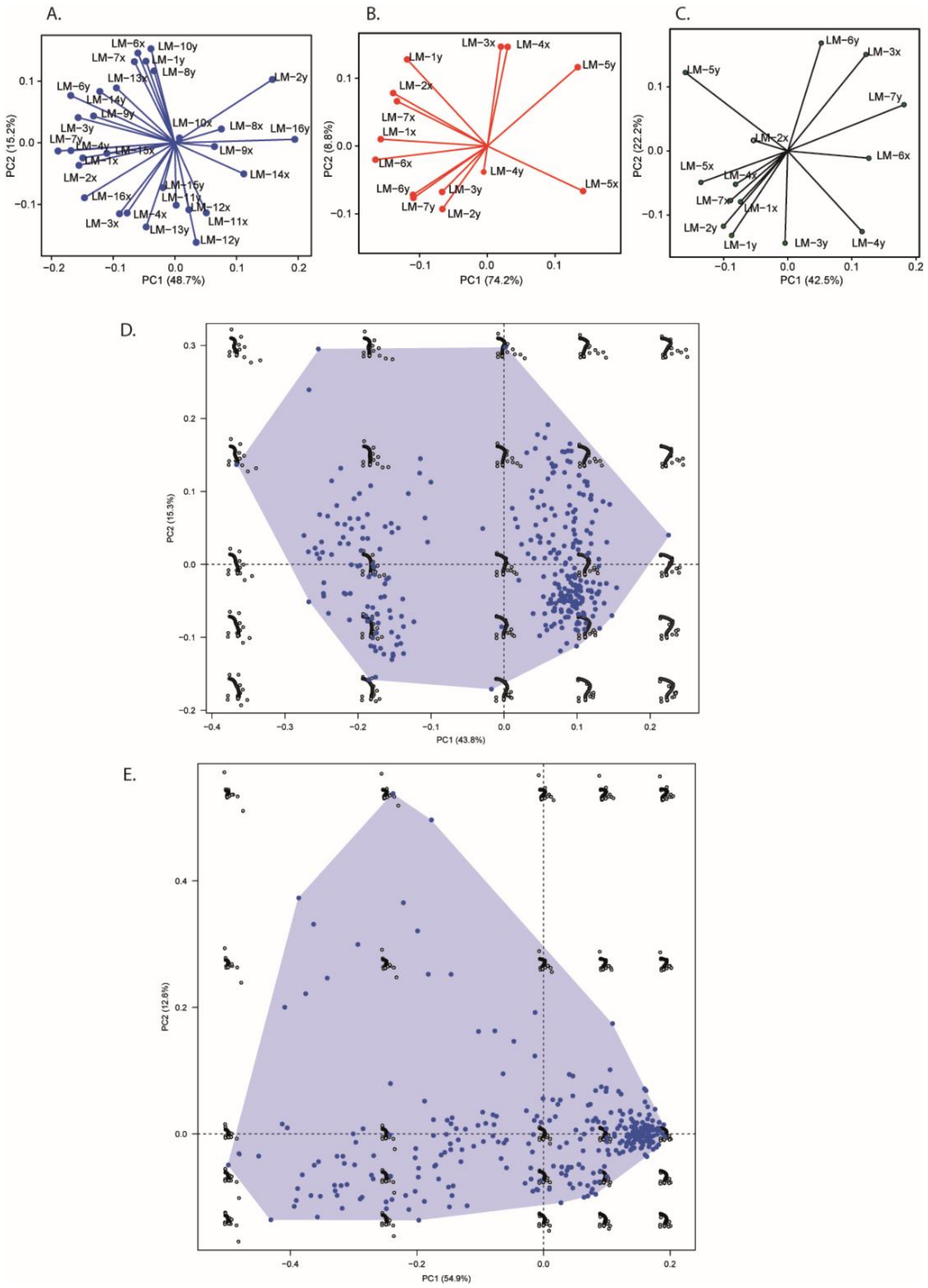

***Figure S1.*** *Results of analyses performed to verify if topological issues occurred with our set of landmarks. Correlation circles of landmarks showing the most contributing variables for: A, cephala; B, cranidia; and C, pygidia. Morphospace defined according to the two first principal component axes performed on Procrustes residuals using cephalon specimens without landmarks 13 and 16 (D) and landmarks 10 and 12 (E).*

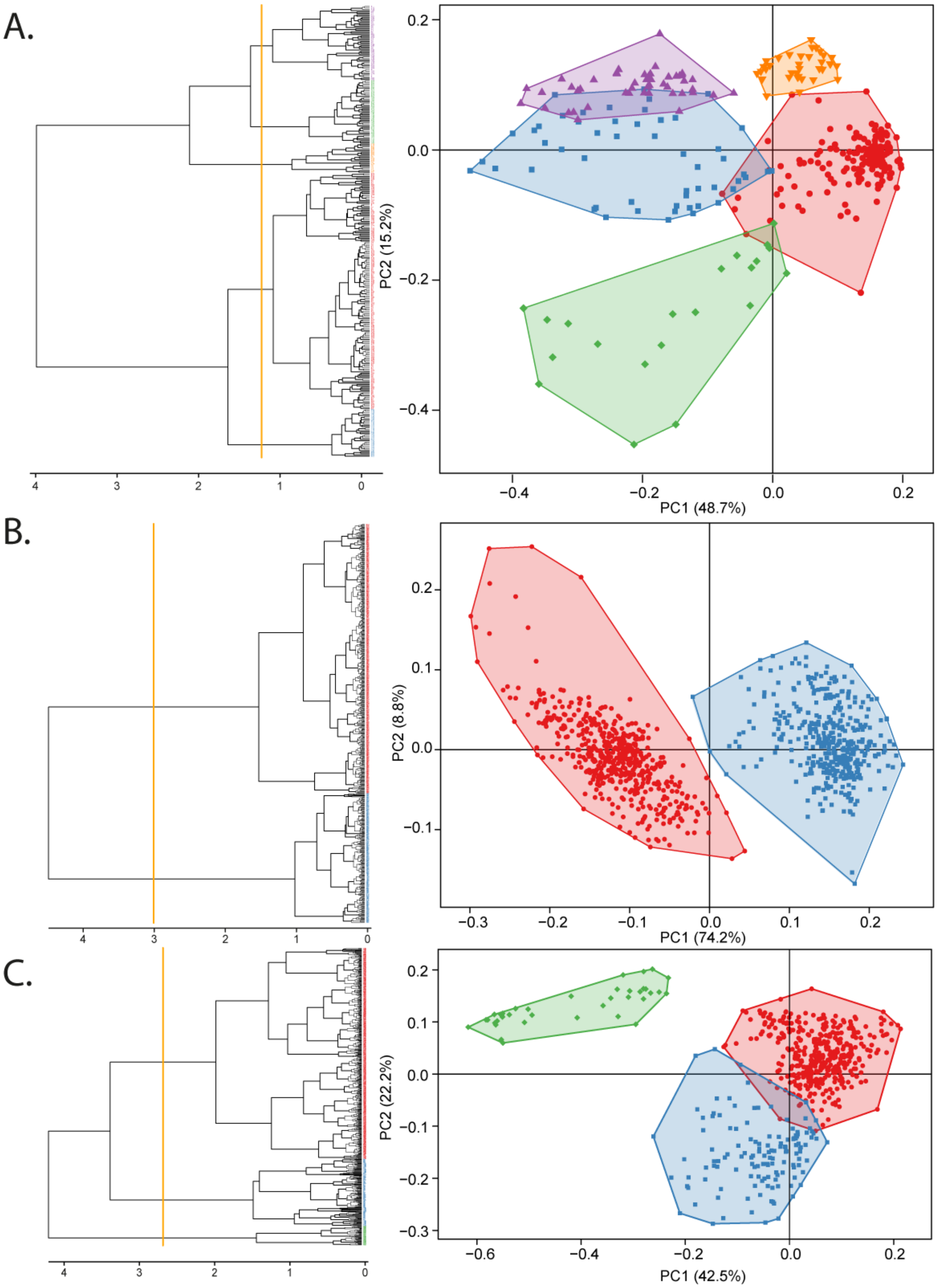

***Figure S2.*** *Clusters identify by a Hierarchical Cluster Analysis (HCA) performed with the Euclidian distance measure and Ward's linkage algorithm on the PC's scores for all specimens, and the global morphospace defined according to the two first principal component axes performed on Procrustes residuals for: A, cephala; B, cranidia; and C, pygidia.*

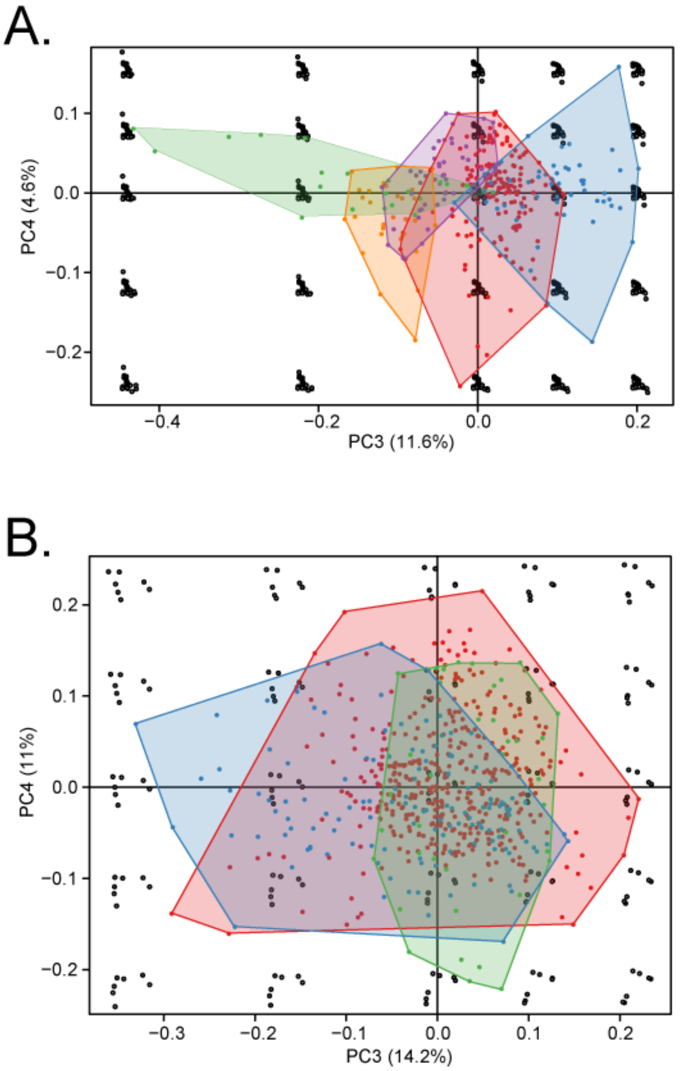

***Figure S3.*** *Location of: A, 328 cephala; and B, 605 pygidia from the Devonian of North Africa in the global morphospace defined according to the third and the fourth principal component axes performed on Procrustes residuals.*

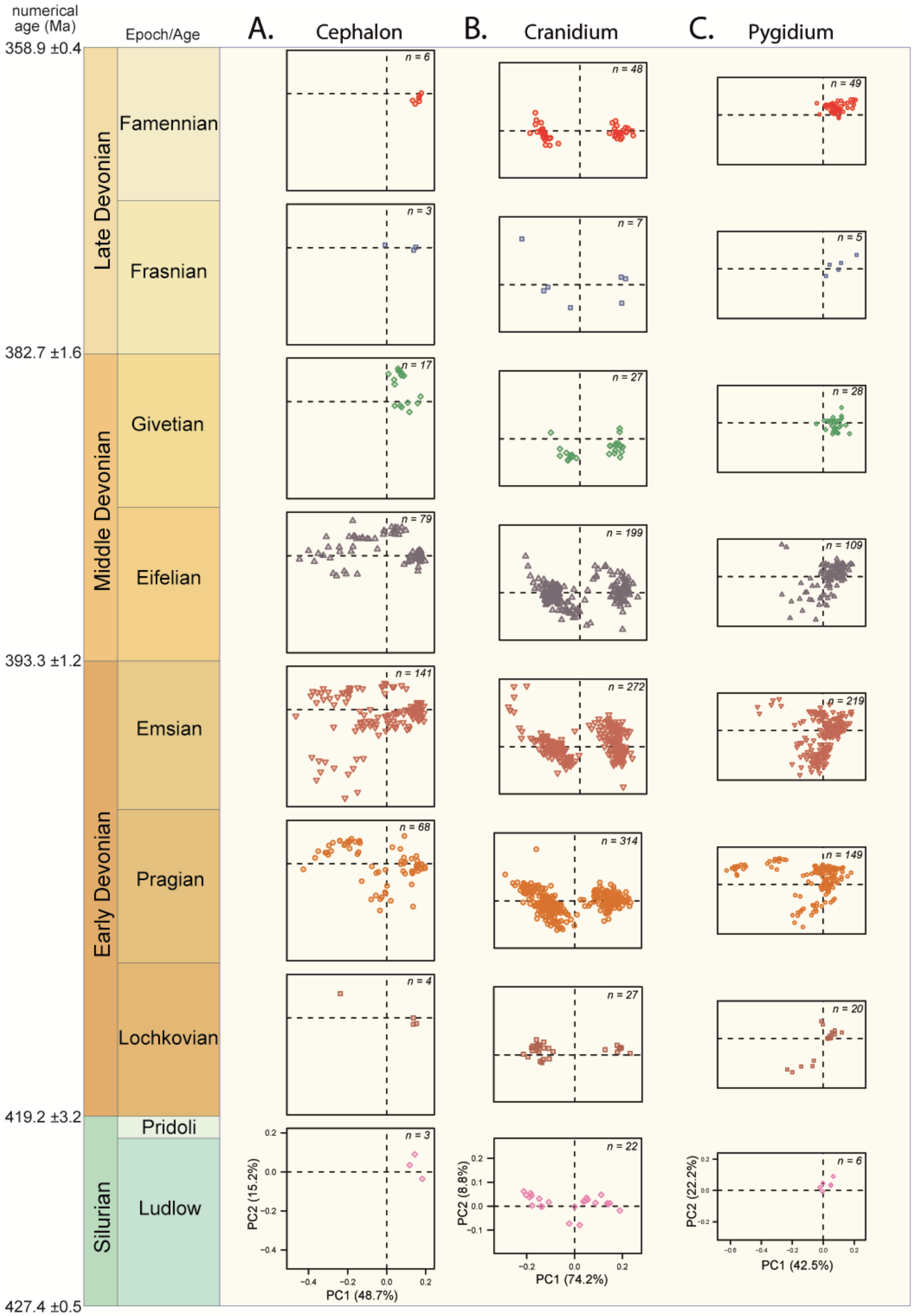

***Figure S4.*** *Location of: A, cephala; B, cranidia; and C, pygidia from the Devonian of North Africa in the global morphospace defined according to the two first principal component axes performed on Procrustes residuals, represented for each Devonian stage. The number of specimens is indicated for each stage. Ages from Cohen et al. (2013, updated with the version of 3/2020).*

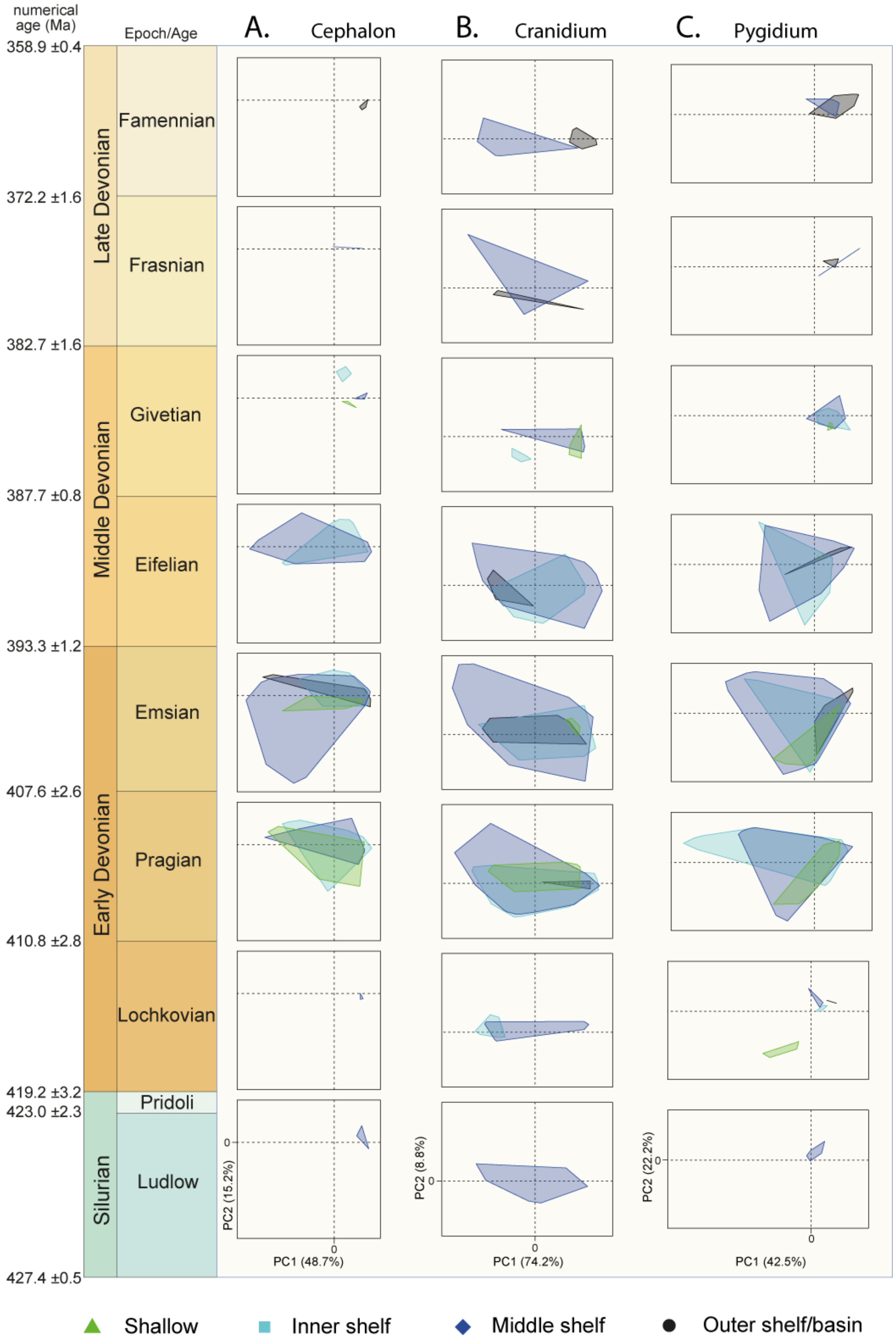

***Figure S5.*** *Location of the morphotypes of: A, cephala; B, cranidia; and C, pygidia from the Devonian of North Africa in the global morphospace defined according to the two first principal component axes performed on Procrustes residuals for bathymetry. Ages from Cohen et al. (2013, updated with the version of 3/2020).*

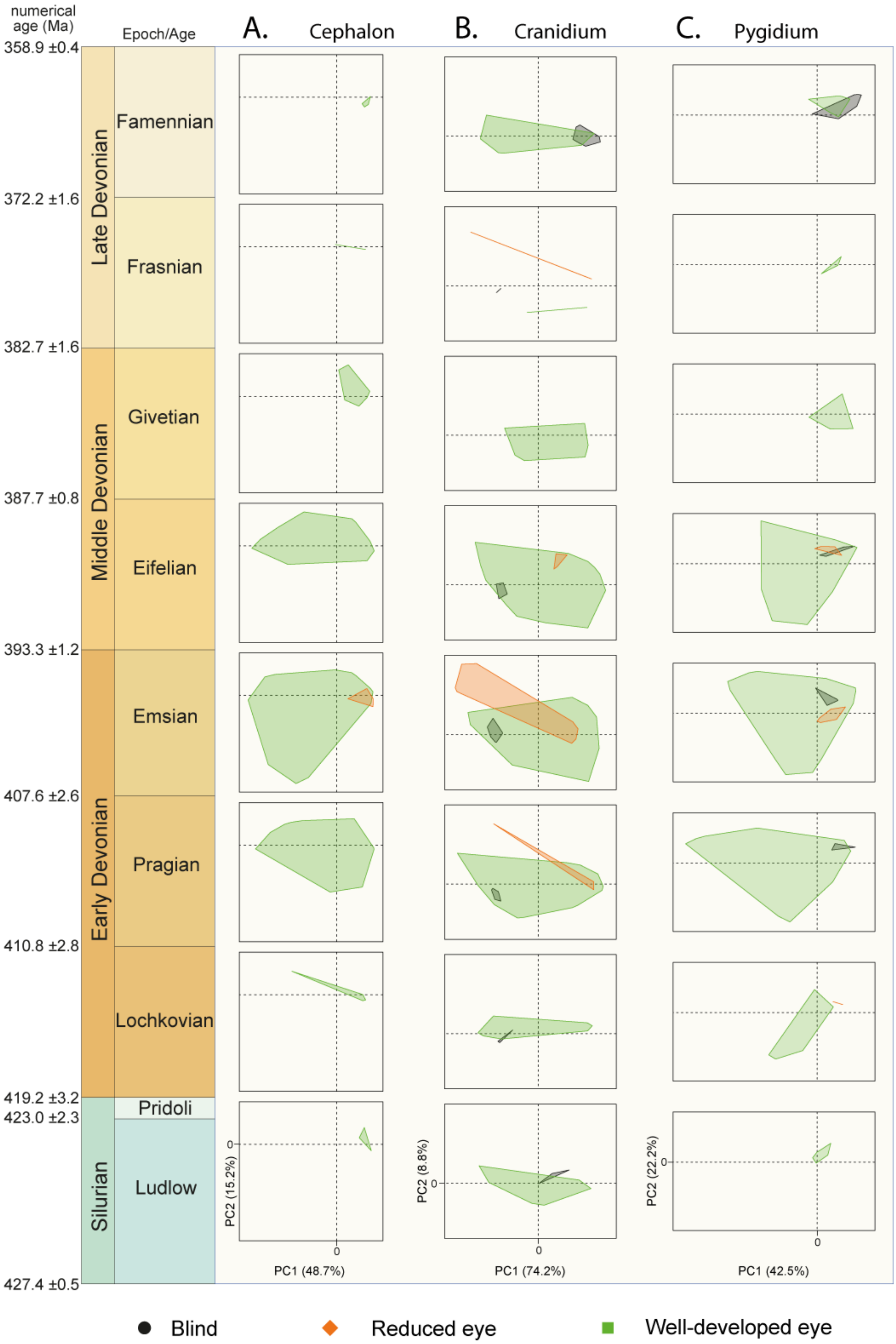

***Figure S6.*** *Location of the morphotypes of: A, cephala; B, cranidia; and C, pygidia from the Devonian of North Africa in the global morphospace defined according to the two first principal component axes performed on Procrustes residuals for vision abilities. Ages from Cohen et al. (2013, updated with the version of 3/2020).*

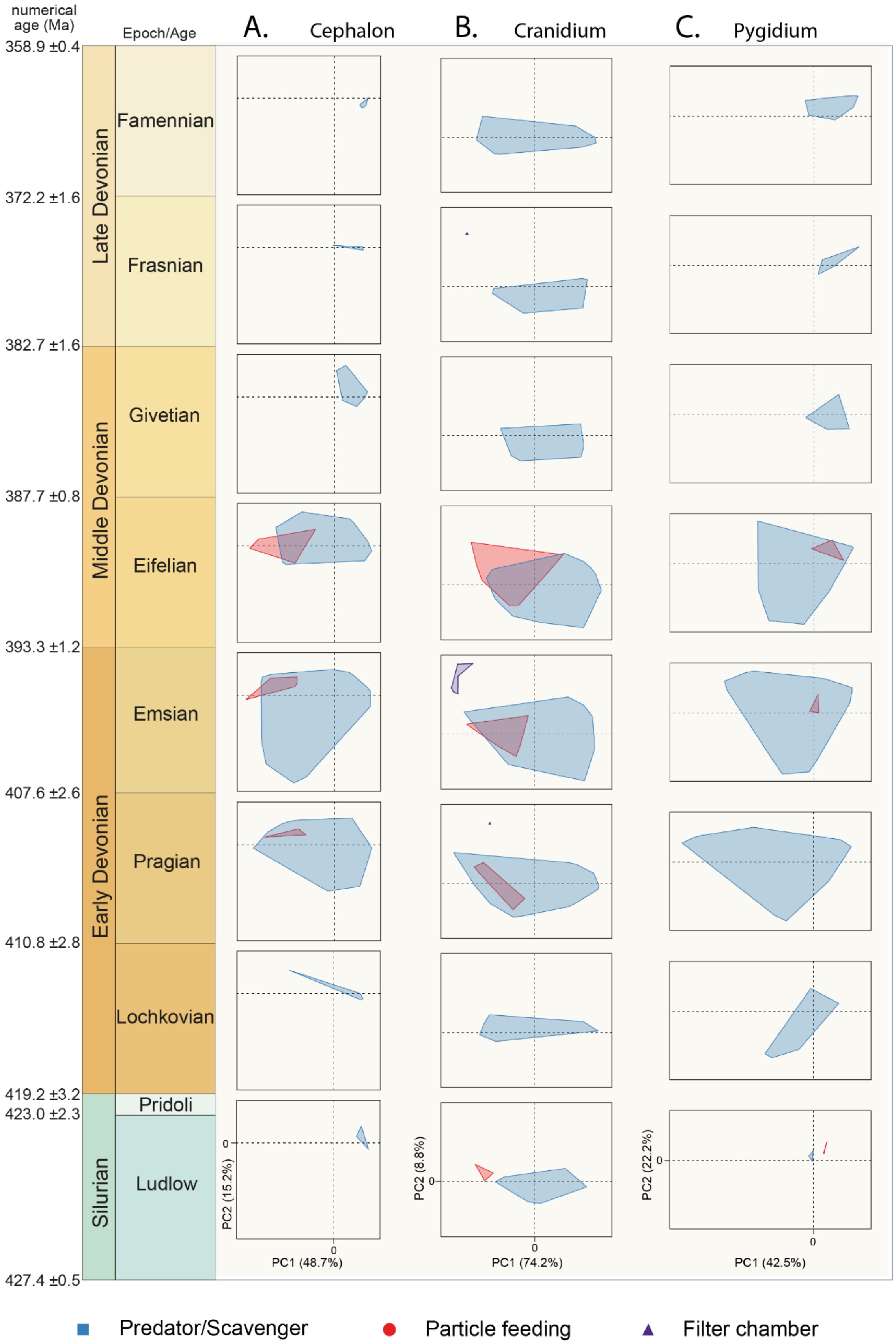

***Figure S7.*** *Location of the morphotypes of: A, cephala; B, cranidia; and C, pygidia from the Devonian of North Africa in the global morphospace defined according to the two first principal component axes performed on Procrustes residuals for feeding habits. Ages from Cohen et al. (2013, updated with the version of 3/2020).*

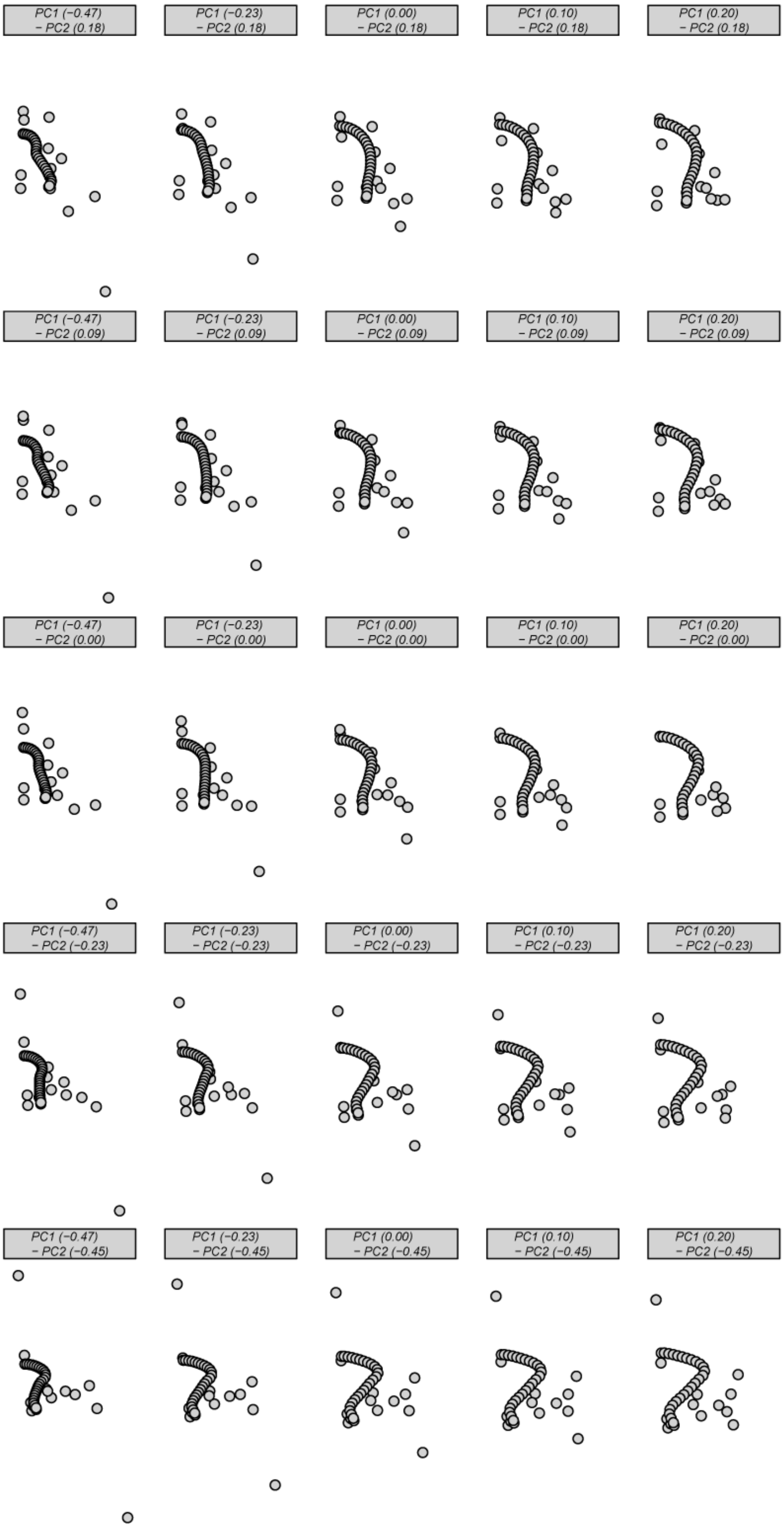

***Figure S8.*** *Reconstruction of virtual shapes for PC1 and PC2 of the cephalon.*

## 2.3. Aucun découplage entre la diversité taxonomique et et la disparité morphologique des trilobites d’Afrique du Nord ?

Article 5 : No decoupling between taxonomic diversity and morphological disparity in the trilobites from the Devonian of North Africa?

Pour être soumis à Historical Biology

# No decoupling between taxonomic diversity and morphological disparity in the trilobites from the Devonian of North Africa?

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## Abstract

Morphological disparity and taxonomic richness are two important often decoupled in time, particularly in the early history of clades. Using morphometric methods and diversity indices, both morphological disparity and taxonomic diversity of Devonian trilobites from North Africa were analysed on three structures, i.e., cephalon, cranidium (without free cheeks) and pygidium. Morphospace occupancy and density as well as trilobite size were estimated and compared to generic richness through time. Whereas the cranidium showed only slight morphological diversification in the Early Devonian, the morphological disparity of the pygidium and the cephalon strongly increased. A disparity peak of pygidia was reached from the Pragian onwards while the cephala continue to innovate. Along with the development of morphological novelties in the Early Devonian, the diversity increased, particularly in the Lochkovian. However, the Middle Devonian events affected the trilobite communities with simultaneous drastic loss of morphologies and richness. This coupling in diversity and disparity dynamics could be explained by either the intensity of extinctions or a high rate of internal constraints. Devonian trilobites represent a 'Top-Heavy Clade' implicating old clades with a more constrained morphology. The weak Famennian recovery did not allow trilobites to reach the Early Devonian diversity level, trilobites constituting a 'Dead Clade Walking' during their late evolutionary history.

**Keywords:**

Arthropods; Palaeozoic; morphology; size; extinction; diversity indices

## 1. Introduction

Studying successful clades (Alfaro et al. 2009, Benton 2015) such as the trilobites during the Palaeozoic times remains fundamental in Macroevolution. Such evolutionary success requires the consideration of taxonomic diversity, assessing changes in the number of species through time, but also morphological disparity, assessing variation in morphology.

The trilobites were probably among the most abundant marine benthic macroinvertebrates during the Palaeozoic. Due to their high taxonomic diversity and their high morphological disparity, these arthropods constitute an important clade for documenting and testing macroevolutionary theories (Eldredge and Gould 1972; Foote 1991b, 1993). They appeared and diversified during the Cambrian explosion (ca. 521 Ma), and showed an important evolutionary success to become one of the major groups of the Early Palaeozoic. However, the Hirnantian mass extinction, recognized as the first, severely affected them, leading to a strong biodiversity decrease (Adrain et al. 1998). While the diversity remained relatively stable in the Silurian, the taxonomic richness changed importantly in the Devonian with the Pragian diversification followed by the Middle and the Late Devonian decline of diversity (Chlupáč 1994; Lerosey-Aubril and Feist 2012). These diversity changes took place in an unstable environmental context including quick sea-level fluctuations, anoxic/hypoxic events and climate upheavals (Walliser 1996; House 2002; Joachimski et al. 2009; Qie et al. 2019). These environmental events mainly affected the marine faunas and so the trilobites (Feist 1991; Lerosey-Aubril and Feist 2012), and triggered major biotic crises such as the Kellwasser events and the Hangenberg event, and subsequently major ecosystem restructuring (Raup and Sepkoski 1982; Buggish 1991; Sepkoski 1996; Bond and Grasby 2017). In the Late Palaeozoic, trilobites showed a low diversity, except for the last diversification in the Tournaisian, and they disappeared at the end of the Permian (Lerosey-Aubril and Feist 2012). Thus, the Devonian constituted a key period in the evolutionary history of trilobites with important increases and decreases of diversity.

At the macroevolutionary , the taxonomic component has been used traditionally as the major metric for a long time (Sepkoski 1978). However, numerous studies have shown the relevance of studying morphological disparity (Wills et al. 1994; Roy and Foote 1997; Foote 1997; Hopkins and Gerber 2017; Guillerme et al. 2020a) as an additional metric of biodiversity (e.g., Foote 1991a, 1993; Roy and Foote 1997; Neige 2003; Adams et al. 2004, 2013; Hopkins 2013; Minelli 2016; Jablonski 2019). Morphological changes could even be a better proxy to understand extinction events (Wan et al. 2021). While selective extinctions led to morphological losses, non-selective extinctions do not necessarily have the same effect (Foote 1991a; Puttick et al. 2020). Studies on trilobite morphology were one of the driving forces behind the development of disparity analyses, notably with the pioneering work of Foote (Foote 1989, 1990, 1991a). Further developments focused on modularity (Gerber and Hopkins 2011; Webster and Zelditch 2011; Oudot et al. 2019). Trilobites showed a constant rate of morphological evolution in the Cambrian (Paterson et al. 2019). With a rapid increase in morphological disparity early in their evolutionary history, trilobites reached maximum disparity in the Middle Ordovician (Foote 1991b, 1993; Webster 2007). Then, the morphological disparity decreased, rather slowly until the Late Devonian and then sharply until their disappearance at the Permian-Triassic boundary. Despite a slight increase of their morphological disparity during the Permian (Foote 1993), no significant increase has been observed in trilobites as a whole. However, at a smaller , trilobites could show reversible trends of morphological variation due to different factors (Webster 2007). Hopkins (2014) showed that environmental conditions affected morphologies, and that effects of some environmental parameters changed through time. Developmental constraints also affected trilobite morphologies (Hughes et al. 2006; Gerber and Hopkins 2011; Crônier 2013; Oudot et al. 2019).

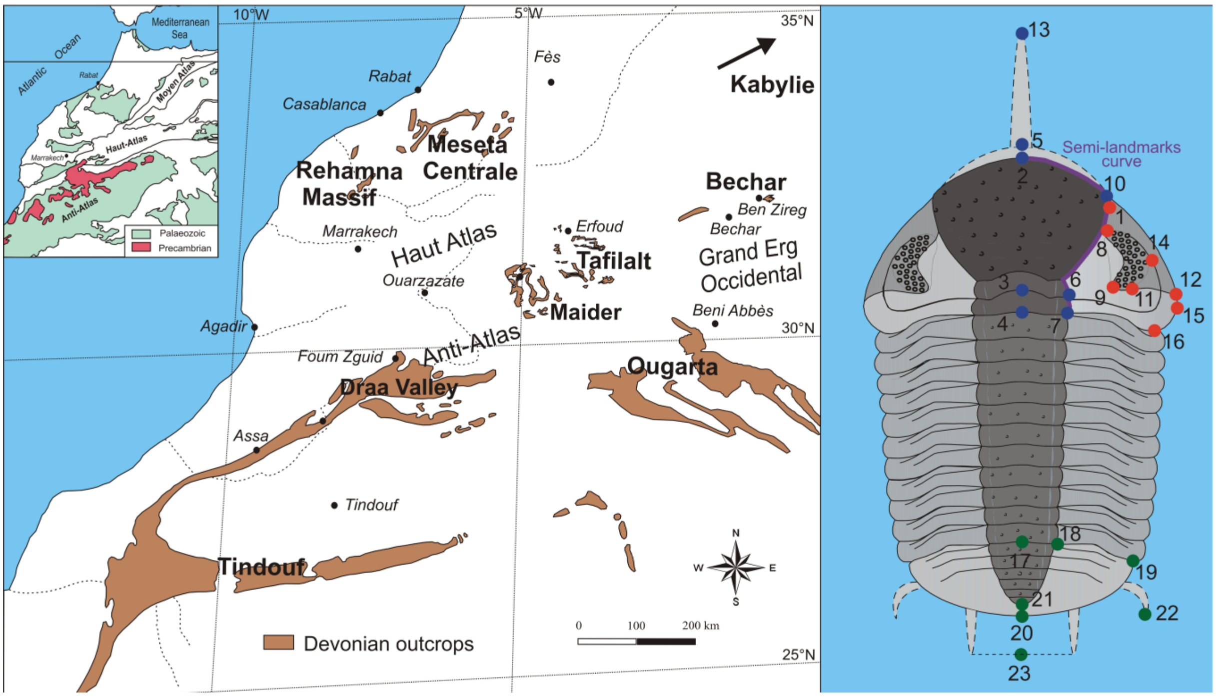
More particularly in the Devonian, trilobites were abundant, diverse and well preserved in North Africa. Due to their richness, they constitute an invaluable fossil record (Alberti 1969, 1981; Lebrun 2018). During the Devonian, North Africa was located in the northern margin of the Gondwana supercontinent, and most of the area was covered by epicontinental seas related to the Paleotethys Ocean (Guiraud et al. 2005). A major Early Devonian diversification was observed in this area before a decline in the Middle Givetian (Bault et al. 2021) related to environmental events (Kaufmann 1998). During the same period, numerous morphological innovations and morphological changes were also observed in trilobites in North Africa (Bault et al. submitted). Therefore, the present study provides a first comparison between the taxonomic diversity and the morphological evolution of trilobites during the Devonian and its unstable environmental context and global events (Joachimski et al. 2009; Becker et al. 2016). The relationship between these two metrics was investigated more accurately by using an updated dataset at the regional , in the well-documented North African fossil record, and using the stage as the temporal resolution . Comparing these two metrics leads to the exploration of large- biodiversity fluctuations, both in terms of patterns and processes, through time (Roy and Foote 1997) and space (Neige 2003).

## 2 Material and methods

### 2.1. Data

Based on North African specimens (Fig. 1A) of trilobites illustrated in the literature (Appendix A), we compared the morphological dataset used in Bault et al. submitted and the associated taxonomic dataset. Analyses were performed to analyse two key structures, i.e., the cephalon and the pygidium (Whittington et al. 1997). Because in the fossil record, cephala are more rarely preserved than cranidia (due to exuviation), cranidia on which numerous studies were done (Gerber and Hopkins 2011; Webster and Zelditch 2011; Hopkins 2013; Oudot et al. 2019) were added. Hopkins (2017) showed that morphological changes among cranidia depicted most of whole changes. From the literature, we selected the specimens with complete cephalon and/or complete cranidium and/or complete structure with a sufficient resolution to be analysed. We only used dorsal views and the right side (or the left side by using mirror image if the preservation was better) for each structure. Consequently, we analysed respectively 308 cephala, 943 cranidia and 604 pygidia for both diversity (i.e., taxonomic diversity) and disparity (i.e., morphological disparity) analyses. Only one cephalon and 35 cranidia used in our study correspond to early juveniles, i.e., meraspid stages, the rest of the dataset corresponds to late juveniles or adults, i.e., holaspid stages. Morphological changes studied correspond to adult morphological variations observed between holaspids and not to ontogenetic series.

***Figure 1.*** *(A) Geographical location of Devonian outcrops of North Africa (from Hollard, 1968) and*



*(B) complete chimeric exoskeleton of trilobite in dorsal view exhibiting eight landmarks for cephalon (in red), plus eight for cranidium (in blue), and seven for pygidium (in green); and some linear measurements. Modified from Crônier (2013).*

## 2.2. Geometric morphometrics and disparity indices

The three studied structures (i.e., cephalon, cranidium, pygidium) were investigated using geometric morphometrics with the acquisition of landmarks and semi-landmark coordinates (for a general overview of geometric morphometrics, see Adams et al. 2004). Twenty three landmarks and one semi-landmark curve were used to digitize each 2D shape from published illustrations. Fifteen landmarks were digitized on the cephalon, 7 on the cranidium and 7 on the pygidium (Fig. 1B; for a description of landmarks, see Bault et al. submitted). Six landmarks between the cephalon and the cranidium and the semi-landmark curve are common (Fig. 1B). The semi-landmark curve was automatically converted into a series of 16 points. The digitalisation was performed using the free software TPSdig 2.32 (Rohlf 2005, 2015); no landmarks were estimated. Landmarks are positioned on the key positions modelling trilobite shapes, known to be changed through time and between clades.

To standardize of the landmarks to remove the effect of size, location and orientation, they were processed using the Generalized Procrustes Analysis (Gower 1975; Rohlf and Slice 1990; Bookstein 1991; O'Higgins 2000; Zelditch et al. 2012). The superimposed landmarks are projected to a linear tangent space at the full Procrustes mean (Rohlf 1999).

In order to quantify accurately the morphological disparity changes through time based on the morphospaces, we used two disparity indices (Foote 1991a; Ciampaglio et al. 2001; Wills 2001; Guillerme et al. 2020b). Indeed, the disparity indices are essential to assess the different aspects of disparity changes (Puttick et al. 2020). Disparity measurement could be summarized in three different categories: the size, the density and the position of the morphological occupancy (Wills 2001; Guillerme et al. 2020b). Indices related to the size of the morphospace occupancy are the sum of range (SoR), the sum of variance (SoV), and the mean Euclidean distance from centroid (MECoid). The SoR is an index of magnitude, corresponding to the total range of morphospace occupancy. This index is particularly sensitive to the sampling effort (Foote 1991a) and could influenced by rare outlier morphologies (Deline 2009). The SoV is an index based on the variance of the specimen scores on each morphospace axis (Foote 1991b, 1993), measuring the average morphological dissimilarity among specimens. This index depends on the taxonomy (Foote 1991a). Nevertheless, to avoid such bias we studied all the specimens available with sufficient quality and not one specimen per taxa. The MECoid corresponds to the Mean Euclidean distances between all pairs of specimens of each geological stage. The Nearest-Neighbour Distance (NND) is used as an index of density, corresponding to the shortest Euclidean distance between two points of a distribution of points.

The sample size being not homogeneous between the different time bins, we computed morphological rarefaction in addition to the raw value per bin for each time bin studied. For this, for 1000 repetitions, we extracted smaller subsamples of the same size from a larger group without replacement and recalculated the morphological indices each time. Confidence intervals correspond to the 25 and 75 percentiles.

Environmental events are known to have an effect on the size of organisms, such as the size reduction known as the 'Lilliput Effect' (Harries and Knorr 2009). In a context of global environmental changes, we analysed whether size changes occurred in the Devonian. Specimen size was estimated as the natural logarithm of the centroid size (CS), i.e., the square root of the sum of squared distances of all the landmarks from the centroid. Logarithmic values allow size to be analysed into convenient values as previously done by Dommergues et al. (2002) on ammonoïds. Trilobite size is plotted using box plots.

### 2.3. Diversity indices and comparison with disparity values

We estimated the taxonomic richness of our dataset to compare the taxonomic diversity and the morphological disparity through time. Diversity was measured here as genus richness at the stage . Taxonomic richness was estimated with the Sample-in-bin diversity (SIB; Foote, 2000; Alroy, 2010) corresponding to the raw count of taxa actually documented (see Bault et al. 2021). To establish the comparison between the two metrics from the same North African area, we used the diversity curves obtained by Bault et al. (2021).

The strength of the correlation between diversity and disparity was tested between the disparity indices and the diversity indices. Correlations were made from the Ludlow to the Famennian except for the Frasnian, which is characterized by a lack of data. In order to have sufficient stages for our analyses, these statistics were based on raw diversity and not on rarefied diversity. Different correlations were made for the cephalon, cranidium and pygidium and in the same way, correlations were made for each disparity indices. The correlation index used is Kendall’s tau (Kendall, 1938) and *p* values are adjusted in case of multiple correlation to avoid false positives.

Finally, a comparison between morphological disparity and taxonomic richness increase during the early Devonian diversification has been done. SIB, SoR and SoV have been standardized and are compared each over. Jablonski (2017) suggested that a higher increase of morphology than diversity suggests a less constrained developmental processes or exceptional ecological opportunities. This type 1 diversification is typical of ‘early burst radiations’. Conversely, when the taxonomic diversification outstrips the morphological one, this type 3 diversification is rather a case of ‘nonadaptive radiation’. An intermediate diversification exists with concordant morphology and diversity increase, this is the type 2 diversification.

All analyses were computed using the R scientific environment (v. 3.6.2; R Core Team 2019; https://cran.r-project.org/) and the ‘geomorph’ (v. 3.2.1; Adams and Otarola-Castillo 2013) and ‘epaleo’ (v. 0.8.41; Monnet, unpub.) packages, as well as the PAST software (version 3.24; Hammer et al. 2001).

## 3. Results

### 3.1. Taxonomic diversity

The taxonomic richness showed the same trend between the three studied structures. Inherited from the reduced diversity of the Silurian, the diversity in the Lochkovian remained low, although it increased slightly especially for pygidia (Fig. 2). A sharp diversification occurred in the Pragian with an important increase of taxa followed by a slowdown in diversity variably marked according to the studied structures (less marked in pygidia, more marked in cephala). This slowdown did not prevent maximum diversity observed at the Emsian, illustrated by the impressive increase of the SIB index recorded through this stage (Fig. 2). Whatever the studied structure, the diversity began to decrease in the Eifelian before a severe decline in the Givetian. Finally, the trilobites did not recover their previous level of diversity despite a slight diversification in the Famennian.

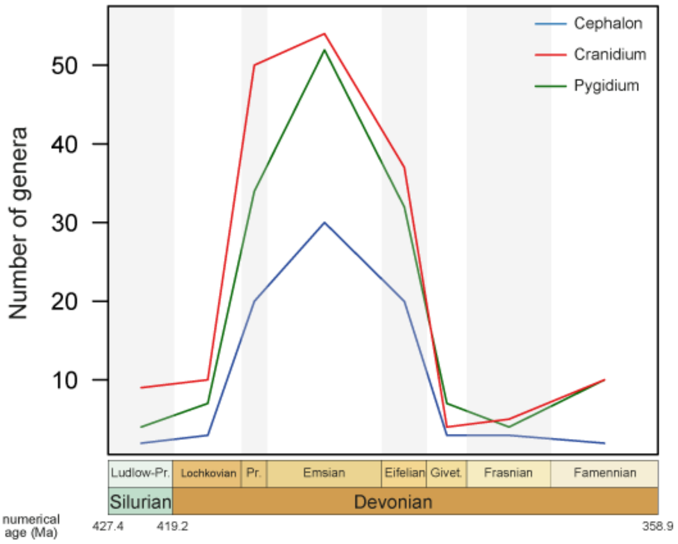


***Figure 2**. Diversity dynamics of Silurian and Devonian trilobites from North Africa. Number of genera per stage represented in each structure are represented in blue for cephalon; red for cranidium and green for pygidium. Modified from Crônier (2013). Ages from Cohen et al. (2013, v. 3/2020).*

### 3.2. Size of the morphospace occupancy

The morphological disparity indices fluctuated differently according to the three studied structures (Fig. 3). Both raw data and rarefacted values show the same trends. There was a low level of morphological extent in the Silurian characterized by very low values of SoR, SoV and MECoïd). An impressive increase of SoR index is recorded during the Lochkovian-Pragian (more impressive for cephala than cranidia or pygidia), which reflects the filling of the morphospace. In the same time, SoV and MECoïd increased for the cephalon and the

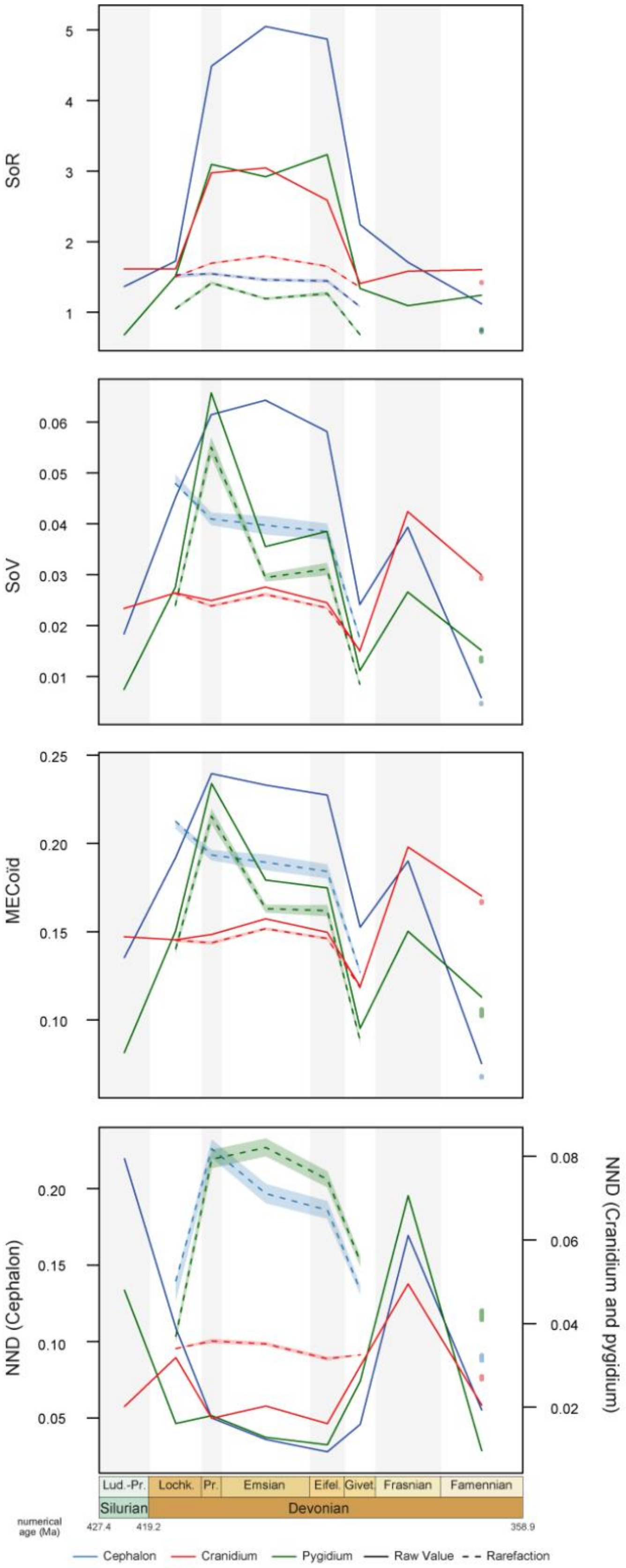


***Figure 3****. Morphological disparity indices according each structure of Silurian and Devonian trilobites from North Africa. Indices used are Sum of Ranges (SoR); Sum of Variance (SoV); Mean Euclidean distance from Centroid (MECoid) and the nearest Neighbour Distance (NND) and displayed for each stage.*

pygidium but not for the cranidium. While the total range of morphospace occupancy remained high during the Emsian for the three studied structures (high values of SoR, Fig. 3), only cephala were characterized by high values of SoV and MECoïd (Fig. 3). A morphological disparity peak occurred either in the Pragian or the Emsian depending on the metrics and the structure studied. Then, there was a slight decrease of morphospace occupancy in the Eifelian except for pygidia. A substantial decrease of SoR index is subsequently recorded during the Eifelian-Givetian (more impressive for cephala than cranidia or pygidia). A low level of morphological disparity characterized the Givetian (all indices, SoR, SoV and MECoïd, show very low values; Fig. 3): morphospace occupancy collapsed in the Givetian for all structures. Then, a moderate but significant increase of the morphological disparity is observed during the Frasnian (increase of SoV and MECoïd index for the three studied structures). Only a moderate but significant decrease of the SoR index is recorded in cephala and cranidia, while an increase is recorded in pygidia. Nevertheless, in the absence of a sufficient number of specimens, this trend remains highly uncertain and should be treated with caution. In the Famennian, while the total range of morphospace occupancy continued to decrease for cephala compared to the Givetian (lower values of SoR, SoV and MECoïd, Fig. 3), cranidia and pygidia show moderate increasing morphological disparity indices. Both SoV and MECoïd indices show roughly similar trends (Fig. 3).

### 3.3. Density of the morphospace occupancy

The NND used as indicator of the density of the morphological occupancy is strongly influenced by the sampling effort (Fig. 3). For this index, raw values seem more reliable than rarefaction ones because the diversity was different between stages and thus the density is strongly modified in the case of a rarefaction method based on a same virtual abundance between stages. This is probably why it is the only index showing different trends between raw data and rarefaction data. The raw NND index sharply decreased in the Lochkovian for both cephala and pygidia, while it increased for cranidia. As was the case for morphological occupancy indices, this density index shows an opposite trend for cranidia, for which it increased. Rarefacted NND also increased for the cranidium, but for the cephalon and the pygidium too. In the Pragian, the NND index shows very low raw values for the three studied structures suggesting a relatively low morphological disparity, whereas the rarefaction data show exactly the opposite, suggesting an evolution from depopulated Lochkovian assemblages to rich Pragian ones. Rarefaction and raw values are maintained at a plateau during the Emsian and Eifelian, two periods where many specimens were encountered in North Africa. The NND index subsequently increased during the Givetian and the Frasnian, followed by a decrease in the Famennian, although rarefaction values indicate the opposite. As with the other indices, the lack of specimens in the Frasnian prevents us from drawing robust conclusions.

### 3.4. Correlation between diversity and disparity indices

Correlations (see Table 1) between the various disparity and diversity (i.e., number of genera) indices were computed. For cephala, diversity trends are correlated to disparity trends, using SoR and SoV (*p*-value = *0.005*, Kendall's tau *t* = *0.93*), MECoïd and NND ($p < 0.05$). For cranidia, disparity and disparity trends are uncorrelated using SoV, MECoïd and NND ($p > 0.05$), except for SoR (*p*-value = 0.021). For pygidia, disparity and disparity trends are uncorrelated, using SoR and NND ($p > 0.05$), but the SoV and MECoïd are correlated to diversity trends ($p < 0.05$). Size of the trilobites was not correlated to diversity whatever the structure studied.

| | SoR | | SoV | | MECoïd | | NND | | CS | |
|---|---|---|---|---|---|---|---|---|---|---|
| | P | Tau | P | Tau | P | Tau | P | Tau | P | Tau |
| Cephalon | 0.005 | 0.93 | 0.005 | 0.93 | 0.013 | 0.82 | 0.041 | -0.68 | 0.351 | 0.31 |
| Cranidium | 0.021 | 0.75 | 0.120 | 0.51 | 0.282 | 0.35 | 0.167 | -0.45 | 0.645 | 0.15 |
| Pygidium | 0.129 | 0.49 | 0.033 | 0.68 | 0.015 | 0.78 | 0.224 | -0.39 | 0.129 | 0.49 |

***Table 1.*** *Correlation results between diversity and each morphological disparity index. P values adjusted and Kendall's tau for each structure are displayed.*

### 3.4. Diversification modes

The morphological disparity for the cephalon, the cranidium and the pygidium increased rather correlatively during the Early Devonian diversification (Fig. 4). This places the Devonian trilobites of North Africa in the type 2 diversification of Jablonski (2017). Nonetheless, the SoV of the cephalon and the cranidium showed higher variation than the taxonomic richness, suggesting a potential type 1 diversification. Conversely, the SoV of the pygidium less increased than the diversity index, indicating a link with the type 3 diversification.

### 3.6. Size range

In the Silurian, the trilobites exhibited large cephala (and also large cranidia) but small pygidia. Cephala and cranidia are characterized by high values for median size and an

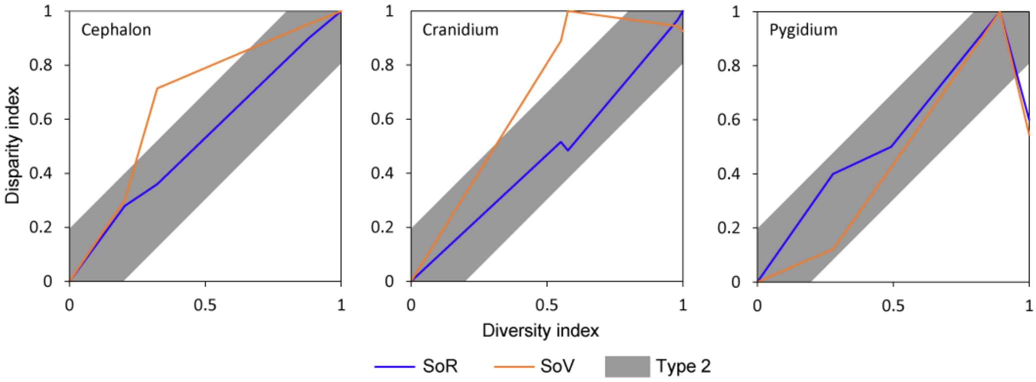


***Figure 4**. Diversity-disparity space (Jablonski, 2017) of the relation between taxonomic and morphological diversification of Devonian trilobites from North Africa. Type 1: Dominance of morphological diversification; Type 2: Morphology concordant with taxonomic diversification; Type 3: Dominance of taxonomic diversification.*

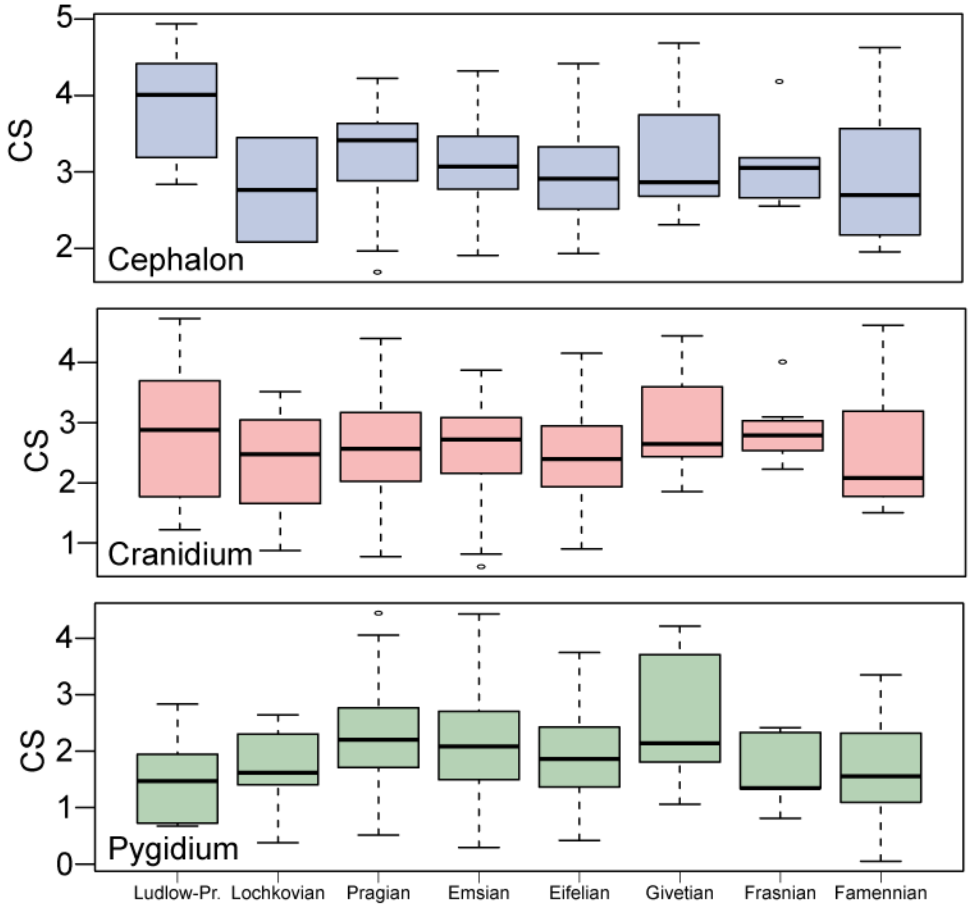


***Figure 5.** Centroïd size through time of Silurian and Devonian trilobites from North Africa for each structure (i.e., cephalon; cranidium and pygidium).*

expanded size range. Subsequently, for cephala as for cranidia, the median size (according to CS) decreased strongly in the Lochkovian, while for pygidia, the median size increased moderately (Fig. 5): there was a loss of trilobites with larger cephala. In the Pragian, an increase in the median size began for cephala (and for cranidia) and continued for pygidia: trilobites exhibited large morphologies, and pygidia were larger than those found in the Silurian. No particular size changes are noticed in the Emsian, and only a slight size reduction for both cephala (and cranidia) and pygidia is recorded in the Eifelian. Major size changes are recorded in the Givetian with a more important size range towards large trilobites with large cranida and pygidia although the median size remains similar to the size recorded in the Emsian. In the Frasnian, only pygidia show a median size reduction. Nevertheless, compared to the Givetian, cephala and cranidia show an impressive reduction in the size range with the disappearance of the largest morphologies. Subsequently, in the Famennian, cephala (and cranidia) recorded an impressive reduction of the median size (not observed in pygidia) and show a significant increase of their size range of the same order of magnitude as that observed in the Silurian or the Lochkovian (Fig. 5).

## 4. Discussion

### 4.1 Diversification: diversity *vs*. disparity

Both morpholological disparity and taxonomic richness were very low at the end of the Silurian. Then, trilobites underwent two periods of diversification in the Devonian, in North Africa as well as at the global (Chlupáč 1994; Lerosey-Aubril and Feist 2012; Bault et al. 2021): in the Early Devonian and in the Famennian. However, these two periods of diversification diverge by their intensity and duration.

In the Early Devonian, the morphological disparity slightly increased in the Lochkovian, but the most important diversity and disparity rise occurred in the Pragian. This stage corresponded to the onset of the Early Devonian diversification (Chlupáč 1994), which arose with the Basal Pragian event, a regression that led to the development of shallow carbonate environments (Chlupáč and Kukal 1986). The morphospace density also progressively increased in the Lochkovian and the Pragian, particularly for the cephala, suggesting the proliferation of taxa with similar shapes. This corresponded especially to the proliferation of some families such as proetids, tropidocoryphids, phacopids and scutelluids (Bault et al. 2021). Simultaneous increase in diversity and morphological disparity could indicate adaptive radiation (Foote 1993, 1997). A morphological disparity increase is generally linked to an ecological disparity increase (Cole and Hopkins 2021), although Bapst et al. (2012) emphasized the necessity to perform more detailed analyses to confirm this theory. With the establishment of new areas in North Africa (Morzadec 2001; Bault et al. 2021), clades rapidly colonised new territories and expanded both in terms of diversity and disparity. Such colonisation has been recognized as the empty ecospace hypothesis (Erwin 1993; Ciampaglio 2002; Hughes et al. 2013; Novack-Gottshall 2016). Exceptional ecological opportunities could even lead to a higher rate of morphological evolution during a diversification (i.e., Type 1 diversification, Jablonski 2017). However, Devonian trilobites were rather in a case of concordant morphological and taxonomical diversification (i.e., Type 2 diversification, Jablonski 2017), an intermediate diversification between 'early burst diversification' and 'nonadaptive radiation' (Jablonski 2017). Nevertheless, it implied a radiation favoured by new environmental niches (Chlupáč 1994). In addition, the exoskeleton enlarged in the Pragian, particularly that of cephala and pygidia, while the cranidia retained their Lochkovian size. This was the consequence of the appearance of spines (Bault et al. submitted).

With the maintenance of favourable environments, particularly in North Africa, the trilobites continued to diversify until they reached a diversity peak in the Emsian (Chlupáč 1994; Bault et al. 2021). During this period of intense taxonomic diversification, the morphological disparity still increased for both cephalon and cranidium. An increase of the size of the morphospace (i.e., SoR) shows that the increase of disparity corresponded to the appearance of new morphologies on the edges of the pre-existing morphospace (Ricklefs and Miles 1994; Roy and Foote 1997), in particular morphologies with both sagittal and genal spines (Bault et al. submitted). The proliferation of morphologies with spines among Early Devonian trilobites was interpreted as a potential response to increasing nektic predation (Brett 2003) in the frame of the Devonian Nekton Revolution (Klug et al. 2010). Moreover, the proliferation of scutelluids contributed to the extension of the morphospace occupancy with the development of long sagittal pygidia with a small rachis (Bault et al. 2021).

On the other hand, decrease of ecological opportunities slow-down the rate of morphologic evolution (Mahler et al. 2010; Hopkins 2013). Trilobites having invaded most of the ecological niches appeared in the Pragian (Chlupáč 1994), it may explain the lower increase in disparity in the Emsian (or even the decrease depending on the structure and the metric observed). Indeed, the pygidium reached its maximum disparity from the Pragian onwards, while the cephalon continued to innovate until the Emsian. In the case of an adaptive radiation, trilobites still diversified morphologically but the novelties were concentrated on the cephalon. Hence, the morphological disparity of the pygidium and the cephalon became decoupled. This explains why both cephalon and cranidium were closer to the Type 1 diversification of Jablonski (2017), whereas for the pygidium, the morphological diversification was lower than the taxonomic one. A greatest cephalon diversification was possible because the cephalon was devoted to a wider range of tasks, including feeding habits (Fortey and Owens 1999) and visual ability (Clarkson 1975; Schoenemann 2021).

The second period of diversification that occurred in the Famennian (Lerosey-Aubril and Feist 2012; Bault et al. 2021) was less intense than the Early Devonian diversification. The Famennian peak of taxonomic richness occurred after a period of low diversity due to the Kellwasser events (Feist 1991; Chlupáč 1994; Lerosey-Aubril and Feist 2012; Bault et al. 2021). In contrast to the Early Devonian diversification, where five orders contributed to diversity peaks, only two orders (i.e., Phacopida and Proetida) were responsible for the Famennian diversity peak. The Famennian recovery was not accompanied by a development of new morphologies except a slight increase of the cranidium and pygidium disparities. The decrease in the morphospace density suggests a clustering trend among the Famennian trilobites (Foote 1990; Wills 2001). The absence of a disparity burst after the Kellwasser mass extinction indicate that biological constraints such as competing clades did not disappear (Oyston et al. 2015). A recovery with few innovations was also reported in other clades like graptolites (Bapst et al. 2012).

### 4.2. Extinctions and recoveries: diversity *vs*. disparity

The diversity strongly dropped during the Middle Devonian of North Africa. At the global , the Middle Devonian ecosystem faced several extinction events, i.e., the Eifelian Choteč and the Kačák events and the Givetian Taghanic event (Walliser 1996; House 2002). Sea-level rise and anoxic/hypoxic conditions characterized these events (Kaufmann 1998; House 2002). At the North African , these successive events led to the loss of many genera and families within trilobites (Bault et al. 2021). This decrease began in the Eifelian to reach a minimum of diversity in the Givetian. The morphological disparity was not affected immediately and most of the morphospace occupancy persisted in the Eifelian. Nevertheless, the acceleration of the extinctions in the Givetian strongly influenced trilobite morphological disparity. Therefore, although the Choteč event greatly affected the Moroccan area (Becker and Aboussalam 2013), the following Kačák and Taghanic events had a stronger effect on trilobite morphologies. In particular, the Taghanic event corresponded to a global faunal overturn due to rapid eustatic changes and overheating pulses and affected Moroccan trilobites (Aboussalam and Becker 2011). This delay in the morphological loss was not specific to trilobites. Among macrobenthos, diplobathrid crinoids showed the same pattern with only a slight morphological loss in the Eifelian despite an important diversity decrease and the main morphospace collapse that occurred only later, in the Late Devonian (Cole and Hopkins 2021). Through the Late Ordovician extinction, graptolites also underwent a decrease of diversity before the morphological disparity drop (Bapst et al. 2012). On the other hand, in ostracods, the morphological disparity declined before the taxonomic richness during the end-Permian mass extinction (Wan et al. 2021). Henceforth, the Middle Devonian events led to several shape losses among trilobites resulting in a collapse of the morphological range and a strong decrease of the variance. These changes indicate a non-random extinction (Ciampaglio et al. 2001) contrary to the Early Palaeozoic decline during which the extinctions were not morphologically selective and so the disparity and diversity were decoupled (Foote 1991a, 1993; Hopkins 2013). The shape losses among trilobites correspond especially to the disappearance of trilobites with genal spines as the aulacopleurid *Cyphaspides* Novák, 1890 or the asteropygin *Mrakibina* Morzadec, 2001 (Morzadec 2001; Chatterton et al. 2019).

The Frasnian-Famennian trends were more difficult to analyse because of the lack of data in the Frasnian. North African trilobites seem to lose their morphological disparity through the Late Devonian extinction, i.e., the Kellwasser events, which was one of five major extinction events in the life history on Earth (Buggisch 1991; McGhee 1996; Racki 2020). The cephalic morphologies were the most affected, notably with the disappearance of the remaining spiny shapes such as the genera *Gondwanaspis* Feist, 2002 or the trilobites with large cephalic shields such as harpetids (Feist 2002). The density of morphologies seemed not strongly affected by this decrease, suggesting only marginal or lateral extinctions (Foote 1991a; Korn et al. 2013). Consequently, not all the trilobite taxa were affected in the same way. In North Africa as at the global , the most impacted taxa were member of the orders Lichida, Odontopleurida, Harpetida and Corynexochida, which disappeared before the Famennian (Feist 1991; Lerosey-Aubril and Feist 2012; Bault et al. 2021).

In addition to the effects of extinctions, ecological constraints can limit the morphological disparity (Oyston et al. 2015). Thus, sea–level rise and a long-term eustatic rise affected the Middle and Late Devonian faunas (Johnson et al. 1985; Kaufman 1998; House 2002) and led to a decrease of the trilobite speciation rate by increasing range expansion (Abe and Lieberman 2009). The morphological disparity was also partly linked to environmental heterogeneities or changes (Hopkins 2014; Bault et al. submitted); a harmonization of environment led to a decrease in the morphological range. However, ecological stresses induced by unfavourable environmental changes could lead to increasing intraspecific variability (Crônier et al. 2015). Such ecological stresses could be induced by the development of potential predators in the second half of the Devonian leading to selective extinction. Non-random extinction is consistent with standard environmental changes, whereas catastrophic events such as the end-Permian extinction were non-selective (Villier and Korn 2004). Moreover, a potential saturated taxonomic richness could favour such a decline, while the diversity reached its maximum during the Emsian (Bault et al. 2021). A self-regulation in a period of high diversity has been previously reported among trilobites (López-Villalta 2016).

Although most innovations occurred during the diversification phase of the Devonian (see previous section), some of them occurred during periods of low diversity across environmental events. The most emblematic case was the strong development of reduced-eyes and blind trilobites in the Late Devonian (Crônier et al., 2004; McNamara and Feist, 2006, 2016; Schoenemann 2018; Feist 2019; Bault et al. 2021). These morphological novelties were the consequences of ecological changes as deepening and turbiditic habitats for endobenthic behaviours (Feist and Clarkson 1989; Feist et al. 2009). In North Africa, this trend was represented by the development among others of the blind genera *Dianops* Richter and Richter, 1923, *Trifoliops* Crônier, 2003, *Trimerocephalus* McCoy, 1849 and *Palpebralia* Richter and Richter, 1927 (Feist 2002; Crônier et al. 2013; Feist et al. 2016). However, despite the availability of ecospace after mass extinctions (Erwin 2015), no extensive morphological innovations occurred, and in North Africa, the Famennian morphological disparity of trilobites remained similar to the Frasnian values. At the global , the morphological innovations occurred later after the Kellwasser crisis, unlike the subsequent Hangenberg event for which the morphological innovations occurred immediately after (Feist 1991).

Following a biotic event, some clades showed a trend to decrease in size, known as ‘Lilliput effect’ (Harries and Knorr 2009). This trend was recorded for different crises and different clades (Twitchett 2007; Song et al. 2011; Brom et al. 2015; Berv and Field 2018; Wiest et al. 2018 among other) among which are some arthropods (Forel et al. 2015; Chu et al. 2015; Martínez-Díaz et al. 2016). However, a ‘Lilliput effect’ has not yet been reported under this name among trilobites although a decrease in size affected trilobites as a whole, for example in Norway in the Late Ordovician (Sigurdsen and Hammer 2016). In the Devonian, such decrease in size was reported in other clades during the early Givetian (Bosetti et al. 2011; Comniskey et al. 2016; Zhuravlev and Sokiran 2020) or in the external platforms after the Taghanic transgression of the mid-Givetian within trilobites (Crônier 2013). Before the Taghanic transgression, trilobites were characterized by their large size and the genera *Hypsipariops* Struve, 1982 and *Drotops* Struve, 1990 (Struve 1995) were among the largest Devonian trilobites. In a context of sea-level rise, presence of large trilobites could have resulted the invasion of deep environments like North African Ordovician trilobites (Saleh et al. 2021).

However, in this case, these phacopids represent assemblages adapted to unstable, high energy environments of shallow internal platforms. They are morphologically characterized by their large, wide and high reniform eyes with numerous lenses, their developed tuberculation and their multisegmented pygidium (Crônier 1999; Crônier and Courville 2003; Crônier 2013). In the Eifelian and in the Famennian, the average size decreases, but only slightly, and large trilobites remained present. Hence, it appears that no 'Lilliput effect' affected North African trilobites throughout the Middle and the Late Devonian events. The late Frasnian Kellwasser events were not characterized by decrease of trilobite size no more than Russian microconchids (Zatoń and Krawczyński 2011) or crinoids, which even experienced body-size increase (Brom et al. 2018). However, our study focused on trilobites as a whole and at the stage level which might not precise enough to identify such a pattern.

### 4.3 Coupled diversity and disparity trends?

At the global , during the Palaeozoic, the Early Devonian represents the second most important period of diversification, after the initial Cambrian radiation (Adrain 2008). This bimodal evolutionary radiation was not unique, being found in other taxa (i.e., dinosaurs, crinoids) and periods (i.e., Mesozoic and Cenozoic) (Romano et al. 2018; Romano 2021). The Devonian diversification was different to the Early Palaeozoic diversification for which diversity and disparity were decoupled (Foote 1993). The Cambrian-Ordovician was the early period of the trilobite evolutionary history, and the increase of their diversity corresponded to the appearance and the development of new orders (Fortey 2001; Paterson et al. 2019). The Devonian diversification, on the other hand, involved high taxonomic ranks (family and above) that already existed before (Chlupáč 1994). This difference could explain why morphological innovations stopped increasing at the same time as diversity during the Devonian Period. In addition, trilobites exhibited greater morphological variation early in their evolutionary life (Webster 2007), and thus, during the Cambrian, their morphologies were less constrained during their ontogenetic development than later during the Devonian (McNamara 1986; Hughes 1991, 2007). The moulting behaviour showed the same decreasing pattern with the disappearance of ventral sutures and the increasing importance of the cephalon moulting to the detriment of the other moulting characteristics (Drage 2019). Thus, the concordant increase in diversity and disparity observed during the Devonian diverge from the 'early burst' diversification characterised by high rates of disparity increases observed during the Cambrian-Ordovician (i.e., Type 1 diversification of Jablonski (2017)). Because a higher level of constraint limits innovations (Oyston et al. 2015), the morphological disparity did not increase after the Emsian diversity peak. This pattern was already reported among trilobites during the Ordovician diversification when Phacopida showed simultaneous morphological and taxonomical changes (Foote 1993). Cole and Hopkins (2021) also noticed coupled diversity and morphological disparity dynamics among diplobathrid crinoids during the Palaeozoic.

The Early Palaeozoic and the Devonian also differ according to their timing of the end-diversification. In the Early Palaeozoic, after the taxonomic richness peak, trilobite diversity decreased progressively before a stronger decline in the Hirnantian (Adrain et al. 1998; Sheehan 2001; Fan et al. 2020). Conversely, in the Devonian, trilobite diversity decreased sharply (Lerosey-Aubril and Feist 2012). This dynamic was not specific to trilobites because the crinoid and conodont diversifications were also interrupted by the Devonian extinction events (Ginot and Goudemand 2020; Cole and Hopkins 2021). Consequently, the increase in disparity in the Devonian could be stopped during its rise and the coupling between changes in diversity and disparity would be a false pattern.

### 4.4. Dynamics and macroevolutionary patterns

Maximum morphospace occupancy occurred in the Early Devonian and then, decreased consistently from the Eifelian onwards until the Famennian. The morphological disparity changes were consistent with the diversity fluctuations (Feist 1991; Chlupáč 1994; Lerosey-Aubril and Feist 2012; Bault et al. 2021). Gould et al. (1977) defined an index to identify if the clades were more diverse before, after or midway through their evolutionary history. Although the Early Palaeozoic clades, including trilobites, showed greater diversity in their early evolutionary history and are characterized as ‘bottom-heavy’ clades (Gould et al. 1987), North African trilobites showed an increase in both diversity and morphological disparity in the Devonian, from the Pragian. Such diversification was unusual because it involved families and subfamilies which appeared in the Ordovician more than 35 Myr before, such as phacopids, proetids or acastids (Adrain 2013). Hence, most Silurian and later clades had higher taxonomic richness midway through their history, and are characterized as symmetrical clades, or later through their history and are characterized as top-heavy clades (Gould et al. 1987).

In Macroevolution, evolutionary rates are often higher in the early history of clades (Hughes et al. 2013) because of a slowdown due to an important morphological space saturation (Foote 1994; Villier and Eble 2004), diminishing ecological opportunities through time (Erwin 1993; Foote 1997) and internal constraints (Wagner 2000; Oyston et al. 2015). However, the evolutionary rates varied through time, and other patterns such as ecomorphological shifts occurred (Hopkins and Smith 2015). The widening of favourable environments since the Pragian (as discussed above) promoted a morphological and taxonomical diversification with new ecological niches. Phenotypic plasticity could foster diversity increase with new environmental opportunities, although its role on disparity remaining uncertain (Minelli 2016). However, phenotypic plasticity seemed less important among Devonian trilobites (McNamara 1986; Hughes 1991, 2007; Webster 2007), although with respect to Devonian trilobites it remains largely unexplored and needs more investigation. Subsequently, a strong decline of diversity and morphological disparity occurred in the second part of the Devonian. Most of the trilobite families disappeared before the Carboniferous with the exception of proetids (Lerosey-Aubril and Feist 2012), confirming that Devonian trilobite families did not constitute a Bottom-heavy clade but rather a Symmetrical or a Top-heavy clade.

After the peak of both diversity and disparity in the Emsian, trilobites strongly declined and never reached their previous taxonomic and morphological richness. The Middle Devonian extinctions occurred at both regional and global  at low taxonomic ranks among trilobites (Lerosey-Aubril and Feist 2012; Bault et al. 2021). However, the demise of several families and orders occurred later, in the Frasnian (Feist 1991). Some extinctions led to evolutionary bottlenecks with a reduction of the morphological and taxonomic diversification afterwards, like the Late Devonian extinction (Sallan and Coates 2010; Cole and Hopkins 2021). Conversely, the disappearance of taxa can trigger new diversification events leading to increase the ecological opportunities (Erwin 1993, 2001). With regard to the trilobites in particular, the Devonian extinctions hampered the subsequent great diversifications (Lerosey-Aubril and Feist 2012) and the new opportunities were not sufficient to reverse this trend, as for Early Triassic anomondonts (Ruta et al. 2013). This delay places many trilobite taxa among the Dead Clade Walking (DCW) of Jablonski (2002). Only the order Proetida, which showed another important diversification later, in the Tournaisian (Lerosey-Aubril and Feist 2012), did not exhibit a DCW pattern. Because Phacopida survived more than one stage after the Middle Devonian extinction, they were not a DCW strictly speaking (Jablonski 2002) but they showed a similar pattern. Nevertheless, Barnes et al. (2021) extended the concept to longer duration, impacts of mass extinction having longer influence than expected. This is partly due to the long-term impact of selective extinctions on the trait distributions of later species (Puttick et al. 2020). Although trilobites slightly recovered after the Kellwasser events (Feist 2019), they remained poorly diversified in the Famennian in North Africa (Fig. 2, Bault et al. 2021) as well as at the global (Feist 1991; Chlupáč 1994). On the contrary, many clades recovered strongly in the Famennian, among which are many nektic organisms (Klug et al. 2010) and some benthic organisms such as echinoderms (Waters and Webster 2009). Other taxa (i.e., brachiopods for instance (Baliński 2002; Curry and Brunton 2007)) were less affected and remained quite diverse despite extinction as they recovered quickly. The Late Devonian events led to bottleneck periods for the trilobites but also for other organisms such as diplobathrid crinoids, which vanished in the Carboniferous after having come close to extinction in the Devonian (Cole and Hopkins 2021). This trend suggests that trilobites were a major clade during the first half of the Palaeozoic but not at the end-Palaeozoic although they survived until the Permian with few periods of diversification (Lerosey-Aubril and Feist 2012). Apart from proetids, trilobites are a Dead Clade Walking (Jablonski 2002; Barnes et al. 2021).

## 5. Conclusion

Trilobites proliferated in North Africa during the Devonian. As on a global , there was an important Early Devonian diversification which led to both an increase of taxonomic richness and morphological disparity. Several innovations occurred, including coupled increases, favoured by welcoming environmental conditions and changing ecological conditions. Because the Early Devonian diversification involved families existing for several million years, the Devonian trilobite families were a Bottom-Heavy clades, characterized by a late diversification. Coupled increases in diversity and morphological disparity are not common in the fossil record and can be explained by the higher morphological constraint in the late evolutionary history of the clade. Another explanation is that the disparity peak could be interrupted by the Middle Devonian extinction. Indeed, the Middle and Late Devonian events affected North African trilobites and the diversity decreased since the Eifelian. At the same time, there were important shape losses, but the majority of losses occurred later, in the Givetian. Lateral extinctions in the morphopace occurred, indicating non-random extinctions in the context of environmental changes, including sea-level variations. Devonian trilobites maintained a relative uniform size throughout the Devonian and no real ‘Lilliput effect’ occurred after extinctions. After the Kellwasser events, another diversification occurred in the Famennian, of a less intensity. Because the trilobites survived for a long time at low level of diversity, in the Middle and the Late Devonian, we can consider them as a Dead Clade Walking.

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## 2.4. Influence de la paléogéographie et de la tectonique sur la répartition des trilobites du Maroc et du Nord-ouest de l'Algérie

Article 6 : The influence of palaeogeography and tectonic events on trilobite distributions in Morocco and north-western Algeria

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# The influence of palaeogeography and tectonic events on trilobite distributions in Morocco and north-western Algeria

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## ABSTRACT

The effects of sea-level changes and anoxia on Devonian trilobites have been studied for a long time but the importance of palaeogeographic and tectonic events in this key-period is still not well understood. In the Devonian, trilobites invaded many different marine environments and areas in North Africa where important palaeogeographic changes occurred. Distribution patterns of trilobites through time and space have been analysed using a hierarchical cluster analysis and diversity indices. Our examination of the literature suggests that trilobites were scarce during the Lochkovian before an important diversification, which occurred during the Pragian. Trilobites flourished in many North African regions without there being important taxonomic differences between basins, because of free migration in relatively flat palaeo-topography and homogeneous environments. During the Middle Devonian, early Variscan tectonic movements transformed the Eastern Anti-Atlas area into a basin with a platform topography. Geographical barriers such as deep basins prevented trilobite migrations. At the beginning of the Eifelian, the reduction of migration between the different regions of this area coincided with a decrease in diversity. Consequently, tectonic events played an important role in the decline of trilobites during the Middle Devonian, especially when these were combined with sea-level changes and anoxic/hypoxic events. A recovery occurred in the Famennian involving only new genera. As at the global , cyrtosymbolines developed in shallow seas whereas phacopids evolved in deeper environments. The basin and platform system still hampered migrations although sea-level variations led to episodic exchanges. The late Famennian regression reduced trilobite diversity and abundance dramatically in the study area.

**Keywords:**
Arthropods, Anti-Atlas, associations, diversity, faunal succession, tectonic, palaeobiogeography

## 1. Introduction

During the Devonian, trilobite communities were strongly influenced by spatial and temporal ecological changes at the global as well as regionally (Crônier & Van Viersen, 2007; Abe & Lieberman, 2012; Crônier & François, 2014; Bignon & Crônier, 2015). The development of hospitable shallow platforms during the Early Devonian led to a trilobite diversification (Chlupáč, 1994) but the sea-level changes and anoxic/hypoxic events during the Middle Devonian caused a sharp decrease of their diversity (Feist, 1991; Lerosey-Aubril & Feist, 2012). These kinds of spatial and temporal palaeoenvironmental changes were observed in the trilobite communities from North Africa (Bault et al., 2021). This area was located on the continental shelf of north-western Gondwana (McKellar & Chatterton, 2009) and was flooded during the Silurian transgression (Bultynck & Walliser, 2000) leading to a Devonian epicontinental sea (Kauffman, 1998). Thus, an abundant and diverse trilobite fauna proliferated during the Early Devonian before a long decline due to events that occurred during the Middle and Late Devonian.

To understand the trilobite response to palaeoenvironmental changes and their biodiversity dynamics at a regional , our study is focused on the Devonian North African communities from two well-known areas, i.e., the Moroccan Anti-Atlas and the Algerian Ougarta Range. These two areas are famous for their detailed stratigraphy, their numerous faunal studies and their recognised environmental changes (Wendt et al., 1984; Wendt, 1985, 1993, 2021a, 2021b; Wendt & Belka, 1991; Benhamou et al., 2004; Ouali Mehadji et al., 2011; Abbache et al., 2019; Frey et al., 2019). The trilobite fauna from this North African area was first studied by Le Maître (1952) followed by numerous publications by G. Alberti (e.g. 1964, 1966a, 1966b, 1967a, 1967b, 1969, 1970, 1981a, 1981b, 1982, 1983) and H. Alberti (e.g. 1972, 1973, 1974, 1975a, 1975b, 1976a, 1976b). This area is still studied nowadays as is reflected in more recent publications by Becker et al. (2018), Crônier et al. (2018a-b), Feist & Belka (2018), Feist & Weyer (2018), Zaplaski & Klug (2018), Van Viersen & Lerouge (2019) and Chatterton et al. (2020). There were many taxonomic changes in the study area throughout the Devonian including periods of great taxonomic diversity among the trilobites, following trends identified on a global  (Chlupáč, 1994; Bault et al., 2021). The Anti-Atlas Range and Ougarta Range also provided a high diversity of environments exhibiting temporal and geographical changes because of sea-level fluctuations. The Variscan tectonic events led to different palaeotopographies (Hollard, 1967, 1981; Wendt, 1985; Bultynck & Walliser, 2000).

The present work concentrates on trilobite occurrences to analyse the dynamic of trilobite faunas confronted with environmental changes in time and space and to thus understand how the diversity of trilobites may be influenced by the diversity and nature of environments. Trilobite associations were determined by performing multivariate analyses before their diversity and ecology were assessed.

## 2. Geological settings

The Moroccan study area, i.e., the Anti-Atlas Range, extends from the Dra region in the south-west toward the north-east, to the Tafilalt in Morocco and ends below the Bechar Basin in Algeria (Hollard, 1967). The Algerian study area, i.e., the Ougarta Range (Saoura Valley, North-western Algerian Sahara), extends towards the north-west, in the Anti-Atlas (Fig. 1A). During the Devonian, the study area included numerous marine basins, which were part of the Sahara platform, a passive continental margin of Gondwana (Wendt et al., 1984). From the south-west toward the north-east, these basins are the Foum Zguid area, the Maïder Basin and Tafilalt Basin in the eastern Anti-Atlas in Morocco, the Ougarta Basin and to the North the Bechar Basin (i.e., Ben Zireg area) in Algeria (Fig. 1B).

The current correlation based on conodonts between the Tafilalt and the Maïders (Bultynck & Walliser, 2000) is associated here with their main environmental characteristics (Fig. 2). The succession ofs of Ougarta was described by Boumendjel et al. (1997). Although the connection between the Devonian strata of the Ougarta Range and those of the Anti-Atlas region are is covered by the Cretaceous ‘Kem-Kem Group’ (Benhamou et al., 2004), the similar basinal facies found in these areas suggests a connection during the Devonian (Hollard, 1967; Wendt et al., 1984). The northern and western parts of the Maïder region were continental during the main part of the Devonian and were only flooded during the Famennian when the sea level rose (Kaufmann, 1998). Figure 2 summarises thes studied along with their dominant lithologies (Fig. 2).

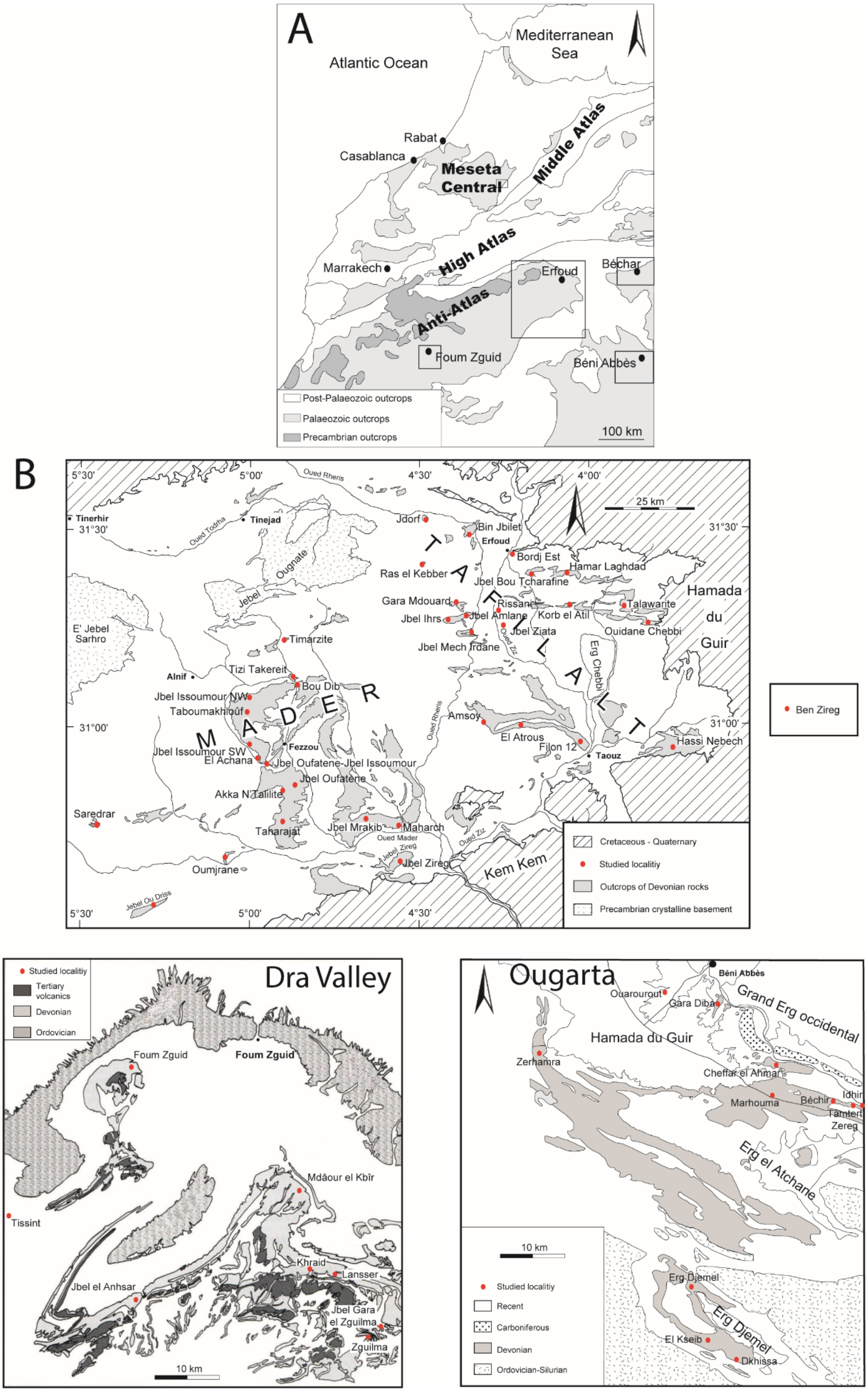

***Fig. 1.*** *(A) Simplified geological map of Morocco and Algeria (modified from Crônier et al. 2018b) and location of the five study areas in North Africa within the Anti-Atlas and Ougarta Ranges. (B) Geographical location of the 69 studied localities from the Maïder/Tafilalt area in Morocco and from the Ougarta area in Algeria.*

### 2.1. Early Devonian

In the Lower Devonian, the eastern Moroccan Anti-Atlas was characterised by rather uniform facies (i.e., Maïder and Tafilalt; Fig. 2) varying mostly in thickness due to a homoclinal carbonate ramp topography (Lubeseder et al., 2010). However, palaeocurrents indicate the presence of a shallow pelagic platform in the Tafilalt with two distinct slope directions - one to the south-west and the other to the north-east (Wendt, 1995). The dominant sedimentology consists of shales interbedded with cephalopod limestones (Kaufmann, 1998). In Algeria, the Ougarta corresponded to a platform (Ouali Mehadji et al., 2011).

