

Journal of Systematic Palaeontology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tjsp20>

The systematics and phylogeny of the Devonian subfamily Asteropyginae (Trilobita: Phacopida)

Arnaud Bignon^{a b} & Catherine Crônier^a

^a Université Lille 1, UFR Sciences de la Terre, UMR 8217 Géosystèmes, Villeneuve d'Ascq cedex, 59655, France

^b Department of Geology and Geophysics, Yale University, New Haven, CT, 06511, USA

Published online: 22 Jul 2013.

To cite this article: Arnaud Bignon & Catherine Crônier, Journal of Systematic Palaeontology (2013): The systematics and phylogeny of the Devonian subfamily Asteropyginae (Trilobita: Phacopida), Journal of Systematic Palaeontology, DOI: [10.1080/14772019.2013.804008](https://doi.org/10.1080/14772019.2013.804008)

To link to this article: <http://dx.doi.org/10.1080/14772019.2013.804008>

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at <http://www.tandfonline.com/page/terms-and-conditions>

The systematics and phylogeny of the Devonian subfamily Asteropyginae (Trilobita: Phacopida)

Arnaud Bignon^{a,b*} and Catherine Crônier^a

^aUniversité Lille 1, UFR Sciences de la Terre, UMR 8217 Géosystèmes, 59655 Villeneuve d'Ascq cedex, France; ^bDepartment of Geology and Geophysics, Yale University, New Haven, CT 06511, USA

(Received 10 August 2012; accepted 26 February 2013)

Traditionally, the evolutionary scenarios of Asteropyginae have been organized in two major clades involving four pygidial patterns. The first cladistic analysis performed on the subfamily maintained the organization in two clades, though the phylogenetic relationships between genera were unexpected compared to the traditional scenarios. Moreover, the previous systematic scheme based on pygidial segmentation was rendered obsolete. In this study, we performed a new phylogenetic analysis from well-known taxa and recent discoveries. Sixty species assigned to 36 genera have been analysed from a dataset of 72 characters. Three more species are used as the outgroup. The 79 most parsimonious trees have a length of 492 steps and a retention index of 0.735. Our analysis confirms the monophyly of Asteropyginae excluding the genus *Protacanthina*. The phylogenetic pattern is unconventional in that a largely pectinate topology is resolved, rather than two clades corresponding to formerly delimited pygidial morphs. Nevertheless, most relationships between genera suggested in the traditional evolutionary scenarios of the subfamily have been recovered, the main differences being the origin of the group. Whereas *Treveropyge* was usually considered as the origin of the remaining Asteropyginae, the present results instead identify *Destombesina* as the sister group to all remaining members of the subfamily. From the new phylogenetic pattern, the diagnoses of genera are rewritten in a standard way and to delimit clades more accurately. This work implies modified generic assignments for some species and the erection of four new genera: *Minicryphaeus* gen. nov., *Gandlops* gen. nov., *Morzadecops* gen. nov. and *Pennarbedops* gen. nov. The systematic position of *Erbenochile* is also discussed, the genus no longer being assigned to Asteropyginae.

<http://zoobank.org/urn:lsid:zoobank.org:pub:C42A54C3-2B8E-439A-8DE0-2F35575F7F40>

Keywords: Acastacea; Acastidae; cladistics; taxonomy

Introduction

Asteropyginae constitutes one of the most famous groups of Devonian trilobites. Indeed, some members of this subfamily present extraordinary morphology such as very long genal or pygidial spines, numerous vertical spines throughout the body, and long blade- or trident-shaped precephalic projections (Chatterton *et al.* 2006). This subfamily persisted from the Lochkovian to the Frasnian (Feist 1991) and comprised more than 250 species (Lieberman & Kloc 1997). A first peak of biodiversity was reached during the Emsian followed by a drastic fall coincident with an important sea level rise during the Emsian–Eifelian transition. A second peak, less important, is recorded in the middle Frasnian. Nevertheless, the Kellwasser event had strongly affected the subfamily and it disappeared before the Famennian (Morzadec 1992). Asteropyginae occurred all over the world, mainly in North Africa, Europe and North America and, to a lesser degree, in Asia and South America (Lieberman & Kloc 1997).

Phylogenetic information is essential for analysing macroevolutionary patterns and processes. Traditionally, Asteropyginae have been divided into two putative clades (Haas 1970; Gandl 1972; Arbizu 1977; Smeenk 1983; Morzadec 1983; Fig. 1). One of these clades belonged to a conservative pygidial type discriminated into *boothi* and *prorotundifrons* patterns and the other, to a progressive pygidial type split into *cometa* and *supradevonicus* patterns (Struve 1959; Fig. 1A–E). Depending on the authors, the generic composition of these clades differed markedly. Moreover, phylogenetic relationships between genera within a single clade were not well understood.

Lieberman & Kloc (1997) performed the first cladistic analysis on Asteropyginae (Fig. 1F). Their study showed also a phyletic division into two different clades. However, the pygidial patterns defined by Struve (1959) were not seen as phylogenetically informative. From this work the pygidial patterns became obsolete.

Here, we present a new study of asteropygine evolution. We performed a cladistic analysis on 60 species assigned

*Corresponding author. Email: arnaudbignon@yahoo.fr

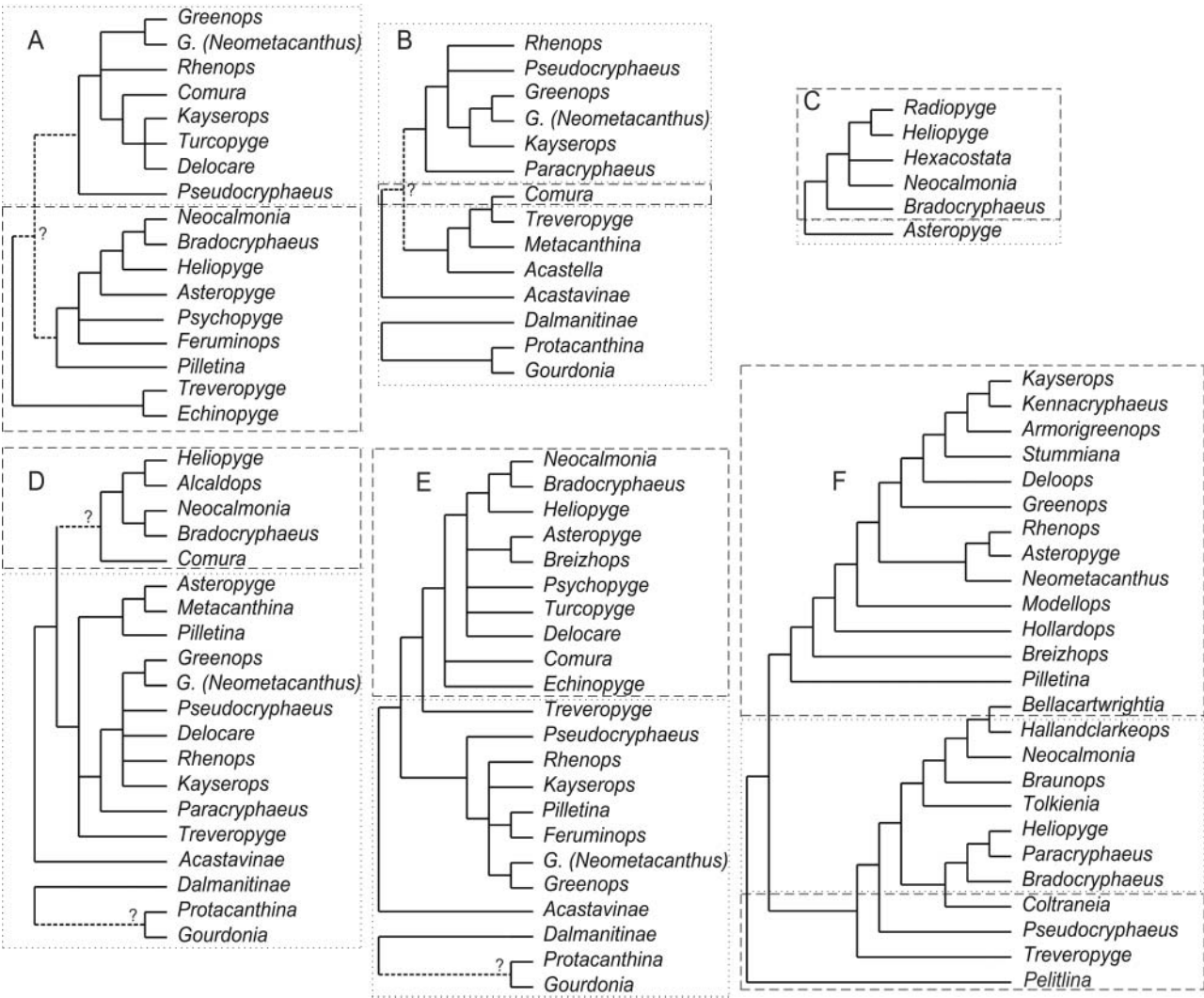


Figure 1. Former hypotheses of Asteropyginae evolution. **A**, Haas 1970; **B**, Gandl 1972; **C**, Farsan 1981; **D**, Smeenk 1983; **E**, Morzadec 1983; **F**, Lieberman & Kloc 1997. Dotted squares correspond to the conservative pygidial type and dashed squares to the progressive pygidial type.

to 36 genera. Our sample proposes an overview of the morphologies existing in this subfamily and considers taxa recently described which have never been tested in a phylogenetical analysis.

The main purpose of this study is to clarify the systematics of the Asteropyginae, (1) to make it easier to identify the genera; and (2) to determine the phylogenetic relationships among genera.

Methods

Ingroup selection

Asteropyginae are represented by 60 species (of 250 described) allocated to 36 genera (online supplemental

material, Appendix 2). Most of these taxa were coded from personal observations. The studied material comes from: samplings in the Ardenne Massif (van Viersien & Bignon 2011), the Mailloux collection housed in the Institut Royal des Sciences Naturelles de Belgique (Belgium), the Morzadec collection of the Museum d'Histoire Naturelle de Nantes (France), and specimens of the Yale Peabody Museum (CT, USA). Moreover, some type species were coded from the literature.

Characters utilized

Seventy-two characters (online supplemental material, Appendix 1) have been selected for the data matrix. Of the 72 selected characters, 42 are from the cephalon, 29 from the pygidium and one from the thorax. The hypostome and the thorax are unknown in many species and

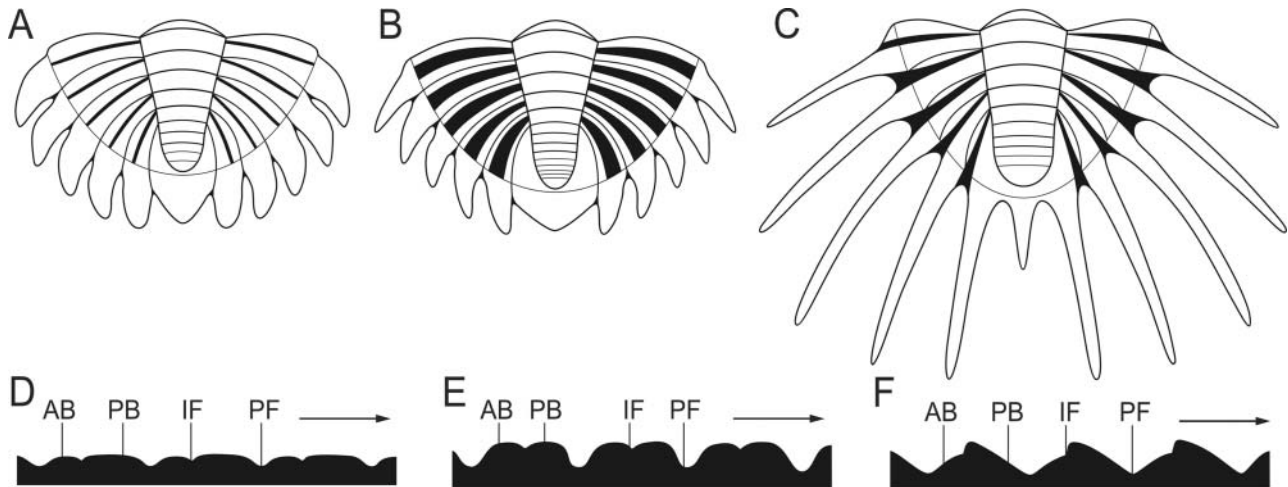


Figure 2. Illustration of some Asteropyginae pygidial characters in dorsal view (A, B, C) and lateral view of the pleurae (D, E, F). The arrow represents the anterior direction. Posterior pleural bands (character 8): more elevated than anterior pleural bands of the posterior segment (state 0; F), as elevated (state 1; D, E); pleural bands (14): rounded (0; E), bent (1; F), flat (2; D); terminal spine (17): wider than axial tip (0; A, B), as large (1; C); terminal spine (18): triangular (0; C), pentagonal (1; A, B); terminal spine (19): shorter than pygidial spines (0; C), as long or longer (1; A, B); pygidial spines developed (20): mostly from anterior pleural bands (0; A), from anterior and posterior bands (1; B), only from posterior bands (2; C).

most of the specimens available for this study are disarticulated. Thus it appeared more judicious not to attempt a hazardous description of these structures. Nevertheless, the number of thoracic segments has been considered because this feature is well known and stable within the Asteropyginae (Morzadec 1997). In the cladistic analysis, the weight of all characters is equal and multistate characters were treated as unordered (Lee 1999). We took care to describe the pygidial segmentation precisely, without overweighting it with an exaggerated number of characters. States of

continuous characters are defined from substantial gaps in growing cumulative curves.

To assist visualization of some diagnostic characters within Asteropyginae, illustrations of pygidia (Fig. 2) and cephalae (Fig. 3) are proposed.