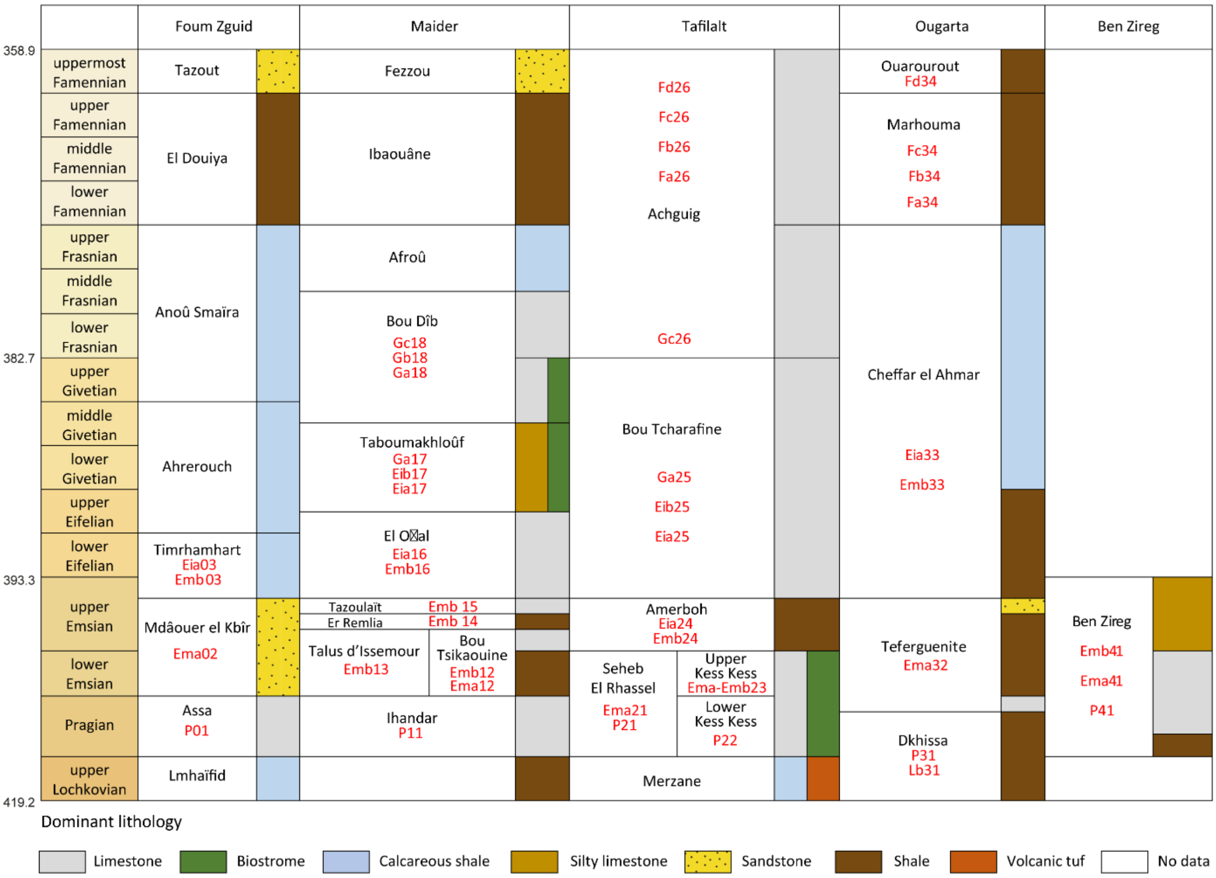

***Fig. 2.*** *Main lithology for each present in the five Moroccan Anti-Atlas and western Algeria basins for the Devonian. names in black, ID of samples in red. Ages from Cohen et al. (2013, updated).*

The Lochkovian deposits of the eastern Anti-Atlas are mainly composed of shales and black graptolite limestones (Fig. 2). These deposits reflect relatively deep environments, which are not favourable for benthic faunas (Morzadec, 2001; Klug et al., 2013; Frey et al., 2014). In the Tafilalt, the particular Hamar Lagdad area is characterised by volcanic tuff deposits (Hollard, 1967; Klug et al., 2018). At the end of Lochkovian and the beginning of Pragian, a regressive phase enabled benthic faunas to develop (Hollard, 1967; Morzadec, 2001). Nevertheless, Bultynck and Walliser (2000) reported a dominance of shales and hemipelagic limestones in the eastern part of the Anti-Atlas whereas the western part was composed of neritic deposits. At the same time, in the Hamar Laghdad area, a reef system settled on volcanic shoals (Hollard, 1981; Brachert et al., 1992). In the Ougarta Basin, the late Lochkovian-Pragian regressive phase led to a mud-dominated platform environment subjected to storm and fair-weather waves while to the north the Bechar Basin corresponded to a carbonate platform (Ouali Mehadji et al., 2011).

During the early Emsian (Fig. 2), limestones and argillaceous limestones still covered the Anti-Atlas without important environmental changes (Hollard, 1967) and are very fossiliferous (Kaufmann, 1998; Klug et al., 2008; De Baets et al., 2010). Conversely, in the Foum Zguid area shallow environmental conditions above storm-wave base led to sandstone deposits despite transgressive sequences (Jansen et al., 2004; Ouanaimi & Lazreq 2008). In Algeria, the Ougarta Basin deepened from the late Pragian due to a subsidence phase and was covered by shales and marls while the Bechar Basin became more siliciclastic (Ouali Mehadji et al., 2011).

The transition between the early and late Emsian was marked by a global transgression: in the Anti-Atlas the Daleje event (House, 1985) led to green shale deposits in a basinal environment (Kaufmann, 1998). Hollard (1967) noted a difference of faunas and facies between the Maïder and the Tafilalt with the Tafilalt becoming more argillaceous with a less diverse benthic fauna than the Maïder (Fig. 2). The northern Tafilalt was a pelagic platform with thinner deposits (Kaufmann, 1998). In Algeria, the Ougarta Basin remained deep and dominated by shales and marls (Ouali Mehadji et al., 2011) whereas the Bechar Basin was covered by shales and siltstones (Massa, 1965). At the end of the Emsian, limestone deposits formed in the Anti-Atlas (Fig. 2) because of a fall in the sea level. Conversely, the Foum Zguid area was characterised by shales and nodular limestones corresponding to more open water and hemipelagic conditions (Jansen et al., 2004). Based on trilobites, Chatterton et al. (2006) confirmed the establishment of a relatively deep environment, which was below the storm wave base but within the photic zone while the north of the Dra Valley was deepening. This area was influenced by the tectonic subsidence triggered by the Variscan extent phase (Ouanaimi & Lazreq, 2008). In Ougarta, the regression led to a shoreface or a foreshore environment with sandstone deposits (Ouali Mehadji et al., 2011).

### 2.2. Middle Devonian

During the Middle Devonian, the collision of Gondwana and Laurussia resulted in the Variscan orogeny. In the Anti-Atlas, this episode is marked by the development of a neritic shelf followed by a platform and basin system, accompanied by palaeoenvironmental changes

(Wendt et al., 1984; Kaufmann, 1998; Baidder et al., 2008; Wendt, 2021a). The first phase of this tectonic movement occurred at the Emsian/Eifelian boundary (Lubeseder et al., 2010). The Maïder Basin separated the Tafilalt Platform in the north-east from the Maïder Platform in the south-west (Fig. 3). While the Maïder Platform was emerging, the Tafilalt Platform remained a pelagic platform with the north-eastern Dra Valley and the Ougarta Basin deepening to a distal ramp (Limam et al., 2021).

The Foum Zguid area continued its transition toward a hemipelagic platform from the Emsian onwards (Jansen et al., 2004). During the Eifelian, marlstones and shales became increasingly important. To the north-east, the environment was less uniform. Kaufmann (1998) explained that three different facies occurred in the Maïder and the Tafilalt. A neritic facies characterised by argillaceous wackestones and numerous fossils was present in the northern and western parts of the Maïder near the emerged Maïder Platform. A neritic fauna including trilobites developed in the limestones of the western side of the Maïder Platform at Jbel Ou Driss (Bultynck, 1985; Feist & Orth, 2000). Condensed pelagic deposits, i.e., condensed nodular limestones and marls with abundant fossils, accumulated in the pelagic Tafilalt Platform. These two platforms corresponded to shallow water environments (Wendt et al., 1984). Finally, a basinal facies existed in the centre of the Maïder Basin and to the east of the Tafilalt Platform in the Tafilalt Basin. It mainly corresponded to marlstones and shales with scattered faunas. Wendt et al. (1984) specified that the Maïder Basin was deeper than the Tafilalt Basin. In Algeria, the Ougarta Basin became deeper during the Eifelian, from a foreshore environment at the end of the Emsian to a distal platform (Maillet et al., 2013; Crônier et al., 2018a). Henceforth, hemipelagic deposits were found as marlstones interbedded with thin-bedded limestones.

The global transgression events of the Middle Devonian were well pronounced in the Anti-Atlas (Kaufmann, 1998). The successive Choteč and Kačák events corresponded to hypoxies, which was probably due to a sea level rise during the Eifelian leading to black shale deposits (Kaufmann, 1998; Döring, 2002).

The differentiation between platforms and basins in the eastern Anti-Atlas continued to intensify in the Givetian. On the edge of the Maïder Platform, coral-stromatoporoid limestones developed and extended to the early Givetian (Kaufmann, 1998). A second tectonic phase of early Variscan movements occurred during the middle Givetian (Lubeseder et al., 2010). It implied the subsidence of the Maïder Basin, which induced the extension of the basinal facies (Kaufmann, 1998). The mid-Givetian Taghanic event was identified in Morocco and Algeria with shale deposits and condensed layers (Kaufmann, 1998). The distal platform of the Ougarta region continued to subside during the Givetian with shale deposits interbedded with limestones (Maillet et al., 2013). To the north, the Bechar Basin showed similar facies to the Tafilalt Platform with the appearance of pseudonodular limestones in the Givetian (Massa, 1965).

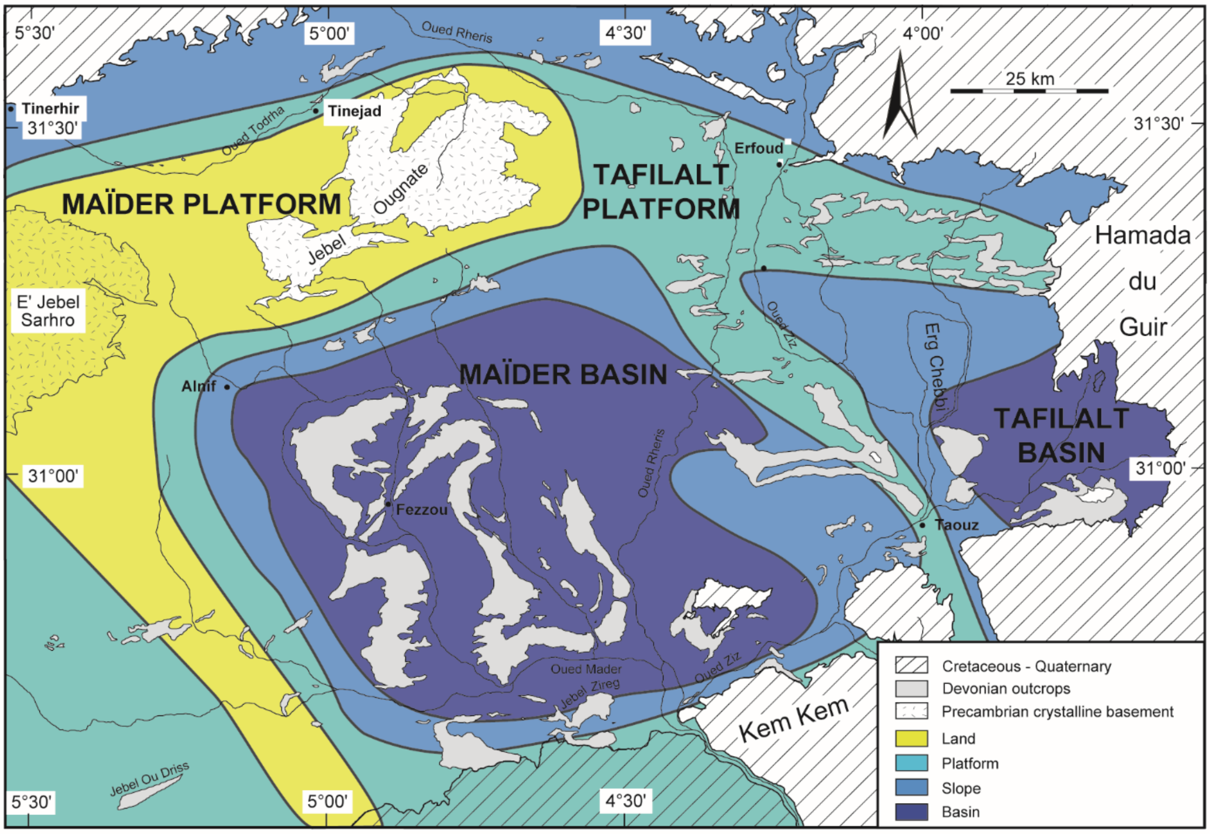

***Fig. 3.*** *Geographical map of the eastern Anti-Atlas in Morocco with the limits of the Maïder Platform and Basin and the Tafilalt Platform and Basin in the Middle and Late Devonian (Modified from Wendt and Belka, 1991 and Frey et al., 2019).*

### 2.3. Late Devonian

During the Late Devonian, the Anti-Atlas Range and Ougarta Range were influenced by the same regional events (Benhamou et al., 2004). Variscan tectonics intensified in the eastern Anti-Atlas, which is reflected in differences of facies and thickness (Hollard, 1974; Wendt, 1985, 1988; Wendt & Belka, 1991; Belka et al., 1999; Frey et al., 2019) resulting in the differentiation of basins and platforms (Wendt et al., 1984, 2021a, 2021b; Michard et al., 2008). The active extensional dislocation of the former platform caused by early Variscan tectonic movements and differential subsidence (Wendt et al., 1984) led to the differentiation of two sub-basins; i.e., the Tafilalt Basin, a slowly subsiding shallow basin in the east and the Maïder Basin, a rapidly subsiding basin in the west (Fig. 3). These two sub-basins were connected *via* the narrow N-S Cephalopod Ridge, i.e., the Tafilalt Platform with shallower water (Wendt, 1985, 1995; Wendt et al., 2006; Toto et al., 2008; Lubeseder et al., 2010). At the beginning of the Frasnian, the

Tafilalt Platform emerged before being flooded again (Michard et al., 2008) and the Maïder Platform partly emerged (Wendt et al., 1985). On the north-western margin of the Algerian Sahara, a tectono-eustatic control is reflected in differences in lateral facies and thickness in sediments accumulated on a distal platform and in basins (Abbache et al., 2019). The Late Devonian marked the most important phase of epirogenic movements in the Saoura leading to an important subsidence (Benhamou et al., 2004). The Upper Devonian is characterised by alternate deposits of clay-sand and limestone, especially including "griottes" nodular limestones with benthic and pelagic faunas, which indicates an opening to marine environments (Crônier et al., 2018a; Abbache et al., 2019).

In North Africa, a transgression occurred during the Late Devonian. In Morocco, the highest sea-level occurred in the late Famennian (Wendt & Belka, 1991; Becker et al., 2004). In the Ougarta, the high stand occurred at the end of the Frasnian but the sea-level stayed high with high stand deposits until the late Famennian (Ouali Mehadji et al., 2012) when a regression led to shallower environments in Morocco and Algeria.

During the Frasnian, in the Anti-Atlas a clay sedimentation with sideritic and nodular levels (Frey et al., 2019) developed in the Tafilalt Basin and the Maïder Basin and even occasionally on the Tafilalt Platform, reflecting rising sea levels (Wendt, 1988; Lubeseder et al., 2010; Frey et al., 2019). At the same time, sandy limestones, thick-bedded crinoid or cephalopod limestones rich in nektonic and planktonic faunas associated with black bituminous shales were deposited on the Tafilalt Platform (Wendt, 1985; Michard et al., 2008; Frey et al., 2019). A condensed sedimentation took place in the south-western Maïder Basin and on the northern Tafilalt Platform (Wendt, 1988; Wendt & Belka, 1991; Hüneke, 2006), probably reflecting a differentiation in both water depth and oxygen availability (Frey et al., 2019). In the late Frasnian, shallow subtidal to supratidal deposits developed in the Tafilalt Platform that are characterised by strongly reduced thicknesses and the Maïder Platform emerged (Wendt et al., 1984; Wendt & Belka, 1991). In the south-eastern part of the Maïder Basin, the Kellwasser levels are represented by dark and massive cephalopod limestones (Wendt & Belka, 1991; Frey et al., 2019). The Ougarta Basin is the continuation of these Tafilalt and Maïder basins to the south-east in the Algerian Sahara (Wendt et al., 1984; Wendt, 1985; Abbache et al., 2019). In this area, the top of the Cheffar el Ahmar is a distal ramp sedimentation with green shales interbedded with nodular limestones followed by “griotte” limestones interbedded with red shales. The fauna consists of ammonoids, ostracods and chitinozoans (Abbache et al., 2019).

During the Famennian, a marly and nodular calcareous sedimentation developed in the Tafilalt Basin, in shallow environments. At the same time basinal facies dominated by shaly and calcareous sedimentation with intercalations of siliciclastic turbidites were laid down in the Maïder Basin, in deeper environments (Wendt et al., 1984; Döring, 2002) with diverse cephalopods (Korn & Bockwinkel, 2017). In the Tafilalt Platform, deposits of quartz-rich brachiopod coquinas, crinoidal limestones, thick-bedded cephalopod limestones and nodular limestones formed during the early Famennian. Similar facies were found in the eastern Maïder Platform (Wendt, 1985). A deeper environment like a slope or basin with shale deposits characterised the Ougarta region. Pyritised ammonoids and brachiopods were found in nodular limestones interbedded with shales (Abbache et al., 2019). The deepening of the Ougarta trough was probably due to subsidence and not to transgression (Ouali Mehadji et al., 2012). The deepening continued during the middle and late Famennian in the Tafilalt Platform where marls and nodular limestones were deposited in slightly deeper environments and debris flows and slumps on the margins during the late Famennian (Wendt et al., 1984). Locally, limestones varied greatly in thickness and fossil content (cephalopods, crinoids, brachiopods). Sedimentology documented phases of moderate to good aeration in more or less shallow water conditions (Wendt et al., 1984; Wendt, 1988). The continuous deepening during the late Famennian led to the decrease of diversity of benthic faunas (Wendt et al., 1984) while the centre of the Maïder Platform was henceforth flooded and pelagic cephalopod limestone accumulated (Wendt, 1985). The Ougarta region remained deep during the middle and the late Famennian and became a basin with a restricted water circulation (Benhamou et al., 2004; Abbache et al., 2019). In this environment, red “griottes” limestones were deposited with shaly beds and turbidites (Ouali Mehadji et al., 2012; Abbache et al., 2019). Ammonoids, brachiopods and trilobites were found within the nodular limestones (Benhamou et al., 2004; Crônier et al., 2013; Mottequin et al., 2015, Allaire et al., 2020). Although this facies is not an indicator of palaeobathymetry (Benhamou et al., 2004), Abbache et al. (2019) concluded that these sediments were deposited in a basinal environment. The *Nereites* ichnofacies confirms this kind of deep environment (Bendella et al., 2014). Ouali Mehadji et al. (2012) identified a narrow basin during the middle Famennian leading to a more homogeneous elongated basin in the late Famennian.

At the end of the Famennian, a fine-grained clastic sedimentation, the Hangenberg Black Shale, was sedimented in most parts of north-western Africa (Kaiser et al., 2011; Klug et al., 2016). Sandy marls and cross-bedded sandstones covered the southern part of the Tafilalt Platform (Wendt et al., 1984). In Ougarta, sandstone beds occurred that were devoid of fossils and sometimes included channels (Abbache et al., 2019). Within sandstones assigned to the “Grès de Ouarourout”, Ouali Mehadji et al. (2012) identified the maximal regression surface.

At the beginning of the Tournaisian, the Tafilalt and southern Maïder Platforms corresponded to a deltaic environment (Wendt et al., 1984). The Ougarta region corresponded to a siliciclastic platform (Abbache et al., 2019) with temporary emersions leading to deltaic environments or lagoons (Ouali Mehadji et al., 2012).

In the southern Ougarta region, in the Erg Djermel area, no trilobites were found within the Upper Devonian deposits, i.e., in black shale deposits corresponding to deep environments from the Frasnian to the late Famennian (Abbache et al., 2019). In the north of Ougarta, in the Ben-Zireg area, trilobites have not yet been recorded within "griottes" calcareous deposits associated with rare shaly layers corresponding to a middle to distal platform (Abbache et al., 2019). In Morocco, the Foum Zguid area and the Dra Valley deepened from the Eifelian to the late Famennian due to global transgression (Becker et al., 2004). These deep environments are not favourable to the development of trilobite communities and thus fossils are rare apart from ammonoids and crinoids (Hollard, 1963; Becker et al., 2004).

## 3. Material and methods

### 3.1. Material

In order to analyse the trilobite records and their shifts, we completed an existing dataset (Bault et al., 2021) based on the occurrence of trilobites from Morocco and Algeria (Fig. 1). 77 studies from the literature were considered because of their updated taxonomy and/or good temporal resolution (Appendix A). The dataset contains 2892 specimens (Appendix B) from the Lochkovian to the Famennian distributed within 69 localities from five basins (Fig. 1). Sections separated by a few hundred metres were combined within the same locality. To avoid possible duplicates the specimen count was restricted to only the highest number of complete exoskeletons plus the disarticulated cephala or pygidia per occurrence. Other parts of trilobites such as free cheeks or hypostomes were not included. For each relevant occurrence, the dataset contains the following information: taxonomic information, abundance, location, stratigraphic position (substages) and lithological information (formations). Throughout our data compilation work, only genera were considered to maximise potential correlations between the distinct assemblages, as many species are only described locally. Species level is often inadequate for biodiversity purposes (Cecca, 2002). As the Late Devonian *Phacops* Emmrich 1839 differs from the Early and the Middle Devonian representatives of the genus, they were counted as a distinct genus called *Phacops* sensu lato (Crônier et al., 2011). We used a preliminary revision of asteropygines in open nomenclature while waiting for the revision of the whole subfamily. As a result, previous *Metacanthina* species *M. issoumourensis* Morzadec, 2001, and *M. maderensis* Morzadec, 2001 are joined with *Minicryphaeus giganteus* Bignon et al., 2014 in the Genus 1, whereas *Asteropyge wallacei* Termier and Termier, 1950 is included in the Genus 2. Overall, the dataset comprises 135 genera (Appendix B) used for biodiversity indices (see section 4.3). However, we excluded genera found in only one sample because they did not provide any linkage with other samples for the clustering, which led to a selection of 67 genera spread over 123 samples (or assemblages) used for a cluster analysis.

### 3.2. Clustering

An analysis of associations was carried out using 123 samples at a given substage and to help us understand the temporal and spatial relationships between trilobite faunas and their environments. The term association is used here for recurrent assemblages of trilobites with a similar taxonomic composition (Brenchley & Harper, 1998; Crônier & Van Viersen, 2007; Crônier & François, 2014; Bignon & Crônier, 2015). To reduce sampling bias the relative abundances of 67 genera were quantified in seven classes, i.e., the percentage of the abundance of each genus in a sample (Harnik, 2009). Indeed, the number of specimens is influenced by the sampling effort (Thompson, 2004), which cannot be estimated as our data were obtained from various bibliographic references.

Data were analysed using a hierarchical cluster analysis (HCA). This agglomerating technique groups recurring samples according to their level of taxonomic similarity (Davis, 1986; Harper, 1999; Hammer & Harper, 2008). It produces dendrograms highlighting the relationships in two modes - an R-mode clustering, grouping the taxa according to their probability of co-occurrence and a Q-mode clustering, grouping the samples, i.e., of similar generic composition. HCA was carried out using the average linkage algorithm and the Pearson correlation similarity index (Hammer & Harper, 2008).

To identify environmental gradients, a Detrended Correspondence Analysis (DCA) was carried out. Correspondence Analysis (CA) is suitable for grouping samples from taxonomic abundance (Greenacre, 1984; Jongman & Jongman, 1995; Legendre & Legendre, 1998) but DCA is more reliable (Hammer & Harper, 2008; Holland et al., 2001; Bonelli & Patzkowsky 2008) for reducing the Pinocchio (Fig. SUPPL. A1) and arch effects (Fig. SUPPL. A2). This ordination method maximises the correspondences between taxa and samples. It also provides ordination scores for both taxa and samples according to the relative abundance of taxa by involving a compression of the total information along the first axis, which often reflects paleoenvironmental gradients (Hammer & Harper, 2008). Unfortunately, several taxa need modern revision to clarify their generic determination. Moreover, microfacies analyses would be suitable for a better characterization of the environments. In their absence, an additional DCA would improve our determination of the relationships between some samples.

Finally, an analysis of similarities (ANOSIM) was carried out to statistically test the differences in the generic composition of groups of taxa. This non-parametric test is based on Bray-Curtis dissimilarity values as it only uses the rank order of dissimilarity values between groups and within groups (Clarke, 1993; Hammer & Harper, 2008). P-values were obtained through 5000 random permutations.

### 3.3. Diversity indices

To complete the multivariate analysis information and help understand the impact of migrations and environmental changes on the diversity, α and β diversities (Whittaker, 1960) were estimated. The total taxa diversity is determined by the mean taxa diversity at the habitat level (α) and the differentiation among habitats (β). The Shannon index H' of α diversity was used to take into account the number of taxa within a sample (taxa richness) and the individual distribution within these taxa (taxa equitability). It considers the relative abundance of each taxon and gives weight to rare species. This index varies from 0 for a sample with only one single taxon to high values for samples with many taxa. $H^{'} = -\sum_{i=1}^{S} p_i log_2 p_i$, with $S$ the number of taxa and $p_i = \frac{n_i}{N}$, with $n_i$ the number of individuals of the taxon $i$ and $N$ the number of individuals for all taxa. The Shannon index H' of α diversity was estimated through time according to substages ors and through environment according to associations. Diversity for associations is calculated as the mean taxonomic richness of samples of each association while the diversity for substages ors is calculated as the total taxonomic richness in these stratigraphic units.

Several measures related to compositional heterogeneity of β diversity were used to quantify differentiation (Baselga, 2010; Balsega & Orme, 2012). The first measure is an index of taxa replacement (i.e., turnover) emphasizing the role of rare taxa as the difference in taxa composition between localities measured as Simpson dissimilarity (i.e., turnover component of Sørensen dissimilarity). This measure enables the identification of the environmental impact or spatial and temporal constraints on the number of taxa that are replaced between localities (Qian et al., 2005). The second measure is an index of nestedness, which occurs when taxa-poor assemblages are a subset of more diverse assemblages (Wright & Reeves, 1992; Ulrich & Gotelli, 2007) measured as nestedness-resultant component of Sørensen dissimilarity (Baselga, 2010). This measure indicates non-random species loss as common species are less likely to disappear (Gaston et al., 2000). The last measure is an index of the Overall β diversity measured as Sørensen dissimilarity (Sørensen, 1948) corresponding to the global taxonomic difference between samples. Components of β diversity were estimated through time between substages and through environment between associations.

HCA, ANOSIM, DCA and Shannon index H' were achieved by using the software PAST v3.24 (Hammer et al., 2001). β diversity was computed by using the 'Betapart' package (Baselga & Orme, 2012) in the R statistical environment (version 3.6.3; R Core Team 2020).

## 4. Results

### 4.1. Delineated associations and faunal gradients

The 67 trilobite genera distributed within the 123 assemblages are grouped into 16 associations or occurrences, in four main clusters by HCA (Fig. 4; details in fig. Suppl. B). Details of each trilobite association are given in table.

Cluster I groups five associations (i.e., *Morzadecops* Association *Ia*, *Ganetops* Association *Ib*, *Montanproetus* Association *Ic*, *Sculptoproetus* Association *Id* and *Piriproetus* Association *Ie*), covering the entire Early Devonian and the early Eifelian; Cluster II groups six associations (i.e., *Hollardops* Association *IIa*, *Morocops* Association *IIb*, *Gerastos* Association *IIc, Chotecops* Association *IId*, *Paralejurus* Association *IIe* and *Psychopyge* Association *IIf*), from the Pragian to the Givetian; Cluster III groups only one association (*Lepidoproetus* Association *IIIa*) mainly found in the Maïder during the Pragian. Finally, Cluster IV groups all four associations (*Cyrtosymbolina* association *IVa, Osmolskabole* Association *IVb, Trimerocephalus* Association *IVc* and *Phacops s.l.* Association *IVd*) restricted to the Late Devonian (Famennian) of the Tafilalt and Ougarta. The ANOSIM results show a significant difference between the 16 associations (R coefficient = 0.59, p value = 0.0002).

| ***Associations*** | ***Samples*** | ***Geological time*** | ***Basins*** | ***Remarks*** |
|---|---|---|---|---|
| *Morzadecops* Association (*Ia*) | JO-Ema12/MEK-Ema03/ F12-Ema21/OC-Ema21 | early Emsian | Dra Valley, Maïder and Tafilalt | • Only OC-Ema21 is diverse with six distinct genera recorded. |
| *Ganetops* Association (*Ib*) | Dkh-Lb31/EK-Lb31 /ED-Lb31/Zer-Lb31 | late Lochkovian | *Ougarta* | • Zer-Lb31 added to the *Ganetops* Association based on the presence of both *Ganetops* and *Protacanthina* and DCA result<br>• Dominated by two asteropygine genera (*Ganetops* and *Protacanthina*)<br>• High overall β diversity. |
| *Montanproetus* Association (*Ic*) | BZ-Emb41/JA-Ema21/JBT-Ema21/JISW-Emb14 | Emsian | Maïder, Tafilalt and Ben Zireg | • In limestone deposits |
| *Sculptoproetus* Association (*Id*) | JA-Eia21/EAt-Emb24/Ris-Emb24/Tim-P11/ EAt-Ema21/JISW-Ema12 | Pragian to Eifelian | Tafilalt and Maïder | • Low overall β diversity<br>• In shales or calcareous-shale alternations |
| *Piriproetus* Association (*Ie*) | GM-Eia24/GM-Emb24/GM-Eia25/JI-Eia25/JA-Eia25/JA-Emb24/HL-Eia25/JBT-Eia25/HL-Emb23/HL-Ema23 | late Emsian to early Eifelian | Tafilalt | • In marly limestones deposits |
| *Hollardops* Association (*IIa*) | Tim-Emb15/BD-Eia16/BD-Emb15/FZ-Emb-02/EK-Emb33/Zer-Emb33/JeA-Emb02/BD-Emb14/Zgu-Eia02/Zer-Ema32/Mar-Emb33 | late Emsian to early Eifelian | the entire Anti-Atlas | • In limestones interbedded with shales from a relatively deep platform.<br>• Association dominated by *Hollardops* and *Timsaloproetus* but they occurred together only in sample Zgu-Eia02 |
| *Morocops* Association (*IIb*) | HL-Emb24/BD-Eia16/FZ-Eia02/BD-Emb15 /Tal-Emb15/JISW-Emb15/TO-Emb15/ED-Eia33/JO-Eia16/ED-Emb33/JGEZ-Emb02/JGEZ-Eia02/Mah-P11/Khr-Emb02/TT-Emb/Tis-Emb02/JO-Emb15/JO-Emb16/Tal-Emb24 | Pragian, **late Emsian to early Eifelian** | Tafilalt, Maïder, Ougarta and Dra Valley | • Five other samples were added according to their taxonomic composition and from DCA results: TT-Emb, Tis-Emb02, JO-Emb15, JO-Emb16 and Tal-Emb25<br>• *Morocops*, *Cyphaspis* and *Austerops* represent the most widespread genera<br>• Most diverse association of the whole Devonian |
| *Gerastos* Association (*IIc*) | JZg-Eia17/JeM-Ga18/ Tab-Gb18/JeM-Eia16/JZg-Eia16/Sar-Eia16/JeM-Eia17/JeM-Eib17/JO-Eib17/Tab-Ga18/JOD-Ga17/JISW-Eia16/JISW-Emb16 | lower Eifelian to middle Givetian | Maïder Basin | • Association dominated by *Gerastos*, which is invariably present in all samples<br>• In limestones |
| *Chotecops* Association (*IId*) | HN-Gc26/Oua-Eia33/JMI-Ga25/JMI-Eib25/JZa-Ga25/JBT-Eib25/Mar-Eia33 | Middle Devonian | Tafilalt and Ougarta | • Association dominated by three genera: *Chotecops*, *Struveaspis* and *Helmutia*<br>• In marly limestones of pelagic environments |
| *Paralejurus* Association (*IIe*) | BZ-P41/MeK-P01/JOJI-P11/F12-P21/HL-P22/JO-P11/Tab-P11/Tis-P01/EAt-P21/BZ-Ema41 | **Pragian**, early Emsian | Maïder, Tafilalt, Ben Zireg and Dra Valley | • Sample BZ-Ema41 was removed from the *Psychopyge* association to be placed in the *Paralejurus* Association based on the presence of *Prodrevermannia* and DCA results<br>• High overall β diversity |
| *Psychopyge* Association (*IIf*) | JBT-Emb24/JO-Emb12/ElH-Emb02/BD-Emb13/Mar-Ema32 | Emsian | Maïder, Tafilalt and Ougarta basins | • Low overall β diversity<br>• In interbedded marl and limestones |
| *Lepidoproetus* Association (*IIIa*) | AnT-P11/JeM-P11/JZg-P11/OJ-P11/JINW-P11/EAc-P11/Ams-P21/Lan-Emb02 | **Pragian**, late Emsian | **Tafilalt**, Dra Valley | • Although Lepidoproetus was the most abundant genus, there is no dominant genus.<br>• Low overall β diversity |
| *Cyrtosymbolina* Association (*IVa*) | BE-Fa26/BJ-Fa26 | early Famennian | Tafilalt Platform | • Low overall β diversity |
| *Osmolskabole* Association (*IVb*) | BE-Fb26/ BE-Fc26/HL-Fb26/JBT-Fb26/OC-Fb26/ BE-Fd26 | middle Famennian to latest Famennian | Tafilalt Platform | • Most diverse association of the Late Devonian<br>• In limestone only |
| *Trimerocephalus* Association (*IVc*) | KeA-Fb26/ Mar-Fa34/CeA-Fb34/GD-Fb34/Mar-Fb34/Bec-Fc34 | early to middle Famennian | **Ougarta Basin**, Tafilalt | • Low overall β diversity<br>• Relatively deep environment |
| *Phacops s.l.* Association (*IVd*) | TZ-Fb34/Idh-Fc34/TZ-Fc34/Mar-Fc34 | middle Famennian to late Famennian | Ougarta Basin | • Poorly diverse |

***Table 1.*** *Trilobite associations and their environmental, faunal and temporal features. The remark column includes data on: diversity (Fig. 9) and occurrences (Appendix A and B). Reattributions of samples were made using DCA data (Fig. 5). Bold font indicates the main characteristic for the associations.*

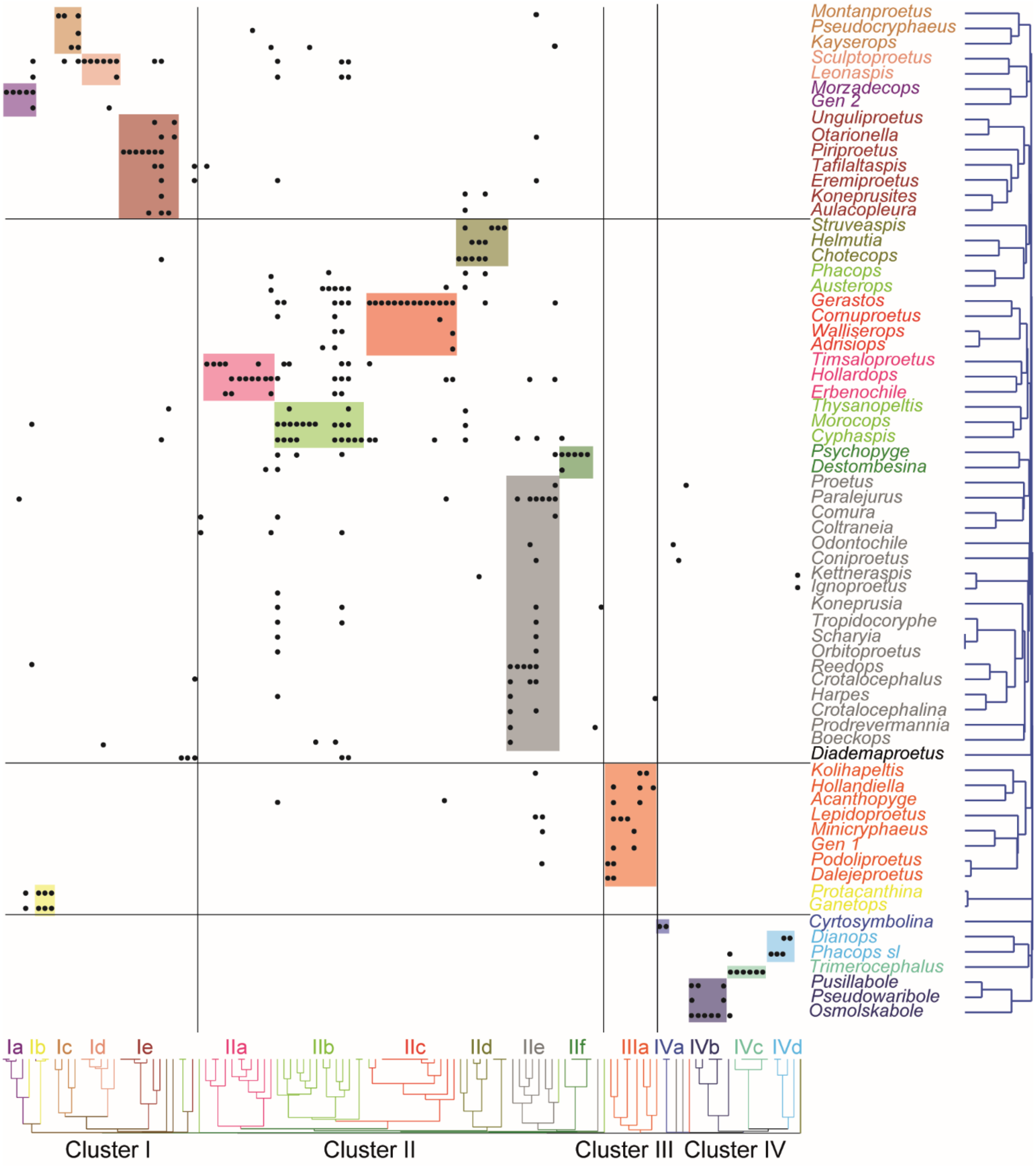

***Fig. 4.*** *Simplified dendogram with R and Q modes from hierarchical cluster analysis (HCA) using the average linkage method as correlation setting and the Pearson correlation index as similarity index (Hammer & Harper, 2008). 67 taxa (genera) are clustered according to 123 analysed samples (localities) from the Devonian of North Africa. Four clusters (I to IV) and 16 associations are identified. Sample names and proportions of each occurrence are given in Fig. SUPPL. B).*

DCA enabled us to offset HCA limits and better understand the spatio-temporal distribution of the assemblages according to their taxonomic record. The Famennian samples did not share trilobites with the Early and Middle Devonian (Fig. 4) so they were removed from DCA to avoid a Pinocchio effect and were analysed in an additional DCA (Fig. 5). Similarly, the early Famennian samples BJ-Fa26 and Be-Fa26 were removed.

For the Early and Middle Devonian, DCA shows a time trend (Fig. 5A). The Early Devonian (Lochkovian, Pragian and early Emsian) associations show the highest values on both DC1 and DC2 axes, whereas the Middle Devonian associations show the lowest values on both DC1 and DC2 axes (Fig. 5A). The Early Devonian associations group mostly the Order Phacopida, whereas the Middle Devonian associations group mostly the Order Proetida (Fig. 5A).

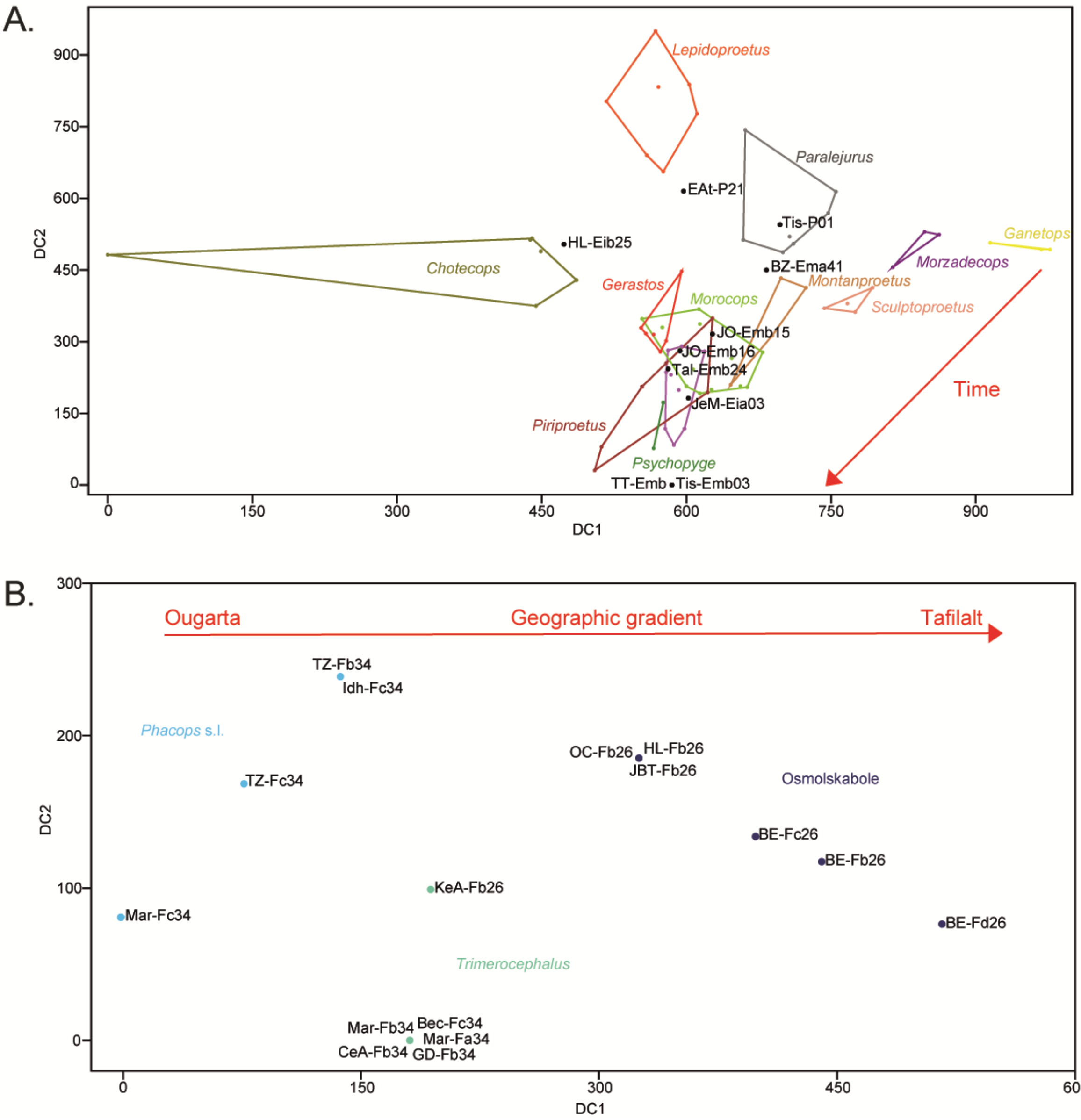

***Fig. 5.*** *Scatter plot of North African samples according to DCA for (A) the Early and Middle Devonian, and (B) the Famennian; DC1 and DC2 axes reflecting potential environment gradient. Eigenvalues for DC1 and DC2 axes are respectively 0.96 and 0.91 for the Early and Middle Devonian with 105 samples, 0.95 and 0.09 for the Famennian with 16 samples. Associations defined by clustering have been reported: 12 associations for the Early and Middle Devonian, and 4 associations for the Famennian.*

However, a look at the results in detail shows five associations are not overlapped by others along one axis of DCA or another. *Chotecops*, *Morzadecops*, *Ganetops* and *Sculptoproetus* associations are clearly independent along the DC1 axis and *Paralejurus* and *Lepidoproetus* associations alone appear along the DC2 axis in the higher values (Fig. 5A). These associations belong to either the Lochkovian, or Pragian, or early Emsian or Givetian. In contrast, late Emsian and Eifelian associations were strongly overlaid on both axes.

For the Famennian, DCA shows a geographic gradient along DC1 axis, from Ougarta with the lowest values to the Tafilalt having the highest ones (Fig. 5B).

## 4.2. Temporal and spatial distribution of clusters

### 4.2.1. Early Devonian

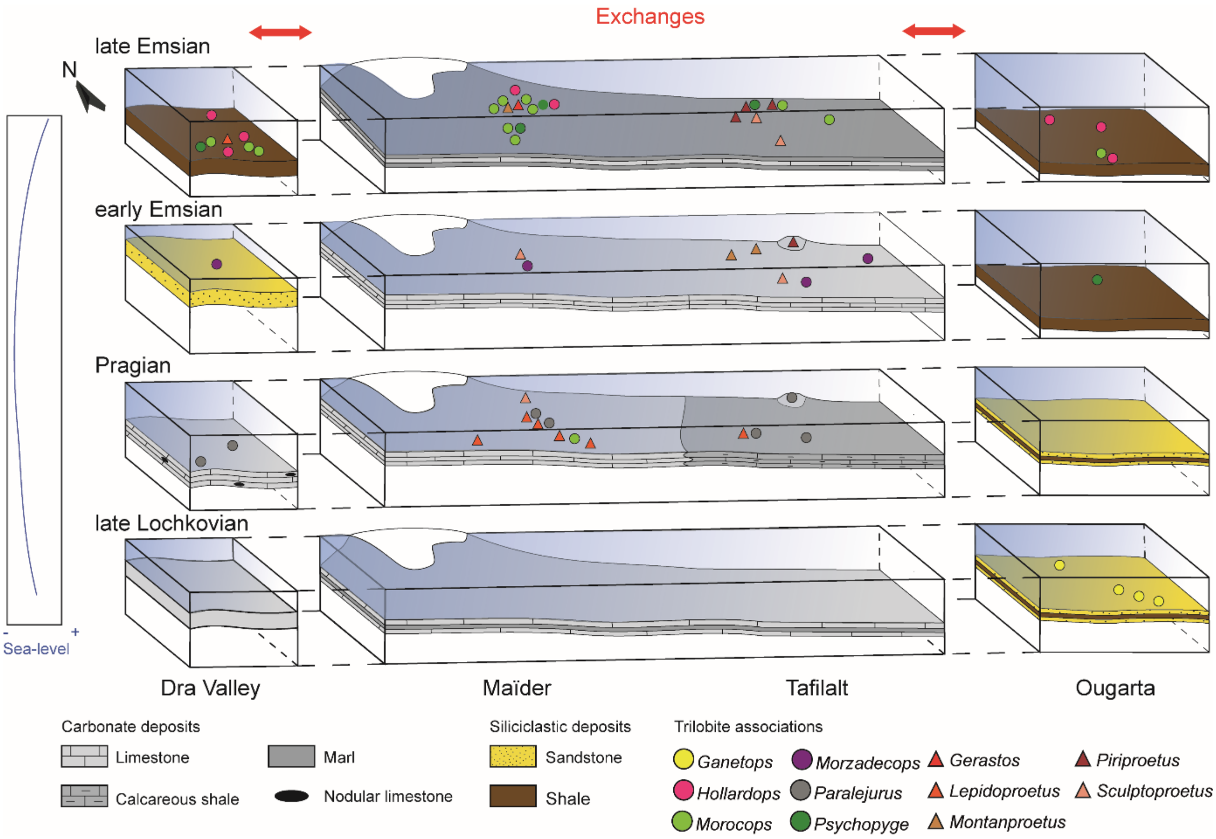

***Fig. 6.*** *Simplified diagrams exhibiting the different facies within five studied areas and their spatio-temporal evolution during the Early Devonian. Associations defined by clustering have been reported.*

## 4.2. Temporal and spatial distribution of clusters

### 4.2.1. Early Devonian

Details of temporal and spatial distributions are given in supplementary figures (Figs. SUPPL. C to H). During the Lochkovian, trilobites seemed restricted to the Ougarta Basin.

They were few and dominated by the *Ganetops* genus (within Ass. *IIb*), which was the sole genus in the southern part of the Ougarta region (Fig. 6). To the North, *Ganetops* was associated with the *Morzadecops* genus at Zerhamra - the only genus capable of persisting in the Pragian, which thus occurs in another association (i.e., *Morzadecops* Association *Ia*).

At the beginning of the Pragian, trilobites flourished in the Anti-Atlas area but are unknown from the Ougarta Basin. Four associations covered this period but two were more dominant, widespread over all the Anti-Atlas and intersected (Fig. 4), the *Lepidoproetus* (*IIIa*) and *Paralejurus* (*IIe*) associations. The *Paralejurus* Association occurred in the Ben Zireg area and developed in the Tafilalt and the Maïder areas too, whereas the *Lepidoproetus* Association occurred predominantly in the Maïder area although it occurred also in the south-western part of the Tafilalt area (Fig. 6). These two widespread associations were strongly affected during the Emsian: the *Paralejurus* Association (*IIe*) disappeared and the *Lepidoproetus* Association (*IIIa*) occurred only in the Dra Valley (at Lansser locality) for the last time in the late Emsian. The *Sculptoproetus* Association (*Id*) and *Morocops* Association (*IIb*) appeared in the Maïder area (respectively at Timarzite and Maharch localities) during the Pragian but were rarer. They developed considerably during the Emsian where they occurred in almost all basins (Fig. 6). The Emsian is represented by nine associations (Fig. 4). In addition to the three associations, which had already occurred in the Pragian, five new ones appeared in the early Emsian and an additional association in the late Emsian. The *Morzadecops* Association (*Ia)* proliferated everywhere in the early Emsian but disappeared immediately afterwards. The *Psychopyge* (*IIf*) and *Hollardops* (*IIa*) associations originated in the early Emsian of Ougarta and then colonised the Anti-Atlas area during the late Emsian (Fig. 6). The *Montanproetus* (*Ic*) Association lasted until the late Emsian and extended from the Anti-Atlas toward the west (Ben Zireg). The two latter associations were rare during the Emsian: The *Piriproetus* Association (*IIe*) is present only in two north-western Tafilalt localities (Gara Mdouard-Jbel Issoumour) and the *Gerastos* Association (*IIc*) only during the late Emsian of the Maïder area (Jbel Issoumour SW).

### 4.2.2. Middle Devonian

Five Early Devonian associations are still found in the Eifelian but the *Hollardops* and *Sculptoproetus* associations disappeared after the early Eifelian. These associations were already rare and restricted to one basin: the *Hollardops* Association was restricted to the western part of the study area (i.e., Maïder and Foum Zguid areas) and the *Sculptoproetus* Association stayed confined in the Tafilalt area (Jbel Amlane, Fig. 7). In contrast, the *Morocops* Association continued to be widespread in different basins during the early Eifelian but also disappeared in the late Eifelian in many places despite a last occurrence (i.e., presence of

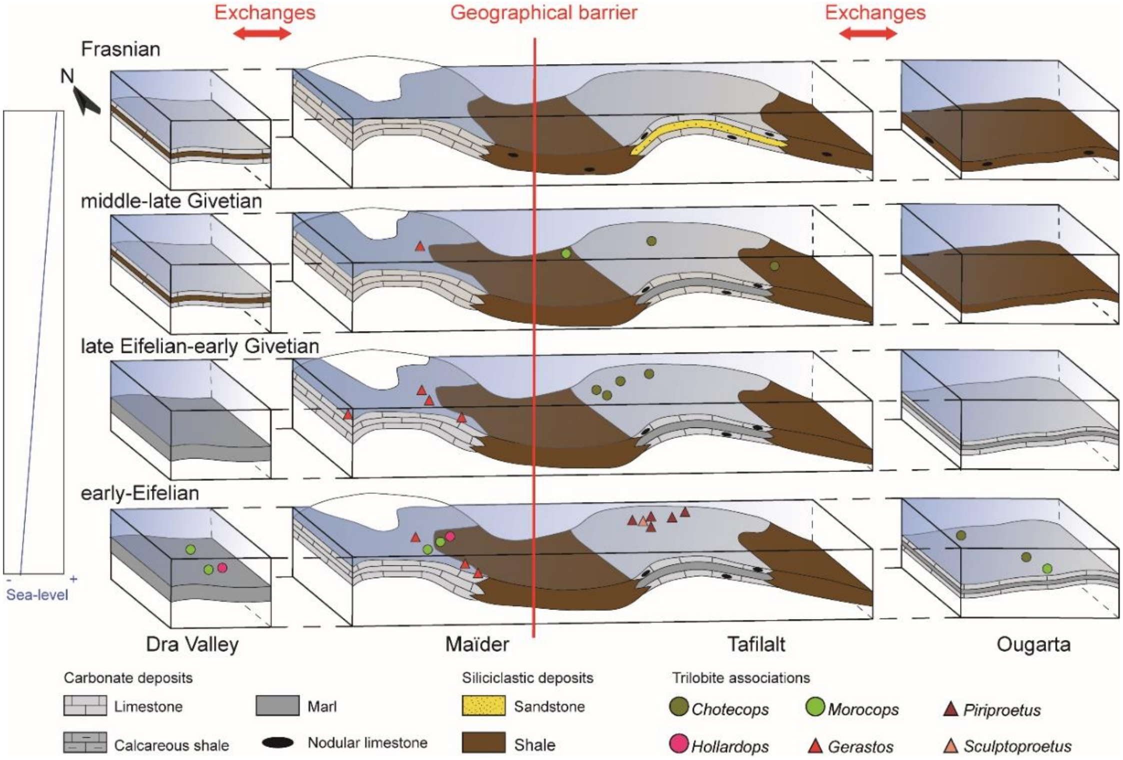

*Fig. 7. Simplified diagrams exhibiting the different facies within five studied areas and their spatio-temporal evolution during the Middle Devonian and Frasnian. Associations defined by clustering have been reported.*

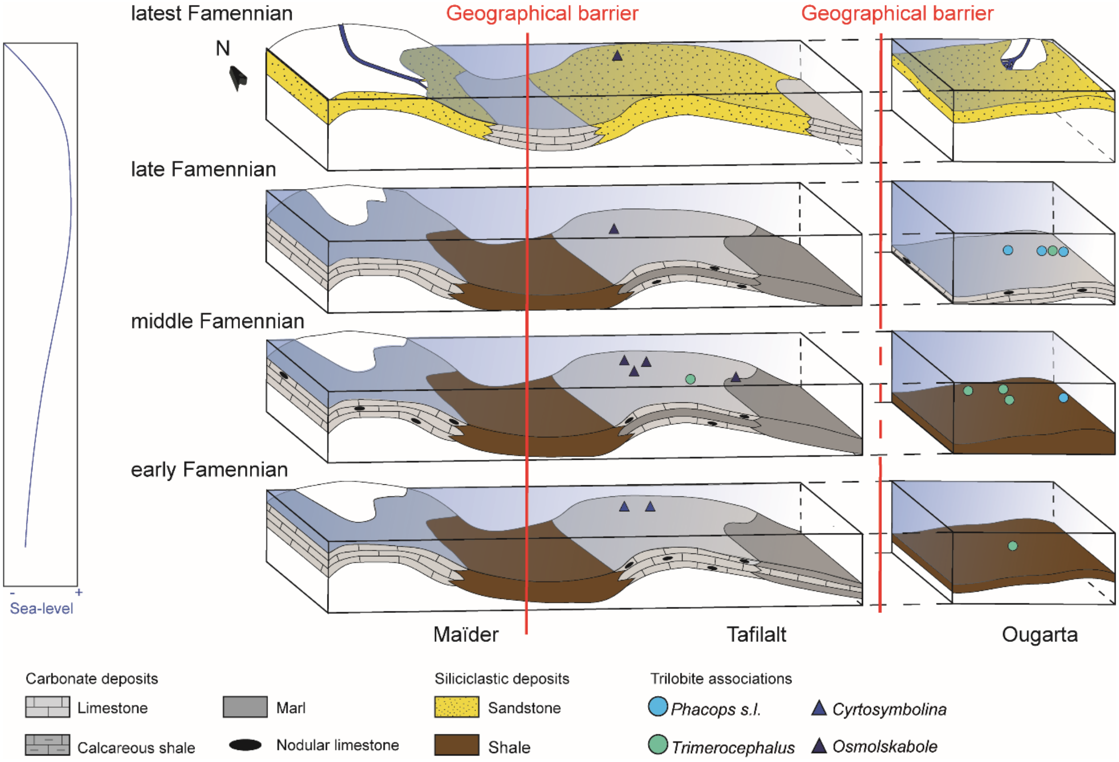

*Fig. 8. Simplified diagrams exhibiting the different facies within five studied areas and their spatio-temporal evolution during the Famennian. Associations defined by clustering have been reported.*

*Koneprusia*) during the late Givetian in the north-western Tafilalt (Ras el Kebbar locality). Similarly, the *Piriproetus* Association (*Ie*), which appeared in the northern Tafilalt during the Emsian, proliferated during the early Eifelian but has not been recorded in strata laid down later. They developed everywhere in the northern Tafilalt area but never occurred elsewhere. Conversely, the *Gerastos* Association (*IIc*) occupied exclusively the Maïder area where it appeared during the late Emsian although some *Gerastos* were also found outnumbered in one Tafilalt locality and one Dra Valley locality. During the Givetian, the *Gerastos* Association (*IIh*) was still limited to the Maïder area but also developed in the western part of the platform at Jbel Ou Driss (Fig. 7). Finally, the *Chotecops* Association (*IId*) was first identified in the Ougarta area (Ouarourout) during the early Eifelian before invading the Tafilalt area during late Eifelian (Fig. 7). The *Chotecops* Association (*IIj*) was still found in the western and the southern Tafilalt area during the Givetian but was apparently no longer present in Algeria. All these associations disappeared at the end of the Givetian.

### 4.2.3. Late Devonian

Only one genus occurred in the study area during the Frasnian, at Marhouma in the Ougarta region. *Chlupacops* is not found in another stage or in another locality and has not been attributed to a particular association.

During the early Famennian, the Tafilalt area was only occupied in its northern part (at Bin Jbilit-Bordj Est locality) by the genus *Cyrtosymbolina* (from Ass. *IVa*, Fig. 8). At the same time, in the western Ougarta (Marhouma), the biodiversity was greater with three identified genera, which are equally abundant within the *Trimerocephalus* Association (*IVc*). When the *Cyrtosymbolina* association disappeared during the middle Famennian, the *Trimerocephalus* Association invaded the Ougarta region but also the western edge of the Tafilalt area. In the extreme south-east of this area (Tamtert Zereg locality), the new *Phacops s.l.* Association (*IVd*) appeared. This genus is also associated with *Trimerocephalus* in the Tafilalt area ('KeA-Fb34' sample) (Fig. 4). The *Phacops s.l.* Association replaced the *Trimerocephalus* Association in many late Famennian localities although *Trimerocephalus* remained only at Bechir locality (Ougarta). However, none of these two associations have been found in the uppermost Famennian. In the Tafilalt area, the *Osmolskabole* Association (*IVb*) replaced the *Cyrtosymbolina* Association (*IVa*) in many places from the middle Famennian and persisted until the latest Famennian where they occurred only in the extreme north-western part (at 'Bordj Est' locality, Fig. 8). *Osmolskabole* was found with *Trimerocephalus* and *Phacops s.l.*

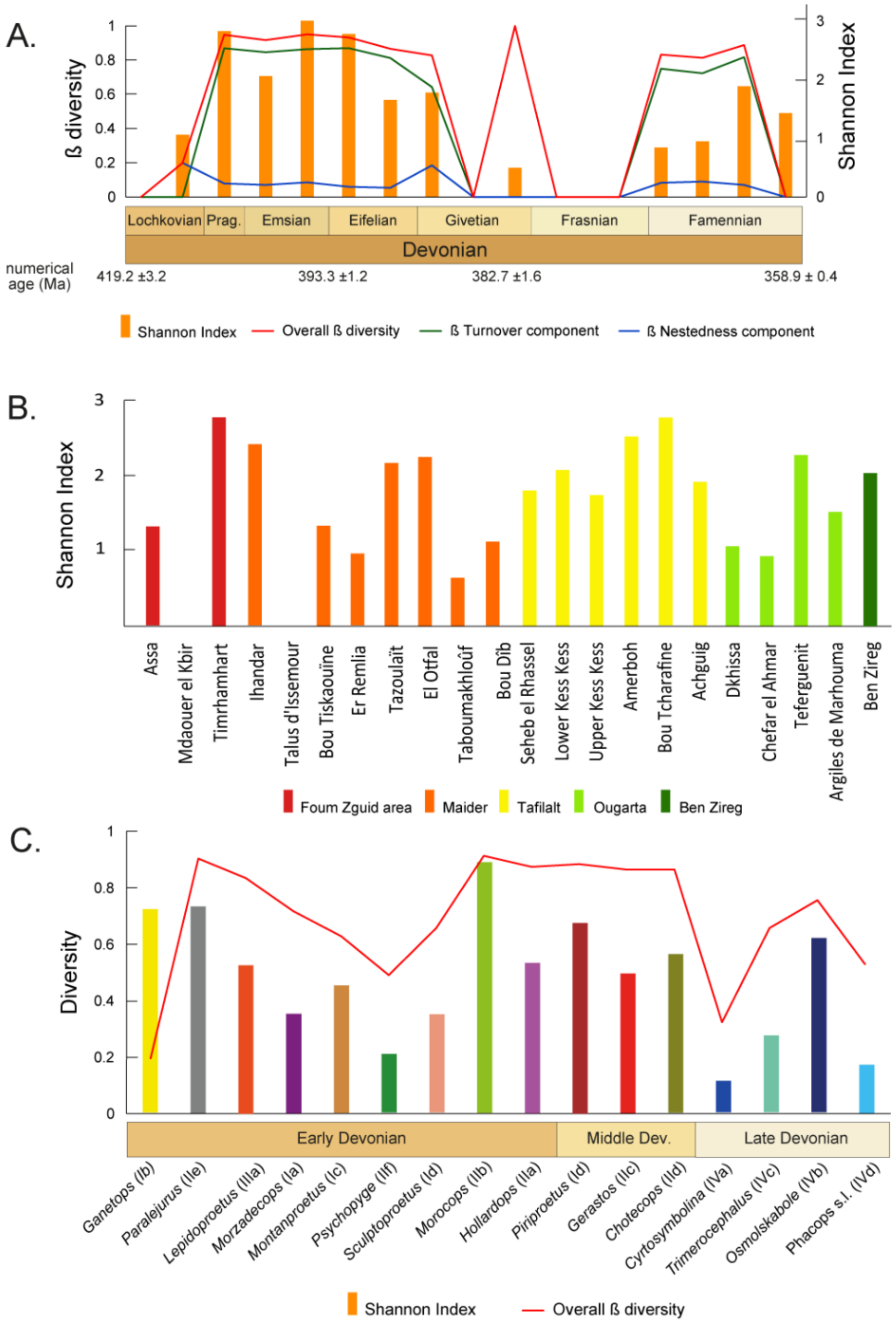

*Fig. 9. Diversity indices. (A) Diversity through time: α diversity estimated with Shannon Index H', Overall β Diversity and its components, i.e., β Turnover component and β Nestedness component determined with Sorensen dissimilarity. (B) α Diversity per from five areas. (C) α Diversity and Overall β Diversity per association. Ages from Cohen et al. (2013, updated).*

### 4.3. Evolution of biodiversity indices through time

α and β diversity were low in the late Lochkovian with Shannon index H' of 1.06 and overall β diversity of 0.2 (Fig. 9A). Then, the diversity indices increased during the Pragian reaching a plateau of high diversity until the early Eifelian with Shannon index H' > 2 and overall β diversity > 0.9. The diversity indices decreased progressively during the late Eifelian to the early Givetian, before a sharp decrease from the middle Givetian to the end of the Frasnian with null or almost null values. In the early Famennian, both α and β diversity indices increased again. However, when the α diversity index stayed low compared to that of the Early and the Middle Devonian with a Shannon index H' of 0.84, overall β diversity reached values similar to the Early Devonian. In the late Famennian, α diversity increased to 1.89 before decreasing in the latest Famennian. During this period, overall β diversity evolved differently with a slight decrease in the middle Famennian followed by an increase in the late Famennian, the time of the highest disparity of the Late Devonian (Fig. 9A). Components related to compositional heterogeneity of β diversity show different trends. The β turnover component follows the overall β diversity trends whereas the β nestedness component always shows lower values (Fig. 9A) indicating that most of the β diversity corresponds to the replacement of genera by others in different localities (Balsega, 2010). Moreover, β nestedness component changed exactly oppositely to the overall β diversity in the Early and the Middle Devonian (Fig. 9A). Consequently, during periods of low diversity, the localities with smaller numbers of species were subsets of biotas found in localities with greater trilobite diversity.

Trilobite association of the Tafilalt remained diverse during nearly all the Devonian contrary to the Maïder and Ougarta where the associations contained in thes were unevenly diverse (Fig. 9B). Although the presence of trilobites at Ben Zireg and Foum Zguid areas were not continuous through time, Shannon index H' was relatively high as in the other basins (Fig. 9B). Thes from the late Emsian and the Eifelian contained the most diverse trilobite faunas in all basins (Fig. 9B).

## 5. Palaeoenvironments of trilobite associations

It is widely known that trilobite associations vary between regions but the ecological drivers are largely unknown. HCA performed on the Devonian trilobite taxa of Morocco and Algeria enabled us to delineate twelve Early and/or Middle Devonian associations and four Late Devonian associations. The associations reflect distinctive taxonomic affinities and palaeoenvironmental preferences. Similar analyses on Devonian trilobites from the Ardenne Massif showed that trilobite associations were dependent on palaeobathymetric domains and sea-level variations (Crônier & Van Viersen, 2007). Subsequently, these associations (most particularly during the Givetian) where highlighted as equilibrated communities were able to maintain their organisation during rather strong and short environmental perturbations. These associations were able to flourish again during similar favourable environmental conditions. Only global events influenced the trilobite association (Bignon & Crônier, 2015).

During the Lochkovian, trilobites were rare in the study area. Only *Ganetops*, *Protacanthina* and to a lesser extent, *Morzadecops*, proliferated during the late Lochkovian in the Ougarta region (Ass. *IIa*). These asteropygines preferred the shallow siliciclastic environment of the Saoura Valley (Fig. 6; Morzadec, 1997) and similar environmental settings, also developing in the Iberian and Cantabric ranges and in the Armorican Massif (Morzadec, 1992). Subsequently, an increasing number of trilobites began to populate the region. Their remains are frequently found in the strata, whose carbonate content is also increasing. This suggests a lower sea-level and concerns distinct invertebrate faunas (Frey et al., 2014). In such environments, *Lepidoproetus* Association (*IIIa*) flourished; proetids like *Lepidoproetus*, *Dalejeproetus* and *Podoliproetus* preferred these rather shallow environments with open marine conditions (Johnson & Fortey, 2012). The *Lepidoproetus* Association survived during the late Emsian of the Dra Valley in deeper water environments. Trilobites of this association are usually found in calcareous shales deposited above the photic zone but probably below the storm weather wave base (Chatterton et al., 2006). However, only *Hollandiella* was encountered in these deeper environments and in layers above the transgressive Daleje event (House, 1985).

During the Pragian, the *Paralejurus* Association (*IId*) also established itself (Fig. 6). *Paralejurus* and *Reedops* were predominant in limestones at intermediate depth but also in shallower environments such as the bioherms of Hamar Laghdad (McKellar & Chatterton, 2009). *Reedops* was probably semi-infaunal or infaunal (McKellar & Chatterton, 2009) whereas Schraut & Feist (2004) excluded a semi-endobenthic life habit for *Paralejurus*. Consequently, these two genera were rarely found together notwithstanding some exceptions - *Paralejurus* co-occurred with *Reedops cephalotes hamlagdadianus* Alberti 1983 but the latter species appears to have been ecologically more flexible with respect to the type of substrate (Chlupáč, 1977). During this period, the *Sculptoproetus* Association (*IIe*) developed and is often found in the nodular marly limestones from the north-eastern part of Jbel Issoumour (Alberti, 1967b, 1969), indicating a slightly deeper environment than those preferred Pragian associations. The *Sculptoproetus* Association evolved during the Emsian; *Sculptoproetus* abounds in marly limestones indicating an intermediate water depth environment (Fig. 6).

During the Emsian, *Morzadecops* first associated with other asteropygines during the Lochkovian, flourished and dominated the *Morzadecops* Association (*Ia*). *Morzadecops* occurs in marls and limestones interbedded with clay in moderately shallow water depth environments (Klug et al., 2008). The *Montanproetus* Association (*Ic*) also developed during the Emsian but it was mainly found in calcareous deposits in shallow carbonate environments (Fig. 6). The associated *Kayserops* preferred a more shallow environment (Morzadec, 2001). *Psychopyge* is widely distributed in several marine basins during the Emsian. It was rarely associated with other genera (Fig. 4) and dominated the *Psychopyge* Association (*IIf*). *Psychopyge* are present in marls or limestones interbedded in thick marl deposits from relatively distal environments dominated by pelagic faunas (Morzadec, 1988).

Although the *Morocops* Association (*IIb*) was first encountered during the Pragian at the Maharch locality with the presence of *Cyphaspis* (Van Viersen & Holland, 2016), it proliferated in the late Emsian and the early Eifelian. This association was dominated by *Morocops*, which co-occurred with *Cyphaspis* and *Austerops*. The presence of *Austerops* could indicate a pioneer community (Khaldi et al., 2016). The *Morocops* Association also developed in the moderately deep-water environment of the Dra Valley (Chatterton et al., 2006) and the platform environment of Ougarta after the late Emsian transgression (Khaldi et al., 2016). It was also able to live in the epicontinental basin between fair weather and storm wave base of Hamar Laghdad (Brachert et al., 1992). Hence, the *Morocops* Association abounded in a water environment below the fair-weather wave base. At the same time, the *Piriproetus* Association (*Ia*) was encountered at the edge of the pelagic Tafilalt Platform in moderate depth below the fair-weather wave base (Figs. 6,7); Kaufmann, 1998; Chatterton et al., 2020). *Piriproetus* occurred in a facies dominated by marly limestones but they disappeared from this environment after the early Eifelian.

During the late Emsian, the *Hollardops* Association (IIa) also flourished and was dominated by *Hollardops*, *Timsaloproetus* and *Erbenochile*. These taxa proliferated in marls or limestones interbedded within marls. They were mostly present in Ougarta, an area considered relatively deep and dominated by shales (Ouali Mehadji et al., 2011) (Fig. 6). A similar environment developed in the western Dra Valley where *Timsaloproetus* was found (Chatterton et al., 2006). *Hollardops* enjoyed intermediate water depth below fair-weather wave base like in the Maïder and the Ougarta region (Chatterton & Gibb, 2010) but they disappeared with a more open marine environment (Morzadec, 2001). Finally, *Erbenochile* proliferated in relatively deep marine environments (Chatterton et al., 2006), which corroborates the moderately deep marine conditions such as an offshore transition for the *Hollardops* Association. The *Gerastos* Association (*IIc*) also flourished during the Emsian at Jbel Issoumour South-west (Fig. 6). In this balanced community (Fig. 4), *Morocops* or *Cyphaspis* did not prevail over *Gerastos* contrary to many late Emsian assemblages affiliated with the *Morocops* Association. Conversely, the *Gerastos* associations from the Middle Devonian were dominated by *Gerastos*, which was the only genus in many localities (Fig. 4). *Gerastos* is found in limestones from the Maïder where they found detritus for food in the shallow shelf marine environment (Gibb &

Chatterton, 2010).

The *Chotecops* Association (*IId*) was the only association to appear and expand during the Middle Devonian and was dominated by *Chotecops* associated with *Helmutia* and *Struveaspis*. The *Chotecops* Association was encountered in Ougarta and Tafilalt (Fig. 7) in marls or in thin limestone layers in marl deposits from the quiet environments of a distal platform or basin (Feist & Orth, 2000; Crônier et al., 2018a).

All the associations that appeared during the Early or Middle Devonian disappeared in the late Givetian. Only *Chlupacops*, a genus with reduced-eyed taxa was found in the limestones of deep marine environments in the Ougarta Basin (Feist et al., 2016).

After the Kellwasser event, trilobites were rare in the study area. The first trilobite after the crisis was *Cyrtosymbolina* in the early Famennian. The increasing depth of water during the Famennian (Wendt et al., 1984; Wendt & Belka, 1991; Abbache et al., 2019) led to trilobites flourishing again, which meant we could use them to examine the relationships between different basins over time. During the early Famennian, only cyrtosymbolines proliferated in the shallow pelagic Tafilalt Platform in the *Cyrtosymbolina* Association (*IVa*). They became common in the photic offshore environments of North Africa and many other places (Lerosey-Aubril & Feist, 2012). Members of the *Cyrtosymbolina* Association occur mainly in limestones but also in marlstones and argillaceous limestones, such as shallow carbonate marine environments (Fig. 8).

In the Ougarta Basin, blind trilobites such as *Trimerocephalus*, *Trifoliops* and *Enygmapyge* occurred since the early Famennian. The *Trimerocephalus* Association (*IVc*) established in many localities of the Ougarta Basin (Fig. 8) in deep marine environments of the slopes and basins. They were collected from rare often nodular limestones indicating a weak water circulation (Benhamou et al., 2004; Crônier et al., 2013). *Trimerocephalus* also occurred at Korb-el-Atil in the Tafilalt Basin associated with *Osmolskabole* and *Phacops sensu lato* (Fig. 8) within a marine environment dominated by shales (Wendt & Belka, 1991). During the late Famennian, the *Trimerocephalus* Association is only found at Béchir, again in a deep marine environment, before its demise at the end of the Famennian.

The *Osmolskabole* Association (*IVb*) appeared during the middle Famennian in the limestones of the Tafilalt Platform (Fig. 8) because they appreciated the photic offshore environment. Consequently, this pelagic platform became convenient for the members of this association because of the sea-level rise (Wendt & Belka 1991). The *Osmolskabole* Association also flourished in the deeper marine environments of the slowly subsiding Tafilalt Basin (at Korb-el-Atil and Ouidane Chebbi localities), in argillaceaous limestones. Nonetheless, this association did not occur in the Maïder Basin because this area was deeper than the Tafilalt Basin (Wendt et al., 1984).

During the late Famennian, Cyrtosymbolines were still abundant in the Tafilalt Platform. However, the *Osmolskabole* Association was no longer present in the Tafilalt Basin, probably due to a transgression (Wendt & Belka, 1991; Becker et al., 2004). At the end of the Famennian, the *Osmolskabole* Association is still found in the limestones of the north Tafilalt Platform whereas the south became a deltaic area (Wendt et al., 1984). Indeed, trilobites did not appreciate brackish water although some attempts to colonize these environments happened in the clade history (Mángano et al., 2021). The *Osmolskabole* Association and cyrtosymbolines in general were restricted to moderate water depth environments from platform to slope, which are represented today by limestone deposits.

Finally, the *Phacops s.l.* Association (*IVd*) flourished in the Ougarta region (at Tamtert Zereg locality) during the Famennian, to the east of the location of the *Trimerocephalus* Association (Fig. 8) in nodular 'griotte' limestones corresponding to a basinal environment (Benhamou et al., 2004). The *Phacops s.l.* Association extended into the late Famennian with the continuous deepening of this area (Wendt et al., 1984; Wendt & Belka, 1991; Abbache et al., 2019) and replaced *Trimerocephalus* Association (at Marhouma locality). The *Phacops s.l.* Association still abounds in nodular limestones alternating with claystones, or in marlstones, in moderate to deep marine environments such as basins. Samples with *Phacops s.l.* are generally slightly younger than those of *Trimerocephalus* even if these two genera may co-occur (Crônier et al., 2013). Therefore, a progressive replacement occurred in the Ougarta Basin in the deeper offshore environment and already recognised at the global (Crônier & François, 2014). At the end of the Famennian, a sea-level drop occurred and all the deep water trilobites disappeared from the studied area.

## 6. Connection between basins and their history through time

### 6.1. Lochkovian

Trilobite diversity was low in the study area in the Lochkovian (Fig. 9A). They only occurred in the Saoura Valley where trilobites populated the sediment surface in the late Lochkovian after a regional regression (Ouali Mehadji et al., 2011). Only asteropygines lived in these shallow siliciclastic environments (Morzadec, 1997). To the west, the eastern Anti-Atlas became too deep to allow benthic faunas to settle during the Lochkovian (Hollard, 1967) and thus, this environment was neither favourable for asteropygines (Morzadec, 1992), nor for other trilobites as they were completely absent from this area.

## 6.2. Pragian

The Pragian regression led to a higher carbonate content with more sand in the Saoura Valley where asteropygines no longer proliferated (Morzadec, 1997; Ouali Mehadji et al., 2011). Indeed, the composition of trilobite associations was linked to the sediment accumulation rate and the type of shelf (Bignon & Crônier, 2015) and no other trilobites replaced them. The eastern Anti-Atlas became more carbonate too (Hollard, 1963; Kaufmann, 1998). New trilobite communities were established (Hollard, 1967; Morzadec, 2001) in these favourable environments leading to a strong increase of their diversity in North Africa (Fig. 9A) simultaneously to the global Pragian diversification (Chlupáč, 1994, Bault et al., 2021). However, despite this high diversity three genera dominated the shallow water environments of the Anti-Atlas region: *Paralejurus*, *Reedops* and *Lepidoproetus*. These genera and some other genera, constituted two associations: the *Paralejurus* Associations was dominant in the Maïder and the *Lepidoproetus* Association was dominant in the Tafilalt (Fig. 6). Nevertheless, the *Paralejurus* Association developed to the west in the Tafilalt and in the north of the Ougarta region at Ben Zireg and to the east near Foum Zguid. Thus, there was a strong connection between these different basins during the Pragian. This is due to a relatively homogeneous environment in the Anti-Atlas region at this time, considered as a homoclinal ramp (Kaufmann, 1998; Lubeseder et al., 2010). Exchanges also occurred with the neighbouring Bechar area, which was facilitated by the same carbonate platform environment (Ouali Mehadji et al., 2011) and with the south-west Foum Zguid area where *Reedops* and *Cyphaspis* were reported. All the Pragian trilobites populated a relatively shallow environment of various carbonate platforms. However, *Paralejurus* and its associated trilobites preferred slightly deeper environments than *Lepidoproetus*, which is why they rarely co-occurred. The shoal of Hamar Laghdad (Hollard, 1981, Brachert et al., 1992; Klug et al., 2018) showed a high diversity of trilobites.

## 6.3. Emsian

In the early Emsian, diversity decreased (Fig. 9A). While the Pragian dominant species almost disappeared from the studied area, other genera proliferated despite no important environmental changes in the Anti-Atlas (Kaufmann, 1998). *Morzadecops* spread over the entire eastern Anti-Atlas and *Sculptoproetus* lived in the Tafilalt. In the Ougarta region, a local transgression (Ouali Mehadji et al., 2011) led to a comeback of trilobites with the moderately deep water genus *Psychopyge* but no connection existed with the Anti-Atlas; the Ougarta region remained isolated from other basins to the west and to the north. The Bechar basin was also excluded from the trilobite dispersal with *Prodrevermannia* the only genus occurring in that region (Alberti, 1983). *Morzadecops*, which preferred a shallow environment (Morzadec, 2001), could not proliferate in the Ougarta region. However, although *Sculptoproetus* lived in moderately deep-water (Chatterton et al., 2006), it was not found in the Ougarta region. Hence, the deep waters of the Tafilalt Basin between Ougarta and Anti-Atlas prevented the dispersal of shallow and moderately deep-water trilobites from one of these regions to the other.

In Morocco, the Maïder and Tafilalt platforms were still connected and the *Morzadecops* Association (*Ia*) flourished in both areas. However, the *Sculptoproetus* Association (*Id*) was restricted to the Tafilalt area while it appeared in the Maïder area during the Pragian. The Tafilalt area being typically shallower than the Maïder area (Wendt, 1995), trilobites migrated to shallower places but no transgression occurred at this time (Kaufmann, 1998). There were no more dispersal to the south-west as the Foum Zguid area became shallower (Jansen et al., 2004) where trilobites did not develop.

During the late Emsian Daleje transgression (Johnson et al., 1985; Kaufmann, 1998; House, 2002), the studied area became deeper (Kaufmann, 1998, Belka et al., 1999). Trilobites developed in this new environment leading to the highest α diversity and a high β diversity (Fig. 9A) simultaneously with the global diversity peak (Chlupáč, 1994; Adrain, 2008). Late Emsian trilobites constituted a stable equilibrium community. Some of the common trilobites of the Pragian persisted into the early Emsian, such as *Paralejurus*, *Reedops* and *Sculptoproetus*. However, no Pragian or early Emsian trilobite genus became common in the late Emsian; they were all declining and restricted to few areas. The only exception was *Psychopyge*, which invaded the Anti-Atlas. Thus, during this period of diversification, the genera quickly renewed themselves by showing innovations and novelties (Chlupáč, 1994). Numerous genera appeared in the late Emsian and among them with the phacopids *Morocops* and *Hollardops* respectively dominating the Anti-Atlas (Crônier et al., 2018b) and the Ougarta region. Connections between the different basins were strong, favoured by the relatively homogeneous environments in North Africa, moderately deep water, with an important proportion of muddy regions (now shales) covering the platforms (Hollard, 1967; Kaufmann, 1998; Jansen et al., 2004; Chatterton et al., 2006; Ouali Mehadji et al., 2011). Exchanges between Anti-Atlas and the deeper Ougarta region became possible: *Hollardops* and *Erbenochile* occurred in Ougarta, Maïder and Dra Valley (Morzadec, 2001; Chatterton et al., 2006; Chatterton & Gibb, 2010; Khaldi et al., 2016). *Psychopyge* were also found in both the eastern Anti-Atlas and the Ougarta region (Fig. 6). Although the Tafilalt and Maïder areas became different during the late Emsian in terms of both facies and fauna (Hollard, 1967), a strong connection was present between these two areas.

*Sculptoproetus* proliferated in the Maïder area, suggesting an invasion from the Tafilalt area. At the same time, *Morocops*, as well as *Cyphaspis*, flourished in the Tafilalt, Maïder and near Foum Zguid areas. Ben Zireg was also involved in the exchanges with *Montanproetus* existing in the Bechar Basin and the Maïder area. Nevertheless, it remains difficult to demonstrate the supply of trilobites from one basin to another without a finer temporal resolution. Although trilobite exchanges were numerous, some trilobites remained restricted to a basin such as *Gerastos* and *Piriproetus* in the Maïder Basin. Significant taxonomic turnovers occurred between the late Emsian localities as is highlighted by the high β diversity (Fig. 9). More important local environment variability in the eastern Anti-Atlas (Hollard, 1967) is a potential explanation for this high taxonomic turnover.

## 6.4. Eifelian

The transition between the Early and Middle Devonian was marked by the onset of tectonic events leading to a platform and basin topography (Wendt et al., 1984; Kaufmann, 1998; Lubeseder et al., 2010). This event is due to the Variscan orogeny, which disrupted the eastern Anti-Atlas. A deep basin (i.e., Maïder Basin) separated two platforms (i.e., Maïder and Tafilalt platforms). As most trilobites lived in shallow environments, they did not cross the basin to invade other localities. More specifically, the deep Maïder Basin acted as a natural barrier, which led to the development of distinct trilobite communities in the Middle Devonian. This barrier also effectively prevented the dispersion of these communities by pelagic or planktonic larvae, which had been identified in several Devonian trilobites (Speyer & Chatterton, 1989; Chatterton et al., 1990; Chatterton & Speyer, 1997). Indeed, these protaspides could not cross this deep basin because of unfavourable paleocurrents, paleoenvironmental conditions, or/and a too wide distance for their life duration. Consequently, in contrast to the Lower Devonian, trilobite distributions of the Eifelian show almost no connections between the Tafilalt and Maïder areas. To the west of the Maïder Basin, *Gerastos* and *Cyphaspis* evolved whereas *Piriproetus* then *Chotecops* developed in the Tafilalt (Fig. 7). The trilobites from the west of the Maïder Basin evolved in a relatively shallow environment (Gibb & Chatterton, 2010) and did not cross the deep Maïder Basin (Wendt et al., 1984). On the other hand, *Cyphaspis* occurred to the south-west at Foum Zguid (Van Viersen & Holland, 2016) showing a connection between the Maïder and the western Anti-Atlas areas. *Gerastos* that appeared in the late Emsian, proliferated in the Maïder during the Eifelian and covered the edges of the Maïder Platform including the western part at the Jbel Ou Driss locality (Fig. 7). *Gerastos* replaced *Morocops* during the Middle Devonian in the shallow neritic environments, while the distribution of this genus decreased from the late Emsian to be restricted in some Maïder localities. To the eastern side of the Maïder Basin, a community of trilobites dominated by the genus *Piriproetus* (Ass. *Id*) expanded in the pelagic Tafilalt Platform. The trilobites from this association living in a moderately deep environment were unable to cross the Maïder Basin. While no connection existed to the west of Tafilalt, trilobite exchanges still occurred to the east. Indeed, *Chotecops*, present in deep environments (Feist & Orth, 2000; Crônier et al., 2018a), occurred in both Tafilalt and Ougarta areas. Variscan orogeny created a basin between the Tafilalt and the Ougarta areas but this basin seems shallower than the Maïder Basin (Kaufmann, 1998) thus enabling *Chotecops* to cross this basin to invade new localities but not *Piriproetus*. *Chotecops* probably never settled in the Maïder because this basin was too deep. Moreover, they did not flourish in the shallow environments of the Maïder Platform margins. *Austerops*, present in Ougarta, Maïder and Dra Valley, was the only genus living on both sides of the Maïder Basin (Chatterton et al., 2006; McKellar & Chatterton, 2009; Crônier et al., 2018a). Its presence in these areas was recorded since the late Emsian (Fig. 6).

In both Tafilalt and Maïder, the Eifelian faunas replaced those of the Emsian and the trilobite associations were influenced by the palaeobathymetry (Crônier & Van Viersen, 2007). The origination rate and trilobite changes were not particularly high at the Emsian/Eifelian boundary on an overall (Chlupáč, 1994; Lerosey-Aubril & Feist, 2012). Thus, North-African faunal changes rather seemed attributed to topographic changes where some trilobite genera took advantage of this new heterogeneous environment.

### 6.5. Givetian

The overall Middle Devonian Choteč, Kačak and Taghanic events (House, 2002; Becker et al., 2016) had an impact on trilobites and their diversity at the global (Lerosey-Aubril & Feist, 2012) and from North Africa (Fig. 9A). Most of them disappeared during the Givetian and only three associations have been reported in the studied area: the *Gerastos* Association with *Gerastos* sometimes associated with *Cornuproetus* or *Cyphaspis* in the Maïder area; the *Chotecops* Association dominated by *Chotecops* and *Helmutia* in the Tafilalt area and the *Morocops* Association at Ras el Kebbar locality (Maïder). The same distinction between areas was identified during the Eifelian. However, the presence of *Gerastos* at the Jbel Ziata locality in the Tafilalt (Feist & Orth, 2000) associated with *Chotecops* showed that trilobite exchanges were rare but remained possible. The weak regressive regime during the early Givetian enabled such migrations from the Maïder to the Tafilalt areas (Lubeseder et al., 2003) as well as the proximity of the Maïder Platform with the Tafilalt Platform to the north of the Maïder Basin

(Kaufmann, 1998). All the trilobites occurred in the eastern Anti-Atlas, whereas the Foum Zguid area and the Ougarta Basin seem relatively depopulated. Unlike in the Ardenne Massif (North of France), the Kačak event did not lead to a replacement of faunas in North Africa (Bignon & Crônier, 2015) but instead to an extinction of existing faunas. However, like in the North of France, the environmental changes favoured *Dechenella* in the Tafilalt (Feist & Orth, 2000).

### 6.6. Frasnian

Overall, the Frasnian trilobite record is scarce (Feist, 1991; Lerosey-Aubril & Feist, 2012). In the studied North African area, the reduced-eyes *Chlupacops* was the only genus encountered in the Ougarta Basin in deep environments (Feist et al., 2016). This basin seems to have been disconnected from the others. The low trilobite diversity recorded during the Frasnian could be explained by unfavourably shallow environmental conditions in the eastern Anti-Atlas (Wendt et al., 1984, Wendt & Belka, 1991) whereas Feist (2002) described trilobites from an outer platform environment in the neighbouring Meseta Central in Morocco.

### 6.7. Famennian

After the Kellwasser crisis, some trilobites developed worldwide. While, cyrtosymbolines proliferated in the shallow outer platform (Lerosey-Aubril & Feist, 2012), in deeper environments such as basins, reduced-eyed and blind phacopids and proetids developed (Chlupáč, 1994; Lerosey-Aubril & Feist, 2012). A similar process occurred in North Africa where cyrtosymbolines appeared during the early Famennian in the shallow Tafilalt Platform and constituted a pioneer community. At the same time, in the deeper Ougarta Basin, the number of blind phacopids increased. No trilobites have been found in the Maïder for this period. No dispersal routes seem to have existed between the different basins at that time: *Trimerocephalus* Association was encountered in the Ougarta Basin, while the *Cyrtosymbolina* Association was encountered in the Tafilalt area. Cyrtosymbolines could not cross the deep Maïder and Tafilalt basins as the Tafilalt Platform acts as a natural barrier to stop deep water trilobites coming from Ougarta. This trend remained through the Late Devonian. In contrast, the distal platform of Ben Zireg (Abbache et al., 2019) seems to have been a favourable environment to host trilobites but none have been found yet in the nodular limestones and shales. Trilobite studies based upon localities at Ben Zireg since Alberti (1983) remain scarce and this could explain the absence of trilobites in addition to the sedimentary gaps (Abbache et al., 2019). Trilobites were absent throughout the Famennian in the Maïder Basin, probably deposited in deeper water than that of the Tafilalt Basin (Wendt et al., 1984; Kaufmann, 1998). Crônier & François (2014) suggested a depth superior to 60 m for blind genera (i.e., *Trimerocephalus*) and Feist et al. (2016) indicated an offshore environment near or beyond the limit of the photic zone. However, with its depth of 200 to 400 metres, the Maïder Basin had much deeper steep slopes according to stratigraphic studies (Wendt et al., 1984). The Tafilalt Platform also acted as a barrier to trilobite dispersal.

The sea-level rise of the middle Famennian (Wendt et al., 1984; Wendt & Belka, 1991; Abbache et al., 2019) allowed the proliferation of deep-sea phacopids. They were present at that time in many Ougarta localities and a connection appeared between the Tafilalt and Ougarta areas. Exchanges were possible because the Tafilalt Basin and the Ougarta Basin were probably interconnected during the Late Devonian (Wendt et al., 1984; Wendt, 1985; Abbache et al., 2019). However, dispersal apparently only occurred from the Ougarta Basin to the Tafilalt area, i.e., from deeper to shallower environments. Indeed, this unidirectional supply of biodiversity suggests that only the deep-living taxa of Ougarta were able to cross the deep basin between the Ougarta and the Tafilalt. The moderately deep-water taxa *Phacops s.l.* and *Trimerocephalus* present in the Ougarta region were able to colonise the margins of the quite deep Tafilalt Basin. Shallower areas also enabled the development of other trilobite communities with new cyrtosymbolines appearing in the Tafilalt Platform dominated by the *Osmolskabole* genus (Alberti, 1973, 1974, 1975a, 1976a, 1976b; Lerosey-Aubril & Feist, 2005; Lerosey-Aubril & Feist, 2006). Because of the deepening of this area, they were adapted to intermediate water depths and could have settled in the margins of this relatively shallow Tafilalt Basin (Wendt et al., 1984) although they were still unable to cross a deep basin to establish themselves in the Ougarta region. Moreover, in the intermediate water/depth, other taxa developed during the middle Famennian. These were the large eyed *Phacops s.l.*, which proliferated in the deeper part of the shallow Tafilalt Platform, associated with *Trimerocephalus* or *Osmolskabole*. On the other hand, *Phacops s.l.* only occurred in the shallower part of Ougarta region to the south-east.

During the late Famennian, this connection was disrupted and the Tafilalt and Ougarta areas are represented by two separate communities (Fig. 8). Despite the deepening of the Tafilalt basin at this time, no trace of deep-water phacopids has been found there although they were still present in the Ougarta Basin. Two explanations are possible - first, that they were present but still not sampled and secondly, that a natural barrier, which has still not been identified between the two basins prevented any trilobite exchange. This kind of natural barrier could have resulted from the deepening between Ougarta and Tafilalt areas, preventing any crossing of trilobites, or, alternatively, from a very shallow barrier, formed in the context of Variscan orogeny, which was not favourable to Famennian trilobites (Hollard, 1974, Wendt et al., 1984). Unfortunately, this area was covered by Cretaceous deposits (Benhamou et al., 2004) thus preventing any information on the evolution of this basin. Cyrtosymbolines were restricted to the shallowest part of Tafilalt, to the North. During this period of highstand sea-level (Wendt & Belka, 1991), the rest of the Tafilalt was probably too deep to host them. In contrast, *Trimerocephalus* has been recorded in the Ougarta region for this time in just one locality, while *Phacops s.l.* dominated the rest of this area. These phacopids tended to replace *Trimerocephalus* in the late Famennian (Crônier & François, 2014).

Finally, at the end of the Famennian, a regression occurred leading to a deltaic environment with sandstone deposits in the eastern Anti-Atlas and Ougarta region (Wendt et al., 1984; Kaiser et al., 2011; Abbache et al., 2019). This environment was unfavourable for many benthic organisms and all deep-sea trilobites disappeared from these areas. Only two cyrtosymbolines (i.e., *Pusillabole* and *Pseudowaribole*) remained in the shallow water environment of the northern Tafilalt and were apparently unable to migrate to the Ougarta Basin, which was probably too deep (Fig. 8). It is difficult to understand the facies distribution of the Tafilalt because of the scarce outcrops and the potential reworking due to debris flows (Wendt et al., 1984).

Originations and migrations always occurred from the shallower part of Tafilalt and Ougarta region. In the Tafilalt, trilobites appeared in the shallowest part of the Tafilalt Platform, located to the north (Wendt & Belka, 1991) before becoming a deeper basin in the south. Trilobite migrations seemed to have started in its south-eastern part of the Ougarta Basin. *Trimerocephalus* Association from the early Famennian and *Phacops s.l.* Association from the middle Famennian appeared respectively at the Marhouma and Tamtert Zereg localities (Fig. 8). These localities corresponded to an epicontinental platform (Benhamou et al., 2004) and represented the shallowest part of the Ougarta Basin. Then, following their occurrences, each genus invaded the deepest north-western part and dominated the basin (Fig. 8). However, an influence from the south-west was unlikely because the environment in the Gourara area was deep with basinal deposits (Benhamou et al., 2004; Abbache et al., 2019).

### 6.8. Tectonic impact on trilobite faunas

During the Early Devonian, the Anti-Atlas area had a rather homogeneous environment (Lubeseder et al., 2010). In this context, faunal changes were linked to global environmental changes with first, the Pragian regression, which led to environmental changes driving faunal changes (Chlupáč, 1994; Morzadec, 1997, 2001). Similar changes occurred in Bohemia with the development of *Reedops* and *Odontochile* (Chlupáč et al., 1985). Then, the Daleje transgression (Kaufmann, 1998; House, 2002) affected the North African trilobites with the development of new faunas dominated among others by *Morocops* and *Hollardops*, adapted to slightly deeper environments (Fig. 6). The same trend occurred worldwide, with diversifications and innovations, particularly in offshore facies (Chlupáč, 1994). From the Middle Devonian, the Variscan orogeny started to influence the regional topography (Wendt et al., 1984; Kaufmann, 1998) and global events (sea-level changes and continental drift) were no longer the only cause of biodiversity changes. Obviously, the Middle Devonian events influenced the trilobite faunas, both quantitatively (Bault et al. 2021) and qualitatively (Fig. 7). Similarly, an important turnover occurred with the Kellwasser events (Lerosey-Aubril & Feist, 2012) and consequently, the Famennian trilobites had nothing in common with their predecessors in North Africa (Fig. 4). However, from the Eifelian, there were faunal differences between nearby areas (Fig. 7). These differences were well marked in Morocco and Algeria with strong differences between Maïder and Tafilalt whereas in other places such as the Ardenne Massif, the faunas were still subject only to global changes (Bignon & Crônier, 2015). The basin and platform topography affected the trilobites because of their bathymetric preferences (Morzadec, 2001; Chatterton et al., 2006). Rapid changes and instability made unpredictable regional conditions indicating that North African trilobite communities conform to Gleasonian models where 'species-individualistic' responses to environmental changes became prevalent in community ecology (Gleason, 1927). Regular local and/or global changes hampered the ecological stasis spotted in other communities (Brett et al., 1996).

Unlike topography, the type of sedimentation had a low impact on North African trilobites, except for those due to global changes at the Lochkovian-Pragian boundary. Moreover, the associations seemed less dependant on the sedimentation type laterally. For instance, *Gerastos* has been found both in thick-layered limestones and in calcareous mudstones interbedded with shales (Gibb & Chatterton, 2010). This kind of equilibrium community has been already noted in the Middle Devonian trilobites of the Ardenne Massif (Bignon & Crônier, 2015). Indeed, the *Dechenella* association raised and flourished when carbonate platform environments appeared at the end of the Eifelian. This community was able to maintain its organization during several dismantling episodes of the platform during the Givetian, corresponding to a mixed carbonate-siliciclatic ramp. Only the global Taghanic event of the late Givetian (House, 1985) broke the stability of this community. A similar signal has currently been highlighted in Morocco regarding the stability of trilobite organization despite environmental variations restricted in local and temporal terms (Hollard, 1963, 1967; Bultynck & Walliser, 2000; Lubeseder et al., 2010).

## 7. Conclusions

During the Devonian, the Anti-Atlas Range and its Algerian extensions were located on the Saharan Platform, a passive continental margin of Gondwana. This area underwent several ecological changes due to regional and global events with many sea-level changes, anoxic/hypoxic events and tectonic events occurring throughout the Devonian. All these changes affected the composition of trilobite communities and their diversity.

Trilobites were not well dispersed between the different areas of Northern Africa because of spatial and temporal environmental changes. Devonian trilobites can be assigned to 16 associations with 12 of these associations existing during the Early and Middle Devonian and four exclusively during the Famennian. Each of these trilobite associations flourished in a specific environment, which was favourable for some genera but less so for others. In siliciclastic environments, asteropygines prospered in the Ougarta region during the Lochkovian, while the Pragian regression allowed the diversification of many trilobites in shallow water environments. Both trilobite diversity and the number of associations further increased during the Emsian. During this period, the different basins were well interconnected. Faunal exchanges were facilitated by the absence of strong ecological or topographical barriers and further favoured by a relatively homogeneous environment. The Variscan orogeny modified the palaeogeographic setting during the Middle Devonian towards a platform and basin topology. Geographical barriers formed and trilobite associations became restricted to smaller areas with poor connections between them. This regional tectonic context coupled with more widespread Middle Devonian events affected trilobites, which were almost eradicated from this area in the Frasnian. After the Kellwasser events, trilobites once again flourished regionally and globally although not to the diversity levels of the Emsian or Eifelian. During the same period, cyrtosymboline associations proliferated in shallow platform environments, while phacopid associations proliferated in deeper water environments. Finally, new sea-level and sedimentological changes in the latest Famennian led to the disappearance of numerous trilobites in the Northern African area under study.

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## Supplemental figures

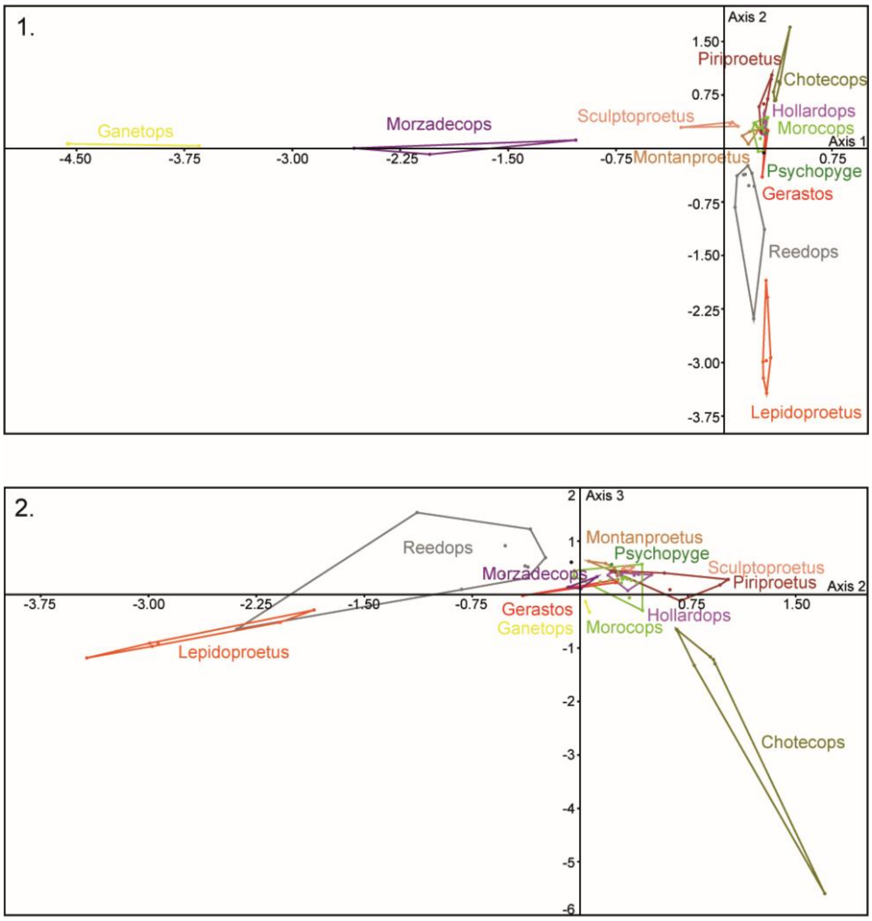

***Fig. A.*** *Scatter plot of North African samples according to Correspondence Analysis (CA) for the Early and Middle Devonian. (1) CA1 and CA2 showing a Pinocchio effect, and (2) CA2 and CA3 showing an arch effect.*

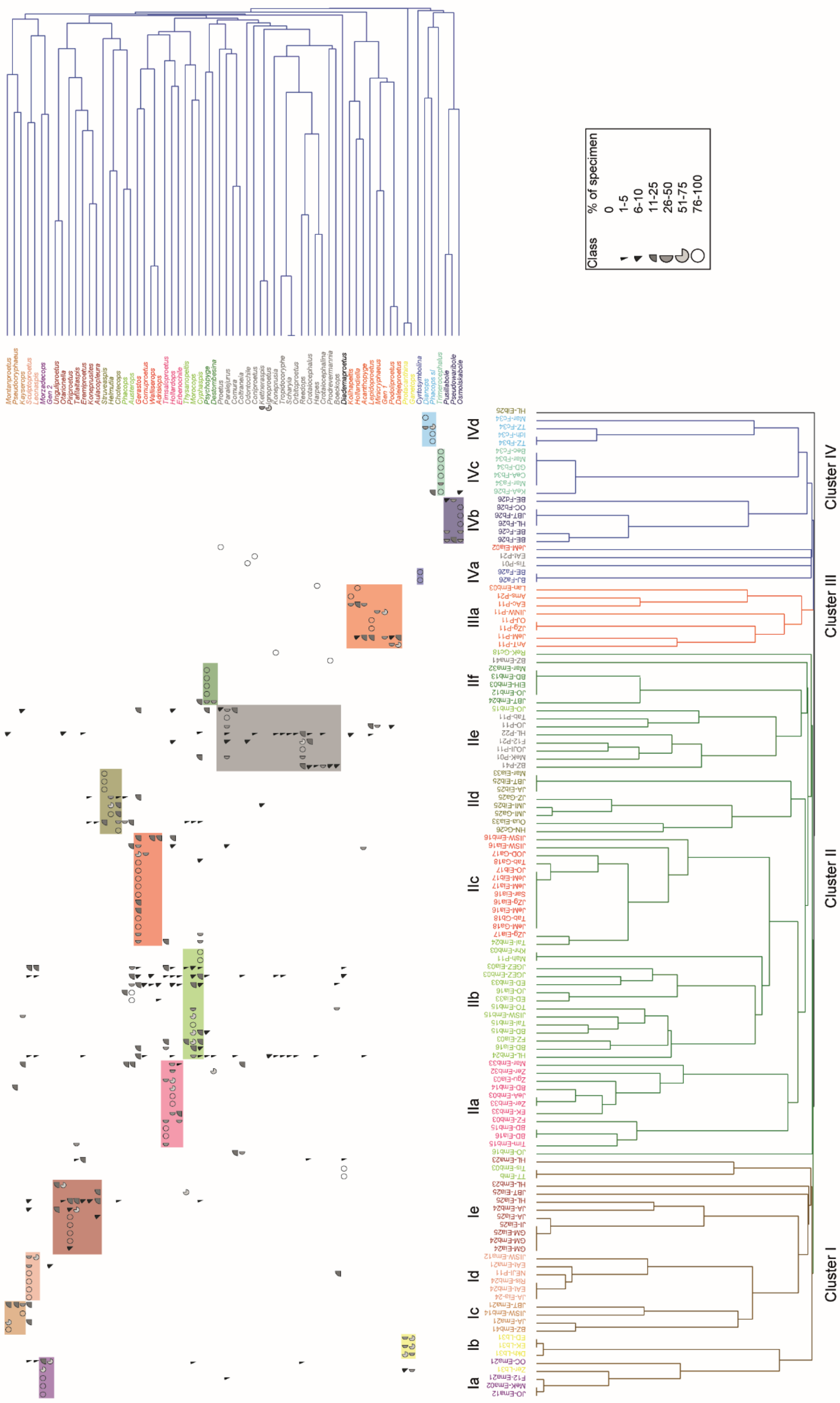

***Fig. B.*** *Dendogram with R and Q modes from hierarchical cluster analysis (HCA) using the average linkage method as correlation setting and the Pearson correlation index as similarity index (Hammer & Harper, 2008). 67 taxa (genera) are clustered according to 123 analysed samples from the Devonian of North Africa. Four clusters and 16 associations are identified. Occurrences of genera in samples are given in proportion of the total number of genera in the sample.*

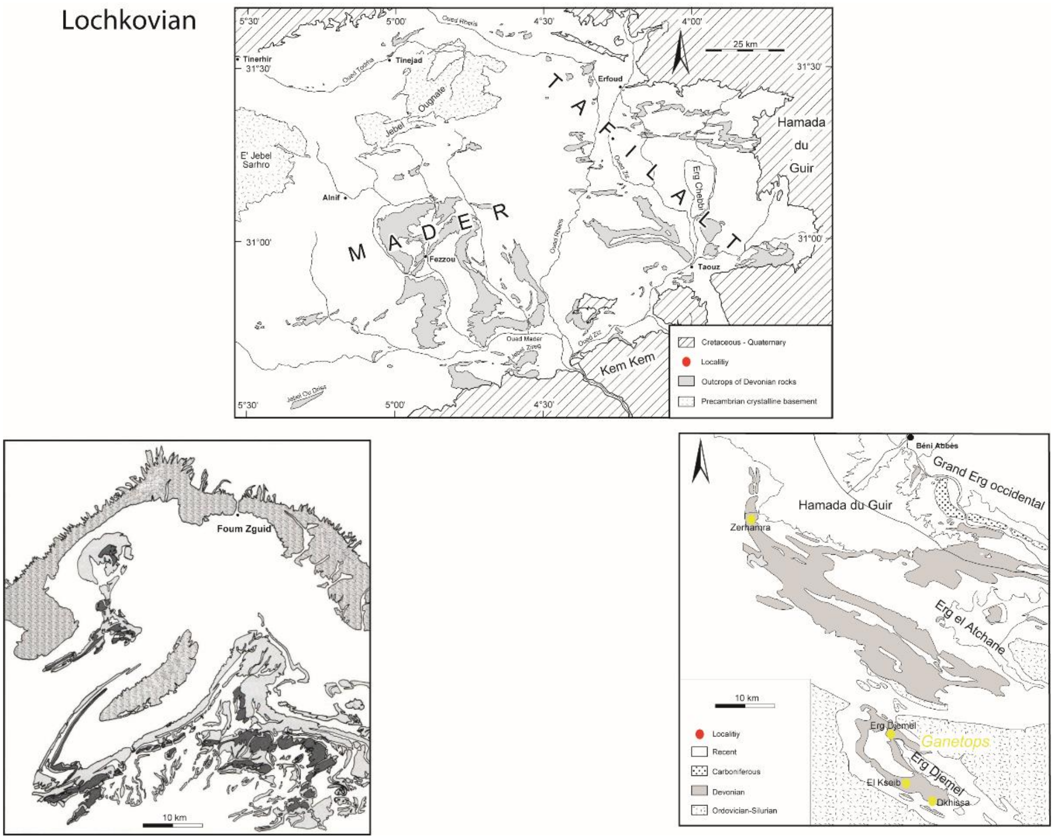

***Fig. C.*** *Geographical localisation of associations defined by clustering in the five studied Moroccan and Algerian areas for the Lochkovian.*

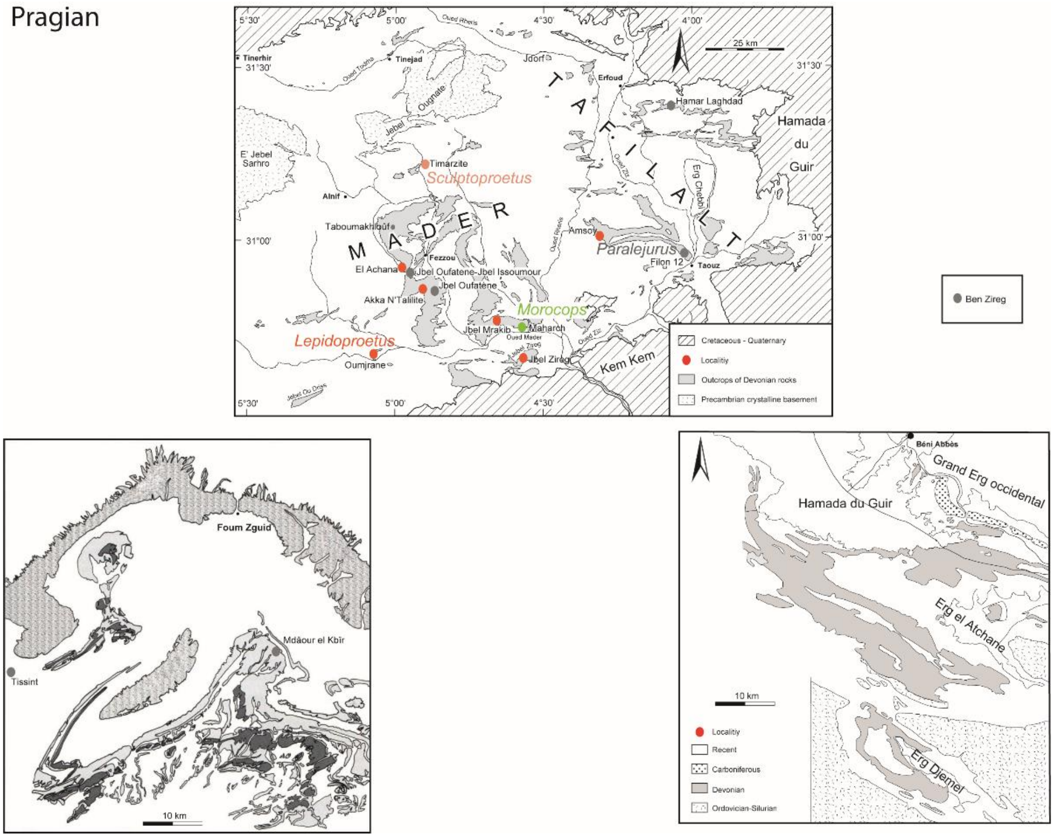

***Fig. D.*** *Geographical localisation of associations defined by clustering in the five studied Moroccan and Algerian areas for the Pragian.*

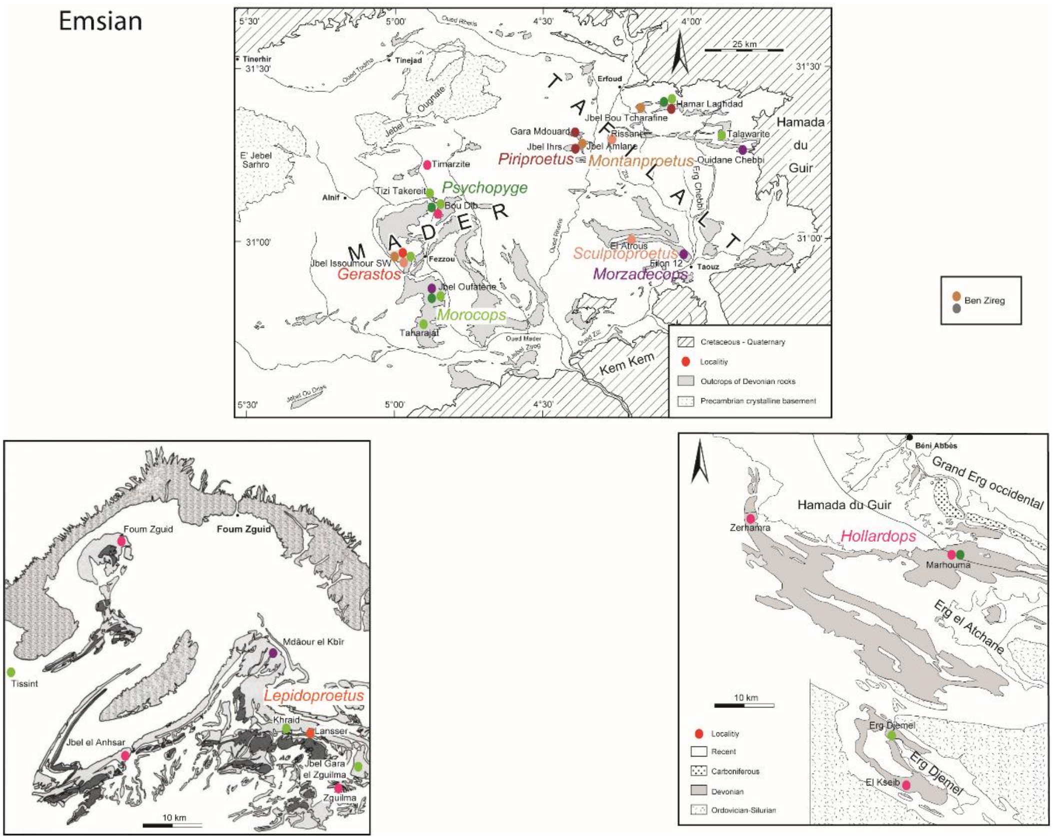

*Fig. E.* *Geographical localisation of associations defined by clustering in the five studied Moroccan and Algerian areas for the Emsian.*

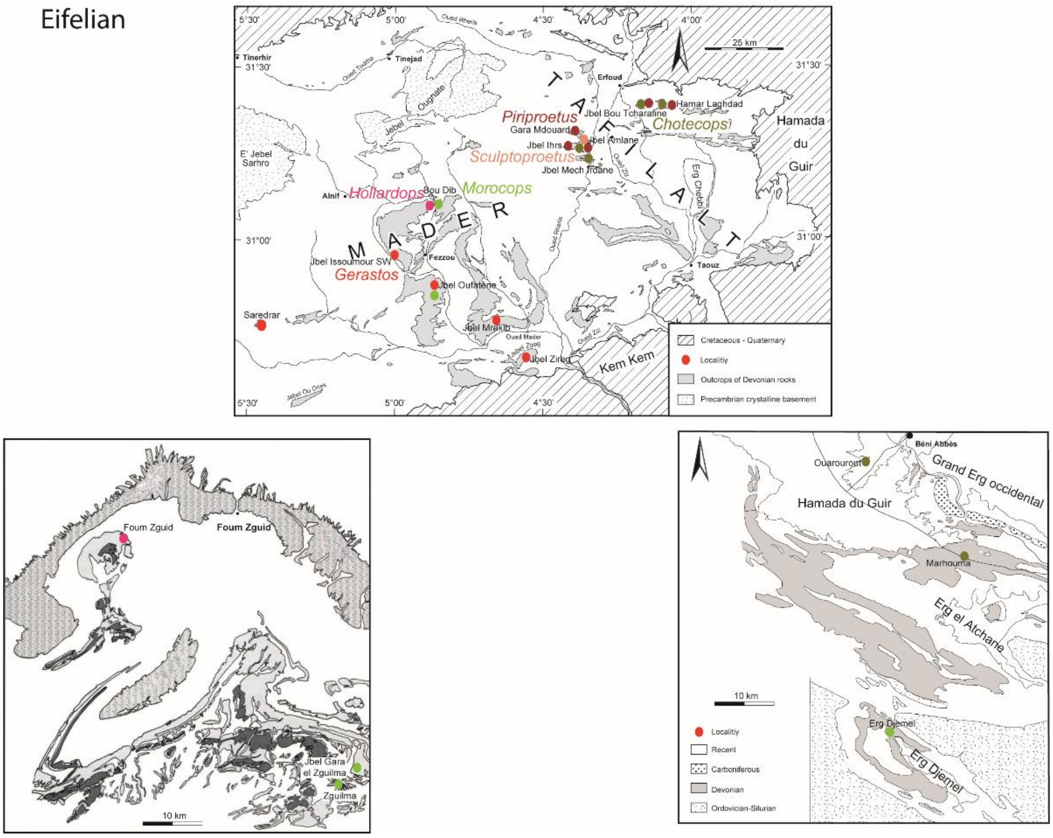

*Fig. F.* *Geographical localisation of associations defined by clustering in the five studied Moroccan and Algerian areas for the Eifelian.*

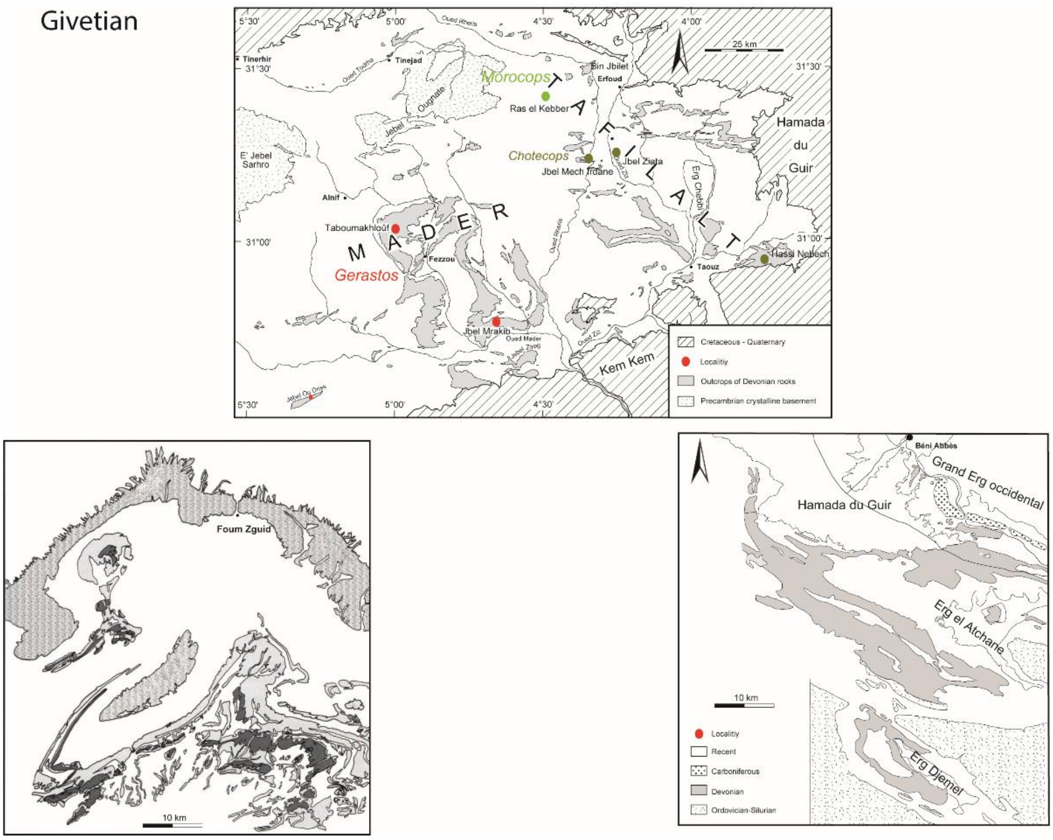

*Fig. G. Geographical localisation of associations defined by clustering in the five studied Moroccan and Algerian areas for the Givetian.*

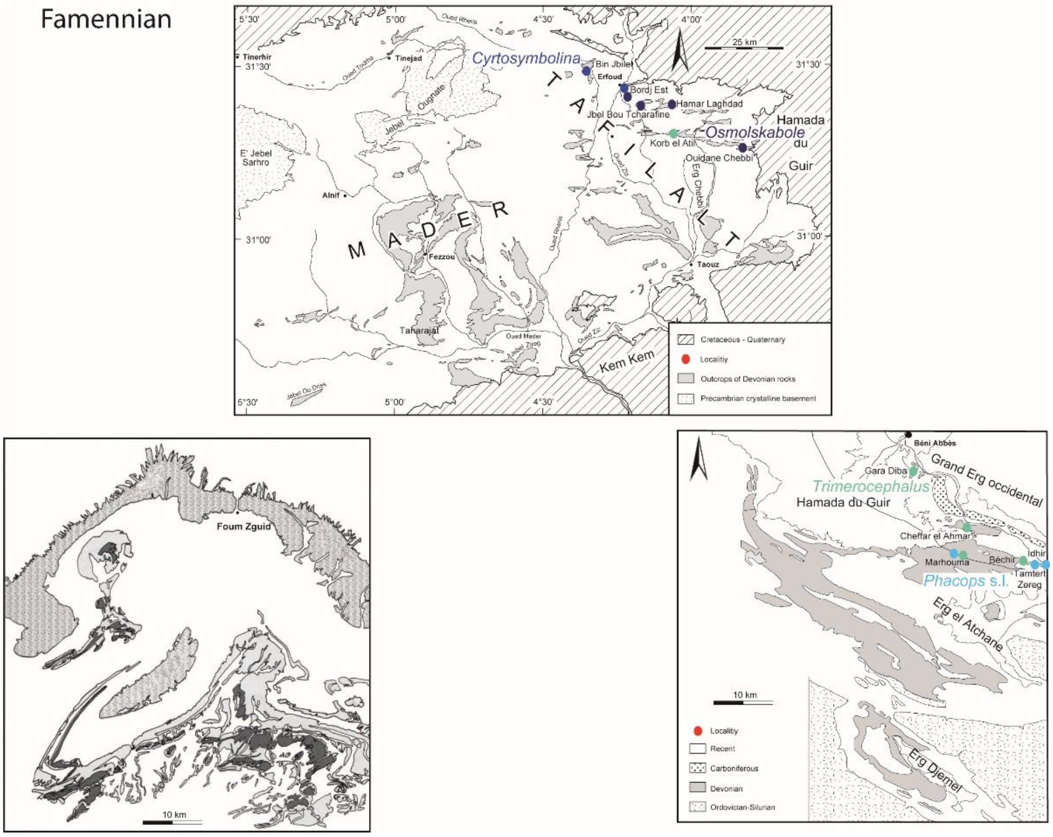

*Fig. H. Geographical localisation of associations defined by clustering in the five studied Moroccan and Algerian areas for the Fammenian.*

## CONCLUSION

Alors qu'elle a commencé avec succès il y a plus de 500 millions d'années au Cambrien, l'histoire évolutive des trilobites s'est perpétuée pendant 250 millions d'années jusqu'à leur disparition lors de la crise de la fin du Permien. Avant cette extinction définitive, plusieurs autres extinctions sont venues perturber ces arthropodes au cours du temps. Cette thèse s'est focalisée sur la seconde partie de l'histoire des trilobites, après l'extinction fini-ordovicienne qui a conduit à la perte de nombreux genres et de plusieurs ordres. Le but a été de comprendre comment les changements environnementaux ont influencé les trilobites afin de mieux comprendre leurs effets sur la biodiversité en général. Les trilobites ont été choisi comme modèle car ils représentent un support de choix en paléontologie, étant abondants et diversifiés en termes de formes et d'écologie. Ils ont connu un succès évolutif au Paléozoïque au cours duquel ils ont survécu à de nombreux événements. Ils abondent dans les terrains du Dévonien d'Afrique du Nord, région très étudiée pour son contenu paléontologique et géologique, offrant une bonne opportunité de recherche. Le Dévonien constitue également une période d'étude idéale en tant que période marquée par d'importants changements écologiques et environnementaux.

Le premier aspect de la biodiversité estimée a été la diversité taxonomique. Pour mieux comprendre les tendances régionales, il a fallu identifier les dynamiques mondiales et élargir la gamme temporelle en partant du Silurien et en allant jusqu'au Permien à l'aide d'une analyse factorielle. Au début du Dévonien, les faunes présentes étaient celles qui ont survécu à la précédente extinction de masse à la transition Ordovicien-Silurien. Ces faunes vont être supplantées par d'autres trilobites lors de la diversification du Dévonien inférieur. Après un pic de diversité à l'Emsien, une succession d'événements environnementaux incluant des changements abrupts du niveau marin et des périodes d'anoxie affectèrent les trilobites. Leur diversité va considérablement diminuer et quelques taxons vont tirer bénéfices de cette période de crise. Une dernière faune de trilobites va se développer à partir du Carbonifère, mais celle-ci ne sera composée que de l'ordre Proetida et n'atteindra jamais les niveaux de diversité précédents. Les événements du Dévonien auront donc eu un impact néfaste et durable sur les trilobites. Les trilobites d'Afrique du Nord montrent les mêmes tendances qu'à l'échelle mondiale. Grâce à des données de bonne qualité, il a été possible d'analyser les dynamiques avec une résolution temporelle relativement fine, au sous-étage. Pour estimer la diversité, il a été possible d'utiliser des méthodes à la pointe permettant de corriger un maximum les biais paléontologiques. Les résultats montrent que la diversité était assez faible au début du Dévonien, mais très vite, elle augmenta lors de deux phases de diversification : au Praguien et à l'Emsien supérieur. Le déclin des trilobites d'Afrique du Nord a été plus soudain à l'échelle régionale qu'à l'échelle mondiale, une importante extinction ayant eu lieu à l'Eifelien. La diversité était donc très faible au Givétien et au Frasnien. La richesse taxonomique a augmenté au Frasnien supérieur et l'extinction de masse du Kellwasser à la limite Frasnien–Famennien s'est plutôt avérée être une phase de *turnover* faunique. L'Afrique du Nord riche en fossiles de différentes faunes a offert l'opportunité unique de comparer les tendances de diversité entre les trilobites benthiques et une faune nectonique, les ammonoïdes, étudiée dans le cadre d'une thèse aux approches similaires (Allaire, 2017 thèse non publiée). Cette comparaison a montré que le necton et le benthos d'une même région pouvaient avoir des dynamiques distinctes et être impactés différemment par les changements environnementaux.

La deuxième partie de ce travail s'est focalisée sur les changements morphologiques des trilobites du Dévonien d'Afrique du Nord. Pour appréhender les variations de forme de ces arthropodes, des séries de points homologues ont été capturées sur des illustrations 2D puis utilisées à l'aide d'analyses Procruste. Des indices de disparité morphologique ont également été utilisés pour caractériser au mieux les variations. Trois structures ont été choisies pour être étudiées car elles concentrent la variation morphologique chez les trilobites : le céphalon, sa partie centrale le cranidium, et le pygidium. Les principales différences mises en évidence entre les individus sont la forme de la glabelle et la position de la suture faciale pour le cephalon et l'élongation du pygidium. La présence ou non d'épines constitue également une divergence importante entre les différents taxons. L'espace morphologique résultant n'a pas été occupé uniformément au Dévonien. En effet, au début du Dévonien inférieur, cet espace était quasiment inoccupé. Ce n'est qu'au Praguien que de nouvelles innovations ont eu lieu chez les trilobites d'Afrique du Nord, en particulier avec l'apparition d'épines de différentes natures. Cette tendance s'est confirmée à l'Emsien mais la plupart des formes ont disparu au Dévonien moyen pour ne plus réapparaitre ensuite. Les analyses mettent en avant une extinction sélective, marginale ou latérale. Les formes déjà présentes à la fin du Silurien sont celles qui ont le mieux supporté les changements environnementaux et qui ont subsisté jusqu'à la fin du Dévonien. Ces formes ont montré une meilleure compatibilité/adaptabilité aux changements d'environnements ou de mode de vie, les aidant à persister au cours du temps. Les deux seuls ordres à avoir survécu jusqu'au Dévonien supérieur avaient un espace morphologique étendu et des morphologies adaptées à une large gamme d'écologie, ce qui a sans doute joué un rôle dans leur survie. Un focus sur les phacopidés, une famille emblématique du Dévonien a permis de confirmer que les innovations ont été réalisées au Dévonien inférieur et que c'est surtout le Givétien qui a conduit à la disparition de nombreuses morphologies. Contrairement à de nombreux clades, les trilobites du Dévonien ont eu des dynamiques de diversité et de disparité relativement couplées. Cela est notamment dû à l'intensité des extinctions dévoniennes qui sont venues interrompre leur diversification.

Outre l'aspect temporel, la configuration spatiale a été étudiée pour une partie de l'Afrique du Nord. En se basant sur quelques bassins riches en trilobites et bien connus du point de vue de la paléogéographie, des associations fauniques ont été déterminées avec des analyses de partitionnement et de correspondance. 16 associations avec des affinités temporelles, géographiques et environnementales ont été identifiées en Afrique du Nord au Dévonien. En analysant leur répartition et évolution, les études réalisées ont mis en évidence le rôle de la paléogéographie sur la biodiversité en favorisant les migrations ou au contraire, en les empêchant. En effet, l'orogénèse varisque a modifié la région à partir du Dévonien moyen impactant fortement les trilobites et accélérant leur déclin en créant des barrières géographiques. Des hauts fonds, des bassins profonds ou des environnements différents ont ainsi empêché des échanges fauniques.

L'Afrique du Nord était donc une région où les trilobites vivaient au Silurien et au début du Dévonien, mais sans y être particulièrement abondants. Ce n'est qu'à partir du Praguien que le nombre de trilobites a explosé à la suite de l'expansion d'environnements peu profonds, favorables à l'établissement de faunes benthiques (Fig. 1). Ces conditions avantageuses perdurèrent jusqu'à l'Emsien. De nombreux échanges et migrations ont eu lieu et l'invasion de ces nouveaux environnements a suscité la mise en place des innovations morphologiques chez les trilobites. La plupart des familles et sous-familles de trilobites ont ainsi participé à cette grande phase de diversification. Le pic de diversité taxonomique et morphologique a été atteint à la fin du Dévonien inférieur mais dès le début du Dévonien moyen, les conditions se sont dégradées pour les trilobites. Les changements rapides et répétés du niveau marin et les phases d'anoxies successives ont grandement affecté les faunes nord-africaines au point que la plupart des genres de trilobites ont disparu au Givétien. L'Afrique du Nord a été particulièrement touchée puisqu'une combinaison de changements environnementaux a accéléré le déclin des trilobites. L'orogénèse varisque et des événements tectoniques qu'elle a induits se sont superposés aux événements marins, morcelant le paysage à partir de l'Eifelien et le rendant ainsi moins avantageux pour le benthos. L'extinction de masse du Frasnien–Famennien est venu accabler une faune déjà meurtrie et a eu davantage d'effets à grande échelle avec des extinctions au niveau des ordres. Si la disparité morphologique est restée faible pendant cette période, il y a néanmoins eu des innovations avec la prolifération de formes aveugles ou à vision réduite. Cette tendance est en partie une adaption à la vie marine en profondeur en réponse à une augmentation du niveau marin. Cette faculté d'adaptation des trilobites a permis une récupération écologique au Famennien avec une légère augmentation de la diversité mais l'événement Hangenberg est venu affecter cette faune déjà fragilisée à la fin du Dévonien, conduisant à l'extinction de l'un des deux derniers ordres de trilobites à l'échelle mondiale et à la quasi-disparition des trilobites en Afrique du Nord. Les trilobites du Dévonien d'Afrique du Nord constituent donc un bon *proxy* pour comprendre les effets des changements environnementaux sur la biodiversité et ont permis de démontrer que ces changements peuvent avoir des effets variables et que la combinaison d'événements néfastes peut être dévastatrice.

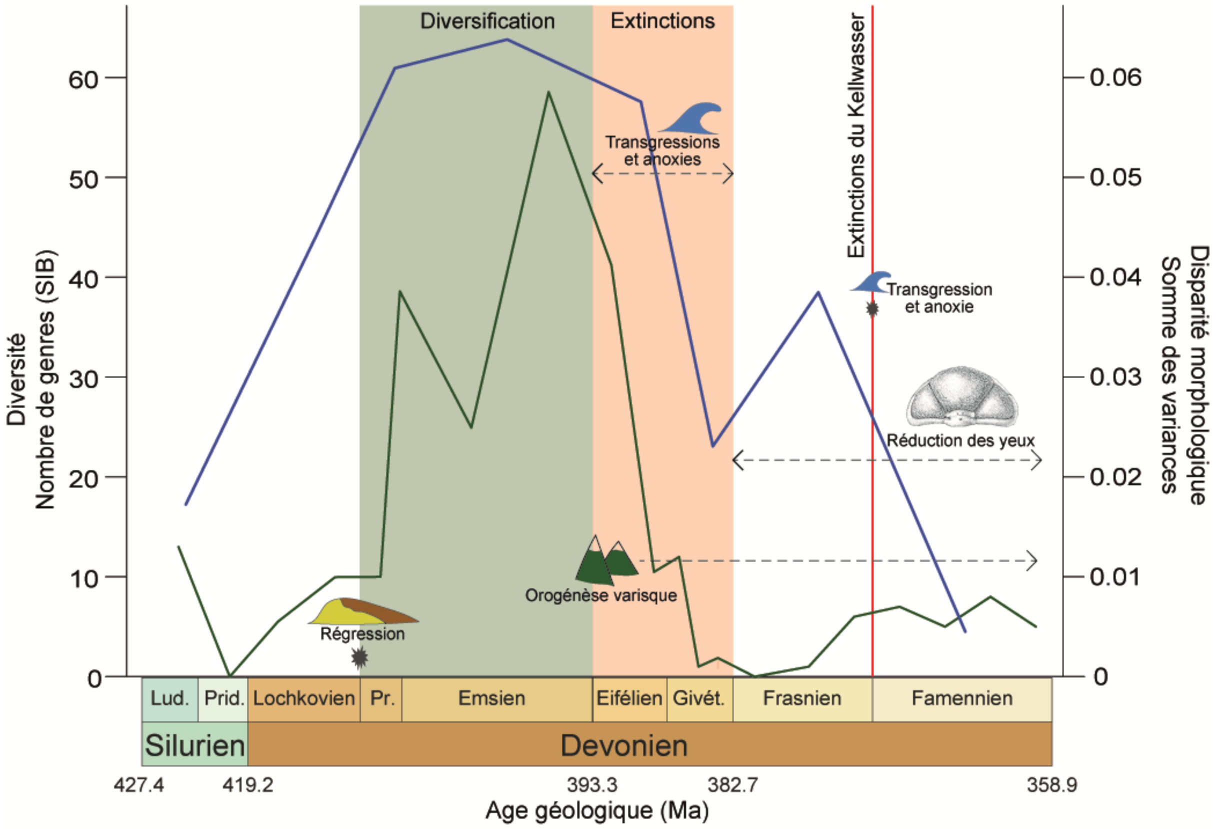

***Figure 1 :*** *Schéma synthétique de l'évolurion de la diversité taxonomique (vert) et morphologique (bleu) des trilobites du Siluro-Dévonien d'Afrique du Nord*

## PERSPECTIVES

Bien que plusieurs aspects de la biodiversité aient été analysés dans le cadre de cette thèse, il reste de nombreuses pistes à étudier pour améliorer notre compréhension des facteurs mis en jeu. Nous l'avons vu, le Dévonien est une période marquée par d'importants changements écologiques et environnementaux : de nouveaux clades apparaissent et les modes de vie se diversifient (Klug et al., 2010 ; Capel et al., 2021). L'influence d'autres taxons sur les trilobites, et inversement, n'a été que brièvement abordée. Cette influence peut s'exercer en termes de compétition entre deux taxons partageant la même niche ou de relation proie/prédateur. Ce dernier aspect mérite un intérêt particulier puisqu'il n'existe que très peu d'articles traitant des chaînes trophiques (Fig. 2) du Paléozoïque dans la littérature. Certes, il reste très compliqué de connaître les véritables liens trophiques au Dévonien mais les quelques recherches réalisées (Mark-Kurik, 1995 ; Brett and Walker, 2002 ; Babcock, 2003 ; Brett, 2003 ; Kriwet et al., 2008) permettent d'avancer des théories plus ou moins étayées et certaines preuves directes semblent exister. Les dépôts sédimentaires d'Afrique du Nord renferment de nombreux fossiles de différents taxons – y compris ceux à corps mous. L'Afrique du Nord représente ainsi un endroit idéal pour faire un état de l'art sur toutes les faunes dévonniennes retrouvées. A l'échelle locale, plusieurs récifs sont bien conservés et permettent de faire une étude des relations trophiques à l'échelle d'un écosystème réduit. En se basant sur des études réalisées sur des écosystèmes cénozoïques (Roopnarine et al., 2007) on pourrait identifier l'effet de l'apparition ou de la disparition d'un ou plusieurs prédateurs (ou proies) sur l'écosystème entier ou les trilobites en particulier.

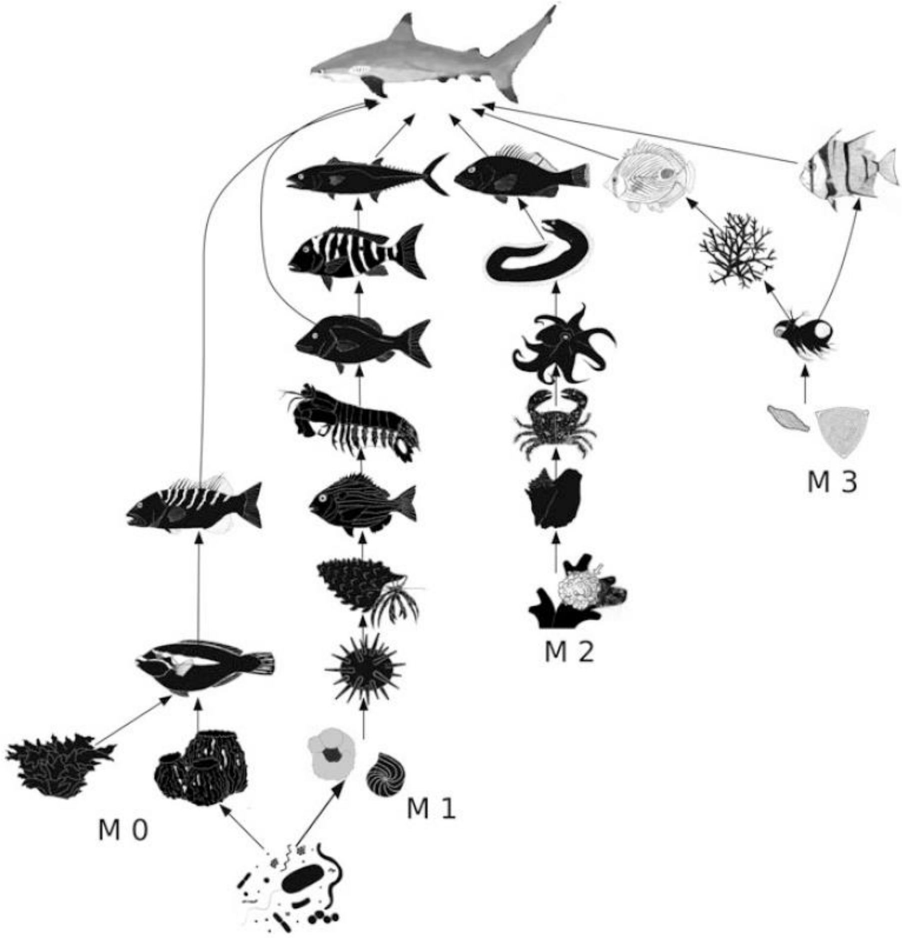

***Figure 2 :*** *Représentation d'une chaîne alimentaire marine actuelle (Roopnarine et Dineen, 2018)*

L’Afrique du Nord est une des régions les plus riches en fossiles de trilobites du Dévonien. Cependant, des restes de ces arthropodes ont également été découverts ailleurs dans le monde (Amérique du Nord, Amérique du Sud, Asie, Australie…) et notamment en Europe. A cette période, le nord de l’Europe actuelle appartenait au continent Laurentia alors que la partie sud était disséminée en une multitude d’îles au milieu de l’océan Rhéique (Fig. 3). L’Europe étant située en face de l’Afrique et au Gondwana, celà offre ainsi une opportunité d’augmenter notre étude et d’analyser d’autres interractions trilobites-environnement. Les trilobites européens étant proches taxonomiquement de ceux d’Afrique du Nord avec beaucoup de genres communs, cela permettrait d’identifier les relations paléobiogéographiques à une plus grande échelle que celle abordée dans ce manuscrit. Cela permettrait notamment de comprendre les liens entre différents continents et d’identifier les grandes routes de migration. La fermeture de l’océan Rhéique et la collision des continents Laurentia et Baltica se mettant en place au Dévonien (Scotese, 2021), on pourrait même étudier l’effet de la tectonique des plaques sur la richesse taxonomique. Les trilobites d’Europe permettraient également de corriger certains biais obtenus en Afrique du Nord comme le manque de données au Givétien–Frasnien puisque l’Europe a un enregistrement relativement continu sur cette période avec de nombreux affleurements au Dévonien moyen et supérieur (Chlupáč, 1992 ; Bignon et Crônier, 2015 par exemple). L’Europe étant une des régions les plus étudiées en géologie, tout comme l’Afrique du Nord, comparer les données de ces deux régions offrirait l’opportunité de mieux comprendre les effets des changements environnementaux à l’échelle inter-régionale. Enfin, la création d’une base de

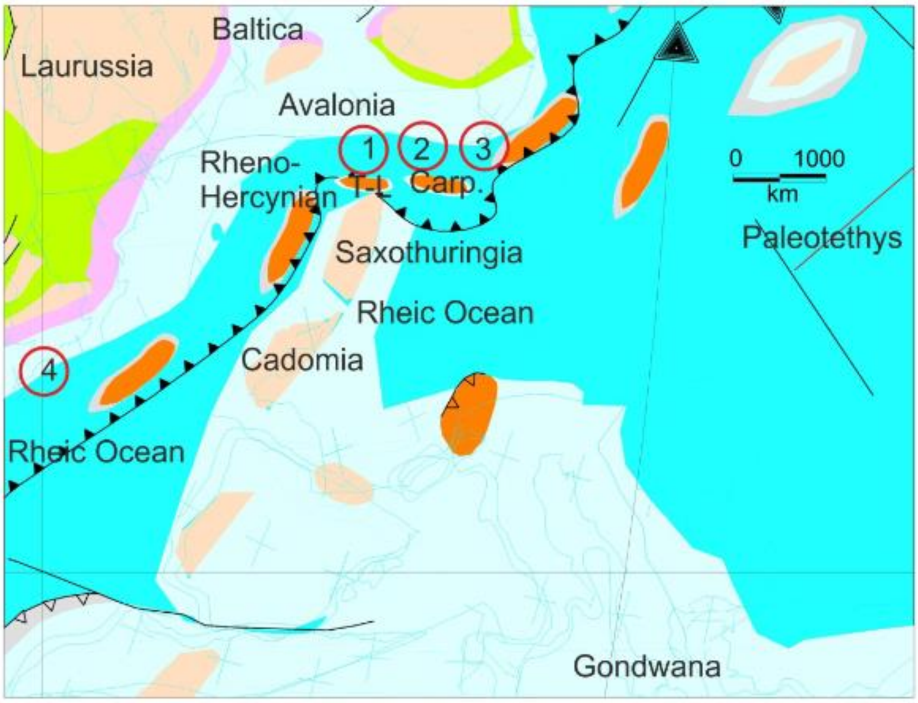

***Figure 3 :*** *Paléogéographie de l’Europe au Dévonien supérieur (Golonka et Gaweda, 2012).*

données fondée sur les gisements européens permettrait de mettre à jour les données de diversité, la base de données mondiale (la Paleobiology database) étant incomplète.

Les analyses morphologiques effectuées lors de ce travail soulèvent également de nouvelles questions sur la relation trilobites-environnement. Cela concerne surtout les effets des changements environnementaux de la deuxième partie du Dévonien qui ont considérablement affecté les trilobites. Sur les deux ordres (Phacopida et Proetida) présents tout au long du Dévonien, seul l'ordre des Proetida subsistera au Carbonifère. Les Phacopida disparaitront en même temps que de nombreux taxons à la frontière Dévonien–Carbonifère, marquée par une crise écologique importante : l'évènement du Hangenberg (Lerosey-Aubril et Feist, 2012 ; Kaiser et al., 2015). Cet événement n'a que peu été évoqué dans ce manuscrit car les données d'Afrique du Nord pour la fin du Famennien sont relativement pauvres et il semble n'y avoir que peu de trilobites au début du Carbonifère. On peut se demander pourquoi cette crise semble n'avoir épargné aucun trilobite dans la région alors que la récupération post-Kellwasser avait été relativement importante. De la même manière, le fait que les Phacopida aient survécu pendant tout le Dévonien mais pas lors de l'évènement Hangenberg interroge. La flexibilité morphologique mise en avant dans l'article 3 (« Trilobite biodiversity trends in the Devonian of North Africa ») n'a-t-elle pas suffit pour permettre d'échapper à l'extinction ? Qu'avaient les Proetida en plus des Phacopida pour survivre ? D'autres questions se posent aussi sur le Kellwasser. En effet, si au Dévonien moyen, la diversité taxonomique et la disparité morphologique ont fortement diminué, il semble que la disparité soit la plus affectée lors de la crise du Frasnien–Famennien. Au niveau de la diversité, il y a eu beaucoup d'extinctions mais ces extinctions ont été compensées par un grand nombre d'apparitions, au point que cette crise soit plutôt une phase de *turnover* qu'une phase de diminution de diversité. Il faudrait confirmer ce postulat avec des données plus globales et comprendre ces changements, pour celle qui reste une des cinq extinctions de masse de l'histoire.

Enfin, toujours dans l'objectif de mieux comprendre les dynamiques géographiques, une étude à l'échelle mondiale fondée sur la Paleobiology database pourrait venir compléter les travaux effectués dans l'article 1 (« Post-Ordovician trilobite diversity and macroevolutionary history »). Cette base de données étant incomplète, de potentiel biais pourrait survenir, liés notamment au manque de données dans certaines régions du globe. Néanmoins, la Paleobiology database constitue un outil pratique avec un grand nombre de données facilement accessibles. Cette étude permettrait donc de voir les grandes voies de migration et les provinces biogéographiques et ainsi de mieux replacer les dynamiques observées en Afrique du Nord dans un cadre global.

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# BASES DE DONNEES

## Article 2 :

| ID | Family | Genus | Species | Type | Cephalon | Type | Paper | Figures | Pygidium | Type | Paper | Figures | Eyes | FAD | LAD |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Phacopidae | Acernaspis | Acernaspis orestes | Type | GSC 2472 | Lectotype | Chatterton & Ludvigsen 2004 | 27.7 | GSC 2472 | Lectotype | Chatterton & Ludvigsen 2004 | 27.8 |  | Rhuddanian | Telychian |
| 2 | Phacopidae | Acuticryphops | Acuticryphops acuticeps | Type | WAM 07.286 |  | Feist et al., 2009 | 5e | WAM 07.290 |  | Feist et al., 2009 | 5n |  | Frasnian | Frasnian |
| 3 | Phacopidae | Adastocephalum | Adastocephalum teleotypicum | Type |  |  | Mitchell 1919 | 16.2 |  |  |  |  |  | Lochkovian? | Lochkovian? |
| 4 | Phacopidae | Adrisiops | Adrisiops weugi | Type | NHMM 2016 007 | Holotype | VanViersen 2017a | 7D | NHMM 2016 007 | Holotype | VanViersen 2017a | 7D |  | Emsian | Eifelian |
| 5 | Phacopidae | Afrops | Afrops larvifer | Type | SH | Holotype | Alberti 1983 | 7.87 |  |  |  |  | Blind | Pragian | Pragian |
| 6 | Phacopidae | Ainasuella | Ainasuella ainasuensis | Type | No information |  | Maksimova 1978 | 2.1a |  |  | Maksimova 1978 | 2.1b |  | Lochkovian | Lochkovian |
| 7 | Phacopidae | Altaesajania | Altaesajania primitiva | Type | No information |  | Maksimova 1978 | 2.3.a |  |  | Maksimova 1978 | 2.3b | Blind | Lochkovian? | Emsian? |
| 8 | Phacopidae | Ananaspis | Ananaspis fecunda fecunda | Type | NM 9324 |  | Chlupac 1977 | 4.1 | NM L 9325 |  | Chlupac 1977 | 4.12 |  | Ludlow | Pridoli |
| 9 | Phacopidae | Angulophacops | Angulophacops angulatus | Type | No information |  | Maksimova 1968 | 20.2 | No information |  | Maksimova 1968 | 20.4 | Blind? | Emsian | Emsian |
| 10 | Phacopidae | Arduennops | Arduennops michelsi | Type | SMF 24603 | Holotype | Franke 2010 | 15.1c | SMF 32032 |  | Basse 2006 | 9.80 |  | Lochkovian | Emsian |
| 11 | Phacopidae | Atopophacops | Atopophacops apiculata | Type | Tr355 |  | Zhou & Campbell 1990 | 5.4 | Tr358 |  | Zhou & Campbell 1990 | 5.7 |  | Emsian? | Givetian? |
| 12 | Phacopidae | Austerops | Austerops kermiti | Type | UA 6884 | Holotype | McKellar & Chatterton 2009 | 8.3 | UA 6884 | Holotype | McKellar & Chatterton 2009 | 8.4 |  | Emsian | Eifelian |
| 13 | Phacopidae | Babinops | Babinops minor |  | WAM 07.273 | Holotype | Feist et al., 2009 | 4t | WAM 07.275 |  | Feist et al., 2009 | 4z2 |  | Famennian | Famennian |
| 14 | Phacopidae | Boeckops | Boeckops stelcki |  | UA 6897 | Holotype | McKellar & Chatterton 2009 | 11.4 | UA 6897 | Holotype | McKellar & Chatterton 2009 | 11.9 |  | Lochkovian | Eifelian |
| 15 | Phacopidae | Burtonops | Burtonops cristatus | Type | No information |  | Becker et al., 2017 | 4d |  |  |  |  |  | Lochkovian | Emsian |
| 16 | Phacopidae | Chlupacops | Chlupacops laticeps | Type | UM-IP 712 | Holotype | Feist et al., 2016 | 3B | UM-IP 713 |  | Feist et al., 2016 | 3F |  | Frasnian | Frasnian |
| 17 | Phacopidae | Chotecops | Chotecops hoseri |  | MU-G-Sr.Tr.A4/Ph123 |  | Crônier et al., 2018 | 5m | MU-G-Sr.Tr.A4/Ph123 |  | Crônier et al., 2018 | 5n |  | Emsian | Frasnian |
| 18 | Phacopidae | Cryphops | Cryphops cryptophthalmus | Type | SMF 57513 |  | Crônier & Feist 2000 | 1.1a |  |  |  |  |  | Famennian | Famennian |
| 19 | Phacopidae | Denckmannites | Denckmannites volborthi | Type | Ich 3441 |  | Chlupac 1977 | 6.6 | Ich 3432 |  | Chlupac 1977 | 6.15 |  | Ludlow | Pragian |
| 20 | Phacopidae | Dianops | Dianops vicarius |  | MUA 1094 011 |  | Crônier et al., 2013 | 5b | MUA/1094/010 |  | Crônier et al. 2013 | 5O | Blind | Famennian | Famennian |
| 21 | Phacopidae | Dienstina | Dienstina diensti | Type |  |  | Brauckmann & Brauckmann 1 | 6.5a |  |  | Brauckmann & Brauckmann 1986 | 6.5b |  | Famennian | Famennian |
| 22 | Phacopidae | Drotops | Drotops megalomanicus | Type | SMF 49340 | Holotype | Struve 1995 | 1.1a | SMF 49357 |  | Struve 1995 | 1.2b |  | Eifelian | Givetian |
| 23 | Phacopidae | Ductina | Ductina ductifrons | Type |  |  | Basse & Müller 2000 | 3.19 |  |  | Basse & Müller 2000 | 3.21 | Blind | Famennian | Famennian |
| 24 | Phacopidae | Echidnops | Echidnops taphomimus |  | CEGH-UNC 26130 |  | Rustan & Balseiro 2016 | 3.7 | CEGH-UNC 24082 | Holotype | Rustan & Balseiro 2016 | 2.5 |  | Lochkovian | Lochkovian |
| 25 | Phacopidae | Echinophacops | Echinophacops mirabilis | Type | Tr 229 |  | Zhou 1983 | 2a | Tr231 |  | Zhou 1983 | 2c |  | Upper Siluriar | Emsian |
| 26 | Phacopidae | Eldredgeops | Eldredgeops rana milleri | Type | AMNH 28896 |  | Burton & Eldredge 1974 | 47.7 | RSM GY 1979.11.3 |  | Miller & Clarkson 1980 | 1.7 |  | Eifelian | Frasnian |
| 27 | Phacopidae | Enigmapyge | Enigmapyge marhoumensis | Type | Do not exist |  |  |  | UM-IP 727 | Holotype | Feist et al., 2016 | 5A |  | Famennian | Famennian |
| 28 | Phacopidae | Eocryphops | Eocryphops albertii |  | NHM It 19284 | Holotype | Holloway 2005 | 1P | NHM It 27131 |  | Holloway 2005 | 1M |  | Emsian | Eifelian |
| 29 | Phacopidae | Eophacops | Eophacops bulliceps |  | Ich 4546 |  | Chlupac 1977 | 3.1 | JV 98 |  | Chlupac 1977 | 3.14 |  | Wenlock | Pridoli |
| 30 | Phacopidae | Geesops | Geesops schlotheimi | Type | NHMM 2016 006 |  | VanViersen et al., 2017 | 7A | Di/UO/004 (Ed3n1) |  | Khaldi et al. 2016 | 4p |  | Emsian | Givetian |
| 31 | Phacopidae | Houseops | Houseops canningensis | Type | WAM 07.266 | Holotype | Feist et al., 2008 | 3n | WAM 07.270 |  | Feist et al., 2008 | 3v |  | Frasnian | Famennian |
| 32 | Phacopidae | Hypsipariops | Hypsipariops vagabundus |  | SMF 49402 | Holotype | Struve 1995 | 8.23a | SMF 49368 |  | Struve 1995 | 8.24c |  | Eifelian | Givetian |
| 33 | Phacopidae | Illaenula | Illaenula struvei |  | SMF 55933 | Paratype | Basse & Müller 2000 | 2.15 | SMF 55933 | Holotype | Basse & Müller 2000 | 2.15 | Blind? | Eifelian | Eifelian |
| 34 | Phacopidae | Kainops | Kainops microps | Type | ANU 35207 | Holotype | Chatterton et al., 1979 | 107.1 | ANU 35217 | Paratype | Chatterton et al., 1979 | 107.18 |  | Lochkovian | Emsian |
| 35 | Phacopidae | Liolophops | Liolophops sublevatus | Type | SMF 24518 | Paratype | Struve 1970 | 6.24a |  |  | Ernst & Bohaty 2010 | 13 |  | Eifelian | Givetian |
| 36 | Phacopidae | Lochkovella | Lochkovella misera | Type | NM L 9332 |  | Chlupac 1977 | 7.9 | NM IT 394 |  | Chlupac 1977 | 7.15 |  | Ludlow | Lochkovian |
| 37 | Phacopidae | Morocops | Morocops granulops | Type | UA 13295 | Holotype | Chatterton et al., 2006 | 1.2 | UA 13295 | Holotype | Chatterton et al., 2006 | 1.5 |  | Emsian | Eifelian |
| 38 | Phacopidae | Nandanaspis | Nandanaspis laevigatus | Type | GT-464 |  | Yin et al., 1978 | 192.11 | GT-464 |  | Yin et al., 1978 | 192.11 | Blind? | Eifelian | Eifelian |
| 39 | Phacopidae | Nephranomma | Nephranomma sweeti |  | P307225 |  | Sandford 2003 | 4.1 | P307303 |  | Sandford 2003 | 3.15 |  | Pragian | Emsian |
| 40 | Phacopidae | Nephranops | Nephranops incisus | Type | SMF 97026 |  | Feist 2019 | 4D | SMF 97027 |  | Feist 2019 | 4F | Blind | Frasnian | Famennian |
| 41 | Phacopidae | Nyterops | Nyterops hollandi |  | IRSBNa12430 | Holotype | VanViersen 2007 | 1.1 |  |  | Megrean and Taghon 2014 | 1 |  | Eifelian | Givetian |
| 42 | Phacopidae | Omegops | Omegops tilabadensis |  | GUGM 1359 | Holotype | Pour et al., 2018 | 4A | GUGM 1359 | Holotype | Pour et al., 2018 | 4G |  | Famennian | Famennian |
| 43 | Phacopidae | Orygmatos | Orygmatos yanyeani | Type | P136135 | Holotype | Sandford 2000 | 18A | P136137 | Paratype | Sandford 2000 | 18J |  | Ludlow | Ludlow |
| 44 | Phacopidae | Paciphacops | Paciphacops logani | Type | YPM 6594-4 |  | Campbell 1977 | 12.4c | YPM 6594 |  | Campbell 1977 | 12.1a |  | Lochkovian | Eifelian |
| 45 | Phacopidae | Pedinopariops | Pedinopariops insequens |  | No information |  | Crônier et al., 2015 | 3J | IRSNB a12671 | Holotype | Van Viersen et al. 2009 | 1.1 |  | Eifelian | Givetian |
| 46 | Phacopidae | Phacopidella | Phacopidella glockeri | Type | NM L 8917 |  | Chlupac 1977 | 1.1 | NM IT 379 |  | Chlupac 1977 | 1.11 |  | Wenlock | Wenlock |
| 47 | Phacopidae | Phacops s.l. | Phacops tamtertensis |  | MUA 1094 001 | Holotype | Crônier et al., 2013 | 3i | MUA/1094/002 |  | Crônier et al. 2013 | 5U |  | Frasnian | Famennian |
| 48 | Phacopidae | Plagiolaria | Plagiolaria senex |  | SH | Holotype | Alberti 1983 | 8.90 | KSGR VI_670/334 | Holotype | Crônier and Tsmeyrek 2011 | 3A |  | Pragian | Eifelian |
| 49 | Phacopidae | Portlockia | Portlockia sublaevis | Type |  | Holotype | McCoy 1846 | 4.13 |  | Holotype | McCoy 1846 | 4.13 | Blind? | Pragian | Pragian |
| 50 | Phacopidae | Prokops | Prokops prokopi | Type | No information |  | Crônier et al., 2015 | 3A | P3071117 |  | Sandford 2004 | 3s |  | Lochkovian | Emsian |
| 51 | Phacopidae | Pulvinocephalus | Pulvinocephalus steinachensis | Type | SMF-X540d | Holotype | Feist 2019 | 6A | SMF-X540e |  | Feist 2019 | 6G | Blind | Famennian | Famennian |
| 52 | Phacopidae | Rabienops | Rabienops wedeckindi |  |  |  | Feist et al. 2020 | 4d |  |  | Feist et al. 2020 | 4e |  | Famennian | Famennian |
| 53 | Phacopidae | Reedops | Reedops bronni | Type | UA 6843 | Plésiotype | McKellar & Chatterton 2009 | 1.9 | UA 6844 |  | McKellar & Chatterton 2009 | 1.8 |  | Lochkovian | Eifelian |
| 54 | Phacopidae | Rhinophacops | Rhinophacops schizoloma | Type | Tr-240 |  | Atsushi & Kaneko 1990 | 2.10a | JP 10003 |  | Atsushi & Kaneko 1990 | 2.3a |  | Emsian | Emsian |
| 55 | Phacopidae | Signatops | Signatops signatus | Type | NM IT 391a |  | Chlupac 1977 | 28.1 |  |  | Chlupac 1977 | 28.1 |  | Eifelian | Eifelian |
| 56 | Phacopidae | Somatrikelon |  |  |  |  |  |  |  |  |  |  |  | Eifelian | Eifelian |
| 57 | Phacopidae | Spinicryphops | Spinicryphops lemkei | Type | SMF X 564e | Holotype | Crônier & Feist 2000 | 2.11 |  |  |  |  |  | Famennian | Famennian |
| 58 | Phacopidae | Struveaspis | Struveaspis maroccanica |  | MU-G-SR.Tr.S7/Ph003 |  | Crônier et al., 2018 | 3b | JC 104 | Paratype | Corbacho 2014 | 1.4 |  | Eifelian | Eifelian |
| 59 | Phacopidae | Struveops | Struveops schlosseri | Type | SMF 57520 |  | Crônier & Feist 2000 | 2.13 | SMF 57525 |  | Crônier & Feist 2000 | 2.18 | Blind | Famennian | Famennian |
| 60 | Phacopidae | Struvephacops | Struvephacops werneri |  | SMF 24417 | Holotype | Struve 1995 | Abb 11 |  |  |  |  |  | Lochkovian | Emsian |
| 61 | Phacopidae | Tangbailaspis | Tangbailaspis beijiangensis | Type |  |  | Zhang 1983 | 183.13 |  |  |  |  |  |  |  |
| 62 | Phacopidae | Teichertops | Teichertops soetenicus |  | SMF 24467 | Holotype | Struve 1970 | 4.13a | SMF 58034a |  | Basse 2006 | 45.447 |  | Eifelian | Givetian |
| 63 | Phacopidae | Toxophacops | Toxophacops cristata | Type | Tr339 | Holotype | Zhou & Campbell 1990 | 3.7A | Tr345 |  | Zhou & Campbell 1990 | 3.9A |  | Emsian | Emsian |
| 64 | Phacopidae | Trifoliops | Trifoliops trifolius | Type | UM-IP 722 |  | Feist et al., 2016 | 5E | UM-IP 723 |  | Feist et al., 2016 | 5F | Blind | Famennian | Famennian |
| 65 | Phacopidae | Trimerocephalus | Trimerocephalus caecus |  | MUA 1094 007 |  | Crônier et al., 2013 | 3a | MUA 1094 007 |  | Crônier et al., 2013 | 3b | Blind | Famennian | Famennian |
| 66 | Phacopidae | Trimerocephaloides | Trimerocephaloides sinevisus | Type | WAM 07.277 | Holotype | Feist et al., 2009 | 4i | WAM 07.278 |  | Feist et al., 2009 | 4k | Blind | Frasnian | Famennian |
| 67 | Phacopidae | Viaphacops | Viaphacops stummi |  | AMNH 28902 | Holotype | Eldredge 1973 | 20A | UMMP 47207 |  | Eldredge 1973 | 20E |  | Lochkovian | Eifelian |
| 68 | Phacopidae | Weyerites | Weyerites wocklumeriae |  | SMF 57512 |  | Crônier & Feist 2000 | Fig-text | M.B.T. 3731 |  | Crônier et al. 1999 | 2.1 |  | Famennian | Famennian |
| 69 | Phacopidae | Zaplaops | Zaplaops zaplensis | Type | MACN-PI-2354 | Holotype | Baldis & Blasco 1976 | 3.4 |  |  |  |  |  | Ludlow? | Pridoli? |
| 70 | Phacopidae | Zhusilengops | Zhusilengops ejinensis | Type | Tr373 | Holotype | Zhou & Campbell 1990 | 4.1a | Tr375 |  | Zhou & Campbell 1990 | 4.4a |  | Emsian | Eifelian |
| 71 | Phacopidae | Phacops | Phacops ouarouroutensis |  | MU-G-Sr.Tr.S7/Ph( | Holotype | Crônier et al., 2018 | 6h-k | MU-G-Sr.Tr.S7/Ph( | Holotype | Crônier et al., 2018 | 6j |  | Eifelian | Givetian |
| 72 | Phacopidae | Feistops | Feistops mongoliensis | Type | MUST-RCSR-TRI.-0( | Holotype | Crônier et al. 2020 | 4.1 | MUST-RCSR-TRI.-0( | Paratype | Crônier et al. 2020 | 4.10 |  | Famennian | Famennian |
| 73 | Phacopidae | Megraneops | Megraneops renateae | Type | IRSBNa13216 | Holotype | Van Viersen and Vanherle 20 | 10e | IRSBNa13216 | Holotype | Van Viersen and Vanherle 2018 | 10d |  | Frasnian | Frasnian |
| 74 | Pterygometo | Calyptaulax | Calyptaulax callirhachis |  | U.A. 1412 |  | Chatterton and Ludvigsen 19 | 16.1 | U.A. 1417 |  | Chatterton and Ludvigsen 1976 | 16.10 |  | Late Ordovicia | Late Ordovician |
| 75 | Phacopidae | Rhinoreedops | Rhinoreedops rhinoceras | Type | No information | Holotype | Maksimova 1978 | 3.9 | No information | Holotype | Maksimova 1978 | 3.9 |  | Eifelian | Eifelian |
| 76 | Phacopidae | Phacopidae | Sambremeusaspis fossesensis | Type | I.R.Sc.N.B. a2511 | Holotype | Lespérance and Sheehan 198 | 3.4 | I.R.Sc.N.B. a2514 | Paratype | Lespérance and Sheehan 1988 |  |  | Late Ordovicia | Late Ordovician |