Outgroup selection

As summarized by Chatterton & Gibb (2010), the phylogenetic relationships within Acastidae have been the subject of debate for a long time. Indeed the subfamilies Acastavinae,

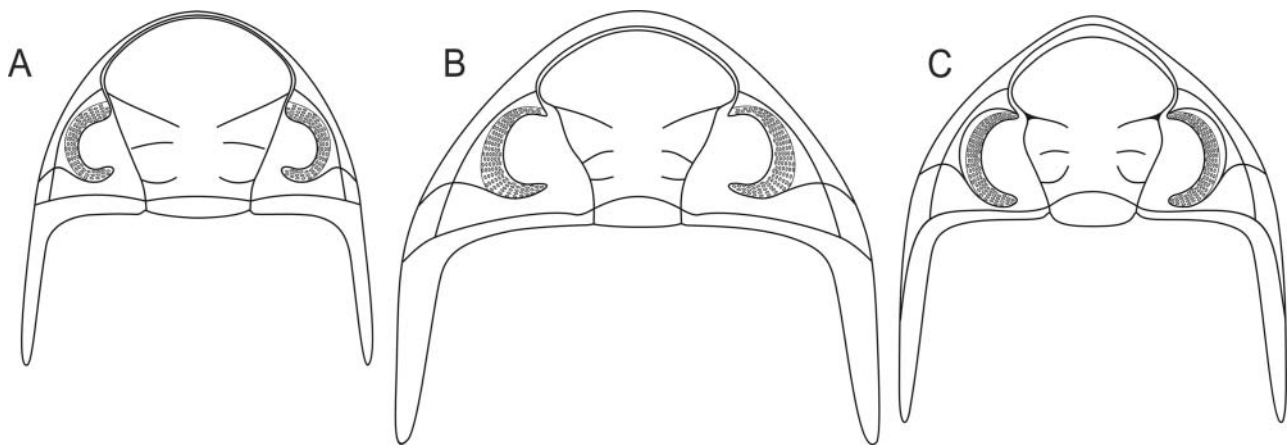


Figure 3. Illustration of some Asteropyginae cephalic characters in dorsal view (A, B, C). Frontal lobe (character 31): diamond shaped (state 0; A, B), rounded (state 1; C); glabella axial furrows (36): straight between S1 and S3 (0; A), curved between S2 and S3 (1; B), curved between S2 and S3 (2; C); S2 (42): in contact with axial furrows (0; B), without contact (1; A, C); eyes upon (48): a vertical wall (0; A, B), a subocular platform (1; C); anterior tip of palpebral lobes (50): opposite intersection of S3 with axial furrows (0; C), posterior (1; A, B); lateral border (66): undeveloped on genal spines (0; A), slightly developed (1; B), strongly developed (2; C).

Acastinae, Odontochilinae and Asteropyginae changed several times with respect to family assignment (Struve 1959; Eldredge 1971, 1979; Edgecombe 1993; Ramsköld & Edgecombe 1993; Morzadec 1995, 1997, 2001; Lieberman & Kloc 1997; Jell & Adrain 2003; Basse 2003). Successively, Asteropygidae have been considered as an independent family (Chatterton *et al.* 2006) and then as a subfamily of the Ascastidae (Chatterton & Gibb 2010).

Asteropyginae are commonly accepted as derived from the paraphyletic subfamily of Acastavinae. Nevertheless, the last common ancestor of Asteropyginae has not reached a consensus subject. Some authors suggested the genera *Acastava* Richter & Richter, 1954 or *Pelitlina* Haas, 1968 as the sister group of Asteropyginae (Ramsköld & Edgecombe 1993; Lieberman & Kloc 1997) whereas others proposed *Acastella* Reed, 1925 as the last common ancestor of the subfamily (Gandl 1972; Timm 1981; Smeenk 1983; Tomczykowa 1991).

We decided not to favour either of these assumptions. Therefore, we include *Acastella tiro* Richter & Richter, 1954 and *Pelitlina goltzi* Haas, 1968 in our cladistic analysis. Moreover, a third species, *Mimocryphaeus altecostatus* Gandl, 1972 is included as outgroup in order to have a more complete overview of the Acastavinae morphology.

Analytical protocols

We subjected our data matrix (online supplemental material, Appendix 2) to a parsimony analysis and used a heuristic search (tree bisection and reconnection, TBR) with 1000 random addition sequence replicates) using the software PAUP* 4.0b10 (Swofford 2002) to obtain the most parsimonious trees. Node robustness was assessed with a parsimony jackknife using fast addition sequence and TBR branch swapping, with 10,000 replicates and 36% character deletion (Farris *et al.* 1996). As branch length is not used as subsequent information, synapomorphies are optimized under delayed transformation assumption (Deltran) in order to reduce ambiguous synapomorphies on internal nodes (Agnarsson & Miller 2008).

Results

The parsimony analysis of our data matrix (online supplemental material, Appendix 2) produced 79 most parsimonious trees (MPTs) of 492 steps (consistency index (CI) of 0.220; retention index (RI) of 0.735). Conflicts between these 79 MPTs are represented in the strict consensus tree (Fig. 4). The italic values given on the nodes were retrieved through the jackknife analysis (Fig. 5).

The cladistic analysis shows Asteropyginae to be monophyletic if the genus *Protacanthina* Gandl, 1972 is excluded from the subfamily. Actually this genus is the sister group of the clade formed by two Acastavinae genera,

Mimocryphaeus and *Acastella*, used as outgroup. Accordingly to these results, *Protacanthina* is still not considered as a member of Asteropyginae. See the Systematic Palaeontology section about *Protacanthina* for further information. Referring to the jackknife results, the monophyly of the Asteropyginae (excluding *Protacanthina*) is rather well supported (51%, Fig. 5).

The jackknife analysis suggests a weak support (less than 50%) for several nodes of the tree. It should be noted that the monophyly of the so-called progressive type of Struve (1959) is unambiguously supported (node 33, 89%; Fig. 5), not only from pygidia but also from cephalic features. The clade formed by *Treveropyge* Struve, 1958 and *Coltraenia* Lieberman & Kloc, 1997 is also well supported (30, 81%). The genera *Minicryphaeus* gen. nov. (7, 78%), *Greenops* Delo, 1935 (11, 80%) and the clade *Deloops* Lieberman & Kloc, 1997 – *Stummiana* Lieberman & Kloc, 1997 (14, 82%) are very well supported. The clades *Pennarbedops* gen. nov. – *Morzadecops* gen. nov. (25, 65%), *Walliserops* Morzadec, 2001 – *Psychopyge* Termier & Termier, 1950 (34, 57%) and the genera *Jaylopygiella* Basse, 2003, *Neocalmonia* Pillet, 1969 and *Radiopyge* Farsan, 1981 (46, 55%) are rather well differentiated.

Two genera considered herein as valid, *Alcaldops* Arbizu, 1977 and *Bradocryphaeus* Haas & Mensink, 1970, are not supported by the topology of the tree. The reasons that led us to take the decision to recognize these groups taxonomically are given in the Systematic Palaeontology sections of these genera.

Main tendencies in morphological evolution of the subfamily

Most previous authors (Haas 1970; Gandl 1972; Morzadec 1983; Smeenk 1983; Lieberman & Kloc 1997) proposed two clades corresponding roughly to the conservative and progressive types of Struve (1959) to explain the evolution of Asteropyginae. The present cladistic analysis suggests a more gradual evolution within a largely pectinate cladogram (Fig. 4).

Treveropyge and allied genera are traditionally proposed as near the subfamily origin (Haas 1970) or as the basis of a conservative or progressive clade (Morzadec 1983; Smeenk 1983; Lieberman & Kloc 1997; Fig. 1). This new phylogenetic analysis proposed the genus *Destombesina* Morzadec, 1997 (node 5) as the sister group (node 4) of all other Asteropyginae (Fig. 5).

The first representatives of the subfamily (node 4) bear few segments on the pygidia (character 1-state 0; Fig. 5 and online supplemental material, Appendix 3), an axial constriction between the third and the fourth ring (2–0) and have only four (16–1) straight (26–0), flat (27–0) and triangular (25–1) pygidial spines as large as the pleural segments (24–1). Short pygidial spines (21–0) emerge mainly from posterior pleural bands (20–0) and the

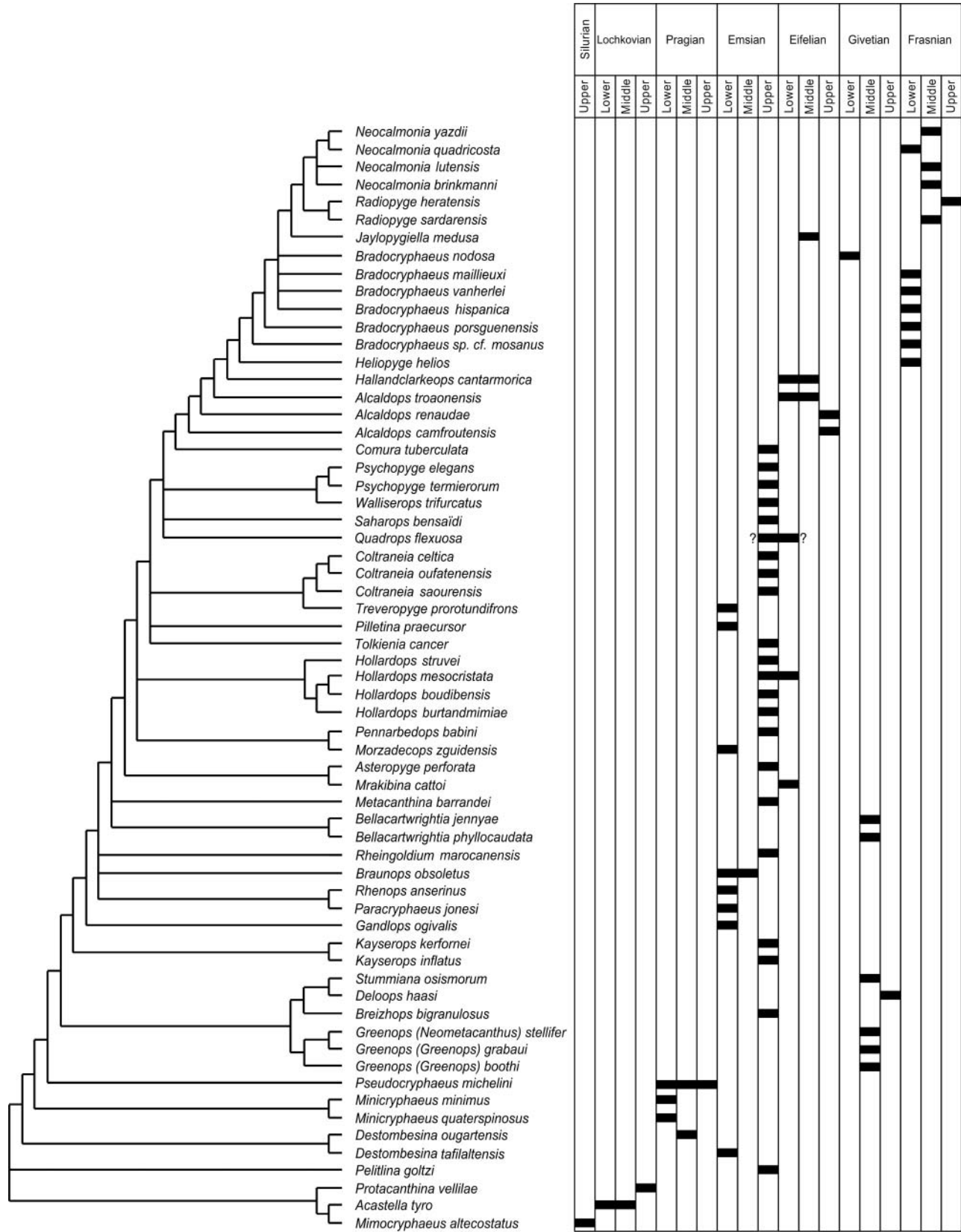


Figure 4. Strict consensus tree of 79 most parsimonious trees (492 steps, CI = 0.220, RI = 0.735) retrieved from a parsimony analysis of the data matrix (see online supplemental material, Appendix 2). The biostratigraphic distribution of each analysed species is reported on the right.