# Articles 4 et 5 :

| Order | Family | Genus | Species | ID | Vision | Depth | Diet | Figures | Specimen | Paper | Scale | Stage | Analysis |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phacopida | Acastidae | Destombesina | Destombesina tafilaltensis | 0 | Large eyes | Middle shelf | Predator/Scavenger | 7.2 |  | Morzadec 2001 | =0,00608 | Emsian | Cephalon |
| Phacopida | Acastidae | Destombesina | Destombesina tafilaltensis | 1 | Large eyes | Middle shelf | Predator/Scavenger | 7.5 |  | Morzadec 2001 | =0,00448 | Emsian | Cephalon |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 2 | Large eyes | Middle shelf | Predator/Scavenger | 6o | GFCL401 | Khaldi 2016 | =0,037036 | Emsian | Cephalon |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 3 | Large eyes | Middle shelf | Predator/Scavenger | 8.3 |  | Morzadec 2001 | =0,02113 | Emsian | Cephalon |
| Phacopida | Acastidae | Hollardops | Hollardops burtandmimiae | 4 | Large eyes | Middle shelf | Predator/Scavenger | 9.8 |  | Morzadec 2001 | =0,00849 | Emsian | Cephalon |
| Phacopida | Acastidae | Hollardops | Hollardops aithassainorum | 5 | Large eyes | Middle shelf | Predator/Scavenger | 17.2 | UA13440 | Chatterton 2006 | =0,116013 | Eifelian | Cephalon |
| Phacopida | Acastidae | Mrakibina | Mrakibina cattoi | 6 | Large eyes | Inner shelf | Predator/Scavenger | 14.5 |  | Morzadec 2001 | =0,010730 | Eifelian | Cephalon |
| Phacopida | Acastidae | Pilletina | Pilletina marokkensis | 7 | Large eyes | Shallow | Predator/Scavenger | 12.1a | SMF 53876 | Schraut 2000c | =0,083331 | Pragian | Cephalon |
| Phacopida | Acastidae | Pilletina | Pilletina marokkensis | 8 | Large eyes | Shallow | Predator/Scavenger | 12.2a | SMF 53866 | Schraut 2000c | =0,100289 | Pragian | Cephalon |
| Phacopida | Acastidae | Pilletina | Pilletina marokkensis | 9 | Large eyes | Shallow | Predator/Scavenger | 12.3a | SMF 53859 | Schraut 2000c | =0,099431 | Pragian | Cephalon |
| Phacopida | Acastidae | Psychopyge | Psychopyge elegans | 10 | Large eyes | Middle shelf | Predator/Scavenger | 13.4 |  | Morzadec 2001 | =0,042040 | Emsian | Cephalon |
| Phacopida | Acastidae | Psychopyge | Psychopyge praestans | 11 | Large eyes | Middle shelf | Predator/Scavenger | 22.6 |  | Chatterton 2006 | =0,176156 | Emsian | Cephalon |
| Phacopida | Acastidae | Psychopyge | Psychopyge praestans | 12 | Large eyes | Middle shelf | Predator/Scavenger | 23.4 | UA13371 | Chatterton 2006 | =0,128859 | Emsian | Cephalon |
| Phacopida | Acastidae | Psychopyge | Psychopyge praestans | 13 | Large eyes | Middle shelf | Predator/Scavenger | 23.6 | UA13372 | Chatterton 2006 | =0,116441 | Emsian | Cephalon |
| Phacopida | Acastidae | Psychopyge | Psychopyge hammerorum | 14 | Large eyes | Middle shelf | Predator/Scavenger | 25.5 | UA13375 | Chatterton 2006 | =0,129346 | Emsian | Cephalon |
| Phacopida | Acastidae | Treveropyge | Treveropyge prorotundifrons iberica | 15 | Large eyes | Shallow | Predator/Scavenger | 11.1a | SMF 53879 | Schraut 2000c | =0,122202 | Pragian | Cephalon |
| Phacopida | Acastidae | Treveropyge | Treveropyge prorotundifrons iberica | 16 | Large eyes | Shallow | Predator/Scavenger | 11.2a | SMF 53790 | Schraut 2000c | =0,077768 | Pragian | Cephalon |
| Phacopida | Acastidae | Treveropyge | Treveropyge prorotundifrons iberica | 17 | Large eyes | Shallow | Predator/Scavenger | 11.4a | SMF 53943 | Schraut 2000c | =0,129336 | Pragian | Cephalon |
| Phacopida | Acastidae | Treveropyge | Treveropyge prorotundifrons iberica | 18 | Large eyes | Shallow | Predator/Scavenger | 42.10 | CGMTA 209 | Alberti 1969 | =0,008503 | Pragian | Cephalon |
| Phacopida | Acastidae | Walliserops | Walliserops trifurcatus | 19 | Large eyes | Middle shelf | Predator/Scavenger | 15.1a |  | Morzadec 2001 | =0,030418 | Emsian | Cephalon |
| Phacopida | Acastidae | Walliserops | Walliserops trifurcatus | 20 | Large eyes | Middle shelf | Predator/Scavenger | 15.3e |  | Morzadec 2001 | =0,028726 | Emsian | Cephalon |
| Proetida | Aulacopleuridae | Aulacopleura | Aulacopleura ignorata | 21 | Large eyes | Middle shelf | Particle feeding | 36;15 | CGMTA 158 | Alberti 1969 | =0,017829 | Eifelian | Cephalon |
| Proetida | Aulacopleuridae | Aulacopleura | Aulacopleura ignorata | 22 | Large eyes | Middle shelf | Particle feeding | 36;16 | SMF 23381 | Alberti 1969 | =0,020068 | Eifelian | Cephalon |
| Proetida | Aulacopleuridae | Chamaeleoaspis | Chamaeleosapis lkomalii | 23 | Large eyes | Middle shelf | Particle feeding | 6a_24 | UA 11821 | Lerosey-Aubril 2008 | =0,014619 | Eifelian | Cephalon |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis walteri | 24 | Large eyes | Middle shelf | Particle feeding | 1b_24 | IRSNB a12875 | Van Viersen 2014 | =0,056453 |  | Cephalon |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis eximia | 25 | Large eyes | Middle shelf | Particle feeding | 6e_24 | IRSNB a13010 | Van Viersen 2016 | =0,022982 | Eifelian | Cephalon |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis bluhmi | 26 | Large eyes | Middle shelf | Particle feeding | 7a_24 | IRSNB a13003 | Van Viersen 2016 | =0,027387 | Eifelian | Cephalon |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis sp A | 27 | Large eyes | Middle shelf | Particle feeding | 7z_24 | MU-G-Sr.Tr.A4/Pr098 | Crônier-Abbache 2018 | =0,054509 | Eifelian | Cephalon |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis kippingi | 28 | Large eyes | Middle shelf | Particle feeding | 14d_24 | IRSNB a13012 | Van Viersen 2016 | =0,026307 | Emsian | Cephalon |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis foumzguidensis | 29 | Large eyes | Middle shelf | Particle feeding | 16b_24 | IRSNB a12996 | Van Viersen 2016 | =0,014805 | Eifelian | Cephalon |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis sp. I | 30 | Large eyes | Middle shelf | Particle feeding | 19c_24 | IRSNB a13008 | Van Viersen 2016 | =0,037031 | Eifelian | Cephalon |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis heisingi | 31 | Large eyes | Middle shelf | Particle feeding | 21b_24 | IRSNB a13011 | Van Viersen 2016 | =0,014919 | Pragian | Cephalon |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis cf. eberhardiei | 32 | Large eyes | Middle shelf | Particle feeding | 23d_24 | IRSNB a13001 | Van Viersen 2016 | =0,020404 | Eifelian | Cephalon |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis agayuara | 33 | Large eyes | Middle shelf | Particle feeding | 42.1_24 | UA13397 | Chatterton 2006 | =0,071700 | Emsian | Cephalon |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis sp A | 34 | Large eyes | Middle shelf | Particle feeding | 45.3_24 | UA13399 | Chatterton 2006 | =0,047565 | Eifelian | Cephalon |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Proetida | Aulacopleuridae | Otarionella | Otarionella magnifica | 35 | Large eyes | Inner shelf | Particle feeding | 35.2a_24 | CGMTA 154 | Alberti 1969 | =0,017824 | Pragian | Cephalon |
| Phacopida | Calmoniidae | Acastoides | Acastoides zguilmensis | 36 | Small eyes | Deep | Predator/Scavenger | 8.8_24 | UA13332 | Chatterton 2006 | =0,062162 | Emsian | Cephalon |
| Phacopida | Calmoniidae | Acastoides | Acastoides zguilmensis | 37 | Small eyes | Deep | Predator/Scavenger | 9.13_24 | UA13340 | Chatterton 2006 | =0,062081 | Emsian | Cephalon |
| Phacopida | Calmoniidae | Acastoides | Acastoides hollardi | 38 | Small eyes | Deep | Predator/Scavenger | 6 | SGMRA 9 | Alberti 1966a | =0,016353 | Emsian | Cephalon |
| Phacopida | Calmoniidae | Acastoides | Acastoides hollardi | 39 | Small eyes | Deep | Predator/Scavenger | 7 | SMF 23017 | Alberti 1966a | =0,009982 | Emsian | Cephalon |
| Phacopida | Calmoniidae | Acastoides | Acastoides hollardi | 40 | Small eyes | Deep | Predator/Scavenger | 18.4 | CGMTA 336 | Alberti 1970a | =0,021200 | Emsian | Cephalon |
| Phacopida | Homalonotidae | Parahomalonotus | Parahomalonotus planus planus | 41 | Large eyes | Inner shelf | Predator/Scavenger | 5.1a_24 | SMF 53914 | Schraut 2000c | =0,085764 | Pragian | Cephalon |
| Phacopida | Homalonotidae | Parahomalonotus | Parahomalonotus planus planus | 42 | Large eyes | Inner shelf | Predator/Scavenger | 5.2a_24 | SMF 53830 | Schraut 2000c | =0,158112 | Pragian | Cephalon |
| Phacopida | Homalonotidae | Parahomalonotus | Parahomalonotus planus planus | 43 | Large eyes | Inner shelf | Predator/Scavenger | 5.4a_24 | SMF 53917 | Schraut 2000c | =0,152597 | Pragian | Cephalon |
| Lichida | Odontopleuridae | Kettneraspis | Kettneraspis prescheri | 44 | Large eyes | Deep | Predator/Scavenger | 2a | IRSNB a1713 | Van Viersen 2015 | =0,035584 | Pragian | Cephalon |
| Lichida | Odontopleuridae | Leonaspis | Leonaspis maura | 45 | Large eyes | Middle shelf | Predator/Scavenger | 40.10a_24 | CGMTA 165 | Alberti 1969 | =0,015812 | | Cephalon |
| Lichida | Odontopleuridae | Leonaspis | Leonaspis haddanei | 46 | Large eyes | Middle shelf | Predator/Scavenger | 50.10_24 | | Chatterton 2006 | =0,042728 | Eifelian | Cephalon |
| Lichida | Odontopleuridae | Leonaspis | Leonaspis haddanei | 47 | Large eyes | Middle shelf | Predator/Scavenger | 51.4_24 | | Chatterton 2006 | =0,033465 | Emsian | Cephalon |
| Phacopida | Phacopidae | Acuticryphops | Acuticryphops acuticeps | 48 | Small eyes | Middle shelf | Predator/Scavenger | 3a_24 | UM2−RF 220 | Feist 2002 | =0,045903 | Frasnian | Cephalon |
| Phacopida | Phacopidae | Adrisiops | Adrisiops fabrei | 49 | Large eyes | Middle shelf | Predator/Scavenger | 4i_24 | Di/UO/016 | Khaldi 2016 | =0,040645 | Emsian | Cephalon |
| Phacopida | Phacopidae | Adrisiops | Adrisiops weugi | 50 | Large eyes | Middle shelf | Predator/Scavenger | 7d_24 | | Van Viersen 2017 | =0,006894 | Emsian | Cephalon |
| Phacopida | Phacopidae | Anaspis | Ananaspis fecunda fecunda | 51 | Large eyes | Middle shelf | Predator/Scavenger | 11.2a_24 | SMF 23512 | Alberti 1970a | =0,017109 | Ludlow-Pridoli | Cephalon |
| Phacopida | Phacopidae | Austerops | Austerops legrandi | 52 | Large eyes | Middle shelf | Predator/Scavenger | 7a_24 | GFCL399 | Khaldi 2016 | =0,047610 | Emsian | Cephalon |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 53 | Large eyes | Middle shelf | Predator/Scavenger | 3.9a_24 | | Schraut 2000c | =0,073473 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Chlupacops | Chlupacops laticeps | 54 | Large eyes | Deep | Predator/Scavenger | 3a_24 | UM-IP 712 | Feist 2016 | =0,076866 | Frasnian | Cephalon |
| Phacopida | Phacopidae | Chlupacops | Chlupacops laticeps | 55 | Large eyes | Deep | Predator/Scavenger | 3b_24 | UM-IP 712 | Feist 2016 | =0,037629 | Frasnian | Cephalon |
| Phacopida | Phacopidae | Austerops | Austerops salamandaroides | 56 | Large eyes | Middle shelf | Predator/Scavenger | 3s_24 | MU-G-Sr.Tr.S6/Ph186 | Crônier-Abbache 2018 | =0,018987 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Eophacops | Eophacops bulliceps | 57 | Large eyes | Middle shelf | Predator/Scavenger | 1.10_24 | | Alberti 1966c | =0.008450 | Ludlow-Pridoli | Cephalon |
| Phacopida | Phacopidae | Hypsipariops | Hypsipariops africanus | 58 | Large eyes | Middle shelf | Predator/Scavenger | 47.9_24 | USNM 174072 | Burton 1974 | =0,140125 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops granulops | 59 | Large eyes | Inner shelf | Predator/Scavenger | 1.2_24 | UA 13295 | Chatterton 2006 | =0,070609 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops granulops | 60 | Large eyes | Inner shelf | Predator/Scavenger | 1.7_24 | UA 13297 | Chatterton 2006 | =0,061025 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops granulops | 61 | Large eyes | Inner shelf | Predator/Scavenger | 1.8_24 | UA 13294 | Chatterton 2006 | =0,075561 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops granulops | 62 | Large eyes | Inner shelf | Predator/Scavenger | 2.9_24 | UA 13301 | Chatterton 2006 | =0,090746 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops torkozensis | 63 | Large eyes | Inner shelf | Predator/Scavenger | 3.4a_24 | SMF 53627 | Schraut 2000c | =0,076227 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops torkozensis | 64 | Large eyes | Inner shelf | Predator/Scavenger | 5d_24 | NHMM 2016 002 | Van Viersen 2017 | =0,038757 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops forteyi | 65 | Large eyes | Inner shelf | Predator/Scavenger | 5g_24 | NHMM 2016 003 | Van Viersen 2017 | =0,048760 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops spinifer | 66 | Large eyes | Inner shelf | Predator/Scavenger | 6a_24 | NHMM 2016 004 | Van Viersen 2017 | =0,050759 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops spinifer | 67 | Large eyes | Inner shelf | Predator/Scavenger | 6f_24 | NHMM 2016 005 | Van Viersen 2017 | =0,042729 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops sparsinodosus struvei | 68 | Large eyes | Inner shelf | Predator/Scavenger | 8j_24 | SMF 57109 | Schraut 2000a | =0.011602 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops sparsinodosus struvei | 69 | Large eyes | Inner shelf | Predator/Scavenger | 8m_24 | SMF 57110 | Schraut 2000a | =0.017740 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops granulops | 70 | Large eyes | Inner shelf | Predator/Scavenger | 18a | | Becker 2018 | =0,038449 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops granulops | 71 | Large eyes | Inner shelf | Predator/Scavenger | 2b | PIMUZ 35146 | Crônier-Oudot 2018 | =0,013089 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops granulops | 72 | Large eyes | Inner shelf | Predator/Scavenger | 2i | PIMUZ 35147 | Crônier-Oudot 2018 | =0,005593 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops granulops | 73 | Large eyes | Inner shelf | Predator/Scavenger | 2k | PIMUZ 35148 | Crônier-Oudot 2018 | =0,009191 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops granulops | 74 | Large eyes | Inner shelf | Predator/Scavenger | 2n | PIMUZ 35149 | Crônier-Oudot 2018 | =0,018315 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops granulops | 75 | Large eyes | Inner shelf | Predator/Scavenger | 2o | PIMUZ 35150 | Crônier-Oudot 2018 | =0,025772 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops forteyi | 76 | Large eyes | Inner shelf | Predator/Scavenger | 2t | PIMUZ 35152 | Crônier-Oudot 2018 | =0,016835 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops sp A | 77 | Large eyes | Inner shelf | Predator/Scavenger | 2w | PIMUZ 35153 | Crônier-Oudot 2018 | =0,029238 | Emsian | Cephalon |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phacopida | Phacopidae | Morocops | Morocops davidbrutoni | 78 | Large eyes | Inner shelf | Predator/Scavenger | 3a_24 | PIMUZ 35154 | Crônier-Oudot 2018 | =0,008944 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops davidbrutoni | 79 | Large eyes | Inner shelf | Predator/Scavenger | 3d | PIMUZ 35155 | Crônier-Oudot 2018 | =0,011085 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops davidbrutoni | 80 | Large eyes | Inner shelf | Predator/Scavenger | 3g | PIMUZ 35156 | Crônier-Oudot 2018 | =0,007072 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops davidbrutoni | 81 | Large eyes | Inner shelf | Predator/Scavenger | 3k | PIMUZ 35157 | Crônier-Oudot 2018 | =0,004153 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops davidbrutoni | 82 | Large eyes | Inner shelf | Predator/Scavenger | 3l | PIMUZ 35159 | Crônier-Oudot 2018 | =0,008547 | Emsian | Cephalon |
| Phacopida | Phacopidae | PHACOPINAE | Indet | 83 | Large eyes | Middle shelf | Predator/Scavenger | 1.1a | Nr 25 | Richter 1943 | =0.035142 | Eifelian | Cephalon |
| Phacopida | Phacopidae | PHACOPINAE | Indet | 84 | Large eyes | Middle shelf | Predator/Scavenger | 1.3a | Nr 8 | Richter 1943 | =0.035142 | | Cephalon |
| Phacopida | Phacopidae | Phacops sl | Phacops tafiuppernsis | 85 | Large eyes | Deep | Predator/Scavenger | 2.a_24 | UM2/CCp002 | Crônier 2001 | =0,015029 | Famennian | Cephalon |
| Phacopida | Phacopidae | Phacops sl | Phacops tafiuppernsis | 86 | Large eyes | Deep | Predator/Scavenger | 2.g_24 | UM2/CCp004 | Crônier 2001 | =0,019872 | Famennian | Cephalon |
| Phacopida | Phacopidae | Phacops sl | Phacops tafiuppernsis | 87 | Large eyes | Deep | Predator/Scavenger | 3.e_24 | UM2/CCp007 | Crônier 2001 | =0,014306 | Famennian | Cephalon |
| Phacopida | Phacopidae | Phacops sl | Phacops zeregensis | 88 | Large eyes | Deep | Predator/Scavenger | 3i_24 | MUA/1094/001 | Crônier 2013 | =0,034246 | Famennian | Cephalon |
| Phacopida | Phacopidae | Phacops | Phacops ouarouroutensis ouarouroutensis | 89 | Large eyes | Middle shelf | Predator/Scavenger | 4z_24 | MU-G-Sr.Tr.S4/Ph054 | Crônier-Abbache 2018 | =0,078920 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Phacops sl | Phacops sensu lato sp B | 90 | Large eyes | Deep | Predator/Scavenger | 5f_24 | Di/UO/033 | Khaldi 2016 | =0,102020 | Emsian | Cephalon |
| Phacopida | Phacopidae | Phacops sl | Phacops zeregensis | 91 | Large eyes | Deep | Predator/Scavenger | 5q_24 | MUA/1094/002 | Crônier 2013 | =0,032461 | Famennian | Cephalon |
| Phacopida | Phacopidae | Phacops | Omegops accipitrinus | 92 | Large eyes | Middle shelf | Predator/Scavenger | 1.2a | Nr 27 | Richter 1943 | =0.023333 | Famennian | Cephalon |
| Phacopida | Phacopidae | Reedops | Reedops bronni | 93 | Large eyes | Inner shelf | Predator/Scavenger | 1.4_24 | UA 6844 | McKellar 2009 | =0,013314 | Pragian | Cephalon |
| Phacopida | Phacopidae | Reedops | Reedops cephalotes hamlagdadianus | 94 | Large eyes | Inner shelf | Predator/Scavenger | 2.8_24 | UA 6861 | McKellar 2009 | =0,023057 | Pragian | Cephalon |
| Phacopida | Phacopidae | Reedops | Reedops intermedius chlupaci | 95 | Large eyes | Inner shelf | Predator/Scavenger | 4.10a_24 | SMF 57095 | Schraut 2000c | =0,088333 | Pragian | Cephalon |
| Phacopida | Phacopidae | Reedops | Reedops maurulus | 96 | Large eyes | Inner shelf | Predator/Scavenger | 15.6a_24 | SMF 23514 | Alberti 1970a | =0,026488 | Pragian | Cephalon |
| Phacopida | Phacopidae | Reedops | Reedops platilegnotor | 97 | Large eyes | Inner shelf | Predator/Scavenger | 15.10a_24 | CGMTA 316 | Alberti 1970a | =0,026488 | Pragian | Cephalon |
| Phacopida | Phacopidae | Struveaspis | Struveaspis bignoni | 98 | Large eyes | Middle shelf | Predator/Scavenger | 1.2_24 | | Corbacho 2014 | =0,025252 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Struveaspis | Struveaspis bignoni | 99 | Large eyes | Middle shelf | Predator/Scavenger | 1.4_24 | | Corbacho 2014 | =0,037726 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Struveaspis | Struveaspis sp A | 100 | Large eyes | Middle shelf | Predator/Scavenger | 1a_24 | SGMRA 8 | Alberti 1966a | =0,016162 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Chotecops | Chotecops hoseri | 101 | Large eyes | Middle shelf | Predator/Scavenger | 5b_24 | Di/UO/035 | Crônier-Abbache 2018 | =0,029999 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Chotecops | Chotecops occidomaurus | 102 | Large eyes | Middle shelf | Predator/Scavenger | 6.60a_24 | CGMTA | Alberti 1981a | =0.080854 | Eifelian | Cephalon |
| Proetida | Proetidae | Dalejeproetus | Dalejeproetus sagaouii | 103 | Large eyes | Inner shelf | Predator/Scavenger | 4.1_24 | NHM It 28946 | Johnson 2012 | =0,013300 | Pragian | Cephalon |
| Proetida | Proetidae | Dalejeproetus | Dalejeproetus sagaouii | 104 | Large eyes | Inner shelf | Predator/Scavenger | 4.6_24 | NHM It 28947 | Johnson 2012 | =0,037207 | Pragian | Cephalon |
| Proetida | Proetidae | Dalejeproetus | Dalejeproetus owensi | 105 | Large eyes | Inner shelf | Predator/Scavenger | 5.1_24 | NHM It 28950 | Johnson 2012 | =0,046180 | Pragian | Cephalon |
| Proetida | Proetidae | Dalejeproetus | Dalejeproetus owensi | 106 | Large eyes | Inner shelf | Predator/Scavenger | 5.3_24 | NHM It 28951 | Johnson 2012 | =0,037324 | Pragian | Cephalon |
| Proetida | Proetidae | Diademaproetus | Diademaproetus mohamedi | 107 | Large eyes | Deep | Predator/Scavenger | 34.6_24 | UA 13382 | Chatterton 2006 | =0,050598 | Eifelian | Cephalon |
| Proetida | Proetidae | Diademaproetus | Diademaproetus praecursor | 108 | Large eyes | Deep | Predator/Scavenger | 35.8_24 | | Chatterton 2006 | =0,084885 | Emsian | Cephalon |
| Proetida | Proetidae | Diademaproetus | Diademaproetus praecursor | 109 | Large eyes | Deep | Predator/Scavenger | 36.6_24 | | Chatterton 2006 | =0,082452 | Emsian | Cephalon |
| Proetida | Proetidae | Diademaproetus | Diademaproetus praecursor | 110 | Large eyes | Deep | Predator/Scavenger | 37.12_24 | | Chatterton 2006 | =0,110567 | Emsian | Cephalon |
| Proetida | Proetidae | Diademaproetus | Diademaproetus holzapfeli praecursor | 111 | Large eyes | Deep | Predator/Scavenger | 16.1a | SMF 53620 | Schraut 2000c | =0,092640 | Emsian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 112 | Large eyes | Inner shelf | Predator/Scavenger | 1.1_24 | UA13526 | Gibb 2010 | =0,012382 | Eifelian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 113 | Large eyes | Inner shelf | Predator/Scavenger | 2.5_24 | UA13464 | Gibb 2010 | =0,010204 | Emsian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 114 | Large eyes | Inner shelf | Predator/Scavenger | 2.12_24 | UA13466 | Gibb 2010 | =0,010751 | Emsian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 115 | Large eyes | Inner shelf | Predator/Scavenger | 4.8_24 | UA13530 | Gibb 2010 | =0,008948 | Emsian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 116 | Large eyes | Inner shelf | Predator/Scavenger | 4.9_24 | UA13530 | Gibb 2010 | =0,008948 | Emsian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos aintawilus | 117 | Large eyes | Inner shelf | Predator/Scavenger | 6.3_24 | UA13454 | Gibb 2010 | =0,003722 | Eifelian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos aintawilus | 118 | Large eyes | Inner shelf | Predator/Scavenger | 5.4_24 | UA13532 | Gibb 2010 | =0,004842 | Eifelian | Cephalon |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 119 | Large eyes | Inner shelf | Predator/Scavenger | 6.12_24 | UA13650 | Chatterton 2010 | =0,040846 | Eifelian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos hammii | 120 | Large eyes | Inner shelf | Predator/Scavenger | 7.10_24 | | Gibb 2010 | =0,009415 | Eifelian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos lisanrasus | 121 | Large eyes | Inner shelf | Predator/Scavenger | 8.3_24 | | Gibb 2010 | =0,009162 | Eifelian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos lisanrasus | 122 | Large eyes | Inner shelf | Predator/Scavenger | 8.8_24 | | Gibb 2010 | =0,005776 | Eifelian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos ainrasifus | 123 | Large eyes | Inner shelf | Predator/Scavenger | 9.8_24 | | Gibb 2010 | =0,014590 | Eifelian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos discombobulatus | 124 | Large eyes | Inner shelf | Predator/Scavenger | 11.11_24 | | Gibb 2010 | =0,006762 | Eifelian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos cuvieri malisus | 125 | Large eyes | Inner shelf | Predator/Scavenger | 13.9_24 | | Gibb 2010 | =0,006350 | Eifelian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos taqus | 126 | Large eyes | Inner shelf | Predator/Scavenger | 16.2_24 | | Gibb 2010 | =0,007241 | Eifelian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos malisjildus | 127 | Large eyes | Inner shelf | Predator/Scavenger | 17.1_24 | | Gibb 2010 | =0,004468 | Eifelian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos raribus | 128 | Large eyes | Inner shelf | Predator/Scavenger | 19.3_24 | | Gibb 2010 | =0,005780 | Givetian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos emmetus | 129 | Large eyes | Inner shelf | Predator/Scavenger | 22.5_24 | | Gibb 2010 | =0,004581 | Givetian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos emmetus | 130 | Large eyes | Inner shelf | Predator/Scavenger | 22.6_24 | | Gibb 2010 | =0,005844 | Givetian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos emmetus | 131 | Large eyes | Inner shelf | Predator/Scavenger | 23.8_24 | | Gibb 2010 | =0,007994 | Givetian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos izius | 132 | Large eyes | Inner shelf | Predator/Scavenger | 24.3_24 | | Gibb 2010 | =0,006982 | Givetian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos izius | 133 | Large eyes | Inner shelf | Predator/Scavenger | 24.9_24 | | Gibb 2010 | =0,006946 | Givetian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos izius | 134 | Large eyes | Inner shelf | Predator/Scavenger | 25.7_24 | | Gibb 2010 | =0,008754 | Givetian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos izius | 135 | Large eyes | Inner shelf | Predator/Scavenger | 25.10_24 | | Gibb 2010 | =0,009129 | Givetian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 136 | Large eyes | Inner shelf | Predator/Scavenger | 37.5_24 | UA13276 | Chatterton 2006 | =0,065026 | Emsian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 137 | Large eyes | Inner shelf | Predator/Scavenger | 39.8_24 | UA13278 | Chatterton 2006 | =0,055102 | Emsian | Cephalon |
| Proetida | Proetidae | Kegeliella | Kegeliella listei bouregregus | 138 | Large eyes | Middle shelf | Predator/Scavenger | 3.2b_24 | SMF 23032 | Alberti 1969 | =0,019092 | Pragian | Cephalon |
| Proetida | Proetidae | Lepidoproetus | Lepidoproetus maharchianus | 139 | Large eyes | Shallow | Predator/Scavenger | 6.1_24 | NHM It 28954 | Johnson 2012 | =0,041042 | Pragian | Cephalon |
| Proetida | Proetidae | Lepidoproetus | Lepidoproetus spendens | 140 | Large eyes | Shallow | Predator/Scavenger | 6.11_24 | NHM It 28956 | Johnson 2012 | =0,028721 | Pragian | Cephalon |
| Proetida | Proetidae | Piriproetus | Piriproetus amblyops oulmesanicus | 141 | Blind | Deep | Predator/Scavenger | 4.10a_24 | SMF23471 | Alberti 1970a | =0,008407 | Eifelian | Blind |
| Proetida | Proetidae | Podoliproetus | Podoliproetus mirdani | 142 | Large eyes | Inner shelf | Predator/Scavenger | 7.3_24 | NHM It 28957 | Johnson 2012 | =0,037131 | Pragian | Cephalon |
| Proetida | Proetidae | Podoliproetus | Podoliproetus mirdani | 143 | Large eyes | Inner shelf | Predator/Scavenger | 7.6_24 | NHM It 28958 | Johnson 2012 | =0,037131 | Pragian | Cephalon |
| Proetida | Proetidae | Podoliproetus | Podoliproetus mirdani | 144 | Large eyes | Inner shelf | Predator/Scavenger | 7.11_24 | NHM It 28959 | Johnson 2012 | =0,037131 | Pragian | Cephalon |
| Proetida | Proetidae | Podoliproetus | Podoliproetus sinespina | 145 | Large eyes | Inner shelf | Predator/Scavenger | 8.3_24 | NHM It 28960 | Johnson 2012 | =0,036862 | Pragian | Cephalon |
| Proetida | Proetidae | Podoliproetus | Podoliproetus mirdani | 146 | Large eyes | Inner shelf | Predator/Scavenger | 8.11_24 | NHM It 28961 | Johnson 2012 | =0,022910 | Pragian | Cephalon |
| Proetida | Proetidae | Proetina | Proetina ihmadii | 147 | Large eyes | Inner shelf | Predator/Scavenger | 9.5_24 | NHM It 28962 | Johnson 2012 | =0,018273 | Pragian | Cephalon |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus haasi | 148 | Large eyes | Middle shelf | Predator/Scavenger | 40.10_24 | UA13269 | Chatterton 2006 | =0,046287 | Eifelian | Cephalon |
| Proetida | Proetidae | Sculptoproetus | Sculptoproetus sp B | 149 | Large eyes | Middle shelf | Predator/Scavenger | 40.13_24 | UA13262 | Chatterton 2006 | =0,038369 | Eifelian | Cephalon |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus haasi | 150 | Large eyes | Middle shelf | Predator/Scavenger | 4.1_24 | UA13272 | Gibb 2007 | =0,005109 | Eifelian | Cephalon |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus haasi | 151 | Large eyes | Middle shelf | Predator/Scavenger | 5.2_24 | UA13256 | Gibb 2007 | =0,011598 | Eifelian | Cephalon |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus haasi | 152 | Large eyes | Middle shelf | Predator/Scavenger | 5.3_24 | UA13269 | Gibb 2007 | =0,007741 | Eifelian | Cephalon |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus haasi | 153 | Large eyes | Middle shelf | Predator/Scavenger | 5.7_24 | UA13269 | Gibb 2007 | =0,015086 | Eifelian | Cephalon |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus elguerrouji | 154 | Large eyes | Middle shelf | Predator/Scavenger | 9.11_24 | UA13260 | Gibb 2007 | =0,010911 | Eifelian | Cephalon |
| Proetida | Proetidae | Warbugella | Warbugella rugulosa maura | 155 | Large eyes | Inner shelf | Predator/Scavenger | 33.5_24 | CGMT | Alberti 1969 | =0,008475 | Lochkovian | Cephalon |
| Proetida | Tropidocoryphe | Tropidocoryphidae | Tropidocoryphe amuri | 156 | Large eyes | Middle shelf | Predator/Scavenger | 41.4_24 | UA13394 | Chatterton 2006 | =0,053329 | Emsian | Cephalon |
| Phacopida | Acastidae | Coltraneia | Coltraneia berbera | 157 | Large eyes | Middle shelf | Predator/Scavenger | 10.2 | | Morzadec 2001 | =0,027925 | Emsian | Cephalon |
| Phacopida | Acastidae | Coltraneia | Coltraneia effelesa | 158 | Large eyes | Middle shelf | Predator/Scavenger | 12.1 | UA 13351 | Chatterton 2006 | =0,089724 | Emsian | Cranidium |
| Phacopida | Acastidae | Comura | Comura bultyncki | 159 | Large eyes | Middle shelf | Predator/Scavenger | 12.2a | | Morzadec 2001 | =0,027972 | Emsian | Cephalon |
| Phacopida | Acastidae | Comura | Comura bultyncki | 160 | Large eyes | Middle shelf | Predator/Scavenger | 12.3a | | Morzadec 2001 | =0,042423 | Emsian | Cephalon |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phacopida | Acastidae | Destombesina | Destombesina ougartensis | 161 | Large eyes | Middle shelf | Predator/Scavenger | 3.6a | | Morzadec 1997 | =0,006728 | Emsian | Cephalon |
| Phacopida | Acastidae | Destombesina | Destombesina ougartensis | 162 | Large eyes | Middle shelf | Predator/Scavenger | 3.10a | | Morzadec 1997 | =0,005262 | Emsian | Cephalon |
| Phacopida | Acastidae | Destombesina | Destombesina tafilaltensis | 163 | Large eyes | Middle shelf | Predator/Scavenger | 7.1a | | Morzadec 2001 | =0,010405 | Emsian | Cephalon |
| Phacopida | Acastidae | Destombesina | Destombesina tafilaltensis | 164 | Large eyes | Middle shelf | Predator/Scavenger | 7.7 | | Morzadec 2001 | =0,00448 | Emsian | Cephalon |
| Phacopida | Acastidae | Destombesina | Destombesina tafilaltensis | 165 | Large eyes | Middle shelf | Predator/Scavenger | 7.8 | | Morzadec 2001 | =0,00448 | Emsian | Cephalon |
| Phacopida | Acastidae | Destombesina | Destombesina tafilaltensis | 166 | Large eyes | Middle shelf | Predator/Scavenger | 7.11 | | Morzadec 2001 | =0,003526 | Emsian | Cephalon |
| Phacopida | Acastidae | Erbenochile | Erbenochile issoumourensis | 167 | Large eyes | Deep | Predator/Scavenger | 3.6 | UA13645 | Chatterton 2010 | =0,060774 | | Cranidium |
| Phacopida | Acastidae | Erbenochile | Erbenochile issoumourensis | 168 | Large eyes | Deep | Predator/Scavenger | 4.11 | UA13647 | Chatterton 2010 | =0,056921 | | Cranidium |
| Phacopida | Acastidae | Erbenochile | Erbenochile issoumourensis | 169 | Large eyes | Deep | Predator/Scavenger | 4.13 | UA13648 | Chatterton 2010 | =0,078486 | | Cranidium |
| Phacopida | Acastidae | Greenops | Indet | 170 | Large eyes | Middle shelf | Predator/Scavenger | 6.2a | | Morzadec 1997 | =0,014105 | Emsian | Cephalon |
| Phacopida | Acastidae | Hollardops | Hollardops lemaitreae | 171 | Large eyes | Middle shelf | Predator/Scavenger | 4.1b | | Morzadec 1997 | =0,007053 | Emsian | Cranidium |
| Phacopida | Acastidae | Hollardops | Hollardops lemaitreae | 172 | Large eyes | Middle shelf | Predator/Scavenger | 4.2a | | Morzadec 1997 | =0,008989 | Emsian | Cephalon |
| Phacopida | Acastidae | Hollardops | Hollardops lemaitreae | 173 | Large eyes | Middle shelf | Predator/Scavenger | 4.3a | | Morzadec 1997 | =0,008285 | Emsian | Cephalon |
| Phacopida | Acastidae | Hollardops | Hollardops lemaitreae | 174 | Large eyes | Middle shelf | Predator/Scavenger | 4.4a | | Morzadec 1997 | =0,014061 | Emsian | Cephalon |
| Phacopida | Acastidae | Hollardops | Hollardops lemaitreae | 175 | Large eyes | Middle shelf | Predator/Scavenger | 4.7 | | Morzadec 1997 | =0,005273 | Emsian | Cranidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 176 | Large eyes | Middle shelf | Predator/Scavenger | 6.1a | | Morzadec 1997 | =0,008360 | Emsian | Cephalon |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 177 | Large eyes | Middle shelf | Predator/Scavenger | 6.3a | | Morzadec 1997 | =0,023627 | Emsian | Cranidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 178 | Large eyes | Middle shelf | Predator/Scavenger | 6.4 | | Morzadec 1997 | =0,017041 | Emsian | Cephalon |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 179 | Large eyes | Middle shelf | Predator/Scavenger | 6.6a | | Morzadec 1997 | =0,013700 | Emsian | Cephalon |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 180 | Large eyes | Middle shelf | Predator/Scavenger | 6m | Di/UO/010 | Khaldi 2016 | =0,053760 | Emsian | Cranidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 181 | Large eyes | Middle shelf | Predator/Scavenger | 7.1a | | Morzadec 1997 | =0,010470 | Emsian | Cephalon |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 182 | Large eyes | Middle shelf | Predator/Scavenger | 7.2a | | Morzadec 1997 | =0,013857 | Emsian | Cranidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 183 | Large eyes | Middle shelf | Predator/Scavenger | 7.3a | | Morzadec 1997 | =0,013857 | Emsian | Cephalon |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 184 | Large eyes | Middle shelf | Predator/Scavenger | 7.4a | | Morzadec 1997 | =0,020849 | Emsian | Cranidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 185 | Large eyes | Middle shelf | Predator/Scavenger | 7.6a | | Morzadec 1997 | =0,027985 | Emsian | Cranidium |
| Phacopida | Acastidae | Hollardops | Hollardops boudibensis | 186 | Large eyes | Middle shelf | Predator/Scavenger | 8.1a | | Morzadec 2001 | =0,013887 | Emsian | Cephalon |
| Phacopida | Acastidae | Hollardops | Hollardops boudibensis | 187 | Large eyes | Middle shelf | Predator/Scavenger | 8.2 | | Morzadec 2001 | =0,010580 | Emsian | Cranidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 188 | Large eyes | Middle shelf | Predator/Scavenger | 8.5a | | Morzadec 1997 | =0,020620 | Emsian | Cephalon |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 189 | Large eyes | Middle shelf | Predator/Scavenger | 8.6a | | Morzadec 2001 | =0,027957 | Emsian | Cephalon |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 190 | Large eyes | Middle shelf | Predator/Scavenger | 8.7a | | Morzadec 1997 | =0,020620 | Emsian | Cranidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 191 | Large eyes | Middle shelf | Predator/Scavenger | 9.5a | | Morzadec 2001 | =0,021051 | Emsian | Cranidium |
| Phacopida | Acastidae | Hollardops | Hollardops aithassainorum | 192 | Large eyes | Middle shelf | Predator/Scavenger | 18.4 | | Chatterton 2006 | =0,050655 | Eifelian | Cranidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 193 | Large eyes | Middle shelf | Predator/Scavenger | 20.8 | | Chatterton 2006 | =0,049175 | Emsian | Cranidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 194 | Large eyes | Middle shelf | Predator/Scavenger | 3z | Di/UO/010 | Crônier Oudot 2018 | =0,014367 | Emsian | Cranidium |
| Phacopida | Acastidae | Kayserops | Kayserops megaspina | 195 | Large eyes | Shallow | Predator/Scavenger | 4.5a | | Morzadec 2001 | =0,041981 | Emsian | Cephalon |
| Phacopida | Acastidae | Kayserops | Kayserops marocanensis | 196 | Large eyes | Shallow | Predator/Scavenger | 5.1a_24 | | Morzadec 2001 | =0,028409 | Emsian | Cephalon |
| Phacopida | Acastidae | Kayserops | Kayserops marocanensis | 197 | Large eyes | Shallow | Predator/Scavenger | 5.2a_24 | | Morzadec 2001 | =0,028409 | Emsian | Cephalon |
| Phacopida | Acastidae | Kayserops | Kayserops tamnrherta | 199 | Large eyes | Shallow | Predator/Scavenger | 19.3 | | Chatterton 2006 | =0,042244 | Emsian | Cranidium |
| Phacopida | Acastidae | Kayserops | Kayserops tamnrherta | 200 | Large eyes | Shallow | Predator/Scavenger | 19.8 | | Chatterton 2006 | =0,044376 | Emsian | Cephalon |
| Phacopida | Acastidae | Kayserops | Kayserops tamnrherta | 201 | Large eyes | Shallow | Predator/Scavenger | 19.9 | | Chatterton 2006 | =0,045418 | Emsian | Cranidium |
| Phacopida | Acastidae | Kayserops | Kayserops tamnrherta | 202 | Large eyes | Shallow | Predator/Scavenger | 19.10 | | Chatterton 2006 | =0,044376 | Emsian | Cranidium |
| Phacopida | Acastidae | Kayserops | Kayserops tamnrherta | 203 | Large eyes | Shallow | Predator/Scavenger | 20.7 | | Chatterton 2006 | =0,051276 | Emsian | Cephalon |

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| Phacopida | Acastidae | Kayserops | Kayserops tamnrherta | 204 | Large eyes | Shallow | Predator/Scavenger | 21.2 | | Chatterton 2006 | =0,072840 | Emsian | Cephalon |
| Phacopida | Acastidae | Kayserops | Kayserops tamnrherta | 205 | Large eyes | Shallow | Predator/Scavenger | 21.7 | | Chatterton 2006 | =0,066804 | Emsian | Cephalon |
| Phacopida | Acastidae | Metacanthina | Metacanthina issoumourensis | 206 | Large eyes | Shallow | Predator/Scavenger | 3.1a | | Morzadec 2001 | =0,028528 | Pragian | Cephalon |
| Phacopida | Acastidae | Metacanthina | Metacanthina issoumourensis | 207 | Large eyes | Shallow | Predator/Scavenger | 3.2a | | Morzadec 2001 | =0,028528 | Pragian | Cephalon |
| Phacopida | Acastidae | Metacanthina | Metacanthina maderensis | 208 | Large eyes | Shallow | Predator/Scavenger | 3.4a | | Morzadec 2001 | =0,021050 | Pragian | Cephalon |
| Phacopida | Acastidae | Metacanthina | Metacanthina wallacei | 209 | Large eyes | Shallow | Predator/Scavenger | 6.1a | | Morzadec 2001 | =0,021183 | Pragian | Cranidium |
| Phacopida | Acastidae | Metacanthina | Metacanthina wallacei | 210 | Large eyes | Shallow | Predator/Scavenger | 6.2a | | Morzadec 2001 | =0,021183 | Pragian | Cephalon |
| Phacopida | Acastidae | Metacanthina | Metacanthina wallacei | 211 | Large eyes | Shallow | Predator/Scavenger | 6.3 | | Morzadec 2001 | =0,021183 | Pragian | Cranidium |
| Phacopida | Acastidae | Metacanthina | Metacanthina wallacei | 212 | Large eyes | Shallow | Predator/Scavenger | 6.4 | | Morzadec 2001 | =0,021183 | Pragian | Cephalon |
| Phacopida | Acastidae | Mrakibina | Mrakibina cattoi | 213 | Large eyes | Inner shelf | Predator/Scavenger | 14.3 | | Morzadec 2001 | =0,021161 | Eifelian | Cephalon |
| Phacopida | Acastidae | Mrakibina | Mrakibina cattoi | 214 | Large eyes | Inner shelf | Predator/Scavenger | 14.7 | | Morzadec 2001 | =0,021161 | Eifelian | Cephalon |
| Phacopida | Acastidae | Morzadecops | Morzadecops zguidensis | 215 | Large eyes | Inner shelf | Predator/Scavenger | 4.1a | | Morzadec 2001 | =0,020901 | Emsian | Cephalon |
| Phacopida | Acastidae | Morzadecops | Morzadecops zguidensis | 216 | Large eyes | Inner shelf | Predator/Scavenger | 4.2 | | Morzadec 2001 | =0,020901 | Emsian | Cephalon |
| Phacopida | Acastidae | Minicryphaeus | Minicryphaeus minimus | 217 | Large eyes | Shallow | Predator/Scavenger | 1.2a | | Morzadec 2001 | =0,008462 | Pragian | Cephalon |
| Phacopida | Acastidae | Minicryphaeus | Minicryphaeus minimus | 218 | Large eyes | Shallow | Predator/Scavenger | 1.3 | | Morzadec 2001 | =0,005248 | Pragian | Cranidium |
| Phacopida | Acastidae | Minicryphaeus | Minicryphaeus minimus | 219 | Large eyes | Shallow | Predator/Scavenger | 1.4a | | Morzadec 2001 | =0,008462 | Pragian | Cephalon |
| Phacopida | Acastidae | Pseudocryphaeus | Pseudocryphaeus sarirus | 220 | Large eyes | Shallow | Predator/Scavenger | 2.1a | | Morzadec 2001 | =0,010281 | Pragian | Cranidium |
| Phacopida | Acastidae | Pseudocryphaeus | Pseudocryphaeus quaterspinosus | 222 | Large eyes | Shallow | Predator/Scavenger | 2.3a | | Morzadec 2001 | =0,013517 | Pragian | Cephalon |
| Phacopida | Acastidae | Pseudocryphaeus | Pseudocryphaeus sp 2 | 223 | Large eyes | Shallow | Predator/Scavenger | 5.7 | | Morzadec 2001 | =0,010095 | Emsian | Cranidium |
| Phacopida | Acastidae | Psychopyge | Psychopyge termierorum | 225 | Large eyes | Middle shelf | Predator/Scavenger | 13.1a | | Morzadec 2001 | =0,021144 | Emsian | Cephalon |
| Phacopida | Acastidae | Psychopyge | Psychopyge praestans | 226 | Large eyes | Middle shelf | Predator/Scavenger | 13.5a | | Morzadec 2001 | =0,039807 | Emsian | Cephalon |
| Phacopida | Acastidae | Psychopyge | Psychopyge praestans | 227 | Large eyes | Middle shelf | Predator/Scavenger | 24.3 | | Chatterton 2006 | =0,164636 | Emsian | Cranidium |
| Phacopida | Acastidae | Psychopyge | Psychopyge hammerorum | 228 | Large eyes | Middle shelf | Predator/Scavenger | 26.5 | | Chatterton 2006 | =0,069324 | Emsian | Cranidium |
| Phacopida | Acastidae | Saharops | Saharops bensaïdi | 229 | Large eyes | Shallow | Predator/Scavenger | 14.1a | | Morzadec 2001 | =0,041660 | Emsian | Cephalon |
| Phacopida | Acastidae | Treveropyge | Treveropyge maura | 230 | Large eyes | Shallow | Predator/Scavenger | 10.1a | | Morzadec 2001 | =0.042420 | Emsian | Cephalon |
| Phacopida | Acastidae | Treveropyge | Treveropyge prorotundifrons iberica | 231 | Large eyes | Shallow | Predator/Scavenger | 11.3a | SMF 53791 | Schraut 2000c | =0.053068 | Pragian | Cranidium |
| Phacopida | Acastidae | Walliserops | Walliserops trifurcatus | 232 | Large eyes | Middle shelf | Predator/Scavenger | 15.2a | | Morzadec 2001 | =0,020595 | Emsian | Cephalon |
| Phacopida | Acastidae | Walliserops | Walliserops hammii | 233 | Large eyes | Middle shelf | Predator/Scavenger | 29.6 | | Chatterton 2006 | =0,049998 | Emsian | Cephalon |
| Phacopida | Acastidae | Walliserops | Walliserops trifurcatus | 234 | Large eyes | Middle shelf | Predator/Scavenger | 31.1 | | Chatterton 2006 | =0,093520 | Emsian | Cephalon |
| Proetida | Aulacopleuridae | Aulacopleura | Aulacopleura beyrichi africana | 235 | Large eyes | Middle shelf | Particle feeding | 9.17a | | Alberti1970a | =0,005291 | Eifelian | Cranidium |
| Proetida | Aulacopleuridae | Aulacopleura | Aulacopleura beyrichi africana | 236 | Large eyes | Middle shelf | Particle feeding | 9.18 | | Alberti1970a | =0,005224 | Eifelian | Cranidium |
| Proetida | Aulacopleuridae | Aulacopleura | Aulacopleurella mauretanica | 237 | Large eyes | Middle shelf | Particle feeding | 5.50a | CGMTA | Alberti1981a | =0,024430 | Eifelian | Cranidium |
| Proetida | Aulacopleuridae | Aulacopleura | Aulacopleura bohemica | 238 | Large eyes | Middle shelf | Particle feeding | 5.51 | SMF 36276 | Alberti1981a | =0,029450 | Eifelian | Cranidium |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis akkae | 239 | Large eyes | Middle shelf | Particle feeding | 3.d | Di/UO/010 | Feist 2018 | =0,010988 | Emsian | Cranidium |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis hamlagdadicus | 240 | Large eyes | Middle shelf | Particle feeding | 5.52a | CGMTA | Alberti 1981a | =0.024515 | Eifelian | Cranidium |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis boutscharafinense | 241 | Large eyes | Middle shelf | Particle feeding | 5.53 | CGMTA | Alberti 1981a | =0.023553 | Emsian | Cranidium |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis boutscharafinense | 242 | Large eyes | Middle shelf | Particle feeding | 5.54 | SMF 36275 | Alberti 1981a | =0.015380 | Emsian | Cranidium |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis lierli | 243 | Large eyes | Middle shelf | Particle feeding | 6.75a | CGMTA | Alberti 1983 | =0.010709 | Pragian | Cranidium |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis lierli | 244 | Large eyes | Middle shelf | Particle feeding | 6.76 | SMF 36567 | Alberti 1983 | =0.010709 | Pragian | Cranidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis sp A | 245 | Large eyes | Middle shelf | Particle feeding | 7w | MU-G-Sr.Tr.A4/Pr144 | Crônier Abbache 2018 | =0,062446 | Eifelian | Cranidium |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis lerougei | 246 | Large eyes | Middle shelf | Particle feeding | 11a | IRSNB a13016 | Van Viersen 2016 | =0,023803 | Emsian | Cephalon |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis lerougei | 247 | Large eyes | Middle shelf | Particle feeding | 11b | IRSNB a13014 | Van Viersen 2016 | =0,012345 | Emsian | Cephalon |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis lerougei | 248 | Large eyes | Middle shelf | Particle feeding | 12c | IRSNB a12998 | Van Viersen 2016 | =0,024383 | Emsian | Cephalon |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis lerougei | 249 | Large eyes | Middle shelf | Particle feeding | 12f | IRSNB a12999 | Van Viersen 2016 | =0,024089 | Emsian | Cephalon |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis lerougei | 250 | Large eyes | Middle shelf | Particle feeding | 13c | IRSNB a13000 | Van Viersen 2016 | =0,023808 | Emsian | Cephalon |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis kippingi | 251 | Large eyes | Middle shelf | Particle feeding | 15c | IRSNB a12997 | Van Viersen 2016 | =0,019996 | Emsian | Cephalon |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis juergenhollandi | 252 | Large eyes | Middle shelf | Particle feeding | 17a | IRSNB a13013 | Van Viersen 2016 | =0,021945 | Emsian | Cephalon |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis smeenki | 253 | Large eyes | Middle shelf | Particle feeding | 18d | IRSNB a13009 | Van Viersen 2016 | =0,037031 | Eifelian | Cephalon |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis maharchensis | 254 | Large eyes | Middle shelf | Particle feeding | 20g | IRSNB a13007 | Van Viersen 2016 | =0,029399 | Pragian | Cephalon |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis khraidensis | 255 | Large eyes | Middle shelf | Particle feeding | 24c | IRSNB a13004 | Van Viersen 2016 | =0,037012 | Emsian | Cephalon |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis khraidensis | 256 | Large eyes | Middle shelf | Particle feeding | 25a | IRSNB a13006 | Van Viersen 2016 | =0,044636 | Emsian | Cranidium |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis tadachachtensis | 257 | Large eyes | Middle shelf | Particle feeding | 26c | IRSNB a13002 | Van Viersen 2016 | =0,022221 | Emsian | Cranidium |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis hamidi | 258 | Large eyes | Middle shelf | Particle feeding | 46.2 | UA 13402 | Chatterton 2006 | =0,024009 | Emsian | Cranidium |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis hamidi | 259 | Large eyes | Middle shelf | Particle feeding | 46.12 | UA 13409 | Chatterton 2006 | =0,026604 | Emsian | Cranidium |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis lata | 260 | Large eyes | Middle shelf | Particle feeding | b.25 | | Alberti 1967b | =0,039842 | Pragian | Cranidium |
| Proetida | Aulacopleuridae | Maurotarion | Maurotarion maurum | 261 | Large eyes | Middle shelf | Particle feeding | 36.1a | CGMTA 159 | Alberti 1969 | =0,005620 | Ludlow-Pridoli | Cranidium |
| Proetida | Aulacopleuridae | Maurotarion | Maurotarion maurum | 262 | Large eyes | Middle shelf | Particle feeding | 36.2a | SMF 23383 | Alberti 1969 | =0,005620 | Ludlow-Pridoli | Cranidium |
| Proetida | Aulacopleuridae | Maurotarion | Maurotarion maurum | 263 | Large eyes | Middle shelf | Particle feeding | 36.3 | SMF 23384 | Alberti 1969 | =0,005966 | Ludlow-Pridoli | Cranidium |
| Proetida | Aulacopleuridae | Maurotarion | Maurotarion maurum | 264 | Large eyes | Middle shelf | Particle feeding | 36.4a | SMF 23386 | Alberti 1969 | =0,004734 | Ludlow-Pridoli | Cranidium |
| Proetida | Aulacopleuridae | Maurotarion | Maurotarion novellum | 265 | Large eyes | Middle shelf | Particle feeding | 36.7 | SMF 23215 | Alberti 1969 | =0,008397 | Ludlow-Pridoli | Cranidium |
| Proetida | Aulacopleuridae | Maurotarion | Maurotarion novellum | 266 | Large eyes | Middle shelf | Particle feeding | 36.8 | CGMTA 206 | Alberti 1969 | =0,007699 | Ludlow-Pridoli | Cranidium |
| Proetida | Aulacopleuridae | Maurotarion | Maurotarion neptis | 267 | Large eyes | Middle shelf | Particle feeding | 36.9a | CGMTA 160 | Alberti 1969 | =0,004853 | Pragian | Cranidium |
| Proetida | Aulacopleuridae | Maurotarion | Maurotarion neptis | 268 | Large eyes | Middle shelf | Particle feeding | 36.10 | SMF 23387 | Alberti 1969 | =0,004589 | Pragian | Cranidium |
| Proetida | Aulacopleuridae | Maurotarion | Maurotarion ambiguum | 269 | Large eyes | Middle shelf | Particle feeding | 36.11a | CGMTA 153 | Alberti 1969 | =0,006397 | | Cranidium |
| Proetida | Aulacopleuridae | Maurotarion | Maurotarion maurum | 270 | Large eyes | Middle shelf | Particle feeding | b.28 | CGMTA 159 | Alberti 1967b | =0,006939 | Ludlow-Pridoli | Cranidium |
| Proetida | Aulacopleuridae | Maurotarion | Maurotarion neptis | 271 | Large eyes | Middle shelf | Particle feeding | b.29 | CGMTA 160 | Alberti 1967b | =0,006379 | Pragian | Cranidium |
| Proetida | Aulacopleuridae | Maurotarion | Maurotarion ambiguum | 272 | Large eyes | Middle shelf | Particle feeding | b.30 | CGMTA 161 | Alberti 1967b | =0,008395 | | Cranidium |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis boutscharafinense | 273 | Large eyes | Middle shelf | Particle feeding | 34.7a | SMF 23444 | Alberti 1969 | =0,007100 | Emsian | Cranidium |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis akkae | 274 | Large eyes | Middle shelf | Particle feeding | 34.1a | CGMTA-AK 112 | Alberti 1969 | =0,010349 | Pragian | Cranidium |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis valida | 275 | Large eyes | Middle shelf | Particle feeding | 34.2a | CGMTA 198 | Alberti 1969 | =0,012955 | Pragian | Cranidium |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis lata | 276 | Large eyes | Middle shelf | Particle feeding | 34.5a | CGMTA 152 | Alberti 1969 | =0,008909 | Pragian | Cranidium |
| Proetida | Aulacopleuridae | Otarionella | Otarionella bensaidi | 277 | Large eyes | Inner shelf | Particle feeding | 6.77 | CGMTA | Alberti 1983 | =0.005137 | Eifelian | Cranidium |
| Proetida | Aulacopleuridae | Otarionella | Otarionella proavus | 278 | Large eyes | Inner shelf | Particle feeding | 9.14a | CGMT | Alberti 1970a | =0,015661 | Lochkovian | Cranidium |
| Proetida | Aulacopleuridae | Otarionella | Otarionella magnifica | 279 | Large eyes | Inner shelf | Particle feeding | 35.1a | SMF 23373 | Alberti 1969 | =0,019122 | Pragian | Cranidium |
| Proetida | Aulacopleuridae | Otarionella | Otarionella magnifica | 280 | Large eyes | Inner shelf | Particle feeding | 35.3a | SMF 23374 | Alberti 1969 | =0,022707 | Pragian | Cranidium |
| Proetida | Aulacopleuridae | Otarionella | Otarionella magnifica | 281 | Large eyes | Inner shelf | Particle feeding | 35.4a | SMF 23375 | Alberti 1969 | =0,022260 | Pragian | Cranidium |
| Proetida | Aulacopleuridae | Otarionella | Otarionella sidiarounium | 282 | Large eyes | Inner shelf | Particle feeding | 35.5a | CGMTA 200 | Alberti 1969 | =0,009356 | Pragian | Cranidium |
| Proetida | Aulacopleuridae | Otarionella | Otarionella tafilaltense | 283 | Large eyes | Inner shelf | Particle feeding | 35.6a | SMF 23377 | Alberti 1969 | =0,009356 | Emsian | Cranidium |
| Proetida | Aulacopleuridae | Otarionella | Otarionella tafilaltense | 284 | Large eyes | Inner shelf | Particle feeding | 35.7a | CGMTA 157 | Alberti 1969 | =0,011646 | Emsian | Cranidium |
| Proetida | Aulacopleuridae | Otarionella | Otarionella magnifica | 285 | Large eyes | Inner shelf | Particle feeding | b.26 | SMF 23375 | Alberti 1967b | =0,028250 | Pragian | Cranidium |
| Proetida | Aulacopleuridae | Otarionella | Otarionella tafilaltense | 286 | Large eyes | Inner shelf | Particle feeding | b.27 | CGMTA 157 | Alberti 1967b | =0,015093 | Emsian | Cranidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Proetida | Aulacopleuridae | Scharya | Scharya maura | 287 | Large eyes | Middle shelf | Particle feeding | 9.1a | CGMTA 299 | Alberti 1970a | =0,003913 | Emsian | Cranidium |
| Phacopida | Calmoniidae | Acastoides | Acastoides zguilmensis | 288 | Small eyes | Deep | Predator/Scavenger | 9.5 | UA 13330 | Chatterton 2006 | =0,082800 | Emsian | Cephalon |
| Phacopida | Calmoniidae | Acastoides | Acastoides zguilmensis | 289 | Small eyes | Deep | Predator/Scavenger | 12.10 | UA 13343 | Chatterton 2006 | =0,036985 | Emsian | Cephalon |
| Phacopida | Calmoniidae | Acastoides | Acastoides hollardi | 290 | Small eyes | Deep | Predator/Scavenger | 18.3a | CGMTA 335 | Alberti 1970a | =0,019067 | Emsian | Cephalon |
| Phacopida | Calmoniidae | Acastoides | Acastoides hollardi | 291 | Small eyes | Deep | Predator/Scavenger | 18.5a* | SMF 23566 | Alberti 1970a | =0,022038 | Emsian | Cephalon |
| Phacopida | Calmoniidae | Acastoides | Acastoides hollardi | 292 | Small eyes | Deep | Predator/Scavenger | 18.6a | SMF 23567 | Alberti 1970a | =0,023200 | Emsian | Cephalon |
| Phacopida | Calymenidae | Gravicalymene | Gravicalymene hamlagdadica | 293 | Large eyes | Middle shelf | Predator/Scavenger | 6.57a | CGMTA | Alberti 1981a | =0.092157 | Pragian | Cranidium |
| Phacopida | Calymenidae | Gravicalymene | Gravicalymene hamlagdadica | 294 | Large eyes | Middle shelf | Predator/Scavenger | 6.58 | SMF 36283 | Alberti 1981a | =0.084178 | Pragian | Cranidium |
| Phacopida | Calymenidae | Gravicalymene | Gravicalymene maura | 295 | Large eyes | Middle shelf | Predator/Scavenger | 42.1a | CGMTA 164 | Alberti 1969 | =0,017787 | Pragian | Cranidium |
| Phacopida | Cheiruridae | Cheirurus | Cheirurus obtusatus | 296 | Blind | Middle shelf | Predator/Scavenger | 39.11 | CGMTA 207 | Alberti 1969 | =0,007724 | Ludlow-Pridoli | Cranidium |
| Phacopida | Cheiruridae | Crotalocephalides | Crotalocephalides africanus | 297 | Large eyes | Middle shelf | Predator/Scavenger | 39.1a | SMF 23401 | Alberti 1969 | =0,051668 | Pragian | Cranidium |
| Phacopida | Cheiruridae | Crotalocephalides | Crotalocephalides africanus | 298 | Large eyes | Middle shelf | Predator/Scavenger | 39.2a | CGMTA 162 | Alberti 1969 | =0,031148 | Pragian | Blind |
| Phacopida | Cheiruridae | Crotalocephalides | Crotalocephalides africanus | 299 | Large eyes | Middle shelf | Predator/Scavenger | a.19 | SMF 23401 | Alberti 1967a | =0.056025 | Pragian | Cranidium |
| Phacopida | Cheiruridae | Crotalocephalina | Crotalocephalina gibbus benziregensis | 300 | Large eyes | Middle shelf | Predator/Scavenger | 1.1a | SMF 36569 | Alberti 1983 | =0.031526 | Pragian | Cranidium |
| Phacopida | Cheiruridae | Crotalocephalina | Crotalocephalina gibbus benziregensis | 301 | Large eyes | Middle shelf | Predator/Scavenger | 1.2 | SH | Alberti 1983 | =0.031526 | Pragian | Cranidium |
| Phacopida | Cheiruridae | Crotalocephalina | Crotalocephalina gibbus benziregensis | 302 | Large eyes | Middle shelf | Predator/Scavenger | 1.5 | SMF 36581 | Alberti 1983 | =0.029187 | Pragian | Cranidium |
| Phacopida | Cheiruridae | Crotalocephalina | Crotalocephalina gibbus tifletensis | 303 | Large eyes | Middle shelf | Predator/Scavenger | 2.1a | SMF 57067 | Schraut 2000c | =0.098363 | Pragian | Cranidium |
| Phacopida | Cheiruridae | Crotalocephalina | Crotalocephalina gibbus auster | 304 | Large eyes | Middle shelf | Predator/Scavenger | 10.6a | CGMTA 307 | Alberti 1970a | =0,032459 | Pragian | Cranidium |
| Phacopida | Cheiruridae | Crotalocephalina | Crotalocephalina gibbus auster | 305 | Large eyes | Middle shelf | Predator/Scavenger | 10.8a | SMF 23510 | Alberti 1970a | =0,030701 | Pragian | Cranidium |
| Phacopida | Cheiruridae | Crotalocephalina | Crotalocephalina gibbus | 306 | Large eyes | Middle shelf | Predator/Scavenger | 38.1a | CGMT | Alberti 1969 | =0,035594 | Pragian | Blind |
| Phacopida | Cheiruridae | Crotalocephalina | Crotalocephalina gibbus | 307 | Large eyes | Middle shelf | Predator/Scavenger | 38.2 | SMF 23447 | Alberti 1969 | =0,016341 | Pragian | Blind |
| Phacopida | Cheiruridae | Crotalocephalina | Crotalocephalina gibbus | 308 | Large eyes | Middle shelf | Predator/Scavenger | 38.3a | CGMT | Alberti 1969 | =0,014603 | Pragian | Cranidium |
| Phacopida | Cheiruridae | Crotalocephalina | Crotalocephalina gibbus | 309 | Large eyes | Middle shelf | Predator/Scavenger | 38.4a | SMF 23448 | Alberti 1969 | =0,020722 | Pragian | Blind |
| Phacopida | Cheiruridae | Crotalocephalina | Crotalocephalina gibbus | 310 | Large eyes | Middle shelf | Predator/Scavenger | 38.5 | CGMTA 173 | Alberti 1969 | =0,019998 | Pragian | Cranidium |
| Phacopida | Cheiruridae | Crotalocephalina | Crotalocephalina sp B | 311 | Large eyes | Middle shelf | Predator/Scavenger | 38.10 | SMF 23449 | Alberti 1969 | =0,024375 | Lochkovian | Blind |
| Phacopida | Cheiruridae | Crotalocephalus | Crotalocephalus pauper saharensis | 312 | Large eyes | Middle shelf | Predator/Scavenger | 7.78 | SH | Alberti 1983 | =0.004549 | Pragian | Cranidium |
| Phacopida | Cheiruridae | Crotalocephalus | Crotalocephalus pauper saharensis | 313 | Large eyes | Middle shelf | Predator/Scavenger | 7.79 | SMF 36593 | Alberti 1983 | =0.033313 | Pragian | Cranidium |
| Phacopida | Cheiruridae | Crotalocephalus | Crotalocephalus meridianus | 314 | Large eyes | Middle shelf | Predator/Scavenger | 37.1a | CGMTA 201 | Alberti 1969 | =0,021165 | Pragian | Blind |
| Phacopida | Cheiruridae | Crotalocephalus | Crotalocephalus meridianus | 315 | Large eyes | Middle shelf | Predator/Scavenger | 37.2a | CGMT | Alberti 1969 | =0,030662 | Pragian | Blind |
| Phacopida | Cheiruridae | Crotalocephalus | Crotalocephalus maurus | 316 | Large eyes | Middle shelf | Predator/Scavenger | 38.6a | CGMTA 161 | Alberti 1969 | =0,026459 | Pragian | Blind |
| Phacopida | Cheiruridae | Crotalocephalus | Crotalocephalus maurus | 317 | Large eyes | Middle shelf | Predator/Scavenger | 38.7a | SMF 23391 | Alberti 1969 | =0,013498 | Pragian | Blind |
| Phacopida | Cheiruridae | Ktenoura | Ktenoura strux | 318 | Large eyes | Inner shelf | Predator/Scavenger | 10.1a | CGMTA 305 | Alberti 1970a | =0,029930 | Ludlow-Pridoli | Cranidium |
| Harpetida | Harpetidae | Harpes | Indet | 319 | Small eyes | Middle shelf | Predator/Scavenger | 2.20 | SH | Alberti 1983 | =0.019083 | Pragian | Cranidium |
| Harpetida | Harpetidae | Harpes | Harpes neogracilis | 320 | Small eyes | Middle shelf | Predator/Scavenger | 2l | UM-RF 220 | Feist 2002 | =0.020642 | Frasnian | Cranidium |
| Harpetida | Harpetidae | Lioharpes | Lioharpes wendti | 321 | Small eyes | Middle shelf | Predator/Scavenger | 4.a | UM-IP 729 | Feist 2018 | =0,015871 | Emsian | Cranidium |
| Harpetida | Harpetidae | Lioharpes | Lioharpes wendti | 322 | Small eyes | Middle shelf | Predator/Scavenger | 4.c | UM-IP 728 | Feist 2018 | =0,013158 | Emsian | Cranidium |
| Harpetida | Harpetidae | Lioharpes | Lioharpes wendti | 323 | Small eyes | Middle shelf | Predator/Scavenger | 4.d | UM-IP 730 | Feist 2018 | =0,019223 | Emsian | Cranidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Lichida | Lichidae | Acanthopyge | Acanthopyge (Belenopyge) estevei | 324 | Large eyes | Middle shelf | Predator/Scavenger | 1.3 | MGSB 79489 | Corbacho Kier 2013 | =0,014005 | Pragian | Cephalon |
| Lichida | Lichidae | Acanthopyge | Acanthopyge (Belenopyge) estevei | 325 | Large eyes | Middle shelf | Predator/Scavenger | 2.1 | MGSB 79489 | Corbacho Kier 2013 | =0,009940 | Pragian | Cephalon |
| Lichida | Lichidae | Acanthopyge | Acanthopyge (Belenopyge) estevei | 326 | Large eyes | Middle shelf | Predator/Scavenger | 2.2 | MGSB 79486 | Corbacho Kier 2013 | =0,019526 | Pragian | Cranidium |
| Lichida | Lichidae | Acanthopyge | Acanthopyge (Belenopyge) estevei | 327 | Large eyes | Middle shelf | Predator/Scavenger | 2.4 | MMB 109 | Corbacho Kier 2013 | =0,006289 | Pragian | Cranidium |
| Lichida | Lichidae | Acanthopyge | Acanthopyge (Belenopyge) estevei | 328 | Large eyes | Middle shelf | Predator/Scavenger | 3.2 | MMB 105 | Corbacho Kier 2013 | =0,020660 | Pragian | Cranidium |
| Lichida | Lichidae | Acanthopyge | Acanthopyge (Belenopyge) estevei | 329 | Large eyes | Middle shelf | Predator/Scavenger | 3.3 | MMB 106 | Corbacho Kier 2013 | =0,013158 | Pragian | Cranidium |
| Lichida | Lichidae | Acanthopyge | Acanthopyge (Belenopyge) estevei | 330 | Large eyes | Middle shelf | Predator/Scavenger | 3.4 | MMB 107 | Corbacho Kier 2013 | =0,011062 | Pragian | Cephalon |
| Lichida | Lichidae | Akantharges | Akantharges mbareki | 332 | Large eyes | Middle shelf | Predator/Scavenger | 3.2 | JC 95 | Corbacho Lopez 2013 | =0,043472 | Eifelian | Blind |
| Lichida | Lichidae | Ceratarges | Ceratarges ziregensis | 333 | Large eyes | Inner shelf | Predator/Scavenger | 1a | NHMM 2011 001 | Van Viersen 2011 | =0,035453 | Eifelian | Cranidium |
| Lichida | Lichidae | Ceratarges | Ceratarges koumalii | 334 | Large eyes | Inner shelf | Predator/Scavenger | 2d | NHMM 2011 002 | Van Viersen 2011 | =0,034227 | Eifelian | Cephalon |
| Lichida | Odontopleuridae | Ceratocephala | Ceratocephala hoernesi | 335 | Large eyes | Middle shelf | Predator/Scavenger | 3.e_24 | UM-IP 786 | Feist 2018 | =0,011293 | Emsian | Cranidium |
| Lichida | Odontopleuridae | Ceratocephala | Ceratocephala hoernesi | 336 | Large eyes | Middle shelf | Predator/Scavenger | 3.h | UM-IP 789 | Feist 2018 | =0,014083 | Emsian | Cranidium |
| Lichida | Odontopleuridae | Ceratocephala | Ceratocephala vesiculosa | 337 | Large eyes | Middle shelf | Predator/Scavenger | 19.10a | CGMTA 344 | Alberti 1970a | =0,013172 | Eifelian | Cranidium |
| Lichida | Odontopleuridae | Isoprusia | Isoprusia laportei | 340 | Large eyes | Middle shelf | Predator/Scavenger | 3.m | UM-IP 804 | Feist 2018 | =0,005747 | Emsian | Cranidium |
| Lichida | Odontopleuridae | Isoprusia | Isoprusia laportei | 341 | Large eyes | Middle shelf | Predator/Scavenger | 41.11a | SMF 23421 | Alberti 1969 | =0,012586 | | Cranidium |
| Lichida | Odontopleuridae | Isoprusia | Isoprusia laportei | 342 | Large eyes | Middle shelf | Predator/Scavenger | 41.12 | CGMTA 168 | Alberti 1969 | =0,005682 | | Cranidium |
| Lichida | Odontopleuridae | Isoprusia | Isoprusia laportei | 343 | Large eyes | Middle shelf | Predator/Scavenger | 41.13a | ISCR | Alberti 1969 | =0,017139 | | Cranidium |
| Lichida | Odontopleuridae | Kettneraspis | Kettneraspis pigra | 344 | Large eyes | Deep | Predator/Scavenger | 41.3 | SMF 23450 | Alberti 1969 | =0,013512 | Eifelian | Cranidium |
| Lichida | Odontopleuridae | Leonaspis | Leonaspis leonhardi | 345 | Large eyes | Middle shelf | Predator/Scavenger | 19.6a | CGMTA 368 | Alberti 1970a | =0,011621 | Ludlow-Pridoli | Cranidium |
| Lichida | Odontopleuridae | Leonaspis | Leonaspis grouensis | 346 | Large eyes | Middle shelf | Predator/Scavenger | 19.7a | CGMTA 342 | Alberti 1970a | =0,007742 | Ludlow-Pridoli | Cranidium |
| Lichida | Odontopleuridae | Leonaspis | Leonaspis hastata | 347 | Large eyes | Middle shelf | Predator/Scavenger | 40.2a | SMF 23408 | Alberti 1969 | =0,011859 | Pragian | Cranidium |
| Lichida | Odontopleuridae | Leonaspis | Leonaspis hastata | 348 | Large eyes | Middle shelf | Predator/Scavenger | 40.3a | SMF 23409 | Alberti 1969 | =0,011859 | Pragian | Cranidium |
| Lichida | Odontopleuridae | Leonaspis | Leonaspis hastata | 349 | Large eyes | Middle shelf | Predator/Scavenger | 40.4 | SMF 23410 | Alberti 1969 | =0,012694 | Pragian | Cranidium |
| Lichida | Odontopleuridae | Leonaspis | Leonaspis hastata | 350 | Large eyes | Middle shelf | Predator/Scavenger | 40.5 | CGMTA 167 | Alberti 1969 | =0,013203 | Pragian | Cranidium |
| Phacopida | Phacopidae | Acuticryphops | Acuticryphops acuticeps | 351 | Small eyes | Middle shelf | Predator/Scavenger | 3.c | UM2-RF 221 | Feist 2002 | =0.011087 | Frasnian | Blind |
| Phacopida | Phacopidae | Adrisiops | Adrisiops fabrei | 352 | Large eyes | Middle shelf | Predator/Scavenger | 4.g | | Khaldi 2016 | =0,041317 | Emsian | Cephalon |
| Phacopida | Phacopidae | Adrisiops | Adrisiops fabrei | 353 | Large eyes | Middle shelf | Predator/Scavenger | 4.n | | Khaldi 2016 | =0,087706 | Emsian | Cranidium |
| Phacopida | Phacopidae | Adrisiops | Adrisiops boudjemaai | 354 | Large eyes | Middle shelf | Predator/Scavenger | 5.n | | Khaldi 2016 | =0,128163 | Emsian | Cranidium |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 355 | Large eyes | Middle shelf | Predator/Scavenger | 4.2 | UA 13306 | Chatterton 2006 | =0,061248 | Emsian | Cranidium |
| Phacopida | Phacopidae | Austerops | Austerops sp D | 356 | Large eyes | Middle shelf | Predator/Scavenger | 4b | | Crônier Abbache 2018 | =0,054536 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Austerops | Austerops sp B | 357 | Large eyes | Middle shelf | Predator/Scavenger | 4s | | Crônier Abbache 2018 | =0,042840 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Austerops | Austerops sp B | 358 | Large eyes | Middle shelf | Predator/Scavenger | 4u | | Crônier Abbache 2018 | =0,061212 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 359 | Large eyes | Middle shelf | Predator/Scavenger | 5.1 | UA 13311 | Chatterton 2006 | =0,058588 | Emsian | Cephalon |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 360 | Large eyes | Middle shelf | Predator/Scavenger | 5.2 | UA 13313 | Chatterton 2006 | =0,065006 | Emsian | Cephalon |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 361 | Large eyes | Middle shelf | Predator/Scavenger | 5.3 | UA 13307 | Chatterton 2006 | =0,059082 | Emsian | Cephalon |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 362 | Large eyes | Middle shelf | Predator/Scavenger | 5.4 | UA 13357 | Chatterton 2006 | =0,087816 | Emsian | Cephalon |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 363 | Large eyes | Middle shelf | Predator/Scavenger | 5.6 | UA 13312 | Chatterton 2006 | =0,050395 | Emsian | Cranidium |
| Phacopida | Phacopidae | Austerops | Austerops speculator punctatus | 364 | Large eyes | Middle shelf | Predator/Scavenger | 6.1 | UA 6878 | McKellar 2009 | =0,015433 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Austerops | Austerops speculator punctatus | 365 | Large eyes | Middle shelf | Predator/Scavenger | 6.3 | UA 6882 | McKellar 2009 | =0,015433 | Eifelian | Cephalon |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phacopida | Phacopidae | Austerops | Austerops speculator speculator | 366 | Large eyes | Middle shelf | Predator/Scavenger | 6.a | | Khaldi 2016 | =0,056176 | Emsian | Cranidium |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 367 | Large eyes | Middle shelf | Predator/Scavenger | 6.e | | Khaldi 2016 | =0,043858 | Emsian | Cranidium |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 368 | Large eyes | Middle shelf | Predator/Scavenger | 6.i | | Khaldi 2016 | =0,063271 | Emsian | Cranidium |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 369 | Large eyes | Middle shelf | Predator/Scavenger | 7.2 | UA 13322 | Chatterton 2006 | =0,059993 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 370 | Large eyes | Middle shelf | Predator/Scavenger | 7.3 | UA 13317 | Chatterton 2006 | =0,041059 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 371 | Large eyes | Middle shelf | Predator/Scavenger | 7.5 | UA 13325 | Chatterton 2006 | =0,043587 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 372 | Large eyes | Middle shelf | Predator/Scavenger | 7.8 | UA 13324 | Chatterton 2006 | =0,053775 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 373 | Large eyes | Middle shelf | Predator/Scavenger | 7.9 | UA 13319 | Chatterton 2006 | =0,067651 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Austerops | Austerops legrandi | 374 | Large eyes | Middle shelf | Predator/Scavenger | 7.d | | Khaldi 2016 | =0,060957 | Emsian | Cephalon |
| Phacopida | Phacopidae | Austerops | Austerops legrandi | 375 | Large eyes | Middle shelf | Predator/Scavenger | 7.k | | Khaldi 2016 | =0,026454 | Emsian | Cephalon |
| Phacopida | Phacopidae | Austerops | Austerops kermiti | 376 | Large eyes | Middle shelf | Predator/Scavenger | 8.3 | UA 6884 | McKellar 2009 | =0,013968 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Austerops | Austerops kermiti | 377 | Large eyes | Middle shelf | Predator/Scavenger | 8.7 | UA 6889 | McKellar 2009 | =0,013275 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Austerops | Austerops kermiti | 378 | Large eyes | Middle shelf | Predator/Scavenger | 8.9 | UA 6888 | McKellar 2009 | =0,011414 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Austerops | Austerops kermiti | 379 | Large eyes | Middle shelf | Predator/Scavenger | 9.2 | UA 6885 | McKellar 2009 | =0,011945 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Austerops | Austerops kermiti | 380 | Large eyes | Middle shelf | Predator/Scavenger | 9.9 | UA 6887 | McKellar 2009 | =0,011945 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Austerops | Austerops salamandar | 381 | Large eyes | Middle shelf | Predator/Scavenger | 10.1 | UA 6892 | McKellar 2009 | =0,010181 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Austerops | Austerops salamandar | 382 | Large eyes | Middle shelf | Predator/Scavenger | 10.6 | UA 6893 | McKellar 2009 | =0,012318 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Austerops | Austerops salamandar | 383 | Large eyes | Middle shelf | Predator/Scavenger | 10.9 | UA 6894 | McKellar 2009 | =0,011295 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Austerops | Austerops speculator speculator | 384 | Large eyes | Middle shelf | Predator/Scavenger | 12;1a | ISCR | Alberti 1970a | =0,018431 | Emsian | Cranidium |
| Phacopida | Phacopidae | Austerops | Austerops speculator speculator | 385 | Large eyes | Middle shelf | Predator/Scavenger | 12.2a | ISCR | Alberti 1970a | =0,018431 | Emsian | Cranidium |
| Phacopida | Phacopidae | Austerops | Austerops speculator speculator | 386 | Large eyes | Middle shelf | Predator/Scavenger | 12.3a | ISCR | Alberti 1970a | =0,019762 | Emsian | Cranidium |
| Harpetida | Harpetidae | Harpes | Harpes hamarlaghdadensis | 387 | Small eyes | Middle shelf | Predator/Scavenger | 6b | PIMUZ 35192 | Crônier Oudot 2018 | =0,010941 | Emsian | Cranidium |
| Harpetida | Harpetidae | Harpes | Harpes hamarlaghdadensis | 388 | Small eyes | Middle shelf | Predator/Scavenger | 6h | PIMUZ 35194 | Crônier Oudot 2018 | =0,004433 | Emsian | Cranidium |
| Harpetida | Harpetidae | Harpes | Harpes hamarlaghdadensis | 389 | Small eyes | Middle shelf | Predator/Scavenger | 6m | PIMUZ 35196 | Crônier Oudot 2018 | =0,008929 | Emsian | Cranidium |
| Phacopida | Phacopidae | Boeckops | Boeckops maidericus | 390 | Large eyes | Middle shelf | Predator/Scavenger | 2.15a | CGMTA | Alberti 1983 | =0.028007 | Pragian | Cranidium |
| Phacopida | Phacopidae | Boeckops | Boeckops algericus | 391 | Large eyes | Middle shelf | Predator/Scavenger | 2.16a | SH | Alberti 1983 | =0.028007 | Pragian | Cranidium |
| Phacopida | Phacopidae | Boeckops | Boeckops algericus | 392 | Large eyes | Middle shelf | Predator/Scavenger | 2.17a | SH | Alberti 1983 | =0.031526 | Pragian | Cranidium |
| Phacopida | Phacopidae | Boeckops | Boeckops slimanensis | 393 | Large eyes | Middle shelf | Predator/Scavenger | 4.38 | SMF 36582 | Alberti 1983 | =0.008749 | Lochkovian | Cephalon |
| Phacopida | Phacopidae | Boeckops | Boeckops sp C | 394 | Large eyes | Middle shelf | Predator/Scavenger | 5k | | Khaldi 2016 | =0,029761 | Emsian | Cranidium |
| Phacopida | Phacopidae | Boeckops | Boeckops maidericus | 395 | Large eyes | Middle shelf | Predator/Scavenger | 8.96a | SMF 36621 | Alberti 1983 | =0.029187 | Pragian | Cranidium |
| Phacopida | Phacopidae | Boeckops | Boeckops stelcki | 396 | Large eyes | Middle shelf | Predator/Scavenger | 11.4 | UA 6897 | McKellar 2009 | =0,016854 | Emsian | Cephalon |
| Phacopida | Phacopidae | Boeckops | Boeckops slimanensis | 397 | Large eyes | Middle shelf | Predator/Scavenger | 16.9a | CGMTA 323 | Alberti 1970a | =0,018561 | Lochkovian | Cranidium |
| Phacopida | Phacopidae | Boeckops | Boeckops slimanensis | 398 | Large eyes | Middle shelf | Predator/Scavenger | 16.10a | CGMTA 322 | Alberti 1970a | =0,012725 | Lochkovian | Cephalon |
| Phacopida | Phacopidae | Denckmanites | Denckmannites miser | 399 | Small eyes | Deep | Predator/Scavenger | 16.1a | CGMTA 321 | Alberti 1970a | =0,019372 | Lochkovian | Blind |
| Phacopida | Phacopidae | Dianops | Dianops vicarius | 400 | Blind | Deep | Predator/Scavenger | 5b | MUA/1094/011 | Crônier 2013 | =0,032677 | Famennian | Cranidium |
| Phacopida | Phacopidae | Dianops | Dianops vicarius | 401 | Blind | Deep | Predator/Scavenger | 5e | MUA/1094/012 | Crônier 2013 | =0,035713 | Famennian | Cranidium |
| Phacopida | Phacopidae | Dianops | Dianops vicarius | 402 | Blind | Deep | Predator/Scavenger | 5j | MUA/1094/013 | Crônier 2013 | =0,032679 | Famennian | Cranidium |
| Phacopida | Phacopidae | Dianops | Dianops typhlops | 403 | Blind | Deep | Predator/Scavenger | 5m | MUA/1094/010 | Crônier 2013 | =0,037309 | Famennian | Cranidium |
| Phacopida | Phacopidae | Dianops | Indet | 404 | Blind | Deep | Predator/Scavenger | 6h | MUA/1094/004 | Crônier 2013 | =0,034719 | Famennian | Cranidium |
| Phacopida | Phacopidae | Dianops | Dianops algeriensis | 405 | Blind | Deep | Predator/Scavenger | 6p | MUA/1094/014 | Crônier 2013 | =0,043477 | Famennian | Cranidium |
| Phacopida | Phacopidae | Drotops | Drotops megalomanicus megalomanicus | 406 | Large eyes | Shallow | Predator/Scavenger | 1.1a | SMF 349340 | Struve 1995 | =0,058274 | Givetian | Cephalon |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phacopida | Phacopidae | Drotops | Drotops megalomanicus megalomanicus | 407 | Large eyes | Shallow | Predator/Scavenger | 1.2a | SMF 49357 | Struve 1995 | =0,066009 | Givetian | Cranidium |
| Phacopida | Phacopidae | Drotops | Drotops megalomanicus subornatus | 408 | Large eyes | Shallow | Predator/Scavenger | 1.3 | SMF 49354 | Struve 1995 | =0,065495 | Givetian | Cranidium |
| Phacopida | Phacopidae | Drotops | Drotops megalomanicus megalomanicus | 409 | Large eyes | Shallow | Predator/Scavenger | 2.4a | SMF 349341 | Struve 1995 | =0,058755 | Givetian | Cranidium |
| Phacopida | Phacopidae | Drotops | Drotops megalomanicus megalomanicus | 410 | Large eyes | Shallow | Predator/Scavenger | 2.5 | MB.T. 1948 | Struve 1995 | =0,059784 | Givetian | Cranidium |
| Phacopida | Phacopidae | Drotops | Drotops armatus | 411 | Large eyes | Shallow | Predator/Scavenger | 6.14a | Kat-Nr. 1011 | Struve 1995 | =0,099663 | Givetian | Cephalon |
| Phacopida | Phacopidae | Drotops | Drotops armatus | 412 | Large eyes | Shallow | Predator/Scavenger | 5.12a | | Struve 1995 | =0,057550 | Givetian | Cephalon |
| Phacopida | Phacopidae | Drotops | Drotops armatus | 413 | Large eyes | Shallow | Predator/Scavenger | 4.11a | SMF 49480/S GPIMH Nr. 3652 | Struve 1995 | =0,048508 | Givetian | Cephalon |
| Phacopida | Phacopidae | Drotops | Drotops armatus | 414 | Large eyes | Shallow | Predator/Scavenger | 6.15a | | Struve 1995 | =0,064712 | Givetian | Cranidium |
| Phacopida | Phacopidae | Drotops | Drotops megalomanicus megalomanicus | 415 | Large eyes | Shallow | Predator/Scavenger | Abb21 | MB.T. 1934 | Struve 1995 | =0,058154 | Givetian | Cranidium |
| Phacopida | Phacopidae | Eldredgeops | Eldredgeops tindoufensis | 416 | Large eyes | Inner shelf | Predator/Scavenger | 47.3 | USNM 174073 | Burton 1974 | =0,104998 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Eophacops | Eophacops bulliceps | 417 | Large eyes | Middle shelf | Predator/Scavenger | 11.4 | CGMTA 332 | Alberti 1970a | =0,009095 | Ludlow-Pridoli | Cephalon |
| Phacopida | Phacopidae | Eophacops | Eophacops bulliceps | 418 | Large eyes | Middle shelf | Predator/Scavenger | 11.5 | CGMTA 333 | Alberti 1970a | =0,011284 | Ludlow-Pridoli | Cranidium |
| Phacopida | Phacopidae | Houseops | Houseops cryphoïdes | 419 | Small eyes | Deep | Predator/Scavenger | 3m | MUA/1094/006 | Crônier 2013 | =0,046727 | Famennian | Cranidium |
| Phacopida | Phacopidae | Hypsipariops | Hypsipariops vagabundus | 420 | Large eyes | Middle shelf | Predator/Scavenger | 8.23a | SMF 49402 | Struve 1995 | =0,059176 | Givetian | Cephalon |
| Phacopida | Phacopidae | Hypsipariops | Hypsipariops vagabundus | 421 | Large eyes | Middle shelf | Predator/Scavenger | 8.24a | SMF 49368 | Struve 1995 | =0,059923 | Givetian | Cranidium |
| Phacopida | Phacopidae | Hypsipariops | Hypsipariops vagabundus | 422 | Large eyes | Middle shelf | Predator/Scavenger | 9.28a | SMF 49403 | Struve 1995 | =0,059724 | Givetian | Cephalon |
| Phacopida | Phacopidae | Hypsipariops | Hypsipariops vagabundus | 423 | Large eyes | Middle shelf | Predator/Scavenger | 9.30a | SMF 49370 | Struve 1995 | =0,059062 | Givetian | Cranidium |
| Phacopida | Phacopidae | Hypsipariops | Hypsipariops vagabundus | 424 | Large eyes | Middle shelf | Predator/Scavenger | 48.4 | In 57166 | Burton 1974 | =0,104829 | Givetian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops granulops | 425 | Large eyes | Inner shelf | Predator/Scavenger | 2.5 | UA 13299 | Chatterton 2006 | =0,081844 | Emsian | Cranidium |
| Phacopida | Phacopidae | Morocops | Morocops granulops | 426 | Large eyes | Inner shelf | Predator/Scavenger | 2.8 | UA 13302 | Chatterton 2006 | =0,132123 | Emsian | Cranidium |
| Phacopida | Phacopidae | Morocops | Moroccops tafilaltanus | 427 | Large eyes | Inner shelf | Predator/Scavenger | 2.12a | CGMTA | Alberti 1983 | =0.024871 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops lebesus | 428 | Large eyes | Inner shelf | Predator/Scavenger | 3.1 | UA 13303 | Chatterton 2006 | =0,094946 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops lebesus | 429 | Large eyes | Inner shelf | Predator/Scavenger | 3.5 | UA 13304 | Chatterton 2006 | =0,044970 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Morocops | Morocops lebesus | 430 | Large eyes | Inner shelf | Predator/Scavenger | 3.8 | UA 13305 | Chatterton 2006 | =0,074292 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops granulops | 431 | Large eyes | Inner shelf | Predator/Scavenger | 3a | Di/UO/028 | Khaldi 2016 | =0,073521 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops granulops | 432 | Large eyes | Inner shelf | Predator/Scavenger | 3e | Di/UO/027 | Khaldi 2016 | =0,048075 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops granulops | 433 | Large eyes | Inner shelf | Predator/Scavenger | 3i | Di/UO/034 | Khaldi 2016 | =0,098020 | Emsian | Cranidium |
| Phacopida | Phacopidae | Morocops | Morocops granulops | 434 | Large eyes | Inner shelf | Predator/Scavenger | 3m | GFCL 405 | Khaldi 2016 | =0,076887 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops chattertoni | 435 | Large eyes | Inner shelf | Predator/Scavenger | 4d | Di/UO/002 | Khaldi 2016 | =0,040317 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops sp F | 436 | Large eyes | Inner shelf | Predator/Scavenger | 7k | MU-G-Sr.Tr.A4/Ph111 | Crônier Abbache 2018 | =0,090867 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops sparsinodosus struvei | 437 | Large eyes | Inner shelf | Predator/Scavenger | 8p | SMF 57112 | Schraut 2000a | =0.041375 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Morocops | Morocops ovatus | 438 | Large eyes | Inner shelf | Predator/Scavenger | 13.1 | UA 6909 | McKellar 2009 | =0,029954 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops ovatus | 439 | Large eyes | Inner shelf | Predator/Scavenger | 13.5 | UA 6910 | McKellar 2009 | =0,012607 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops ovatus | 440 | Large eyes | Inner shelf | Predator/Scavenger | 13.8 | UA 6913 | McKellar 2009 | =0,013091 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops forteyi | 441 | Large eyes | Inner shelf | Predator/Scavenger | 15.1 | UA 6926 | McKellar 2009 | =0,018943 | Emsian | Cranidium |
| Phacopida | Phacopidae | Morocops | Morocops forteyi | 442 | Large eyes | Inner shelf | Predator/Scavenger | 15.4 | UA 6932 | McKellar 2009 | =0,019821 | Emsian | Cephalon |
| Phacopida | Phacopidae | Morocops | Morocops granulops | 443 | Large eyes | Inner shelf | Predator/Scavenger | 2A3 | PIMUZ 27077 | Klug 2009 | =0,008504 | Emsian | Cranidium |
| Phacopida | Phacopidae | PHACOPINAE | Indet | 444 | Large eyes | Middle shelf | Predator/Scavenger | 2.11a | CGMTA | Alberti 1983 | =0.028007 | Eifelian | Cranidium |
| Phacopida | Phacopidae | PHACOPINAE | Indet | 445 | Large eyes | Middle shelf | Predator/Scavenger | 2.13a | CGMTA | Alberti 1983 | =0.028007 | Pragian | Cranidium |
| Phacopida | Phacopidae | Phacops | Phacops sensu lato sp A | 446 | Large eyes | Middle shelf | Predator/Scavenger | 3n | Di/UO/032 | Khaldi 2016 | =0,062480 | Emsian | Cranidium |

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| Phacopida | Phacopidae | Phacops | Phacops sensu lato sp B | 447 | Large eyes | Middle shelf | Predator/Scavenger | 5b | Di/UO/035 | Khaldi 2016 | =0,101956 | Emsian | Cephalon |
| Phacopida | Phacopidae | Phacops | Phacops ouarouroutensis ouarouroutensis | 448 | Large eyes | Middle shelf | Predator/Scavenger | 6b | MU-G-Sr.Tr.S7/Ph032 | Crônier Abbache 2018 | =0,039986 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Phacops | Phacops ouarouroutensis ouarouroutensis | 449 | Large eyes | Middle shelf | Predator/Scavenger | 6e | MU-G-Sr.Tr.S4/Ph064 | Crônier Abbache 2018 | =0,046869 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Phacops | Phacops ouarouroutensis ouarouroutensis | 450 | Large eyes | Middle shelf | Predator/Scavenger | 6i | MU-G-Sr.Tr.S7/Ph001 | Crônier Abbache 2018 | =0,062486 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Phacops | Phacops ouarouroutensis ouarouroutensis | 451 | Large eyes | Middle shelf | Predator/Scavenger | 6m | MU-G-Sr.Tr.S7/Ph036 | Crônier Abbache 2018 | =0,090867 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Phacops | Phacops ouarouroutensis ouarouroutensis | 452 | Large eyes | Middle shelf | Predator/Scavenger | 6p | MU-G-Sr.Tr.S4/Ph050 | Crônier Abbache 2018 | =0,081051 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Phacops | Phacops sp E | 453 | Large eyes | Middle shelf | Predator/Scavenger | 7b | MU-G-Sr.Tr.A4/Ph124 | Crônier Abbache 2018 | =0,066650 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Phacops | Phacops sp E | 454 | Large eyes | Middle shelf | Predator/Scavenger | 7f | MU-G-Sr.Tr.A4/Ph074 | Crônier Abbache 2018 | =0,088197 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Phacops | Phacops ouarouroutensis ouarouroutensoides | 455 | Large eyes | Middle shelf | Predator/Scavenger | 7n | MU-G-Sr.Tr.A2/Ph156 | Crônier Abbache 2018 | =0,046869 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Phacops | Phacops ouarouroutensis ouarouroutensoides | 456 | Large eyes | Middle shelf | Predator/Scavenger | 7r | MU-G-Sr.Tr.A2/Ph165 | Crônier Abbache 2018 | =0,065156 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Phacops | Phacops ouarouroutensis ouarouroutensoides | 457 | Large eyes | Middle shelf | Predator/Scavenger | 7t | MU-G-Sr.Tr.A2/Ph166 | Crônier Abbache 2018 | =0,078920 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Adrisiops | Adrisiops fabrei | 458 | Large eyes | Middle shelf | Predator/Scavenger | 48.5 | ULL 256 d 49 | Burton 1974 | =0,060076 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Plagiolaria | Plagiolaria senex | 459 | Small eyes | Deep | Predator/Scavenger | 8.90a | SH | Alberti 1983 | =0.019434 | Pragian | Cranidium |
| Phacopida | Phacopidae | Plagiolaria | Plagiolaria senex | 460 | Small eyes | Deep | Predator/Scavenger | 8.91 | SH | Alberti 1983 | =0.021832 | Pragian | Cranidium |
| Phacopida | Phacopidae | Prokops | Prokops chlupaci | 461 | Large eyes | Middle shelf | Predator/Scavenger | 4.31a | SH | Alberti 1983 | =0.029187 | Pragian | Cranidium |
| Phacopida | Phacopidae | Prokops | Prokops chlupaci | 462 | Large eyes | Middle shelf | Predator/Scavenger | 4.32a | SH | Alberti 1983 | =0.026021 | Pragian | Cranidium |
| Phacopida | Phacopidae | Prokops | Prokops chlupaci | 463 | Large eyes | Middle shelf | Predator/Scavenger | 4.33 | SH | Alberti 1983 | =0.031526 | Pragian | Cranidium |
| Phacopida | Phacopidae | Prokops | Prokops chlupaci | 464 | Large eyes | Middle shelf | Predator/Scavenger | 4.35 | SH | Alberti 1983 | =0.026021 | Pragian | Cranidium |
| Phacopida | Phacopidae | Prokops | Prokops benziregensis ezzhiligensis | 465 | Large eyes | Middle shelf | Predator/Scavenger | 18.1a | CGMTA 329 | Alberti 1970a | =0,016029 | Lochkovian | Cephalon |
| Phacopida | Phacopidae | Prokops | Prokops benziregensis ezzhiligensis | 466 | Large eyes | Middle shelf | Predator/Scavenger | 18.2a | CGMTA 330 | Alberti 1970a | =0,022725 | Lochkovian | Cranidium |
| Phacopida | Phacopidae | Prokops | Prokops benziregensis benziregensis | 467 | Large eyes | Middle shelf | Predator/Scavenger | 4.40 | SH | Alberti 1983 | =0.014140 | Pragian | Cranidium |
| Phacopida | Phacopidae | Prokops | Prokops benziregensis benziregensis | 468 | Large eyes | Middle shelf | Predator/Scavenger | 8.88a | SH | Alberti 1983 | =0.009214 | Pragian | Cranidium |
| Phacopida | Phacopidae | Prokops | Prokops benziregensis ezzhiligensis | 469 | Large eyes | Middle shelf | Predator/Scavenger | 16.14a | CGMTA 328 | Alberti 1970a | =0,012259 | Pragian | Cranidium |
| Phacopida | Phacopidae | Prokops | Prokops benziregensis ezzhiligensis | 470 | Large eyes | Middle shelf | Predator/Scavenger | 16.15 | SMF 23524 | Alberti 1970a | =0,015009 | Pragian | Cephalon |
| Phacopida | Phacopidae | Prokops | Prokops benziregensis ezzhiligensis | 471 | Large eyes | Middle shelf | Predator/Scavenger | 42.13 | CGMTA | Alberti 1969 | =0,012935 | Pragian | Cranidium |
| Phacopida | Phacopidae | Reedops | Reedops bronni | 472 | Large eyes | Inner shelf | Predator/Scavenger | 1.9 | UA 6843 | McKellar 2009 | =0,014485 | Pragian | Cephalon |
| Phacopida | Phacopidae | Reedops | Reedops cephalotes hamlagdadianus | 473 | Large eyes | Inner shelf | Predator/Scavenger | 2.1 | UA 6848 | McKellar 2009 | =0,023115 | Pragian | Cephalon |
| Phacopida | Phacopidae | Reedops | Reedops cephalotes hamlagdadianus | 474 | Large eyes | Inner shelf | Predator/Scavenger | 2.4 | UA 6848 | McKellar 2009 | =0,023115 | Pragian | Cranidium |
| Phacopida | Phacopidae | Reedops | Reedops cephalotes hamlagdadianus | 475 | Large eyes | Inner shelf | Predator/Scavenger | 2.9 | UA 6861 | McKellar 2009 | =0,023115 | Pragian | Cephalon |
| Phacopida | Phacopidae | Reedops | Reedops cephalotes hamlagdadianus | 476 | Large eyes | Inner shelf | Predator/Scavenger | 3.11 | UA 6851 | McKellar 2009 | =0,017547 | Pragian | Cephalon |
| Phacopida | Phacopidae | Reedops | Reedops cephalotes hamlagdadianus | 477 | Large eyes | Inner shelf | Predator/Scavenger | 3.21a | CGMTA | Alberti 1983 | =0.026021 | Pragian | Cranidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phacopida | Phacopidae | Reedops | Reedops cephalotes hamlagdadianus | 478 | Large eyes | Inner shelf | Predator/Scavenger | 3.22 | CGMTA | Alberti 1983 | =0.026021 | Pragian | Cranidium |
| Phacopida | Phacopidae | Reedops | Reedops cephalotes hamlagdadianus | 479 | Large eyes | Inner shelf | Predator/Scavenger | 3.23a | CGMTA | Alberti 1983 | =0.031502 | Pragian | Cranidium |
| Phacopida | Phacopidae | Reedops | Reedops cephalotes hamlagdadianus | 480 | Large eyes | Inner shelf | Predator/Scavenger | 3.24a | Coll. Lierl (Hamburg) | Alberti 1983 | =0.031502 | Pragian | Cephalon |
| Phacopida | Phacopidae | Reedops | Reedops cephalotes hamlagdadianus | 481 | Large eyes | Inner shelf | Predator/Scavenger | 3.25 | SMF 32498 | Alberti 1983 | =0.029187 | Pragian | Cranidium |
| Phacopida | Phacopidae | Reedops | Reedops cephalotes hamlagdadianus | 482 | Large eyes | Inner shelf | Predator/Scavenger | 3.26 | SMF 36580 | Alberti 1983 | =0.034545 | Pragian | Cranidium |
| Phacopida | Phacopidae | Reedops | Reedops cephalotes algericanus | 483 | Large eyes | Inner shelf | Predator/Scavenger | 3.27a | SH | Alberti 1983 | =0.026021 | Pragian | Cranidium |
| Phacopida | Phacopidae | Reedops | Reedops cephalotes algericanus | 484 | Large eyes | Inner shelf | Predator/Scavenger | 3.28a | SH | Alberti 1983 | =0.028007 | Pragian | Cranidium |
| Phacopida | Phacopidae | Reedops | Reedops pembertoni | 485 | Large eyes | Inner shelf | Predator/Scavenger | 4.10 | UA 6862 | McKellar 2009 | =0,014815 | Pragian | Cephalon |
| Phacopida | Phacopidae | Reedops | Reedops struveianus | 486 | Large eyes | Inner shelf | Predator/Scavenger | 4.29 | SH | Alberti 1983 | =0.028007 | Pragian | Cranidium |
| Phacopida | Phacopidae | Reedops | Reedops pembertoni | 487 | Large eyes | Inner shelf | Predator/Scavenger | 5.4 | UA 6863 | McKellar 2009 | =0,015113 | Pragian | Cephalon |
| Phacopida | Phacopidae | Reedops | Reedops cephalotes hamlagdadianus | 488 | Large eyes | Inner shelf | Predator/Scavenger | 7.81a | SMF 36602 | Alberti 1983 | =0.028219 | Pragian | Cranidium |
| Phacopida | Phacopidae | Reedops | Reedops cephalotes cephalotes | 489 | Large eyes | Inner shelf | Predator/Scavenger | 14.1a | CGMTA 313 | Alberti 1970a | =0,027185 | Pragian | Cranidium |
| Phacopida | Phacopidae | Reedops | Reedops bronni | 490 | Large eyes | Inner shelf | Predator/Scavenger | 14.3a | CGMTA 312 | Alberti 1970a | =0,014709 | Pragian | Cranidium |
| Phacopida | Phacopidae | Reedops | Reedops bronni | 491 | Large eyes | Inner shelf | Predator/Scavenger | 14.4a | SMF 23513 | Alberti 1970a | =0,019785 | Pragian | Cranidium |
| Phacopida | Phacopidae | Reedops | Reedops intermedius chlupaci | 492 | Large eyes | Inner shelf | Predator/Scavenger | 14.5a | CGMTA 314 | Alberti 1970a | =0,027185 | Pragian | Cephalon |
| Phacopida | Phacopidae | Reedops | Reedops sternbergi | 493 | Large eyes | Inner shelf | Predator/Scavenger | 14.6a | CGMTA 315 | Alberti 1970a | =0,022044 | Pragian | Cranidium |
| Phacopida | Phacopidae | Reedops | Reedops maurulus | 494 | Large eyes | Inner shelf | Predator/Scavenger | 15.1a | CGMTA 319 | Alberti 1970a | =0,028952 | Pragian | Cranidium |
| Phacopida | Phacopidae | Reedops | Reedops maurulus | 495 | Large eyes | Inner shelf | Predator/Scavenger | 15.2a | SMF 23516 | Alberti 1970a | =0,011608 | Pragian | Cranidium |
| Phacopida | Phacopidae | Reedops | Reedops maurulus | 496 | Large eyes | Inner shelf | Predator/Scavenger | 15.3a | CGMTA 320 | Alberti 1970a | =0,016014 | Pragian | Cranidium |
| Phacopida | Phacopidae | Reedops | Reedops maurulus | 497 | Large eyes | Inner shelf | Predator/Scavenger | 15.7 | CGMTA 318 | Alberti 1970a | =0,015067 | Pragian | Cranidium |
| Phacopida | Phacopidae | Reedops | Reedops maurulus | 498 | Large eyes | Inner shelf | Predator/Scavenger | 15.8a | SMF 23515 | Alberti 1970a | =0,015067 | Pragian | Cranidium |
| Phacopida | Phacopidae | Reedops | Reedops maurulus | 499 | Large eyes | Inner shelf | Predator/Scavenger | 15.9a | CGMTA 317 | Alberti 1970a | =0,026065 | Pragian | Cranidium |
| Phacopida | Phacopidae | Struveaspis | Struveaspis maroccanica | 500 | Large eyes | Middle shelf | Predator/Scavenger | 3b | MU-G-SR.Tr.S7/Ph024 | Crônier Abbache 2018 | =0,047613 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Struveaspis | Struveaspis maroccanica | 501 | Large eyes | Middle shelf | Predator/Scavenger | 3f | MU-G-SR.Tr.S7/Ph004 | Crônier Abbache 2018 | =0,085679 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Struveaspis | Struveaspis maroccanica | 502 | Large eyes | Middle shelf | Predator/Scavenger | 3i | MU-G-SR.Tr.S4/Ph065 | Crônier Abbache 2018 | =0,031577 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Struveaspis | Struveaspis maroccanica | 503 | Large eyes | Middle shelf | Predator/Scavenger | 3l | MU-G-SR.Tr.S4/Ph150 | Crônier Abbache 2018 | =0,074906 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Struveaspis | Struveaspis maroccanica | 504 | Large eyes | Middle shelf | Predator/Scavenger | 6.64a | LGFSSA | Alberti 1981a | =0.084400 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Struveaspis | Struveaspis maroccanica | 505 | Large eyes | Middle shelf | Predator/Scavenger | 13.1a | SMF 23561 | Alberti 1970a | =0,011396 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Struveaspis | Struveaspis maroccanica | 506 | Large eyes | Middle shelf | Predator/Scavenger | 13.2a | GCGMTA 331 | Alberti 1970a | =0,020908 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Struveaspis | Struveaspis maroccanica | 507 | Large eyes | Middle shelf | Predator/Scavenger | 13.3a | SMF 23562 | Alberti 1970a | =0,019335 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Struveaspis | Struveaspis maroccanica | 508 | Large eyes | Middle shelf | Predator/Scavenger | 13.4a | CGMTA 8 | Alberti 1970a | =0,016382 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Trifoliops | Trifoliops nigritus | 509 | Blind | Deep | Predator/Scavenger | 3d | MUA/1094/008 | Crônier 2013 | =0,044636 | Famennian | Cranidium |
| Phacopida | Phacopidae | Trifoliops | Trifoliops trifolius | 510 | Blind | Deep | Predator/Scavenger | 5e | UM-IP 722 | Feist 2016 | =0,027387 | Famennian | Blind |
| Phacopida | Phacopidae | Trimerocephalus | Trimerocephalus lelievrei | 511 | Blind | Deep | Predator/Scavenger | 1.1b | UM2-CCt26 | Crônier 1997 | =0,017863 | Famennian | Blind |
| Phacopida | Phacopidae | Trimerocephalus | Trimerocephalus lelievrei | 512 | Blind | Deep | Predator/Scavenger | 1.6 | UM2-CCt48 | Crônier 1997 | =0,007911 | Famennian | Cranidium |
| Phacopida | Phacopidae | Trimerocephalus | Trimerocephalus caecus | 513 | Blind | Deep | Predator/Scavenger | 3a | MUA/1094/007 | Crônier 2013 | =0,037878 | Famennian | Cranidium |
| Phacopida | Phacopidae | Trimerocephalus | Trimerocephalus mahboubii | 514 | Blind | Deep | Predator/Scavenger | 4a | UM-IP 718 | Feist 2016 | =0,052613 | Famennian | Blind |
| Phacopida | Phacopidae | Trimerocephalus | Trimerocephalus mahboubii | 515 | Blind | Deep | Predator/Scavenger | 4c | UM-IP 719 | Feist 2016 | =0,074023 | Famennian | Blind |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phacopida | Phacopidae | Trimerocephalus | Trimerocephalus mahboubii | 516 | Blind | Deep | Predator/Scavenger | 4j | UM-IP 720 | Feist 2016 | =0,043437 | Famennian | Blind |
| Phacopida | Phacopidae | Trimerocephalus | Trimerocephalus caecus | 517 | Blind | Deep | Predator/Scavenger | 4l | UM-IP 721 | Feist 2016 | =0,016391 | Famennian | Cranidium |
| Phacopida | Phacopidae | Chotecops | Chotecops zizensis | 518 | Large eyes | Middle shelf | Predator/Scavenger | 2.13 | UM2 - RF 162 | Feist 2000 | =0.016246 | Eifelian | Cephalon |
| Phacopida | Phacopidae | Chotecops | Chotecops zizensis | 519 | Large eyes | Middle shelf | Predator/Scavenger | 2.14a | CGMTA | Alberti 1983 | =0.024660 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Chotecops | Chotecops hoseri | 520 | Large eyes | Middle shelf | Predator/Scavenger | 4d | MU-G-Sr.Tr.A6/Ph008 | Crônier Abbache 2018 | =0,090867 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Chotecops | Chotecops hoseri | 521 | Large eyes | Middle shelf | Predator/Scavenger | 4i | MU-G-Sr.Tr.A6/Ph013 | Crônier Abbache 2018 | =0,076898 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Chotecops | Chotecops hoseri | 522 | Large eyes | Middle shelf | Predator/Scavenger | 5e | | Crônier Abbache 2018 | =0,107075 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Chotecops | Chotecops hoseri | 523 | Large eyes | Middle shelf | Predator/Scavenger | 5h | | Crônier Abbache 2018 | =0,041663 | Eifelian | Cranidium |
| Phacopida | Phacopidae | Chotecops | Chotecops hoseri | 524 | Large eyes | Middle shelf | Predator/Scavenger | 5m | | Crônier Abbache 2018 | =0,066601 | Eifelian | Cephalon |
| Proetida | Proetidae | Buchiproetus | Buchiproetus pribyli pribyli | 525 | Large eyes | Middle shelf | Predator/Scavenger | 2.8a | CGMTA 41 | Alberti 1981a | =0.033893 | Pragian | Cranidium |
| Proetida | Proetidae | Buchiproetus | Buchiproetus rudrichteri | 526 | Large eyes | Middle shelf | Predator/Scavenger | 3.u | UM-IP 822 | Feist 2018 | =0,005376 | Emsian | Cranidium |
| Proetida | Proetidae | Buchiproetus | Buchiproetus mauretanicus | 527 | Large eyes | Middle shelf | Predator/Scavenger | 9.2a | SMF 23124 | Alberti 1969 | =0,013727 | Pragian | Cranidium |
| Proetida | Proetidae | Buchiproetus | Buchiproetus mauretanicus | 528 | Large eyes | Middle shelf | Predator/Scavenger | 9.3a | CGMTA 42 | Alberti 1969 | =0,013305 | Pragian | Cranidium |
| Proetida | Proetidae | Buchiproetus | Buchiproetus mauretanicus | 529 | Large eyes | Middle shelf | Predator/Scavenger | 9.4 | SMF 23125 | Alberti 1969 | =0,017389 | Pragian | Cranidium |
| Proetida | Proetidae | Buchiproetus | Buchiproetus mauretanicus | 530 | Large eyes | Middle shelf | Predator/Scavenger | 9.5a | SMF 23126 | Alberti 1969 | =0,014012 | Pragian | Cranidium |
| Proetida | Proetidae | Buchiproetus | Buchiproetus mauretanicus | 531 | Large eyes | Middle shelf | Predator/Scavenger | 9.6a | CGMTA 43 | Alberti 1969 | =0,011731 | Pragian | Cranidium |
| Proetida | Proetidae | Buchiproetus | Buchiproetus mauretanicus | 532 | Large eyes | Middle shelf | Predator/Scavenger | 9.7a | SMF 23127 | Alberti 1969 | =0,015169 | Pragian | Cranidium |
| Proetida | Proetidae | Buchiproetus | Buchiproetus mauretanicus | 533 | Large eyes | Middle shelf | Predator/Scavenger | 9.8a | SMF 23128 | Alberti 1969 | =0,012032 | Pragian | Cranidium |
| Proetida | Proetidae | Buchiproetus | Buchiproetus mauretanicus | 534 | Large eyes | Middle shelf | Predator/Scavenger | 9.9a | SMF 23129 | Alberti 1969 | =0,012032 | Pragian | Cranidium |
| Proetida | Proetidae | Buchiproetus | Buchiproetus pribyli pribyli | 535 | Large eyes | Middle shelf | Predator/Scavenger | 9.13a | CGMTA 40 | Alberti 1969 | =0,015503 | Pragian | Cranidium |
| Proetida | Proetidae | Buchiproetus | Buchiproetus pribyli pribyli | 536 | Large eyes | Middle shelf | Predator/Scavenger | 9.14 | SMF 23118 | Alberti 1969 | =0,008316 | Pragian | Cranidium |
| Proetida | Proetidae | Buchiproetus | Buchiproetus pribyli pribyli | 537 | Large eyes | Middle shelf | Predator/Scavenger | 9.15a | SMF 23119 | Alberti 1969 | =0,008560 | Pragian | Cranidium |
| Proetida | Proetidae | Buchiproetus | Buchiproetus mauretanicus | 538 | Large eyes | Middle shelf | Predator/Scavenger | a.2 | SMF 23124 | Alberti 1967a | =0.014160 | Pragian | Cranidium |
| Proetida | Proetidae | Coniproetus | Coniproetus finitimus tenuigranifer | 539 | Large eyes | Inner shelf | Predator/Scavenger | 4.2a | CGMTA 187 | Alberti 1969 | =0,020711 | Pragian | Cranidium |
| Proetida | Proetidae | Coniproetus | Coniproetus condensus mesembrinus | 540 | Large eyes | Inner shelf | Predator/Scavenger | 4.3a | CGMTA 16 | Alberti 1969 | =0,012781 | Pragian | Cranidium |
| Proetida | Proetidae | Coniproetus | Coniproetus eurysthenes nomas | 541 | Large eyes | Inner shelf | Predator/Scavenger | 4.5a | CGMT-TM 132 | Alberti 1969 | =0,014208 | Pragian | Cranidium |
| Proetida | Proetidae | Coniproetus | Indet | 542 | Large eyes | Inner shelf | Predator/Scavenger | b.3 | CGMTA 180 | Alberti 1967b | =0,008507 | Emsian | Cranidium |
| Proetida | Proetidae | PROETINAE | Indet | 543 | Large eyes | Inner shelf | Predator/Scavenger | 4.1a | CGMTA 180 | Alberti 1969 | =0,013686 | Emsian | Cranidium |
| Proetida | Proetidae | Coniproetus | Coniproetus foucauldi | 544 | Large eyes | Inner shelf | Predator/Scavenger | 4.4a | ISCR | Alberti 1969 | =0,008157 | Lochkovian | Cranidium |
| Proetida | Proetidae | Cornuproetus | Cornuproetus sp A | 545 | Large eyes | Middle shelf | Predator/Scavenger | 1.4 | No name | Alberti 1966c | =0,003343 | | Cranidium |
| Proetida | Proetidae | Cornuproetus | Cornuproetus cornutus djemelensis | 546 | Large eyes | Middle shelf | Predator/Scavenger | 1.5a | GPIH | Alberti 1981a | =0.025873 | Emsian | Cranidium |
| Proetida | Proetidae | Cornuproetus | Cornuproetus pusulosus | 547 | Large eyes | Middle shelf | Predator/Scavenger | 3.w | UM-IP 820 | Feist 2018 | =0,009801 | Emsian | Cranidium |
| Proetida | Proetidae | Cornuproetus | Cornuproetus cornutus nssp A | 548 | Large eyes | Middle shelf | Predator/Scavenger | 4.3 | CGMTA 241 | Alberti 1970a | =0,005166 | Givetian | Cranidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Proetida | Proetidae | Cornuproetus | Cornuproetus cornutus marrakechensis | 549 | Large eyes | Middle shelf | Predator/Scavenger | 7.11 | CGMTA 28 | Alberti 1969 | =0,009958 | Eifelian | Cranidium |
| Proetida | Proetidae | Cornuproetus | Cornuproetus cornutus marrakechensis | 550 | Large eyes | Middle shelf | Predator/Scavenger | 7.12a | SMF 23093 | Alberti 1969 | =0,008831 | Eifelian | Cranidium |
| Proetida | Proetidae | Cornuproetus | Cornuproetus cornutus djemelensis | 551 | Large eyes | Middle shelf | Predator/Scavenger | 7m | Di/UO/011 | Khaldi 2016 | =0,059507 | Emsian | Cranidium |
| Proetida | Proetidae | Cornuproetus | Cornuproetus cornutus djemelensis | 552 | Large eyes | Middle shelf | Predator/Scavenger | 8f | Di/UO/037 | Khaldi 2016 | =0,073521 | Emsian | Cephalon |
| Proetida | Proetidae | Cornuproetus | Cornuproetus walliseri | 553 | Large eyes | Middle shelf | Predator/Scavenger | 9.1a | CGMTA 28 | Alberti 1969 | =0,005213 | | Cranidium |
| Proetida | Proetidae | Cornuproetus | Cornuproetus rudrichteri | 554 | Large eyes | Middle shelf | Predator/Scavenger | 9.11a | SMF 23122 | Alberti 1969 | =0,012058 | Pragian | Cranidium |
| Proetida | Proetidae | Cornuproetus | Cornuproetus taciturnus nssp A | 555 | Large eyes | Middle shelf | Predator/Scavenger | 9.12a | SMF 23186 | Alberti 1969 | =0,016807 | Pragian | Cranidium |
| Proetida | Proetidae | Cornuproetus | Cornuproetus taciturnus | 556 | Large eyes | Middle shelf | Predator/Scavenger | 10.1a | SMF 23132 | Alberti 1969 | =0,017012 | Pragian | Cranidium |
| Proetida | Proetidae | Cornuproetus | Cornuproetus taciturnus | 557 | Large eyes | Middle shelf | Predator/Scavenger | 10.2a | SMF 23133 | Alberti 1969 | =0,017012 | Pragian | Cranidium |
| Proetida | Proetidae | Cornuproetus | Cornuproetus taciturnus | 558 | Large eyes | Middle shelf | Predator/Scavenger | 10.3a | SMF 23134 | Alberti 1969 | =0,014847 | Pragian | Cranidium |
| Proetida | Proetidae | Cornuproetus | Cornuproetus taciturnus | 559 | Large eyes | Middle shelf | Predator/Scavenger | 10.4 | CGMTA 45 | Alberti 1969 | =0,019028 | Pragian | Cranidium |
| Proetida | Proetidae | Cornuproetus | Cornuproetus pernix pernix | 560 | Large eyes | Middle shelf | Predator/Scavenger | 10.5a | SMF 23111 | Alberti 1969 | =0,021412 | Pragian | Cranidium |
| Proetida | Proetidae | Cornuproetus | Cornuproetus pernix pernix | 561 | Large eyes | Middle shelf | Predator/Scavenger | 10.6a | SMF 23112 | Alberti 1969 | =0,011384 | Pragian | Cranidium |
| Proetida | Proetidae | Cornuproetus | Cornuproetus rudrichteri | 562 | Large eyes | Middle shelf | Predator/Scavenger | a.4 | SMF 23122 | Alberti 1967a | =0.012563 | Pragian | Cranidium |
| Proetida | Proetidae | Paralepidoproetus | Paralepidoproetus fauremuretae | 563 | Large eyes | Middle shelf | Predator/Scavenger | Doublon_ | SMF 23115 | Alberti 1969 | =0,010668 | | Cranidium |
| Proetida | Proetidae | Paralepidoproetus | Paralepidoproetus fauremuretae | 564 | Large eyes | Middle shelf | Predator/Scavenger | Doublon_ | CGMTA 38 | Alberti 1969 | =0,009894 | | Cranidium |
| Proetida | Proetidae | Cornuproetus | Indet | 565 | Large eyes | Middle shelf | Predator/Scavenger | Crônier_2 | PIMUZ 35177 | Crônier Oudot 2018 | =0,008665 | Emsian | Cranidium |
| Proetida | Proetidae | Cyrtosymbole | Cyrtosymbole rectifrons | 566 | Large eyes | Middle shelf | Predator/Scavenger | 1.2 | UMC-IP 434 | Lerosey-Aubril 2006 | =0,001886 | Famennian | Cranidium |
| Proetida | Proetidae | Cyrtosymbole | Cyrtosymbole rectifrons | 567 | Large eyes | Middle shelf | Predator/Scavenger | 1.3 | UMC-IP 435 | Lerosey-Aubril 2006 | =0,002809 | Famennian | Cranidium |
| Proetida | Proetidae | Cyrtosymbole | Cyrtosymbole rectifrons | 568 | Large eyes | Middle shelf | Predator/Scavenger | 1.4 | UMC-IP 436 | Lerosey-Aubril 2006 | =0,002841 | Famennian | Cranidium |
| Proetida | Proetidae | Cyrtosymbole | Cyrtosymbole rectifrons | 569 | Large eyes | Middle shelf | Predator/Scavenger | 1.5 | UMC-IP 437 | Lerosey-Aubril 2006 | =0,003597 | Famennian | Cranidium |
| Proetida | Proetidae | Cyrtosymbole | Cyrtosymbole rectifrons | 570 | Large eyes | Middle shelf | Predator/Scavenger | 1.6 | UMC-IP 438 | Lerosey-Aubril 2006 | =0,004424 | Famennian | Cranidium |
| Proetida | Proetidae | Cyrtosymbole | Cyrtosymbole rectifrons | 571 | Large eyes | Middle shelf | Predator/Scavenger | 1.7 | UMC-IP 439 | Lerosey-Aubril 2006 | =0,004672 | Famennian | Cranidium |
| Proetida | Proetidae | Cyrtosymbole | Cyrtosymbole rectifrons | 572 | Large eyes | Middle shelf | Predator/Scavenger | 1.8 | UMC-IP 440 | Lerosey-Aubril 2006 | =0,004672 | Famennian | Cranidium |
| Proetida | Proetidae | Cyrtosymbole | Cyrtosymbole rectifrons | 573 | Large eyes | Middle shelf | Predator/Scavenger | 1.9 | UMC-IP 441 | Lerosey-Aubril 2006 | =0,005100 | Famennian | Cranidium |
| Proetida | Proetidae | Cyrtosymbole | Cyrtosymbole rectifrons | 574 | Large eyes | Middle shelf | Predator/Scavenger | 1.10 | UMC-IP 442 | Lerosey-Aubril 2006 | =0,005263 | Famennian | Cranidium |
| Proetida | Proetidae | Cyrtosymbole | Cyrtosymbole rectifrons | 575 | Large eyes | Middle shelf | Predator/Scavenger | 1.11 | UMC-IP 443 | Lerosey-Aubril 2006 | =0,004715 | Famennian | Cranidium |
| Proetida | Proetidae | Cyrtosymbole | Cyrtosymbole sp A | 576 | Large eyes | Middle shelf | Predator/Scavenger | 2.32 | UMC-IP 486 | Lerosey-Aubril 2006 | =0,004347 | Famennian | Cranidium |
| Proetida | Proetidae | Cyrtosymboloides | Cyrtosymboloides samum | 577 | Large eyes | Middle shelf | Predator/Scavenger | 5.9a | CGMTA 260 | Alberti 1970a | =0,006258 | Eifelian | Cranidium |
| Proetida | Proetidae | Cyrtosymboloides | Cyrtosymboloides samum | 578 | Large eyes | Middle shelf | Predator/Scavenger | 5.10 | SMF 23479 | Alberti 1970a | =0,006359 | Eifelian | Cranidium |
| Proetida | Proetidae | Cyrtosymboloides | Cyrtosymboloides samum | 579 | Large eyes | Middle shelf | Predator/Scavenger | 5.11 | CGMTA 261 | Alberti 1970a | =0,005580 | Eifelian | Cranidium |
| Proetida | Proetidae | Cyrtosymboloides | Cyrtosymboloides samum | 580 | Large eyes | Middle shelf | Predator/Scavenger | 5.12 | SMF 23480 | Alberti 1970a | =0,005335 | Eifelian | Cranidium |
| Proetida | Proetidae | Cyrtosymboloides | Cyrtosymboloides termieri | 581 | Large eyes | Middle shelf | Predator/Scavenger | 14.19a | CGMTA 58 | Alberti 1969 | =0,004664 | Emsian | Cranidium |
| Proetida | Proetidae | Cyrtosymboloides | Cyrtosymboloides samum | 582 | Large eyes | Middle shelf | Predator/Scavenger | 14.22 | SMF 23163 | Alberti 1969 | =0,006545 | Eifelian | Cranidium |
| Proetida | Proetidae | Cyrtosymboloides | Cyrtosymboloides termieri | 583 | Large eyes | Middle shelf | Predator/Scavenger | 16.2 | SMF 18189 | Alberti 1964 | =0,003282 | Emsian | Cranidium |
| Proetida | Proetidae | Dalejeproetus | Dalejeproetus owensi | 584 | Large eyes | Inner shelf | Predator/Scavenger | 4.13 | NHM It 28949 | Johnson 2012 | =0,037207 | Pragian | Cephalon |
| Proetida | Proetidae | Diademaproetus | Diademaproetus praecursor | 585 | Large eyes | Deep | Predator/Scavenger | 16.1a | CGMT-AT 159 | Alberti 1969 | =0,014471 | Emsian | Cranidium |
| Proetida | Proetidae | Diademaproetus | Diademaproetus praecursor | 586 | Large eyes | Deep | Predator/Scavenger | 16.2 | CGMTA 70 | Alberti 1969 | =0,011453 | Emsian | Cranidium |
| Proetida | Proetidae | Diademaproetus | Diademaproetus praecursor | 587 | Large eyes | Deep | Predator/Scavenger | 16.3 | SMF 23185 | Alberti 1969 | =0,011453 | Emsian | Cranidium |

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| Proetida | Proetidae | Diademaproetus | Diademaproetus praecursor | 588 | Large eyes | Deep | Predator/Scavenger | 16.4a | SMF 23184 | Alberti 1969 | =0,009663 | Emsian | Cranidium |
| Proetida | Proetidae | Diademaproetus | Diademaproetus antatlasius | 589 | Large eyes | Deep | Predator/Scavenger | 16.7a | CGMT-As 38 | Alberti 1969 | =0,014471 | Eifelian | Cranidium |
| Proetida | Proetidae | Diademaproetus | Diademaproetus mohamedi | 590 | Large eyes | Deep | Predator/Scavenger | 40.14 | UA 13393 | Chatterton 2006 | =0,071908 | Eifelian | Cranidium |
| Proetida | Proetidae | DREVERMANNIINAE | Indet | 591 | Blind | Deep | Predator/Scavenger | 28.16 | SMF 23319 | Alberti 1969 | =0,004482 | Emsian | Cranidium |
| Proetida | Proetidae | DREVERMANNIINAE | Indet | 592 | Blind | Deep | Predator/Scavenger | 28.18a | SMF 23320 | Alberti 1969 | =0,004581 | Emsian | Cranidium |
| Proetida | Proetidae | DREVERMANNIINAE | Indet | 593 | Blind | Deep | Predator/Scavenger | 28.19 | CGMTA 126 | Alberti 1969 | =0,005077 | Emsian | Cranidium |
| Proetida | Proetidae | Eopalpebralia | Eopalpebralia herrmanni | 594 | Blind | Middle shelf | Predator/Scavenger | 3.21 | SMF 36268 | Alberti 1981a | =0.012245 | Emsian | Cranidium |
| Proetida | Proetidae | Eopalpebralia | Eopalpebralia herrmanni | 595 | Blind | Middle shelf | Predator/Scavenger | 18;1 | CGMT | Alberti 1969 | =0,006228 | Emsian | Cranidium |
| Proetida | Proetidae | Eopiriproetus | Eopiriproetus microphtalmus | 596 | Blind | Middle shelf | Predator/Scavenger | 18.15a | CGMTA 84 | Alberti 1969 | =0,007315 | Pragian | Cranidium |
| Proetida | Proetidae | Erbenaspis | | 597 | Large eyes | Middle shelf | Predator/Scavenger | 6.69 | SH | Alberti 1983 | =0.011412 | Pragian | Cranidium |
| Proetida | Proetidae | Erbenaspis | Erbenaspis erbeni | 598 | Large eyes | Middle shelf | Predator/Scavenger | 6.70 | SH | Alberti 1983 | =0.005533 | Pragian | Cranidium |
| Proetida | Proetidae | Erbenaspis | Erbenaspis cicatricosa | 599 | Large eyes | Middle shelf | Predator/Scavenger | 6.71 | CGMTA | Alberti 1983 | =0.005866 | Lochkovian | Cranidium |
| Proetida | Proetidae | Erbenaspis | Erbenaspis arabica | 600 | Large eyes | Middle shelf | Predator/Scavenger | 8.17a | CGMTA 358 | Alberti 1970a | =0,004407 | Pragian | Cranidium |
| Proetida | Proetidae | Erbenaspis | Erbenaspis cicatricosa | 601 | Large eyes | Middle shelf | Predator/Scavenger | 8.18a | CGMTA 304 | Alberti 1970a | =0,006501 | Lochkovian | Cranidium |
| Proetida | Proetidae | Erbenaspis | Erbenaspis arabica | 603 | Large eyes | Middle shelf | Predator/Scavenger | 28.7 | SMF 23013 | Alberti 1969 | =0,004558 | Pragian | Cranidium |
| Proetida | Proetidae | Erbenaspis | Erbenaspis arabica | 604 | Large eyes | Middle shelf | Predator/Scavenger | 28;8 | SMF 23014 | Alberti 1969 | =0,004895 | Pragian | Cranidium |
| Proetida | Proetidae | Erbenaspis | Erbenaspis arabica | 605 | Large eyes | Middle shelf | Predator/Scavenger | 28.9a | SMF 23015 | Alberti 1969 | =0,004066 | Pragian | Cranidium |
| Proetida | Proetidae | Erbenaspis | Erbenaspis arabica | 606 | Large eyes | Middle shelf | Predator/Scavenger | 28.10 | CGMTA 5 | Alberti 1969 | =0,004826 | Pragian | Cranidium |
| Proetida | Proetidae | Erbenaspis | Erbenaspis arabica | 607 | Large eyes | Middle shelf | Predator/Scavenger | 28;11 | CGMTA 6 | Alberti 1969 | =0,004600 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus emerita | 608 | Large eyes | Middle shelf | Predator/Scavenger | 3.j | UM-IP 817 | Feist 2018 | =0,010983 | Emsian | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus notabilis | 609 | Large eyes | Middle shelf | Predator/Scavenger | 3.s | UM-IP 819 | Feist 2018 | =0,011975 | Emsian | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus dufresnoyi saharae | 610 | Large eyes | Middle shelf | Predator/Scavenger | 6.67 | SMF 36563 | Alberti 1983 | =0.015440 | Emsian | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus dufresnoyi australomaurus | 611 | Large eyes | Middle shelf | Predator/Scavenger | 6.68 | CGMTA | Alberti 1983 | =0.018698 | Eifelian | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus dufresnoyi australis | 612 | Large eyes | Middle shelf | Predator/Scavenger | 7.7 | CGMTA 283 | Alberti 1970a | =0,018651 | Emsian | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus dufresnoyi australis | 613 | Large eyes | Middle shelf | Predator/Scavenger | 7.8a | SMF 23495 | Alberti 1970a | =0,015383 | Emsian | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus ferentarius | 614 | Large eyes | Middle shelf | Predator/Scavenger | 16.5 | SMF 18185 | Alberti 1964 | =0,007160 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus tafilaltanus | 615 | Large eyes | Middle shelf | Predator/Scavenger | 23.1a | SMF 23256 | Alberti 1969 | =0,014209 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus tafilaltanus | 616 | Large eyes | Middle shelf | Predator/Scavenger | 23.2a | CGMTA 102 | Alberti 1969 | =0,016176 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus tafilaltanus | 617 | Large eyes | Middle shelf | Predator/Scavenger | 23.3a | SMF 23257 | Alberti 1969 | =0,012008 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus tafilaltanus | 618 | Large eyes | Middle shelf | Predator/Scavenger | 23.4a | CGMTA 193 | Alberti 1969 | =0,008688 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus dufresnoyi australis | 619 | Large eyes | Middle shelf | Predator/Scavenger | 23.5a | SMF 23264 | Alberti 1969 | =0,014211 | Emsian | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus dufresnoyi australis | 620 | Large eyes | Middle shelf | Predator/Scavenger | 23.6a | SMF 23265 | Alberti 1969 | =0,009691 | Emsian | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus dufresnoyi australis | 621 | Large eyes | Middle shelf | Predator/Scavenger | 23.7 | SMF 23266 | Alberti 1969 | =0,012157 | Emsian | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus dufresnoyi australis | 622 | Large eyes | Middle shelf | Predator/Scavenger | 23.8a | CGMTA 106 | Alberti 1969 | =0,013226 | Emsian | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus dufresnoyi saharae | 623 | Large eyes | Middle shelf | Predator/Scavenger | 23.10a | CGMTA 181 | Alberti 1969 | =0,011096 | Emsian | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus notabilis | 624 | Large eyes | Middle shelf | Predator/Scavenger | 26.1a | SMF 23284 | Alberti 1969 | =0,016580 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus notabilis | 625 | Large eyes | Middle shelf | Predator/Scavenger | 262a | SMF 23285 | Alberti 1969 | =0,025959 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus notabilis | 626 | Large eyes | Middle shelf | Predator/Scavenger | 26.3a | SMF 23286 | Alberti 1969 | =0,019441 | Pragian | Cranidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus notabilis | 627 | Large eyes | Middle shelf | Predator/Scavenger | 26.4a | CGMTA 112 | Alberti 1969 | =0,016580 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus notabilis | 628 | Large eyes | Middle shelf | Predator/Scavenger | 26.5a | CGMTA 113 | Alberti 1969 | =0,019273 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus cacuminatus | 629 | Large eyes | Middle shelf | Predator/Scavenger | 26.8a | SMF 23271 | Alberti 1969 | =0,024955 | | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus cacuminatus | 630 | Large eyes | Middle shelf | Predator/Scavenger | 26.9 | SMF 23272 | Alberti 1969 | =0,007369 | | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus cacuminatus | 631 | Large eyes | Middle shelf | Predator/Scavenger | 26.10a | CGMTA 109 | Alberti 1969 | =0,004998 | | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus cacuminatus | 632 | Large eyes | Middle shelf | Predator/Scavenger | 26.11 | SMF 23273 | Alberti 1969 | =0,007111 | | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus cacuminatus | 633 | Large eyes | Middle shelf | Predator/Scavenger | 26.12 | SMF 23274 | Alberti 1969 | =0,008583 | | Cranidium |
| Proetida | Proetidae | Xiphogonium | Xiphogonium trautensteinensis crassus | 634 | Large eyes | Inner shelf | Predator/Scavenger | 27.5a | CGMTA 116 | Alberti 1969 | =0,006911 | Emsian | Cranidium |
| Proetida | Proetidae | Xiphogonium | Xiphogonium trautensteinensis crassus | 635 | Large eyes | Inner shelf | Predator/Scavenger | 27.6a | SMF 23291 | Alberti 1969 | =0,004348 | Emsian | Cranidium |
| Proetida | Proetidae | Xiphogonium | Xiphogonium trautensteinensis crassus | 636 | Large eyes | Inner shelf | Predator/Scavenger | 27.7 | SMF 23292 | Alberti 1969 | =0,005976 | Emsian | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus munitus | 638 | Large eyes | Middle shelf | Predator/Scavenger | 27.13a | CGMTA 123 | Alberti 1969 | =0,010548 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus tafilaltanus | 639 | Large eyes | Middle shelf | Predator/Scavenger | a.13 | CGMTA 102 | Alberti 1967a | =0.020001 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus dufresnoyi saharae | 640 | Large eyes | Middle shelf | Predator/Scavenger | b.14 | CGMTA 181 | Alberti 1967b | =0,014743 | Emsian | Cranidium |
| Proetida | Proetidae | Gerastos | Gerastos akrechanus | 641 | Large eyes | Inner shelf | Predator/Scavenger | 1.1a | ISCR | Alberti 1969 | =0,014885 | Emsian | Cranidium |
| Proetida | Proetidae | Gerastos | Gerastos akrechanus | 642 | Large eyes | Inner shelf | Predator/Scavenger | 1.2 | ISCR | Alberti 1969 | =0,014239 | Emsian | Cranidium |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 643 | Large eyes | Inner shelf | Predator/Scavenger | 1.3 | UA 13278 | Gibb 2010 | =0,008811 | Eifelian | Cranidium |
| Proetida | Proetidae | Gerastos | Gerastos akrechanus | 644 | Large eyes | Inner shelf | Predator/Scavenger | 1.3a | ISCR | Alberti 1969 | =0,014239 | Emsian | Cranidium |
| Proetida | Proetidae | Gerastos | Gerastos prox umerbianus | 645 | Large eyes | Inner shelf | Predator/Scavenger | 1.4a | CGMTA 11 | Alberti 1969 | =0,011058 | | Cranidium |
| Proetida | Proetidae | Gerastos | Gerastos prox umerbianus | 646 | Large eyes | Inner shelf | Predator/Scavenger | 1.5a | SMF 23020 | Alberti 1969 | =0,012011 | | Cranidium |
| Proetida | Proetidae | Gerastos | Gerastos prox umerbianus | 647 | Large eyes | Inner shelf | Predator/Scavenger | 1.6a | SMF 23021 | Alberti 1969 | =0,008546 | | Cranidium |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 648 | Large eyes | Inner shelf | Predator/Scavenger | 2.8 | UA 13465 | Gibb 2010 | =0,013213 | Emsian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos rehamnanus | 649 | Large eyes | Inner shelf | Predator/Scavenger | 3.6b | ISCR | Alberti 1969 | =0,013067 | | Cranidium |
| Proetida | Proetidae | Gerastos | Gerastos hammii | 650 | Large eyes | Inner shelf | Predator/Scavenger | 7.1 | UA 13534 | Gibb 2010 | =0,008451 | Eifelian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 651 | Large eyes | Inner shelf | Predator/Scavenger | 8i | Di/UO/030 | Khaldi 2016 | =0,048535 | Emsian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos discombobulatus | 652 | Large eyes | Inner shelf | Predator/Scavenger | 11.12 | UA 13469 | Gibb 2010 | =0,012255 | Eifelian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos cuvieri malisus | 653 | Large eyes | Inner shelf | Predator/Scavenger | 13.3 | UA 13551 | Gibb 2010 | =0,012902 | Eifelian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos raribus | 654 | Large eyes | Inner shelf | Predator/Scavenger | 18.8 | UA 13463 | Gibb 2010 | =0,006039 | Givetian | Cranidium |
| Proetida | Proetidae | Gerastos | Gerastos izius | 655 | Large eyes | Inner shelf | Predator/Scavenger | 24.6 | UA 13570 | Gibb 2010 | =0,009669 | Givetian | Cephalon |
| Proetida | Proetidae | Gerastos | Gerastos izius | 656 | Large eyes | Inner shelf | Predator/Scavenger | 24.8 | UA 13529 | Gibb 2010 | =0,009446 | Givetian | Cephalon |
| Proetida | Proetidae | Interproetus | Interproetus walliseri | 657 | Large eyes | Middle shelf | Predator/Scavenger | 2.16 | SMF 23098 | Alberti 1981a | =0.012028 | Ludlow-Pridoli | Cranidium |
| Proetida | Proetidae | Kegeliella | Kegeliella listei bouregregus | 658 | Large eyes | Middle shelf | Predator/Scavenger | 3.1b | CGMTA 15 | Alberti 1969 | =0,020975 | Pragian | Cranidium |
| Proetida | Proetidae | Kegeliella | Kegeliella listei bouregregus | 659 | Large eyes | Middle shelf | Predator/Scavenger | 3.3 | SMF 23033 | Alberti 1969 | =0,019580 | Pragian | Cranidium |
| Proetida | Proetidae | Kegeliella | Kegeliella listei prolistei | 660 | Large eyes | Middle shelf | Predator/Scavenger | 3.4b | CGMTA 186 | Alberti 1969 | =0,019612 | Pragian | Cranidium |
| Proetida | Proetidae | Koneprusites | Koneprusites moestus | 661 | Large eyes | Middle shelf | Predator/Scavenger | 4m | MU-G-Sr.Tr.A4/Pr141 | Crônier Abbache 2018 | =0,033325 | Eifelian | Cranidium |
| Proetida | Proetidae | Koneprusites | Koneprusites insons africus | 662 | Large eyes | Middle shelf | Predator/Scavenger | 6.11a | CGMTA 271 | Alberti 1970a | =0,008166 | Eifelian | Cranidium |
| Proetida | Proetidae | Koneprusites | Koneprusites insons africus | 663 | Large eyes | Middle shelf | Predator/Scavenger | 6.12a | SMF 23488 | Alberti 1970a | =0,006081 | Eifelian | Cranidium |
| Proetida | Proetidae | Koneprusites | Koneprusites insons africus | 664 | Large eyes | Middle shelf | Predator/Scavenger | 6.13a | SMF 23489 | Alberti 1970a | =0,010058 | Eifelian | Cranidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Proetida | Proetidae | Koneprusites | Koneprusites insons africus | 665 | Large eyes | Middle shelf | Predator/Scavenger | 6.14 | CGMTA 272 | Alberti 1970a | =0,005079 | Eifelian | Cranidium |
| Proetida | Proetidae | Koneprusites | Koneprusites insons africus | 666 | Large eyes | Middle shelf | Predator/Scavenger | 6.15 | CGMTA 273 | Alberti 1970a | =0,005131 | Eifelian | Cranidium |
| Proetida | Proetidae | Koneprusites | Koneprusites insons africus | 667 | Large eyes | Middle shelf | Predator/Scavenger | 6.16 | CGMTA 274 | Alberti 1970a | =0,005878 | Eifelian | Cranidium |
| Proetida | Proetidae | Koneprusites | Koneprusites baconi saharae | 668 | Large eyes | Middle shelf | Predator/Scavenger | 20.2a | CGMTA 101 | Alberti 1969 | =0,006120 | Eifelian | Cranidium |
| Proetida | Proetidae | Koneprusites | Koneprusites baconi saharae | 669 | Large eyes | Middle shelf | Predator/Scavenger | 20.3 | SMF 23253 | Alberti 1969 | =0,006537 | Eifelian | Cranidium |
| Proetida | Proetidae | Koneprusites | Koneprusites baconi saharae | 670 | Large eyes | Middle shelf | Predator/Scavenger | 20.4a | SMF 23254 | Alberti 1969 | =0,005704 | Eifelian | Cranidium |
| Proetida | Proetidae | Lepidoproetus | Lepidoproetus solutus | 671 | Large eyes | Shallow | Predator/Scavenger | 1.3 | No name | Alberti 1966c | =0,006219 | | Cranidium |
| Proetida | Proetidae | Lepidoproetus | Lepidoproetus lahceni | 672 | Large eyes | Shallow | Predator/Scavenger | 5.5 | NHM It 28952 | Johnson 2012 | =0,031096 | Pragian | Cephalon |
| Proetida | Proetidae | Lepidoproetus | Lepidoproetus maharchianus | 673 | Large eyes | Shallow | Predator/Scavenger | 6.6 | NHM It 28955 | Johnson 2012 | =0,046560 | Pragian | Cephalon |
| Proetida | Proetidae | Lepidoproetus | Lepidoproetus lorae | 674 | Large eyes | Shallow | Predator/Scavenger | 15.9a | SMF 23176 | Alberti 1969 | =0,008917 | Pragian | Cranidium |
| Proetida | Proetidae | Lepidoproetus | Lepidoproetus lorae | 675 | Large eyes | Shallow | Predator/Scavenger | 15.10 | CGMTA 66 | Alberti 1969 | =0,010668 | Pragian | Cranidium |
| Proetida | Proetidae | Lepidoproetus | Lepidoproetus praematurus | 676 | Large eyes | Shallow | Predator/Scavenger | 15.12 | CGMTA 61 | Alberti 1969 | =0,005404 | Pragian | Cranidium |
| Proetida | Proetidae | Lepidoproetus | Lepidoproetus praematurus | 677 | Large eyes | Shallow | Predator/Scavenger | 15.13 | CGMTA 62 | Alberti 1969 | =0,005975 | Pragian | Cranidium |
| Proetida | Proetidae | Lepidoproetus | Lepidoproetus praematurus | 678 | Large eyes | Shallow | Predator/Scavenger | 15.14a | SMF 23168 | Alberti 1969 | =0,006065 | Pragian | Cranidium |
| Proetida | Proetidae | Lepidoproetus | Lepidoproetus lepidus | 679 | Large eyes | Shallow | Predator/Scavenger | 15.18a | SMF 23465 | Alberti 1969 | =0,005281 | Lochkovian | Cranidium |
| Proetida | Proetidae | Lepidoproetus | Lepidoproetus solutus | 680 | Large eyes | Shallow | Predator/Scavenger | 15.19a | CGMTA 63 | Alberti 1969 | =0,007333 | | Cranidium |
| Proetida | Proetidae | Lepidoproetus | Lepidoproetus praematurus | 681 | Large eyes | Shallow | Predator/Scavenger | 17.1 | SMF 18186 | Alberti 1964 | =0,005577 | Pragian | Cranidium |
| Proetida | Proetidae | Lepidoproetus | Lepidoproetus lorae | 682 | Large eyes | Shallow | Predator/Scavenger | a.8 | SMF 23176 | Alberti 1967a | =0.009317 | Pragian | Cranidium |
| Proetida | Proetidae | Linguaproetus | Linguaproetus saharensis | 683 | Blind | Shallow | Predator/Scavenger | 18.2a | CGMTA 184 | Alberti 1969 | =0,004314 | Eifelian | Cranidium |
| Proetida | Proetidae | Macroblepharum | Macroblepharum africanum iunior | 684 | Large eyes | Middle shelf | Predator/Scavenger | 2.15 | CGMTA | Alberti 1981a | =0.015427 | Eifelian | Cranidium |
| Proetida | Proetidae | Macroblepharum | Macroblepharum africanum ribatelfatanum | 685 | Large eyes | Middle shelf | Predator/Scavenger | 5.1a | SMF 23465 | Alberti 1970a | =0,005779 | Emsian | Cranidium |
| Proetida | Proetidae | Macroblepharum | Macroblepharum africanum ribatelfatanum | 686 | Large eyes | Middle shelf | Predator/Scavenger | 5.2a | CGMTA 247 | Alberti 1970a | =0,006357 | Emsian | Cranidium |
| Proetida | Proetidae | Macroblepharum | Macroblepharum africanum ribatelfatanum | 687 | Large eyes | Middle shelf | Predator/Scavenger | 5.4 | CGMTA 248 | Alberti 1970a | =0,006186 | Emsian | Cranidium |
| Proetida | Proetidae | Macroblepharum | Macroblepharum africanum ribatelfatanum | 688 | Large eyes | Middle shelf | Predator/Scavenger | 5.48 | SMF 36555 | Alberti 1983 | =0.006584 | Eifelian | Cranidium |
| Proetida | Proetidae | Macroblepharum | Macroblepharum africanum africanum | 689 | Large eyes | Middle shelf | Predator/Scavenger | 5.58 | SMF 36556 | Alberti 1983 | =0.005326 | Eifelian | Cranidium |
| Proetida | Proetidae | Macroblepharum | Macroblepharum africanum africanum | 690 | Large eyes | Middle shelf | Predator/Scavenger | 14.1a | SMF 23145 | Alberti 1969 | =0,005622 | Eifelian | Cranidium |
| Proetida | Proetidae | Macroblepharum | Macroblepharum africanum africanum | 691 | Large eyes | Middle shelf | Predator/Scavenger | 14.2a | SMF 23146 | Alberti 1969 | =0,004633 | Eifelian | Cranidium |
| Proetida | Proetidae | Macroblepharum | Macroblepharum africanum africanum | 692 | Large eyes | Middle shelf | Predator/Scavenger | 14.3 | SMF 23147 | Alberti 1969 | =0,005982 | Eifelian | Cranidium |
| Proetida | Proetidae | Macroblepharum | Macroblepharum africanum africanum | 693 | Large eyes | Middle shelf | Predator/Scavenger | 14.4a | SMF 23148 | Alberti 1969 | =0,004633 | Eifelian | Cranidium |
| Proetida | Proetidae | Macroblepharum | Macroblepharum africanum africanum | 694 | Large eyes | Middle shelf | Predator/Scavenger | 14.5 | SMF 23149 | Alberti 1969 | =0,004322 | Eifelian | Cranidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Proetida | Proetidae | Macroblepharum | Macroblepharum africanum africanum | 695 | Large eyes | Middle shelf | Predator/Scavenger | 14.6 | SMF 23150 | Alberti 1969 | =0,004472 | Eifelian | Cranidium |
| Proetida | Proetidae | Macroblepharum | Macroblepharum africanum africanum | 696 | Large eyes | Middle shelf | Predator/Scavenger | 14.7 | SMF 23151 | Alberti 1969 | =0,005511 | Eifelian | Cranidium |
| Proetida | Proetidae | Macroblepharum | Macroblepharum africanum africanum | 697 | Large eyes | Middle shelf | Predator/Scavenger | 14.9 | SMF 23153 | Alberti 1969 | =0,004952 | Eifelian | Cranidium |
| Proetida | Proetidae | Macroblepharum | Macroblepharum africanum africanum | 698 | Large eyes | Middle shelf | Predator/Scavenger | 14.10a | SMF 23155 | Alberti 1969 | =0,004946 | Eifelian | Cranidium |
| Proetida | Proetidae | Macroblepharum | Macroblepharum africanum africanum | 699 | Large eyes | Middle shelf | Predator/Scavenger | 14.12 | CGMTA 51 | Alberti 1969 | =0,004238 | Eifelian | Cranidium |
| Proetida | Proetidae | Macroblepharum | Macroblepharum africanum africanum | 700 | Large eyes | Middle shelf | Predator/Scavenger | 14.15 | SMF 23433 | Alberti 1969 | =0,004633 | Eifelian | Cranidium |
| Proetida | Proetidae | Macroblepharum | Macroblepharum africanum africanum | 701 | Large eyes | Middle shelf | Predator/Scavenger | 14.16 | SMF 23434 | Alberti 1969 | =0,004941 | Eifelian | Cranidium |
| Proetida | Proetidae | Macroblepharum | Macroblepharum africanum africanum | 702 | Large eyes | Middle shelf | Predator/Scavenger | 16.1 | SMF 18188 | Alberti 1964 | =0,003938 | Eifelian | Cranidium |
| Proetida | Proetidae | Montanproetus | Montanproetus midas amlanensis | 703 | Large eyes | Inner shelf | Predator/Scavenger | 1.6 | CGMTA 37 | Alberti 1981a | =0.020741 | Emsian | Cranidium |
| Proetida | Proetidae | Montanproetus | Montanproetus midas amlanensis | 704 | Large eyes | Inner shelf | Predator/Scavenger | 1.7 | LGFSA | Alberti 1981a | =0.019600 | Emsian | Cranidium |
| Proetida | Proetidae | Montanproetus | Montanproetus chlupaci | 705 | Large eyes | Inner shelf | Predator/Scavenger | 8.1a | SMF 23099 | Alberti 1969 | =0,014124 | Pragian | Cranidium |
| Proetida | Proetidae | Montanproetus | Montanproetus chlupaci | 706 | Large eyes | Inner shelf | Predator/Scavenger | 8.2a | SMF 23100 | Alberti 1969 | =0,015039 | Pragian | Cranidium |
| Proetida | Proetidae | Montanproetus | Montanproetus chlupaci | 707 | Large eyes | Inner shelf | Predator/Scavenger | 8.3 | CGMTA 30 | Alberti 1969 | =0,013072 | Pragian | Cranidium |
| Proetida | Proetidae | Montanproetus | Montanproetus chlupaci | 708 | Large eyes | Inner shelf | Predator/Scavenger | 8.4a | CGMTA 31 | Alberti 1969 | =0,011422 | Pragian | Cranidium |
| Proetida | Proetidae | Montanproetus | Montanproetus chlupaci | 709 | Large eyes | Inner shelf | Predator/Scavenger | 8.5a | SMF 23101 | Alberti 1969 | =0,007096 | Pragian | Cranidium |
| Proetida | Proetidae | Montanproetus | Montanproetus chlupaci | 710 | Large eyes | Inner shelf | Predator/Scavenger | 8.6a | SMF 23102 | Alberti 1969 | =0,008003 | Pragian | Cranidium |
| Proetida | Proetidae | Montanproetus | Montanproetus chlupaci | 711 | Large eyes | Inner shelf | Predator/Scavenger | 8.8 | CGMTA 320 | Alberti 1969 | =0,012097 | Pragian | Cranidium |
| Proetida | Proetidae | Montanproetus | Montanproetus chlupaci | 712 | Large eyes | Inner shelf | Predator/Scavenger | 8.9 | SMF 23104 | Alberti 1969 | =0,010974 | Pragian | Cranidium |
| Proetida | Proetidae | Montanproetus | Montanproetus chlupaci | 713 | Large eyes | Inner shelf | Predator/Scavenger | 8.10a | SMF 23105 | Alberti 1969 | =0,006027 | Pragian | Cranidium |
| Proetida | Proetidae | Montanproetus | Montanproetus chlupaci | 714 | Large eyes | Inner shelf | Predator/Scavenger | 8.11 | GSTIH | Alberti 1969 | =0,015455 | Pragian | Cranidium |
| Proetida | Proetidae | Montanproetus | Montanproetus tindoufanus | 715 | Large eyes | Inner shelf | Predator/Scavenger | 8.13a | SMF 23106 | Alberti 1969 | =0,010801 | Pragian | Cranidium |
| Proetida | Proetidae | Montanproetus | Montanproetus tindoufanus | 716 | Large eyes | Inner shelf | Predator/Scavenger | 8.14a | CGMTA 33 | Alberti 1969 | =0,008363 | Pragian | Cranidium |
| Proetida | Proetidae | Montanproetus | Montanproetus tindoufanus | 717 | Large eyes | Inner shelf | Predator/Scavenger | 8.15a | SMF 23107 | Alberti 1969 | =0,008905 | Pragian | Cranidium |
| Proetida | Proetidae | Montanproetus | Montanproetus midas amlanensis | 718 | Large eyes | Inner shelf | Predator/Scavenger | 10.10a | CGMTA 36 | Alberti 1969 | =0,012616 | Emsian | Cranidium |
| Proetida | Proetidae | Montanproetus | Montanproetus midas amlanensis | 719 | Large eyes | Inner shelf | Predator/Scavenger | 10.11a | SMF 23114 | Alberti 1969 | =0,013049 | Emsian | Cranidium |
| Proetida | Proetidae | Montanproetus | Montanproetus pernix boutsharafinensis | 720 | Large eyes | Inner shelf | Predator/Scavenger | 10.14a | CGMTA 35 | Alberti 1969 | =0,006897 | Emsian | Cranidium |
| Proetida | Proetidae | Montanproetus | Montanproetus chlupaci | 721 | Large eyes | Inner shelf | Predator/Scavenger | a.1 | SMF 23099 | Alberti 1967a | =0.014959 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Nagaproetus | Nagaproetus frequens | 722 | Large eyes | Middle shelf | Predator/Scavenger | 3.L | UM-IP 818 | Feist 2018 | =0,007117 | Emsian | Cranidium |
| Proetida | Tropidocoryphidae | Nagaproetus | Nagaproetus frequens | 723 | Large eyes | Middle shelf | Predator/Scavenger | 27.1a | CGMTA 119 | Alberti 1969 | =0,007318 | Emsian | Cranidium |
| Proetida | Tropidocoryphidae | Nagaproetus | Nagaproetus frequens | 724 | Large eyes | Middle shelf | Predator/Scavenger | 27.2 | SMF 23296 | Alberti 1969 | =0,007549 | Emsian | Cranidium |
| Proetida | Tropidocoryphidae | Nagaproetus | Nagaproetus frequens | 725 | Large eyes | Middle shelf | Predator/Scavenger | 27.3 | CGMTA 120 | Alberti 1969 | =0,009678 | Emsian | Cranidium |
| Proetida | Tropidocoryphidae | Nagaproetus | Nagaproetus frequens | 726 | Large eyes | Middle shelf | Predator/Scavenger | 27.4a | SMF 23297 | Alberti 1969 | =0,009678 | Emsian | Cranidium |
| Proetida | Proetidae | Orbitoproetus | Orbitoproetus lecointrei | 727 | Large eyes | Middle shelf | Predator/Scavenger | 1.13a | CGMTA 193 | Alberti 1969 | =0,015611 | Pragian | Cranidium |
| Proetida | Proetidae | Orbitoproetus | Orbitoproetus africanus | 728 | Large eyes | Middle shelf | Predator/Scavenger | 2.3b | CGMTA 12 | Alberti 1969 | =0,017317 | Pragian | Cranidium |
| Proetida | Proetidae | Orbitoproetus | Orbitoproetus africanus | 729 | Large eyes | Middle shelf | Predator/Scavenger | 2.4b | SMF 23024 | Alberti 1969 | =0,019969 | Pragian | Cranidium |
| Proetida | Proetidae | Orbitoproetus | Orbitoproetus ovalis | 730 | Large eyes | Middle shelf | Predator/Scavenger | 2.6a | CGMTA 13 | Alberti 1969 | =0,017317 | Pragian | Cranidium |
| Proetida | Proetidae | Orbitoproetus | Orbitoproetus ovalis | 731 | Large eyes | Middle shelf | Predator/Scavenger | 2.7a | SMF 23027 | Alberti 1969 | =0,012819 | Pragian | Cranidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Proetida | Proetidae | Orbitoproetus | Orbitoproetus africanus | 732 | Large eyes | Middle shelf | Predator/Scavenger | 46.5 | CGMTA 211 | Alberti 1969 | =0,015551 | Pragian | Cranidium |
| Proetida | Proetidae | Orbitoproetus | Orbitoproetus africanus | 733 | Large eyes | Middle shelf | Predator/Scavenger | b.1 | CGMTA 12 | Alberti 1967b | =0,021188 | Pragian | Cranidium |
| Proetida | Proetidae | Orbitoproetus | Orbitoproetus africanus | 734 | Large eyes | Middle shelf | Predator/Scavenger | 6 | SMF 23024 | Alberti 1982 | =0,014796 | Pragian | Cranidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 735 | Large eyes | Middle shelf | Predator/Scavenger | 2.19 | Gö 693-192 | H. Alberti 1975a | =0.036994 | Famennian | Cranidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 736 | Large eyes | Middle shelf | Predator/Scavenger | 2.21 | CGMT-HA 26 | H. Alberti 1975a | =0.036994 | Famennian | Cranidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 737 | Large eyes | Middle shelf | Predator/Scavenger | 2.22 | Gö 693-197 | H. Alberti 1975a | =0.036994 | Famennian | Cranidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 738 | Large eyes | Middle shelf | Predator/Scavenger | 2.b | UMC-IP 424 | Lerosey-Aubril Feist 2008 | =0,004098 | Famennian | Cranidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 739 | Large eyes | Middle shelf | Predator/Scavenger | 2.c1 | UMC-IP 425 | Lerosey-Aubril Feist 2008 | =0,004545 | Famennian | Cranidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 740 | Large eyes | Middle shelf | Predator/Scavenger | 2.d1 | UMC-IP 426 | Lerosey-Aubril Feist 2008 | =0,004806 | Famennian | Cranidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 741 | Large eyes | Middle shelf | Predator/Scavenger | 3.g | UMC-IP 367 | Lerosey-Aubril Feist 2008 | =0,001582 | Famennian | Cranidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 742 | Large eyes | Middle shelf | Predator/Scavenger | 3.i | UMC-IP 369 | Lerosey-Aubril Feist 2008 | =0,002551 | Famennian | Cranidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 743 | Large eyes | Middle shelf | Predator/Scavenger | 3.j | UMC-IP 370 | Lerosey-Aubril Feist 2008 | =0,002747 | Famennian | Cranidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 744 | Large eyes | Middle shelf | Predator/Scavenger | 3.k | UMC-IP 371 | Lerosey-Aubril Feist 2008 | =0,003205 | Famennian | Cranidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 745 | Large eyes | Middle shelf | Predator/Scavenger | 3.m | UMC-IP 313 | Lerosey-Aubril Feist 2008 | =0,003448 | Famennian | Cranidium |
| Proetida | Proetidae | Paralepidoproetus | Paralepidoproetus wragei | 746 | Large eyes | Middle shelf | Predator/Scavenger | 2.11 | SMF 36235 | Alberti 1981a | =0.015504 | Eifelian | Cranidium |
| Proetida | Proetidae | Paralepidoproetus | Paralepidoproetus wragei | 747 | Large eyes | Middle shelf | Predator/Scavenger | 2.13 | CGMTA | Alberti 1981a | =0.013985 | Eifelian | Cranidium |
| Proetida | Proetidae | Paralepidoproetus | Paralepidoproetus haentzscheli | 748 | Large eyes | Middle shelf | Predator/Scavenger | 7.1a | CGMTA 64 | Alberti 1969 | =0,006906 | Pragian | Cranidium |
| Proetida | Proetidae | Paralepidoproetus | Paralepidoproetus haentzscheli | 749 | Large eyes | Middle shelf | Predator/Scavenger | 7.2a | SMF 23174 | Alberti 1969 | =0,005335 | Pragian | Cranidium |
| Proetida | Proetidae | Paralepidoproetus | Paralepidoproetus haentzscheli | 750 | Large eyes | Middle shelf | Predator/Scavenger | 7.3 | SMF 23175 | Alberti 1969 | =0,005681 | Pragian | Cranidium |
| Proetida | Proetidae | Paralepidoproetus | Paralepidoproetus chouberti | 751 | Large eyes | Middle shelf | Predator/Scavenger | 7.4 | CGMTA 39 | Alberti 1969 | =0,009656 | | Cranidium |
| Proetida | Proetidae | Paralepidoproetus | Paralepidoproetus chouberti | 752 | Large eyes | Middle shelf | Predator/Scavenger | 7.5a | SMF 23116 | Alberti 1969 | =0,007848 | | Cranidium |
| Proetida | Proetidae | Paralepidoproetus | Paralepidoproetus fauremuretae | 753 | Large eyes | Middle shelf | Predator/Scavenger | 16.3 | SMF 18184 | Alberti 1964 | =0,006741 | | Cranidium |
| Proetida | Proetidae | Paralepidoproetus | Paralepidoproetus chouberti | 754 | Large eyes | Middle shelf | Predator/Scavenger | 17.6 | SMF 18183 | Alberti 1964 | =0,007844 | | Cranidium |
| Proetida | Tropidocoryphidae | Phaetonellus | Phaetonellus planicauda africanus | 755 | Large eyes | Middle shelf | Predator/Scavenger | 3.27 | SMF 36259 | Alberti 1981a | =0.029274 | Emsian | Cranidium |
| Proetida | Tropidocoryphidae | Phaetonellus | Phaetonellus planicauda africanus | 756 | Large eyes | Middle shelf | Predator/Scavenger | 3.31 | CGMTA | Alberti 1981a | =0.031667 | Emsian | Cranidium |
| Proetida | Tropidocoryphidae | Phaetonellus | Phaetonellus maurusius | 757 | Large eyes | Middle shelf | Predator/Scavenger | 7.17a | CGMTA 287 | Alberti 1970a | =0,005519 | Emsian | Cranidium |
| Proetida | Proetidae | Piriproetus | Piriproetus ornatissimus maurus | 758 | Blind | Deep | Predator/Scavenger | 16.4 | SMF 18187 | Alberti 1964 | =0,003469 | Emsian | Cranidium |
| Proetida | Proetidae | Piriproetus | Piriproetus ornatissimus maurus | 759 | Blind | Deep | Predator/Scavenger | 18.3a | SMF 23219 | Alberti 1969 | =0,004611 | Emsian | Cranidium |
| Proetida | Proetidae | Piriproetus | Piriproetus amblyops austromaurus | 760 | Blind | Deep | Predator/Scavenger | 19.1a | SMF 23222 | Alberti 1969 | =0,006449 | Eifelian | Cranidium |
| Proetida | Proetidae | Piriproetus | Piriproetus amblyops austromaurus | 761 | Blind | Deep | Predator/Scavenger | 19.2a | CGMTA 89 | Alberti 1969 | =0,006622 | Eifelian | Cranidium |
| Proetida | Proetidae | Piriproetus | Piriproetus amblyops austromaurus | 762 | Blind | Deep | Predator/Scavenger | 19.3a | SMF 23223 | Alberti 1969 | =0,004932 | Eifelian | Cranidium |
| Proetida | Proetidae | Piriproetus | Piriproetus amblyops austromaurus | 763 | Blind | Deep | Predator/Scavenger | 19.4 | SMF 23224 | Alberti 1969 | =0,005298 | Eifelian | Cranidium |
| Proetida | Proetidae | Piriproetus | Piriproetus amblyops austromaurus | 764 | Blind | Deep | Predator/Scavenger | 19.5 | SMF 23226 | Alberti 1969 | =0,005624 | Eifelian | Cranidium |
| Proetida | Proetidae | Piriproetus | Piriproetus amblyops austromaurus | 765 | Blind | Deep | Predator/Scavenger | 19.7 | SMF 23227 | Alberti 1969 | =0,007439 | Eifelian | Cranidium |
| Proetida | Proetidae | Piriproetus | Piriproetus amblyops austromaurus | 766 | Blind | Deep | Predator/Scavenger | 19.8 | SMF 23228 | Alberti 1969 | =0,004336 | Eifelian | Cranidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Proetida | Proetidae | Piriproetus | Piriproetus amblyops austromaurus | 767 | Blind | Deep | Predator/Scavenger | 19.9a | SMF 23229 | Alberti 1969 | =0,006449 | Eifelian | Cranidium |
| Proetida | Proetidae | Piriproetus | Piriproetus amblyops austromaurus | 768 | Blind | Deep | Predator/Scavenger | 19.10 | CGMTA 92 | Alberti 1969 | =0,005202 | Eifelian | Cranidium |
| Proetida | Proetidae | Piriproetus | Piriproetus amblyops austromaurus | 769 | Blind | Deep | Predator/Scavenger | 19.11a | SMF 23230 | Alberti 1969 | =0,006900 | Eifelian | Cranidium |
| Proetida | Proetidae | Piriproetus | Piriproetus amblyops austromaurus | 770 | Blind | Deep | Predator/Scavenger | 19.12 | SMF 23231 | Alberti 1969 | =0,004046 | Eifelian | Cranidium |
| Proetida | Proetidae | Piriproetus | Piriproetus amblyops austromaurus | 771 | Blind | Deep | Predator/Scavenger | 19.13 | SMF 23232 | Alberti 1969 | =0,004519 | Eifelian | Cranidium |
| Proetida | Proetidae | Piriproetus | Piriproetus amblyops patruelis | 772 | Blind | Deep | Predator/Scavenger | 19.16 | CGMTA 95? | Alberti 1969 | =0,005048 | Eifelian | Cranidium |
| Proetida | Proetidae | Piriproetus | Piriproetus amblyops patruelis | 773 | Blind | Deep | Predator/Scavenger | 19.17 | CGMTA 95 | Alberti 1969 | =0,005202 | Eifelian | Cranidium |
| Proetida | Proetidae | Piriproetus | Piriproetus amblyops patruelis | 774 | Blind | Deep | Predator/Scavenger | 19.18 | CGMTA 96 | Alberti 1969 | =0,005375 | Eifelian | Cranidium |
| Proetida | Proetidae | Piriproetus | Piriproetus amblyops patruelis | 775 | Blind | Deep | Predator/Scavenger | 19.19 | SMF 23234 | Alberti 1969 | =0,004599 | Eifelian | Cranidium |
| Proetida | Proetidae | Podoliproetus | Podoliproetus rabatanus | 776 | Large eyes | Inner shelf | Predator/Scavenger | 2.1 | SMF 23028 | Alberti 1969 | =0,018035 | Pragian | Cranidium |
| Proetida | Proetidae | Podoliproetus | Podoliproetus rabatanus | 777 | Large eyes | Inner shelf | Predator/Scavenger | 2.2a | CGMTA 14 | Alberti 1969 | =0,014006 | Pragian | Cranidium |
| Proetida | Proetidae | Pragoproetus | Pragoproetus medius | 778 | Large eyes | Inner shelf | Predator/Scavenger | 4.7a | CGMTA 19 | Alberti 1969 | =0,006616 | Pragian | Cranidium |
| Proetida | Proetidae | Pragoproetus | Pragoproetus gibbosus | 779 | Large eyes | Inner shelf | Predator/Scavenger | 4.10a | CGMTA 20 | Alberti 1969 | =0,012450 | Pragian | Cranidium |
| Proetida | Proetidae | Pragoproetus | Pragoproetus gibbosus | 780 | Large eyes | Inner shelf | Predator/Scavenger | 4.11a | SMF 23044 | Alberti 1969 | =0,013543 | Pragian | Cranidium |
| Proetida | Proetidae | Pragoproetus | Pragoproetus tafilaltensis | 781 | Large eyes | Inner shelf | Predator/Scavenger | 5.1a | SMF 23046 | Alberti 1969 | =0,007969 | Pragian | Cranidium |
| Proetida | Proetidae | Pragoproetus | Pragoproetus tafilaltensis | 782 | Large eyes | Inner shelf | Predator/Scavenger | 5.2a | SMF 23047 | Alberti 1969 | =0,007246 | Pragian | Cranidium |
| Proetida | Proetidae | Pragoproetus | Pragoproetus tafilaltensis | 783 | Large eyes | Inner shelf | Predator/Scavenger | 5.3a | SMF 23048 | Alberti 1969 | =0,013922 | Pragian | Cranidium |
| Proetida | Proetidae | Pragoproetus | Pragoproetus tafilaltensis | 784 | Large eyes | Inner shelf | Predator/Scavenger | 5.4 | SMF 23049 | Alberti 1969 | =0,008404 | Pragian | Cranidium |
| Proetida | Proetidae | Pragoproetus | Pragoproetus tafilaltensis | 785 | Large eyes | Inner shelf | Predator/Scavenger | 5.5a | SMF 23050 | Alberti 1969 | =0,007246 | Pragian | Cranidium |
| Proetida | Proetidae | Pragoproetus | Pragoproetus tafilaltensis | 786 | Large eyes | Inner shelf | Predator/Scavenger | 5.6 | SMF 23051 | Alberti 1969 | =0,012086 | Pragian | Cranidium |
| Proetida | Proetidae | Pragoproetus | Pragoproetus tafilaltensis | 787 | Large eyes | Inner shelf | Predator/Scavenger | 5.7a | SMF 23052 | Alberti 1969 | =0,010304 | Pragian | Cranidium |
| Proetida | Proetidae | Pragoproetus | Pragoproetus tafilaltensis | 788 | Large eyes | Inner shelf | Predator/Scavenger | 5.8a | CGMTA 211 | Alberti 1969 | =0,009280 | Pragian | Cranidium |
| Proetida | Proetidae | Pragoproetus | Pragoproetus tafilaltensis | 789 | Large eyes | Inner shelf | Predator/Scavenger | 5.9a | SMF 23053 | Alberti 1969 | =0,010017 | Pragian | Cranidium |
| Proetida | Proetidae | Pragoproetus | Pragoproetus tafilaltensis | 790 | Large eyes | Inner shelf | Predator/Scavenger | 5.10a | SMF 23054 | Alberti 1969 | =0,009603 | Pragian | Cranidium |
| Proetida | Proetidae | Pragoproetus | Pragoproetus tafilaltensis | 791 | Large eyes | Inner shelf | Predator/Scavenger | 5.11a | CGMTA 22 | Alberti 1969 | =0,007222 | Pragian | Cranidium |
| Proetida | Proetidae | Pragoproetus | Pragoproetus tafilaltensis | 792 | Large eyes | Inner shelf | Predator/Scavenger | 5.12a | CGMTA 23 | Alberti 1969 | =0,005940 | Pragian | Cranidium |
| Proetida | Proetidae | Pragoproetus | Pragoproetus tafilaltensis | 793 | Large eyes | Inner shelf | Predator/Scavenger | 5.13a | CGMTA 24 | Alberti 1969 | =0,007444 | Pragian | Cranidium |
| Proetida | Proetidae | Pragoproetus | Pragoproetus tafilaltensis | 794 | Large eyes | Inner shelf | Predator/Scavenger | 5.15 | SMF 23055 | Alberti 1969 | =0,004918 | Pragian | Cranidium |
| Proetida | Proetidae | Pragoproetus | Pragoproetus tafilaltensis | 795 | Large eyes | Inner shelf | Predator/Scavenger | 5.16 | SMF 23056 | Alberti 1969 | =0,004739 | Pragian | Cranidium |
| Proetida | Proetidae | Pragoproetus | Pragoproetus tafilaltensis | 796 | Large eyes | Inner shelf | Predator/Scavenger | 5.17 | SMF 23057 | Alberti 1969 | =0,013318 | Pragian | Cranidium |
| Proetida | Proetidae | Pragoproetus | Pragoproetus tafilaltensis | 797 | Large eyes | Inner shelf | Predator/Scavenger | 17.3 | SMF 18191 | Alberti 1964 | =0,005958 | Pragian | Cranidium |
| Proetida | Proetidae | Prodrevermannia | Prodrevermannia jaegeri jaegeri | 798 | Blind | Middle shelf | Predator/Scavenger | 6.61 | SMF 36561 | Alberti 1983 | =0.006425 | Pragian | Cranidium |
| Proetida | Proetidae | Prodrevermannia | Prodrevermannia jaegeri jaegeri | 799 | Blind | Middle shelf | Predator/Scavenger | 6.62 | SH | Alberti 1983 | =0.005866 | Pragian | Cranidium |
| Proetida | Proetidae | Prodrevermannia | Prodrevermannia jaegeri jaegeri | 800 | Blind | Middle shelf | Predator/Scavenger | 6.63 | SH | Alberti 1983 | =0.005866 | Pragian | Cranidium |
| Proetida | Proetidae | Prodrevermannia | Prodrevermannia baghdadlii | 801 | Blind | Middle shelf | Predator/Scavenger | 6.66 | SH | Alberti 1983 | =0.011412 | Emsian | Cranidium |
| Proetida | Proetidae | Prodrevermannia | Prodrevermannia rabatensis senior | 802 | Blind | Middle shelf | Predator/Scavenger | 8.1a | CGMTA 257 | Alberti 1970a | =0,006070 | Lochkovian | Cranidium |
| Proetida | Proetidae | Prodrevermannia | Prodrevermannia rabatensis senior | 803 | Blind | Middle shelf | Predator/Scavenger | 8.2 | CGMTA 258 | Alberti 1970a | =0,006616 | Lochkovian | Cranidium |
| Proetida | Proetidae | Prodrevermannia | Prodrevermannia rabatensis senior | 804 | Blind | Middle shelf | Predator/Scavenger | 8.3 | SMF 23477 | Alberti 1970a | =0,005485 | Lochkovian | Cranidium |