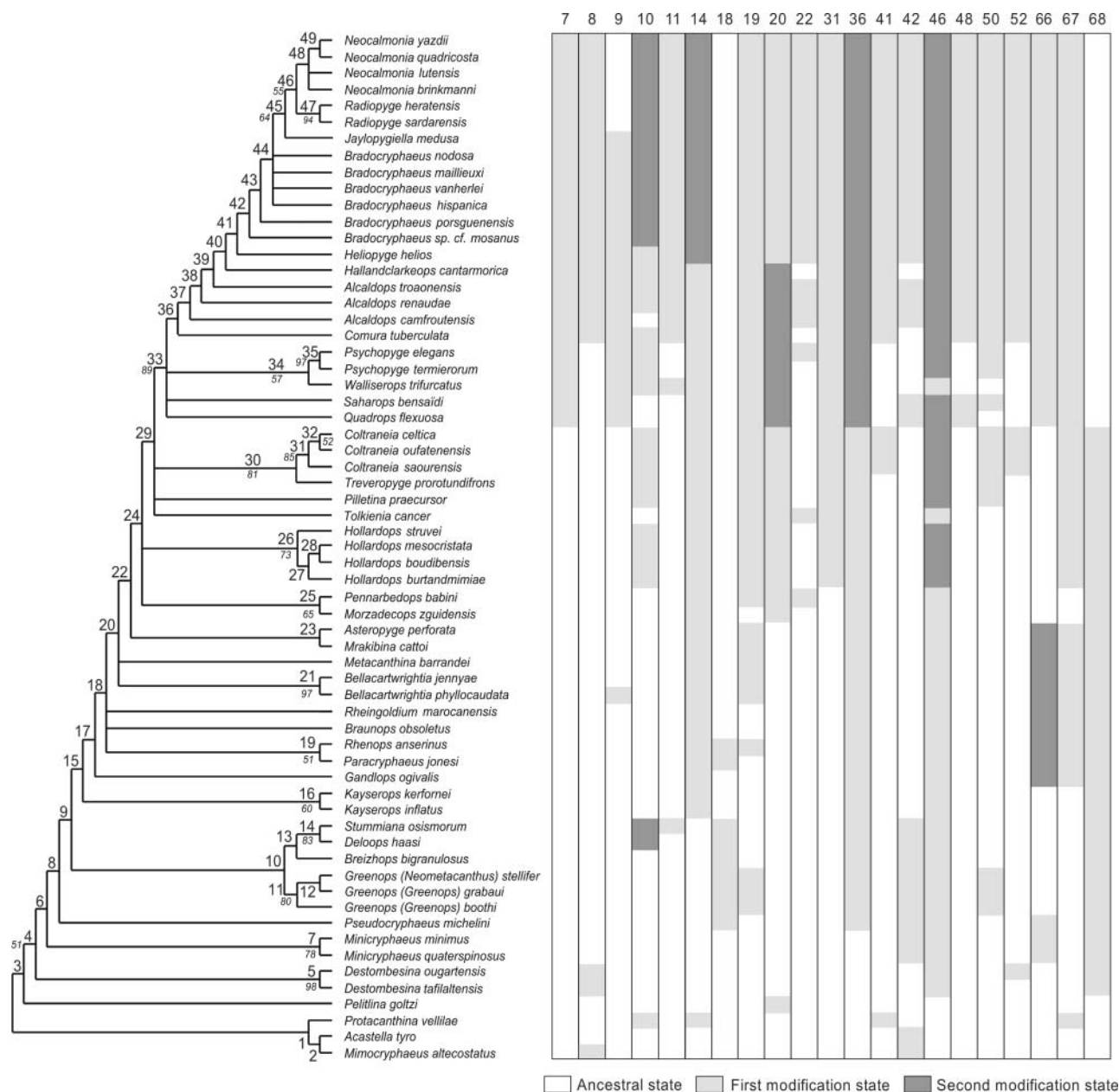


Figure 5. Strict consensus of the 79 most parsimonious trees. Values on the nodes are to identify them. Italic values on the nodes were retrieved through jackknife analysis (36% character deletion, 10 000 repetitions), node values lower to 50% are not reported. The evolution of main characters used in the phylogeny is reported on the right.

triangle-shaped terminal spine (18–0) is equal or longer than other spines (19–1). Pleural furrows are moderately incised (10–1), interpleural furrows are deep (11–1), posterior and anterior pleural bands have an equal width (7–1), are flat (14–2), posterior bands are more elevated (8–0) than the anterior bands, and there is only a slight distal enlargement (transversal, tr.) of pleurae (9–0). The frontal lobe is diamond shaped (31–0); axial furrows are straight between S1 and S3 (36–0); glabellar furrows S1

converge anteriorly (38–1) and are curved (39–0); S2 are convergent anteriorly (40–1), in contact with axial furrows (42–0), and the proximal tip is more distal than S1 and S3 (45–0); L3 is more inflated than L2 and L1 (46–0); L2 is narrow (44–0). The eyes are small (50–1; 52–1) and the posterior border is curved opposite the middle part of palpebral lobe (60–1). Genal spines have a rectangular section (68–0), the proximal portion is narrow (67–1), and the lateral border is not developed on genal spines (66–0).

Minicryphaeus (node 7) has posterior and anterior pleural bands of the same height (8–1). Its posterior border is curved opposite the most proximal portion of palpebral lobe (60–2). S2 distal tips do not contact axial furrows (42–1) and their proximal tips are aligned exsagittally with S1 and S3 (45–1).

From *Pseudocryphaeus* Pillet, 1954 (node 8) there is an increase of the axial rings number on the pygidium (1–1). The terminal pygidial spine is pentagonal (18–1) and glabellar axial furrows are curved between S2 and S3 (36–1).

Asteropyginae, from the clade formed by *Breizhops* Morzadec, 1983, *Deloops*, *Stummiana* and *Greenops* (node 9) have the pygidial axis constriction between the fifth and sixth axial ring (2–2) and a wide L2 (44–1).

From *Kayserops* Delo, 1935 (node 15) the members of the subfamily show rounded pygidial pleural bands (14–0), pointed pygidial spines (25–0), a triangular terminal medial spine (18–0) and a contact between the distal tip of S2 and the glabellar axial furrows (42–0).

From *Gandlops* gen. nov. (node 17), S2 furrows are transverse (40–0), the proximal part of the genal spines is as wide as the distal one (67–0) and the lateral border is strongly developed on them (66–2).

Starting with *Bellacartwrightia* Lieberman & Kloc, 1997 (node 20), Asteropyginae can present a greater number of pygidial axial rings (1–2); the pygidial terminal spine is shorter than the fifth spine pair (19–0), width of the occipital ring may be as great as L1 (33–1) and S1 can be straight (39–1).

With *Metacanthina* Pillet, 1954 (node 20), Asteropyginae have a terminal pygidial spine wider than the posterior axial tip (17–0), curved pygidial spines (26–1), and the curve of cephalic posterior border is opposite the middle of the eye (60–1).

From the clade formed with *Mrakibina* Morzadec, 2001 and *Asteropyge* Hawle & Corda, 1847 (node 22), glabellar furrows S1 are straight (39–1) and converge anteriorly (38–1).

New innovations appear with the clade *Morzadecops* and *Pennarbedops* (node 24): the origin of pygidial spines comes from anterior and posterior pleural bands (20–1) and the lateral border is undeveloped on the genal spine (66–0).

Several features are developed in the genus *Hollardops* (node 24) such as a strong enlargement of pleural furrows (10–2), L3 and L2 more elevated than L1 (46–1), and a more rounded frontal lobe (31–1).

The main innovations in *Pilletina* Haas, 1970 (node 29) concern the cephalon: L2 becomes longer (44–1), the anterior border of the eye is opposite the distal tip of S3 (50–0), and its posterior border is in contact with the posterior border furrow (52–0).

From the clade formed with *Treveropyge* and *Coltraneia* (node 29), S1 glabellar furrows become curved again (39–0)

and the proximal tip of S2 is more distal than S1–S3 (45–0).

A significant step in Asteropyginae evolution corresponds to the genera *Quadrops* Morzadec, 2001, *Saharops* Morzadec, 2001, *Walliserops* and *Psychopyge* (node 33) where pygidia and cephalia are affected by important changes. Posterior pleural bands of the pygidium become twice as wide as the anterior band of the posterior segment (7–0), pleural segments are twice larger distally (9–1) and pygidial spines only come from posterior pleural bands (20–2). Pygidial spines are longer (21–2), have a rounded section (27–1) and are as wide as the posterior pleural bands (24–0). Glabellar furrows are curved between S1 and S3 (36–2) and the lateral border is developed on genal spines (66–1), which have a square section (68–1).

The main changes occurring in *Comura* Richter & Richter, 1926 (node 36) are: an elevation of posterior pleural bands in comparison to the anterior band of the posterior segment (8–0), faintly incised pygidial pleural furrows (11–0), S2 anteriorly curved (41–0), and a subocular platform (48–0).

From the genus *Alcaldops* (node 37), modifications are: pygidial spines with different lengths (22–1) and loss of the contact between the distal tip of S2 and axial furrows (42–1).

Heliopyge Haas & Mensink, 1970 (node 41) presents modification of pygidial pleural bands which become bent (14–1) and pygidial spines which take their origin from both the anterior and posterior pleural bands (20–1).

Bradocryphaeus (node 42) has faintly incised interpleural furrows (10–0), pygidial spines with a reduced length (21–1), a greater width (24–1), and the proximal tip of S2 being aligned exsagittally with those of S1 and S3 (45–1).

The clade comprising *Neocalmonia* and *Radiopyge* (node 46) shows a slight distal increase of pygidial width segment (9–0) and pygidial spines become shorter (21–0). The number of pygidial spine pairs is six for *Radiopyge* (16–2; node 47) and four for *Neocalmonia* (16–1; node 48).

Morphological patterns

In order to characterize the morphological diversity within Asteropyginae, Struve (1959) proposed four pygidial patterns regrouped into both conservative (*prorotundifrons* and *boothi* patterns) and progressive types (*supradevonicus* and *cometa* patterns). These patterns were based on pleural bands, the furrow organization and their relation with pygidial spines. These groups were, for a long time, fundamental in the description of the subfamily in spite of some subsequent redefinitions (Haas 1970; Gandl 1972; Pillet 1972). New models were also added, as *mic helini* (Gandl 1972), *alcaldi* (Arbizu 1977) and *medusa* (Basse 2003) to complete the morphological variability of the group. The phylogenetic analysis of Lieberman & Kloc (1997) did not support the monophyly of these models and since this

work only few authors used these patterns to describe the Asteropyginae.

The present analysis confirms this conclusion; these patterns should not be used. The consensus tree supports only the *supradevonicus* pattern as corresponding to a monophyletic group, the three others being paraphyletic. Moreover, the conservative and progressive distinction is not maintained because only the second type is monophyletic.

Systematic palaeontology

Superfamily **Acastacea** Delo, 1935

Family **Acastidae** Delo, 1935

Subfamily **Acastavinae** Delo, 1935

Protacanthina Gandl, 1972

Type species. *Protacanthina vellilae* Gandl, 1972.

Additional species. *Protacanthina gandli* Morzadec, 1990; *P. robusticostata* Gandl, 1972; *P. sagittaeformis* Morzadec, 1976a.

Diagnosis. Frontal lobe diamond shaped; axial furrows straight between S1 and S3; eyes not in contact with posterior border furrow and S3 distal tip; L3 above L1 and L2; genal spine well separated from genal field. Eight to 12 pygidial axial rings; 5 to 7 pleural segments; pleural bands flat; anterior bands as wide as posteriors; pleural furrows wide; interpleural furrows well incised; 5 to 7 very small and narrow pygidial spine pairs originated from anterior and posterior pleural bands; wide and very long terminal spine closed to pygidial length.

Occurrence. *Protacanthina robusticostata* is the oldest species, occurring in the upper Lochkovian of Algeria, France and Spain. *Protacanthina* persists in the lower Pragian of France (Armorican Massif) and Smeenk (1983) identified two specimens in the middle Pragian of Spain.

Discussion. Several authors considered *Protacanthina* as the ancestor of *Gourdonia* Pillet, 1954 (Gandl 1972; Morzadec 1976a, 1983, 1990, 1994; Smeenk 1983). These genera share small palpebral lobes, numerous pygidial axial rings, numerous pygidial spines and pleurae (5–7), a very long terminal spine and very short pygidial spines. However, several characters make *Gourdonia* closer to *Destombesina*: axial furrows slightly curved forming an obtuse angle; longer genal, pygidial and terminal spines; pygidial spines originated from posterior and slightly anterior bands. Nevertheless, *Destombesina* differs from *Gourdonia* in having a small number of pygidial spines (4), pleural segments (4–5) and axial rings (6–7), and a slightly smaller terminal spine. The number of pygidial segments and axial rings seems not to be fixed in the first representa-

tives of Asteropyginae (characters 6 and 16). Consequently, *Destombesina* and *Gourdonia* seem to be more similar to each other than either is to *Protacanthina*.

For a long time, authors have assigned *Protacanthina* to Asteropyginae with doubt (Morzadec 1983; Smeenk 1983). In our cladistic analysis, *P. vellilae* was resolved a posteriori within the outgroup members. *Protacanthina* is consequently closer to Acastavinae than any Asteropyginae. Indeed as is likewise the case in Acastavinae, this genus has small palpebral lobes, a terminal pygidial spine much longer than other very reduced spines and developed from posterior pleural bands. Consequently, we do not consider *Protacanthina* as a member of the Asteropyginae.

Subfamily **Asteropyginae** Delo, 1935

Destombesina Morzadec, 1997

(Fig. 6A)

Type species. *Destombesina ougartensis* Morzadec, 1997.

Additional species. *Destombesina tafilaltensis* Morzadec, 2001.

Diagnosis. Frontal lobe diamond shaped; axial furrows straight between S1 and S3; L3 above L1 and L2; anteriormost portion of the palpebral lobe posterior to intersection of S3 and axial furrow, 4 lenses per dorsoventral file of visual surface; genal spines weak, shorter than glabella with a narrow proximal portion; lateral border rather large, undeveloped on genal spine. Pygidium with anterior pleural bands lower and narrower than posterior, flat pleural bands; axis with 6–7 rings, constricted between the 3rd and 4th rings; 4–5 pleural segments; 4 pairs of reduced pygidial spines, mainly developed from posterior pleural bands; terminal pygidial spine larger than axis, triangular, twice as long as other pygidial spines.

Occurrence. The two known species occur in the upper Emsian; *Destombesina ougartensis* comes from Algeria and *D. tafilaltensis* from Morocco.

Discussion. *Destombesina* seems closer to the Acastavinae than are other studied Asteropyginae. *Destombesina* resembles Acastavinae in having small palpebral lobes with few lenses per dorsoventral file, a slightly pointed anterior border, a wide lateral border, a weak genal spine, very small pygidial spines, and a very long terminal pygidial spine compared to other pygidial spines. However, *Destombesina* differs from Acastavinae in having pygidial spines that originate mostly from the posterior bands and only slightly from the anterior bands. This feature supports its attribution to the Asteropyginae.

Nevertheless, we cannot reject the assumption that very short or absent pygidial spines and the presence of a very long terminal pygidial spine in *Destombesina* could be diagnostic to discriminate Acastavinae from Asteropyginae. Indeed, such features are present in some Acastavinae such as *Acastella* Reed, 1925, *Mimocryphaeus* Gandl, 1972

and *Chimaerastella* Gandl, 1972. Bearing in mind this possibility, the assignment of *Destombesina* to Asteropyginae is not assured.

***Minicryphaeus* gen. nov.**
(Fig. 6B)

Type species. *Pseudocryphaeus minimus* Morzadec, 2001.

Additional species. *Minicryphaeus quaterspinosus* (Morzadec, 2001); *M. sarirus* (Morzadec, 2001).

Derivation of name. After the type species name.

Diagnosis. Cephalon may have a prefrontal spine; frontal lobe diamond shaped; axial furrows straight between S1 and S3; 5–8 lenses per dorsoventral file of visual surface; genal spine shorter than glabella with narrow proximal portion; narrow anterior border, lateral border very large, poorly developed on genal spine. Pygidium with anterior pleural bands as wide and elevated as posterior bands, flat pleural bands; axis with 7–10 rings; 5 pleural segments; 4 or 5 pairs of pygidial spines shorter than pleural width (tr.), mainly developed from posterior pleural bands; terminal pygidial spine slightly wider than axis, roughly triangular, twice as long as other pygidial spines.

Occurrence. The three species are restricted to Pragian of the Anti-Atlas (Morocco).

Discussion. Although originally described as *Pseudocryphaeus* (Morzadec 2001), the tree topology and the jackknife analysis (78%, Fig. 5) strongly support the splitting of these species in a new genus. *Minicryphaeus* presents affinities with *Pseudocryphaeus* in having axial furrows straight between S1 and S3, L2 and L3 with similar width, an angle of 30–39° formed by axial furrows, S2 distal tip not in contact with axial furrows, wide lateral borders, small eyes, anterior pleural bands as wide and elevated as the posterior bands, small pygidial spines and a longer terminal spine. However, the erection of this new genus is well sustained by several differences, such as more robust and slightly longer genal spines, a wider S1, wider posterior and anterior border, a more rounded anterior border, pygidial spines squeezed up against their neighbours, and a longer and triangular terminal pygidial spine.

Minicryphaeus has some morphological characters that are highly variable. For example, *Minicryphaeus minimus* has a strong prefrontal spine that is totally absent in *M. quaterspinosus* and *M. sarirus*. *Minicryphaeus quaterspinosus* has only 4 pairs of pygidial spines against 5 in the two other species. Presently, we consider this evolutionary ontogenetic change as a heterometry (*sensu* Webster & Zelditch 2005) where the number of pygidial spines changes from 5 to 4. Nevertheless, if a deceleration in the rate of ontogenetic changes within *M. quaterspinosus* could be demonstrated, that pattern would correspond to neoteny, as suggested by Morzadec (2001).

***Pseudocryphaeus* Pillet, 1954**
(Fig. 6C)

Type species. *Phacops michelini* Rouault, 1851.

Additional species. *Pseudocryphaeus occidentalis* Haas, 1970; *P. vernensis* Morzadec, 1971.

Diagnosis. Frontal lobe diamond shaped; axial furrow straight between S1 and S3, S2 and S3 wide; S2 transverse, without or with a light contact with axial furrows; axial furrows slightly curved between S2 and S3; 10 lenses per dorsoventral file of visual surface; genal spine shorter than glabella; anterior border narrow; lateral border very wide, poorly developed on genal spine. Pygidium with anterior pleural bands as wide and elevated as posterior bands, flat pleural bands; axis with 10–11 rings; 5 pleural segments; 5 pairs of pygidial spines shorter than pleural width (tr.), mainly developed from posterior pleural bands; terminal pygidial spine slightly larger than axis, pentagonal, slightly longer than other pygidial spines.

Occurrence. *Pseudocryphaeus michelini* and *P. vernensis* are restricted to the Pragian of France (Armorican Massif). *Pseudocryphaeus occidentalis* occurs in the lower Emsian of Spain (Asturias).

Discussion. Morzadec (1971) described 11 species attributed to the genus *Pseudocryphaeus*. From the present analysis, it appears that only the three species determined herein as *Pseudocryphaeus* belong to this genus. *Paracryphaeus jonesi* (Oehlert, 1877) and *Paracryphaeus izensis* (Morzadec, 1971) present an excessively long terminal spine, only 7 lenses in the dorsoventral files of the eyes, and a lateral border developed on the genal spine, characters that are incongruent with the diagnosis of *Pseudocryphaeus*. The other six species have pygidial spines originating from both anterior and posterior pleural bands and should not be assigned to this genus. Moreover ‘*Pseudocryphaeus*’ *astrictus* Gandl, 1972 and ‘*Pseudocryphaeus*?’ *demoulini* Smeenk, 1983 have a terminal pygidial spine that is too wide and pygidial spines too small to consider them as *Pseudocryphaeus*. Likewise, ‘*Pseudocryphaeus*’ *rothei* Haas, 1970 has an excessively wide terminal pygidial spine and pygidial spine tips too pointed to maintain this species in *Pseudocryphaeus*. *Pseudocryphaeus occidentalis* was assigned to *Paracryphaeus* by Smeenk (1983) because of its excessively long terminal spine. We do not agree with this proposition after examination of specimens. Moreover this terminal spine is pentagonal whereas it is triangular in *Paracryphaeus*.

In the present study, *Pseudocryphaeus* is close to the clade formed by *Greenops*, *Breizhops*, *Deloops* and *Stummiana* (node 10, Fig. 5) according to the number of pygidial axial rings, the pentagonal terminal pygidial spine and the axial furrows curved between S2 and S3. *Pseudocryphaeus* differs from this clade based on its more granulated pygidial

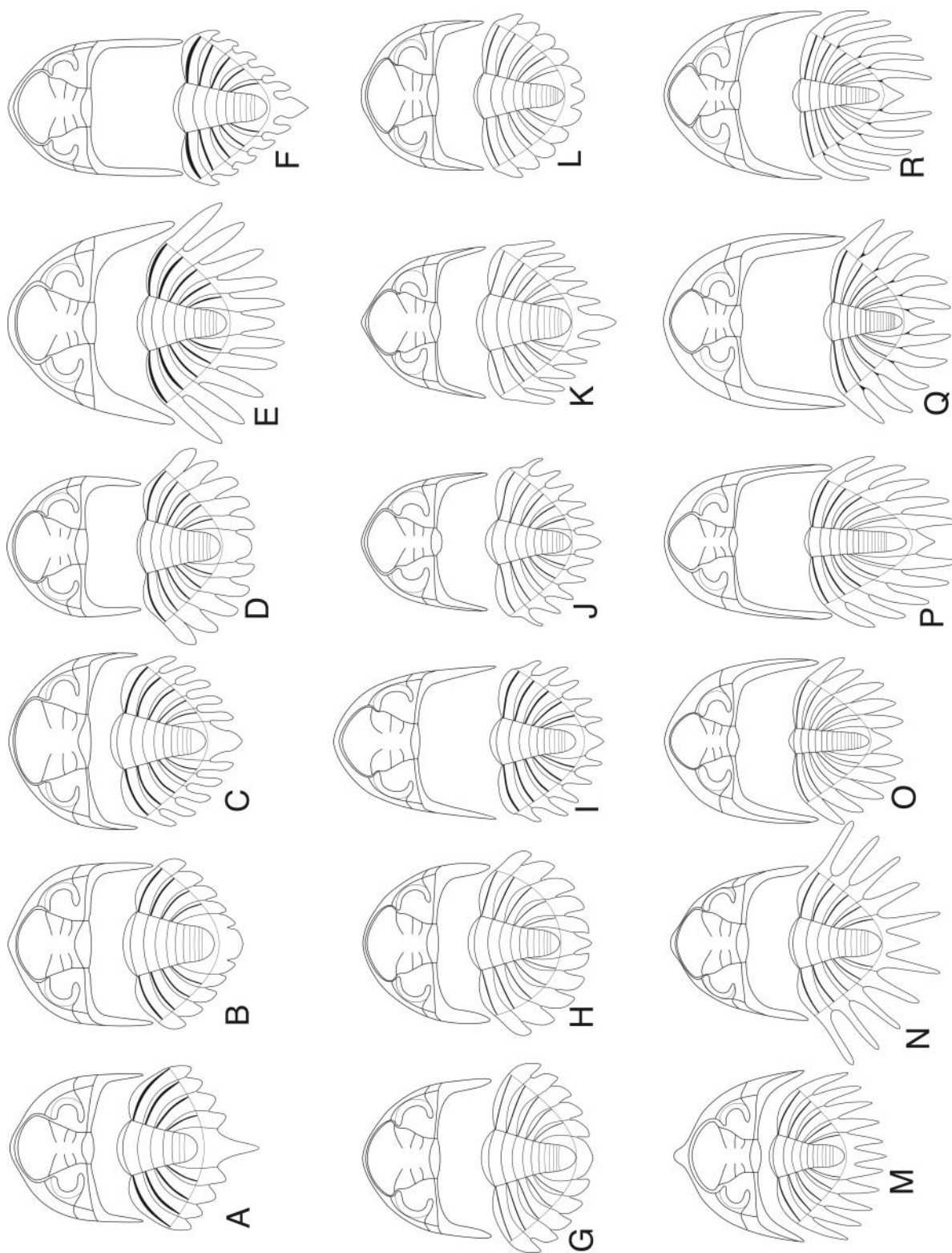


Figure 6. Line drawings of **A**, *Dextombesina*; **B**, *Minicryphaeus*; **C**, *Pseudocryphaeus*; **D**, *Greenops*; **E**, *Greenops* (*Neometacanthus*); **F**, *Breizhops*; **G**, *Deloops*; **H**, *Stummiana*; **I**, *Kayserops*; **J**, *Gandlops*; **K**, *Paracryphaeus*; **L**, *Rhenops*; **M**, *Braunops*; **N**, *Rheingoldium*; **O**, *Bellacartwrightia*; **P**, *Metacanthina*; **Q**, *Mrakibina*; **R**, *Asteropyge*;

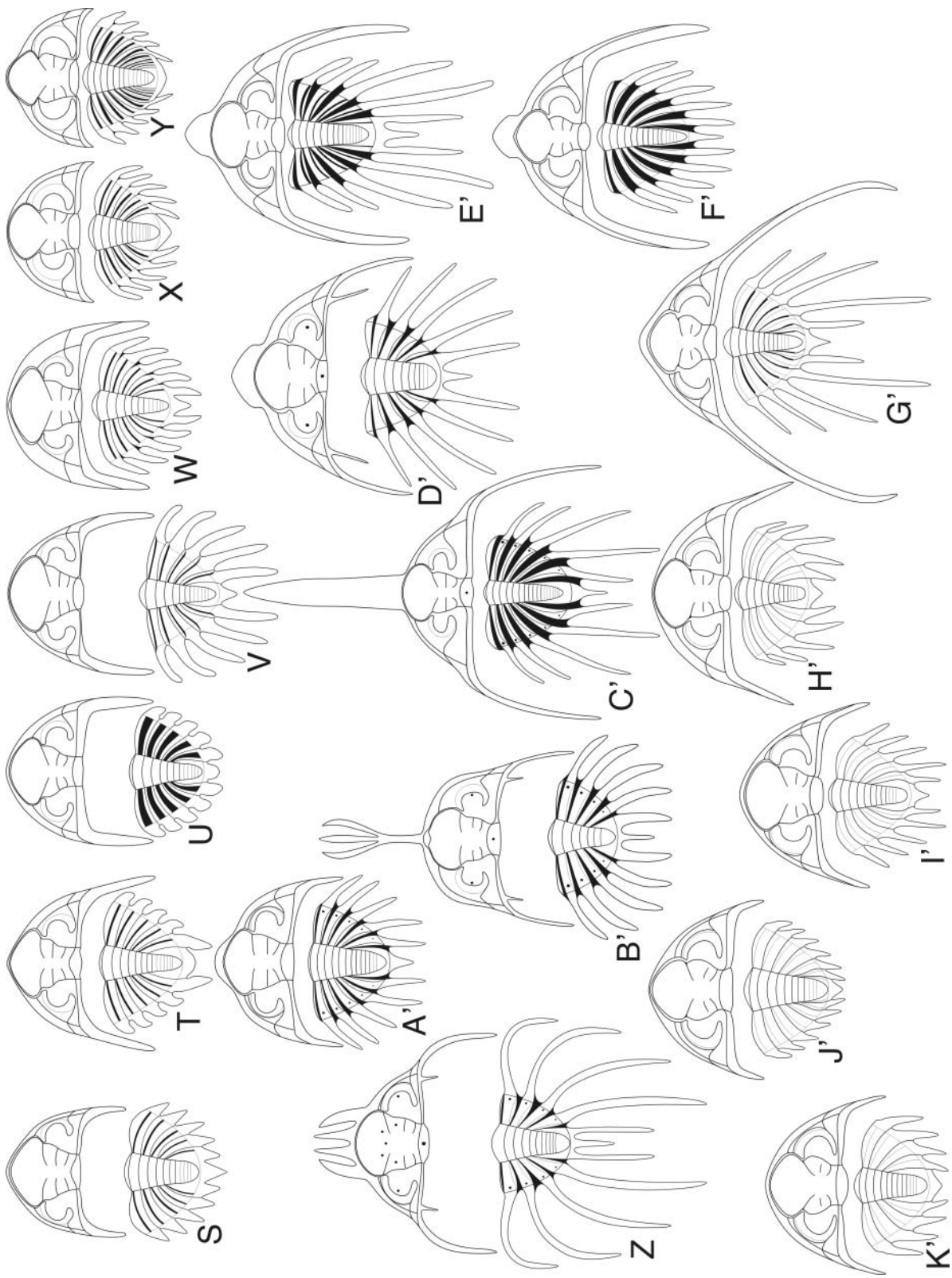


Figure 6. (Continued) *S*, *Morzedecops*; *T*, *Pennarbedops*; *U*, *Hollardops*; *V*, *Tolkienia*; *W*, *Pilletina*; *X*, *Treveropyge*; *Y*, *Coltranea*; *Z*, *Quadrops*; *A'*, *Saharops*; *B'*, *Walliserops*; *C'*, *Psychopyge*; *D'*, *Comura*; *E'*, *Alcaldops*; *F'*, *Hallandclarkeops*; *G'*, *Heliopyge*; *H'*, *Bradocryphaeus*; *I'*, *Jaylopygiella*; *J'*, *Radiopyge*; *K'*, *Neocalmonia*.

axis, the axial furrows that form a more acute angle (30–40°), the larger pygidial border furrow, and the slightly more developed lateral border on the genal spines.