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| Proetida | Proetidae | Prodrevermannia | Prodrevermannia medioxima | 805 | Blind | Middle shelf | Predator/Scavenger | 21.4a | SMF 23244 | Alberti 1969 | =0,008880 | Pragian | Cranidium |
| Proetida | Proetidae | Prodrevermannia | Prodrevermannia medioxima | 806 | Blind | Middle shelf | Predator/Scavenger | 21.5a | CGMTA 99 | Alberti 1969 | =0,008880 | Pragian | Cranidium |
| Proetida | Proetidae | Prodrevermannia | Prodrevermannia jaegeri zemmoura | 807 | Blind | Middle shelf | Predator/Scavenger | 21.11a | SMF 23241 | Alberti 1969 | =0,007551 | Pragian | Cranidium |
| Proetida | Proetidae | Prodrevermannia | Prodrevermannia jaegeri zemmoura | 808 | Blind | Middle shelf | Predator/Scavenger | 21.12a | CGMTA 97 | Alberti 1969 | =0,007436 | Pragian | Cranidium |
| Proetida | Proetidae | Prodrevermannia | Prodrevermannia jaegeri zemmoura | 809 | Blind | Middle shelf | Predator/Scavenger | 21.13a | SMF 23242 | Alberti 1969 | =0,005482 | Pragian | Cranidium |
| Proetida | Proetidae | Prodrevermannia | Prodrevermannia jaegeri zemmoura | 810 | Blind | Middle shelf | Predator/Scavenger | 21.15 | CGMTA 204 | Alberti 1969 | =0,006265 | Pragian | Cranidium |
| Proetida | Proetidae | PROETINAE | Indet | 811 | Large eyes | Middle shelf | Predator/Scavenger | 1.12a | CGMT | Alberti 1969 | =0,020104 | | Cranidium |
| Proetida | Proetidae | Ignoproetus | Ignoproetus waldschmidti | 812 | Large eyes | Middle shelf | Predator/Scavenger | 6.1 | SMF 23589 | Alberti 1970a | =0,010147 | Emsian | Cranidium |
| Proetida | Proetidae | Ignoproetus | Ignoproetus waldschmidti | 813 | Large eyes | Middle shelf | Predator/Scavenger | 6.2a | SMF 23590 | Alberti 1970a | =0,007831 | Emsian | Cranidium |
| Proetida | Proetidae | Ignoproetus | Ignoproetus waldschmidti | 814 | Large eyes | Middle shelf | Predator/Scavenger | 6.3 | CGMTA 354 | Alberti 1970a | =0,008874 | Emsian | Cranidium |
| Proetida | Proetidae | Ignoproetus | Ignoproetus waldschmidti | 815 | Large eyes | Middle shelf | Predator/Scavenger | 17.1a | SMF 23203 | Alberti 1969 | =0,009810 | Eifelian | Cranidium |
| Proetida | Proetidae | Ignoproetus | Ignoproetus waldschmidti | 816 | Large eyes | Middle shelf | Predator/Scavenger | 17.2a | CGMTA 79 | Alberti 1969 | =0,006894 | Eifelian | Cranidium |
| Proetida | Proetidae | Proetopeltis | Proetopeltis neglectus hamlagdadicus | 817 | Large eyes | Middle shelf | Predator/Scavenger | 17.10a | CGMTA 78 | Alberti 1969 | =0,007830 | Eifelian | Cranidium |
| Proetida | Proetidae | Proetopeltis | Proetopeltis neglectus hamlagdadicus | 818 | Large eyes | Middle shelf | Predator/Scavenger | 17.11a | SMF 23201 | Alberti 1969 | =0,008525 | Eifelian | Cranidium |
| Proetida | Proetidae | Proetopeltis | Proetopeltis neglectus hamlagdadicus | 819 | Large eyes | Middle shelf | Predator/Scavenger | 17.12 | SMF 23202 | Alberti 1969 | =0,007324 | Eifelian | Cranidium |
| Proetida | Proetidae | Proetus | Proetus orbitatus | 820 | Large eyes | Middle shelf | Predator/Scavenger | 2.8a | CGMT | Alberti 1969 | =0,016502 | | Cranidium |
| Proetida | Proetidae | Proetus | Proetus proetus sp A aff granulosus | 821 | Large eyes | Middle shelf | Predator/Scavenger | 3.5a | CGMT-TM 21 | Alberti 1970a | =0,016616 | Emsian | Cephalon |
| Proetida | Proetidae | Proetus | Proetus proetus sp L | 822 | Large eyes | Middle shelf | Predator/Scavenger | 3.6a | ISCR | Alberti 1970a | =0,015535 | Emsian | Cranidium |
| Proetida | Proetidae | Sculptoproetus | Sculptoproetus maghrebus | 823 | Large eyes | Middle shelf | Predator/Scavenger | 4.5 | CGMTA 242 | Alberti 1970a | =0,005539 | Emsian | Cranidium |
| Proetida | Proetidae | Sculptoproetus | Scultoproetus sculptus posterior | 824 | Large eyes | Middle shelf | Predator/Scavenger | 4.7a | SMF 23461 | Alberti 1970a | =0,006022 | Emsian | Cranidium |
| Proetida | Proetidae | Sculptoproetus | Scultoproetus sculptus posterior | 825 | Large eyes | Middle shelf | Predator/Scavenger | 4.8 | CGMTA 244 | Alberti 1970a | =0,006258 | Emsian | Cranidium |
| Proetida | Proetidae | Sculptoproetus | Sculptoproetus maghrebus | 826 | Large eyes | Middle shelf | Predator/Scavenger | 5.46 | SMF 36554 | Alberti 1983 | =0.007006 | Emsian | Cranidium |
| Proetida | Proetidae | Sculptoproetus | Sculptoproetus sculptus antiquus | 827 | Large eyes | Middle shelf | Predator/Scavenger | 13.1a | SMF 23138 | Alberti 1969 | =0,007688 | Pragian | Cranidium |
| Proetida | Proetidae | Sculptoproetus | Sculptoproetus sculptus antiquus | 828 | Large eyes | Middle shelf | Predator/Scavenger | 13.2a | CGMTA 46 | Alberti 1969 | =0,006921 | Pragian | Cranidium |
| Proetida | Proetidae | Sculptoproetus | Sculptoproetus sculptus antiquus | 829 | Large eyes | Middle shelf | Predator/Scavenger | 13.3a | SMF 23137 | Alberti 1969 | =0,007327 | Pragian | Cranidium |
| Proetida | Proetidae | Sculptoproetus | Sculptoproetus sculptus antiquus | 830 | Large eyes | Middle shelf | Predator/Scavenger | 13.4a | CGMT-AT 204/1 | Alberti 1969 | =0,007199 | Pragian | Cranidium |
| Proetida | Proetidae | Sculptoproetus | Sculptoproetus sculptus antiquus | 831 | Large eyes | Middle shelf | Predator/Scavenger | 13.5 | CGMT-AT 204/1 | Alberti 1969 | =0,007659 | Pragian | Cranidium |
| Proetida | Proetidae | Sculptoproetus | Sculptoproetus sculptus antiquus | 832 | Large eyes | Middle shelf | Predator/Scavenger | 13.6a | CGMTA 48 | Alberti 1969 | =0,006085 | Pragian | Cranidium |
| Proetida | Proetidae | Sculptoproetus | Sculptoproetus sculptus antiquus | 833 | Large eyes | Middle shelf | Predator/Scavenger | 13.7a | SMF 23141 | Alberti 1969 | =0,005399 | Pragian | Cranidium |
| Proetida | Proetidae | Sculptoproetus | Sculptoproetus sculptus antiquus | 834 | Large eyes | Middle shelf | Predator/Scavenger | 13.8 | SMF 23142 | Alberti 1969 | =0,004598 | Pragian | Cranidium |
| Proetida | Proetidae | Sculptoproetus | Sculptoproetus sculptus antiquus | 835 | Large eyes | Middle shelf | Predator/Scavenger | 13.9a | SMF 23143 | Alberti 1969 | =0,004398 | Pragian | Cranidium |
| Proetida | Proetidae | Sculptoproetus | Sculptoproetus sp A | 836 | Large eyes | Middle shelf | Predator/Scavenger | 40.1 | UA 13259 | Chatterton 2006 | =0,026225 | Emsian | Cranidium |
| Proetida | Proetidae | Sculptoproetus | Sculptoproetus haasi | 837 | Large eyes | Middle shelf | Predator/Scavenger | 40.8 | UA 13265 | Chatterton 2006 | =0,023544 | Eifelian | Cranidium |
| Proetida | Proetidae | Sculptoproetus | Sculptoproetus sp B | 838 | Large eyes | Middle shelf | Predator/Scavenger | 40.11 | UA 13260 | Chatterton 2006 | =0,034202 | Eifelian | Cranidium |
| Proetida | Tropidocoryphidae | Tafilaltaspis | Tafilaltaspis creber creber | 840 | Large eyes | Middle shelf | Predator/Scavenger | 6.7a | SMF 23472 | Alberti 1970a | =0,005288 | Emsian | Cranidium |
| Proetida | Tropidocoryphidae | Tafilaltaspis | Tafilaltaspis creber tenuigranifer | 841 | Large eyes | Middle shelf | Predator/Scavenger | 12.1 | SMF 23192 | Alberti 1969 | =0,006148 | Eifelian | Cranidium |
| Proetida | Tropidocoryphidae | Tafilaltaspis | Tafilaltaspis creber tenuigranifer | 842 | Large eyes | Middle shelf | Predator/Scavenger | 12.2a | CGMTA 75 | Alberti 1969 | =0,009026 | Eifelian | Cranidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Proetida | Tropidocoryphidae | Tafilaltaspis | Tafilaltaspis creber tenuigranifer | 843 | Large eyes | Middle shelf | Predator/Scavenger | 12.3 | CGMTA 76 | Alberti 1969 | =0,008473 | Eifelian | Cranidium |
| Proetida | Tropidocoryphidae | Tafilaltaspis | Tafilaltaspis creber tenuigranifer | 844 | Large eyes | Middle shelf | Predator/Scavenger | 12.4a | SMF 23193 | Alberti 1969 | =0,008048 | Eifelian | Cranidium |
| Proetida | Tropidocoryphidae | Tafilaltaspis | Tafilaltaspis creber tenuigranifer | 845 | Large eyes | Middle shelf | Predator/Scavenger | 12.5 | SMF 23194 | Alberti 1969 | =0,006148 | Eifelian | Cranidium |
| Proetida | Tropidocoryphidae | Tafilaltaspis | Tafilaltaspis creber tenuigranifer | 846 | Large eyes | Middle shelf | Predator/Scavenger | 12.6a | CGMTA 77 | Alberti 1969 | =0,007122 | Eifelian | Cranidium |
| Proetida | Tropidocoryphidae | Tafilaltaspis | Tafilaltaspis nitidus | 847 | Large eyes | Middle shelf | Predator/Scavenger | 12.15a | CGMTA 192 | Alberti 1969 | =0,008673 | Emsian | Cranidium |
| Proetida | Tropidocoryphidae | Tafilaltaspis | Tafilaltaspis maidericus | 848 | Large eyes | Middle shelf | Predator/Scavenger | 12.16a | CGMTA 188 | Alberti 1969 | =0,004789 | Emsian | Cranidium |
| Proetida | Tropidocoryphidae | Tafilaltaspis | Tafilaltaspis creber creber | 849 | Large eyes | Middle shelf | Predator/Scavenger | 12.7a | SMF 23001 | Alberti 1969 | =0,005132 | Emsian | Cranidium |
| Proetida | Tropidocoryphidae | Tafilaltaspis | Tafilaltaspis creber creber | 850 | Large eyes | Middle shelf | Predator/Scavenger | 12.8 | SMF 23002 | Alberti 1969 | =0,004494 | Emsian | Cranidium |
| Proetida | Tropidocoryphidae | Tafilaltaspis | Tafilaltaspis creber creber | 851 | Large eyes | Middle shelf | Predator/Scavenger | 12.9 | SMF 23428 | Alberti 1969 | =0,004448 | Emsian | Cranidium |
| Proetida | Tropidocoryphidae | Tafilaltaspis | Tafilaltaspis creber creber | 852 | Large eyes | Middle shelf | Predator/Scavenger | 12.10a | SMF 23429 | Alberti 1969 | =0,005349 | Emsian | Cranidium |
| Proetida | Tropidocoryphidae | Tafilaltaspis | Tafilaltaspis creber creber | 853 | Large eyes | Middle shelf | Predator/Scavenger | 12.11a | CGMTA 1 | Alberti 1969 | =0,006189 | Emsian | Cranidium |
| Proetida | Tropidocoryphidae | Tafilaltaspis | Tafilaltaspis creber creber | 854 | Large eyes | Middle shelf | Predator/Scavenger | 12.12 | SMF 23430 | Alberti 1969 | =0,005429 | Emsian | Cranidium |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus haasi | 855 | Large eyes | Middle shelf | Predator/Scavenger | 4.2 | UA 13275 | Gibb 2007 | =0,007013 | Eifelian | Cranidium |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus haasi | 856 | Large eyes | Middle shelf | Predator/Scavenger | 6.3 | UA 13282 | Gibb 2007 | =0,003799 | Eifelian | Cranidium |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus dibbanus | 857 | Large eyes | Middle shelf | Predator/Scavenger | 7.4 | UA 13257 | Gibb 2007 | =0,007550 | Emsian | Cranidium |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus elguerrouji | 858 | Large eyes | Middle shelf | Predator/Scavenger | 8.5 | UA 13262 | Gibb 2007 | =0,007366 | Eifelian | Cranidium |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus elguerrouji | 859 | Large eyes | Middle shelf | Predator/Scavenger | 9.2 | UA 13261 | Gibb 2007 | =0,008787 | Eifelian | Cranidium |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus haasi | 860 | Large eyes | Middle shelf | Predator/Scavenger | 9.6 | UA 13267 | Gibb 2007 | =0,007487 | Eifelian | Cranidium |
| Proetida | Proetidae | Unguliproetus | Unguliproetus unguloides tener | 861 | Large eyes | Middle shelf | Predator/Scavenger | 6.7 | CGMTA 17 | Alberti 1969 | =0,007606 | Emsian | Cranidium |
| Proetida | Proetidae | Unguliproetus | Unguliproetus unguloides tener | 862 | Large eyes | Middle shelf | Predator/Scavenger | 17.2 | SMF 18190 | Alberti 1964 | =0,005589 | Emsian | Cranidium |
| Proetida | Proetidae | Vicinoproetus | Vicinoproetus vicinus vicinus | 863 | Large eyes | Middle shelf | Predator/Scavenger | 15.1a | SMF 23177 | Alberti 1969 | =0,011339 | Pragian | Cranidium |
| Proetida | Proetidae | Vicinoproetus | Vicinoproetus vicinus vicinus | 864 | Large eyes | Middle shelf | Predator/Scavenger | 15.2 | SMF 23178 | Alberti 1969 | =0,009166 | Pragian | Cranidium |
| Proetida | Proetidae | Vicinoproetus | Vicinoproetus vicinus vicinus | 865 | Large eyes | Middle shelf | Predator/Scavenger | 15.3 | CGMTA 67 | Alberti 1969 | =0,006712 | Pragian | Cranidium |
| Proetida | Proetidae | Vicinoproetus | Vicinoproetus vicinus vicinus | 866 | Large eyes | Middle shelf | Predator/Scavenger | 15.4 | SMF 23179 | Alberti 1969 | =0,005095 | Pragian | Cranidium |
| Proetida | Proetidae | Vicinoproetus | Vicinoproetus vicinus subtenuis | 867 | Large eyes | Middle shelf | Predator/Scavenger | 15.6a | CGMTA 69 | Alberti 1969 | =0,009051 | Pragian | Cranidium |
| Proetida | Proetidae | Vicinoproetus | Vicinoproetus vicinus subtenuis | 868 | Large eyes | Middle shelf | Predator/Scavenger | 15.7a | SMF 23180 | Alberti 1969 | =0,007111 | Pragian | Cranidium |
| Proetida | Proetidae | Vicinoproetus | Vicinoproetus vicinus subtenuis | 869 | Large eyes | Middle shelf | Predator/Scavenger | 15.8 | SMF 23181 | Alberti 1969 | =0,007111 | Pragian | Cranidium |
| Proetida | Proetidae | Vicinoproetus | Vicinoproetus boucoti | 870 | Large eyes | Middle shelf | Predator/Scavenger | 27.15a | SMF 23302 | Alberti 1969 | =0,008428 | Pragian | Cranidium |
| Proetida | Proetidae | Vicinoproetus | Vicinoproetus boucoti | 871 | Large eyes | Middle shelf | Predator/Scavenger | 27.16a | SMF 23303 | Alberti 1969 | =0,008556 | Pragian | Cranidium |
| Proetida | Proetidae | Vicinoproetus | Vicinoproetus boucoti | 872 | Large eyes | Middle shelf | Predator/Scavenger | 27.17 | CGMTA 124 | Alberti 1969 | =0,007447 | Pragian | Cranidium |
| Proetida | Proetidae | Warbugella | Warbugella rugulosa maura | 873 | Large eyes | Inner shelf | Predator/Scavenger | 32.1a | CGMTA 137 | Alberti 1969 | =0,007667 | Lochkovian | Cranidium |
| Proetida | Proetidae | Warbugella | Warbugella rugulosa maura | 874 | Large eyes | Inner shelf | Predator/Scavenger | 32.2a | SMF 23351 | Alberti 1969 | =0,005801 | Lochkovian | Cranidium |
| Proetida | Proetidae | Warbugella | Warbugella rugulosa maura | 875 | Large eyes | Inner shelf | Predator/Scavenger | 32.3a | SMF 23352 | Alberti 1969 | =0,006147 | Lochkovian | Cranidium |
| Proetida | Proetidae | Warbugella | Warbugella rugulosa maura | 876 | Large eyes | Inner shelf | Predator/Scavenger | 32.4 | CGMTA 138 | Alberti 1969 | =0,005801 | Lochkovian | Cranidium |
| Proetida | Proetidae | Warbugella | Warbugella rugulosa maura | 877 | Large eyes | Inner shelf | Predator/Scavenger | 32.5 | SMF 23353 | Alberti 1969 | =0,006654 | Lochkovian | Cranidium |
| Proetida | Proetidae | Warbugella | Warbugella rugulosa maura | 878 | Large eyes | Inner shelf | Predator/Scavenger | 32.6a | SMF 23354 | Alberti 1969 | =0,006410 | Lochkovian | Cranidium |
| Proetida | Proetidae | Warbugella | Warbugella rugulosa maura | 879 | Large eyes | Inner shelf | Predator/Scavenger | 32.7 | CGMTA 139 | Alberti 1969 | =0,004853 | Lochkovian | Cranidium |
| Proetida | Proetidae | Warbugella | Warbugella rugulosa maura | 880 | Large eyes | Inner shelf | Predator/Scavenger | 32.8 | CGMT | Alberti 1969 | =0,004853 | Lochkovian | Cranidium |
| Proetida | Proetidae | Warbugella | Warbugella rugulosa maura | 881 | Large eyes | Inner shelf | Predator/Scavenger | 32.9 | SMF 23355 | Alberti 1969 | =0,005821 | Lochkovian | Cranidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Proetida | Proetidae | Warbugella | Warbugella rugulosa maura | 882 | Large eyes | Inner shelf | Predator/Scavenger | 32.10a | SMF 23356 | Alberti 1969 | =0,005896 | Lochkovian | Cranidium |
| Proetida | Proetidae | Warbugella | Warbugella rugulosa maura | 883 | Large eyes | Inner shelf | Predator/Scavenger | 32.11 | SMF 23357 | Alberti 1969 | =0,004433 | Lochkovian | Cranidium |
| Proetida | Proetidae | Haasproetus | Haasproetus wildungensis | 884 | Large eyes | Middle shelf | Predator/Scavenger | 9.6 | CGMT-HA 3 | H. Alberti 1973 | =0.008309 | Famennian | Cranidium |
| Asaphida | Raphiophoridae | Raphiophorus | Raphiophorus rouaulti | 885 | Blind | Middle shelf | Predator/Scavenger | 1.8 | No name | Alberti 1966c | =0,005265 | Ludlow-Pridoli | Cranidium |
| Asaphida | Raphiophoridae | Raphiophorus | Raphiophorus rouaulti | 886 | Blind | Middle shelf | Predator/Scavenger | 1.9 | No name | Alberti 1966c | =0,003980 | Ludlow-Pridoli | Cranidium |
| Asaphida | Raphiophoridae | Raphiophorus | Raphiophorus rouaulti | 887 | Blind | Middle shelf | Predator/Scavenger | 5.55 | LGFSA | Alberti 1981a | =0.014017 | Ludlow-Pridoli | Cranidium |
| Asaphida | Raphiophoridae | Raphiophorus | Raphiophorus rouaulti | 888 | Blind | Middle shelf | Predator/Scavenger | 5.56 | LGFSA | Alberti 1981a | =0.014017 | Ludlow-Pridoli | Cranidium |
| Asaphida | Raphiophoridae | Raphiophorus | Raphiophorus rouaulti | 889 | Blind | Middle shelf | Predator/Scavenger | 42.7 | CGMTA 208 | Alberti 1969 | =0,005505 | Ludlow-Pridoli | Cranidium |
| Corynexoch | Scutelluidae | Cavetia | Cavetia furcifera hamlagdadiana | 891 | Large eyes | Middle shelf | Predator/Scavenger | 7 | No name | Alberti 1981b | =0.016818 | Emsian | Cranidium |
| Corynexoch | Scutelluidae | Heliopeltis | Heliopeltis ihmadii | 894 | Large eyes | Inner shelf | Predator/Scavenger | 12a | UM-IP 705 | Feist 2015 | =0,021048 | | Cranidium |
| Corynexoch | Scutelluidae | Heliopeltis | Heliopeltis ihmadii | 895 | Large eyes | Inner shelf | Predator/Scavenger | 13a | UM-IP 706 | Feist 2015 | =0,017241 | | Cranidium |
| Corynexoch | Scutelluidae | Heliopeltis | Heliopeltis ihmadii | 896 | Large eyes | Inner shelf | Predator/Scavenger | 13e | UM-IP 707 | Feist 2015 | =0,015998 | | Cranidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis hamlaghdadica | 897 | Large eyes | Inner shelf | Predator/Scavenger | 1.8a | CGMTA 239 | Alberti 1970a | =0,030878 | Pragian | Cranidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis chlupaci hollardi | 899 | Large eyes | Inner shelf | Predator/Scavenger | 4f | UA 14326 | Feist 2015 | =0,032255 | Pragian | Cranidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis bassei | 900 | Large eyes | Inner shelf | Predator/Scavenger | 5b | UM-IP 654 | Feist 2015 | =0,023805 | Pragian | Cranidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis hamlaghdadica | 901 | Large eyes | Inner shelf | Predator/Scavenger | 6a | UM-IP 658 | Feist 2015 | =0,030118 | Pragian | Cranidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis hamlaghdadica | 902 | Large eyes | Inner shelf | Predator/Scavenger | 6e | UA 14328 | Feist 2015 | =0,011234 | Pragian | Cranidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis maghrebia | 903 | Large eyes | Inner shelf | Predator/Scavenger | 7a | UM-IP 666 | Feist 2015 | =0,025509 | Pragian | Cranidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis maghrebia | 904 | Large eyes | Inner shelf | Predator/Scavenger | 7d | UM-IP 667 | Feist 2015 | =0,022522 | Pragian | Cranidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis tafilaltensis | 905 | Large eyes | Inner shelf | Predator/Scavenger | 8a | UA 14329 | Feist 2015 | =0,007220 | Pragian | Cranidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis tafilaltensis | 906 | Large eyes | Inner shelf | Predator/Scavenger | 8d | UM-IP 679 | Feist 2015 | =0,012193 | Pragian | Cranidium |
| Corynexoch | Scutelluidae | Platyscutellum | Platyscutellum massai | 914 | Large eyes | Middle shelf | Predator/Scavenger | 4 | | Alberti 1981b | =0.032443 | Pragian | Cranidium |
| Corynexoch | Scutelluidae | Platyscutellum | Platyscutellum massai | 915 | Large eyes | Middle shelf | Predator/Scavenger | 5 | SMF 36336 | Alberti 1981b | =0.032443 | Pragian | Cranidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Corynexoch | Scutelluidae | Platyscutellum | Platyscutellum massai | 916 | Large eyes | Middle shelf | Predator/Scavenger | 5 | | Alberti 1982 | =0,065376 | Pragian | Cranidium |
| Corynexoch | Scutelluidae | Sagittapeltis | Sagittapeltis belkai | 917 | Large eyes | Inner shelf | Predator/Scavenger | 9a | UM-IP 694 | Feist 2015 | =0,020614 | Emsian | Cranidium |
| Corynexoch | Scutelluidae | Sagittapeltis | Sagittapeltis belkai | 918 | Large eyes | Inner shelf | Predator/Scavenger | 9g | UM-IP 695 | Feist 2015 | =0,024969 | Emsian | Cranidium |
| Corynexoch | Scutelluidae | Scabriscutellum | Scabriscutellum frix | 919 | Large eyes | Middle shelf | Predator/Scavenger | 2.1a | CGMTA 234 | Alberti 1970a | =0,025916 | Pragian | Cephalon |
| Corynexoch | Scutelluidae | Scabriscutellum | Scabriscutellum lahceni | 920 | Large eyes | Middle shelf | Predator/Scavenger | 47.2 | UA 13410 | Chatterton 2006 | =0,057221 | Emsian | Cranidium |
| Corynexoch | Scutelluidae | Scabriscutellum | Scabriscutellum hammadi | 921 | Large eyes | Middle shelf | Predator/Scavenger | 48.3 | UA 13411 | Chatterton 2006 | =0,097256 | Emsian | Cephalon |
| Corynexoch | Scutelluidae | Scabriscutellum | Scabriscutellum hammadi | 922 | Large eyes | Middle shelf | Predator/Scavenger | 48.6 | UA 13412 | Chatterton 2006 | =0,099918 | Emsian | Cephalon |
| Corynexoch | Scutelluidae | Thysanopeltis | Thysanopeltis speciosa austromaura | 923 | Large eyes | Middle shelf | Predator/Scavenger | 1.2 | GPIH | Alberti 1981a | =0.009406 | Eifelian | Cranidium |
| Proetida | Tropidocoryphidae | Alberticoryphe | Alberticoryphe cogneyi | 924 | Large eyes | Middle shelf | Predator/Scavenger | 17.4 | SMF 18193 | Alberti 1964 | =0,004936 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Alberticoryphe | Alberticoryphe cogneyi | 925 | Large eyes | Middle shelf | Predator/Scavenger | 17.5 | SMF 18192 | Alberti 1964 | =0,005724 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Alberticoryphe | Alberticoryphe stirps | 926 | Large eyes | Middle shelf | Predator/Scavenger | 29.17 | SMF 23197 | Alberti 1969 | =0,011674 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Alberticoryphe | Alberticoryphe rugosa | 927 | Large eyes | Middle shelf | Predator/Scavenger | 30.15a | CGMTA 31 | Alberti 1969 | =0,006373 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Alberticoryphe | Alberticoryphe rugosa | 928 | Large eyes | Middle shelf | Predator/Scavenger | 30.16a | SMF 23342 | Alberti 1969 | =0,010973 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Alberticoryphe | Alberticoryphe stirps | 929 | Large eyes | Middle shelf | Predator/Scavenger | 4.33 | SMF 36288 | Alberti 1981a | =0.021374 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Decoroproetus | Decoroproetus decorus maurulus | 930 | Large eyes | Middle shelf | Predator/Scavenger | 29.14 | CGMTA 197 | Alberti 1969 | =0,012815 | Ludlow-Pridoli | Cranidium |
| Proetida | Tropidocoryphidae | Decoroproetus | Decoroproetus decorus maurulus | 931 | Large eyes | Middle shelf | Predator/Scavenger | 29.15 | SMF 23341 | Alberti 1969 | =0,013187 | Ludlow-Pridoli | Cranidium |
| Proetida | Tropidocoryphidae | Decoroproetus | Decoroproetus concentricus meridianus | 932 | Large eyes | Middle shelf | Predator/Scavenger | 31.17a | CGMTA 135 | Alberti 1969 | =0,008098 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Decoroproetus | Decoroproetus concentricus meridianus | 933 | Large eyes | Middle shelf | Predator/Scavenger | 31.18 | SMF 23347 | Alberti 1969 | =0,007191 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Denemarkia | Denemarkia tafilaltensis | 934 | Large eyes | Middle shelf | Predator/Scavenger | 6.73 | SMF 36586 | Alberti 1983 | =0.006438 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Denemarkia | Denemarkia tafilaltensis | 935 | Large eyes | Middle shelf | Predator/Scavenger | 31.1a | CGMTA 183 | Alberti 1969 | =0,005704 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Denemarkia | Denemarkia africana | 936 | Large eyes | Middle shelf | Predator/Scavenger | 31.2 | SMF 23333 | Alberti 1969 | =0,006834 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Denemarkia | Denemarkia africana | 937 | Large eyes | Middle shelf | Predator/Scavenger | 31.3a | SMF 23334 | Alberti 1969 | =0,005089 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Denemarkia | Denemarkia africana | 938 | Large eyes | Middle shelf | Predator/Scavenger | 31.4 | SMF 23335 | Alberti 1969 | =0,005089 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Denemarkia | Denemarkia africana | 939 | Large eyes | Middle shelf | Predator/Scavenger | 31.5 | CGMTA 128 | Alberti 1969 | =0,005353 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Denemarkia | Denemarkia africana | 940 | Large eyes | Middle shelf | Predator/Scavenger | 31.6 | SMF 23336 | Alberti 1969 | =0,005594 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Denemarkia | Denemarkia africana | 941 | Large eyes | Middle shelf | Predator/Scavenger | 31.7 | SMF 23337 | Alberti 1969 | =0,005465 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Denemarkia | Denemarkia africana | 942 | Large eyes | Middle shelf | Predator/Scavenger | 31.8 | SMF 23338 | Alberti 1969 | =0,005353 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Galbertianus | Galbertianus hollardi | 943 | Large eyes | Middle shelf | Predator/Scavenger | 16.7a | SMF 18199 | Alberti 1964 | =0,004967 | | Cranidium |
| Proetida | Tropidocoryphidae | Galbertianus | Galbertianus draae | 944 | Large eyes | Middle shelf | Predator/Scavenger | 31.15a | CGMTA 132 | Alberti 1969 | =0,005704 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Tropidocoryphe | Tropidocoryphe mediterranea | 945 | Large eyes | Middle shelf | Predator/Scavenger | 3.v | UM-IP 815 | Feist 2018 | =0,005682 | Emsian | |
| Proetida | Tropidocoryphidae | Tropidocoryphe | Tropidocoryphe mauretanica | 946 | Large eyes | Middle shelf | Predator/Scavenger | 30.1 | SMF 23331 | Alberti 1969 | =0,006062 | Pragian | Cranidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Proetida | Tropidocoryphidae | Tropidocoryphe | Tropidocoryphe hamlaghdadica | 947 | Large eyes | Middle shelf | Predator/Scavenger | 30.6 | SMF 23329 | Alberti 1969 | =0,007041 | Pragian | Cranidium |
| Proetida | Tropidocoryphidae | Tropidocoryphe | Tropidocoryphe maroccanica | 948 | Large eyes | Middle shelf | Predator/Scavenger | a.18 | SMF 23332 | Alberti 1967a | =0.007899 | Pragian | Cranidium |
| Phacopida | Acastidae | Minicryphaeus | Minicryphaeus giganteus | 949 | Large eyes | Shallow | Predator/Scavenger | 3.2 | 80202 | Bignon 2014 | =0,048541 | Pragian | Cephalon |
| Phacopida | Acastidae | Minicryphaeus | Minicryphaeus giganteus | 950 | Large eyes | Shallow | Predator/Scavenger | 3.4 | JC 101 | Bignon 2014 | =0,046727 | Pragian | Cephalon |
| Phacopida | Acastidae | Minicryphaeus | Minicryphaeus giganteus | 951 | Large eyes | Shallow | Predator/Scavenger | 4.2 | JC 103 | Bignon 2014 | =0,055858 | Pragian | Cephalon |
| Phacopida | Acastidae | Minicryphaeus | Minicryphaeus giganteus | 952 | Large eyes | Shallow | Predator/Scavenger | 4.3 | JC 102 | Bignon 2014 | =0,053763 | Pragian | Cephalon |
| Proetida | Proetidae | Perliproetus | Perliproetus africanus | 953 | Large eyes | Middle shelf | Predator/Scavenger | 1O | MB.T 6223 | FeistWeyer 2018 | =0,030289 | Famennian | Cranidium |
| Proetida | Proetidae | Perliproetus | Perliproetus africanus | 954 | Large eyes | Middle shelf | Predator/Scavenger | 1Z | MB.T 6228 | FeistWeyer 2018 | =0.036936 | Famennian | Cranidium |
| Proetida | Proetidae | Perliproetus | Perliproetus africanus | 955 | Large eyes | Middle shelf | Predator/Scavenger | 1T | MB.T 6221 | FeistWeyer 2018 | =0.028560 | Famennian | Cranidium |
| Proetida | Aulacopleuridae | Cyphaspides | Cyphaspides ammari | 956 | Small eyes | Middle shelf | Particle feeding | 2.3 | UA 14313 | Chatterton 2019 | =0,058823 | Eifelian | Cranidium |
| Proetida | Aulacopleuridae | Cyphaspides | Cyphaspides ammari | 957 | Small eyes | Middle shelf | Particle feeding | 3.1 | UA 14315 | Chatterton 2019 | =0,049998 | Eifelian | Cranidium |
| Proetida | Aulacopleuridae | Cyphaspides | Cyphaspides ammari | 958 | Small eyes | Middle shelf | Particle feeding | 4.1 | UA 14318 | Chatterton 2019 | =0,005780 | Eifelian | Cranidium |
| Proetida | Aulacopleuridae | Cyphaspides | Cyphaspides pankowskiorum | 959 | Small eyes | Middle shelf | Particle feeding | 5.2 | UA 14316 | Chatterton 2019 | =0,058136 | Eifelian | Cranidium |
| Proetida | Aulacopleuridae | Cyphaspides | Cyphaspides pankowskiorum | 960 | Small eyes | Middle shelf | Particle feeding | 5.4 | UA 14264 | Chatterton 2019 | =0,079355 | Eifelian | Cephalon |
| Proetida | Aulacopleuridae | Cyphaspides | Cyphaspides nicoleae | 961 | Small eyes | Middle shelf | Particle feeding | 5.5 | UA 14317 | Chatterton 2019 | =0,084743 | Eifelian | Cranidium |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis lata | 962 | Large eyes | Middle shelf | Particle feeding | 34.6a | SMF 23368 | Alberti 1969 | =0,006541 | Pragian | Cranidium |
| Phacopida | Phacopidae | Morocops | Morocops torkozensis | 963 | Large eyes | Inner shelf | Predator/Scavenger | 10.6 | PIMUZ 7287 | Klug 2008 | =0,037315 | Emsian | Cephalon |
| Phacopida | Acastidae | Morzadecops | Morzadecops zguidensis | 964 | Large eyes | Inner shelf | Predator/Scavenger | 11.6 | PIMUZ 7296 | Klug 2008 | =0,065673 | Emsian | Cephalon |
| Phacopida | Acastidae | Metacanthina | Metacanthina wallacei | 965 | Large eyes | Shallow | Predator/Scavenger | 11.10 | PIMUZ 7291 | Klug 2008 | =0,086926 | Emsian | Cephalon |
| Lichida | Odontopleuridae | Gondwanaspis | Gondwanaspis mrirtensis | 966 | Large eyes | Middle shelf | Predator/Scavenger | 2a | UM2-RF 172 | Feist 2002 | =0,005959 | Frasnian | Cephalon |
| Phacopida | Dalmanitidae | Morocconites | Morocconites malladoides | 967 | Large eyes | Inner shelf | Predator/Scavenger | 2c | No name | Edgecombe 1991 | =0.008003 | | Cephalon |
| Phacopida | Acastidae | Lanceaspis | Lanceaspis hammondi | 968 | Large eyes | Inner shelf | Predator/Scavenger | 1.1 | JC106 | Corbacho 2014 | =0,084224 | Pragian | Cephalon |
| Phacopida | Acastidae | Lanceaspis | Lanceaspis hammondi | 969 | Large eyes | Inner shelf | Predator/Scavenger | 1.2 | MGSB80843 | Corbacho 2014 | =0,057371 | Pragian | Cephalon |
| Phacopida | Acastidae | Lanceaspis | Lanceaspis hammondi | 970 | Large eyes | Inner shelf | Predator/Scavenger | 2.2 | JC107 | Corbacho 2014 | =0,083734 | Pragian | Cephalon |
| Phacopida | Acastidae | Lanceaspis | Lanceaspis hammondi | 971 | Large eyes | Inner shelf | Predator/Scavenger | 2.5 | BPM1091 | Corbacho 2014 | =0,113406 | Pragian | Cephalon |
| Proetida | Proetidae | Sculptoproetus | Sculptoproetus raki | 972 | Large eyes | Middle shelf | Predator/Scavenger | 3d | IRSBNa13414 | Van Viersen 2019 | =0,022975 | Emsian | Cephalon |
| Proetida | Proetidae | Lepidoproetus | Lepidoproetus arenicolus | 973 | Large eyes | Shallow | Predator/Scavenger | 3l | IRSBNa13434 | Van Viersen 2019 | =0,045408 | Pragian | Cephalon |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus haasi | 974 | Large eyes | Middle shelf | Predator/Scavenger | 4a | IRSBNa13416 | Van Viersen 2019 | =0,027395 | Eifelian | Cephalon |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus haasi | 975 | Large eyes | Middle shelf | Predator/Scavenger | 5a | IRSBNa13420 | Van Viersen 2019 | =0,033879 | Eifelian | Cephalon |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus haasi | 976 | Large eyes | Middle shelf | Predator/Scavenger | 5g | IRSBNa13419 | Van Viersen 2019 | =0,036340 | Emsian | Cephalon |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus haasi | 977 | Large eyes | Middle shelf | Predator/Scavenger | 5m | IRSBNa13421 | Van Viersen 2019 | =0,043468 | Emsian | Cephalon |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus sp. A | 978 | Large eyes | Middle shelf | Predator/Scavenger | 6e | IRSBNa13422 | Van Viersen 2019 | =0,045443 | | Cephalon |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus pulchistriatus pulchistriatus | 979 | Large eyes | Middle shelf | Predator/Scavenger | 6j | IRSBNa13424 | Van Viersen 2019 | =0,048766 | Emsian | Cephalon |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus gibbae | 980 | Large eyes | Middle shelf | Predator/Scavenger | 7h | IRSBNa13423 | Van Viersen 2019 | =0,020829 | Emsian | Cephalon |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus pulchistriatus repens | 981 | Large eyes | Middle shelf | Predator/Scavenger | 8a | IRSBNa13425 | Van Viersen 2019 | =0,025972 | Emsian | Cephalon |
| Proetida | Proetidae | Hollandiella | Hollandiella curvirostris | 982 | Large eyes | Inner shelf | Predator/Scavenger | 10c | IRSBNa13427 | Van Viersen 2019 | =0,051265 | Pragian | Cephalon |
| Proetida | Proetidae | Hollandiella | Hollandiella curvirostris | 983 | Large eyes | Inner shelf | Predator/Scavenger | 10d | IRSBNa13426 | Van Viersen 2019 | =0,031235 | Pragian | Cephalon |
| Proetida | Proetidae | Hollandiella | Hollandiella curvirostris | 984 | Large eyes | Inner shelf | Predator/Scavenger | 10i | IRSBNa13428 | Van Viersen 2019 | =0,035709 | Pragian | Cephalon |
| Proetida | Proetidae | Hollandiella | Hollandiella lebruni | 985 | Large eyes | Inner shelf | Predator/Scavenger | 11d | IRSBNa13429 | Van Viersen 2019 | =0,019604 | Emsian | Cephalon |
| Proetida | Proetidae | Hollandiella | Hollandiella lebruni | 986 | Large eyes | Inner shelf | Predator/Scavenger | 11g | IRSBNa13430 | Van Viersen 2019 | =0,024383 | Emsian | Cephalon |
| Proetida | Proetidae | Hollandiella | Hollandiella sp. A | 987 | Large eyes | Inner shelf | Predator/Scavenger | 12a | IRSBNa13431 | Van Viersen 2019 | =0,028569 | | Cephalon |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Proetida | Proetidae | Hollandiella | Hollandiella verecunda | 988 | Large eyes | Inner shelf | Predator/Scavenger | 13a | IRSBNa13432 | Van Viersen 2019 | =0,031235 | Pragian | Cephalon |
| Proetida | Proetidae | Lepidoproetus | Lepidoproetus maharchianus | 989 | Large eyes | Shallow | Predator/Scavenger | 13h | IRSBNa13433 | Van Viersen 2019 | =0,047606 | Pragian | Cephalon |
| Proetida | Tropidocoryphidae | Tafilaltaspis | Tafilaltaspis rufa | 990 | Large eyes | Middle shelf | Predator/Scavenger | 15a | IRSBNa13435 | Van Viersen 2019 | =0,035709 | Eifelian | Cephalon |
| Proetida | Tropidocoryphidae | Tafilaltaspis | Tafilaltaspis spA | 991 | Large eyes | Middle shelf | Predator/Scavenger | 15l | IRSBNa13436 | Van Viersen 2019 | =0,027017 | | Cephalon |
| Proetida | Proetidae | Palpebralia | Palpebralia brecciae | 992 | Blind | Deep | Predator/Scavenger | 2c | UM2-RF179 | Feist 2002 | =0,017953 | Frasnian | Cranidium |
| Proetida | Proetidae | Palpebralia | Palpebralia brecciae | 993 | Blind | Deep | Predator/Scavenger | 2j | UM2-RF182 | Feist 2002 | =0,017057 | Frasnian | Cranidium |
| Phacopida | Acastidae | Coltraneia | Coltraneia oufatenensis | 0 | Large eyes | Middle shelf | Predator/Scavenger | 11.1a | No name | Morzadec 2001 | =0,035829 | Emsian | Pygidium |
| Phacopida | Acastidae | Coltraneia | Coltraneia oufatenensis | 1 | Large eyes | Middle shelf | Predator/Scavenger | 11.3a | No name | Morzadec 2001 | =0,021489 | Emsian | Pygidium |
| Phacopida | Acastidae | Coltraneia | Coltraneia oufatenensis | 2 | Large eyes | Middle shelf | Predator/Scavenger | 11.4 | No name | Morzadec 2001 | =0,021489 | Emsian | Pygidium |
| Phacopida | Acastidae | Coltraneia | Coltraneia oufatenensis | 3 | Large eyes | Middle shelf | Predator/Scavenger | 11.6 | No name | Morzadec 2001 | =0,041974 | Emsian | Pygidium |
| Phacopida | Acastidae | Comura | Comura bultyncki | 4 | Large eyes | Middle shelf | Predator/Scavenger | 12.3c | No name | Morzadec 2001 | =0,042611 | Emsian | Pygidium |
| Phacopida | Acastidae | Comura | Comura bultyncki | 5 | Large eyes | Middle shelf | Predator/Scavenger | 12.4a | No name | Morzadec 2001 | =0,033862 | Emsian | Pygidium |
| Phacopida | Acastidae | Destombesina | Destombesina ougartensis | 6 | Large eyes | Middle shelf | Predator/Scavenger | 3.1 | No name | Morzadec 1997 | =0,002491 | Emsian | Pygidium |
| Phacopida | Acastidae | Destombesina | Destombesina ougartensis | 7 | Large eyes | Middle shelf | Predator/Scavenger | 3.2 | No name | Morzadec 1997 | =0,002914 | Emsian | Pygidium |
| Phacopida | Acastidae | Destombesina | Destombesina ougartensis | 8 | Large eyes | Middle shelf | Predator/Scavenger | 3.3 | No name | Morzadec 1997 | =0,003469 | Emsian | Pygidium |
| Phacopida | Acastidae | Destombesina | Destombesina ougartensis | 9 | Large eyes | Middle shelf | Predator/Scavenger | 3.4 | No name | Morzadec 1997 | =0,004731 | Emsian | Pygidium |
| Phacopida | Acastidae | Destombesina | Destombesina ougartensis | 10 | Large eyes | Middle shelf | Predator/Scavenger | 3.7 | No name | Morzadec 1997 | =0,001867 | Emsian | Pygidium |
| Phacopida | Acastidae | Destombesina | Destombesina ougartensis | 11 | Large eyes | Middle shelf | Predator/Scavenger | 3.8a | No name | Morzadec 1997 | =0,003275 | Emsian | Pygidium |
| Phacopida | Acastidae | Destombesina | Destombesina ougartensis | 12 | Large eyes | Middle shelf | Predator/Scavenger | 3.9 | No name | Morzadec 1997 | =0,004198 | Emsian | Pygidium |
| Phacopida | Acastidae | Destombesina | Destombesina tafilaltensis | 13 | Large eyes | Middle shelf | Predator/Scavenger | 6.6 | No name | Morzadec 2001 | =0,003495 | Emsian | Pygidium |
| Phacopida | Acastidae | Destombesina | Destombesina tafilaltensis | 14 | Large eyes | Middle shelf | Predator/Scavenger | 6.7 | No name | Morzadec 2001 | =0,003495 | Emsian | Pygidium |
| Phacopida | Acastidae | Destombesina | Destombesina tafilaltensis | 15 | Large eyes | Middle shelf | Predator/Scavenger | 7.6 | No name | Morzadec 2001 | =0,004140 | Emsian | Pygidium |
| Phacopida | Acastidae | Destombesina | Destombesina tafilaltensis | 16 | Large eyes | Middle shelf | Predator/Scavenger | 7.9 | No name | Morzadec 2001 | =0,003231 | Emsian | Pygidium |
| Phacopida | Acastidae | Destombesina | Destombesina tafilaltensis | 17 | Large eyes | Middle shelf | Predator/Scavenger | 7.10 | No name | Morzadec 2001 | =0,004140 | Emsian | Pygidium |
| Phacopida | Acastidae | Erbenochile | Erbenochile erbeni | 18 | Large eyes | Deep | Predator/Scavenger | 2.F | IGR 11943 | Morzadec 1995 | =0,010391 | Emsian | Pygidium |
| Phacopida | Acastidae | Erbenochile | Erbenochile issoumourensis | 19 | Large eyes | Deep | Predator/Scavenger | 3.5 | UA13645 | Chatterton 2010 | =0,059680 | | Pygidium |
| Phacopida | Acastidae | Erbenochile | Erbenochile issoumourensis | 20 | Large eyes | Deep | Predator/Scavenger | 4.12 | UA13646 | Chatterton 2010 | =0,125876 | | Pygidium |
| Phacopida | Acastidae | Erbenochile | Erbenochile issoumourensis | 21 | Large eyes | Deep | Predator/Scavenger | 4.13 | UA13648 | Chatterton 2010 | =0,079381 | | Pygidium |
| Phacopida | Acastidae | Erbenochile | Erbenochile erbeni | 22 | Large eyes | Deep | Predator/Scavenger | 7p | Di/UO/036 | Khaldi 2016 | =0,069418 | Emsian | Pygidium |
| Phacopida | Acastidae | Erbenochile | Erbenochile erbeni | 23 | Large eyes | Deep | Predator/Scavenger | 13.9 | It27126 | Chatterton 2006 | =0,103597 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops lemaitreae | 24 | Large eyes | Middle shelf | Predator/Scavenger | 5.2 | IGR 11974 | Morzadec 1997 | =0,006032 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops lemaitreae | 25 | Large eyes | Middle shelf | Predator/Scavenger | 5.5 | IGR 11977 | Morzadec 1997 | =0,004176 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops lemaitreae | 26 | Large eyes | Middle shelf | Predator/Scavenger | 5.6a | IGR 11978 | Morzadec 1997 | =0,007015 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops lemaitreae | 27 | Large eyes | Middle shelf | Predator/Scavenger | 5.7a | IGR 11979 | Morzadec 1997 | =0,008497 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops burtandmimiae | 28 | Large eyes | Middle shelf | Predator/Scavenger | 6.4 | UA13655 | Chatterton 2010 | =0,025069 | | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 29 | Large eyes | Middle shelf | Predator/Scavenger | 6.5 | IGR 11984 | Morzadec 1997 | =0,014217 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops burtandmimiae | 30 | Large eyes | Middle shelf | Predator/Scavenger | 6.9 | UA13643 | Chatterton 2010 | =0,046688 | | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 31 | Large eyes | Middle shelf | Predator/Scavenger | 6n | Di/UO/010 | Khaldi 2016 | =0,053188 | Emsian | Pygidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 32 | Large eyes | Middle shelf | Predator/Scavenger | 7.2c | IGR 11988 | Morzadec 1997 | =0,014178 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 33 | Large eyes | Middle shelf | Predator/Scavenger | 7.4b | IGR 11990 | Morzadec 1997 | =0,021326 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 34 | Large eyes | Middle shelf | Predator/Scavenger | 7.5 | IGR 11991 | Morzadec 1997 | =0,021326 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 35 | Large eyes | Middle shelf | Predator/Scavenger | 7.6a | IGR 11992 | Morzadec 1997 | =0,042542 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops boudibensis | 36 | Large eyes | Middle shelf | Predator/Scavenger | 8.1c | CPM | Morzadec 2001 | =0,012912 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops boudibensis | 37 | Large eyes | Middle shelf | Predator/Scavenger | 8.4 | CPM | Morzadec 2001 | =0,010999 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops boudibensis | 38 | Large eyes | Middle shelf | Predator/Scavenger | 8.5a | CPM | Morzadec 2001 | =0,010999 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 39 | Large eyes | Middle shelf | Predator/Scavenger | 8.6 | IGR 11995 | Morzadec 1997 | =0,005275 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 40 | Large eyes | Middle shelf | Predator/Scavenger | 8.6a | CPM | Morzadec 2001 | =0,028055 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops boudibensis | 41 | Large eyes | Middle shelf | Predator/Scavenger | 8.7 | CPM | Morzadec 2001 | =0,010999 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 42 | Large eyes | Middle shelf | Predator/Scavenger | 8.8 | IGR 11996 | Morzadec 1997 | =0,008581 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 43 | Large eyes | Middle shelf | Predator/Scavenger | 8.9 | CPM | Morzadec 2001 | =0,004290 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops boudibensis | 44 | Large eyes | Middle shelf | Predator/Scavenger | 8.10 | CPM | Morzadec 2001 | =0,019599 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 45 | Large eyes | Middle shelf | Predator/Scavenger | 9.1a | CPM | Morzadec 2001 | =0,020935 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 46 | Large eyes | Middle shelf | Predator/Scavenger | 9.2a | CPM | Morzadec 2001 | =0,010590 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 47 | Large eyes | Middle shelf | Predator/Scavenger | 9.3 | CPM | Morzadec 2001 | =0,010590 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 48 | Large eyes | Middle shelf | Predator/Scavenger | 9.4a | CPM | Morzadec 2001 | =0,010590 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops burtandmimiae | 49 | Large eyes | Middle shelf | Predator/Scavenger | 9.5b | CPM | Morzadec 2001 | =0,020935 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops burtandmimiae | 50 | Large eyes | Middle shelf | Predator/Scavenger | 9.6a | CPM | Morzadec 2001 | =0,013945 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops burtandmimiae | 51 | Large eyes | Middle shelf | Predator/Scavenger | 9.7 | CPM | Morzadec 2001 | =0,008462 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 52 | Large eyes | Middle shelf | Predator/Scavenger | 13.2a | SMF 53769 | Schraut 2000c | =0,081760 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 53 | Large eyes | Middle shelf | Predator/Scavenger | 13.4a | SMF 53735 | Schraut 2000c | =0,140378 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 54 | Large eyes | Middle shelf | Predator/Scavenger | 13.5 | SMF 53742 | Schraut 2000c | =0,087222 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 55 | Large eyes | Middle shelf | Predator/Scavenger | 14.1a | SMF 53644 | Schraut 2000c | =0,097024 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops mesocristata | 56 | Large eyes | Middle shelf | Predator/Scavenger | 14.2a | SMF 53764 | Schraut 2000c | =0,121010 | Emsian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops aithassainorum | 57 | Large eyes | Middle shelf | Predator/Scavenger | 17.1 | UA 13440 | Chatterton 2006 | =0,117647 | Eifelian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops aithassainorum | 58 | Large eyes | Middle shelf | Predator/Scavenger | 18.7 | UA 13442 | Chatterton 2006 | =0,081231 | Eifelian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops aithassainorum | 59 | Large eyes | Middle shelf | Predator/Scavenger | 18.8 | UA 13441 | Chatterton 2006 | =0,065404 | Eifelian | Pygidium |
| Phacopida | Acastidae | Hollardops | Hollardops aithassainorum | 60 | Large eyes | Middle shelf | Predator/Scavenger | 18.9 | UA 13444 | Chatterton 2006 | =0,065404 | Eifelian | Pygidium |
| Phacopida | Acastidae | Kayserops | Kayserops megaspina | 61 | Large eyes | Shallow | Predator/Scavenger | 4.5b | CPC | Morzadec 2001 | =0,042596 | Emsian | Pygidium |
| Phacopida | Acastidae | Kayserops | Kayserops marocanensis | 62 | Large eyes | Shallow | Predator/Scavenger | 5.2b | CPM | Morzadec 2001 | =0,028844 | Emsian | Pygidium |
| Phacopida | Acastidae | Kayserops | Kayserops marocanensis | 63 | Large eyes | Shallow | Predator/Scavenger | 5.3 | CPM | Morzadec 2001 | =0,010603 | Emsian | Pygidium |
| Phacopida | Acastidae | Kayserops | Kayserops djazaïrensis | 64 | Large eyes | Shallow | Predator/Scavenger | 8.4 | IGR 12000 | Morzadec 1997 | =0,021195 | Emsian | Pygidium |
| Phacopida | Acastidae | Kayserops | Kayserops tamnrherta | 65 | Large eyes | Shallow | Predator/Scavenger | 21.6 | UA 13329 | Chatterton 2006 | =0,073683 | Emsian | Pygidium |
| Phacopida | Acastidae | Kayserops | Kayserops tamnrherta | 66 | Large eyes | Shallow | Predator/Scavenger | 21.9 | UA 13356 | Chatterton 2006 | =0,067521 | Emsian | Pygidium |
| Phacopida | Acastidae | Metacanthina | Metacanthina matutina | 67 | Large eyes | Shallow | Predator/Scavenger | 2.6 | IGR 11953 | Morzadec 1997 | =0,006952 | Lochkovian | Pygidium |
| Phacopida | Acastidae | Metacanthina | Metacanthina matutina | 68 | Large eyes | Shallow | Predator/Scavenger | 2.7a | IGR 11954 | Morzadec 1997 | =0,014217 | Lochkovian | Pygidium |
| Phacopida | Acastidae | Metacanthina | Metacanthina issoumourensis | 69 | Large eyes | Shallow | Predator/Scavenger | 3.2a | CPC | Morzadec 2001 | =0,027831 | Pragian | Pygidium |
| Phacopida | Acastidae | Metacanthina | Metacanthina issoumourensis | 70 | Large eyes | Shallow | Predator/Scavenger | 3.3b | CPC | Morzadec 2001 | =0,027831 | Pragian | Pygidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phacopida | Acastidae | Metacanthina | Metacanthina maderensis | 71 | Large eyes | Shallow | Predator/Scavenger | 3.4c | CPC | Morzadec 2001 | =0,020987 | Pragian | Pygidium |
| Phacopida | Acastidae | Mrakibina | Mrakibina cattoi | 72 | Large eyes | Inner shelf | Predator/Scavenger | 14.3 | CPC | Morzadec 2001 | =0,021012 | Eifelian | Pygidium |
| Phacopida | Acastidae | Mrakibina | Mrakibina cattoi | 73 | Large eyes | Inner shelf | Predator/Scavenger | 14.4 | CPC | Morzadec 2001 | =0,010616 | Eifelian | Pygidium |
| Phacopida | Acastidae | Mrakibina | Mrakibina cattoi | 74 | Large eyes | Inner shelf | Predator/Scavenger | 14.7 | CPC | Morzadec 2001 | =0,021012 | Eifelian | Pygidium |
| Phacopida | Acastidae | Odontochile | Odontochile magrebianum | 75 | Large eyes | Middle shelf | Predator/Scavenger | 15.9a | SMF 57066 | Schraut 2000c | =0,147471 | Pragian | Pygidium |
| Phacopida | Acastidae | Morzadecops | Morzadecops zguidensis | 76 | Large eyes | Inner shelf | Predator/Scavenger | 4.1b | CPC | Morzadec 2001 | =0,021189 | Emsian | Pygidium |
| Phacopida | Acastidae | Morzadecops | Morzadecops zguidensis | 77 | Large eyes | Inner shelf | Predator/Scavenger | 4.4 | CPM | Morzadec 2001 | =0,021189 | Emsian | Pygidium |
| Phacopida | Acastidae | Protacanthina | Protacanthina robusticostata | 78 | Large eyes | Shallow | Predator/Scavenger | 1.5a | IGR11921 | Morzadec 1990 | =0,008442 | Lochkovian | Pygidium |
| Phacopida | Acastidae | Protacanthina | Protacanthina robusticostata | 79 | Large eyes | Shallow | Predator/Scavenger | 2.1a | IGR 11924 | Morzadec 1990 | =0,008394 | Lochkovian | Pygidium |
| Phacopida | Acastidae | Protacanthina | Protacanthina robusticostata | 80 | Large eyes | Shallow | Predator/Scavenger | 2.4a | IGR 11926 | Morzadec 1990 | =0,006034 | Lochkovian | Pygidium |
| Phacopida | Acastidae | Protacanthina | Protacanthina robusticostata | 81 | Large eyes | Shallow | Predator/Scavenger | Doublon_ | IGR11921 | Morzadec 1997 | =0,008574 | Lochkovian | Pygidium |
| Phacopida | Acastidae | Minicryphaeus | Minicryphaeus minimus | 82 | Large eyes | Shallow | Predator/Scavenger | 1.7a | CPM | Morzadec 2001 | =0,006089 | Pragian | Pygidium |
| Phacopida | Acastidae | Minicryphaeus | Minicryphaeus minimus | 83 | Large eyes | Shallow | Predator/Scavenger | 1.10 | CPM | Morzadec 2001 | =0,006089 | Pragian | Pygidium |
| Phacopida | Acastidae | Pseudocryphaeus | Pseudocryphaeus sarirus | 84 | Large eyes | Shallow | Predator/Scavenger | 2.2b | CPC | Morzadec 2001 | =0,014029 | Pragian | Pygidium |
| Phacopida | Acastidae | Pseudocryphaeus | Pseudocryphaeus quaterspinosus | 85 | Large eyes | Shallow | Predator/Scavenger | 2.3b | CPC | Morzadec 2001 | =0,014029 | Pragian | Pygidium |
| Phacopida | Acastidae | Pseudocryphaeus | Pseudocryphaeus quaterspinosus | 86 | Large eyes | Shallow | Predator/Scavenger | 2.4a | CPM | Morzadec 2001 | =0,003521 | Pragian | Pygidium |
| Phacopida | Acastidae | Pseudocryphaeus | Pseudocryphaeus sp 1 | 87 | Large eyes | Shallow | Predator/Scavenger | 2.5 | CPM | Morzadec 2001 | =0,008372 | Emsian | Pygidium |
| Phacopida | Acastidae | Pseudocryphaeus | Pseudocryphaeus quaterspinosus | 88 | Large eyes | Shallow | Predator/Scavenger | 2.6 | CPM | Morzadec 2001 | =0,002643 | Pragian | Pygidium |
| Phacopida | Acastidae | Psychopyge | Psychopyge termierorum | 89 | Large eyes | Middle shelf | Predator/Scavenger | 2.7a | IGR 10289 | Morzadec 1988 | =0,021298 | Emsian | Pygidium |
| Phacopida | Acastidae | Psychopyge | Psychopyge termierorum | 90 | Large eyes | Middle shelf | Predator/Scavenger | 13.1c | CPC | Morzadec 2001 | =0,021066 | Emsian | Pygidium |
| Phacopida | Acastidae | Psychopyge | Psychopyge praestans | 91 | Large eyes | Middle shelf | Predator/Scavenger | 13.5a | CPC | Morzadec 2001 | =0,042507 | Emsian | Pygidium |
| Phacopida | Acastidae | Psychopyge | Psychopyge elegans | 92 | Large eyes | Middle shelf | Predator/Scavenger | 15.1 | SMF 53622 | Schraut 2000c | =0,128705 | Emsian | Pygidium |
| Phacopida | Acastidae | Psychopyge | Psychopyge elegans | 93 | Large eyes | Middle shelf | Predator/Scavenger | 22.5 | UA 13370 | Chatterton 2006 | =0,188533 | Emsian | Pygidium |
| Phacopida | Acastidae | Psychopyge | Psychopyge praestans | 94 | Large eyes | Middle shelf | Predator/Scavenger | 22.6 | UA 13369 | Chatterton 2006 | =0,177508 | Emsian | Pygidium |
| Phacopida | Acastidae | Psychopyge | Psychopyge praestans | 95 | Large eyes | Middle shelf | Predator/Scavenger | 23.6 | UA 13372 | Chatterton 2006 | =0,115084 | Emsian | Pygidium |
| Phacopida | Acastidae | Psychopyge | Psychopyge hammerorum | 96 | Large eyes | Middle shelf | Predator/Scavenger | 25.6 | UA 13375 | Chatterton 2006 | =0,125687 | Emsian | Pygidium |
| Phacopida | Acastidae | Quadrops | Quadrops flexuosa | 97 | Large eyes | Inner shelf | Predator/Scavenger | 11.6b | CPC | Morzadec 2001 | =0,042279 | Emsian | Pygidium |
| Phacopida | Acastidae | Saharops | Saharops bensaïdi | 98 | Large eyes | Shallow | Predator/Scavenger | 14.1b | No name | Morzadec 2001 | =0,042580 | Emsian | Pygidium |
| Phacopida | Acastidae | Saharops | Saharops bensaïdi | 99 | Large eyes | Shallow | Predator/Scavenger | 14.2a | No name | Morzadec 2001 | =0,042580 | Emsian | Pygidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phacopida | Acastidae | Coltraneia | Coltraneia saourensis | 100 | Large eyes | Middle shelf | Predator/Scavenger | 2.1a | IGR 11948 | Morzadec 1997 | =0,010461 | Emsian | Pygidium |
| Phacopida | Acastidae | Coltraneia | Coltraneia saourensis | 101 | Large eyes | Middle shelf | Predator/Scavenger | 2.3a | IGR11950 | Morzadec 1997 | =0,010554 | Emsian | Pygidium |
| Phacopida | Acastidae | Coltraneia | Coltraneia saourensis | 102 | Large eyes | Middle shelf | Predator/Scavenger | 2.3b | IGR11950 | Morzadec 1997 | =0,014032 | Emsian | Pygidium |
| Phacopida | Acastidae | Treveropyge | Treveropyge maura | 103 | Large eyes | Shallow | Predator/Scavenger | 10.1b | CPC | Morzadec 2001 | =0,042142 | Emsian | Pygidium |
| Phacopida | Acastidae | Walliserops | Walliserops trifurcatus | 104 | Large eyes | Middle shelf | Predator/Scavenger | 15.1a | No name | Morzadec 2001 | =0,029645 | Emsian | Pygidium |
| Phacopida | Acastidae | Walliserops | Walliserops trifurcatus | 105 | Large eyes | Middle shelf | Predator/Scavenger | 15.3a | CPC | Morzadec 2001 | =0,024057 | Emsian | Pygidium |
| Phacopida | Acastidae | Walliserops | Walliserops trifurcatus | 106 | Large eyes | Middle shelf | Predator/Scavenger | 15.3b | CPC | Morzadec 2001 | =0,024057 | Emsian | Pygidium |
| Phacopida | Acastidae | Walliserops | Walliserops trifurcatus | 107 | Large eyes | Middle shelf | Predator/Scavenger | 15.4b | COW n°1.3.83 | Morzadec 2001 | =0,021216 | Emsian | Pygidium |
| Phacopida | Acastidae | Walliserops | Walliserops hammii | 108 | Large eyes | Middle shelf | Predator/Scavenger | 27.6 | UA 13446 | Chatterton 2006 | =0,071182 | Emsian | Pygidium |
| Phacopida | Acastidae | Walliserops | Walliserops hammii | 109 | Large eyes | Middle shelf | Predator/Scavenger | 28.5 | UA 13449 | Chatterton 2006 | =0,073179 | Emsian | Pygidium |
| Phacopida | Acastidae | Walliserops | Walliserops hammii | 110 | Large eyes | Middle shelf | Predator/Scavenger | 29.6 | UA 13450 | Chatterton 2006 | =0,101524 | Emsian | Pygidium |
| Phacopida | Acastidae | Walliserops | Walliserops trifurcatus | 111 | Large eyes | Middle shelf | Predator/Scavenger | 31.5 | UA 13447 | Chatterton 2006 | =0,125319 | Emsian | Pygidium |
| Proetida | Aulacopleuridae | Aulacopleura | Aulacopleura ignorata | 112 | Large eyes | Middle shelf | Particle feeding | Alberti196 | CGMTA 158 | Alberti 1969 | =0,017829 | Eifelian | Pygidium |
| Proetida | Aulacopleuridae | Aulacopleura | Aulacopleura ignorata | 113 | Large eyes | Middle shelf | Particle feeding | Alberti196 | SMF 23381 | Alberti 1969 | =0,020068 | Eifelian | Pygidium |
| Proetida | Aulacopleuridae | Chamaeleoaspis | Chamaeleosapis lkomalii | 114 | Large eyes | Middle shelf | Particle feeding | 6a | UA11821 | Lerosey-Aubril 2008 | =0,015150 | Eifelian | Pygidium |
| Proetida | Aulacopleuridae | Cyphaspides | Indet | 115 | Small eyes | Middle shelf | Particle feeding | 46.20 | CGMTA 225 | Alberti 1969 | =0,007879 | Eifelian | Pygidium |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis walteri | 116 | Large eyes | Middle shelf | Particle feeding | 1b | IRSNB a12875 | Van Viersen 2014 | =0,057033 | | Pygidium |
| Proetida | Aulacopleuridae | Cyphaspis | Cyphaspis lerougei | 117 | Large eyes | Middle shelf | Particle feeding | 11d | IRSNB a13014 | Van Viersen 2016 | =0,016611 | Emsian | Pygidium |
| Proetida | Aulacopleuridae | Maurotarion | Maurotarion maurum | 118 | Large eyes | Middle shelf | Particle feeding | 9.24 | No name | Alberti 1970a | =0,004647 | Ludlow-Pridoli | Pygidium |
| Proetida | Aulacopleuridae | Maurotarion | Maurotarion maurum | 119 | Large eyes | Middle shelf | Particle feeding | 46.19 | CGMTA 220 | Alberti 1969 | =0,004534 | Ludlow-Pridoli | Pygidium |
| Proetida | Aulacopleuridae | Scharya | Scharya hamlagdadica | 120 | Large eyes | Middle shelf | Particle feeding | 4.44 | CGMTA | Alberti 1981a | =0.015257 | Emsian | Pygidium |
| Proetida | Aulacopleuridae | Scharya | Scharya hamlagdadica | 121 | Large eyes | Middle shelf | Particle feeding | 4.45 | SMF 36271 | Alberti 1981a | =0.015257 | Emsian | Pygidium |
| Proetida | Aulacopleuridae | Scharya | Scharya hamlagdadica | 122 | Large eyes | Middle shelf | Particle feeding | 4.46 | SMF 36272 | Alberti 1981a | =0.016424 | Emsian | Pygidium |
| Proetida | Aulacopleuridae | Scharya | Scharya yolkiniana | 123 | Large eyes | Middle shelf | Particle feeding | 6.74 | CGMTA | Alberti 1983 | =0.005227 | Pragian | Pygidium |
| Proetida | Aulacopleuridae | Scharya | Scharya maura | 124 | Large eyes | Middle shelf | Particle feeding | 9.3 | CGMTA 298 | Alberti 1970a | =0,004256 | Emsian | Pygidium |
| Proetida | Aulacopleuridae | Scharya | Scharya meridiana | 125 | Large eyes | Middle shelf | Particle feeding | 9.5 | CGMTA 295 | Alberti 1970a | =0,004334 | Ludlow-Pridoli | Pygidium |
| Proetida | Aulacopleuridae | Scharya | Scharya tafilaltensis | 126 | Large eyes | Middle shelf | Particle feeding | 9.6a | CGMTA 301 | Alberti 1970a | =0,004159 | Emsian | Pygidium |
| Phacopida | Calmoniidae | Acastoides | Acastoides zguilmensis | 127 | Small eyes | Deep | Predator/Scavenger | 8.12 | UA 13337 | Chatterton 2006 | =0,017563 | Emsian | Pygidium |
| Phacopida | Calmoniidae | Acastoides | Acastoides zguilmensis | 128 | Small eyes | Deep | Predator/Scavenger | 9.2 | UA 13332 | Chatterton 2006 | =0,040075 | Emsian | Pygidium |
| Phacopida | Calmoniidae | Acastoides | Acastoides zguilmensis | 129 | Small eyes | Deep | Predator/Scavenger | 9.12 | UA 13343 | Chatterton 2006 | =0,026108 | Emsian | Pygidium |
| Phacopida | Calmoniidae | Acastoides | Acastoides zguilmensis | 130 | Small eyes | Deep | Predator/Scavenger | 9.13 | UA 13340 | Chatterton 2006 | =0,061451 | Emsian | Pygidium |
| Phacopida | Calmoniidae | Acastoides | Acastoides hollardi | 131 | Small eyes | Deep | Predator/Scavenger | Alberti_19 | SGMRA 10 | Alberti 1966a | =0,013237 | Emsian | Pygidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phacopida | Calmoniidae | Acastoides | Acastoides hollardi | 132 | Small eyes | Deep | Predator/Scavenger | Alberti_19 | SMF 235 | Alberti 1970a | =0,014553 | Emsian | Pygidium |
| Phacopida | Calmoniidae | Acastoides | Acastoides hollardi | 133 | Small eyes | Deep | Predator/Scavenger | Alberti_19 | CGMTA 337 | Alberti 1970a | =0,014074 | Emsian | Pygidium |
| Phacopida | Calmoniidae | Acastoides | Acastoides hollardi | 134 | Small eyes | Deep | Predator/Scavenger | Alberti_19 | CGMTA 338 | Alberti 1970a | =0,013829 | Emsian | Pygidium |
| Phacopida | Calymenidae | Gravicalymene | Gravicalymene hamlagdadica | 135 | Large eyes | Middle shelf | Predator/Scavenger | 6.59 | CGMTA | Alberti 1981a | =0.096483 | Pragian | Pygidium |
| Phacopida | Calymenidae | Gravicalymene | Gravicalymene maura | 136 | Large eyes | Middle shelf | Predator/Scavenger | 42.2 | SMF 23135 | Alberti 1969 | =0,020592 | Pragian | Pygidium |
| Phacopida | Cheiruridae | Crotalocephalus | Crotalocephalus maurus | 137 | Large eyes | Middle shelf | Predator/Scavenger | 5a | SMF 23016 | Alberti 1966a | =0,015934 | Pragian | Pygidium |
| Phacopida | Cheiruridae | Crotalocephalus | Crotalocephalus maurus | 138 | Large eyes | Middle shelf | Predator/Scavenger | 38.9 | SMF 23016 | Alberti 1969 | =0,018402 | Pragian | Pygidium |
| Phacopida | Acastidae | Morocconites | Morocconites maurus | 139 | Large eyes | Inner shelf | Predator/Scavenger | Alberti_19 | CGMTA 341 | Alberti 1970a | =0,020970 | | Pygidium |
| Phacopida | Homalonotidae | Parahomalonotus | Parahomalonotus planus planus | 140 | Large eyes | Inner shelf | Predator/Scavenger | 6.2a | SMF 53836 | Schraut 2000c | =0,087822 | Pragian | Pygidium |
| Phacopida | Homalonotidae | Parahomalonotus | Parahomalonotus planus planus | 141 | Large eyes | Inner shelf | Predator/Scavenger | 6.3a | SMF 53837 | Schraut 2000c | =0,100230 | Pragian | Pygidium |
| Phacopida | Homalonotidae | Parahomalonotus | Parahomalonotus planus planus | 142 | Large eyes | Inner shelf | Predator/Scavenger | 6.4a | SMF 53842 | Schraut 2000c | =0,149784 | Pragian | Pygidium |
| Phacopida | Homalonotidae | Indet | | 143 | | | Predator/Scavenger | 11.7a | CGMTA 364 | Alberti 1970a | =0,021155 | Ludlow-Pridoli | Pygidium |
| Phacopida | Homalonotidae | Wenndorfia | Wenndorfia calvus | 144 | Large eyes | Middle shelf | Predator/Scavenger | 32.6 | UA 13378 | Chatterton 2006 | =0,262733 | Emsian | Pygidium |
| Lichida | Lichidae | Acanthopyge | Acanthopyge (Belenopyge) bassei | 145 | Large eyes | Middle shelf | Predator/Scavenger | 7.5 | UA 13653 | Chatterton 2010 | =0,022202 | Eifelian | Pygidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Lichida | Lichidae | Acanthopyge | Acanthopyge (Belenopyge) bassei | 146 | Large eyes | Middle shelf | Predator/Scavenger | 7.6 | UA 16854 | Chatterton 2010 | =0,021012 | Eifelian | Pygidium |
| Lichida | Lichidae | Acanthopyge | Acanthopyge (Belenopyge) estevei | 147 | Large eyes | Middle shelf | Predator/Scavenger | Corbacho | MGSB79489 | Corbacho Kier 2013 | =0,014005 | Pragian | Pygidium |
| Lichida | Lichidae | Acanthopyge | Acanthopyge (Belenopyge) estevei | 148 | Large eyes | Middle shelf | Predator/Scavenger | Corbacho | MGSB79489 | Corbacho Kier 2013 | =0,007153 | Pragian | Pygidium |
| Lichida | Lichidae | Acanthopyge | Acanthopyge (Belenopyge) estevei | 149 | Large eyes | Middle shelf | Predator/Scavenger | Corbacho | MGSB79486 | Corbacho Kier 2013 | =0,019230 | Pragian | Pygidium |
| Lichida | Lichidae | Acanthopyge | Acanthopyge (Belenopyge) bassei | 150 | Large eyes | Middle shelf | Predator/Scavenger | Corbacho | BPM1049 | Corbacho Kier 2013 | =0,010183 | Eifelian | Pygidium |
| Lichida | Lichidae | Acanthopyge | Acanthopyge (Belenopyge) estevei | 151 | Large eyes | Middle shelf | Predator/Scavenger | Corbacho | MMB101 | Corbacho Kier 2013 | =0,013440 | Pragian | Pygidium |
| Lichida | Lichidae | Acanthopyge | Acanthopyge (Belenopyge) estevei | 152 | Large eyes | Middle shelf | Predator/Scavenger | Corbacho | MMB106 | Corbacho Kier 2013 | =0,013190 | Pragian | Pygidium |
| Lichida | Lichidae | Acanthopyge | Acanthopyge (Belenopyge) estevei | 153 | Large eyes | Middle shelf | Predator/Scavenger | Corbacho | MMB108 | Corbacho Kier 2013 | =0,013812 | Pragian | Pygidium |
| Lichida | Lichidae | Akantharges | Akantharges mbareki | 154 | Large eyes | Middle shelf | Predator/Scavenger | 3.2 | JC95 | Corbacho Lopez-Soriano 2013 | =0,044246 | Eifelian | Pygidium |
| Lichida | Lichidae | Akantharges | Akantharges mbareki | 155 | Large eyes | Middle shelf | Predator/Scavenger | 3.5 | MGSB79879 | Corbacho Lopez-Soriano 2013 | =0,053188 | Eifelian | Pygidium |
| Lichida | Lichidae | Akantharges | Akantharges mbareki | 156 | Large eyes | Middle shelf | Predator/Scavenger | 3.6 | JC96 | Corbacho Lopez-Soriano 2013 | =0,048541 | Eifelian | Pygidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Lichida | Lichidae | Besseiarges | Basseiarges mellishae | 157 | Large eyes | Middle shelf | Predator/Scavenger | 1.1 | MMB104 | Corbacho Lopez-Soriano 2013 | =0,059520 | Eifelian | Pygidium |
| Lichida | Lichidae | Besseiarges | Basseiarges mellishae | 158 | Large eyes | Middle shelf | Predator/Scavenger | 1.2 | MMB102 | Corbacho Lopez-Soriano 2013 | =0,056815 | Eifelian | Pygidium |
| Lichida | Lichidae | Besseiarges | Basseiarges mellishae | 159 | Large eyes | Middle shelf | Predator/Scavenger | 1.3 | MMB103 | Corbacho Lopez-Soriano 2013 | =0,046727 | Eifelian | Pygidium |
| Lichida | Lichidae | Besseiarges | Basseiarges mellishae | 160 | Large eyes | Middle shelf | Predator/Scavenger | 1.4 | MGSB79774 | Corbacho Lopez-Soriano 2013 | =0,061724 | Eifelian | Pygidium |
| Lichida | Lichidae | Ceratarges | Ceratarges ziregensis | 161 | Large eyes | Inner shelf | Predator/Scavenger | 1a | NHMM 2011 001 | Van Viersen 2011 | =0,035711 | Eifelian | Pygidium |
| Lichida | Lichidae | Ceratarges | Ceratarges koumalii | 162 | Large eyes | Inner shelf | Predator/Scavenger | 2d | NHMM 2011 002 | Van Viersen 2011 | =0,033321 | Eifelian | Pygidium |
| Lichida | Lichidae | Ceratarges | Ceratarges aries | 163 | Large eyes | Inner shelf | Predator/Scavenger | 3b | NHMM 2011 003 | Van Viersen 2011 | =0,038741 | Eifelian | Pygidium |
| Lichida | Lichidae | Perunaspis | Perunaspis longispinus | 164 | Large eyes | Middle shelf | Predator/Scavenger | 20.21 | No name | Alberti 1970a | =0,005224 | Eifelian | Pygidium |
| Lichida | Lichidae | Perunaspis | Perunaspis longispinus | 165 | Large eyes | Middle shelf | Predator/Scavenger | 20.22 | CGMTA 375 | Alberti 1970a | =0,008187 | Eifelian | Pygidium |
| Lichida | Odontopleuridae | Ceratocephala | Ceratocephala hoernesi | 166 | Large eyes | Middle shelf | Predator/Scavenger | 3f | MGSB79774 | Feist 2018 | =0,007690 | Emsian | Pygidium |
| Lichida | Odontopleuridae | Ceratocephala | Ceratocephala hoernesi | 167 | Large eyes | Middle shelf | Predator/Scavenger | 19.11 | CGMTA 345 | Alberti 1970a | =0,017006 | Emsian | Pygidium |
| Lichida | Odontopleuridae | Isoprusia | Isoprusia laportei | 168 | Large eyes | Middle shelf | Predator/Scavenger | 3.q | UM-IP 810 | Feist 2018 | =0,007662 | Emsian | Pygidium |
| Lichida | Odontopleuridae | Kettneraspis | Kettneraspis pigra | 169 | Large eyes | Deep | Predator/Scavenger | 2.7 | UM2-RF 169 | Feist 2000 | =0.007394 | Eifelian | Pygidium |
| Lichida | Odontopleuridae | Kettneraspis | Kettneraspis pigra | 170 | Large eyes | Deep | Predator/Scavenger | 19.9 | CGMTA 369 | Alberti 1970a | =0,012961 | Eifelian | Pygidium |
| Lichida | Odontopleuridae | Kettneraspis | Kettneraspis pigra | 171 | Large eyes | Deep | Predator/Scavenger | 41.5 | SMF 23451 | Alberti 1969 | =0,021288 | Eifelian | Pygidium |
| Lichida | Odontopleuridae | Koneprusia | Koneprusia subtermata | 172 | Large eyes | Middle shelf | Predator/Scavenger | 19.14 | CGMTA 348 | Alberti 1970a | =0,007701 | Emsian | Pygidium |
| Lichida | Odontopleuridae | Koneprusia | Koneprusia maura | 173 | Large eyes | Middle shelf | Predator/Scavenger | 19.15a | CGMTA 349 | Alberti 1970a | =0,007999 | Pragian | Pygidium |
| Lichida | Odontopleuridae | Koneprusia | Koneprusia maura | 174 | Large eyes | Middle shelf | Predator/Scavenger | 19.15b | CGMTA 349 | Alberti 1970a | =0,007999 | Pragian | Pygidium |
| Lichida | Odontopleuridae | Leonaspis | Leonaspis issoumourensis | 175 | Large eyes | Middle shelf | Predator/Scavenger | 19.8 | CGMTA 343 | Alberti 1970a | =0,006330 | Emsian | Pygidium |
| Lichida | Odontopleuridae | Leonaspis | Leonaspis hastata | 176 | Large eyes | Middle shelf | Predator/Scavenger | 40.6 | CGMTA 166 | Alberti 1969 | =0,012072 | Pragian | Pygidium |
| Lichida | Odontopleuridae | Leonaspis | Leonaspis hastata | 177 | Large eyes | Middle shelf | Predator/Scavenger | 40.8 | SMF 23412 | Alberti 1969 | =0,014277 | Pragian | Pygidium |
| Lichida | Odontopleuridae | Leonaspis | Leonaspis maura | 178 | Large eyes | Middle shelf | Predator/Scavenger | 40.11 | SMF 23406 | Alberti 1969 | =0,011581 | | Pygidium |
| Lichida | Odontopleuridae | Leonaspis | Leonaspis haddanei | 179 | Large eyes | Middle shelf | Predator/Scavenger | 50.10 | UA 13417 | Chatterton 2006 | =0,037586 | Eifelian | Pygidium |
| Lichida | Odontopleuridae | Leonaspis | Leonaspis hastata | 180 | Large eyes | Middle shelf | Predator/Scavenger | b.31 | CGMTA 166 | Alberti 1967b | =0,014854 | Pragian | Pygidium |
| Phacopida | Phacopidae | Acuticryphops | Acuticryphops acuticeps | 181 | Small eyes | Middle shelf | Predator/Scavenger | 3f | UM2−RF 222 | Feist 2002 | =0.007416 | Frasnian | Pygidium |
| Phacopida | Phacopidae | Morocops | Morocops chattertoni | 182 | Large eyes | Inner shelf | Predator/Scavenger | 4e | Di/UO/002 | Khaldi 2016 | =0,040649 | Emsian | Pygidium |
| Phacopida | Phacopidae | Adrisiops | Adrisiops fabrei | 183 | Large eyes | Middle shelf | Predator/Scavenger | 4p | Di/UO/004 | Khaldi 2016 | =0,096136 | Emsian | Pygidium |
| Phacopida | Phacopidae | Adrisiops | Adrisiops boudjemaai | 184 | Large eyes | Middle shelf | Predator/Scavenger | 5r | Di/UO/005 | Khaldi 2016 | =0,116248 | Emsian | Pygidium |
| Phacopida | Phacopidae | Adrisiops | Adrisiops weugi | 185 | Large eyes | Middle shelf | Predator/Scavenger | 7d | NHMM 2016 007 | Van Viersen 2017 | =0,006711 | Emsian | Pygidium |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 186 | Large eyes | Middle shelf | Predator/Scavenger | 4.1 | UA 13306 | Chatterton 2006 | =0,063851 | Emsian | Pygidium |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 187 | Large eyes | Middle shelf | Predator/Scavenger | 4.3 | UA 13306 | Chatterton 2006 | =0,063851 | Emsian | Pygidium |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 188 | Large eyes | Middle shelf | Predator/Scavenger | 4.6 | UA 13308 | Chatterton 2006 | =0,058471 | Emsian | Pygidium |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 189 | Large eyes | Middle shelf | Predator/Scavenger | 4.7 | UA 13309 | Chatterton 2006 | =0,098781 | Emsian | Pygidium |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 190 | Large eyes | Middle shelf | Predator/Scavenger | 4.9 | UA 13306 | Chatterton 2006 | =0,063851 | Emsian | Pygidium |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 191 | Large eyes | Middle shelf | Predator/Scavenger | 5.5 | UA 13307 | Chatterton 2006 | =0,059370 | Emsian | Pygidium |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 192 | Large eyes | Middle shelf | Predator/Scavenger | 5.7 | UA 13308 | Chatterton 2006 | =0,054830 | Emsian | Pygidium |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 193 | Large eyes | Middle shelf | Predator/Scavenger | 5.8 | UA 13314 | Chatterton 2006 | =0,065539 | Emsian | Pygidium |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 194 | Large eyes | Middle shelf | Predator/Scavenger | 5.9 | UA 13312 | Chatterton 2006 | =0,050383 | Emsian | Pygidium |
| Phacopida | Phacopidae | Austerops | Austerops speculator speculator | 195 | Large eyes | Middle shelf | Predator/Scavenger | 6.c | Di/UO/013 | Khaldi 2016 | =0,057467 | Emsian | Pygidium |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 196 | Large eyes | Middle shelf | Predator/Scavenger | 6.g | Di/UO/026 | Khaldi 2016 | =0,044246 | Emsian | Pygidium |
| Phacopida | Phacopidae | Austerops | Austerops speculator punctatus | 197 | Large eyes | Middle shelf | Predator/Scavenger | 7.4 | UA 13538 | McKellar 2009 | =0,010215 | Eifelian | Pygidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phacopida | Phacopidae | Austerops | Austerops speculator punctatus | 198 | Large eyes | Middle shelf | Predator/Scavenger | 7.6 | UA 13535 | McKellar 2009 | =0,012682 | Eifelian | Pygidium |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 199 | Large eyes | Middle shelf | Predator/Scavenger | 7.10 | UA 13328 | Chatterton 2006 | =0,055801 | Eifelian | Pygidium |
| Phacopida | Phacopidae | Austerops | Austerops menchikoffi | 200 | Large eyes | Middle shelf | Predator/Scavenger | 7.12 | UA 13327 | Chatterton 2006 | =0,066837 | Eifelian | Pygidium |
| Phacopida | Phacopidae | Austerops | Austerops legrandi | 201 | Large eyes | Middle shelf | Predator/Scavenger | 7g | Di/UO/009 | Khaldi 2016 | =0,048068 | Emsian | Pygidium |
| Phacopida | Phacopidae | Austerops | Austerops legrandi | 202 | Large eyes | Middle shelf | Predator/Scavenger | 7i | Di/UO/025 | Khaldi 2016 | =0,046288 | Emsian | Pygidium |
| Phacopida | Phacopidae | Austerops | Austerops kermiti | 203 | Large eyes | Middle shelf | Predator/Scavenger | 8.8 | UA 13548 | McKellar 2009 | =0,008684 | Eifelian | Pygidium |
| Phacopida | Phacopidae | Austerops | Austerops salamandar | 204 | Large eyes | Middle shelf | Predator/Scavenger | 10.2 | UA 13549 | McKellar 2009 | =0,010177 | Eifelian | Pygidium |
| Phacopida | Phacopidae | Austerops | Austerops speculator speculator | 205 | Large eyes | Middle shelf | Predator/Scavenger | Alberti197 | ISCR | Alberti 1970a | =0,015217 | Emsian | Pygidium |
| Phacopida | Phacopidae | Boeckops | Boeckops sp C | 206 | Large eyes | Middle shelf | Predator/Scavenger | 5m | Di/UO/015 | Khaldi 2016 | =0,029938 | Emsian | Pygidium |
| Phacopida | Phacopidae | Boeckops | Boeckops stelcki | 207 | Large eyes | Middle shelf | Predator/Scavenger | 11.9 | UA 13469 | McKellar 2009 | =0,013171 | Emsian | Pygidium |
| Phacopida | Phacopidae | Boeckops | Boeckops slimanensis | 208 | Large eyes | Middle shelf | Predator/Scavenger | 16.12a | SMF 23519 | Alberti 1970a | =0,017513 | Lochkovian | Pygidium |
| Phacopida | Phacopidae | Boeckops | Boeckops slimanensis | 209 | Large eyes | Middle shelf | Predator/Scavenger | 16.13 | CGMTA 325 | Alberti 1970a | =0,018614 | Lochkovian | Pygidium |
| Phacopida | Phacopidae | Chlupacops | Chlupacops laticeps | 210 | Large eyes | Deep | Predator/Scavenger | 3f | UM-IP 713 | Feist 2016 | =0,049984 | Frasnian | Pygidium |
| Phacopida | Phacopidae | Chlupacops | Chlupacops cryphoides | 211 | Large eyes | Deep | Predator/Scavenger | 3l | UM-IP 714 | Feist 2016 | =0,051265 | Frasnian | Pygidium |
| Phacopida | Phacopidae | Denckmanites | Denckmannites miser | 212 | Small eyes | Deep | Predator/Scavenger | 16.2 | CGMTA 367 | Alberti 1970a | =0,009884 | Lochkovian | Pygidium |
| Phacopida | Phacopidae | Denckmanites | Denckmannites miser | 213 | Small eyes | Deep | Predator/Scavenger | 16.3 | No name | Alberti 1970a | =0,010933 | Lochkovian | Pygidium |
| Phacopida | Phacopidae | Dianops | Dianops algeriensis | 214 | Blind | Deep | Predator/Scavenger | 5l | UM-IP 726 | Feist 2016 | =0,042544 | Famennian | Pygidium |
| Phacopida | Phacopidae | Dianops | Indet | 215 | Blind | Deep | Predator/Scavenger | 6l | MUA/1094/004 | Crônier 2013 | =0,039995 | Famennian | Pygidium |
| Phacopida | Phacopidae | Drotops | Drotops megalomanicus megalomanicus | 216 | Large eyes | Shallow | Predator/Scavenger | 1.1b | SMF 49341 | Struve 1995 | =0,058707 | Givetian | Pygidium |
| Phacopida | Phacopidae | Drotops | Drotops megalomanicus megalomanicus | 217 | Large eyes | Shallow | Predator/Scavenger | 1.2b | SMF 49357 | Struve 1995 | =0,065033 | Givetian | Pygidium |
| Phacopida | Phacopidae | Drotops | Drotops megalomanicus megalomanicus | 218 | Large eyes | Shallow | Predator/Scavenger | 2.4b | SMF 49354 | Struve 1995 | =0,057167 | Givetian | Pygidium |
| Phacopida | Phacopidae | Drotops | Drotops megalomanicus megalomanicus | 219 | Large eyes | Shallow | Predator/Scavenger | 2.5 | MB.T 1948 | Struve 1995 | =0,057827 | Givetian | Pygidium |
| Phacopida | Phacopidae | Drotops | Drotops armatus | 220 | Large eyes | Shallow | Predator/Scavenger | 5.12c | No name | Struve 1995 | =0,089152 | Givetian | Pygidium |
| Phacopida | Phacopidae | Drotops | Drotops armatus | 221 | Large eyes | Shallow | Predator/Scavenger | 6.15a | No name | Struve 1995 | =0,065485 | Givetian | Pygidium |
| Phacopida | Phacopidae | Enygmapyge | Enigmapyge marhoumensis | 222 | Blind | Deep | Predator/Scavenger | 5a | UM-IP 727 | Feist 2016 | =0,039186 | Famennian | Pygidium |
| Phacopida | Phacopidae | Enygmapyge | Enigmapyge marhoumensis | 223 | Blind | Deep | Predator/Scavenger | 5c | UM-IP 727 | Feist 2016 | =0,058798 | Famennian | Pygidium |
| Phacopida | Phacopidae | Eocryphops | Eocryphops termieri | 224 | Small eyes | Middle shelf | Predator/Scavenger | Richter_2. | Nr 40 | Richter 1943 | =0.023208 | Emsian | Pygidium |
| Phacopida | Phacopidae | Eophacops | Eophacops bulliceps | 225 | Large eyes | Middle shelf | Predator/Scavenger | 11.6 | CGMTA 374 | Alberti 1970a | =0,010952 | Ludlow-Pridoli | Pygidium |
| Phacopida | Phacopidae | Hypsipariops | Hypsipariops vagabundus | 226 | Large eyes | Middle shelf | Predator/Scavenger | 8.24c | SMF 49368 | Struve 1995 | =0,058661 | Givetian | Pygidium |
| Phacopida | Phacopidae | Hypsipariops | Hypsipariops vagabundus | 227 | Large eyes | Middle shelf | Predator/Scavenger | 8.23h | SMF 49402 | Struve 1995 | =0,059221 | Givetian | Pygidium |
| Phacopida | Phacopidae | Hypsipariops | Hypsipariops vagabundus | 228 | Large eyes | Middle shelf | Predator/Scavenger | 8.25 | SMF 49372 | Struve 1995 | =0,058095 | Givetian | Pygidium |
| Phacopida | Phacopidae | Hypsipariops | Hypsipariops vagabundus | 229 | Large eyes | Middle shelf | Predator/Scavenger | 9.26 | SMF 49611A | Struve 1995 | =0,058976 | Givetian | Pygidium |
| Phacopida | Phacopidae | Hypsipariops | Hypsipariops vagabundus | 230 | Large eyes | Middle shelf | Predator/Scavenger | 9.27 | SMF 49374 | Struve 1995 | =0,056245 | Givetian | Pygidium |
| Phacopida | Phacopidae | Hypsipariops | Hypsipariops vagabundus | 231 | Large eyes | Middle shelf | Predator/Scavenger | 9.30b | SMF 49373 | Struve 1995 | =0,059301 | Givetian | Pygidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phacopida | Phacopidae | Hypsipariops | Hypsipariops africanus | 232 | Large eyes | Middle shelf | Predator/Scavenger | 48.2 | In 56877 | Burton 1974 | =0,211154 | Eifelian | Pygidium |
| Phacopida | Phacopidae | Morocops | Morocops granulops | 233 | Large eyes | Inner shelf | Predator/Scavenger | 1.5 | UA 13295 | Chatterton 2006 | =0,057838 | Emsian | Pygidium |
| Phacopida | Phacopidae | Morocops | Morocops granulops | 234 | Large eyes | Inner shelf | Predator/Scavenger | 1.8 | UA 13294 | Chatterton 2006 | =0,075606 | Emsian | Pygidium |
| Phacopida | Phacopidae | Morocops | Morocops granulops | 235 | Large eyes | Inner shelf | Predator/Scavenger | 1.10 | UA 13298 | Chatterton 2006 | =0,077125 | Emsian | Pygidium |
| Phacopida | Phacopidae | Morocops | Morocops granulops | 236 | Large eyes | Inner shelf | Predator/Scavenger | 2.10 | UA 13302 | Chatterton 2006 | =0,136848 | Emsian | Pygidium |
| Phacopida | Phacopidae | Morocops | Morocops granulops | 237 | Large eyes | Inner shelf | Predator/Scavenger | 2.12 | UA 13302 | Chatterton 2006 | =0,097288 | Emsian | Pygidium |
| Phacopida | Phacopidae | Morocops | Morocops lebesus | 238 | Large eyes | Inner shelf | Predator/Scavenger | 3.4 | UA 13304 | Chatterton 2006 | =0,047408 | Eifelian | Pygidium |
| Phacopida | Phacopidae | Morocops | Morocops torkozensis | 239 | Large eyes | Inner shelf | Predator/Scavenger | 3.5 | SMF 53624 | Schraut 2000c | =0,076035 | Emsian | Pygidium |
| Phacopida | Phacopidae | Morocops | Morocops torkozensis | 240 | Large eyes | Inner shelf | Predator/Scavenger | 3.6a | SMF 53719 | Schraut 2000c | =0,092503 | Emsian | Pygidium |
| Phacopida | Phacopidae | Morocops | Morocops granulops | 241 | Large eyes | Inner shelf | Predator/Scavenger | 3k | Di/UO/034 | Khaldi 2016 | =0,098020 | Emsian | Pygidium |
| Phacopida | Phacopidae | Morocops | Morocops chattertoni | 242 | Large eyes | Inner shelf | Predator/Scavenger | 4c | Di/UO/001 | Khaldi 2016 | =0,051544 | Emsian | Pygidium |
| Phacopida | Phacopidae | Adrisiops | Adrisiops fabrei | 243 | Large eyes | Middle shelf | Predator/Scavenger | 4j | Di/UO/016 | Khaldi 2016 | =0,040649 | Emsian | Pygidium |
| Phacopida | Phacopidae | Morocops | Morocops spinifer | 244 | Large eyes | Inner shelf | Predator/Scavenger | 6d | NHMM 2016 004 | Van Viersen 2017 | =0,042373 | Emsian | Pygidium |
| Phacopida | Phacopidae | Morocops | Morocops ovatus | 245 | Large eyes | Inner shelf | Predator/Scavenger | 13.3 | UA 6909 | McKellar 2009 | =0,029862 | Emsian | Pygidium |
| Phacopida | Phacopidae | Morocops | Morocops ovatus | 246 | Large eyes | Inner shelf | Predator/Scavenger | 13.6 | UA 6913 | McKellar 2009 | =0,012969 | Emsian | Pygidium |
| Phacopida | Phacopidae | Morocops | Morocops forteyi | 247 | Large eyes | Inner shelf | Predator/Scavenger | 15.6 | UA 6921 | McKellar 2009 | =0,020262 | Emsian | Pygidium |
| Phacopida | Phacopidae | Morocops | Morocops granulops | 248 | Large eyes | Inner shelf | Predator/Scavenger | Cronier_2 | PIMUZ 35146 | Crônier Oudot 2018 | =0,013121 | Emsian | Pygidium |
| Phacopida | Phacopidae | Morocops | Morocops davidbrutoni | 249 | Large eyes | Inner shelf | Predator/Scavenger | Cronier_2 | PIMUZ 35159 | Crônier Oudot 2018 | =0,008576 | Emsian | Pygidium |
| Phacopida | Phacopidae | Phacops sl | Phacops tafiuppernsis | 250 | Large eyes | Deep | Predator/Scavenger | 2f | UM2/CCp003 | Crônier 2001 | =0,013294 | Famennian | Pygidium |
| Phacopida | Phacopidae | Phacops sl | Phacops tafiuppernsis | 251 | Large eyes | Deep | Predator/Scavenger | 3g | UM2/CCp010 | Crônier 2001 | =0,011045 | Famennian | Pygidium |
| Phacopida | Phacopidae | Phacops sl | Phacops tafiuppernsis | 252 | Large eyes | Deep | Predator/Scavenger | 3h | UM2/CCp009 | Crônier 2001 | =0,011568 | Famennian | Pygidium |
| Phacopida | Phacopidae | Phacops | Phacops sensu lato sp B | 253 | Large eyes | Middle shelf | Predator/Scavenger | 5g | Di/UO/033 | Khaldi 2016 | =0,104144 | Emsian | Pygidium |
| Phacopida | Phacopidae | Phacops sl | Phacops zeregensis | 254 | Large eyes | Deep | Predator/Scavenger | 5u | MUA/1094/002 | Crônier 2013 | =0,032255 | Famennian | Pygidium |
| Phacopida | Phacopidae | Phacops | Phacops ouarouroutensis ouarouroutensis | 255 | Large eyes | Middle shelf | Predator/Scavenger | 6f | MU-G-Sr.Tr.S4/Ph064 | Crônier Abbache 2018 | =0,047613 | Eifelian | Pygidium |
| Phacopida | Phacopidae | Phacops | Phacops ouarouroutensis ouarouroutensis | 256 | Large eyes | Middle shelf | Predator/Scavenger | 6j | MU-G-Sr.Tr.S7/Ph001 | Crônier Abbache 2018 | =0,062486 | Eifelian | Pygidium |
| Phacopida | Phacopidae | Phacops sl | Indet | 257 | Large eyes | Deep | Predator/Scavenger | 6k | MUA/1094/004 | Crônier 2013 | =0,038755 | Famennian | Pygidium |
| Phacopida | Phacopidae | Phacops sl | Indet | 258 | Large eyes | Deep | Predator/Scavenger | 6m | MUA/1094/005 | Crônier 2013 | =0,050495 | Famennian | Pygidium |
| Phacopida | Phacopidae | Phacops | Phacops ouarouroutensis ouarouroutensis | 259 | Large eyes | Middle shelf | Predator/Scavenger | 6n | MU-G-Sr.Tr.S7/Ph036 | Crônier Abbache 2018 | =0,099944 | Eifelian | Pygidium |
| Phacopida | Phacopidae | Phacops | Phacops ouarouroutensis ouarouroutensoides | 260 | Large eyes | Middle shelf | Predator/Scavenger | 7u | MU-G-Sr.Tr.A2/Ph163 | Crônier Abbache 2018 | =0,096724 | Eifelian | Pygidium |
| Phacopida | Phacopidae | Prokops | Prokops benziregensis ezzhiligensis | 261 | Large eyes | Middle shelf | Predator/Scavenger | 46.23 | CGMTA 223 | Alberti 1969 | =0,020395 | Pragian | Pygidium |
| Phacopida | Phacopidae | Prokops | Prokops benziregensis benziregensis | 262 | Large eyes | Middle shelf | Predator/Scavenger | 8.88c | SH | Alberti 1983 | =0.009214 | Pragian | Pygidium |
| Phacopida | Phacopidae | Prokops | Prokops benziregensis ezzhiligensis | 263 | Large eyes | Middle shelf | Predator/Scavenger | 16.16 | CGMTA 223 | Alberti 1970a | =0,034247 | Pragian | Pygidium |
| Phacopida | Phacopidae | Prokops | Prokops benziregensis benziregensis | 264 | Large eyes | Middle shelf | Predator/Scavenger | 4.42 | SH | Alberti 1983 | =0.010473 | Pragian | Pygidium |
| Phacopida | Phacopidae | Reedops | Reedops bronni | 265 | Large eyes | Inner shelf | Predator/Scavenger | 1.8 | UA 6844 | McKellar 2009 | =0,010059 | Pragian | Pygidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phacopida | Phacopidae | Reedops | Reedops cephalotes hamlagdadianus | 266 | Large eyes | Inner shelf | Predator/Scavenger | 2.10 | UA 6861 | McKellar 2009 | =0,019746 | Pragian | Pygidium |
| Phacopida | Phacopidae | Reedops | Reedops cephalotes hamlagdadianus | 267 | Large eyes | Inner shelf | Predator/Scavenger | 3.8 | UA 6853 | McKellar 2009 | =0,014556 | Pragian | Pygidium |
| Phacopida | Phacopidae | Reedops | Reedops pembertoni | 268 | Large eyes | Inner shelf | Predator/Scavenger | 4.6 | UA 6875 | McKellar 2009 | =0,012229 | Pragian | Pygidium |
| Phacopida | Phacopidae | Reedops | Reedops pembertoni | 269 | Large eyes | Inner shelf | Predator/Scavenger | 4.9 | UA 6871 | McKellar 2009 | =0,012229 | Pragian | Pygidium |
| Phacopida | Phacopidae | Reedops | Reedops intermedius chlupaci | 270 | Large eyes | Inner shelf | Predator/Scavenger | 4.11a | SMF 57095 | Schraut 2000c | =0.083464 | Pragian | Pygidium |
| Phacopida | Phacopidae | Struveaspis | Struveaspis bignoni | 271 | Large eyes | Middle shelf | Predator/Scavenger | 1.2 | 80534 | Corbacho 2014 | =0,025707 | Eifelian | Pygidium |
| Phacopida | Phacopidae | Struveaspis | Struveaspis bignoni | 272 | Large eyes | Middle shelf | Predator/Scavenger | 1.4 | JC 104 | Corbacho 2014 | =0,037732 | Eifelian | Pygidium |
| Phacopida | Phacopidae | Struveaspis | Struveaspis micromma | 273 | Large eyes | Middle shelf | Predator/Scavenger | 1.7 | JC 105 | Corbacho 2014 | =0,039365 | Eifelian | Pygidium |
| Phacopida | Phacopidae | Struveaspis | Struveaspis micromma | 274 | Large eyes | Middle shelf | Predator/Scavenger | 14.7 | CGMTA 366 | Alberti 1970a | =0,009784 | Eifelian | Pygidium |
| Phacopida | Phacopidae | Trifoliops | Trifoliops trifolius | 275 | Blind | Deep | Predator/Scavenger | 5f | Di/UO/033 | Khaldi 2016 | =0,102020 | Famennian | Pygidium |
| Phacopida | Phacopidae | Trifoliops | Trifoliops croniera | 276 | Blind | Deep | Predator/Scavenger | 5o | Di/UO/007 | Khaldi 2016 | =0,135086 | Famennian | Pygidium |
| Phacopida | Phacopidae | Trimerocephalus | Trimerocephalus lelievrei | 277 | Blind | Deep | Predator/Scavenger | 1.13 | UM2-CCt55 | Crônier 1997 | =0,010599 | Famennian | Pygidium |
| Phacopida | Phacopidae | Trimerocephalus | Trimerocephalus lelievrei | 278 | Blind | Deep | Predator/Scavenger | 1.15a | UM2-CCt32 | Crônier 1997 | =0,003176 | Famennian | Pygidium |
| Phacopida | Phacopidae | Trimerocephalus | Trimerocephalus caecus | 279 | Blind | Deep | Predator/Scavenger | 3b | MUA/1094/007 | Crônier 2013 | =0,037874 | Famennian | Pygidium |
| Phacopida | Phacopidae | Trimerocephalus | Trimerocephalus mahboubii | 280 | Blind | Deep | Predator/Scavenger | 4f | UM-IP 718 | Feist 2016 | =0,036358 | Famennian | Pygidium |
| Phacopida | Phacopidae | Chotecops | Chotecops hoseri | 281 | Large eyes | Middle shelf | Predator/Scavenger | 5o | MU-G-Sr.Tr.A4/Ph136 | Crônier Abbache 2018 | =0,015544 | Eifelian | Pygidium |
| Phacopida | Phacopidae | Chotecops | Chotecops hoseri | 282 | Large eyes | Middle shelf | Predator/Scavenger | 5u | MU-G-Sr.Tr.A4/Ph109 | Crônier Abbache 2018 | =0,093704 | Eifelian | Pygidium |
| Corynexoch | Scutelluidae | Paralejurus | Paralejurus sp A | 283 | Large eyes | Inner shelf | Predator/Scavenger | 1.4 | SMF 36233 | Alberti 1981a | =0.059873 | Pragian | Pygidium |
| Proetida | Proetidae | Buchiproetus | Buchiproetus mendax | 284 | Large eyes | Middle shelf | Predator/Scavenger | 11.21 | CGMTA 190 | Alberti 1969 | =0,013816 | Pragian | Pygidium |
| Proetida | Proetidae | Coniproetus | Coniproetus affinis | 285 | Large eyes | Inner shelf | Predator/Scavenger | 3.10 | CGMTA 212a | Alberti 1970a | =0,013225 | Lochkovian | Pygidium |
| Proetida | Proetidae | Cornuproetus | Cornuproetus oudrissensis | 286 | Large eyes | Middle shelf | Predator/Scavenger | 1.12 | UM2-RF 160 | Feist 2000 | =0.008824 | Givetian | Pygidium |
| Proetida | Proetidae | Cornuproetus | Cornuproetus pusulosus | 287 | Large eyes | Middle shelf | Predator/Scavenger | 3x | UM-IP 820a | Feist 2018 | =0,007896 | Emsian | Pygidium |
| Proetida | Proetidae | Cornuproetus | Cornuproetus cornutus marrakechensis | 288 | Large eyes | Middle shelf | Predator/Scavenger | 4.4 | SMF 23095 | Alberti 1970a | =0,010529 | Eifelian | Pygidium |
| Proetida | Proetidae | Cornuproetus | Indet | 289 | Large eyes | Middle shelf | Predator/Scavenger | 46.11 | CGMTA 216 | Alberti 1969 | =0,009167 | Emsian | Pygidium |
| Proetida | Proetidae | Cyrtosymbole | Cyrtosymbole rectifrons | 290 | Large eyes | Middle shelf | Predator/Scavenger | 2.14 | UMC-IP 469 | Lerosey-Aubril 2006 | =0.002857 | Famennian | Pygidium |
| Proetida | Proetidae | Cyrtosymbole | Cyrtosymbole rectifrons | 291 | Large eyes | Middle shelf | Predator/Scavenger | 2.15 | UMC-IP 470 | Lerosey-Aubril 2006 | =0.003267 | Famennian | Pygidium |
| Proetida | Proetidae | Cyrtosymbole | Cyrtosymbole rectifrons | 292 | Large eyes | Middle shelf | Predator/Scavenger | 2.16 | UMC-IP 471 | Lerosey-Aubril 2006 | =0.003649 | Famennian | Pygidium |
| Proetida | Proetidae | Cyrtosymbole | Cyrtosymbole rectifrons | 293 | Large eyes | Middle shelf | Predator/Scavenger | 2.17 | UMC-IP 472 | Lerosey-Aubril 2006 | =0.003906 | Famennian | Pygidium |
| Proetida | Proetidae | Cyrtosymbole | Cyrtosymbole rectifrons | 294 | Large eyes | Middle shelf | Predator/Scavenger | 2.18 | UMC-IP 473 | Lerosey-Aubril 2006 | =0.004504 | Famennian | Pygidium |
| Proetida | Proetidae | Cyrtosymbole | Cyrtosymbole rectifrons | 295 | Large eyes | Middle shelf | Predator/Scavenger | 2.19 | UMC-IP 474 | Lerosey-Aubril 2006 | =0.005680 | Famennian | Pygidium |
| Proetida | Proetidae | Cyrtosymbole | Cyrtosymbole rectifrons | 296 | Large eyes | Middle shelf | Predator/Scavenger | 2.20 | UMC-IP 475 | Lerosey-Aubril 2006 | =0.006577 | Famennian | Pygidium |
| Proetida | Proetidae | Cyrtosymbole | Cyrtosymbole rectifrons | 297 | Large eyes | Middle shelf | Predator/Scavenger | 2.22 | UMC-IP 477 | Lerosey-Aubril 2006 | =0.005554 | Famennian | Pygidium |
| Proetida | Proetidae | Cyrtosymbole | Cyrtosymbole rectifrons | 298 | Large eyes | Middle shelf | Predator/Scavenger | 2.23 | UMC-IP 478 | Lerosey-Aubril 2006 | =0.002673 | Famennian | Pygidium |
| Proetida | Proetidae | Cyrtosymbole | Cyrtosymbole sp A | 299 | Large eyes | Middle shelf | Predator/Scavenger | 2.31 | UMC-IP 486 | Lerosey-Aubril 2006 | =0.004545 | Famennian | Pygidium |
| Proetida | Proetidae | Cyrtosymboloides | Cyrtosymboloides samum | 300 | Large eyes | Middle shelf | Predator/Scavenger | 5.14 | CGMTA 266 | Alberti 1970a | =0,005413 | Eifelian | Pygidium |
| Proetida | Proetidae | Cyrtosymboloides | Cyrtosymboloides samum | 301 | Large eyes | Middle shelf | Predator/Scavenger | 5.15 | CGMTA 259 | Alberti 1970a | =0,005780 | Eifelian | Pygidium |
| Proetida | Proetidae | Cyrtosymboloides | Cyrtosymboloides samum | 302 | Large eyes | Middle shelf | Predator/Scavenger | 5.16 | SMF 23483a | Alberti 1970a | =0,006392 | Eifelian | Pygidium |
| Proetida | Proetidae | Cyrtosymboloides | Cyrtosymboloides samum | 303 | Large eyes | Middle shelf | Predator/Scavenger | 5.17 | SMF 23484a | Alberti 1970a | =0,006530 | Eifelian | Pygidium |
| Proetida | Proetidae | Dalejeproetus | Dalejeproetus owensi | 304 | Large eyes | Inner shelf | Predator/Scavenger | 4.10 | NHM It 28949 | Johnson 2012 | =0,036642 | Pragian | Pygidium |
| Proetida | Proetidae | Dalejeproetus | Dalejeproetus owensi | 305 | Large eyes | Inner shelf | Predator/Scavenger | 4.14 | NHM It 28950 | Johnson 2012 | =0,045975 | Pragian | Pygidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Proetida | Proetidae | Dalejeproetus | Dalejeproetus owensi | 306 | Large eyes | Inner shelf | Predator/Scavenger | 5.3 | NHM It 28951 | Johnson 2012 | =0,036559 | Pragian | Pygidium |
| Proetida | Proetidae | Dechenella | Dechenella ziatensis | 307 | Large eyes | Inner shelf | Predator/Scavenger | 2.2a | IMGP Gö Orig K 1122-37 | Feist 2000 | =0.006290 | Givetian | Pygidium |
| Proetida | Proetidae | Diademaproetus | Diademaproetus praecursor | 308 | Large eyes | Deep | Predator/Scavenger | 20.11 | SMF 23124 | Alberti 1969 | =0,012361 | Emsian | Pygidium |
| Proetida | Proetidae | Diademaproetus | Diademaproetus praecursor | 309 | Large eyes | Deep | Predator/Scavenger | 20.12 | CGMT-TD 32 | Alberti 1969 | =0,014380 | Emsian | Pygidium |
| Proetida | Proetidae | Diademaproetus | Diademaproetus praecursor | 310 | Large eyes | Deep | Predator/Scavenger | 35.7 | UA 13383 | Chatterton 2006 | =0,076087 | Emsian | Pygidium |
| Proetida | Proetidae | Diademaproetus | Diademaproetus praecursor | 311 | Large eyes | Deep | Predator/Scavenger | 36.3 | UA 13384 | Chatterton 2006 | =0,084187 | Emsian | Pygidium |
| Proetida | Proetidae | Diademaproetus | Diademaproetus praecursor | 312 | Large eyes | Deep | Predator/Scavenger | 36.7 | UA 13384 | Chatterton 2006 | =0,043840 | Emsian | Pygidium |
| Proetida | Proetidae | Diademaproetus | Diademaproetus praecursor | 313 | Large eyes | Deep | Predator/Scavenger | 37.9 | UA 13444 | Chatterton 2006 | =0,086669 | Emsian | Pygidium |
| Proetida | Proetidae | DREVERMANNIINAE | 314 | Blind | Deep | Predator/Scavenger | 28.20 | SMF 23321 | Alberti 1969 | =0,004364 | Emsian | | Pygidium |
| Proetida | Proetidae | DREVERMANNIINAE | 315 | Blind | Deep | Predator/Scavenger | 28.21 | SMF 23322 | Alberti 1969 | =0,003273 | Emsian | | Pygidium |
| Proetida | Proetidae | Eodrevermannia | Eodrevermannia rara africana | 316 | Blind | Middle shelf | Predator/Scavenger | 8.10 | CGMTA 292 | Alberti 1970a | =0,004457 | Emsian | Pygidium |
| Proetida | Proetidae | Erbenaspis | Erbenaspis arabica | 317 | Large eyes | Middle shelf | Predator/Scavenger | 3 | SMF 23012 | Alberti 1966a | =0,004083 | Pragian | Pygidium |
| Proetida | Proetidae | Erbenaspis | Erbenaspis erbeni | 318 | Large eyes | Middle shelf | Predator/Scavenger | 8.14 | CGMTA 293 | Alberti 1970a | =0,004199 | Lochkovian | Pygidium |
| Proetida | Proetidae | Erbenaspis | Erbenaspis erbeni | 319 | Large eyes | Middle shelf | Predator/Scavenger | 8.15 | SMF 23586 | Alberti 1970a | =0,004348 | Lochkovian | Pygidium |
| Proetida | Proetidae | Erbenaspis | Erbenaspis arabica | 320 | Large eyes | Middle shelf | Predator/Scavenger | 8.16 | CGMTA 357 | Alberti 1970a | =0,004795 | Pragian | Pygidium |
| Proetida | Proetidae | Erbenaspis | Erbenaspis arabica | 321 | Large eyes | Middle shelf | Predator/Scavenger | Doublon_ | CGMTA 7 | Alberti 1969 | =0.004884 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus cacuminatus | 322 | Large eyes | Middle shelf | Predator/Scavenger | 1.2 | No name | Alberti 1966c | =0,010381 | Emsian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus subobscurus | 323 | Large eyes | Middle shelf | Predator/Scavenger | 3.26 | CGMTA | Alberti 1981a | =0.013224 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus tafilaltanus | 324 | Large eyes | Middle shelf | Predator/Scavenger | 7.4 | SMF 23495 | Alberti 1970a | =0,018375 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus dufresnoyi australis | 325 | Large eyes | Middle shelf | Predator/Scavenger | 7.9 | CGMTA 284 | Alberti 1970a | =0,018375 | Emsian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus dufresnoyi australis | 326 | Large eyes | Middle shelf | Predator/Scavenger | 7.10 | SMF 23496 | Alberti 1970a | =0,013076 | Emsian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus notabilis | 327 | Large eyes | Middle shelf | Predator/Scavenger | 16.6 | No name | Alberti 1964 | =0,013338 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus meridianomaurus | 328 | Large eyes | Middle shelf | Predator/Scavenger | 22.13a | CGMT-AT 204/1 | Alberti 1969 | =0,008136 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus meridianomaurus | 329 | Large eyes | Middle shelf | Predator/Scavenger | 22.13b | CGMT-AT 204/1 | Alberti 1969 | =0,008136 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus tafilaltanus | 330 | Large eyes | Middle shelf | Predator/Scavenger | 24.1 | SMF 23258 | Alberti 1969 | =0,017552 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus tafilaltanus | 331 | Large eyes | Middle shelf | Predator/Scavenger | 24.2 | SMF 23259 | Alberti 1969 | =0,017189 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus tafilaltanus | 332 | Large eyes | Middle shelf | Predator/Scavenger | 24.3 | CGMTA 103 | Alberti 1969 | =0,011404 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus tafilaltanus | 333 | Large eyes | Middle shelf | Predator/Scavenger | 24.4 | SMF 23260 | Alberti 1969 | =0,017147 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus tafilaltanus | 334 | Large eyes | Middle shelf | Predator/Scavenger | 24.5a | SMF 23261 | Alberti 1969 | =0,014640 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus tafilaltanus | 335 | Large eyes | Middle shelf | Predator/Scavenger | 24.6 | CGMTA 104 | Alberti 1969 | =0,012156 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus helmuti helmuti | 336 | Large eyes | Middle shelf | Predator/Scavenger | 24.7 | CGMTA 114 | Alberti 1969 | =0,010162 | Pragian | Pygidium |