Greenops Delo, 1935
(Fig. 6D)

Type species. *Cryphaeus boothi* Green, 1837.

Additional species. *Greenops barberi* Lieberman & Kloc, 1997; *G. chilmanae* Stumm, 1965; *G. grabau* Lieberman & Kloc, 1997; *G. (Neometacanthus) stellifer* Burmeister, 1843; *G. widderensis* Lieberman & Kloc, 1997.

Diagnosis. Frontal lobe diamond shaped; L3 wide (exsagittal, exsag.) compared to L2; tubercles variably present on L0; axial furrows curved between S2 and S3; S2 anteriorly converging; 4–7 lenses per dorsoventral file of visual surface; genal spine shorter or as long as glabella; very narrow anterior and lateral borders undeveloped on genal spine with a narrow proximal portion. Pygidial axis with 10–12 rings; 5 pleural segments, flat pleural bands; pleural furrows rather large; 5 pairs of pygidial spines mainly developed from posterior pleural bands, longer or as long as pleural width (tr.), with a sharp triangular tip; terminal spine not wider than axis, roughly pentagonal and slightly shorter than other pygidial spines.

Occurrence. All species assigned to *Greenops* are recorded in the Givetian of North America, except *G. (N.) stellifer* which occurs in the Eifelian of Germany.

Discussion. *Greenops* is included in a clade with *Breizhops*, *Deloops* and *Stummiana*. This group is based on the following synapomorphies: a pygidial constriction between the 5th and 6th ring, increased pygidial length compared to the width, a narrow pygidial axis compared to pleural width, the first glabellar furrow straight, a narrow posterior border furrow, and a lateral border undeveloped on genal spines. This clade does not differ that much from the clade defined by Lieberman & Kloc (1997) except that *Breizhops* and *Greenops (Neometacanthus)* were outside and *Kayserops* was included (*Armorigreenops* and *Kennacryphaeus* are not analysed herein). This group is based on an S3 straight and transverse or distally posteriorly oriented, a posteromedial impression rounded, a longer genal spine, and 11 rings in the pygidial axis. However the origin of Lieberman & Kloc's clade is associated with *Neometacanthus*, *Asteropyge* and *Rhenops* whereas in the present work it seems more closely related to *Pseudocryphaeus*.

The determination of *Greenops* as the sister group of the other members of this clade is very well supported, following the jackknife analysis (80%, Fig. 5) and from the following synapomorphies: a terminal spine shorter than other pygidial spines, longer pygidial spines, S1 straight, anterior and posterior tips of the eye on the same exsagittal line, anterior tip of eye opposite the intersection between

S3 and axial furrow, and the posterior border curved in the middle of the eye.

Greenops (Neometacanthus) Richter & Richter, 1948
(Fig. 6E)

Type species. *Phacops stellifer* Burmeister, 1843.

Additional species. None.

Diagnosis. S2 distal tips in contact with axial furrows; 4–5 lenses per dorsoventral file of visual surface; genal spine as long as glabella. Pygidial axis with 11 rings; 5 pleural segments; 5 pairs of pygidial spines longer than pleural width (tr.), with a sharp triangular tip; terminal spine narrower than axis, pentagonal.

Occurrence. *Greenops (Neometacanthus) stellifer* is known in the middle Eifelian of Germany.

Discussion. The status of *Greenops (Neometacanthus)* has been discussed for a long time. Haas (1970), Gandl (1972), Arbizu (1977), Smeenk (1983) and Morzadec (1983) all suggested that this group is a subgenus of *Greenops*. However the analysis of Lieberman & Kloc (1997) showed a clear phylogenetic distinction between *Greenops* and *Greenops (Neometacanthus)*. In the present work, the topology of our tree suggests that *Greenops (Neometacanthus)* should be considered a subgenus, as keeping both of these taxa at the generic level would make *Greenops* paraphyletic. Indeed, we found no significant morphological features that would separate *Greenops grabau* (the sister taxa of the subgenus; node 12, Fig. 5) from *Greenops* (the only way to maintain *Greenops (Neometacanthus)* at a generic level without making it paraphyletic). The integration of *Neometacanthus* in *Greenops* as a subgenus is supported by the following synapomorphies: a terminal spine that does not project further back than the 5th pygidial spine pair, straight S1, the anterior and posterior extremities of the palpebral lobes on the same exsagittal lines, the anteriormost points of the palpebral lobes opposite the intersection of S3 and the axial furrows. The species of the subgenus *Greenops (Greenops)* can be differentiated from *Greenops (Neometacanthus)* based on: eyes with 6–7 lens files, pygidial spines as long as the pleural segments, a terminal spine as wide as the axis with its pentagonal shape more defined.

Contrary to Lieberman & Kloc (1997), who considered *Neometacanthus* close to *Asteropyge*, in the present analysis these genera are distantly related. Indeed, *Asteropyge* has rounded pleural bands, a triangular terminal spine wider than the axis, an occipital ring not wider than L1, axial furrows forming a large angle (up to 40°), 6 to 9 lenses per dorsoventral file in the eye, an anterior tip of the palpebral lobe not in contact with the intersection of S3 and the axial furrow, genal spines as long as the glabella with the proximal part narrow and the lateral border strongly developed.

Basse (2003) proposed that *Greenops* (*Neometacanthus*) is monotypic, contrary to Lieberman & Kloc (1997) who suggested that several North American species may be assigned to that taxon. We follow Basse's proposal because these American specimens are too poorly preserved to defend their assignment. Smeenk (1983, pl. 27, fig. 2) assigned a specimen to *Greenops* (*Neometacanthus*) sp. This specimen has an excessively large and long terminal pygidial spine and pygidial spines too short to be assigned to this genus. According to Lieberman & Kloc (1997), it is difficult to assign formally '*Asteropyge* (*Neometacanthus*)' sp. *M. aff. aequituberculatus* to this genus. The pygidial spines appear too wide and too short in comparison to *N. stellifer*. Moreover the terminal spine of this species is much narrower than the posterior tip of the axis.

Breizhops Morzadec, 1983
(Fig. 6F)

Type species. *Breizhops lanceolatus* Morzadec, 1983.

Additional species. *Breizhops bigranulosus* Morzadec, 1983; *B. chaconae* (Arbizu, 1977); *B. hercyniae* (Gandl, 1972).

Diagnosis. Frontal lobe diamond shaped; axial furrows curved between S2 and S3; 4–7 lenses per dorsoventral file of visual surface; genal spines mostly longer than glabella with a narrow proximal portion; anterior border large; lateral border poorly developed on genal spines. Triangular pygidium; 9–10 axial rings; 5 pleural segments; flat pleural bands; 5 pairs of pygidial spines mainly developed from posterior pleural bands, shorter than pleural width (tr.); posterior border very large; terminal spine as wide as axis, sharply pentagonal, twice as long as other pygidial spines.

Occurrence. *Breizhops* occurs in the upper Emsian of France (Armorican Massif) and Spain (Cantabrian and Celtiberian Mountains).

Discussion. Morzadec (1983) reassigned *Breizhops hercyniae* (Gandl, 1972) to *Breizhops* whereas Lieberman & Kloc (1997) considered this species as *Paracryphaeus*. We agree with Morzadec on the basis of the wide L1, the wide anterior border forming an acute angle, the wide posterior border, and the long pentagonal terminal spine with its base slightly narrower than the spine body. Nevertheless, the genal spines are very short compared to other *Breizhops* species.

In our cladistic analysis, *Breizhops* was added a posteriori and forms a clade with the genera *Stummiana* and *Deloops* (node 13, Fig. 5). These genera are distinguished from *Greenops* by the following synapomorphies: a terminal spine projecting further back than the 5th pygidial spine pair, the anterior tip of palpebral lobes being more proximal than posterior tips and being posterior to the intersection of S3 with the axial furrows, and a posterior border curved opposite the most proximal point of the eye. However,

Breizhops differs from *Deloops* and *Stummiana* in having narrower and longer genal spines and its anterior border is more developed. The terminal spine of *Deloops* is wider than the pygidial axis and as long as other pygidial spines. *Stummiana* has also a short terminal spine but the pentagonal shape is not as well defined. Moreover, *Breizhops* has a strongly triangular pygidium.

Deloops Lieberman & Kloc, 1997
(Fig. 6G)

Type species. *Greenops haasi* Morzadec, 1983.

Additional species. None.

Diagnosis. Frontal lobe diamond shaped; axial furrows curved between S2 and S3; 7 lenses per dorsoventral file of visual surface; genal spines shorter than glabella with a narrow proximal part, very narrow lateral border undeveloped on genal spines. Eleven pygidial axial rings; 5 pleural segments; flat pleural bands; narrow pleural and interpleural furrows; 5 pairs of pygidial spines mainly developed from posterior pleural bands, shorter than pleural width (tr.), with extremity as sharp triangle; terminal spine wider than axis, sharply pentagonal and as long as other pygidial spines.

Occurrence. *Deloops haasi* comes from the upper Givetian of France (Armorican Massif).

Discussion. The present cladistic analysis places *Deloops* as the sister genus of *Stummiana*. Following the jackknife analysis, this clade is well supported (83%, Fig. 5). This relationship is based on the following synapomorphies: lightly incised pleural furrows, the anteriormost point of the posterior branch of the facial suture opposite L2, the junction of the facial suture and lateral border opposite L1, a horizontal lateral border, and a glabella with a similar length and width. *Deloops* can be differentiated from *Stummiana* by having its palpebral anterior tip extending back to the intersection between S3 and the axial furrow, a wider and pentagonal terminal spine, interpleural furrows more clearly incised, and pygidial spines shorter than the pleurae.

Stummiana Lieberman & Kloc, 1997
(Fig. 6H)

Type species. *Greenops arkonensis* Stumm, 1953.

Additional species. *Stummiana osismorum* (Morzadec, 1983); *S. perijaensis* (De Carvalho & Moody, 2000).

Diagnosis. Frontal lobe diamond shaped; axial furrows curved between S2 and S3; tubercle variably present on L0; 4–7 lenses per dorsoventral file of visual surface; genal spines shorter than glabella; narrow anterior and lateral borders undeveloped on genal spines with a narrow proximal portion. Ten to 12 pygidial axial rings; 5 pleural segments; flat pleural bands; pleural furrows rather narrow, and faint interpleural furrows; 5 pairs of pygidial spines,

mainly developed from posterior pleural bands, as long as pleural width (tr.), with tip as sharp triangle; terminal spine as wide as axis, roughly triangular and as long as other pygidial spines.

Occurrence. *Stummiana* occurs in the Givetian of North America and in the middle Givetian of France (Armorican Massif). *Stummiana perijaensis* is recorded in the Eifelian–Givetian of Venezuela (Perijá Mountains).

Discussion. *Stummiana osismorum* differs from *S. arkonensis* in having a slightly narrower cephalic border, no contact between S2 and the axial furrow, a frontal lobe slightly more developed laterally, more lenses in dorsoventral files (7 for *S. osismorum* and 4 for *S. arkonensis*), a pygidial outline that is less laterally developed and flatter pleurae. Within Asteropyginae, the contact between S2 and the axial furrow seems to be an effective feature to determine genera. However, in the present genus, this character is not paired with other important ones to justify such discrimination between these species.

De Carvalho & Moody (2000) described a poorly preserved species from Venezuela, *S. perijaensis*, that they considered a member of *Greenops*. We considered that this species does not belong to *Greenops* because the terminal pygidial spine is triangular and as long as the other pygidial spines, whereas it is pentagonal and shorter in *Greenops*. However, *S. perijaensis* is very close to the type species, the main differences being a frontal lobe closer to *S. osismorum*, the anterior and posterior tips of the eye aligned on the same extrasagittal line, and a narrower axis. These differences not being diagnostic, we attribute this species to *Stummiana*.

Lieberman & Kloc (1997) described a new species that they attributed to a new genus, *Armorigreenops*. The terminal spine being triangular and as long as the fifth spine pairs make this species, *A. leoi*, very close to *Stummiana*, and indeed these character states tempted us to regroup *A. leoi* with the genus *Stummiana*. However this species presents some characters which are not in accordance with this assignment, such as the anterior tip of the palpebral lobe being posterior to the intersection of S3 and the axial furrow, and the terminal spine being slightly wider than the posterior tip of the axis. For the present we follow Lieberman & Kloc's (1997) classification.

***Kayserops* Delo, 1935**
(Fig. 6I)

Type species. *Cryphaeus kochi* Kayser, 1883.

Additional species. *Kayserops daleidensis* Basse, 2003; *K. gahardensis* Morzadec, 1981; *K. heisdorfensis* Basse, 2003; *K. inflatus* Morzadec, 1983; *K. kerfornei* (Pichard, 1930); *K. pluton* Basse, 2003; *K. wetteldorfensis* Basse, 2003.

Diagnosis. Frontal lobe diamond shaped; axial furrows curved between S2 and S3; L3 inflated; medial spine on L0; 8–10 lenses per dorsoventral file of visual surface; genal spine as long as glabella, very narrow lateral border undeveloped on the genal spine with narrow proximal part. Nine to 12 pygidial axial rings; 5 pleural segments; rounded pleural bands; pleural furrows rather wide; 5 pairs of pygidial spines mainly developed from posterior pleural bands, shorter than pleural width (tr.); terminal spine triangular, as wide as axis and as long as other pygidial spines.

Occurrence. *Kayserops* occurs in the upper Emsian of Germany and France (Armorican Massif).

Discussion. *Kayserops* presents strong affinities with *Gandlops*, *Paracryphaeus* and *Rhenops* (Fig. 5). We enumerate the main differences between these genera to make their determination easier (Table 1). *Kayserops* differs from *Gandlops* in having L3 strongly inflated, longer genal and pygidial spines, and a slightly shorter terminal pygidial spine. Compared to *Paracryphaeus*, *Kayserops* has L3 strongly inflated, a narrow lateral border lightly developed on longer genal spines, shorter pygidial and terminal spines, a triangular terminal spine and narrower pleural furrows. *Kayserops* differs from *Rhenops* in having L3 strongly inflated, a narrow lateral border lightly developed on longer genal spines, a triangular terminal spine, and more pointed pygidial spine extremity.

Kayserops inflatus and *K. kerfornei* differ from the type species in having L3 more strongly inflated, which could be a diagnostic feature for a new genus. Nevertheless, these three species share a lateral border undeveloped on the genal spines, the same number of pygidial axial rings (10) and pygidial spines developed mainly from posterior pleural bands, suggesting a strong affinity.

As noticed by Morzadec (1983) and Lieberman & Kloc (1997), the morphology of *Kayserops kerfornei* is marginal within the genus. Indeed, the long prefrontal and occipital spines make its determination problematic. *Braunops obsoletus* (Gandl 1972) possesses such structures but not as well developed. These two species cannot be considered as congeneric because their genal spine differs both in length and width of the proximal border and in the development of the lateral border. Moreover, pygidial spines of *B. obsoletus* are longer than pleural width and the number of axial rings is greater compared to *K. kerfornei*.

Lieberman & Kloc (1997) considered *Greenops traversensis* Stumm, 1953 as an American representative of *Kayserops*. *Greenops traversensis* does not have the characteristic L3 strongly inflated of the genus *Kayserops*. Moreover, this species has large granules on the cephalon and axis, large pleural perforations, a maximum of only 7 lenses per dorsoventral file of the visual surface, genal spines shorter than glabellar length, pygidial spines longer than the pleurae, and a terminal spine shorter than the other pygidial spines.

Table 1. Main features of *Kayserops* Delo, 1935; *Gandlops* gen. nov.; *Rheingoldium* Basse, 2003; *Braunops* Lieberman & Kloc, 1997; *Paracryphaeus* Gandl, 1972; and *Rhenops* Richter & Richter, 1943

	<i>Kayserops</i>	<i>Gandlops</i>	<i>Rheingoldium</i>	<i>Braunops</i>	<i>Paracryphaeus</i>	<i>Rhenops</i>
L3 inflated	Yes	No	No	No	No	No
Genal spine compared to cephalic length (sag.)	As long	Shorter	As long	As long–shorter	Shorter	Shorter
Lateral border	Thin	Thin	Thin	Large	Large	Large
Lateral border developed on genal spines	Slightly	Strongly	Slightly	Strongly	Strongly	Strongly
Pleural furrows	Rather wide	Rather wide	Rather wide	Wide	Wide	Rather wide
Pygidial spines compared to pleural width (tr.)	Shorter	Much shorter	Slightly longer	Slightly longer	Equal	Shorter
Pygidial spines oriented	Mainly posteriorly	Mainly posteriorly	Aligned with pleural segments	Mainly posteriorly	Mainly posteriorly	Mainly posteriorly
Terminal spine length compared to other pygidial spines	Equal	Slightly longer	Shorter–longer	Slightly longer	Longer	Equal
Terminal spine shape	Triangular	Triangular	Triangular	Triangular	Pentagonal	Pentagonal

***Gandlops* gen. nov.**
(Fig. 6J)

Type species. *Kayserops brevispinosus* Gandl, 1972.

Additional species. *Gandlops ogivalis* (Morzadec, 1976b); *G. palenciae* (Smeenk, 1983); *G. tamnrherta* (Chatterton *et al.*, 2006).

Derivation of name. After Josef Gandl, the discoverer of the type species.

Diagnosis. Frontal lobe diamond shaped; axial furrows curved between S2 and S3; 6–10 lenses per dorsoventral file of visual surface; genal spine shorter than glabella; lateral border narrow and developed on genal spine. Eight to 11 pygidial axial rings without median tubercle; 5 pleural segments with pleural furrows rather wide, rounded pleural bands; 5 very small and narrow pairs of pygidial spines mainly developed from posterior pleural bands, separated from each other; triangular terminal spine as wide as axis and slightly longer than other pygidial spines.

Occurrence. *Gandlops ogivalis* occurs in the lower Emsian of France. *Gandlops brevispinosus* and *G. palenciae* from Spain occur in the upper Emsian as *G. tamnrherta* from Morocco.

Discussion. The most plausible synapomorphies sustaining the erection of this genus are the very small and separated pygidial spines associated with a narrow and triangular terminal spine that is slightly longer than the other spines.

Paracryphaeus differs from *Gandlops* with the following features: a short L1, a narrow lateral border, a pentagonal terminal pygidial spine, slightly longer pygidial spines with their tips bluntly triangular and less spaced between each other (Table 1).

The main features making *Rhenops* distinct from *Gandlops* are longer pygidial spines associated with a pentagonal shaped terminal pygidial spine and a larger cephalic lateral border lightly developed on genal spines (Table 1).

Gandlops palenciae was assigned with uncertainty to the genus *Delocare* Struve, 1958 in the original description and by Basse (2003). Unlike the species assigned to *Delocare*, which have pygidial spines longer than adjacent pleurae and the terminal spine shorter than other pygidial spines, *Gandlops palenciae* has very narrow terminal and pygidial spines, as in the type species *G. brevispinosus*.

Gandlops ogivalis has a terminal spine longer than the rather short and narrow pygidial spines. Nevertheless, these terminal and pygidial spines are slightly larger than in *G. brevispinosus* and *G. palenciae*. The narrow lateral border not strongly developed on the short genal spine confirms the assignment of *G. ogivalis* to the genus *Gandlops*.

Chatterton *et al.* (2006) placed *Gandlops tamnrherta* within *Kayserops* with difficulties. Indeed, its short pairs of pygidial spines and its long and triangular terminal spine are not characteristic of this genus. Instead, these features make them closer to the genus *Gandlops*.

Kayserops pluton has a similar pygidium to *Gandlops*: the pygidial spines are very short and the terminal spine is very narrow. Nevertheless, the terminal spine as long as other pygidial spines, the third occipital lobe inflated, and

the lateral border not developed on the genal spine confirm the assignment to the genus *Kayserops*.

***Paracryphaeus* Gandl, 1972**
(Fig. 6K)

Type species. *Cryphaeus jonesi* Oehlert, 1877.

Additional species. *Paracryphaeus izensis* (Morzadec, 1971); *P. alcoleae* Gandl, 1972.

Species doubtfully assigned. *Paracryphaeus? praejonesi* (Gandl, 1972).

Diagnosis. Frontal lobe diamond shaped; axial furrows curved between S2 and S3; 7 lenses per dorsoventral file of visual surface; wide cranial furrows; genal spine very short; wide lateral border, strongly developed on genal spine. Eleven pygidial axial rings; 5 pleural segments with wide pleural furrows, rounded pleural bands; 5 pairs of pygidial spines mainly developed from posterior pleural bands with a length close to the pleural width (tr.); terminal spine pentagonal, as wide as axis and longer than other pygidial spines.

Occurrence. *Paracryphaeus alcoleae* comes from basal Pragian of Spain (Celtiberian mountains). *Paracryphaeus izensis* and *P. jonesi* occur in the Pragian of France (Armorican Massif).

Discussion. *Paracryphaeus* is separated from *Rhenops* by a shorter (exsag.) L1, wider occipital furrows, shorter genal spines, a terminal spine longer than other pygidial spines, these spines being as long as the pleurae and their distal tips being more pointed (Table 1).

The cephalon of *Paracryphaeus izensis* is not presently known. However as already noticed by Morzadec (1971), this species presents strong affinities with *P. jonesi*, except for its smaller size and pygidial spines.

The cephalon of *Paracryphaeus alcoleae* is likewise unknown. Nevertheless, the species is close to the type species *P. jonesi*. The main differences are the wider pygidium and the more developed axial constriction in *P. alcoleae*.

Paracryphaeus? praejonesi is doubtfully placed within this genus due to the triangular terminal spine smaller than pygidial axis. Its cephalon is still unknown. However, this species has characteristic features of the genus such as large pleural furrows, pygidial spines as long as the pleural field, 11 axial rings and a terminal spine that is longer than the other pygidial spines. Its pairs of pygidial spines seem to be too small to assign this species to *Braunops*.

***Rhenops* Richter & Richter, 1943**
(Fig. 6L)

Type species. *Cryphaeus anserinus* Richter, 1916.

Additional species. *Rhenops australocustos* Basse *et al.*, 2006; *R. daleidianus* Basse, 2003; *R. lethaeae* (Kayser, 1889); *R. odremani* De Carvalho & Moody, 2000.

Species doubtfully assigned. *Rhenops? index* Richter & Richter, 1943; *R.? redonesianus* Morzadec, 1981.

Diagnosis. Frontal lobe diamond shaped; axial furrows curved between S2 and S3, S2 without or with poorly defined contact with axial furrows; 9–10 lenses per dorsoventral file of visual surface; genal spine shorter than glabellar length; lateral border wide, strongly developed on genal spine. Twelve to 13 pygidial axial rings; 5 pleural segments with narrow pleural furrows, rounded pleural bands; 5 pairs of pygidial spine mainly developed from posterior pleural bands, shorter than pleural width (tr.); terminal pygidial spine pentagonal, as wide as axis and either as long as other pygidial spines or shorter.

Occurrence. *Rhenops anserinus* and *R.? index* occur in the lower Emsian and *R. daleidianus* in the upper Emsian of Germany (Eifel). *Rhenops? redonesianus* and *R. lethaeae* occur in the upper Emsian of France (Armorican Massif) and the latter is also present in Spain (Aragon) and Germany (Eifel). *Rhenops australocustos* comes from the lower Emsian of Luxembourg. *Rhenops odremani* has been found in the Eifelian–Givetian of Venezuela (Perijá Mountains).

Discussion. *Rhenops? redonesianus* and *R.? index* are doubtfully assigned to this genus because the former has a slightly shorter terminal spine and the latter a slightly longer one compared to the other pygidial spines. No other feature of the pygidium allows the discrimination of these species from *Rhenops*. Moreover, the cephalon of *R.? redonesianus* and that of *R.? index* are presently poorly known (Basse 2003). Nevertheless, Morzadec (1981) stated that *R.? redonesianus* has genal spines longer than the thorax, which keeps the doubtful attribution of this species to *Rhenops*. More complete descriptions of their cephalon could solve their assignments.

Rhenops odremani is one of the rare Asteropyginae of the Malvinokaffric Realm (*sensu* Eldredge & Ormiston 1979). The material is not well preserved. Nevertheless, the main generic features are preserved, including a wide lateral border developed on a genal spine that is shorter than cephalon, and a terminal spine that seems pentagonal and close to the length of the other pygidial spines, which are shorter than the pleurae. De Carvalho & Moody (2000) reported that *R. odremani* lacks tubercles on the pygidial axis as in the type species, *R. anserinus*, and *R. daleidianus*.

For the morphological differentiation between *Rhenops*, *Kayserops*, *Gandlops*, *Rheingoldium* and *Paracryphaeus* see discussions of those genera and Table 1.

***Braunops* Lieberman & Kloc, 1997**
(Fig. 6M)

Type species. *Kayserops obsoletus* Gandl, 1972.

Additional species. *Braunops champagnensis* (Morzadec, 1971); *B. djazaïrensis* (Morzadec, 1997); *B. longispinosa* (Haas, 1970).

Diagnosis. Frontal lobe diamond shaped; axial furrows curved between S2 and S3; 5–8 lenses per dorsoventral file of visual surface; genal spine with a wide proximal part; large lateral border strongly developed on genal spine. Ten to 13 pygidial axial rings with median tubercle; 5 pleural segments with wide pleural furrows, rounded pleural bands; 5 pairs of pygidial spines mainly developed from posterior pleural bands, slightly longer than pleural width (tr.); triangular terminal spine as wide as axis and as long as other pygidial spines or slightly longer.

Occurrence. *Braunops champagnensis* occurs in the Pragian of France. *Braunops longispinosa* occurs in the lower Emsian of Germany and *B. djazaïrensis* in the upper Emsian of Algeria.

Discussion. Cephalo of *Braunops djazaïrensis* and *B. longispinosus* are not well known. However, Basse (2003) described several preserved individuals attributed to *Braunops?* sp. n. 1. These specimens have the diagnostic pygidial characters of *Braunops*, i.e. pairs of pygidial spines slightly longer than the pleural field and a terminal pygidial spine as long as the other spines. If this attribution is correct, it confirms the presence of a spine on the occipital ring and a wide lateral cephalic border that is well developed on the genal spine. However, it highlights intra-generic variation because the genal spine is more or less as long as the cephalon and no prefrontal projection is present, contrary to *B. obsoletus*.