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| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus helmuti helmuti | 337 | Large eyes | Middle shelf | Predator/Scavenger | 24.8 | SMF 23287 | Alberti 1969 | =0,011404 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus helmuti junior | 338 | Large eyes | Middle shelf | Predator/Scavenger | 24.9 | CGMTA 115 | Alberti 1969 | =0,011539 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus helmuti junior | 339 | Large eyes | Middle shelf | Predator/Scavenger | 24.10 | SMF 23289 | Alberti 1969 | =0,011404 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus helmuti junior | 340 | Large eyes | Middle shelf | Predator/Scavenger | 24.11 | SMF 23288 | Alberti 1969 | =0,010162 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus notabilis | 341 | Large eyes | Middle shelf | Predator/Scavenger | 24.12a | SMF 23282 | Alberti 1969 | =0,010744 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus notabilis | 342 | Large eyes | Middle shelf | Predator/Scavenger | 24.13 | SMF 23283 | Alberti 1969 | =0,017526 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus cacuminatus | 343 | Large eyes | Middle shelf | Predator/Scavenger | 24.16 | SMF 23276 | Alberti 1969 | =0,017526 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus cacuminatus | 344 | Large eyes | Middle shelf | Predator/Scavenger | 24.17 | SMF 23275 | Alberti 1969 | =0,007076 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus cacuminatus | 345 | Large eyes | Middle shelf | Predator/Scavenger | 24.18 | CGMTA 111 | Alberti 1969 | =0,015109 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus cacuminatus | 346 | Large eyes | Middle shelf | Predator/Scavenger | 24.19 | SMF 23278 | Alberti 1969 | =0,007260 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus cacuminatus | 347 | Large eyes | Middle shelf | Predator/Scavenger | 24.20 | SMF 23277 | Alberti 1969 | =0,005916 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus maurulus | 348 | Large eyes | Middle shelf | Predator/Scavenger | 25.1 | CGMTA 194 | Alberti 1969 | =0,008243 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus papilio exornatus | 349 | Large eyes | Middle shelf | Predator/Scavenger | 25.4 | SMF 23301 | Alberti 1969 | =0,015090 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus papilio exornatus | 350 | Large eyes | Middle shelf | Predator/Scavenger | 25.5 | CGMTA 122 | Alberti 1969 | =0,013004 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus papilio exornatus | 351 | Large eyes | Middle shelf | Predator/Scavenger | 25.6 | CGMTA 73 | Alberti 1969 | =0,015956 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus dufresnoyi australis | 352 | Large eyes | Middle shelf | Predator/Scavenger | 25.8 | CGMTA 105 | Alberti 1969 | =0,013028 | Emsian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus dufresnoyi australis | 353 | Large eyes | Middle shelf | Predator/Scavenger | 25.9 | SMF 23267 | Alberti 1969 | =0,011544 | Emsian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus dufresnoyi australis | 354 | Large eyes | Middle shelf | Predator/Scavenger | 25.10 | CGMTA 107 | Alberti 1969 | =0,013455 | Emsian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus dufresnoyi australis | 355 | Large eyes | Middle shelf | Predator/Scavenger | 25.11 | SMF 23268 | Alberti 1969 | =0,012140 | Emsian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus dufresnoyi australis | 356 | Large eyes | Middle shelf | Predator/Scavenger | 25.12 | SMF 23269 | Alberti 1969 | =0,013455 | Emsian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus cacuminatus | 357 | Large eyes | Middle shelf | Predator/Scavenger | 46.17 | CGMTA | Alberti 1969 | =0,019125 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus berberus | 358 | Large eyes | Middle shelf | Predator/Scavenger | a.14 | SMF 23298 | Alberti 1967a | =0.013211 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus helmuti helmuti | 359 | Large eyes | Middle shelf | Predator/Scavenger | b.15 | CGMTA 114 | Alberti 1967b | =0,012962 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus meridianomaurus | 360 | Large eyes | Middle shelf | Predator/Scavenger | b.17 | CGMTA 182 | Alberti 1967b | =0,008266 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus meridianomaurus | 361 | Large eyes | Middle shelf | Predator/Scavenger | Doublon_ | CGMTA 182 | Alberti 1969 | =0,006687 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Eremiproetus | Eremiproetus berberus | 362 | Large eyes | Middle shelf | Predator/Scavenger | Doublon_ | SMF 23298 | Alberti 1969 | =0,012136 | Pragian | Pygidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Proetida | Proetidae | Gerastos | Gerastos prox umerbianus | 363 | Large eyes | Inner shelf | Predator/Scavenger | 1.2 | IMGP Gö Orig K 1122-5 | Feist 2000 | =0.003913 | Givetian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos sp C | 364 | Large eyes | Inner shelf | Predator/Scavenger | Crônier_2 | PIMUZ 35183 | Crônier Oudot 2018 | =0,010570 | Emsian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 365 | Large eyes | Inner shelf | Predator/Scavenger | 1.7 | UA 13527 | Gibb 2010 | =0,008365 | Eifelian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 366 | Large eyes | Inner shelf | Predator/Scavenger | 2.2 | UA 13464 | Gibb 2010 | =0,011817 | Emsian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos granulosus sensu | 367 | Large eyes | Inner shelf | Predator/Scavenger | 2.6 | UM2-RF 130 | Feist 2000 | =0.007625 | Givetian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 368 | Large eyes | Inner shelf | Predator/Scavenger | 2.8 | UA 13465 | Gibb 2010 | =0,013304 | Emsian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 369 | Large eyes | Inner shelf | Predator/Scavenger | 2.13 | UA 13466 | Gibb 2010 | =0,010499 | Emsian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 370 | Large eyes | Inner shelf | Predator/Scavenger | 3.2 | UA 13280 | Gibb 2010 | =0,003871 | Emsian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 371 | Large eyes | Inner shelf | Predator/Scavenger | 4.5 | UA 13530 | Gibb 2010 | =0,008880 | Emsian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 372 | Large eyes | Inner shelf | Predator/Scavenger | 4.10 | UA 13531 | Gibb 2010 | =0,007036 | Emsian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 373 | Large eyes | Inner shelf | Predator/Scavenger | 4.11 | UA 13531 | Gibb 2010 | =0,005463 | Emsian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos aintawilus | 374 | Large eyes | Inner shelf | Predator/Scavenger | 6.4 | UA 13454 | Gibb 2010 | =0,003478 | Eifelian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 375 | Large eyes | Inner shelf | Predator/Scavenger | 5.6 | UA 13533 | Gibb 2010 | =0,004153 | Emsian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 376 | Large eyes | Inner shelf | Predator/Scavenger | 5.8 | UA 13533 | Gibb 2010 | =0,006851 | Emsian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos aintawilus | 377 | Large eyes | Inner shelf | Predator/Scavenger | 6.5 | UA 13455 | Gibb 2010 | =0,002762 | Eifelian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 378 | Large eyes | Inner shelf | Predator/Scavenger | 6.10 | UA13651 | Chatterton 2010 | =0,036752 | Eifelian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos hammii | 379 | Large eyes | Inner shelf | Predator/Scavenger | 7.7 | UA 13537 | Gibb 2010 | =0,006961 | Eifelian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos hammii | 380 | Large eyes | Inner shelf | Predator/Scavenger | 7.8 | UA 13536 | Gibb 2010 | =0,006520 | Eifelian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos hammii | 381 | Large eyes | Inner shelf | Predator/Scavenger | 7.10 | UA 13538 | Gibb 2010 | =0,009337 | Eifelian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos lisanrasus | 382 | Large eyes | Inner shelf | Predator/Scavenger | 8.7 | UA 13548 | Gibb 2010 | =0,005817 | Eifelian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 383 | Large eyes | Inner shelf | Predator/Scavenger | 8k | Di/UO/031 | Khaldi 2016 | =0,038460 | Emsian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 384 | Large eyes | Inner shelf | Predator/Scavenger | 8n | Di/UO/029 | Khaldi 2016 | =0,041317 | Emsian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos ainrasifus | 385 | Large eyes | Inner shelf | Predator/Scavenger | 9.8 | UA 13460 | Gibb 2010 | =0,014195 | Eifelian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos ainrasifus | 386 | Large eyes | Inner shelf | Predator/Scavenger | 9.11 | UA 13459 | Gibb 2010 | =0,013969 | Eifelian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos ainrasifus | 387 | Large eyes | Inner shelf | Predator/Scavenger | 10.5 | UA 13549 | Gibb 2010 | =0,006638 | Eifelian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos discombobulatus | 388 | Large eyes | Inner shelf | Predator/Scavenger | 11.7 | UA 13469 | Gibb 2010 | =0,008608 | Eifelian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos discombobulatus | 389 | Large eyes | Inner shelf | Predator/Scavenger | 11.11 | UA 13467 | Gibb 2010 | =0,006632 | Eifelian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos discombobulatus | 390 | Large eyes | Inner shelf | Predator/Scavenger | 11.12 | UA 13469 | Gibb 2010 | =0,012448 | Eifelian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos cuvieri malisus | 391 | Large eyes | Inner shelf | Predator/Scavenger | 12.9 | UA 13458 | Gibb 2010 | =0,011682 | Eifelian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos sp C | 392 | Large eyes | Inner shelf | Predator/Scavenger | Crônier_2 | Di/UO/029 | Crônier Oudot 2018 | =0,007704 | Emsian | Pygidium |

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| Proetida | Proetidae | Gerastos | Gerastos cuvieri malisus | 393 | Large eyes | Inner shelf | Predator/Scavenger | 13.13 | UA 13553 | Gibb 2010 | =0,012081 | Eifelian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos cuvieri malisus | 394 | Large eyes | Inner shelf | Predator/Scavenger | 14.6 | UA 13457 | Gibb 2010 | =0,005350 | Eifelian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos taqus | 395 | Large eyes | Inner shelf | Predator/Scavenger | 15.1 | UA 13554 | Gibb 2010 | =0,004519 | Eifelian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 396 | Large eyes | Inner shelf | Predator/Scavenger | 18.3 | UA 13558 | Gibb 2010 | =0,008501 | Emsian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos raribus | 397 | Large eyes | Inner shelf | Predator/Scavenger | 18.7 | UA 13463 | Gibb 2010 | =0,005228 | Givetian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos raribus | 398 | Large eyes | Inner shelf | Predator/Scavenger | 18.8 | UA 13463 | Gibb 2010 | =0,006018 | Givetian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos emmetus | 399 | Large eyes | Inner shelf | Predator/Scavenger | 21.4 | UA 13561 | Gibb 2010 | =0,009256 | Givetian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos emmetus | 400 | Large eyes | Inner shelf | Predator/Scavenger | 21.5 | UA 13472 | Gibb 2010 | =0,006170 | Givetian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos emmetus | 401 | Large eyes | Inner shelf | Predator/Scavenger | 22.5 | UA 13560 | Gibb 2010 | =0,004590 | Givetian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos emmetus | 402 | Large eyes | Inner shelf | Predator/Scavenger | 22.6 | UA 13562 | Gibb 2010 | =0,005849 | Givetian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos emmetus | 403 | Large eyes | Inner shelf | Predator/Scavenger | 23.9 | UA 13569 | Gibb 2010 | =0,003408 | Givetian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos emmetus | 404 | Large eyes | Inner shelf | Predator/Scavenger | 23.10 | UA 13568 | Gibb 2010 | =0,004169 | Givetian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos izius | 405 | Large eyes | Inner shelf | Predator/Scavenger | 24.10 | UA 13570 | Gibb 2010 | =0,006702 | Givetian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos izius | 406 | Large eyes | Inner shelf | Predator/Scavenger | 24.11 | UA 13529 | Gibb 2010 | =0,009798 | Givetian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos izius | 407 | Large eyes | Inner shelf | Predator/Scavenger | 25.7 | UA 13473 | Gibb 2010 | =0,009050 | Givetian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos izius | 408 | Large eyes | Inner shelf | Predator/Scavenger | 25.9 | UA 13473 | Gibb 2010 | =0,008047 | Givetian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 409 | Large eyes | Inner shelf | Predator/Scavenger | 37.7 | UA 13276 | Chatterton 2006 | =0,054866 | Emsian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 410 | Large eyes | Inner shelf | Predator/Scavenger | 39.9 | UA 13277 | Chatterton 2006 | =0,063487 | Emsian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 411 | Large eyes | Inner shelf | Predator/Scavenger | 39.11 | UA 13278 | Chatterton 2006 | =0,043132 | Emsian | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos prox umerbianus | 412 | Large eyes | Inner shelf | Predator/Scavenger | 46.6a | CGMTA 212b | Alberti 1969 | =0,011593 | | Pygidium |
| Proetida | Proetidae | Gerastos | Gerastos tuberculatus marocensis | 413 | Large eyes | Inner shelf | Predator/Scavenger | 54.7 | UA 13438 | Chatterton 2006 | =0,021757 | Emsian | Pygidium |
| Proetida | Proetidae | Helmutia | Helmutia rissanensis | 414 | Large eyes | Deep | Predator/Scavenger | 1.6b | IMGP Gö Orig K 1122-25 | Feist 2000 | =0.006480 | | Pygidium |
| Proetida | Proetidae | Helmutia | Helmutia rissanensis | 415 | Large eyes | Deep | Predator/Scavenger | 1.7 | UM2-RF 150 | Feist 2000 | =0.006825 | | Pygidium |
| Proetida | Proetidae | Helmutia | Helmutia rissanensis | 416 | Large eyes | Deep | Predator/Scavenger | 1.9a | UM2-RF 151 | Feist 2000 | =0.005683 | | Pygidium |
| Proetida | Proetidae | Koneprusites | Indet | 417 | Large eyes | Middle shelf | Predator/Scavenger | 2.11 | IMGP Gö Orig K 1122-48 | Feist 2000 | =0.005980 | Givetian | Pygidium |
| Proetida | Proetidae | Koneprusites | Koneprusites insons africus | 418 | Large eyes | Middle shelf | Predator/Scavenger | 6.18a | CGMTA 281 | Alberti 1970a | =0,007665 | Eifelian | Pygidium |
| Proetida | Proetidae | Koneprusites | Koneprusites insons africus | 419 | Large eyes | Middle shelf | Predator/Scavenger | 6.19 | SMF 23491 | Alberti 1970a | =0,005577 | Eifelian | Pygidium |
| Proetida | Proetidae | Koneprusites | Koneprusites insons africus | 420 | Large eyes | Middle shelf | Predator/Scavenger | 6.20 | CGMTA 282 | Alberti 1970a | =0,006873 | Eifelian | Pygidium |
| Proetida | Proetidae | Koneprusites | Koneprusites insons africus | 421 | Large eyes | Middle shelf | Predator/Scavenger | 6.21 | SMF 23492 | Alberti 1970a | =0,007918 | Eifelian | Pygidium |
| Proetida | Proetidae | Lepidoproetus | Lepidoproetus solutus | 422 | Large eyes | Shallow | Predator/Scavenger | 1.6 | No name | Alberti 1966c | =0.004703 | Pragian | Pygidium |
| Proetida | Proetidae | Lepidoproetus | Lepidoproetus lahceni | 423 | Large eyes | Shallow | Predator/Scavenger | 5.7 | NHM It 28952 | Johnson 2012 | =0,030310 | Pragian | Pygidium |
| Proetida | Proetidae | Lepidoproetus | Lepidoproetus lahceni | 424 | Large eyes | Shallow | Predator/Scavenger | 5.13 | NHM It 28953 | Johnson 2012 | =0,018320 | Pragian | Pygidium |
| Proetida | Proetidae | Lepidoproetus | Lepidoproetus maharchianus | 425 | Large eyes | Shallow | Predator/Scavenger | 6.1 | NHM It 28954 | Johnson 2012 | =0,039976 | Pragian | Pygidium |
| Proetida | Proetidae | Lepidoproetus | Lepidoproetus maharchianus | 426 | Large eyes | Shallow | Predator/Scavenger | 6.8 | NHM It 28955 | Johnson 2012 | =0,045789 | Pragian | Pygidium |
| Proetida | Proetidae | Lepidoproetus | Lepidoproetus spendens | 427 | Large eyes | Shallow | Predator/Scavenger | 6.13 | NHM It 28956 | Johnson 2012 | =0,028182 | Pragian | Pygidium |
| Proetida | Proetidae | Lepidoproetus | Lepidoproetus spendens | 428 | Large eyes | Shallow | Predator/Scavenger | 11.10 | SMF 23169 | Alberti 1969 | =0,006215 | Pragian | Pygidium |
| Proetida | Proetidae | Linguaproetus | Linguaproetus saharensis | 429 | Blind | Shallow | Predator/Scavenger | 28.22 | SMF 23439 | Alberti 1969 | =0,004873 | Eifelian | Pygidium |
| Proetida | Proetidae | Linguaproetus | Linguaproetus saharensis | 430 | Blind | Shallow | Predator/Scavenger | 28.23 | SMF 23440 | Alberti 1969 | =0,004749 | Eifelian | Pygidium |
| Proetida | Proetidae | Macroblepharum | Macroblepharum africanum ribatelfatanum | 431 | Large eyes | Middle shelf | Predator/Scavenger | 5.6 | CGMTA 250 | Alberti 1970a | =0,006093 | Emsian | Pygidium |
| Proetida | Proetidae | Macroblepharum | Macroblepharum africanum ribatelfatanum | 432 | Large eyes | Middle shelf | Predator/Scavenger | 5.7a | CGMTA 251 | Alberti 1970a | =0,005876 | Emsian | Pygidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Proetida | Proetidae | Macroblepharum | Macroblepharum africanum ribatelfatanum | 433 | Large eyes | Middle shelf | Predator/Scavenger | 5.8 | SMF 23468 | Alberti 1970a | =0,005228 | Emsian | Pygidium |
| Proetida | Proetidae | Macroblepharum | Macroblepharum africanum africanum | 434 | Large eyes | Middle shelf | Predator/Scavenger | 11.12 | CGMTA 203 | Alberti 1969 | =0,005557 | Eifelian | Pygidium |
| Proetida | Proetidae | Macroblepharum | Macroblepharum africanum africanum | 435 | Large eyes | Middle shelf | Predator/Scavenger | 46.15 | CGMTA 219 | Alberti 1969 | =0,005732 | Eifelian | Pygidium |
| Proetida | Proetidae | Montanproetus | Montanproetus tindoufanus | 436 | Large eyes | Inner shelf | Predator/Scavenger | 11.6 | SMF 23109 | Alberti 1969 | =0,010133 | Pragian | Pygidium |
| Proetida | Proetidae | Montanproetus | Montanproetus chlupaci | 437 | Large eyes | Inner shelf | Predator/Scavenger | 11.7 | SMF 23187? | Alberti 1969 | =0,011096 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Nagaproetus | Nagaproetus frequens | 438 | Large eyes | Middle shelf | Predator/Scavenger | 25.17 | CGMTA 117 | Alberti 1969 | =0,006742 | Emsian | Pygidium |
| Proetida | Tropidocoryphidae | Nagaproetus | Nagaproetus frequens | 439 | Large eyes | Middle shelf | Predator/Scavenger | 25.18 | CGMTA 118 | Alberti 1969 | =0,008587 | Emsian | Pygidium |
| Proetida | Tropidocoryphidae | Nagaproetus | Nagaproetus frequens | 440 | Large eyes | Middle shelf | Predator/Scavenger | 25.19 | CGMTA 119 | Alberti 1969 | =0,008749 | Emsian | Pygidium |
| Proetida | Tropidocoryphidae | Nagaproetus | Nagaproetus frequens | 441 | Large eyes | Middle shelf | Predator/Scavenger | 25.20 | SMF 23294 | Alberti 1969 | =0,008398 | Emsian | Pygidium |
| Proetida | Tropidocoryphidae | Nagaproetus | Nagaproetus frequens | 442 | Large eyes | Middle shelf | Predator/Scavenger | 25.21 | SMF 23295 | Alberti 1969 | =0,007810 | Emsian | Pygidium |
| Proetida | Tropidocoryphidae | Nagaproetus | Nagaproetus frequens | 443 | Large eyes | Middle shelf | Predator/Scavenger | b.16 | CGMTA 120 | Alberti 1967b | =0,011164 | Emsian | Pygidium |
| Proetida | Proetidae | Oehlertaspis | Oehlertaspis subpinguis | 444 | Large eyes | Middle shelf | Predator/Scavenger | 46.9a | CGMTA 214 | Alberti 1969 | =0,011589 | Emsian | Pygidium |
| Proetida | Proetidae | Orbitoproetus | Orbitoproetus africanus | 445 | Large eyes | Middle shelf | Predator/Scavenger | 46.1 | CGMTA 210 | Alberti 1969 | =0,015661 | Pragian | Pygidium |
| Proetida | Proetidae | Orbitoproetus | Orbitoproetus africanus | 446 | Large eyes | Middle shelf | Predator/Scavenger | 46.2 | SMF 23483b | Alberti 1969 | =0,016670 | Pragian | Pygidium |
| Proetida | Proetidae | Orbitoproetus | Orbitoproetus africanus | 447 | Large eyes | Middle shelf | Predator/Scavenger | 46.3 | SMF 23484b | Alberti 1969 | =0,013846 | Pragian | Pygidium |
| Proetida | Proetidae | Orbitoproetus | Indet | 448 | Large eyes | Middle shelf | Predator/Scavenger | Crônier_2 | Di/UO/029 | Crônier Oudot 2018 | =0,008725 | Emsian | Pygidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 449 | Large eyes | Middle shelf | Predator/Scavenger | 2.20 | No name | H. Alberti 1975a | =0.036994 | Famennian | Pygidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 450 | Large eyes | Middle shelf | Predator/Scavenger | 2.25 | No name | H. Alberti 1975a | =0.036994 | Famennian | Pygidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 451 | Large eyes | Middle shelf | Predator/Scavenger | 2.27 | No name | H. Alberti 1975a | =0.036994 | Famennian | Pygidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 452 | Large eyes | Middle shelf | Predator/Scavenger | 2.E2 | UMC−IP427 | Lerosey-Aubril 2005 | =0.004460 | Famennian | Pygidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 453 | Large eyes | Middle shelf | Predator/Scavenger | 2.F1 | UMC−IP428 | Lerosey-Aubril 2005 | =0.005746 | Famennian | Pygidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 454 | Large eyes | Middle shelf | Predator/Scavenger | 3.1 | No name | H. Alberti 1975a | =0.036994 | Famennian | Pygidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 455 | Large eyes | Middle shelf | Predator/Scavenger | 3.2 | No name | H. Alberti 1975a | =0.036994 | Famennian | Pygidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 456 | Large eyes | Middle shelf | Predator/Scavenger | 3.3 | No name | H. Alberti 1975a | =0.036994 | Famennian | Pygidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 457 | Large eyes | Middle shelf | Predator/Scavenger | 3.4 | No name | H. Alberti 1975a | =0.036994 | Famennian | Pygidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 458 | Large eyes | Middle shelf | Predator/Scavenger | 3.5 | No name | H. Alberti 1975a | =0.036994 | Famennian | Pygidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 459 | Large eyes | Middle shelf | Predator/Scavenger | 3.6 | No name | H. Alberti 1975a | =0.036994 | Famennian | Pygidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 460 | Large eyes | Middle shelf | Predator/Scavenger | 4q | UMC−IP400 | Lerosey-Aubril 2005 | =0,001623 | Famennian | Pygidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 461 | Large eyes | Middle shelf | Predator/Scavenger | 4r | UMC−IP401 | Lerosey-Aubril 2005 | =0,001742 | Famennian | Pygidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 462 | Large eyes | Middle shelf | Predator/Scavenger | 4s | UMC−IP402 | Lerosey-Aubril 2005 | =0,001930 | Famennian | Pygidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 463 | Large eyes | Middle shelf | Predator/Scavenger | 4t | UMC−IP403 | Lerosey-Aubril 2005 | =0,002128 | Famennian | Pygidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 464 | Large eyes | Middle shelf | Predator/Scavenger | 4u | UMC−IP404 | Lerosey-Aubril 2005 | =0,002686 | Famennian | Pygidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 465 | Large eyes | Middle shelf | Predator/Scavenger | 4v | UMC−IP405 | Lerosey-Aubril 2005 | =0,003496 | Famennian | Pygidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 466 | Large eyes | Middle shelf | Predator/Scavenger | 4w | UMC−IP406 | Lerosey-Aubril 2005 | =0,004310 | Famennian | Pygidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 467 | Large eyes | Middle shelf | Predator/Scavenger | 4x | UMC−IP407 | Lerosey-Aubril 2005 | =0,004306 | Famennian | Pygidium |
| Proetida | Proetidae | Osmolskabole | Osmolskabole prima | 468 | Large eyes | Middle shelf | Predator/Scavenger | 4y | UMC−IP408 | Lerosey-Aubril 2005 | =0,003937 | Famennian | Pygidium |
| Proetida | Proetidae | Palpebralia | Palpebralia brecciae | 469 | Blind | Deep | Predator/Scavenger | 2i | UM2−RF 181 | Feist 2002 | =0.015746 | Frasnian | Pygidium |
| Proetida | Proetidae | Paralepidoproetus | Paralepidoproetus wragei | 470 | Large eyes | Middle shelf | Predator/Scavenger | 2.14 | SMF 36237 | Alberti 1981a | =0.020358 | Eifelian | Pygidium |
| Proetida | Proetidae | Paralepidoproetus | Paralepidoproetus chouberti | 471 | Large eyes | Middle shelf | Predator/Scavenger | 11.5 | SMF 23427 | Alberti 1969 | =0,009640 | | Pygidium |
| Proetida | Tropidocoryphidae | Phaetonellus | Phaetonellus planicauda africanus | 472 | Large eyes | Middle shelf | Predator/Scavenger | 3.29 | CGMTA | Alberti 1981a | =0.035772 | Emsian | Pygidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Proetida | Tropidocoryphidae | Phaetonellus | Phaetonellus planicauda africanus | 473 | Large eyes | Middle shelf | Predator/Scavenger | 3.30 | SMF 36264 | Alberti 1981a | =0.036200 | Emsian | Pygidium |
| Proetida | Proetidae | Piriproetus | Indet | 474 | Blind | Deep | Predator/Scavenger | 3.24 | SMF 36257 | Alberti 1981a | =0.020358 | Emsian | Pygidium |
| Proetida | Proetidae | Piriproetus | Piriproetus amblyops austromaurus | 475 | Blind | Deep | Predator/Scavenger | 3.32 | SMF 36291 | Alberti 1981a | =0.012760 | Eifelian | Pygidium |
| Proetida | Proetidae | Piriproetus | Piriproetus amblyops austromaurus | 476 | Blind | Deep | Predator/Scavenger | 19.14 | SMF 23225 | Alberti 1969 | =0,005336 | Eifelian | Pygidium |
| Proetida | Proetidae | Piriproetus | Piriproetus amblyops patruelis | 477 | Blind | Deep | Predator/Scavenger | 46.13 | CGMTA 217 | Alberti 1969 | =0,005031 | Eifelian | Pygidium |
| Proetida | Proetidae | Piriproetus | Piriproetus amblyops austromaurus | 478 | Blind | Deep | Predator/Scavenger | Doublon_ | CGMTA 218 | Alberti 1969 | =0,005745 | Eifelian | Pygidium |
| Proetida | Proetidae | Podoliproetus | Podoliproetus mirdani | 479 | Large eyes | Inner shelf | Predator/Scavenger | 7.4 | NHM It 28957 | Johnson 2012 | =0,037283 | Pragian | Pygidium |
| Proetida | Proetidae | Podoliproetus | Podoliproetus mirdani | 480 | Large eyes | Inner shelf | Predator/Scavenger | 7.7 | NHM It 28958 | Johnson 2012 | =0,037283 | Pragian | Pygidium |
| Proetida | Proetidae | Podoliproetus | Podoliproetus mirdani | 481 | Large eyes | Inner shelf | Predator/Scavenger | 7.11 | NHM It 28959 | Johnson 2012 | =0,037283 | Pragian | Pygidium |
| Proetida | Proetidae | Podoliproetus | Podoliproetus sinespina | 482 | Large eyes | Inner shelf | Predator/Scavenger | 8.5 | NHM It 28960 | Johnson 2012 | =0,037035 | Pragian | Pygidium |
| Proetida | Proetidae | Podoliproetus | Podoliproetus mirdani | 483 | Large eyes | Inner shelf | Predator/Scavenger | 8.11 | NHM It 28961 | Johnson 2012 | =0,023295 | Pragian | Pygidium |
| Proetida | Proetidae | Podoliproetus | Podoliproetus mirdani | 484 | Large eyes | Inner shelf | Predator/Scavenger | 8.12 | NHM It 28961 | Johnson 2012 | =0,023295 | Pragian | Pygidium |
| Proetida | Proetidae | Pragoproetus | Pragoproetus tafilaltensis | 485 | Large eyes | Inner shelf | Predator/Scavenger | 6.16 | SMF 23087 | Alberti 1969 | =0,009070 | Pragian | Pygidium |
| Proetida | Proetidae | Pragoproetus | Pragoproetus tafilaltensis | 486 | Large eyes | Inner shelf | Predator/Scavenger | 6.17 | SMF 23088 | Alberti 1969 | =0,010015 | Pragian | Pygidium |
| Proetida | Proetidae | Pragoproetus | Pragoproetus tafilaltensis | 487 | Large eyes | Inner shelf | Predator/Scavenger | 6.18 | CGMTA 26 | Alberti 1969 | =0,010015 | Pragian | Pygidium |
| Proetida | Proetidae | Pragoproetus | Pragoproetus gibbosus | 488 | Large eyes | Inner shelf | Predator/Scavenger | 6.22 | SMF 23045 | Alberti 1969 | =0,012510 | Pragian | Pygidium |
| Proetida | Proetidae | Prodrevermannia | Prodrevermannia jaegeri zemmoura | 489 | Blind | Middle shelf | Predator/Scavenger | 3.25 | SMF 36258 | Alberti 1981a | =0.014330 | Pragian | Pygidium |
| Proetida | Proetidae | Prodrevermannia | Prodrevermannia jaegeri jaegeri | 490 | Blind | Middle shelf | Predator/Scavenger | 6.64 | SMF 36562 | Alberti 1983 | =0.005866 | Pragian | Pygidium |
| Proetida | Proetidae | Prodrevermannia | Prodrevermannia jaegeri jaegeri | 491 | Blind | Middle shelf | Predator/Scavenger | 6.65 | SH | Alberti 1983 | =0.005462 | Pragian | Pygidium |
| Proetida | Proetidae | Proetina | Proetina ihmadii | 492 | Large eyes | Inner shelf | Predator/Scavenger | 9.5 | NHM It 28962 | Johnson 2012 | =0,018080 | Pragian | Pygidium |
| Proetida | Proetidae | Ignoproetus | Proetopeltis waldschmidti | 493 | Large eyes | Middle shelf | Predator/Scavenger | 6.4 | CGMTA 355 | Alberti 1970a | =0,008322 | Emsian | Pygidium |
| Proetida | Proetidae | Ignoproetus | Proetopeltis waldschmidti | 494 | Large eyes | Middle shelf | Predator/Scavenger | 6.5 | SMF 23591 | Alberti 1970a | =0,006750 | Emsian | Pygidium |
| Proetida | Proetidae | CORNUPROETINAE | Indet | 495 | | | Predator/Scavenger | 17.13 | SMF 23205 | Alberti 1969 | =0,010335 | Emsian | Pygidium |
| Proetida | Proetidae | CORNUPROETINAE | Indet | 496 | | | Predator/Scavenger | 17.14 | SMF 23206 | Alberti 1969 | =0,010335 | Emsian | Pygidium |
| Proetida | Proetidae | Proetus | Proetus proetus sp B aff granulosus | 497 | Large eyes | Middle shelf | Predator/Scavenger | 3.2 | CGMT | Alberti 1970a | =0,014710 | Eifelian | Pygidium |
| Proetida | Proetidae | Proetus | Proetus proetus sp A aff granulosus | 498 | Large eyes | Middle shelf | Predator/Scavenger | 3.5d | CGMT-TM 21 | Alberti 1970a | =0,013346 | Emsian | Pygidium |
| Proetida | Proetidae | Proetus | Indet | 499 | Large eyes | Middle shelf | Predator/Scavenger | 46.7 | CGMTA 213 | Alberti 1969 | =0,010674 | Emsian | Pygidium |
| Proetida | Proetidae | Proetus | Indet | 500 | Large eyes | Middle shelf | Predator/Scavenger | 46.10 | CGMTA 215 | Alberti 1969 | =0,004838 | Emsian | Pygidium |
| Proetida | Proetidae | Sculptoproetus | Sculptoproetus maghrebus | 501 | Large eyes | Middle shelf | Predator/Scavenger | 4.6 | CGMTA 243 | Alberti 1970a | =0,005260 | Emsian | Pygidium |
| Proetida | Proetidae | Sculptoproetus | Sculptoproetus sculptus antiquus | 502 | Large eyes | Middle shelf | Predator/Scavenger | 11.8 | SMF 23139 | Alberti 1969 | =0,005793 | Pragian | Pygidium |
| Proetida | Proetidae | Sculptoproetus | Sculptoproetus sp A | 503 | Large eyes | Middle shelf | Predator/Scavenger | 40.4 | UA 13259 | Chatterton 2006 | =0,023965 | Emsian | Pygidium |
| Proetida | Proetidae | Sculptoproetus | Sculptoproetus sp A | 504 | Large eyes | Middle shelf | Predator/Scavenger | 40.5 | UA 13258 | Chatterton 2006 | =0,026375 | Emsian | Pygidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Proetida | Proetidae | Sculptoproetus | Sculptoproetus haasi | 505 | Large eyes | Middle shelf | Predator/Scavenger | 40.9 | UA 13266 | Chatterton 2006 | =0,030728 | Eifelian | Pygidium |
| Proetida | Proetidae | Sculptoproetus | Sculptoproetus haasi | 506 | Large eyes | Middle shelf | Predator/Scavenger | 40.10 | UA 13269 | Chatterton 2006 | =0,050878 | Eifelian | Pygidium |
| Proetida | Proetidae | Sculptoproetus | Sculptoproetus sp B | 507 | Large eyes | Middle shelf | Predator/Scavenger | 40.13 | UA 13262 | Chatterton 2006 | =0,040703 | Eifelian | Pygidium |
| Proetida | Proetidae | Tafilaltaspis | Tafilaltaspis creber creber | 508 | Large eyes | Middle shelf | Predator/Scavenger | 4 | SMF 23000 | Alberti 1966a | =0,005627 | Emsian | Pygidium |
| Proetida | Proetidae | Tafilaltaspis | Tafilaltaspis creber creber | 509 | Large eyes | Middle shelf | Predator/Scavenger | 6.9 | CGMTA 254 | Alberti 1970a | =0,005651 | Emsian | Pygidium |
| Proetida | Proetidae | Tafilaltaspis | Tafilaltaspis creber creber | 510 | Large eyes | Middle shelf | Predator/Scavenger | 6.10 | CGMTA 356 | Alberti 1970a | =0,009132 | Emsian | Pygidium |
| Proetida | Proetidae | Tafilaltaspis | Tafilaltaspis creber tenuigranifer | 511 | Large eyes | Middle shelf | Predator/Scavenger | 11.20 | SMF 23195 | Alberti 1969 | =0,008644 | Eifelian | Pygidium |
| Proetida | Proetidae | Tafilaltaspis | Tafilaltaspis creber creber | 512 | Large eyes | Middle shelf | Predator/Scavenger | Doublon_ | CGMTA 3 | Alberti 1969 | =0,004906 | Emsian | Pygidium |
| Proetida | Proetidae | Tafilaltaspis | Tafilaltaspis creber creber | 513 | Large eyes | Middle shelf | Predator/Scavenger | Doublon_ | CGMTA 4 | Alberti 1969 | =0,007054 | Emsian | Pygidium |
| Proetida | Proetidae | Tafilaltaspis | Tafilaltaspis creber creber | 514 | Large eyes | Middle shelf | Predator/Scavenger | Doublon_ | SMF 23003 | Alberti 1969 | =0,004899 | Emsian | Pygidium |
| Proetida | Proetidae | Tafilaltaspis | Tafilaltaspis creber creber | 515 | Large eyes | Middle shelf | Predator/Scavenger | Doublon_ | SMF 23000 | Alberti 1969 | =0,006388 | Emsian | Pygidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus haasi | 516 | Large eyes | Middle shelf | Predator/Scavenger | 4.6 | UA13272 | Gibb 2007 | =0,005460 | Eifelian | Pygidium |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus haasi | 517 | Large eyes | Middle shelf | Predator/Scavenger | 4.7 | UA13273 | Gibb 2007 | =0,004004 | Eifelian | Pygidium |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus haasi | 518 | Large eyes | Middle shelf | Predator/Scavenger | 5.1 | UA13256 | Gibb 2007 | =0,011808 | Eifelian | Pygidium |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus haasi | 519 | Large eyes | Middle shelf | Predator/Scavenger | 5.10 | UA13269 | Gibb 2007 | =0,015089 | Eifelian | Pygidium |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus haasi | 520 | Large eyes | Middle shelf | Predator/Scavenger | 6.14 | UA13288 | Gibb 2007 | =0,004756 | Eifelian | Pygidium |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus dibbanus | 521 | Large eyes | Middle shelf | Predator/Scavenger | 7.5 | UA13258 | Gibb 2007 | =0,007913 | Emsian | Pygidium |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus dibbanus | 522 | Large eyes | Middle shelf | Predator/Scavenger | 7.8 | UA13258 | Gibb 2007 | =0,008185 | Emsian | Pygidium |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus dibbanus | 523 | Large eyes | Middle shelf | Predator/Scavenger | 7.9 | UA13259 | Gibb 2007 | =0,007714 | Emsian | Pygidium |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus dibbanus | 524 | Large eyes | Middle shelf | Predator/Scavenger | 7.10 | UA13281 | Gibb 2007 | =0,003636 | Emsian | Pygidium |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus elguerrouji | 525 | Large eyes | Middle shelf | Predator/Scavenger | 8.1 | UA13262 | Gibb 2007 | =0,009831 | Eifelian | Pygidium |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus haasi | 526 | Large eyes | Middle shelf | Predator/Scavenger | 9.10 | UA13268 | Gibb 2007 | =0,005522 | Eifelian | Pygidium |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus elguerrouji | 527 | Large eyes | Middle shelf | Predator/Scavenger | 9.12 | UA13260 | Gibb 2007 | =0,011700 | Eifelian | Pygidium |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus haasi | 528 | Large eyes | Middle shelf | Predator/Scavenger | 9.13 | UA13266 | Gibb 2007 | =0,009031 | Eifelian | Pygidium |
| Proetida | Proetidae | Unguliproetus | Unguliproetus unguloides tener | 529 | Large eyes | Middle shelf | Predator/Scavenger | 6.9 | SMF 23039 | Alberti 1969 | =0,007372 | Emsian | Pygidium |
| Proetida | Proetidae | Unguliproetus | Unguliproetus unguloides tener | 530 | Large eyes | Middle shelf | Predator/Scavenger | 6.10 | CGMTA 18 | Alberti 1969 | =0,007110 | Emsian | Pygidium |
| Proetida | Proetidae | Unguliproetus | Unguliproetus unguloides tener | 531 | Large eyes | Middle shelf | Predator/Scavenger | 6.11 | SMF 23042 | Alberti 1969 | =0,007566 | Emsian | Pygidium |
| Proetida | Proetidae | Voigtaspis | Voigtaspis voigti | 532 | Large eyes | Middle shelf | Predator/Scavenger | 11.1 | SMF 23208 | Alberti 1969 | =0,009630 | Pragian | Pygidium |
| Proetida | Proetidae | Voigtaspis | Voigtaspis voigti | 533 | Large eyes | Middle shelf | Predator/Scavenger | 11.2 | CGMTA 83 | Alberti 1969 | =0,007340 | Pragian | Pygidium |
| Proetida | Proetidae | Voigtaspis | Voigtaspis voigti | 534 | Large eyes | Middle shelf | Predator/Scavenger | 11.3 | SMF 23209 | Alberti 1969 | =0,008663 | Pragian | Pygidium |
| Proetida | Proetidae | Voigtaspis | Voigtaspis voigti | 535 | Large eyes | Middle shelf | Predator/Scavenger | 11.4a | CGMTA 82 | Alberti 1969 | =0,014387 | Pragian | Pygidium |
| Proetida | Proetidae | Voigtaspis | Voigtaspis voigti | 536 | Large eyes | Middle shelf | Predator/Scavenger | b.8 | CGMTA 82 | Alberti 1967b | =0,018963 | Pragian | Pygidium |
| Proetida | Proetidae | Warbugella | Warbugella rugulosa maura | 537 | Large eyes | Inner shelf | Predator/Scavenger | 33.4 | CGMT | Alberti 1969 | =0,007672 | Lochkovian | Pygidium |
| Proetida | Proetidae | Warbugella | Warbugella rugulosa maura | 538 | Large eyes | Inner shelf | Predator/Scavenger | 33.5 | No name | Alberti 1969 | =0,008485 | Lochkovian | Pygidium |
| Proetida | Proetidae | Warbugella | Warbugella rugulosa maura | 539 | Large eyes | Inner shelf | Predator/Scavenger | 33.6 | SMF 23358 | Alberti 1969 | =0,006860 | Lochkovian | Pygidium |
| Proetida | Proetidae | Warbugella | Warbugella rugulosa maura | 540 | Large eyes | Inner shelf | Predator/Scavenger | 33.7 | CGMTA 145 | Alberti 1969 | =0,007588 | Lochkovian | Pygidium |
| Proetida | Proetidae | Warbugella | Warbugella rugulosa maura | 541 | Large eyes | Inner shelf | Predator/Scavenger | 33.8 | SMF 23359 | Alberti 1969 | =0,006744 | Lochkovian | Pygidium |
| Proetida | Proetidae | Warbugella | Warbugella rugulosa maura | 542 | Large eyes | Inner shelf | Predator/Scavenger | 33.9 | SMF 23360 | Alberti 1969 | =0,006308 | Lochkovian | Pygidium |
| Proetida | Proetidae | Warbugella | Warbugella rugulosa maura | 543 | Large eyes | Inner shelf | Predator/Scavenger | 33.10 | SMF 23361 | Alberti 1969 | =0,007012 | Lochkovian | Pygidium |
| Proetida | Proetidae | Warbugella | Warbugella rugulosa maura | 544 | Large eyes | Inner shelf | Predator/Scavenger | 33.11 | CGMTA 205 | Alberti 1969 | =0,007012 | Lochkovian | Pygidium |
| Proetida | Proetidae | Yuanjia | Yuanjia wildungensis | 545 | Large eyes | Middle shelf | Predator/Scavenger | 9.2 | Gö 693-210 | H. Alberti 1973 | =0.009415 | Famennian | Pygidium |
| Corynexoch | Scutelluidae | Cavetia | Cavetia furcifera hamlagdadiana | 546 | Large eyes | Middle shelf | Predator/Scavenger | 3y | UA13266 | Feist 2018 | =0,024302 | Emsian | Pygidium |
| Corynexoch | Scutelluidae | Cavetia | Cavetia furcifera hamlagdadiana | 547 | Large eyes | Middle shelf | Predator/Scavenger | 8 | No name | Alberti 1981b | =0.047222 | Emsian | Pygidium |
| Corynexoch | Scutelluidae | Heliopeltis | Heliopeltis johnsoni | 548 | Large eyes | Inner shelf | Predator/Scavenger | 12e | UM-IP 705 | Feist 2015 | =0,007352 | | Pygidium |
| Corynexoch | Scutelluidae | Heliopeltis | Heliopeltis johnsoni | 549 | Large eyes | Inner shelf | Predator/Scavenger | 13h | UM-IP 710 | Feist 2015 | =0,008889 | | Pygidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis chlupaci hollardi | 550 | Large eyes | Inner shelf | Predator/Scavenger | 2 | No name | Alberti 1966b | =0.017114 | Pragian | Pygidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis bassei | 551 | Large eyes | Inner shelf | Predator/Scavenger | 3 | Nr 1126 | Alberti 1966b | =0.015531 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis chlupaci hollardi | 552 | Large eyes | Inner shelf | Predator/Scavenger | 4a | UA 14327 | Feist 2015 | =0,029065 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis chlupaci hollardi | 553 | Large eyes | Inner shelf | Predator/Scavenger | 4c | UM-IP 658 | Feist 2015 | =0,045043 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis chlupaci hollardi | 554 | Large eyes | Inner shelf | Predator/Scavenger | 4d | UA 14326 | Feist 2015 | =0,018796 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis bassei | 555 | Large eyes | Inner shelf | Predator/Scavenger | 4h | UA 14325 | Feist 2015 | =0,023363 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis chlupaci rabatensis | 556 | Large eyes | Inner shelf | Predator/Scavenger | 5 | No name | Alberti 1966b | =0.017989 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis bassei | 557 | Large eyes | Inner shelf | Predator/Scavenger | 5a | UM-IP 653 | Feist 2015 | =0,022726 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis bassei | 558 | Large eyes | Inner shelf | Predator/Scavenger | 5e | UM-IP 655 | Feist 2015 | =0,017482 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis maghrebia | 559 | Large eyes | Inner shelf | Predator/Scavenger | 6 | No name | Alberti 1966b | =0.032786 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis hamlaghdadica | 560 | Large eyes | Inner shelf | Predator/Scavenger | 6i | UM-IP 663 | Feist 2015 | =0,021644 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis hamlaghdadica | 561 | Large eyes | Inner shelf | Predator/Scavenger | 6k | UM-IP 664 | Feist 2015 | =0,025124 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis hamlaghdadica | 562 | Large eyes | Inner shelf | Predator/Scavenger | 6l | UM-IP 665 | Feist 2015 | =0,036488 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis maghrebia | 563 | Large eyes | Inner shelf | Predator/Scavenger | 7l | SMF 36590 | Feist 2015 | =0,014083 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis tafilaltensis | 564 | Large eyes | Inner shelf | Predator/Scavenger | 8e | UM-IP 682 | Feist 2015 | =0,019793 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis tafilaltensis | 565 | Large eyes | Inner shelf | Predator/Scavenger | 8i | UM-IP 683 | Feist 2015 | =0,019417 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis tafilaltensis | 566 | Large eyes | Inner shelf | Predator/Scavenger | 8k | UM-IP 678 | Feist 2015 | =0,019230 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Kolihapeltis | Kolihapeltis maghrebia | 567 | Large eyes | Inner shelf | Predator/Scavenger | Doublon_ | No name | Alberti 1982 | =0.038210 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Paralejurus | Paralejurus elayounensis | 568 | Large eyes | Inner shelf | Predator/Scavenger | 1.2a | SMF 57073 | Schraut 2000c | =0,086718 | Pragian | Pygidium |
| Proetida | Proetidae | Buchiproetus | Buchiproetus pribyli pribyli | 569 | Large eyes | Middle shelf | Predator/Scavenger | 2.9 | SMF 36234 | Alberti 1981a | =0.036146 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Paralejurus | Paralejurus hamlagdadicus | 570 | Large eyes | Inner shelf | Predator/Scavenger | 1.10a | CGMTA | Alberti 1983 | =0.035397 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Paralejurus | Paralejurus brongniarti menanensis | 571 | Large eyes | Inner shelf | Predator/Scavenger | 4.3 | SMF 76649 | Schraut 2004 | =0,053175 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Paralejurus | Paralejurus bohemicus | 572 | Large eyes | Inner shelf | Predator/Scavenger | 4.10 | SMF 76654 | Schraut 2004 | =0,045057 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Paralejurus | Paralejurus spatuliformis | 573 | Large eyes | Inner shelf | Predator/Scavenger | 5.6 | SMF 76658 | Schraut 2004 | =0,051371 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Paralejurus | Paralejurus spatuliformis | 574 | Large eyes | Inner shelf | Predator/Scavenger | 5.8 | SMF 76662 | Schraut 2004 | =0,051371 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Paralejurus | Paralejurus spatuliformis | 575 | Large eyes | Inner shelf | Predator/Scavenger | 5.10 | SMF 76663 | Schraut 2004 | =0,050497 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Paralejurus | Paralejurus rehamnanus | 576 | Large eyes | Inner shelf | Predator/Scavenger | 6.7 | UA13652 | Chatterton 2010 | =0,052633 | Eifelian | Pygidium |
| Corynexoch | Scutelluidae | Paralejurus | Paralejurus tenuistriatus | 577 | Large eyes | Inner shelf | Predator/Scavenger | 7.7 | SMF 76676 | Schraut 2004 | =0,047420 | Emsian | Pygidium |
| Corynexoch | Scutelluidae | Paralejurus | Paralejurus rehamnanus | 578 | Large eyes | Inner shelf | Predator/Scavenger | 7.9 | SMF 76669 | Schraut 2004 | =0,029352 | Emsian | Pygidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Corynexoch | Scutelluidae | Paralejurus | Paralejurus tenuistriatus | 579 | Large eyes | Inner shelf | Predator/Scavenger | 7.10 | SMF 76676 | Schraut 2004 | =0,032031 | Emsian | Pygidium |
| Corynexoch | Scutelluidae | Platyscutellum | Platyscutellum megranense | 580 | Large eyes | Middle shelf | Predator/Scavenger | 1.14a | CGMTA 231 | Alberti 1970a | =0,020435 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Platyscutellum | Platyscutellum massai | 581 | Large eyes | Middle shelf | Predator/Scavenger | 6 | No name | Alberti 1981b | =0.033551 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Platyscutellum | Platyscutellum massai | 582 | Large eyes | Middle shelf | Predator/Scavenger | Alberti_19 | No name | Alberti 1982 | =0.065376 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Scabriscutellum | Scabriscutellum frix | 583 | Large eyes | Middle shelf | Predator/Scavenger | 2.2 | CGMTA 235 | Alberti 1970a | =0,017046 | Pragian | Pygidium |
| Corynexoch | Scutelluidae | Scabriscutellum | Scabriscutellum hammadi | 584 | Large eyes | Middle shelf | Predator/Scavenger | 48.6 | UA 13412 | Chatterton 2006 | =0,101153 | Emsian | Pygidium |
| Corynexoch | Scutelluidae | Scabriscutellum | Scabriscutellum hammadi | 585 | Large eyes | Middle shelf | Predator/Scavenger | 48.7 | UA 13410 | Chatterton 2006 | =0,102334 | Emsian | Pygidium |
| Corynexoch | Scutelluidae | Thysanopeltis | Thysanopeltis speciosa | 586 | Large eyes | Middle shelf | Predator/Scavenger | 8r | SMF 57113 | Schraut 2000a | =0.030650 | Eifelian | Pygidium |
| Proetida | Tropidocoryphidae | Chlupaciparia | Chlupaciparia ziegleri maroccania | 587 | Large eyes | Middle shelf | Predator/Scavenger | 3p | UM2−RF 254 | Feist 2002 | =0.003445 | Frasnian | Pygidium |
| Proetida | Tropidocoryphidae | Decoroproetus | Decoroproetus decorus maurulus | 588 | Large eyes | Middle shelf | Predator/Scavenger | 8.21 | SMF 23501 | Alberti 1970a | =0,007165 | Ludlow-Pridoli | Pygidium |
| Proetida | Tropidocoryphidae | Decoroproetus | Decoroproetus decorus maurulus | 589 | Large eyes | Middle shelf | Predator/Scavenger | 29.16 | SMF 23236 | Alberti 1969 | =0,011776 | Ludlow-Pridoli | Pygidium |
| Proetida | Tropidocoryphidae | Decoroproetus | Decoroproetus concentricus meridianus | 590 | Large eyes | Middle shelf | Predator/Scavenger | 31.20 | CGMTA 136 | Alberti 1969 | =0,006349 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Decoroproetus | Decoroproetus concentricus meridianus | 591 | Large eyes | Middle shelf | Predator/Scavenger | 31.21 | SMF 23349 | Alberti 1969 | =0,008060 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Tropidocoryphe | Tropidocoryphe memmon nepos | 592 | Large eyes | Middle shelf | Predator/Scavenger | 4.37 | SMF 36269 | Alberti 1981a | =0.041156 | Emsian | Pygidium |
| Proetida | Tropidocoryphidae | Tropidocoryphe | Tropidocoryphe hamlaghdadica | 593 | Large eyes | Middle shelf | Predator/Scavenger | 30.7 | SMF 23330 | Alberti 1969 | =0,009016 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Tropidocoryphe | Tropidocoryphe hamlaghdadica | 594 | Large eyes | Middle shelf | Predator/Scavenger | 30.8 | CGMTA 127 | Alberti 1969 | =0,008140 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Tropidocoryphe | Tropidocoryphe amuri | 595 | Large eyes | Middle shelf | Predator/Scavenger | 41.6 | UA 13394 | Chatterton 2006 | =0,035555 | Emsian | Pygidium |
| Phacopida | Acastidae | Minicryphaeus | Minicryphaeus giganteus | 596 | Large eyes | Shallow | Predator/Scavenger | 3.3 | 80202 | Bignon 2014 | =0,042371 | Pragian | Pygidium |
| Phacopida | Acastidae | Minicryphaeus | Minicryphaeus giganteus | 597 | Large eyes | Shallow | Predator/Scavenger | 3.5 | JC 101 | Bignon 2014 | =0,040981 | Pragian | Pygidium |
| Phacopida | Acastidae | Minicryphaeus | Minicryphaeus giganteus | 598 | Large eyes | Shallow | Predator/Scavenger | 4.5 | JC 103 | Bignon 2014 | =0,042015 | Pragian | Pygidium |
| Phacopida | Acastidae | Minicryphaeus | Minicryphaeus giganteus | 599 | Large eyes | Shallow | Predator/Scavenger | 4.6 | JC 102 | Bignon 2014 | =0,042011 | Pragian | Pygidium |
| Proetida | Proetidae | Perliproetus | Perliproetus africanus | 600 | Large eyes | Middle shelf | Predator/Scavenger | 1W | MB.T 6225 | FeistWeyer 2018 | =0.029399 | Famennian | Pygidium |
| Proetida | Proetidae | Perliproetus | Perliproetus africanus | 601 | Large eyes | Middle shelf | Predator/Scavenger | 1U | MB.T 6222 | FeistWeyer 2018 | =0.035692 | Famennian | Pygidium |
| Phacopida | Phacopidae | Nephranops | Nephranops (Nephranops) incisus | 602 | Blind | Deep | Predator/Scavenger | 4V | UM-IP 820b | Feist 2019 | =0.011110 | Famennian | Pygidium |
| Proetida | Aulacopleuridae | Cyphaspides | Cyphaspides ammari | 603 | Small eyes | Middle shelf | Particle feeding | 3.6 | UA 14313 | Chatterton 2019 | =0.028900 | Eifelian | Pygidium |
| Proetida | Aulacopleuridae | Cyphaspides | Cyphaspides ammari | 604 | Small eyes | Middle shelf | Particle feeding | 4.3 | UA 14320 | Chatterton 2019 | =0.007810 | Eifelian | Pygidium |
| Proetida | Aulacopleuridae | Cyphaspides | Cyphaspides ammari | 605 | Small eyes | Middle shelf | Particle feeding | 4.5 | UA 14322 | Chatterton 2019 | =0.007873 | Eifelian | Pygidium |
| Proetida | Aulacopleuridae | Cyphaspides | Cyphaspides pankowskiorum | 606 | Small eyes | Middle shelf | Particle feeding | 5.2 | UA 14316 | Chatterton 2019 | =0.058819 | Eifelian | Pygidium |
| Proetida | Aulacopleuridae | Cyphaspides | Cyphaspides pankowskiorum | 607 | Small eyes | Middle shelf | Particle feeding | 5.4 | UA 14264 | Chatterton 2019 | =0.079363 | Eifelian | Pygidium |
| Proetida | Aulacopleuridae | Cyphaspides | Cyphaspides nicoleae | 608 | Small eyes | Middle shelf | Particle feeding | 5.5 | UA 14317 | Chatterton 2019 | =0.085442 | Eifelian | Pygidium |
| Phacopida | Phacopidae | Reedops | Reedops bronni | 609 | Large eyes | Inner shelf | Predator/Scavenger | Frey8g_py | PIMUZ 30647 | Frey 2014 | =0,059938 | Pragian | Pygidium |
| Phacopida | Phacopidae | Reedops | Reedops cephalotes | 610 | Large eyes | Inner shelf | Predator/Scavenger | Klug_11.2 | PIMUZ 7289 | Klug 2008 | =0,064841 | Emsian | Pygidium |
| Phacopida | Acastidae | Metacanthina | Metacanthina wallacei | 611 | Large eyes | Shallow | Predator/Scavenger | Klug_11.1 | PIMUZ 7291 | Klug 2008 | =0,051938 | Emsian | Pygidium |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Phacopida | Dalmanitidae | Morocconites | Morocconites malladoides | 612 | Large eyes | Inner shelf | Predator/Scavenger | Edgecomb | No name | Edgecombe 1991 | =0,015954 | | Pygidium |
| Phacopida | Acastidae | Lanceaspis | Lanceaspis hammondi | 613 | Large eyes | Inner shelf | Predator/Scavenger | Corbacho | JC106 | Corbacho 2014 | =0,087062 | Pragian | Pygidium |
| Phacopida | Acastidae | Lanceaspis | Lanceaspis hammondi | 614 | Large eyes | Inner shelf | Predator/Scavenger | Corbacho | KH200 | Corbacho 2014 | =0,144261 | Pragian | Pygidium |
| Phacopida | Acastidae | Lanceaspis | Lanceaspis hammondi | 615 | Large eyes | Inner shelf | Predator/Scavenger | Corbacho | JC107 | Corbacho 2014 | =0,073056 | Pragian | Pygidium |
| Proetida | Proetidae | Sculptoproetus | Sculptoproetus raki | 616 | Large eyes | Middle shelf | Predator/Scavenger | 3h | IRSBNa13414 | Van Viersen 2019 | =0,012048 | Emsian | Pygidium |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus haasi | 617 | Large eyes | Middle shelf | Predator/Scavenger | 4f | IRSBNa13416 | Van Viersen 2019 | =0,027387 | Eifelian | Pygidium |
| Proetida | Proetidae | Koneprusites | Koneprusites oresibios | 618 | Large eyes | Middle shelf | Predator/Scavenger | 4p | IRSBNa13415 | Van Viersen 2019 | =0,029847 | Eifelian | Pygidium |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus haasi | 619 | Large eyes | Middle shelf | Predator/Scavenger | 5a | IRSBNa13420 | Van Viersen 2019 | =0,033879 | Eifelian | Pygidium |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus haasi | 620 | Large eyes | Middle shelf | Predator/Scavenger | 5r | IRSBNa13421 | Van Viersen 2019 | =0,016666 | Emsian | Pygidium |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus sp. A | 621 | Large eyes | Middle shelf | Predator/Scavenger | 6d | IRSBNa13422 | Van Viersen 2019 | =0,045443 | | Pygidium |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus gibbae | 622 | Large eyes | Middle shelf | Predator/Scavenger | 7i | IRSBNa13423 | Van Viersen 2019 | =0,020198 | Emsian | Pygidium |
| Proetida | Proetidae | Timsaloproetus | Timsaloproetus pulchistriatus repens | 623 | Large eyes | Middle shelf | Predator/Scavenger | 8e | IRSBNa13425 | Van Viersen 2019 | =0,037709 | Emsian | Pygidium |
| Proetida | Proetidae | Hollandiella | Hollandiella curvirostris | 624 | Large eyes | Inner shelf | Predator/Scavenger | 10d | IRSBNa13426 | Van Viersen 2019 | =0,031235 | Pragian | Pygidium |
| Proetida | Proetidae | Hollandiella | Hollandiella lebruni | 625 | Large eyes | Inner shelf | Predator/Scavenger | 11d | IRSBNa13429 | Van Viersen 2019 | =0,019604 | Emsian | Pygidium |
| Proetida | Proetidae | Hollandiella | Hollandiella lebruni | 626 | Large eyes | Inner shelf | Predator/Scavenger | 11g | IRSBNa13430 | Van Viersen 2019 | =0,024383 | Emsian | Pygidium |
| Proetida | Proetidae | Hollandiella | Hollandiella verecunda | 627 | Large eyes | Inner shelf | Predator/Scavenger | 13a | IRSBNa13432 | Van Viersen 2019 | =0,031235 | Pragian | Pygidium |
| Proetida | Proetidae | Lepidoproetus | Lepidoproetus maharchianus | 628 | Large eyes | Shallow | Predator/Scavenger | 13j | IRSBNa13433 | Van Viersen 2019 | =0,023254 | Pragian | Pygidium |
| Proetida | Tropidocoryphidae | Tafilaltaspis | Tafilaltaspis rufa | 629 | Large eyes | Middle shelf | Predator/Scavenger | 15e | IRSBNa13435 | Van Viersen 2019 | =0,022221 | Eifelian | Pygidium |
| Lichida | Odontopleuridae | Koneprusia | Koneprusia aboussalamae | 630 | Large eyes | Middle shelf | Predator/Scavenger | 3n | MB.T. 4572 | Feist McNamara 2007 | =0.013329 | Givetian | Pygidium |

# Article 6 :

| reference | species | genus | family | order | section | basin | stage | substage | count | Formation |
|---|---|---|---|---|---|---|---|---|---|---|
| Corbacho Kier 2013 Bettaleria | Acanthopyge (Belenopyge) estevei | Acanthopyge | Lichidae | Lichida | El Achana | Maider | Pragian | Pragian | 7 | Ihandar |
| Cronier Oudot Klug DeBaets 2018 NJb Geol Pal | Indet | Acanthopyge | Lichidae | Lichida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 3 | Amerboh |
| Corbacho Kier 2013 Bettaleria | Acanthopyge (Belenopyge) estevei | Acanthopyge | Lichidae | Lichida | Jbel el Mrakib | Maider | Pragian | Pragian | 3 | Ihandar |
| Corbacho Kier 2013 Bettaleria | Acanthopyge (Belenopyge) bassei | Acanthopyge | Lichidae | Lichida | Jbel Issoumour SW | Maider | Eifelian | lower Eifelian | 1 | El Otfal |
| Chatterton Gibbs 2010 Jpal | Acanthopyge (Belenopyge) bassei | Acanthopyge | Lichidae | Lichida | Jbel Issoumour SW | Maider | Eifelian | lower Eifelian | 2 | El Otfal |
| Hollard 1963 Notes et Mémoires du SGM | Acastella jacquemonti levis | Acastella | Acastidae | Phacopida | Tanzida | Draa Valley | Lochkovian | lower Lochkovian | 1 | Lmhaïfid |
| Hollard 1963 Notes et Mémoires du SGM | Acastella jacquemonti tanzidensis | Acastella | Acastidae | Phacopida | Tanzida | Draa Valley | Lochkovian | lower Lochkovian | 1 | Lmhaïfid |
| Hollard 1963 Notes et Mémoires du SGM | Acastella patula | Acastella | Acastidae | Phacopida | Tanzida | Draa Valley | Lochkovian | lower Lochkovian | 1 | Lmhaïfid |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Acastoides haddadi | Acastoides | Calmoniidae | Phacopida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 1 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Acastoides zguilmensis | Acastoides | Calmoniidae | Phacopida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 19 | Timrhamhart |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Adrisiops boudjemaai | Adrisiops | Phacopidae | Phacopida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 4 | Chefar el Ahmar |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Adrisiops fabrei | Adrisiops | Phacopidae | Phacopida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 2 | Chefar el Ahmar |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Adrisiops fabrei | Adrisiops | Phacopidae | Phacopida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 3 | Chefar el Ahmar |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Adrisiops fabrei | Adrisiops | Phacopidae | Phacopida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 2 | Chefar el Ahmar |
| Burton Eldredge 1974 Palaeont | Adrisiops fabrei | Adrisiops | Phacopidae | Phacopida | Erg Djemel | Ougarta basin | Eifelian | lower Eifelian | 1 | Chefar el Ahmar |
| vanViersen Holland Koppka 2017 Bull geo | Adrisiops weugi | Adrisiops | Phacopidae | Phacopida | Jbel Issoumour SW | Maider | Emsian | upper Emsian | 1 | El Otfal |
| Alberti 1983 Senck lethaea | Afrops larvifer | Afrops | Phacopidae | Phacopida | Ben Zireg | Ougarta basin | Pragian | Pragian | 1 |  |
| Thomas Holloway 1988 Phil. TRSL | Akantharges mbarki | Akantharges | Lichidae | Lichida | Jdorf | Tafilalt | Eifelian |  | 1 |  |
| Cobacho Lopez-Soriano 2013 Batalleria | Akantharges mbarki | Akantharges | Lichidae | Lichida | Tinejad | Tafilalt | Eifelian |  | 4 |  |
| Alberti 1969 SenckNaturGesell | Alberticoryphe stirps | Alberticoryphe | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Alberti 1981a Senck lethaea | Alberticoryphe stirps | Alberticoryphe | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Alberti 1969 SenckNaturGesell | Aulacopleura beyrichi africana | Aulacopleura | Aulacopleuridae | Proetida | Hamar Laghdad | Tafilalt | Eifelian | lower Eifelian | 1 | Bou Tcharafine |
| Alberti 1970a SenckNaturGesell | Aulacopleura beyrichi africana | Aulacopleura | Aulacopleuridae | Proetida | Hamar Laghdad | Tafilalt | Eifelian | lower Eifelian | 2 | Bou Tcharafine |
| Alberti 1981a Senck lethaea | Aulacopleura beyrichi africana | Aulacopleura | Aulacopleuridae | Proetida | Hamar Laghdad | Tafilalt | Eifelian | lower Eifelian | 8 | Bou Tcharafine |
| Alberti 1970a SenckNaturGesell | Aulacopleura beyrichi africana | Aulacopleura | Aulacopleuridae | Proetida | Jbel Amlane | Tafilalt | Eifelian | lower Eifelian | 1 | Bou Tcharafine |
| Alberti 1981a Senck lethaea | Aulacopleura bohemica | Aulacopleura | Aulacopleuridae | Proetida | Jbel Bou Tscharafine | Tafilalt | Eifelian | lower Eifelian | 1 | Bou Tcharafine |
| Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag | Aulacopleura beyrichi africana | Aulacopleura | Aulacopleuridae | Proetida | Ouarourout | Ougarta basin | Eifelian | lower Eifelian | 1 | Chefar el Ahmar |
| Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag | Aulacopleura | Aulacopleuridae | Proetida | Ouarourout | Ougarta basin | Eifelian | lower Eifelian | 1 | Chefar el Ahmar |  |
| Alberti 1981a Senck lethaea | Aulacopleurella mauretanica | Aulacopleurella | Aulacopleuridae | Proetida | Hamar Laghdad | Tafilalt | Eifelian | lower Eifelian | 1 | Bou Tcharafine |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Austerops legrandi | Austerops | Phacopidae | Phacopida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 7 | Chefar el Ahmar |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Austerops legrandi | Austerops | Phacopidae | Phacopida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 35 | Chefar el Ahmar |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Austerops menchikoffi | Austerops | Phacopidae | Phacopida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 1 | Chefar el Ahmar |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Austerops menchikoffi | Austerops | Phacopidae | Phacopida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 2 | Chefar el Ahmar |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Austerops menchikoffi | Austerops | Phacopidae | Phacopida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 12 | Chefar el Ahmar |
| Le Maître 1952 Mémoire de la Carte géologique de l'Algérie | Austerops menchikoffi | Austerops | Phacopidae | Phacopida | Erg Djemel | Ougarta basin | Eifelian | lower Eifelian | 20 | Chefar el Ahmar |

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|---|---|---|---|---|---|---|---|---|---|---|
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Austerops speculator speculator | Austerops | Phacopidae | Phacopida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 5 | Chefar el Ahmar |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Austerops speculator speculator | Austerops | Phacopidae | Phacopida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 4 | Chefar el Ahmar |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Austerops speculator speculator | Austerops | Phacopidae | Phacopida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 3 | Chefar el Ahmar |
| McKellar Chatterton 2009 Pal Canadiana | Austerops menchikoffi | Austerops | Phacopidae | Phacopida | Jbel Gara el Zguilma | Maider | Emsian | upper Emsian | 10 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Austerops menchikoffi | Austerops | Phacopidae | Phacopida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 11 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Austerops menchikoffi | Austerops | Phacopidae | Phacopida | Jbel Gara el Zguilma | Draa Valley | Eifelian | lower Eifelian | 13 | Timrhamhart |
| Chatterton Gibbs 2010 Jpal | Austerops menchikoffi | Austerops | Phacopidae | Phacopida | Jbel Issoumour SW | Maider | Eifelian | lower Eifelian | 2 | El Otfal |
| McKellar Chatterton 2009 Pal Canadiana | Austerops kermiti | Austerops | Phacopidae | Phacopida | Jbel Oufatene | Maider | Eifelian | lower Eifelian | 8 | El Otfal |
| McKellar Chatterton 2009 Pal Canadiana | Austerops salamandar | Austerops | Phacopidae | Phacopida | Jbel Oufatene | Maider | Eifelian | lower Eifelian | 5 | El Otfal |
| McKellar Chatterton 2009 Pal Canadiana | Austerops speculator punctatus | Austerops | Phacopidae | Phacopida | Jbel Oufatene | Maider | Eifelian | lower Eifelian | 3 | El Otfal |
| McKellar Chatterton 2009 Pal Canadiana | Austerops speculator punctatus | Austerops | Phacopidae | Phacopida | Jbel Oufatene | Maider | Eifelian | lower Eifelian | 4 | El Otfal |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Austerops menchikoffi | Austerops | Phacopidae | Phacopida | Marhouma | Ougarta basin | Emsian | upper Emsian | 3 | Chefar el Ahmar |
| Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag | Austerops salamandaroides | Austerops | Phacopidae | Phacopida | Ouarourout | Ougarta basin | Eifelian | lower Eifelian | 11 | Chefar el Ahmar |
| Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag | Austerops sp B | Austerops | Phacopidae | Phacopida | Ouarourout | Ougarta basin | Eifelian | lower Eifelian | 3 | Chefar el Ahmar |
| Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag | Austerops sp D | Austerops | Phacopidae | Phacopida | Ouarourout | Ougarta basin | Eifelian | lower Eifelian | 3 | Chefar el Ahmar |
| Cobacho Lopez-Soriano 2013 Batalleria | Basseiarges mellishae | Basseiarges | Lichidae | Lichida | Jdorf | Tafilalt | Eifelian | | 4 | |
| Alberti 1983 Senck lethaea | Boeckops algericus | Boeckops | Phacopidae | Phacopida | Ben Zireg | Ougarta basin | Pragian | Pragian | 6 | |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Boeckops sp C | Boeckops | Phacopidae | Phacopida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 1 | Chefar el Ahmar |
| Alberti 1983 Senck lethaea | Boeckops maidericus | Boeckops | Phacopidae | Phacopida | Timarzite | Maider | Pragian | Pragian | 1 | Ihandar |
| McKellar Chatterton 2009 Pal Canadiana | Boeckops stelcki | Boeckops | Phacopidae | Phacopida | Taharajat Oufatene | Maider | Emsian | upper Emsian | 7 | Tazoulaït |
| Alberti 1969 SenckNaturGesell | Buchiproetus mauretanicus | Buchiproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 2 | lower Kess Kess |
| Alberti 1967a Senck leth | Buchiproetus mauretanicus | Buchiproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Alberti 1969 SenckNaturGesell | Buchiproetus mauretanicus | Buchiproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 6 | lower Kess Kess |
| Feist Belka 2018 N.Jb Geol | Buchiproetus rudrichteri | Buchiproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | | 1 | upper Kess Kess |
| Feist Belka 2018 N.Jb Geol | Cavetia furcifera hamlagdadiana | Cavetia | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Emsian | lower Emsian | 12 | upper Kess Kess |
| Becker ElHassani Hartenfels Luddecke 2018 Frontiers Science | Cavetia furcifera hamlagdadiana | Cavetia | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Emsian | lower Emsian | | upper Kess Kess |
| Alberti 1970a SenckNaturGesell | Cavetia furcifera hamlagdadiana | Cavetia | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Emsian | lower Emsian | 1 | upper Kess Kess |
| Alberti 1981b Senck lethaea | Cavetia furcifera hamlagdadiana | Cavetia | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Emsian | lower Emsian | 2 | upper Kess Kess |
| Alberti 1983 Senck lethaea | Cavetia furcifera hamlagdadiana | Cavetia | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Emsian | lower Emsian | 4 | upper Kess Kess |
| vanViersen Prescher 2011 GeolBelgica | Ceratarges aries | Ceratarges | Lichidae | Lichida | Jbel Zireg | Maider | Eifelian | lower Eifelian | 1 | El Otfal |
| vanViersen Prescher 2011 GeolBelgica | Ceratarges koumalii | Ceratarges | Lichidae | Lichida | Jbel Zireg | Maider | Eifelian | lower Eifelian | 1 | El Otfal |
| vanViersen Prescher 2011 GeolBelgica | Ceratarges ziregensis | Ceratarges | Lichidae | Lichida | Jbel Zireg | Maider | Eifelian | lower Eifelian | 1 | El Otfal |
| Feist Belka 2018 N.Jb Geol | Ceratocephala hoernesi | Ceratocephala | Odontopleuridae | Lichida | Hamar Laghdad | Tafilalt | Emsian | | 12 | upper Kess Kess |
| Alberti 1970a SenckNaturGesell | Ceratocephala hoernesi | Ceratocephala | Odontopleuridae | Lichida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| Cronier Oudot Klug DeBaets 2018 NJb Geol Pal | Ceratocephala vesiculosa | Ceratocephala | Odontopleuridae | Lichida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 3 | Amerboh |
| Lerosey-Aubril Feist Chatterton 2008 Geol Mag | Chamaeleoaspis lkomalii | Chamaeleoaspis | Aulacopleuridae | Proetida | Jbel Zireg | Maider | Eifelian | lower Eifelian | 1 | El Otfal |
| H.Alberti 1974 NJb Geol Pal | Chaunoproetus berberus | Chaunoproetus | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | upper Famennian | 7 | Achguig |
| Feist Mahboubi Girard 2016 Bull geo | Chlupacops cryphoides | Chlupacops | Phacopidae | Phacopida | Marhouma | Ougarta basin | Frasnian | middle Frasnian | 4 | Chefar el Ahmar |
| Feist Mahboubi Girard 2016 Bull geo | Chlupacops laticeps | Chlupacops | Phacopidae | Phacopida | Marhouma | Ougarta basin | Frasnian | middle Frasnian | 2 | Chefar el Ahmar |
| Alberti 1983 Senck lethaea | Chotecops zizensis | Chotecops | Phacopidae | Phacopida | Hamar Laghdad | Tafilalt | Eifelian | lower Eifelian | 1 | Bou Tcharafine |

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|---|---|---|---|---|---|---|---|---|---|---|
| Stegemann 2006 Münstersche Forschungen Geol Pal | Chotecops sp1 | Chotecops | Phacopidae | Phacopida | Hassi Nebech | Tafilalt | Givetian | upper Givetian | 3 | Achguig |
| Stegemann 2006 Münstersche Forschungen Geol Pal | Chotecops sp1 | Chotecops | Phacopidae | Phacopida | Hassi Nebech | Tafilalt | Givetian | upper Givetian | 1 | Achguig |
| Feist Orth 2000 ProcSDS | Chotecops zizensis | Chotecops | Phacopidae | Phacopida | Jbel Mech Irdane | Tafilalt | Eifelian | upper Eifelian | 3 | Bou Tcharafine |
| Feist Orth 2000 ProcSDS | Chotecops zizensis | Chotecops | Phacopidae | Phacopida | Jbel Mech Irdane | Tafilalt | Givetian | lower Givetian | 2 | Bou Tcharafine |
| Feist Orth 2000 ProcSDS | Chotecops zizensis | Chotecops | Phacopidae | Phacopida | Jbel Ziata | Tafilalt | Givetian | lower Givetian | 1 | Bou Tcharafine |
| Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag | Chotecops hoseri | Chotecops | Phacopidae | Phacopida | Ouarourout | Ougarta basin | Eifelian | lower Eifelian | 4 | Chefar el Ahmar |
| Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag | Chotecops hoseri | Chotecops | Phacopidae | Phacopida | Ouarourout | Ougarta basin | Eifelian | lower Eifelian | 47 | Chefar el Ahmar |
| Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag | Chotecops hoseri | Chotecops | Phacopidae | Phacopida | Ouarourout | Ougarta basin | Eifelian | lower Eifelian | 5 | Chefar el Ahmar |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Coltraneia effelesa | Coltraneia | Acastidae | Phacopida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 3 | Timrhamhart |
| Morzadec 2001 PalaeontA | Coltraneia oufatenensis | Coltraneia | Acastidae | Phacopida | Jbel Oufatene | Maider | Emsian | upper Emsian | 2 | El Otfal |
| Morzadec 1997 PalaeontA | Coltraneia saourensis | Coltraneia | Acastidae | Phacopida | Marhouma | Ougarta basin | Emsian | upper Emsian | 1 | Chefar el Ahmar |
| Morzadec 1997 PalaeontA | Coltraneia saourensis | Coltraneia | Acastidae | Phacopida | Marhouma | Ougarta basin | Emsian | upper Emsian | 2 | Chefar el Ahmar |
| Morzadec 1997 PalaeontA | Coltraneia saourensis | Coltraneia | Acastidae | Phacopida | Marhouma | Ougarta basin | Emsian | upper Emsian | 1 | Chefar el Ahmar |
| Cronier Oudot Klug DeBaets 2018 NJb Geol Pal | Indet | Comura | Acastidae | Phacopida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| Morzadec 2001 PalaeontA | Comura bultyncki | Comura | Acastidae | Phacopida | Jbel Oufatene | Maider | Emsian | upper Emsian | 2 | Tazoulaït |
| Morzadec 2001 PalaeontA | Comura bultyncki | Comura | Acastidae | Phacopida | Jbel Oufatene | Maider | Emsian | upper Emsian | 1 | El Otfal |
| Alberti 1969 SenckNaturGesell | Coniproetus eurysthenes nomas | Coniproetus | Proetidae | Proetida | El Atrous | Tafilalt | Pragian | Pragian | 1 | Seheb el Rhassel |
| Alberti 1969 SenckNaturGesell | Coniproetus condensus mesembrinus | Coniproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 2 | lower Kess Kess |
| Alberti 1981a Senck lethaea | Cornuproetus cornutus djemelensis | Cornuproetus | Proetidae | Proetida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 3 | Chefar el Ahmar |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Cornuproetus cornutus djemelensis | Cornuproetus | Proetidae | Proetida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 3 | Chefar el Ahmar |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Cornuproetus cornutus djemelensis | Cornuproetus | Proetidae | Proetida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 3 | Chefar el Ahmar |
| Feist Belka 2018 N.Jb Geol | Cornuproetus pusulosus | Cornuproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | | 1 | upper Kess Kess |
| Cronier Oudot Klug DeBaets 2018 NJb Geol Pal | Indet | Cornuproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 4 | Amerboh |
| Feist Orth 2000 ProcSDS | Cornuproetus oudrissensis | Cornuproetus | Proetidae | Proetida | Jbel Ou Driss | Maider | Givetian | lower Givetian | 2 | Taboumakhloûf |
| Alberti 1970a SenckNaturGesell | Cornuproetus cornutus sspA | Cornuproetus | Proetidae | Proetida | Jbel Ouhalane | Maider | Givetian | | 1 | |
| Alberti 1983 Senck lethaea | Crotalocephalina gibbus benziregensis | Crotalocephalina | Cheiruridae | Phacopida | Ben Zireg | Ougarta basin | Pragian | Pragian | 20 | |
| Alberti 1969 SenckNaturGesell | Crotalocephalina gibbus | Crotalocephalina | Cheiruridae | Phacopida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Alberti 1969 SenckNaturGesell | Crotalocephalina gibbus | Crotalocephalina | Cheiruridae | Phacopida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 2 | lower Kess Kess |
| Alberti 1983 Senck lethaea | Crotalocephalina gibbus auster | Crotalocephalina | Cheiruridae | Phacopida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Alberti 1983 Senck lethaea | Crotalocephalus meridianus | Crotalocephalus | Cheiruridae | Phacopida | Ben Zireg | Ougarta basin | Pragian | Pragian | 1 | |
| Alberti 1983 Senck lethaea | Crotalocephalus pauper saharensis | Crotalocephalus | Cheiruridae | Phacopida | Ben Zireg | Ougarta basin | Pragian | Pragian | 4 | |
| Alberti 1983 Senck lethaea | Crotalocephalus pauper saharensis | Crotalocephalus | Cheiruridae | Phacopida | Ben Zireg | Ougarta basin | Pragian | Pragian | 1 | |
| Alberti 1983 Senck lethaea | Chrotalocephalus sternbergi | Crotalocephalus | Cheiruridae | Phacopida | Hamar Laghdad | Tafilalt | Emsian | lower Emsian | 1 | upper Kess Kess |
| Alberti 1983 Senck lethaea | Crotalocephalus pauper hamlagdadicus | Crotalocephalus | Cheiruridae | Phacopida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Alberti 1981b Senck lethaea | Crotalocephalus pauper hamlagdadicus | Crotalocephalus | Cheiruridae | Phacopida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 3 | lower Kess Kess |
| Frey Naglik Hofmann Schemm-Gregory Fryda Kröger Taylor 2014 Bull geo | Crotalocephalus | Cheiruridae | Phacopida | Jbel | Tafilalt | Pragian | Pragian | 2 | Seheb el | |
| Basse in Basse and Müller 2004 Wiebelsheim | Cyberella lemkei | Cyberella | Proetidae | Proetida | Taboumakhloûf | Maider | Eifelian | lower Eifelian | 1 | Taboumakhloûf |
| Chatterton Gibb McKellar 2019 | Cyphaspides ammari | Cyphaspides | Aulacopleuridae | Proetida | Hamar Laghdad | Tafilalt | Eifelian | | 2 | |
| Cronier Oudot Klug DeBaets 2018 NJb Geol Pal | Cyphaspides ammari | Cyphaspides | Aulacopleuridae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 5 | Amerboh |

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|---|---|---|---|---|---|---|---|---|---|---|
| Chatterton Gibb McKellar 2019 | Cyphaspides nicoleae | Cyphaspides | Aulacopleuridae | Proetida | Jdorf | Tafilalt | Eifelian | | 1 | Bou Tcharafine |
| Chatterton Gibb McKellar 2019 | Cyphaspides pankowskiorum | Cyphaspides | Aulacopleuridae | Proetida | Jdorf | Tafilalt | Eifelian | | 2 | Bou Tcharafine |
| Chatterton Gibb McKellar 2019 | Cyphaspides ammari | Cyphaspides | Aulacopleuridae | Proetida | Talawarite | Tafilalt | Eifelian | | 8 | Bou Tcharafine |
| vanViersen Holland 2016 GeolBelgica | Cyphaspis khraidensis | Cyphaspis | Aulacopleuridae | Proetida | Bou Dîb | Maider | Emsian | | 1 | |
| vanViersen Holland 2016 GeolBelgica | Cyphaspis kippingi | Cyphaspis | Aulacopleuridae | Proetida | Bou Dîb | Maider | Emsian | upper Emsian | 2 | Tazoulaït |
| vanViersen Holland 2016 GeolBelgica | Cyphaspis smeenki | Cyphaspis | Aulacopleuridae | Proetida | Bou Dîb | Maider | Eifelian | lower Eifelian | 1 | El Otfal |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Cyphaspis agayuara | Cyphaspis | Aulacopleuridae | Proetida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 5 | Chefar el Ahmar |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Cyphaspis agayuara | Cyphaspis | Aulacopleuridae | Proetida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 2 | Chefar el Ahmar |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Cyphaspis hamidi | Cyphaspis | Aulacopleuridae | Proetida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 1 | Chefar el Ahmar |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Cyphaspis hamidi | Cyphaspis | Aulacopleuridae | Proetida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 1 | Chefar el Ahmar |
| vanViersen Holland 2016 GeolBelgica | Cyphaspis eberhardiei | Cyphaspis | Aulacopleuridae | Proetida | Foum Zguid | Draa Valley | Eifelian | lower Eifelian | 1 | Timrhamhart |
| vanViersen Holland 2016 GeolBelgica | Cyphaspis foumzguidensis | Cyphaspis | Aulacopleuridae | Proetida | Foum Zguid | Draa Valley | Eifelian | lower Eifelian | 1 | Timrhamhart |
| Feist Belka 2018 N.Jb Geol | Cyphaspis akkae | Cyphaspis | Aulacopleuridae | Proetida | Hamar Laghdad | Tafilalt | Emsian | | 3 | upper Kess Kess |
| Alberti 1981a Senck lethaea | Cyphaspis boutscharafinense | Cyphaspis | Aulacopleuridae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| Alberti 1981a Senck lethaea | Cyphaspis hamlagdadicus | Cyphaspis | Aulacopleuridae | Proetida | Hamar Laghdad | Tafilalt | Eifelian | lower Eifelian | 1 | Bou Tcharafine |
| Alberti 1983 Senck lethaea | Cyphaspis lierli | Cyphaspis | Aulacopleuridae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 3 | lower Kess Kess |
| Cronier Oudot Klug DeBaets 2018 NJb Geol Pal | Cyphaspis sp Aprim | Cyphaspis | Aulacopleuridae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 3 | Amerboh |
| Cronier Oudot Klug DeBaets 2018 NJb Geol Pal | Cyphaspis sp B boutscharafinense | Cyphaspis | Aulacopleuridae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| Alberti 1969 SenckNaturGesell | Indet | Cyphaspis | Aulacopleuridae | Proetida | Hamar Laghdad | Tafilalt | Eifelian | | 1 | lower Kess Kess |
| Alberti 1981a Senck lethaea | Cyphaspis boutscharafinense | Cyphaspis | Aulacopleuridae | Proetida | Jbel Bou Tscharafine | Tafilalt | Emsian | upper Emsian | 3 | Amerboh |
| Alberti 1969 SenckNaturGesell | Cyphaspis boutscharafinense | Cyphaspis | Aulacopleuridae | Proetida | Jbel Bou Tscharafine | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| vanViersen Prescher 2014 GeolBelgica | Cyphaspis walteri | Cyphaspis | Aulacopleuridae | Proetida | Jbel el Mrakib | Maider | | | | Bou Dîb |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Cyphaspis agayuara | Cyphaspis | Aulacopleuridae | Proetida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 1 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Cyphaspis eberhardiei | Cyphaspis | Aulacopleuridae | Proetida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 4 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Cyphaspis hamidi | Cyphaspis | Aulacopleuridae | Proetida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 3 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Cyphaspis hamidi | Cyphaspis | Aulacopleuridae | Proetida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 8 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Cyphaspis sp A | Cyphaspis | Aulacopleuridae | Proetida | Jbel Gara el Zguilma | Draa Valley | Eifelian | lower Eifelian | 1 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Cyphaspis | Aulacopleuridae | Proetida | Jbel Gara el | Draa Valley | Emsian | upper Emsian | 2 | Timrhamh | |
| vanViersen Holland 2016 GeolBelgica | Cyphaspis lerougei | Cyphaspis | Aulacopleuridae | Proetida | Jbel Issoumour Unknown | Maider | Emsian | | 1 | |
| vanViersen Holland 2016 GeolBelgica | Cyphaspis sp I | Cyphaspis | Aulacopleuridae | Proetida | Jbel Issoumour Unknown | Maider | Eifelian | | 1 | |
| vanViersen Holland 2016 GeolBelgica | Cyphaspis eximia | Cyphaspis | Aulacopleuridae | Proetida | Jbel Oufatene | Maider | Eifelian | | 1 | Taboumakhloûf |
| vanViersen Holland 2016 GeolBelgica | Cyphaspis bluhmi | Cyphaspis | Aulacopleuridae | Proetida | Jbel Zireg | Maider | Eifelian | lower Eifelian | 1 | Taboumakhloûf |
| vanViersen Holland 2016 GeolBelgica | Cyphaspis khraidensis | Cyphaspis | Aulacopleuridae | Proetida | Khraid | Draa Valley | Emsian | upper Emsian | 1 | Timrhamhart |
| vanViersen Holland 2016 GeolBelgica | Cyphaspis maharchensis | Cyphaspis | Aulacopleuridae | Proetida | Maharch | Maider | Pragian | Pragian | 1 | Ihandar |
| vanViersen Holland 2016 GeolBelgica | Cyphaspis heisingi | Cyphaspis | Aulacopleuridae | Proetida | Mdâour el Kbîr | Draa Valley | Pragian | Pragian | 1 | Assa |
| Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag | Cyphaspis sp A | Cyphaspis | Aulacopleuridae | Proetida | Ouarourout | Ougarta basin | Eifelian | lower Eifelian | 2 | Chefar el Ahmar |
| vanViersen Holland 2016 GeolBelgica | Cyphaspis ihmadii | Cyphaspis | Aulacopleuridae | Proetida | Taboumakhloûf | Maider | Givetian | lower Givetian | 1 | Bou Dîb |
| vanViersen Holland 2016 GeolBelgica | Cyphaspis agayuara | Cyphaspis | Aulacopleuridae | Proetida | Talawarite | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| vanViersen Holland 2016 GeolBelgica | Cyphaspis juergenhollandi | Cyphaspis | Aulacopleuridae | Proetida | Talawarite | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| Lerosey-Aubril Feist 2006 Pal | Cyrtosymbole rectifrons | Cyrtosymbole | Proetidae | Proetida | Korb el Atil | Tafilalt | Famennian | lower Famennian | 85 | Achguig |
| Lerosey-Aubril Feist 2006 Pal | Cyrtosymbole sp A | Cyrtosymbole | Proetidae | Proetida | Korb el Atil | Tafilalt | Famennian | lower Famennian | 1 | Achguig |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| H.Alberti 1976a NJb Geol Pal | Cyrtosymbolina varica | Cyrtosymbolina | Proetidae | Proetida | Bin Jbilet | Tafilalt | Famennian | lower Famennian | 5 | Achguig |
| H.Alberti 1976a NJb Geol Pal | Cyrtosymbolina varica | Cyrtosymbolina | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | lower Famennian | 15 | Achguig |
| H.Alberti 1976a NJb Geol Pal | Cyrtosymbolina varica | Cyrtosymbolina | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | lower Famennian | 1 | Achguig |
| Alberti 1970a SenckNaturGesell | Cyrtosymboloides samum | Cyrtosymboloides | Proetidae | Proetida | Gara Mdouard | Tafilalt | Eifelian | lower Eifelian | 10 | Amerboh |
| Johnson Fortey 2012 Jpal | Dalejeproetus owensi | Dalejeproetus | Proetidae | Proetida | Akka n'Talilite | Maider | Pragian | Pragian | 3 | Ihandar |
| Johnson Fortey 2012 Jpal | Dalejeproetus sagaouii | Dalejeproetus | Proetidae | Proetida | Jbel el Mrakib | Maider | Pragian | Pragian | 3 | Ihandar |
| Feist Orth 2000 ProcSDS | Dechenella gigouti | Dechenella | Proetidae | Proetida | Jbel Ziata | Tafilalt | Givetian | lower Givetian | 1 | Bou Tcharafine |
| Feist Orth 2000 ProcSDS | Dechenella ziatensis | Dechenella | Proetidae | Proetida | Jbel Ziata | Tafilalt | Givetian | lower Givetian | 8 | Bou Tcharafine |
| Alberti 1983 Senck lethaea | Denckmannites morator | Denckmannites | Phacopidae | Phacopida | Ben Zireg | Ougarta basin | Pragian | Pragian | 1 | |
| Alberti 1967b Senck leth | Denemarkia tafilaltensis | Denemarkia | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Alberti 1983 Senck lethaea | Denemarkia tafilaltensis | Denemarkia | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Becker ElHassani Hartenfels Luddecke 2018 Frontiers Science Engineering | Destombesina tafilaltensis | Destombesina | Acastidae | Phacopida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| Cronier Oudot Klug DeBaets 2018 NJb Geol Pal | Destombesina tafilaltensis | Destombesina | Acastidae | Phacopida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 3 | Amerboh |
| Morzadec 2001 PalaeontA | Destombesina tafilaltensis | Destombesina | Acastidae | Phacopida | Jbel Bou Tscharafine | Tafilalt | Emsian | upper Emsian | 8 | Amerboh |
| Morzadec 1997 PalaeontA | Destombesina ougartensis | Destombesina | Acastidae | Phacopida | Zerhamra | Ougarta basin | Emsian | upper Emsian | 11 | Teferguenit |
| Alberti 1969 SenckNaturGesell | Diademaproetus praecursor | Diademaproetus | Proetidae | Proetida | Tissint | Draa Valley | Emsian | upper Emsian | 1 | Timrhamhart |
| Alberti 1969 SenckNaturGesell | Diademaproetus praecursor | Diademaproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | lower Emsian | 2 | upper Kess Kess |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Diademaproetus mohamedi | Diademaproetus | Proetidae | Proetida | Jbel Gara el Zguilma | Draa Valley | Eifelian | lower Eifelian | 2 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Diademaproetus praecursor | Diademaproetus | Proetidae | Proetida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 1 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Diademaproetus praecursor | Diademaproetus | Proetidae | Proetida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 10 | Timrhamhart |
| Alberti 1969 SenckNaturGesell | Diademaproetus praecursor | Diademaproetus | Proetidae | Proetida | Tizi Takereit | Maider | Emsian | upper Emsian | 1 | |
| Feist Mahboubi Girard 2016 Bull geo | Dianops algeriensis | Dianops | Phacopidae | Phacopida | Marhouma | Ougarta basin | Famennian | upper Famennian | 2 | Argiles de Marhouma |
| Crônier Malti François Benyoucef Brice 2013 Geol Mag | Dianops algeriensis | Dianops | Phacopidae | Phacopida | Tamtert Zereg | Ougarta basin | Famennian | upper Famennian | 1 | Argiles de Marhouma |
| Crônier Malti François Benyoucef Brice 2013 Geol Mag | Dianops typhlops | Dianops | Phacopidae | Phacopida | Tamtert Zereg | Ougarta basin | Famennian | upper Famennian | 1 | Argiles de Marhouma |
| Crônier Malti François Benyoucef Brice 2013 Geol Mag | Dianops vicarius | Dianops | Phacopidae | Phacopida | Tamtert Zereg | Ougarta basin | Famennian | upper Famennian | 3 | Argiles de Marhouma |
| Crônier Malti François Benyoucef Brice 2013 Geol Mag | Dianops | Phacopidae | Phacopida | Tamtert | Ougarta basin | Famennian | upper Famennian | 1 | Argiles de | |
| Struve 1995 Senck lethaea | Drotops armatus | Drotops | Phacopidae | Phacopida | Jbel Issoumour Unknown | Maider | Givetian | lower Givetian | 6 | |
| Struve 1995 Senck lethaea | Drotops megalomanicus megalomanicus | Drotops | Phacopidae | Phacopida | Jbel Issoumour Unknown | Maider | Givetian | lower Givetian | 26 | |
| Struve 1995 Senck lethaea | Drotops megalomanicus subornatus | Drotops | Phacopidae | Phacopida | Jbel Issoumour Unknown | Maider | Givetian | lower Givetian | 5 | |
| McKellar Chatterton 2009 Pal Canadiana | Drotops armatus | Drotops | Phacopidae | Phacopida | Taboumakhloûf | Maider | Givetian | lower Givetian | 1 | Bou Dîb |
| McKellar Chatterton 2009 Pal Canadiana | Drotops megalomanicus megalomanicus | Drotops | Phacopidae | Phacopida | Taboumakhloûf | Maider | Givetian | lower Givetian | 1 | Bou Dîb |
| Feist Mahboubi Girard 2016 Bull geo | Enigmapyge marhoumensis | Enigmapyge | Phacopidae | Phacopida | Marhouma | Ougarta basin | Famennian | lower Famennian | 1 | Argiles de Marhouma |
| Holloway 2005 Pal Zeit | Eocryphops albertii | Eocryphops | Phacopidae | Phacopida | Jdorf | Maider | Eifelian | lower Eifelian | 9 | Bou Tcharafine |
| Alberti 1983 Senck lethaea | Erbenaspis erbeni | Erbenaspis | Proetidae | Proetida | Ben Zireg | Ougarta basin | Pragian | Pragian | 2 | |
| Morzadec 1995 NJb Geol Pal | Erbenochile erbeni | Erbenochile | Dalmanitidae | Phacopida | El Kseib | Ougarta basin | Emsian | upper Emsian | 1 | Chefar el Ahmar |
| Le Maître 1952 Mémoire de la Carte géologique de l'Algérie | Erbenochile erbeni | Erbenochile | Dalmanitidae | Phacopida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 1 | Chefar el Ahmar |
| Chatterton Gibbs 2010 Jpal | Erbenochile erbeni | Erbenochile | Dalmanitidae | Phacopida | Foum Zguid | Draa Valley | Emsian | upper Emsian | 1 | Timrhamhart |