Rheingoldium Basse, 2003
(Fig. 6N)

Type species. *Rheingoldium feldbergensis* Basse, 2003.

Additional species. *Rheingoldium marocanensis* (Morzadec, 2001).

Diagnosis. Frontal lobe diamond shaped; axial furrows curved between S2 and S3; 6–10 lenses per dorsoventral file of visual surface; genal spine as long as glabella; lateral border rather narrow and developed on genal spine. Eleven to 13 pygidial axial rings; 5 pleural segments, rounded pleural bands; pleural furrows rather wide; 5 pairs of pygidial spines mainly developed from posterior pleural bands, slightly longer than pleural width (tr.) aligned with corresponding pleural segments; triangular terminal spine as wide as axis.

Occurrence. The two species occur in the upper Emsian of Morocco (*Rheingoldium marocanensis*) and Germany (*R. feldbergensis*).

Discussion. The short terminal spine of *Rheingoldium feldbergensis* is strongly different to *R. marocanensis*, which is as long as the other pygidial spines. Nevertheless, these two species share diagnostic characters of the genus such as the orientation of pygidial spines where each spine is rather straight and has a completely different orien-

tation compared to adjacent spines. Conversely, the closely related *Kayserops*, *Paracryphaeus*, *Rhenops*, *Braunops* and *Gandlops* have pygidial spines mostly posteriorly oriented (Table 1).

In the consensus tree, the phylogenetic relationships are not resolved between the clades *Paracryphaeus*–*Rhenops*, *Rheingoldium* and *Braunops*. These taxa share several features such as: 10 to 13 pygidial axial rings, a transverse course of S2, contact of the facial suture with the lateral margin opposite L0, and a narrow anterior border. *Rheingoldium* and *Braunops* have pygidial spines slightly longer than pleurae, a pentagonal terminal spine, a tubercle on the occipital ring, a transverse course of S1 and the anterior curve of the posterior branch of the facial suture opposite L2. The clades *Paracryphaeus*–*Rhenops* and *Rheingoldium* share genal spines forming an angle of 0–15° with the exsagittal line and a wide glabella. Finally, the clades *Paracryphaeus*–*Rhenops* and *Braunops* have a wide posterior border, genal spines as long as the glabella, and a relatively narrow cephalon.

Bellacartwrightia Lieberman & Kloc, 1997
(Fig. 6O)

Type species. *Bellacartwrightia jennyae* Lieberman & Kloc, 1997.

Additional species. *Bellacartwrightia calderonae* Lieberman & Kloc, 1997, *B. calliteles* (Green, 1837), *B. phyllocaudata* Lieberman & Kloc, 1997, *B. pleione* (Hall, 1861) and *B. whiteleyi* Lieberman & Kloc, 1997.

Diagnosis. Frontal lobe diamond shaped; axial furrows curved between S2 and S3; 8–10 lenses per dorsoventral file of visual surface; anterior border as wide as lateral borders; no anterior extension; length of genal spine close to that of glabella; lateral border strongly developed on genal spine. Fourteen to 16 pygidial axial rings; 5 pleural segments with a posterior narrowing, rounded pleural bands; 5 pairs of pygidial spines mainly developed from posterior pleural bands; triangular terminal spine shorter than other pygidial spines and as wide as axis.

Occurrence. *Bellacartwrightia* is recorded in the Eastern North American Basin. Most species are dated from the middle Givetian except for *B. pleione*, from the Eifelian.

Discussion. According to Lieberman & Kloc (1997) the species of the genus *Bellacartwrightia* traditionally considered as *Greenops* (*Greenops*), sometimes as *Greenops* (*Neometacanthus*), could not be associated with these genera. *Greenops* (*Neometacanthus*) differs from *Bellacartwrightia* in the following: only up to 12 pygidial axial rings, a flat section of the pygidial pleural bands, a pentagonal terminal pygidial spine; occipital rings wider than L1, eyes having up to 6 lenses in a dorsoventral file; and a narrow proximal part of the genal spine. In addition to the characters mentioned for *Greenops* (*Neometacanthus*),

Greenops (*Greenops*) differs also from *Bellacartwrightia* in having very lightly incised pleural furrows, a terminal pygidial spine that projects backward as far as the fifth pygidial spine pair, and a S2 distal tip not in contact with the axial furrow.

However, contrary to Lieberman & Kloc (1997), the present cladistic analysis does not suggest a close relationship between *Bellacartwrightia* and *Hallandclarkeops*. Indeed, the latter genus could not be considered as the sister group of *Bellacartwrightia* because *Hallandclarkeops* has pygidial posterior bands twice as elevated and as wide as the anterior bands of posterior segments, wide pleural furrows, pygidial spines based on the pleural posterior band, a rounded frontal lobe, axial furrows curved between S1 and S3, L3 as elevated as L2, the eye resting on a narrow horizontal platform, and genal spine with a square section.

Metacanthina Pillet, 1954
(Fig. 6P)

Type species. *Cryphaeus barrandei* (De Tromelin & Lebesconte, 1876 emend. Oehlert, 1889).

Additional species. None.

Diagnosis. Frontal lobe diamond shaped; axial furrows curved between S2 and S3; wide occipital ring; genal spine longer than glabella; lateral border strongly developed on genal spine. Fifteen pygidial axial rings; 5 pleural segments with constant width, rounded pleural bands; 5 pairs of pygidial spines mainly developed from posterior pleural bands, as long as pleural width (tr.); triangular terminal spine shorter than other pygidial spines and wider than axis.

Occurrence. *Metacanthina barrandei* is only known from the lower Eifelian of France (Armorican Massif).

Discussion. Gandl (1972) assigned several species to *Metacanthina*. These morphologically related species are too distant from the type species, *M. barrandei*, to be considered as members of this genus. They have genal spines that are too short, pygidial spines developed from posterior and anterior pleural bands, a backward length reduction of pygidial pleurae, fewer pygidial axial rings and, in most of them, the terminal pygidial spine is as long as or longer than the other pygidial spines. Thus, at present *M. barrandei* is the only representative of this genus.

Metacanthina barrandei shares a constant width of pleurae with *Hallandclarkeops cantarmorica* (Morzadec & Arbizu 1978). Nevertheless, this particularity has no phylogenetic significance because these species are too distantly related (Fig. 4). Indeed, *Hallandclarkeops* has a rounded frontal lobe, axial furrows curved between S1 and S3, L2 as elevated as L3, posterior pygidial pleural bands twice as wide and as elevated as the anterior bands, and pygidial spines developed almost completely from the posterior pleural bands.

Basse (2003, pl. 2, fig. 40) reported a poorly preserved pygidium attributed doubtfully to *Metacanthina*. The pygidial spines seem to originate from both the anterior and posterior pleural bands of the segments. Moreover, the terminal spine is too wide and too long to attribute this species to *Metacanthina*.

Mrakibina Morzadec, 2001
(Fig. 6Q)

Type species. *Mrakibina cattoi* Morzadec, 2001.

Additional species. None.

Diagnosis. Frontal lobe diamond shaped; axial furrows curved between S2 and S3; narrow palpebral lobe (tr.) allowing important development of lateral border; 7 lenses per dorsoventral file of visual surface; smooth occipital ring; genal spine longer than glabella; lateral border strongly developed on genal spine. Fifteen pygidial axial rings without median tubercle; 5 pleural segments, rounded pleural bands; 5 pairs of pygidial spines mainly developed from posterior pleural bands, slightly longer than pleural width (tr.); terminal spine shorter than other pygidial spines.

Occurrence. This genus is only known from the lower Eifelian of Morocco (Anti-Atlas).

Discussion. In our cladistic analysis *Mrakibina* is positioned as the sister group of *Asteropyge*. These two genera share a diamond shaped frontal lobe, axial furrows curved between S2 and S3, long genal spines, a wide anterior border, curved pygidial spines mainly developed from posterior pleural bands and longer than pleural width, and a terminal spine shorter than the adjacent pygidial spines. *Mrakibina* differs from *Asteropyge* in having shorter eyes and a wider lateral border, slightly shorter and wider genal and pygidial spines, and a narrower terminal spine.

As already noticed by Morzadec (2001), *Mrakibina* is very close to the North American genus *Bellacartwrightia*. *Bellacartwrightia* has more developed eyes and a narrower lateral border that does not extend as far on the genal spine as in *Mrakibina*. *Mrakibina cattoi* has longer pygidial spines, pleural field not perforated, and no median tubercle or spine on the pygidial rings.

Asteropyge Hawle & Corda, 1847
(Fig. 6R)

Type species. *Olenus punctatus* Steininger, 1831.

Additional species. *Asteropyge lauchensis* Basse, 2003; *A. perforata olpensis* (Basse, 2003); *A. perforata perforata* Morzadec, 2003; *A. plana* Basse, 2003; *A. pruemensis* Basse, 2003; *A. remscheidensis* Basse, 2003; *A. schoeneckenensis* Basse, 2003.

Diagnosis. Frontal lobe diamond shaped; axial furrows curved between S2 and S3; large anterior border; 6–9 lenses per dorsoventral file of visual surface; genal spine

longer than glabella; lateral border developed on the genal spine. Twelve to 14 pygidial axial rings; 5 pleural segments mainly developed from posterior pleural bands with a slight decrease of the posterior width (tr.); 5 pairs of pygidial spines, usually granulated, longer than pleural width (tr.), with approximately the same length except the 5th which may be shorter; wide terminal pygidial spine.

Occurrence. All species occur in the lower and middle Eifelian of Germany (Eifel district) except the subspecies *Asteropyge perforata perforata* which is present in the upper Emsian of France (Armorican Massif).

Discussion. *Asteropyge* shares with *Greenops* and *Bellacartwrightia* the characteristic pronounced perforations of the pleural field as well as a diamond-shaped frontal lobe, axial furrows curved between S2 and S3, and pygidial spines mainly developed from the posterior pleural bands. However, *Asteropyge* shares more features with *Bellacartwrightia*. Indeed, only slight differences allow their discrimination: *Bellacartwrightia* has wider genal spines that could be as long as the glabella, wider pygidial spines with their length close to pleural width, a terminal spine usually narrow, and few perforations could be present on the pygidial pleural field. *Asteropyge* can be more easily distinguished from *Greenops* because this genus has: very small genal and pygidial spines, a narrow anterior border, eyes less developed, a lateral border not developed on the genal spine, a pygidial axis with 11 rings, the width of pleural segments strongly reduced posteriorly, and a narrow terminal spine.

Lieberman & Kloc (1997) considered '*Asteropyge* (*Neometacanthus*)' *czarnockii* Kielan, 1954 as a member of *Asteropyge*. We do not agree with this proposal because this species presents features different from diagnostic ones: a maximum of 5 lenses per dorsoventral file of the visual surface, genal spines shorter than the glabella, a reduced anterior border, only 8–9 pygidial axial rings, a noticeable posterior reduction of pleural segment width, pygidial spines with significant size variations, and an unperforated pleural field. Nor does this species seem to belong to *Greenops* (*Neometacanthus*) because its terminal pygidial spine is not pentagonal and is too short. The swollen L3 is suggestive of *Kayserops*, but in this genus the lens number is greater, the pygidial spines are shorter and the terminal spine is as long as the other spines. Unfortunately, due to the poor preservation, it is difficult to give a precise generic determination of this species.

***Morzadecops* gen. nov.**
(Fig. 6S)

Type species. *Pillettina zguidensis* Morzadec, 2001.

Additional species. *Morzadecops aequisulcata matutina* (Gandl, 1972).

Derivation of name. In honour of Pierre Morzadec for his great contributions on Asteropyginae.

Diagnosis. Frontal lobe diamond shaped; axial furrows curved between S2 and S3; L3 more elevated than L1 and L2; 8 lenses per dorsoventral file of visual surface; genal spine shorter than glabella, without development of lateral border. Ten to 11 pygidial axial rings; 5 pleural segments, rounded pleural bands; pleural furrows rather large; 5 pairs of pygidial spines developed from posterior and anterior pleural bands with a similar length, shorter or as long as pleural width (tr.); terminal spine as wide as axial extremity and as long as other pygidial spines.

Occurrence. *Morzadecops zguidensis* is recorded in the lower Emsian of Morocco and *M. matutina* in the middle Pragian of Spain.

Discussion. In our cladistic analysis, *Morzadecops* gen. nov. has been resolved as the sister group of *Pennarbedops* gen. nov. and this clade is reasonably well supported according to the jackknife analysis (65%, Fig. 5). They share a diamond-shaped frontal lobe, axial furrows curved between S2 and S3, and pygidial spines mainly developed from posterior pleural bands. They also share anteriorly divergent axial furrows posterior to S1, a posterior border twice as narrow as L0, and genal spines with a narrow proximal side. *Pennarbedops* differs from *Morzadecops* in having a greater number of pygidial axial rings (14–15), longer pygidial spines, a wider and shorter terminal spine, a length of pleural segments slightly decreasing posteriorly, a wider cephalon, genal spines longer than glabellar length, and axial furrows forming a more acute angle.

Morzadecops zguidensis was previously attributed to the genus *Pillettina* (Morzadec 2001). These genera share a constant length of pairs of pygidial spines, a backward decrease of pleural segment width (tr.), a triangular terminal spine and short pygidial spines. However, *Pillettina* differs in having more than five pleural segments, a terminal spine wider than the axis with more pygidial axial rings (12–15) and without median tubercles, a wider pygidium and cephalon compared to their length, a lateral border running onto a genal spine that is longer than the glabella, and the presence of a prefrontal projection.

The other species included in this new genus is *Morzadecops matutina*. Unfortunately, the cephalon of this species is not yet known, but their pygidia share the same number of pleural segments (5) and axial rings (11), the width of the terminal spine and the wide pygidial shape.