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|---|---|---|---|---|---|---|---|---|---|---|
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Erbenochile erbeni | Erbenochile | Dalmanitidae | Phacopida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 1 | Timrhamhart |
| Chatterton Gibbs 2010 Jpal | Erbenochile issoumourensis | Erbenochile | Dalmanitidae | Phacopida | Jbel Issoumour SW | Maider | | | 4 | El Otfal |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Erbenochile erbeni | Erbenochile | Dalmanitidae | Phacopida | Marhouma | Ougarta basin | Emsian | upper Emsian | 1 | Chefar el Ahmar |
| Alberti 1969 SenckNaturGesell | Eremiproetus dufresnoyi australis | Eremiproetus | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | lower Emsian | 5 | upper Kess Kess |
| Alberti 1970a SenckNaturGesell | Eremiproetus dufresnoyi australis | Eremiproetus | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | lower Emsian | 2 | upper Kess Kess |
| Alberti 1983 Senck lethaea | Eremiproetus dufresnoyi australomaurus | Eremiproetus | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Eifelian | lower Eifelian | 5 | Bou Tcharafine |
| Cronier Oudot Klug DeBaets 2018 NJb Geol Pal | Eremiproetus dufresnoyi saharae | Eremiproetus | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 6 | Amerboh |
| Alberti 1967b Senck leth | Eremiproetus dufresnoyi saharae | Eremiproetus | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| Alberti 1969 SenckNaturGesell | Eremiproetus dufresnoyi saharae | Eremiproetus | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| Alberti 1983 Senck lethaea | Eremiproetus dufresnoyi saharae | Eremiproetus | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| Feist Belka 2018 N.Jb Geol | Eremiproetus emerita | Eremiproetus | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | | 1 | upper Kess Kess |
| Alberti 1969 SenckNaturGesell | Eremiproetus erfoudanus | Eremiproetus | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Alberti 1967b Senck leth | Eremiproetus helmuti helmuti | Eremiproetus | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Alberti 1969 SenckNaturGesell | Eremiproetus helmuti helmuti | Eremiproetus | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 2 | lower Kess Kess |
| Alberti 1969 SenckNaturGesell | Eremiproetus helmuti junior | Eremiproetus | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 3 | lower Kess Kess |
| Alberti 1967b Senck leth | Eremiproetus meridianomaurus | Eremiproetus | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Alberti 1969 SenckNaturGesell | Eremiproetus munitus | Eremiproetus | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Feist Belka 2018 N.Jb Geol | Eremiproetus notabilis | Eremiproetus | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | | 1 | upper Kess Kess |
| Alberti 1967a Senck leth | Eremiproetus tafilaltanus | Eremiproetus | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Alberti 1969 SenckNaturGesell | Eremiproetus tafilaltanus | Eremiproetus | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 7 | lower Kess Kess |
| Alberti 1970a SenckNaturGesell | Eremiproetus tafilaltanus | Eremiproetus | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| H.Alberti 1973 NJb Geol Pal | Franconicabole bordjensis maroccana | Franconicabole | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | upper Famennian | 3 | Achguig |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Gandlops tamnrhertus | Gandlops | Acastidae | Phacopida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 8 | Timrhamhart |
| Morzadec 1997 PalaeontA | Ganetops djemelensis | Ganetops | Acastidae | Phacopida | Dkhissa | Ougarta basin | Lochkovian | upper Lochkovian | 4 | Dkhissa |
| Morzadec 1997 PalaeontA | Ganetops djemelensis | Ganetops | Acastidae | Phacopida | El Kseib | Ougarta basin | Lochkovian | upper Lochkovian | 2 | Dkhissa |
| Morzadec 1997 PalaeontA | Ganetops djemelensis | Ganetops | Acastidae | Phacopida | Erg Djemel | Ougarta basin | Lochkovian | upper Lochkovian | 3 | Dkhissa |
| Morzadec 1997 PalaeontA | Ganetops djemelensis | Ganetops | Acastidae | Phacopida | Zerhamra | Ougarta basin | Lochkovian | upper Lochkovian | 3 | Dkhissa |
| Bignon Corbacho Lopez-Soriano 2014 Geobios | Minicryphaeus giganteus | Gen1 | Acastidae | Phacopida | Jbel el Mrakib | Maider | Pragian | Pragian | 4 | Ihandar |
| Morzadec 2001 PalaeontA | Metacanthina issoumourensis | Gen1 | Acastidae | Phacopida | Jbel Issoumour NW | Maider | Pragian | Pragian | 3 | Ihandar |
| Morzadec 2001 PalaeontA | Metacanthina maderensis | Gen1 | Acastidae | Phacopida | Jbel Issoumour NW | Maider | Pragian | Pragian | 1 | Ihandar |
| Klug Kröger Korn Rücklin Schemm-Gregory DeBaets Mapes 2008 Pal Abt A | Metacanthina wallacei | Gen2 | Acastidae | Phacopida | El Atrous | Tafilalt | Emsian | lower Emsian | 1 | Seheb el Rhassel |
| Frey Naglik Hofmann Schemm-Gregory Fryda Kröger Taylor 2014 Bull geo | Metacanthina wallacei | Gen2 | Acastidae | Phacopida | Jbel Ouafilal-Filon 12 | Tafilalt | Emsian | lower Emsian | 3 | Seheb el Rhassel |
| Klug Kröger Korn Rücklin Schemm-Gregory DeBaets Mapes 2008 Pal Abt A | Metacanthina wallacei | Gen2 | Acastidae | Phacopida | Ouidane Chebbi | Tafilalt | Emsian | lower Emsian | 43 | Seheb el Rhassel |
| Gibb Chatterton 2010 Pal Canadiana | Gerastos aintawilus | Gerastos | Proetidae | Proetida | Bou Dîb | Maider | Eifelian | lower Eifelian | 2 | El Otfal |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Gerastos marocensis | Gerastos | Proetidae | Proetida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 6 | Chefar el Ahmar |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Gerastos marocensis | Gerastos | Proetidae | Proetida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 5 | Chefar el Ahmar |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Gerastos marocensis | Gerastos | Proetidae | Proetida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 14 | Chefar el Ahmar |
| Cronier Oudot Klug DeBaets 2018 NJb Geol Pal | Gerastos sp A vel Rhenocynproetus sp A | Gerastos | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 7 | Amerboh |

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|---|---|---|---|---|---|---|---|---|---|---|
| Cronier Oudot Klug DeBaets 2018 NJb Geol Pal | Gerastos sp B vel Rhenocynproetus sp B | Gerastos | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 16 | Amerboh |
| Cronier Oudot Klug DeBaets 2018 NJb Geol Pal | Gerastos sp C | Gerastos | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 3 | Amerboh |
| Gibb Chatterton 2010 Pal Canadiana | Gerastos ainrasifus | Gerastos | Proetidae | Proetida | Jbel el Mrakib | Maider | Eifelian | lower Eifelian | 3 | Taboumakhloûf |
| Gibb Chatterton 2010 Pal Canadiana | Gerastos discombobulatus | Gerastos | Proetidae | Proetida | Jbel el Mrakib | Maider | Eifelian | upper Eifelian | 4 | Taboumakhloûf |
| Gibb Chatterton 2010 Pal Canadiana | Gerastos emmetus | Gerastos | Proetidae | Proetida | Jbel el Mrakib | Maider | Givetian | lower Givetian | 1 | Bou Dîb |
| Gibb Chatterton 2010 Pal Canadiana | Gerastos izius | Gerastos | Proetidae | Proetida | Jbel el Mrakib | Maider | Givetian | lower Givetian | 5 | Bou Dîb |
| Gibb Chatterton 2010 Pal Canadiana | Gerastos lisanrasus | Gerastos | Proetidae | Proetida | Jbel el Mrakib | Maider | Eifelian | lower Eifelian | 1 | El Otfal |
| Gibb Chatterton 2010 Pal Canadiana | Gerastos taqus | Gerastos | Proetidae | Proetida | Jbel el Mrakib | Maider | Eifelian | lower Eifelian | 2 | Taboumakhloûf |
| Gibb Chatterton 2010 Pal Canadiana | Gerastos aintawilus | Gerastos | Proetidae | Proetida | Jbel Gara el Zguilma | Draa Valley | Eifelian | lower Eifelian | 1 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Gerastos marocensis | Gerastos | Proetidae | Proetida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 7 | Timrhamhart |
| Gibb Chatterton 2010 Pal Canadiana | Gerastos marocensis | Gerastos | Proetidae | Proetida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 6 | Timrhamhart |
| Chatterton Gibbs 2010 Jpal | Gerastos marocensis | Gerastos | Proetidae | Proetida | Jbel Issoumour SW | Maider | Eifelian | lower Eifelian | 2 | El Otfal |
| Gibb Chatterton 2010 Pal Canadiana | Gerastos marocensis | Gerastos | Proetidae | Proetida | Jbel Issoumour SW | Maider | Eifelian | lower Eifelian | 1 | El Otfal |
| Gibb Chatterton 2010 Pal Canadiana | Gerastos marocensis | Gerastos | Proetidae | Proetida | Jbel Issoumour SW | Maider | Emsian | upper Emsian | 1 | El Otfal |
| Feist Orth 2000 ProcSDS | Gerastos granulosus sensu | Gerastos | Proetidae | Proetida | Jbel Ou Driss | Maider | Givetian | lower Givetian | 3 | Taboumakhloûf |
| Gibb Chatterton 2010 Pal Canadiana | Gerastos cuvieri malisus | Gerastos | Proetidae | Proetida | Jbel Oufatene | Maider | Eifelian | upper Eifelian | 3 | Taboumakhloûf |
| Gibb Chatterton 2010 Pal Canadiana | Gerastos cuvieri malisus | Gerastos | Proetidae | Proetida | Jbel Oufatene | Maider | Eifelian | upper Eifelian | 3 | Taboumakhloûf |
| Gibb Chatterton 2010 Pal Canadiana | Gerastos marocensis | Gerastos | Proetidae | Proetida | Jbel Oufatene | Maider | Emsian | upper Emsian | 3 | Tazoulaït |
| Feist Orth 2000 ProcSDS | Gerastos prox umerbianus | Gerastos | Proetidae | Proetida | Jbel Ziata | Tafilalt | Givetian | lower Givetian | 3 | Bou Tcharafine |
| Gibb Chatterton 2010 Pal Canadiana | Gerastos lisanrasus | Gerastos | Proetidae | Proetida | Jbel Zireg | Maider | Eifelian | lower Eifelian | 1 | El Otfal |
| Gibb Chatterton 2010 Pal Canadiana | Gerastos malisjildus | Gerastos | Proetidae | Proetida | Jbel Zireg | Maider | Eifelian | lower Eifelian | 1 | Taboumakhloûf |
| Gibb Chatterton 2010 Pal Canadiana | Gerastos hammii | Gerastos | Proetidae | Proetida | Saredrar | Maider | Eifelian | lower Eifelian | 7 | El Otfal |
| Gibb Chatterton 2010 Pal Canadiana | Gerastos emmetus | Gerastos | Proetidae | Proetida | Taboumakhloûf | Maider | Givetian | lower Givetian | 1 | Bou Dîb |
| Gibb Chatterton 2010 Pal Canadiana | Gerastos emmetus | Gerastos | Proetidae | Proetida | Taboumakhloûf | Maider | Givetian | lower Givetian | 6 | Bou Dîb |
| Gibb Chatterton 2010 Pal Canadiana | Gerastos emmetus | Gerastos | Proetidae | Proetida | Taboumakhloûf | Maider | Givetian | lower Givetian | 2 | Bou Dîb |
| Gibb Chatterton 2010 Pal Canadiana | Gerastos emmetus | Gerastos | Proetidae | Proetida | Taboumakhloûf | Maider | Givetian | middle Givetian | 1 | Bou Dîb |
| Gibb Chatterton 2010 Pal Canadiana | Gerastos raribus | Gerastos | Proetidae | Proetida | Taboumakhloûf | Maider | Givetian | lower Givetian | 2 | Bou Dîb |
| Gibb Chatterton 2010 Pal Canadiana | Gerastos marocensis | Gerastos | Proetidae | Proetida | Talawarite | Tafilalt | Emsian | upper Emsian | 3 | Amerboh |
| Alberti 1981a Senck lethaea | Gravicalymene hamlagdadica | Gravicalymene | Calymenidae | Phacopida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 5 | lower Kess Kess |
| Morzadec 1997 PalaeontA | Indet | Greenops | Acastidae | Phacopida | El Kseib | Ougarta basin | Emsian | upper Emsian | 1 | Chefar el Ahmar |
| H.Alberti 1973 NJb Geol Pal | Haasproetus wildungensis | Haasproetus | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | uppermost Famennian | 4 | Achguig |
| Alberti 1983 Senck lethaea | Indet | Harpes | Harpetidae | Harpetida | Ben Zireg | Ougarta basin | Pragian | Pragian | 1 | |
| Cronier Oudot Klug DeBaets 2018 NJb Geol Pal | Harpes hamarlaghdadensis | Harpes | Harpetidae | Harpetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 6 | Amerboh |
| Zapalski Klug 2018 NJb Geol Pal | Harpes hamarlaghdadensis | Harpes | Harpetidae | Harpetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| Feist Chatterton 2015 Palaeontology | Heliopeltis ihmadii | Heliopeltis | Scutelluidae | Corynexoch | Jbel Oufatene | Maider | | | 3 | Tazoulaït |
| Feist Chatterton 2015 Palaeontology | Heliopeltis johnsoni | Heliopeltis | Scutelluidae | Corynexoch | Jbel Oufatene | Maider | | | 1 | Tazoulaït |
| Feist Chatterton 2015 Palaeontology | Indet | Heliopeltis | Scutelluidae | Corynexoch | Jbel Oufatene | Maider | Emsian | upper Emsian | 1 | Tazoulaït |
| Feist Orth 2000 ProcSDS | Helmutia rissanensis | Helmutia | Proetidae | Proetida | Jbel Mech Irdane | Tafilalt | Eifelian | upper Eifelian | 7 | Bou Tcharafine |
| Feist Orth 2000 ProcSDS | Helmutia rissanensis | Helmutia | Proetidae | Proetida | Jbel Mech Irdane | Tafilalt | Givetian | lower Givetian | 7 | Bou Tcharafine |
| Feist Orth 2000 ProcSDS | Helmutia sp A | Helmutia | Proetidae | Proetida | Jbel Mech Irdane | Tafilalt | Eifelian | upper Eifelian | 1 | Bou Tcharafine |
| Feist Orth 2000 ProcSDS | Helmutia tuberculatus | Helmutia | Proetidae | Proetida | Jbel Mech Irdane | Tafilalt | Eifelian | upper Eifelian | 1 | Bou Tcharafine |
| Feist Orth 2000 ProcSDS | Helmutia rissanensis | Helmutia | Proetidae | Proetida | Jbel Ziata | Tafilalt | Givetian | lower Givetian | 9 | Bou Tcharafine |
| vanViersen Lerouge 2019 Pal Zeit | Hollandiella curvirostris | Hollandiella | Proetidae | Proetida | El Achana | Maider | Pragian | Pragian | 3 | Ihandar |
| vanViersen Lerouge 2019 Pal Zeit | Hollandiella lebruni | Hollandiella | Proetidae | Proetida | Lansser | Draa Valley | Emsian | upper Emsian | 2 | Timrhanrhart |

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|---|---|---|---|---|---|---|---|---|---|---|
| vanViersen Lerouge 2019 Pal Zeit | Hollandiella verecunda | Hollandiella | Proetidae | Proetida | Tafraoute | Maider | Pragian | Pragian | 1 | Ihandar |
| Morzadec 2001 PalaeontA | Hollardops boudibensis | Hollardops | Acastidae | Phacopida | Bou Dîb | Maider | Emsian | upper Emsian | 3 | Er Remlia |
| Morzadec 1997 PalaeontA | Hollardops mesocristata | Hollardops | Acastidae | Phacopida | El Kseib | Ougarta basin | Emsian | upper Emsian | 2 | Chefar el Ahmar |
| Morzadec 1997 PalaeontA | Hollardops mesocristata | Hollardops | Acastidae | Phacopida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 3 | Chefar el Ahmar |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Hollardops mesocristata | Hollardops | Acastidae | Phacopida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 5 | Chefar el Ahmar |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Hollardops mesocristata | Hollardops | Acastidae | Phacopida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 2 | Chefar el Ahmar |
| Le Maître 1952 Mémoire de la Carte géologique de l’Algérie | Hollardops mesocristata | Hollardops | Acastidae | Phacopida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 2 | Chefar el Ahmar |
| Cronier Oudot Klug DeBaets 2018 NJb Geol Pal | Hollardops mesocristata | Hollardops | Acastidae | Phacopida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 2 | Amerboh |
| Morzadec 2001 PalaeontA | Hollardops burtandmimiae | Hollardops | Acastidae | Phacopida | Jbel el Anhsar | Draa Valley | Emsian | upper Emsian | 3 | Timrhamhart |
| Morzadec 2001 PalaeontA | Hollardops mesocristata | Hollardops | Acastidae | Phacopida | Jbel el Anhsar | Draa Valley | Emsian | upper Emsian | 4 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Hollardops aithassainorum | Hollardops | Acastidae | Phacopida | Jbel Gara el Zguilma | Draa Valley | Eifelian | lower Eifelian | 2 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Hollardops mesocristata | Hollardops | Acastidae | Phacopida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 6 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Hollardops mesocristata | Hollardops | Acastidae | Phacopida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 1 | Timrhamhart |
| Chatterton Gibbs 2010 Jpal | Hollardops burtandmimiae | Hollardops | Acastidae | Phacopida | Jbel Issoumour SW | Maider | Eifelian | lower Eifelian | 1 | El Otfal |
| Chatterton Gibbs 2010 Jpal | Hollardops burtandmimiae | Hollardops | Acastidae | Phacopida | Jbel Issoumour SW | Maider | Emsian | upper Emsian | 1 | El Otfal |
| Frey Naglik Hofmann Schemm-Gregory Fryda Kröger Taylor 2014 Bull geo | Hollardops | Acastidae | Phacopida | Jbel | Tafilalt | Pragian | Pragian | 1 | Seheb el | |
| Morzadec 2001 PalaeontA | Hollardops mesocristata | Hollardops | Acastidae | Phacopida | Jbel Oufatene | Maider | Emsian | upper Emsian | 1 | Tazoulaït |
| Morzadec 1997 PalaeontA | Hollardops mesocristata | Hollardops | Acastidae | Phacopida | Marhouma | Ougarta basin | Emsian | upper Emsian | 11 | Chefar el Ahmar |
| Le Maître 1952 Mémoire de la Carte géologique de l’Algérie | Hollardops mesocristata | Hollardops | Acastidae | Phacopida | Marhouma | Ougarta basin | Emsian | upper Emsian | 1 | Chefar el Ahmar |
| Morzadec 1997 PalaeontA | Hollardops lemaitreae | Hollardops | Acastidae | Phacopida | Zerhamra | Ougarta basin | Emsian | upper Emsian | 10 | Teferguenit |
| Morzadec 1997 PalaeontA | Hollardops mesocristata | Hollardops | Acastidae | Phacopida | Zerhamra | Ougarta basin | Emsian | upper Emsian | 1 | Chefar el Ahmar |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Hollardops aithassainorum | Hollardops | Acastidae | Phacopida | Zguilma | Draa Valley | Eifelian | lower Eifelian | 2 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Hollardops aithassainorum | Hollardops | Acastidae | Phacopida | Zguilma | Draa Valley | Eifelian | lower Eifelian | 1 | Timrhamhart |
| Crônier Malti François Benyoucef Brice 2013 Geol Mag | Houseops cryphoïdes | Houseops | Phacopidae | Phacopida | Gara Diba | Ougarta basin | Famennian | lower Famennian | 1 | Argiles de Marhouma |
| Stegemann 2006 Münstersche Forschungen Geol Pal | Hypsipariops torleyi | Hypsipariops | Phacopidae | Phacopida | Dar Kaoua | Tafilalt | Givetian | | 1 | |
| Stegemann 2006 Münstersche Forschungen Geol Pal | Hypsipariops torleyi | Hypsipariops | Phacopidae | Phacopida | Hassi Nebech | Tafilalt | Givetian | | 1 | |
| Stegemann 2006 Münstersche Forschungen Geol Pal | Hypsipariops torleyi | Hypsipariops | Phacopidae | Phacopida | Hassi Nebech | Tafilalt | Givetian | | 1 | |
| Stegemann 2006 Münstersche Forschungen Geol Pal | Hypsipariops torleyi | Hypsipariops | Phacopidae | Phacopida | Jbel Amlane | Tafilalt | Givetian | | 1 | |
| Stegemann 2006 Münstersche Forschungen Geol Pal | Hypsipariops torleyi | Hypsipariops | Phacopidae | Phacopida | Jbel Bou Tscharafine | Tafilalt | Givetian | | 1 | |
| McKellar Chatterton 2009 Pal Canadiana | Hypsipariops vagabundus | Hypsipariops | Phacopidae | Phacopida | Jbel Issoumour SW | Maider | Givetian | lower Givetian | 1 | Bou Dîb |
| Struve 1995 Senck lethaea | Hypsipariops vagabundus | Hypsipariops | Phacopidae | Phacopida | Jbel Issoumour Unknown | Maider | Givetian | lower Givetian | 36 | |
| Stegemann 2006 Münstersche Forschungen Geol Pal | Hypsipariops torleyi | Hypsipariops | Phacopidae | Phacopida | Ouidane Chebbi | Tafilalt | Givetian | | 1 | |
| Stegemann 2006 Münstersche Forschungen Geol Pal | Hypsipariops torleyi | Hypsipariops | Phacopidae | Phacopida | Ras el Kebbar | Tafilalt | Givetian | | 1 | |
| Stegemann 2006 Münstersche Forschungen Geol Pal | Hypsipariops torleyi | Hypsipariops | Phacopidae | Phacopida | Seheb el Rhassal 2 | Tafilalt | Givetian | | 1 | |
| Alberti 1981a Senck lethaea | Ignoproetus erfoudanus | Ignoproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 11 | Amerboh |
| Alberti 1970a SenckNaturGesell | Ignoproetus waldschmidti | Ignoproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 3 | Amerboh |
| Alberti 1969 SenckNaturGesell | Ignoproetus waldschmidti | Ignoproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Eifelian | upper Eifelian | 4 | Bou Tcharafine |
| Feist Belka 2018 N.Jb Geol | Isoprusia laportei | Isoprusia | Odontopleuridae | Lichida | Hamar Laghdad | Tafilalt | Emsian | | 1 | upper Kess Kess |
| Morzadec 2001 PalaeontA | Indet | Kayserops | Acastidae | Phacopida | Jbel Bou Tscharafine | Tafilalt | Emsian | lower Emsian | 3 | Seheb el Rhassel |

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|---|---|---|---|---|---|---|---|---|---|---|
| Morzadec 2001 PalaeontA | Kayserops marocanensis | Kayserops | Acastidae | Phacopida | Jbel Issoumour SW | Maider | Emsian | upper Emsian | 1 | Er Remlia |
| Morzadec 2001 PalaeontA | Kayserops marocanensis | Kayserops | Acastidae | Phacopida | Jbel Issoumour SW | Maider | Emsian | upper Emsian | 1 | Tazoulaït |
| Morzadec 2001 PalaeontA | Kayserops marocanensis | Kayserops | Acastidae | Phacopida | Jbel Oufatene | Maider | Emsian | upper Emsian | 1 | Tazoulaït |
| Morzadec 1997 PalaeontA | Kayserops djazaïrensis | Kayserops | Acastidae | Phacopida | Marhouma | Ougarta basin | Emsian | upper Emsian | 2 | Chefar el Ahmar |
| Morzadec 1997 PalaeontA | Kayserops djazaïrensis | Kayserops | Acastidae | Phacopida | Marhouma | Ougarta basin | Emsian | upper Emsian | 1 | Chefar el Ahmar |
| Morzadec 1997 PalaeontA | Kayserops djazaïrensis | Kayserops | Acastidae | Phacopida | Marhouma | Ougarta basin | Emsian | upper Emsian | 1 | Chefar el Ahmar |
| Alberti 1969 SenckNaturGesell | Kegeliella listei prolistei | Kegeliella | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Alberti 1969 SenckNaturGesell | Kettneraspis pigra | Kettneraspis | Odontopleuridae | Lichida | Hamar Laghdad | Tafilalt | Eifelian | upper Eifelian | 3 | Bou Tcharafine |
| vanViersen Heising 2015 GeolBelgica | Kettneraspis prescheri | Kettneraspis | Odontopleuridae | Lichida | Jbel Issoumour Unknown | Maider | Pragian | Pragian | 1 | Ihandar |
| Feist Orth 2000 ProcSDS | Kettneraspis pigra | Kettneraspis | Odontopleuridae | Lichida | Jbel Mech Irdane | Tafilalt | Eifelian | upper Eifelian | 1 | Bou Tcharafine |
| Feist Chatterton 2015 Palaeontology | Kolihapeltis hamlaghdadica | Kolihapeltis | Scutelluidae | Corynexoch | Amsoy | Tafilalt | Pragian | Pragian | 3 | Seheb el Rhassel |
| Feist Chatterton 2015 Palaeontology | Kolihapeltis bassei | Kolihapeltis | Scutelluidae | Corynexoch | El Achana | Maider | Pragian | Pragian | 4 | Ihandar |
| Feist Chatterton 2015 Palaeontology | Kolihapeltis chlupaci hollardi | Kolihapeltis | Scutelluidae | Corynexoch | El Achana | Maider | Pragian | Pragian | 3 | Ihandar |
| Feist Chatterton 2015 Palaeontology | Kolihapeltis bassei | Kolihapeltis | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Alberti 1966b Pal Zeitschrift | Kolihapeltis bassei | Kolihapeltis | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Alberti 1966b Pal Zeitschrift | Kolihapeltis chlupaci hollardi | Kolihapeltis | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Pragian | Pragian | 2 | lower Kess Kess |
| Feist Chatterton 2015 Palaeontology | Kolihapeltis chlupaci hollardi | Kolihapeltis | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Pragian | Pragian | 5 | lower Kess Kess |
| Alberti 1970a SenckNaturGesell | Kolihapeltis hamlaghdadica | Kolihapeltis | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Feist Chatterton 2015 Palaeontology | Kolihapeltis hamlaghdadica | Kolihapeltis | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Pragian | Pragian | 2 | lower Kess Kess |
| Alberti 1966b Pal Zeitschrift | Kolihapeltis maghrebia | Kolihapeltis | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Alberti 1983 Senck lethaea | Kolihapeltis maghrebia | Kolihapeltis | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Pragian | Pragian | 4 | lower Kess Kess |
| Feist Chatterton 2015 Palaeontology | Kolihapeltis maghrebia | Kolihapeltis | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Pragian | Pragian | 4 | lower Kess Kess |
| Feist Chatterton 2015 Palaeontology | Kolihapeltis tafilaltensis | Kolihapeltis | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Pragian | Pragian | 8 | lower Kess Kess |
| Alberti 1983 Senck lethaea | Koneprusia brutoni | Koneprusia | Odontopleuridae | Lichida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Alberti 1970a SenckNaturGesell | Koneprusia subtermata | Koneprusia | Odontopleuridae | Lichida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 3 | Amerboh |
| Alberti 1967b Senck leth | Koneprusia tafilaltana | Koneprusia | Odontopleuridae | Lichida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Koneprusia dahmani | Koneprusia | Odontopleuridae | Lichida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 4 | Timrhamhart |
| Feist McNamara 2007 Geol Mag | Koneprusia aboussalamae | Koneprusia | Odontopleuridae | Lichida | SW El Jorf | Maider | Givetian | upper Givetian | 1 | Bou Dîb |
| Alberti 1969 SenckNaturGesell | Koneprusites baconi saharae | Koneprusites | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Eifelian | lower Eifelian | 3 | Bou Tcharafine |
| vanViersen Lerouge 2019 Pal Zeit | Koneprusites oresibios | Koneprusites | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Eifelian | lower Eifelian | 1 | Bou Tcharafine |
| Feist Orth 2000 ProcSDS | Indet | Koneprusites | Proetidae | Proetida | Jbel Ziata | Tafilalt | Givetian | lower Givetian | 1 | Bou Tcharafine |
| Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag | Koneprusites moestus | Koneprusites | Proetidae | Proetida | Ouarourout | Ougarta basin | Eifelian | lower Eifelian | 1 | Chefar el Ahmar |
| Corbacho 2014a Bettaleria | Lanceaspis hammondi | Lanceaspis | Acastidae | Phacopida | Oumjrane | Maider | Pragian | Pragian | 25 | Ihandar |
| Cronier Oudot Klug DeBaets 2018 NJb Geol Pal | Indet | Leonaspis | Odontopleuridae | Lichida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Leonaspis haddanei | Leonaspis | Odontopleuridae | Lichida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 3 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Leonaspis haddanei | Leonaspis | Odontopleuridae | Lichida | Jbel Gara el Zguilma | Draa Valley | Eifelian | lower Eifelian | 5 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Leonaspis spinicurva | Leonaspis | Odontopleuridae | Lichida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 4 | Timrhamhart |
| Alberti 1970a SenckNaturGesell | Leonaspis issoumourensis | Leonaspis | Odontopleuridae | Lichida | Jbel Issoumour SW | Maider | Emsian | lower Emsian | 2 | Bou Tiskaouïne |
| Klug Kröger Korn Rücklin Schemm-Gregory DeBaets Mapes 2008 Pal Abt A | Leonaspis issoumourensis | Leonaspis | Odontopleuridae | Lichida | Ouidane Chebbi | Tafilalt | Emsian | lower Emsian | 1 | Seheb el Rhassel |
| Alberti 1969 SenckNaturGesell | Lepidoproetus praematurus | Lepidoproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Johnson Fortey 2012 Jpal | Lepidoproetus maharchianus | Lepidoproetus | Proetidae | Proetida | Jbel el Mrakib | Maider | Pragian | Pragian | 2 | Ihandar |
| Johnson Fortey 2012 Jpal | Lepidoproetus lahceni | Lepidoproetus | Proetidae | Proetida | Jbel Oufatene | Maider | Pragian | Pragian | 2 | Ihandar |

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|---|---|---|---|---|---|---|---|---|---|---|
| Johnson Fortey 2012 Jpal | Lepidoproetus spendens | Lepidoproetus | Proetidae | Proetida | Jbel Oufatene | Maider | Pragian | Pragian | 1 | Ihandar |
| vanViersen Lerouge 2019 Pal Zeit | Lepidoproetus maharchianus | Lepidoproetus | Proetidae | Proetida | Jbel Zireg | Maider | Pragian | Pragian | 1 | Ihandar |
| vanViersen Lerouge 2019 Pal Zeit | Lepidoproetus arenicolus | Lepidoproetus | Proetidae | Proetida | Oum Jerane | Maider | Pragian | Pragian | 1 | Ihandar |
| Alberti 1969 SenckNaturGesell | Linguaproetus saharensis | Linguaproetus | Proetidae | Proetida | Jbel Amlane | Tafilalt | Eifelian | | 2 | |
| Alberti 1970a SenckNaturGesell | Linguaproetus saharensis | Linguaproetus | Proetidae | Proetida | Jbel Amlane | Tafilalt | Eifelian | | 1 | |
| Alberti 1967b Senck leth | Linguaproetus saharensis | Linguaproetus | Proetidae | Proetida | Jbel Ihrs | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| Feist Belka 2018 N.Jb Geol | Lioharpes wendti | Lioharpes | Harpetidae | Harpetida | Hamar Laghdad | Tafilalt | Emsian | | 15 | upper Kess Kess |
| Klug Kröger Korn Rücklin Schemm-Gregory DeBaets Mapes 2008 Pal Abt A | Metacanthina | Acastidae | Phacopida | Ouidane | Tafilalt | Emsian | lower Emsian | 4 | Seheb el | |
| Morzadec 2001 PalaeontA | Minicryphaeus quaterspinosus | Minicryphaeus | Acastidae | Phacopida | Jbel Issoumour NW | Maider | Pragian | Pragian | 1 | Ihandar |
| Morzadec 2001 PalaeontA | Minicryphaeus sarirus | Minicryphaeus | Acastidae | Phacopida | Jbel Issoumour NW | Maider | Pragian | Pragian | 2 | Ihandar |
| Morzadec 2001 PalaeontA | Minicryphaeus minimus | Minicryphaeus | Acastidae | Phacopida | Jbel Oufatene | Maider | Pragian | Pragian | 10 | Ihandar |
| Morzadec 2001 PalaeontA | Minicryphaeus quaterspinosus | Minicryphaeus | Acastidae | Phacopida | Jbel Oufatene | Maider | Pragian | Pragian | 2 | Ihandar |
| H.Alberti 1974 NJb Geol Pal | Mirabole kielanae | Mirabole | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | uppermost Famennian | 7 | Achguig |
| Alberti 1981a Senck lethaea | Montanproetus midas amlanensis | Montanproetus | Proetidae | Proetida | Ben Zireg | Ougarta basin | Emsian | upper Emsian | 1 | |
| Alberti 1967a Senck leth | Montanproetus chlupaci | Montanproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Alberti 1969 SenckNaturGesell | Montanproetus chlupaci | Montanproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 30 | lower Kess Kess |
| Alberti 1969 SenckNaturGesell | Montanproetus midas amlanensis | Montanproetus | Proetidae | Proetida | Jbel Amlane | Tafilalt | Emsian | lower Emsian | 4 | Seheb el Rhassel |
| Alberti 1981a Senck lethaea | Montanproetus midas amlanensis | Montanproetus | Proetidae | Proetida | Jbel Amlane | Tafilalt | Emsian | lower Emsian | 1 | Seheb el Rhassel |
| Alberti 1969 SenckNaturGesell | Montanproetus midas amlanensis | Montanproetus | Proetidae | Proetida | Jbel Amlane | Tafilalt | Emsian | lower Emsian | 1 | Seheb el Rhassel |
| Alberti 1969 SenckNaturGesell | Montanproetus pernix boutsharafinensis | Montanproetus | Proetidae | Proetida | Jbel Bou Tscharafine | Tafilalt | Emsian | lower Emsian | 1 | Seheb el Rhassel |
| Struve 1992 Senck lethaea | Morocconites expansus | Morocconites | Dalmanitidae | Phacopida | Alnif | Maider | Emsian | upper Emsian | 1 | Tazoulaït |
| Struve 1992 Senck lethaea | Morocconites lemkei | Morocconites | Dalmanitidae | Phacopida | Alnif | Maider | Emsian | upper Emsian | 1 | Tazoulaït |
| Struve in Boucot et al. 1989 Senck lethaea | Morocconites malladoides | Morocconites | Dalmanitidae | Phacopida | Alnif | Maider | Emsian | upper Emsian | 1 | Tazoulaït |
| McKellar Chatterton 2009 Pal Canadiana | Morocops forteyi | Morocops | Phacopidae | Phacopida | Bou Dîb | Maider | Emsian | upper Emsian | 6 | Tazoulaït |
| vanViersen Holland Koppka 2017 Bull geo | Morocops forteyi | Morocops | Phacopidae | Phacopida | Bou Dîb | Maider | Emsian | upper Emsian | 1 | Tazoulaït |
| McKellar Chatterton 2009 Pal Canadiana | Morocops lebesus | Morocops | Phacopidae | Phacopida | Bou Dîb | Maider | Eifelian | lower Eifelian | 2 | El Otfal |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Morocops chattertoni | Morocops | Phacopidae | Phacopida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 1 | Chefar el Ahmar |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Morocops chattertoni | Morocops | Phacopidae | Phacopida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 3 | Chefar el Ahmar |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Morocops granulops | Morocops | Phacopidae | Phacopida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 3 | Chefar el Ahmar |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Morocops granulops | Morocops | Phacopidae | Phacopida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 27 | Chefar el Ahmar |
| Le Maître 1952 Mémoire de la Carte géologique de l'Algérie | Morocops granulops | Morocops | Phacopidae | Phacopida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 2 | Chefar el Ahmar |
| Schraut 2000a Senck Lethaea | Morocops sparsinodosus struvei | Morocops | Phacopidae | Phacopida | Foum Zguid | Draa Valley | Eifelian | lower Eifelian | 5 | Timrhamhart |
| Alberti 1983 Senck lethaea | Moroccops tafilaltanus | Morocops | Phacopidae | Phacopida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| Cronier Oudot Klug DeBaets 2018 NJb Geol Pal | Morocops davidbrutoni | Morocops | Phacopidae | Phacopida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 69 | Amerboh |
| Cronier Oudot Klug DeBaets 2018 NJb Geol Pal | Morocops forteyi | Morocops | Phacopidae | Phacopida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 5 | Amerboh |
| Becker ElHassani Hartenfels Luddecke 2018 Frontiers Science Engineering | Morocops granulops | Morocops | Phacopidae | Phacopida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| Cronier Oudot Klug DeBaets 2018 NJb Geol Pal | Morocops granulops | Morocops | Phacopidae | Phacopida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 30 | Amerboh |
| Klug Schulz DeBaets 2009 APP | Morocops granulops | Morocops | Phacopidae | Phacopida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 3 | Amerboh |
| Zapalski Klug 2018 NJb Geol Pal | Morocops granulops | Morocops | Phacopidae | Phacopida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| Cronier Oudot Klug DeBaets 2018 NJb Geol Pal | Morocops sp A | Morocops | Phacopidae | Phacopida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 2 | Amerboh |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| McKellar Chatterton 2009 Pal Canadiana | Morocops granulops | Morocops | Phacopidae | Phacopida | Jbel Gara el Zguilma | Maider | Emsian | upper Emsian | 7 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Morocops granulops | Morocops | Phacopidae | Phacopida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 1 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Morocops granulops | Morocops | Phacopidae | Phacopida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 8 | Timrhamhart |
| McKellar Chatterton 2009 Pal Canadiana | Morocops lebesus | Morocops | Phacopidae | Phacopida | Jbel Gara el Zguilma | Maider | Eifelian | lower Eifelian | 1 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Morocops lebesus | Morocops | Phacopidae | Phacopida | Jbel Gara el Zguilma | Draa Valley | Eifelian | lower Eifelian | 3 | Timrhamhart |
| McKellar Chatterton 2009 Pal Canadiana | Morocops forteyi | Morocops | Phacopidae | Phacopida | Jbel Issoumour SW | Maider | Emsian | upper Emsian | 1 | Tazoulaït |
| McKellar Chatterton 2009 Pal Canadiana | Morocops forteyi | Morocops | Phacopidae | Phacopida | Jbel Issoumour SW | Maider | Emsian | upper Emsian | 1 | Tazoulaït |
| Le Maître 1952 Mémoire de la Carte géologique de l'Algérie | Morocops granulops | Morocops | Phacopidae | Phacopida | Marhouma | Ougarta basin | Emsian | | 2 | |
| Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag | Morocops sp F | Morocops | Phacopidae | Phacopida | Ouarourout | Ougarta basin | Eifelian | lower Eifelian | 3 | Chefar el Ahmar |
| Klug Kröger Korn Rücklin Schemm-Gregory DeBaets Mapes 2008 Pal Abt A | Morocops torkozensis | Morocops | Phacopidae | Phacopida | Ouidane Chebbi | Tafilalt | Emsian | lower Emsian | 2 | Seheb el Rhassel |
| McKellar Chatterton 2009 Pal Canadiana | Morocops ovatus | Morocops | Phacopidae | Phacopida | Taharajat Oufatene | Maider | Emsian | upper Emsian | 1 | Tazoulaït |
| McKellar Chatterton 2009 Pal Canadiana | Morocops ovatus | Morocops | Phacopidae | Phacopida | Taharajat Oufatene | Maider | Emsian | upper Emsian | 6 | Tazoulaït |
| McKellar Chatterton 2009 Pal Canadiana | Morocops forteyi | Morocops | Phacopidae | Phacopida | Talawarite | Tafilalt | Emsian | upper Emsian | 9 | Tazoulaït |
| Frey Naglik Hofmann Schemm-Gregory Fryda Kröger Taylor 2014 Bull geo | Morzadecops zguidensis | Morzadecops | Acastidae | Phacopida | Jbel Ouafilal-Filon 12 | Tafilalt | Emsian | lower Emsian | 60 | Seheb el Rhassel |
| Klug Kröger Korn Rücklin Schemm-Gregory DeBaets Mapes 2008 Pal Abt A | Morzadecops zguidensis | Morzadecops | Acastidae | Phacopida | Jbel Ouafilal-Filon 12 | Tafilalt | Emsian | lower Emsian | 4 | Seheb el Rhassel |
| Morzadec 2001 PalaeontA | Morzadecops zguidensis | Morzadecops | Acastidae | Phacopida | Jbel Oufatene | Maider | Emsian | lower Emsian | 1 | Bou Tiskaouïne |
| Morzadec 2001 PalaeontA | Morzadecops zguidensis | Morzadecops | Acastidae | Phacopida | Mdâour el Kbîr | Draa Valley | Emsian | lower Emsian | 3 | Mdaouer el Kbir |
| Klug Kröger Korn Rücklin Schemm-Gregory DeBaets Mapes 2008 Pal Abt A | Morzadecops zguidensis | Morzadecops | Acastidae | Phacopida | Ouidane Chebbi | Tafilalt | Emsian | lower Emsian | 12 | Seheb el Rhassel |
| Morzadec 1997 PalaeontA | Morzadecops matutina | Morzadecops | Acastidae | Phacopida | Zerhamra | Ougarta basin | Lochkovian | upper Lochkovian | 2 | Dkhissa |
| Morzadec 1997 PalaeontA | Morzadecops matutina | Morzadecops | Acastidae | Phacopida | Zerhamra | Ougarta basin | Lochkovian | upper Lochkovian | 4 | Dkhissa |
| Morzadec 2001 PalaeontA | Mrakibina cattoi | Mrakibina | Acastidae | Phacopida | Jbel el Mrakib | Maider | Eifelian | lower Eifelian | 3 | El Otfal |
| Alberti 1981b Senck lethaea | Mulciberaspis georgei | Mulciberaspis | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Emsian | lower Emsian | 1 | upper Kess Kess |
| Feist Belka 2018 N.Jb Geol | Nagaproetus frequens | Nagaproetus | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | lower Emsian | 1 | upper Kess Kess |
| Alberti 1967b Senck leth | Nagaproetus frequens | Nagaproetus | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | lower Emsian | 1 | upper Kess Kess |
| Alberti 1969 SenckNaturGesell | Nagaproetus frequens | Nagaproetus | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | lower Emsian | 10 | upper Kess Kess |
| Frey Naglik Hofmann Schemm-Gregory Fryda Kröger Taylor 2014 Bull geo | Odontochile hausmanni | Odontochile | Dalmanitidae | Phacopida | Jbel Ouafilal-Filon 12 | Tafilalt | Pragian | Pragian | 1 | Seheb el Rhassel |
| Schraut 2000c Senck Lethaea | Odontochile magrebianum | Odontochile | Dalmanitidae | Phacopida | Tissint | Draa Valley | Pragian | Pragian | 3 | Assa |
| H.Alberti 1972 NJb Geol Pal | Omegops accipitrinus | Omegops | Phacopidae | Phacopida | Bordj Est | Tafilalt | Famennian | uppermost Famennian | 9 | Achguig |
| Alberti 1967b Senck leth | Orbitoproetus africanus | Orbitoproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Alberti 1969 SenckNaturGesell | Orbitoproetus africanus | Orbitoproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 2 | lower Kess Kess |
| Alberti 1969 SenckNaturGesell | Orbitoproetus ovalis | Orbitoproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 2 | lower Kess Kess |
| Cronier Oudot Klug DeBaets 2018 NJb Geol Pal | Indet | Orbitoproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 3 | Amerboh |
| Lerosey-Aubril Feist 2005 APP | Osmolskabole prima | Osmolskabole | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | middle Famennian | 5 | Achguig |
| H.Alberti 1975a NJb Geol Pal | Osmolskabole prima | Osmolskabole | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | upper Famennian | 17 | Achguig |
| Lerosey-Aubril Feist 2005 APP | Osmolskabole prima | Osmolskabole | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Famennian | middle Famennian | 14 | Achguig |
| Lerosey-Aubril Feist 2005 APP | Osmolskabole prima | Osmolskabole | Proetidae | Proetida | Jbel Bou Tscharafine | Tafilalt | Famennian | middle Famennian | 12 | Achguig |
| Lerosey-Aubril Feist 2005 APP | Osmolskabole prima | Osmolskabole | Proetidae | Proetida | Korb el Atil | Tafilalt | Famennian | middle Famennian | 14 | Achguig |
| Lerosey-Aubril Feist 2005 APP | Osmolskabole prima | Osmolskabole | Proetidae | Proetida | Ouidane Chebbi | Tafilalt | Famennian | middle Famennian | 1 | Achguig |
| Feist Orth 2000 ProcSDS | Indet | Otarion | Aulacopleuridae | Proetida | Jbel Ziata | Tafilalt | Givetian | lower Givetian | 1 | Bou Tcharafine |

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|---|---|---|---|---|---|---|---|---|---|---|
| Alberti 1983 Senck lethaea | Otarionella bensaidi | Otarionella | Aulacopleuridae | Proetida | Hamar Laghdad | Tafilalt | Eifelian | lower Eifelian | 1 | Bou Tcharafine |
| Alberti 1969 SenckNaturGesell | Otarionella magnifica | Otarionella | Aulacopleuridae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 25 | lower Kess Kess |
| Alberti 1967b Senck leth | Otarionella magnifica | Otarionella | Aulacopleuridae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Alberti 1967b Senck leth | Otarionella tafilaltense | Otarionella | Aulacopleuridae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 1 | upper Kess Kess |
| Alberti 1969 SenckNaturGesell | Otarionella tafilaltense | Otarionella | Aulacopleuridae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 2 | upper Kess Kess |
| Alberti 1983 Senck lethaea | Paralejurus hamlagdadicus | Paralejurus | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Pragian | Pragian | 2 | lower Kess Kess |
| Alberti 1981a Senck lethaea | Paralejurus sp A | Paralejurus | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Chatterton Gibbs 2010 Jpal | Paralejurus rehamnanus | Paralejurus | Scutelluidae | Corynexoch | Jbel Issoumour SW | Maider | Eifelian | lower Eifelian | 1 | El Otfal |
| Frey Naglik Hofmann Schemm-Gregory Fryda Kröger Taylor 2014 Bull geo | Paralejurus campanifer | Paralejurus | Scutelluidae | Corynexoch | Jbel Ouafilal-Filon 12 | Tafilalt | Emsian | lower Emsian | 2 | Seheb el Rhassel |
| Frey Naglik Hofmann Schemm-Gregory Fryda Kröger Taylor 2014 Bull geo | Paralejurus elayounensis | Paralejurus | Scutelluidae | Corynexoch | Jbel Ouafilal-Filon 12 | Tafilalt | Pragian | Pragian | 1 | Seheb el Rhassel |
| Schraut Feist 2004 Jpal | Paralejurus rehamnanus | Paralejurus | Scutelluidae | Corynexoch | Jbel Oufatene | Maider | Emsian | upper Emsian | 4 | Tazoulaït |
| Schraut Feist 2004 Jpal | Paralejurus spatuliformis | Paralejurus | Scutelluidae | Corynexoch | Jbel Oufatene | Maider | Pragian | Pragian | 7 | Ihandar |
| Schraut Feist 2004 Jpal | Paralejurus tenuistriatus | Paralejurus | Scutelluidae | Corynexoch | Jbel Oufatene | Maider | Emsian | upper Emsian | 2 | Tazoulaït |
| Schraut Feist 2004 Jpal | Paralejurus brongniarti menanensis | Paralejurus | Scutelluidae | Corynexoch | Mdâour el Kbîr | Draa Valley | Pragian | Pragian | 3 | Assa |
| Schraut Feist 2004 Jpal | Paralejurus bohemicus | Paralejurus | Scutelluidae | Corynexoch | Taboumakhloûf | Maider | Pragian | Pragian | 2 | Ihandar |
| Alberti 1981a Senck lethaea | Paralepidoproetus wragei | Paralepidoproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Eifelian | lower Eifelian | 3 | Bou Tcharafine |
| Feist Weyer 2018 NJb Geol Pal | Perliproetus africanus | Perliproetus | Proetidae | Proetida | Bou Ifarherioun | Tafilalt | Famennian | upper Famennian | 12 | Achguig |
| Alberti 1970a SenckNaturGesell | Perunaspis longispinus | Perunaspis | Lichidae | Lichida | Gara Mdouard | Tafilalt | Eifelian | lower Eifelian | 1 | Amerboh |
| Crônier Malti François Benyoucef Brice 2013 Geol Mag | Phacops | Phacopidae | Phacopida | Idhir | Ougarta basin | Famennian | upper Fam | 1 | Argiles de | |
| McKellar Chatterton 2009 Pal Canadiana | Phacops araw | Phacops | Phacopidae | Phacopida | Jbel Oufatene | Maider | Eifelian | lower Eifelian | 4 | El Otfal |
| Feist Orth 2000 ProcSDS | Indet | Phacops | Phacopidae | Phacopida | Jbel Ziata | Tafilalt | Givetian | lower Givetian | 1 | Bou Tcharafine |
| Crônier Clarkson 2001 TRSE | Phacops tafilaltensis | Phacops | Phacopidae | Phacopida | Korb el Atil | Tafilalt | Famennian | middle Famennian | 40 | Achguig |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Phacops sl spA | Phacops | Phacopidae | Phacopida | Marhouma | Ougarta basin | Emsian | upper Emsian | 1 | Chefar el Ahmar |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Phacops sl spB | Phacops | Phacopidae | Phacopida | Marhouma | Ougarta basin | Emsian | upper Emsian | 2 | Chefar el Ahmar |
| Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag | Phacops ouarouroutensis ouarouroutensis | Phacops | Phacopidae | Phacopida | Ouarourout | Ougarta basin | Eifelian | lower Eifelian | 19 | Chefar el Ahmar |
| Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag | Phacops ouarouroutensis ouarouroutensis | Phacops | Phacopidae | Phacopida | Ouarourout | Ougarta basin | Eifelian | lower Eifelian | 20 | Chefar el Ahmar |
| Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag | Phacops ouarouroutensis ouarouroutensis | Phacops | Phacopidae | Phacopida | Ouarourout | Ougarta basin | Eifelian | lower Eifelian | 4 | Chefar el Ahmar |
| Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag | Phacops ouarouroutensis ouarouroutensoides | Phacops | Phacopidae | Phacopida | Ouarourout | Ougarta basin | Eifelian | lower Eifelian | 18 | Chefar el Ahmar |
| Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag | Phacops sp E | Phacops | Phacopidae | Phacopida | Ouarourout | Ougarta basin | Eifelian | lower Eifelian | 4 | Chefar el Ahmar |
| Crônier Malti François Benyoucef Brice 2013 Geol Mag | Phacops tamtertensis | Phacops | Phacopidae | Phacopida | Tamtert Zereg | Ougarta basin | Famennian | middle Famennian | 1 | Argiles de Marhouma |
| Crônier Malti François Benyoucef Brice 2013 Geol Mag | Phacops zeregensis | Phacops | Phacopidae | Phacopida | Tamtert Zereg | Ougarta basin | Famennian | middle Famennian | 1 | Argiles de Marhouma |
| Crônier Malti François Benyoucef Brice 2013 Geol Mag | Phacops | Phacopidae | Phacopida | Tamtert | Ougarta basin | Famennian | upper Famennian | 5 | Argiles de | |
| Crônier Malti François Benyoucef Brice 2013 Geol Mag | Phacops | Phacopidae | Phacopida | Tamtert | Ougarta basin | Famennian | upper Famennian | 2 | Argiles de | |
| Alberti 1981a Senck lethaea | Phaetonellus planicauda africanus | Phaetonellus | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 12 | Amerboh |

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|---|---|---|---|---|---|---|---|---|---|---|
| Alberti 1970a SenckNaturGesell | Phaetonellus planicauda ulcifrons | Phaetonellus | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 2 | Amerboh |
| Alberti 1981a Senck lethaea | Piriproetus amblyops austromaurus | Piriproetus | Proetidae | Proetida | Gara Mdouard | Tafilalt | Eifelian | lower Eifelian | 1 | Amerboh |
| Alberti 1970a SenckNaturGesell | Piriproetus ornatissimus maurus | Piriproetus | Proetidae | Proetida | Gara Mdouard | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| Alberti 1981a Senck lethaea | Piriproetus ornatissimus rissaniensis | Piriproetus | Proetidae | Proetida | Gara Mdouard | Tafilalt | Eifelian | lower Eifelian | 2 | Bou Tcharafine |
| Alberti 1967b Senck leth | Piriproetus amblyops patruelis | Piriproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Eifelian | lower Eifelian | 1 | Bou Tcharafine |
| Alberti 1969 SenckNaturGesell | Piriproetus amblyops patruelis | Piriproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Eifelian | lower Eifelian | 5 | Bou Tcharafine |
| Alberti 1969 SenckNaturGesell | Piriproetus amblyops austromaurus | Piriproetus | Proetidae | Proetida | Jbel Amlane | Tafilalt | Eifelian | lower Eifelian | 11 | Bou Tcharafine |
| Alberti 1981a Senck lethaea | Indet | Piriproetus | Proetidae | Proetida | Jbel Amlane | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| Alberti 1967b Senck leth | Piriproetus amblyops austromaurus | Piriproetus | Proetidae | Proetida | Jbel Ihrs | Tafilalt | Eifelian | lower Eifelian | 1 | Bou Tcharafine |
| Alberti 1983 Senck lethaea | Plagiolaria senex | Plagiolaria | Phacopidae | Phacopida | Ben Zireg | Ougarta basin | Pragian | Pragian | 3 | |
| Alberti 1981b Senck lethaea | Platyscutellum massai | Platyscutellum | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Pragian | Pragian | 2 | lower Kess Kess |
| Alberti 1982 Natur und Museum | Platyscutellum massai | Platyscutellum | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Alberti 1982 Natur und Museum | Platyscutellum massai | Platyscutellum | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Alberti 1981b Senck lethaea | Platyscutellum massai | Platyscutellum | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Pragian | Pragian | 2 | lower Kess Kess |
| Alberti 1970a SenckNaturGesell | Platyscutellum tafilaltense | Platyscutellum | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Pragian | Pragian | 2 | lower Kess Kess |
| Alberti 1981a Senck lethaea | Platyscutellum tafilaltense | Platyscutellum | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Johnson Fortey 2012 Jpal | Podoliproetus mirdani | Podoliproetus | Proetidae | Proetida | Akka n'Talilite | Maider | Pragian | Pragian | 1 | Ihandar |
| Johnson Fortey 2012 Jpal | Podoliproetus sinespina | Podoliproetus | Proetidae | Proetida | Akka n'Talilite | Maider | Pragian | Pragian | 1 | Ihandar |
| Johnson Fortey 2012 Jpal | Podoliproetus mirdani | Podoliproetus | Proetidae | Proetida | Jbel el Mrakib | Maider | Pragian | Pragian | 1 | Ihandar |
| Johnson Fortey 2012 Jpal | Podoliproetus mirdani | Podoliproetus | Proetidae | Proetida | Jbel Oufatene | Maider | Pragian | Pragian | 2 | Ihandar |
| Alberti 1964 SenckNaturGesell | Pragoproetus tafilaltensis | Pragoproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 40 | lower Kess Kess |
| Alberti 1969 SenckNaturGesell | Pragoproetus tafilaltensis | Pragoproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 112 | lower Kess Kess |
| Alberti 1983 Senck lethaea | Prodrevermannia baghdadlii | Prodrevermannia | Proetidae | Proetida | Ben Zireg | Ougarta basin | Emsian | lower Emsian | 1 | |
| Alberti 1983 Senck lethaea | Prodrevermannia jaegeri jaegeri | Prodrevermannia | Proetidae | Proetida | Ben Zireg | Ougarta basin | Pragian | Pragian | 5 | |
| Johnson Fortey 2012 Jpal | Proetina ihmadii | Proetina | Proetidae | Proetida | Jbel el Mrakib | Maider | Pragian | Pragian | 1 | Ihandar |
| Alberti 1969 SenckNaturGesell | Proetopeltis neglecta hamlagdadica | Proetopeltis | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Eifelian | lower Eifelian | 3 | Bou Tcharafine |
| Alberti 1970a SenckNaturGesell | Proetus proetus sp B granulosus | Proetus | Proetidae | Proetida | Jbel el Mrakib | Maider | Eifelian | lower Eifelian | 2 | Timrhamhart |
| Alberti 1970a SenckNaturGesell | Proetus proetus sp A granulosus | Proetus | Proetidae | Proetida | Jbel Oufatene | Maider | Emsian | upper Emsian | 1 | Tazoulaït |
| Alberti 1983 Senck lethaea | Prokops benziregensis benziregensis | Prokops | Phacopidae | Phacopida | Ben Zireg | Ougarta basin | Pragian | Pragian | 7 | |
| Alberti 1983 Senck lethaea | Prokops chlupaci | Prokops | Phacopidae | Phacopida | Ben Zireg | Ougarta basin | Pragian | Pragian | 15 | |
| Morzadec 1990 Geobios | Protacanthina robusticostata | Protacanthina | Acastidae | Phacopida | Dkhissa | Ougarta basin | Lochkovian | upper Lochkovian | 6 | Dkhissa |
| Morzadec 1990 Geobios | Protacanthina robusticostata | Protacanthina | Acastidae | Phacopida | El Kseib | Ougarta basin | Lochkovian | upper Lochkovian | 1 | Dkhissa |
| Morzadec 1990 Geobios | Protacanthina robusticostata | Protacanthina | Acastidae | Phacopida | Erg Djemel | Ougarta basin | Lochkovian | upper Lochkovian | 2 | Dkhissa |
| Morzadec 1990 Geobios | Protacanthina robusticostata | Protacanthina | Acastidae | Phacopida | Zerhamra | Ougarta basin | Lochkovian | upper Lochkovian | 1 | Dkhissa |
| Morzadec 2001 PalaeontA | Pseudocryphaeus sp 1 | Pseudocryphaeus | Acastidae | Phacopida | Bou Dîb | Maider | Emsian | upper Emsian | 1 | Er Remlia |
| Morzadec 2001 PalaeontA | Pseudocryphaeus sp 2 | Pseudocryphaeus | Acastidae | Phacopida | Jbel Bou Tscharafine | Tafilalt | Emsian | lower Emsian | 1 | Seheb el Rhassel |
| H.Alberti 1975a NJb Geol Pal | Pseudowaribole (Pseudowaribole) conifer | Pseudowaribole (Pseudowaribole) | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | uppermost Famennian | 5 | Achguig |
| H.Alberti 1975a NJb Geol Pal | Pseudowaribole (Pseudowaribole) conifer | Pseudowaribole (Pseudowaribole) | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | uppermost Famennian | 2 | Achguig |
| H.Alberti 1975a NJb Geol Pal | Pseudowaribole (Pseudowaribole) conifer gibber | Pseudowaribole (Pseudowaribole) | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | uppermost Famennian | 3 | Achguig |

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|---|---|---|---|---|---|---|---|---|---|---|
| H.Alberti 1975a NJb Geol Pal | Pseudowaribole (Pseudowaribole) conifer gibber | Pseudowaribole (Pseudowaribole) | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | uppermost Famennian | 3 | Achguig |
| H.Alberti 1975a NJb Geol Pal | Pseudowaribole (Pseudowaribole) conifer palmeus | Pseudowaribole (Pseudowaribole) | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | uppermost Famennian | 3 | Achguig |
| H.Alberti 1975a NJb Geol Pal | Pseudowaribole (Pseudowaribole) conifer palmeus | Pseudowaribole (Pseudowaribole) | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | uppermost Famennian | 3 | Achguig |
| H.Alberti 1975a NJb Geol Pal | Pseudowaribole (Pseudowaribole) conifer speculator | Pseudowaribole (Pseudowaribole) | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | uppermost Famennian | 2 | Achguig |
| H.Alberti 1975a NJb Geol Pal | Pseudowaribole (Pseudowaribole) conifer speculator | Pseudowaribole (Pseudowaribole) | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | uppermost Famennian | 1 | Achguig |
| H.Alberti 1975b NJb Geol Pal | Pseudowaribole (Pseudowaribole) familiaris | Pseudowaribole (Pseudowaribole) | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | middle Famennian | 4 | Achguig |
| Morzadec 1988 PalaeontA | Psychopyge elegans | Psychopyge | Acastidae | Phacopida | Bou Dîb | Maider | Emsian | upper Emsian | 2 | Talus d'Issemour |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Psychopyge elegans | Psychopyge | Acastidae | Phacopida | Bou Dîb | Maider | Emsian | upper Emsian | 1 | Tazoulaït |
| Morzadec 1988 PalaeontA | Psychopyge termierorum | Psychopyge | Acastidae | Phacopida | El Haidouriya | Draa Valley | Emsian | upper Emsian | 1 | Chefar el Ahmar |
| Cronier Oudot Klug DeBaets 2018 NJb Geol Pal | Psychopyge elegans | Psychopyge | Acastidae | Phacopida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| Morzadec 1988 PalaeontA | Psychopyge termierorum | Psychopyge | Acastidae | Phacopida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 5 | Amerboh |
| Morzadec 1988 PalaeontA | Psychopyge termierorum | Psychopyge | Acastidae | Phacopida | Jbel Bou Tscharafine | Tafilalt | Emsian | upper Emsian | 8 | Amerboh |
| Morzadec 1988 PalaeontA | Psychopyge elegans | Psychopyge | Acastidae | Phacopida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 1 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Psychopyge hammerorum | Psychopyge | Acastidae | Phacopida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 1 | Timrhamhart |
| Morzadec 2001 PalaeontA | Psychopyge praestans | Psychopyge | Acastidae | Phacopida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 1 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Psychopyge praestans | Psychopyge | Acastidae | Phacopida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 5 | Timrhamhart |
| Morzadec 2001 PalaeontA | Psychopyge elegans | Psychopyge | Acastidae | Phacopida | Jbel Issoumour Unknown | Maider | Emsian | upper Emsian | 1 | Tazoulaït |
| Morzadec 2001 PalaeontA | Psychopyge elegans | Psychopyge | Acastidae | Phacopida | Jbel Oufatene | Maider | Emsian | upper Emsian | 2 | Tazoulaït |
| Morzadec 2001 PalaeontA | Psychopyge termierorum | Psychopyge | Acastidae | Phacopida | Jbel Oufatene | Maider | Emsian | upper Emsian | 1 | Bou Tiskaouïne |
| Morzadec 1997 PalaeontA | Psychopyge elegans | Psychopyge | Acastidae | Phacopida | Marhouma | Ougarta basin | Emsian | upper Emsian | 1 | Teferguenit |
| Morzadec 1988 PalaeontA | Psychopyge termierorum | Psychopyge | Acastidae | Phacopida | Marhouma | Ougarta basin | Emsian | upper Emsian | 1 | Teferguenit |
| H.Alberti 1973 NJb Geol Pal | Pusillabole bordjensis | Pusillabole | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | middle Famennian | 2 | Achguig |
| H.Alberti 1973 NJb Geol Pal | Pusillabole bordjensis | Pusillabole | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | middle Famennian | 1 | Achguig |
| H.Alberti 1973 NJb Geol Pal | Pusillabole bordjensis | Pusillabole | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | middle Famennian | 1 | Achguig |
| H.Alberti 1973 NJb Geol Pal | Pusillabole cognata | Pusillabole | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | upper Famennian | 1 | Achguig |
| H.Alberti 1973 NJb Geol Pal | Pusillabole cornicula jebelensis | Pusillabole | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | upper Famennian | 2 | Achguig |
| H.Alberti 1973 NJb Geol Pal | Pusillabole cornicula sobrina | Pusillabole | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | upper Famennian | 8 | Achguig |
| H.Alberti 1973 NJb Geol Pal | Pusillabole cornicula tafilaltensis | Pusillabole | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | uppermost Famennian | 2 | Achguig |
| H.Alberti 1973 NJb Geol Pal | Pusillabole erfoudensis | Pusillabole | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | middle Famennian | 3 | Achguig |
| H.Alberti 1973 NJb Geol Pal | Pusillabole erfoudensis zizensis | Pusillabole | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | upper Famennian | 3 | Achguig |
| H.Alberti 1973 NJb Geol Pal | Pusillabole radiata pusillaformis | Pusillabole | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | uppermost Famennian | 5 | Achguig |
| Morzadec 2001 PalaeontA | Quadrops flexosus | Quadrops | Acastidae | Phacopida | Jbel Oufatene | Maider | Emsian | upper Emsian | 2 | El Otfal |
| Feist Orth 2000 ProcSDS | Indet | Radiaspis | Odontopleuridae | Lichida | Jbel Ziata | Tafilalt | Givetian | lower Givetian | 1 | Bou Tcharafine |
| Alberti 1983 Senck lethaea | Reedops cephalotes algericanus | Reedops | Phacopidae | Phacopida | Ben Zireg | Ougarta basin | Pragian | Pragian | 2 | |
| Alberti 1983 Senck lethaea | Reedops struveianus | Reedops | Phacopidae | Phacopida | Ben Zireg | Ougarta basin | Pragian | Pragian | 6 | |
| Alberti 1983 Senck lethaea | Reedops cephalotes hamlagdadianus | Reedops | Phacopidae | Phacopida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 40 | lower Kess Kess |
| McKellar Chatterton 2009 Pal Canadiana | Reedops cephalotes hamlagdadianus | Reedops | Phacopidae | Phacopida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 13 | lower Kess Kess |

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|---|---|---|---|---|---|---|---|---|---|---|
| Frey Naglik Hofmann Schemm-Gregory Fryda Kröger Taylor 2014 Bull geo | Reedops bronni | Reedops | Phacopidae | Phacopida | Jbel Ouafilal-Filon 12 | Tafilalt | Pragian | Pragian | 1 | Seheb el Rhassel |
| Frey Naglik Hofmann Schemm-Gregory Fryda Kröger Taylor 2014 Bull geo | Reedops cephalotes hamlagdadianus | Reedops | Phacopidae | Phacopida | Jbel Ouafilal-Filon 12 | Tafilalt | Pragian | Pragian | 7 | Seheb el Rhassel |
| McKellar Chatterton 2009 Pal Canadiana | Reedops bronni | Reedops | Phacopidae | Phacopida | Jbel Oufatene Jbel Issoumour | Maider | Pragian | Pragian | 2 | Ihandar |
| McKellar Chatterton 2009 Pal Canadiana | Reedops bronni | Reedops | Phacopidae | Phacopida | Jbel Oufatene Jbel Issoumour | Maider | Pragian | Pragian | 1 | Ihandar |
| McKellar Chatterton 2009 Pal Canadiana | Reedops pembertoni | Reedops | Phacopidae | Phacopida | Jbel Oufatene Jbel Issoumour | Maider | Pragian | Pragian | 14 | Ihandar |
| McKellar Chatterton 2009 Pal Canadiana | Reedops pembertoni | Reedops | Phacopidae | Phacopida | Jbel Oufatene Jbel Issoumour | Maider | Pragian | Pragian | 1 | Ihandar |
| McKellar Chatterton 2009 Pal Canadiana | Reedops cephalotes hamlagdadianus | Reedops | Phacopidae | Phacopida | Mdâour el Kbîr | Draa Valley | Pragian | Pragian | 2 | Assa |
| Klug Kröger Korn Rücklin Schemm-Gregory DeBaets Mapes 2008 Pal Abt A | Reedops cephalotes cephalotes | Reedops | Phacopidae | Phacopida | Ouidane Chebbi | Tafilalt | Emsian | lower Emsian | 1 | Seheb el Rhassel |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Rheiscutellum hammadi | Rheiscutellum | Scutelluidae | Corynexoch | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 2 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Rheiscutellum lahceni | Rheiscutellum | Scutelluidae | Corynexoch | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 1 | Timrhamhart |
| Feist Chatterton 2015 Palaeontology | Sagittapeltis belkai | Sagittapeltis | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Emsian | lower Emsian | 2 | upper Kess Kess |
| Müller 2005 Geol et Pal | Scabrella aithssainei | Scabrella | Homalonotidae | Phacopida | Jbel Issoumour Unknown | Maider | Pragian | Pragian | 1 | Ihandar |
| Müller 2005 Geol et Pal | Scabrella propradoana | Scabrella | Homalonotidae | Phacopida | Jbel Issoumour Unknown | Maider | Pragian | Pragian | 1 | Ihandar |
| Cronier Oudot Klug DeBaets 2018 NJb Geol Pal | Indet | Scabriscutellum | Scutelluidae | Corynexoch | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 4 | Amerboh |
| Alberti 1981a Senck lethaea | Scharyia hamlagdadica | Scharyia | Aulacopleuridae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 7 | Amerboh |
| Alberti 1970a SenckNaturGesell | Scharyia tafilaltensis | Scharyia | Aulacopleuridae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| Alberti 1983 Senck lethaea | Scharyia yolkiniana | Scharyia | Aulacopleuridae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Alberti 1981a Senck lethaea | Sculptoporetus africanus africanus | Sculptoproetus | Proetidae | Proetida | Ben Zireg | Ougarta basin | Emsian | | 1 | |
| Alberti 1967a Senck leth | Sculptoproetus maghrebus | Sculptoproetus | Proetidae | Proetida | El Atrous | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| Alberti 1969 SenckNaturGesell | Sculptoproetus maghrebus | Sculptoproetus | Proetidae | Proetida | El Atrous | Tafilalt | Emsian | lower Emsian | 5 | Seheb el Rhassel |
| Alberti 1983 Senck lethaea | Sculptoporetus africanus africanus | Sculptoproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Eifelian | lower Eifelian | 1 | Bou Tcharafine |
| Alberti 1981a Senck lethaea | Sculptoporetus africanus iunior | Sculptoproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Eifelian | lower Eifelian | 3 | Bou Tcharafine |
| Alberti 1983 Senck lethaea | Sculptoporetus africanus ribatelfatanus | Sculptoproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Eifelian | lower Eifelian | 1 | Bou Tcharafine |
| Alberti 1970a SenckNaturGesell | Scultoproetus sculptus posterior | Sculptoproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 7 | Amerboh |
| Alberti 1969 SenckNaturGesell | Sculptoporetus africanus africanus | Sculptoproetus | Proetidae | Proetida | Jbel Amlane | Tafilalt | Eifelian | lower Eifelian | 40 | Amerboh |
| Alberti 1964 SenckNaturGesell | Sculptoporetus africanus africanus | Sculptoproetus | Proetidae | Proetida | Jbel Amlane | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| Alberti 1983 Senck lethaea | Sculptoporetus spAA | Sculptoproetus | Proetidae | Proetida | Jbel Amlane | Tafilalt | Emsian | lower Emsian | 1 | Seheb el Rhassel |
| Alberti 1983 Senck lethaea | Sculptoproetus maghrebus | Sculptoproetus | Proetidae | Proetida | Jbel Amlane | Tafilalt | Emsian | lower Emsian | 1 | Seheb el Rhassel |
| Alberti 1970a SenckNaturGesell | Sculptoproetus maghrebus | Sculptoproetus | Proetidae | Proetida | Jbel Bou Tscharafine | Tafilalt | Emsian | lower Emsian | 1 | Seheb el Rhassel |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Sculptoproetus haasi | Sculptoproetus | Proetidae | Proetida | Jbel Gara el Zguilma | Draa Valley | Eifelian | lower Eifelian | 3 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Sculptoproetus sp B | Sculptoproetus | Proetidae | Proetida | Jbel Gara el Zguilma | Draa Valley | Eifelian | lower Eifelian | 2 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Sculptoproetus spA | Sculptoproetus | Proetidae | Proetida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 2 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Sculptoproetus spA | Sculptoproetus | Proetidae | Proetida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 1 | Timrhamhart |
| Alberti 1970a SenckNaturGesell | Sculptoproetus maghrebus | Sculptoproetus | Proetidae | Proetida | Jbel Issoumour SW | Maider | Emsian | lower Emsian | 1 | Bou Tiskaouïne |
| Alberti 1967b Senck leth | Sculptoproetus sculptus antiquus | Sculptoproetus | Proetidae | Proetida | Timarzite | Maider | Pragian | Pragian | 1 | Ihandar |

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|---|---|---|---|---|---|---|---|---|---|---|
| Alberti 1969 SenckNaturGesell | Sculptoproetus sculptus antiquus | Sculptoproetus | Proetidae | Proetida | Timarzite | Maider | Pragian | Pragian | 3 | Ihandar |
| Klug Kröger Korn Rücklin Schemm-Gregory DeBaets Mapes 2008 Pal Abt A | Sculptoproetus maghrebus | Sculptoproetus | Proetidae | Proetida | Ouidane Chebbi | Tafilalt | Emsian | lower Emsian | 2 | Seheb el Rhassel |
| vanViersen Lerouge 2019 Pal Zeit | Sculptoproetus raki | Sculptoproetus | Proetidae | Proetida | Rissani South | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| Schraut 2000b Senck Lethaea | Spiniscabrella struvei | Spiniscabrella | Homalonotidae | Phacopida | Jbel Issoumour N | Maider | Emsian | upper Emsian | 2 | Tazoulaït |
| Alberti 1970a SenckNaturGesell | Struveaspis maroccanica | Struveaspis | Phacopidae | Phacopida | Jbel Amlane | Tafilalt | Eifelian | upper Eifelian | 3 | Bou Tcharafine |
| Alberti 1981a Senck lethaea | Struveaspis maroccanica | Struveaspis | Phacopidae | Phacopida | Jbel Amlane | Tafilalt | Eifelian | upper Eifelian | 3 | Bou Tcharafine |
| Alberti 1966a Senck leth | Struveaspis sp A | Struveaspis | Phacopidae | Phacopida | Jbel Amlane | Tafilalt | Eifelian | upper Eifelian | 1 | Bou Tcharafine |
| Alberti 1970a SenckNaturGesell | Struveaspis maroccanica | Struveaspis | Phacopidae | Phacopida | Jbel Bou Tscharafine | Tafilalt | Eifelian | upper Eifelian | 3 | Bou Tcharafine |
| Alberti 1981a Senck lethaea | Struveaspis maroccanica | Struveaspis | Phacopidae | Phacopida | Jbel Bou Tscharafine | Tafilalt | Eifelian | upper Eifelian | 3 | Bou Tcharafine |
| Corbacho 2014b Sc. Musei Geologici Seminarii Barcinonensis | Struveaspis bignoni | Struveaspis | Phacopidae | Phacopida | Jdorf | Tafilalt | Eifelian | | 2 | |
| Corbacho 2014b Sc. Musei Geologici Seminarii Barcinonensis | Struveaspis micromma | Struveaspis | Phacopidae | Phacopida | Jdorf | Tafilalt | Eifelian | | 1 | |
| Alberti 1981a Senck lethaea | Struveaspis maroccanica | Struveaspis | Phacopidae | Phacopida | Marhouma | Ougarta basin | Eifelian | lower Eifelian | 2 | Chefar el Ahmar |
| Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag | Struveaspis maroccanica | Struveaspis | Phacopidae | Phacopida | Ouarourout | Ougarta basin | Eifelian | lower Eifelian | 7 | Chefar el Ahmar |
| Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag | Struveaspis maroccanica | Struveaspis | Phacopidae | Phacopida | Ouarourout | Ougarta basin | Eifelian | lower Eifelian | 9 | Chefar el Ahmar |
| Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag | Struveaspis maroccanica | Struveaspis | Phacopidae | Phacopida | Ouarourout | Ougarta basin | Eifelian | lower Eifelian | 1 | Chefar el Ahmar |
| Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag | Struveaspis maroccanica | Struveaspis | Phacopidae | Phacopida | Ouarourout | Ougarta basin | Eifelian | lower Eifelian | 4 | Chefar el Ahmar |
| Alberti 1967b Senck leth | Tafilaltaspis creber tenuigranifer | Tafilaltaspis | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Eifelian | lower Eifelian | 1 | Bou Tcharafine |
| Alberti 1969 SenckNaturGesell | Tafilaltaspis creber tenuigranifer | Tafilaltaspis | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Eifelian | lower Eifelian | 10 | Bou Tcharafine |
| Alberti 1969 SenckNaturGesell | Tafilaltaspis nitidus | Tafilaltaspis | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | lower Emsian | 1 | upper Kess Kess |
| Alberti 1966a Senck leth | Tafilaltaspis creber creber | Tafilaltaspis | Tropidocoryphidae | Proetida | Jbel Amlane | Tafilalt | Emsian | upper Emsian | 5 | Amerboh |
| Alberti 1970a SenckNaturGesell | Tafilaltaspis creber creber | Tafilaltaspis | Tropidocoryphidae | Proetida | Jbel Amlane | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| Alberti 1969 SenckNaturGesell | Tafilaltaspis maidericus | Tafilaltaspis | Tropidocoryphidae | Proetida | Timarzite | Maider | Emsian | upper Emsian | 1 | |
| vanViersen Lerouge 2019 Pal Zeit | Tafilaltaspis rufa | Tafillataspis | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Eifelian | lower Eifelian | 1 | Bou Tcharafine |
| vanViersen Lerouge 2019 Pal Zeit | Tafilaltaspis spA | Tafillataspis | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | | | 1 | |
| Schraut 2000a Senck Lethaea | Thysanopeltis speciosa | Thysanopeltis | Scutelluidae | Corynexoch | Foum Zguid | Draa Valley | Eifelian | lower Eifelian | 1 | Timrhamhart |
| Alberti 1981a Senck lethaea | Thysanopeltis speciosa austromaura | Thysanopeltis | Scutelluidae | Corynexoch | Jbel Bou Tscharafine | Tafilalt | Eifelian | lower Eifelian | 3 | Bou Tcharafine |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Thysanopeltis speciosa | Thysanopeltis | Scutelluidae | Corynexoch | Jbel Gara el Zguilma | Draa Valley | Eifelian | lower Eifelian | 2 | Timrhamhart |
| Crônier Abbache Khaldi Oudot Maillet Ouali-Mehadji 2018 Geol Mag | Thysanopeltis speciosa | Thysanopeltis | Scutelluidae | Corynexoch | Ouarourout | Ougarta basin | Eifelian | lower Eifelian | 1 | Chefar el Ahmar |
| Gibb Chatterton 2007 JPaleont | Timsaloproetus haasi | Timsaloproetus | Proetidae | Proetida | Bou Dîb | Maider | Eifelian | lower Eifelian | 5 | El Otfal |
| vanViersen Lerouge 2019 Pal Zeit | Timsaloproetus haasi | Timsaloproetus | Proetidae | Proetida | Foum Zguid | Draa Valley | Eifelian | lower Eifelian | 1 | Timrhamhart |
| vanViersen Lerouge 2019 Pal Zeit | Timsaloproetus pulchistriatus repens | Timsaloproetus | Proetidae | Proetida | Foum Zguid | Draa Valley | Emsian | upper Emsian | 1 | Timrhamhart |
| Gibb Chatterton 2007 JPaleont | Timsaloproetus dibbanus | Timsaloproetus | Proetidae | Proetida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 3 | Timrhamhart |
| Gibb Chatterton 2007 JPaleont | Timsaloproetus elguerrouji | Timsaloproetus | Proetidae | Proetida | Jbel Gara el Zguilma | Draa Valley | Eifelian | lower Eifelian | 3 | Timrhamhart |
| Gibb Chatterton 2007 JPaleont | Timsaloproetus haasi | Timsaloproetus | Proetidae | Proetida | Jbel Gara el Zguilma | Draa Valley | Eifelian | lower Eifelian | 3 | Timrhamhart |
| vanViersen Lerouge 2019 Pal Zeit | Timsaloproetus haasi | Timsaloproetus | Proetidae | Proetida | Talawarite | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| vanViersen Lerouge 2019 Pal Zeit | Timsaloproetus pulchistriatus pulchistriatus | Timsaloproetus | Proetidae | Proetida | Timarzite | Maider | Emsian | upper Emsian | 1 | Tazoulait |
| vanViersen Lerouge 2019 Pal Zeit | Timsaloproetus haasi | Timsaloproetus | Proetidae | Proetida | Bou Dîb | Maider | Eifelian | lower Eifelian | 1 | El Otfal |
| vanViersen Lerouge 2019 Pal Zeit | Timsaloproetus haasi | Timsaloproetus | Proetidae | Proetida | Bou Dîb | Maider | Emsian | upper Emsian | 1 | Tazoulaït |
| Gibb Chatterton 2007 JPaleont | Timsaloproetus haasi | Timsaloproetus | Proetidae | Proetida | Zguilma | Draa Valley | Eifelian | lower Eifelian | 1 | Timrhamhart |

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|---|---|---|---|---|---|---|---|---|---|---|
| vanViersen Lerouge 2019 Pal Zeit | Timsaloproetus haasi | Timsaloproetus | Proetidae | Proetida | Zguilma | Draa Valley | Eifelian | lower Eifelian | 1 | Timrhamhart |
| Morzadec 2001 PalaeontA | Treveropyge maura | Treveropyge | Acastidae | Phacopida | Jbel Oufatene | Maider | Emsian | upper Emsian | 1 | Tazoulaït |
| Feist Mahboubi Girard 2016 Bull geo | Trifoliops croniera | Trifoliops | Phacopidae | Phacopida | Marhouma | Ougarta basin | Famennian | lower Famennian | 1 | Argiles de Marhouma |
| Feist Mahboubi Girard 2016 Bull geo | Trifoliops septimanicus | Trifoliops | Phacopidae | Phacopida | Marhouma | Ougarta basin | Famennian | lower Famennian | 2 | Argiles de Marhouma |
| Crônier Malti François Benyoucef Brice 2013 Geol Mag | Trimerocephalus nigritus | Trimerocephalus | Phacopidae | Phacopida | Béchir | Ougarta basin | Famennian | upper Famennian | 1 | Argiles de Marhouma |
| Crônier Malti François Benyoucef Brice 2013 Geol Mag | Trimerocephalus caecus | Trimerocephalus | Phacopidae | Phacopida | Cheffar-el-Ahmar | Ougarta basin | Famennian | middle Famennian | 1 | Argiles de Marhouma |
| Crônier Malti François Benyoucef Brice 2013 Geol Mag | Trimerocephalus nigritus | Trimerocephalus | Phacopidae | Phacopida | Gara Diba | Ougarta basin | Famennian | middle Famennian | 1 | Argiles de Marhouma |
| Crônier Feist 1997 Geobios | Trimerocephalus lelievrei | Trimerocephalus | Phacopidae | Phacopida | Korb el Atil | Tafilalt | Famennian | middle Famennian | 213 | Achguig |
| Feist Mahboubi Girard 2016 Bull geo | Trimerocephalus caecus | Trimerocephalus | Phacopidae | Phacopida | Marhouma | Ougarta basin | Famennian | middle Famennian | 1 | Argiles de Marhouma |
| Feist Mahboubi Girard 2016 Bull geo | Trimerocephalus mahboubii | Trimerocephalus | Phacopidae | Phacopida | Marhouma | Ougarta basin | Famennian | lower Famennian | 3 | Argiles de Marhouma |
| Alberti 1967a Senck leth | Tropidocoryphe hamlaghdadica | Tropidocoryphe | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 1 | lower Kess Kess |
| Alberti 1969 SenckNaturGesell | Tropidocoryphe hamlaghdadica | Tropidocoryphe | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Pragian | Pragian | 2 | lower Kess Kess |
| Feist Belka 2018 N.Jb Geol | Tropidocoryphe mediterranea | Tropidocoryphe | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | | 1 | upper Kess Kess |
| Alberti 1981a Senck lethaea | Tropidocoryphe memmon nepos | Tropidocoryphe | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| Becker ElHassani Hartenfels Luddecke 2018 Frontiers Science Engineering | Tropidocoryphe memnon nepos | Tropidocoryphe | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 1 | Amerboh |
| Alberti 1970a SenckNaturGesell | Tropidocoryphe memnon nepos | Tropidocoryphe | Tropidocoryphidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 3 | Amerboh |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Tropidocoryphe amuri | Tropidocoryphe | Tropidocoryphidae | Proetida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 1 | Timrhamhart |
| Alberti 1969 SenckNaturGesell | Unguliproetus unguloides unguloides | Unguliproetus | Proetidae | Proetida | Hamar Laghdad | Tafilalt | Emsian | upper Emsian | 1 | upper Kess Kess |
| Alberti 1969 SenckNaturGesell | Unguliproetus unguloides tener | Unguliproetus | Proetidae | Proetida | Jbel Amlane | Tafilalt | Emsian | upper Emsian | 2 | Amerboh |
| H.Alberti 1976b NJb Geol Pal | Vittaella vitta | Vittaella | Proetidae | Proetida | Bordj Est | Tafilalt | Famennian | lower Famennian | 1 | Achguig |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Walliserops sp A | Walliserops | Acastidae | Phacopida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 1 | Chefar el Ahmar |
| Khaldi Crônier Hainaut Abbacke Mehadji 2016 Geol Mag | Walliserops sp B | Walliserops | Acastidae | Phacopida | Erg Djemel | Ougarta basin | Emsian | upper Emsian | 1 | Chefar el Ahmar |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Walliserops hammii | Walliserops | Acastidae | Phacopida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 3 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Walliserops tridens | Walliserops | Acastidae | Phacopida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 1 | Timrhamhart |
| Morzadec 2001 PalaeontA | Walliserops trifurcatus | Walliserops | Acastidae | Phacopida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 4 | Timrhamhart |
| vanViersen 2004 GEA | Walliserops trifurcatus | Walliserops | Acastidae | Phacopida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 1 | Timrhamhart |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Walliserops trifurcatus | Walliserops | Acastidae | Phacopida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 2 | Timrhamhart |
| Chatterton Gibbs 2010 Jpal | Walliserops lindoei | Walliserops | Acastidae | Phacopida | Jbel Issoumour SW | Maider | Emsian | upper Emsian | 1 | El Otfal |
| Chatterton Fortey Brett Gibb McKellar 2006 Pal Canadiana | Wenndorfia calvus | Wenndorfia | Homalonotidae | Phacopida | Jbel Gara el Zguilma | Draa Valley | Emsian | upper Emsian | 6 | Timrhamhart |
| Alberti 1969 SenckNaturGesell | Xiphogonium trautensteinensis crassus | Xiphogonium | Tropidocoryphidae | Proetida | El Atrous | Tafilalt | Emsian | lower Emsian | 4 | Seheb el Rhassel |