***Pennarbedops* gen. nov.**
(Fig. 6T)

Type species. *Rhenops babini* Morzadec, 1983.

Additional species. *Pennarbedops circumapodemus* (Smeenk, 1983).

Derivation of name. After Penn ar Bed, Breton name of the Finistère department, the type locality of the type species.

Diagnosis. Frontal lobe diamond shaped; axial furrows curved between S2 and S3, forming anteriorly a 30–40° angle; L3 more elevated than L1 and L2; 9 lenses per dorsoventral file of visual surface; genal spine as long as glabella. Fourteen to 15 pygidial axial rings without median tubercle; 5 pleural segments with a slight posterior width (tr.) decrease, rounded pleural bands, pleural furrows rather wide; 5 pairs of pygidial spines developed from posterior and anterior pleural bands, shorter than pleural width (tr.), longer posteriorly, with the 5th twice as long as other pairs; terminal spine wide and short.

Occurrence. *Pennarbedops* occurs in the upper Emsian of France (Armorican Massif) and Spain (Cantabrian Mountains).

Discussion. The two species belonging to *Pennarbedops* gen. nov. were previously assigned to *Rhenops*. These genera differ in their pygidial configurations. *Rhenops* has 12–14 pygidial rings, pygidial spines mainly developed from posterior pleural bands, pygidial spines with a similar length, a terminal spine more or less as long as other pygidial spines and its width is roughly equivalent to the axis. *Rhenops* differs also in the cephalic configuration: the posterior extremity of the palpebral lobe is more laterally displaced than the anterior extremity but is aligned (exsag.) with the distal extremity of the frontal lobe.

Pennarbedops babini differs from the other species, *P. circumapodemus*, in having a significant length increase from the first to the fifth pairs of pygidial spines, and posterior pleural bands have the same width and level as anterior bands. In *P. circumapodemus*, the length increase between the first and the fourth pairs of pygidial spines is more restricted and the posterior pleural bands are slightly higher and wider than the anterior pleural bands.

Hollardops Morzadec, 1997
(Fig. 6U)

Type species. *Asteropyge mesocristata* Le Maître, 1952.

Additional species. *Hollardops aithassainorum* Chatterton *et al.*, 2006; *H. boudibensis* Morzadec, 2001; *H. burtandmimiae* (Lieberman & Kloc, 1997); *H. lemaitreae* Morzadec, 1997; *H. struvei* (Morzadec, 1969).

Diagnosis. Frontal lobe rounded; axial furrows curved between S2 and S3; L2 and L3 more elevated than L1; 6–11 lenses per dorsoventral file of visual surface; genal spine as long as glabella, anterior tip of palpebral lobe posterior to intersection of axial furrows and S3. Thorax with 10 segments. Ten to 16 pygidial axial rings; 5 pleural segments, rounded pleural bands; very wide pleural furrows; 5 pairs of pygidial spines developed from posterior and anterior pleu-

ral bands, shorter than pleural width (tr.); terminal medial spine shorter than adjacent pygidial spines, wider than axis.

Occurrence. *Hollardops* is mostly represented in North Africa (two species in Algeria and four in Morocco). One species, *Hollardops struvei*, has been recognized in France (Armorican Massif). Most species occur in the upper Emsian except *H. aithassainorum* in the Eifelian and *H. burtandmimiae* in the upper Emsian and Eifelian.

Discussion. In the original diagnosis of the genus, Morzadec (1997) considered this genus to belong to the *boothi* pygidial pattern as defined by Struve (1959). This pattern was related to pygidia with flat pleural bands, faint interpleural furrows, and spines mainly developed from the posterior pleural bands. We do not agree with this description because in *Hollardops* the pleural bands are rounded, interpleural furrows are deep, and spine pairs are equally developed from the posterior and anterior pleural bands.

Lieberman & Kloc (1997) placed *Hollardops struvei* in their new monotypic genus *Modellops*. However, Morzadec (2001) considered this genus to be a junior subjective synonym of *Hollardops*. The tree topology of this work does not favour either of these assumptions but we are inclined to agree with the synonymy. Indeed, the exclusion of *H. struvei* is supported by only three unstable characters: the terminal pygidial ring well differentiated from the posterior border, the occipital ring lacking a medial spine, and a wider glabella compared to its length. After re-examination of the characters used in the cladistic analysis of Lieberman & Kloc (1997), they do not appear satisfactorily to support a differentiation between *Hollardops* and *Modellops*. Re-examined specimens share a palpebral lobe posterior to the intersection between S3 and axial furrow, an anterior cephalic border forming an approximately 140° angle, tubercles on L3 and L2, pygidial rings with an anterior margin anteriorly curved before the constriction, a pygidial pleural field prominently excavated flanking posterior part of pygidial axis, very wide (exsag.) pleural furrows, and an axis with 11–16 axial rings. The discriminating features are the slope of the librigena under the eyes and the anterior margin shape of the pygidial rings, which show too much intraspecific variability to justify the differentiation of *H. struvei* into a genus other than *Hollardops*.

Tolkienia Lieberman & Kloc, 1997
(Fig. 6V)

Type species. *Comura (Comura) granulispina* Morzadec, 1983.

Additional species. *Tolkienia cancer* Morzadec, 1983; *T. nova* Arbizu, 1977; *T. wiltzense* (Basse, 2003).

Diagnosis. Frontal lobe rounded; axial furrows curved between S2 and S3; anterior tip of palpebral lobe posterior to intersection of axial furrows and S3; genal spine as

long as glabella. Ten to 14 pygidial axial rings; 5 pleural segments, rather wide and long pleural furrows, rounded pleural bands; 5 pairs of pygidial spines, developed from posterior and anterior pleural bands, longer than pleural width (tr.); terminal pygidial spine twice as narrow as 5th pair of pygidial spines, slightly wider than axis.

Occurrence. *Tolkienia* has been recorded from France (Armorican massif), Germany (Eifel) and Spain (Cantabrian Mountains), from the upper Emsian to the lower Eifelian.

Discussion. Lieberman & Kloc (1997) suggested a close phylogenetic relationship between *Tolkienia* and *Comura*, based on long, rounded section and curved pygidial spines, a narrow and tear-drop shaped terminal spine, and posterior pleural bands wider and higher than the anterior bands. Unfortunately, they could not test this assumption in their analysis. In our cladistic analysis, these genera appear clearly distinct, sharing features with numerous other Asteropyginae taxa such as S2 anteriorly curved, axial furrows forming anteriorly a 30–40° angle, and the palpebral lobe in contact with the posterior border. These authors were probably misled by the long (tr.) pleural furrows suggesting no connection of spines with the anterior pleural bands as in pygidia of *Comura*. However, some specimens of *Tolkienia* bear the connection between anterior pleural bands and pygidial spines. For example, this is obvious in the original description of the type species, *T. granulispina* (Morzadec 1983, pl. 21, figs 3a, 4). Moreover, several cephalic features also support a distinct phylogenetic position. Indeed, *Tolkienia* differs from *Comura* in having no precephalic projection, a third glabellar lobe higher than the first two lobes, axial furrows curved only between S3 and S2, and an anterior edge of the palpebral lobe posterior to the intersection between S3 and the axial furrows.

Tolkienia wiltzense was doubtfully placed in this genus by Basse (2003). Nevertheless, this species presents the diagnostic characters of *Tolkienia*: axial furrows curved between S2 and S3, L3 above L1 and L2, pygidial spines developed from anterior and posterior pleural bands, pairs of long pygidial spines and long pleural furrows. Consequently, we confirm Basse's assignment and retain this species in *Tolkienia*.

Considering *Greenops* sp. A Stumm, 1953, Lieberman & Kloc (1997) identified this poorly preserved specimen as a member of *Tolkienia*. We did not have the opportunity to check if this pygidium collected from the Givetian of Michigan (USA) belongs to this genus.

Pilletina Haas, 1970

(Fig. 6W)

Type species. *Asteropyge* (*Metacanthina*) *oehlerti praecursor* Pillet, 1958.

Additional species. *Pilletina andegevensis* (Pillet, 1950); *P. oehlerti* (Pillet, 1958).

Species doubtfully assigned. *Pilletina? aequisulcata aequisulcata* (Gandl, 1972); *P? aequisulcata matutina* (Gandl, 1972); *P? aulnensis* Morzadec, 1976b; *P? luxembourgensis* Basse *et al.*, 2006; *P? oeslingiana* Basse & Franke, 2006.

Diagnosis. Frontal lobe rounded; axial furrows curved between S2 and S3; L3 and L2 more elevated than L1; anteriormost portion of palpebral lobe opposite the intersection of S3 with axial furrows, posteriormost portion not in contact with posterior border furrows. Twelve to 13 pygidial axial rings; 6 pleural segments, large pleural furrows, rounded pleural bands; 5 pygidial spine pairs developed from posterior and anterior pleural bands, slightly shorter than pleural width (tr.); terminal pygidial spine triangular, slightly shorter than 5th pygidial spine pair, slightly wider than axis.

Occurrence. Except for *Pilletina? luxembourgensis* and *P? oeslingiana* from Luxembourg and *P? aequisulcata aequisulcata*, *P? aequisulcata matutina* from Spain, all species come from France (Armorican Massif). *Pilletina praecursor* is doubtfully dated from middle Pragian–lower Emsian. *Pilletina andegavensis* and *P? aequisulcata aequisulcata* occur in the upper Pragian, *P? aequisulcata matutina* in the middle Pragian and the other species in the lower Emsian.

Discussion. *Pilletina? luxembourgensis*, *P? oeslingiana*, *P? aequisulcata* and *P? aulnensis* are doubtfully placed within *Pilletina* because they differ from the type species *P. praecursor* in sharing interpleural furrows with a distal widening and a terminal spine that is slightly pentagonal. These species may constitute a new genus.

Haas (1968) described several species from Turkey, *Metacanthina asiatica* (de Verneuil, 1867), *M. anatolica* Haas, 1968 and *M. incisa* Haas, 1968, reattributed later in *Pilletina* (Haas, 1970). We do not agree to place these species within *Metacanthina* (see above discussion about *Metacanthina*), but nor do we agree to place them in *Pilletina*. Indeed, these species have a pentagonal terminal spine, a very deep interpleural furrow distally, a pygidial shape wider anteriorly, and pygidial spines narrower than the pleurae. These features make them too different to be included in *Pilletina*. However, the interpleural furrows and the terminal spine make them close to the species doubtfully placed herein in *Pilletina*. We can reject the assumption that the doubtfully attributed *Pilletina* are closer to the Turkish species than other species included in *Pilletina*. A detailed study must be performed on these taxa to solve this question.

Pilletina appears to have a close relationship with a clade comprising *Treveropyge* and *Coltraneia*. These taxa share more than 6 pleurae in the pygidium, L2 and L3 with a

similar width, anterior and posterior extremities of the eye on the same exsagittal line, an anterior extremity of eye opposite the intersection with S3 and axial furrow, a posterior extremity of the eye in contact with the posterior border furrow, and a posterior border twice as narrow as the occipital ring.

Treveropyge Struve, 1958
(Fig. 6X)

Type species. *Asteropyge (Asteropyge) prorotundifrons* Richter & Richter, 1943.

Additional species. *Treveropyge aranea* Haas, 1970; *T. hattalensis* Basse, 2003; *T. kassandra* Basse, 2003; *T. rotundifrons* (Emmrich, 1839); *T. wiltziana* Basse, 2003.

Diagnosis. Frontal lobe rounded; axial furrows curved between S2 and S3; L3 and L2 more elevated than L1; large eyes, anteriormost portion of palpebral lobe opposite intersection of S3 with axial furrows, posterior portion contacts posterior border furrow, with 8–12 lenses in a dorsoventral file on visual surface; anterior border flat, without anterior spine. Twelve to 13 pygidial axial rings, axial constriction between 4th and 5th rings; 6 pleural segments, rounded pleural bands; 5 pairs of pygidial spines, developed from posterior and anterior pleural bands, as long as pleural width (tr.); wide (tr.); triangular terminal medial spine at least twice as short as other pygidial spines.

Occurrence. The genus occurred in Germany (Eifel) from lower to upper Emsian. *Treveropyge hattalensis* is perhaps present until the lower Eifelian.

Discussion. *Treveropyge* is traditionally interpreted as one of the most ancestral Asteropyginae (Haas 1970; Gandl 1972; Arbizu 1977; Morzadec 1983; Smeenk 1983; Lieberman & Kloc 1997). In our cladistic analysis, this genus is determined a posteriori as deeply nested within the group. This interpretation is supported by axial furrows curved between S2 and S3, L2 and L3 above L1, the anterior tip of the eye opposite the intersection of the axial furrows and S3, and pygidial spines developed from anterior and posterior pleural bands, all of which are characteristic derived features within the Asteropyginae.

Dunopyge Struve in Becker & Jansen 1998, not included in our analysis, is a genus close to *Treveropyge*, sharing axial furrows curved between S2 and S3, L3 and L2 above L1, and pygidial spines originating from anterior and posterior pleural bands. *Dunopyge* can be differentiated by the small precephalic spine, smaller eyes, and the narrow terminal pygidial spine. Thus, from these features, *Dunopyge lebanzaensis* (Smeenk 1983), originally described in *Treveropyge*, could not be considered as a member of this genus.

Several species described previously in the genus *Treveropyge*, in spite of being close to this genus, can no longer be considered to be members of this genus,

such as '*Treveropyge?*' *hunsrueckensis* Basse, 2003 and '*T.*' *maura* Morzadec, 2002, which have excessively short eyes (exsag.) and too many segments in the pygidium. '*Treveropyge?*' *procerospinosa* Gandl, 1972 has a long terminal pygidial spine and too many pygidial segments. '*Treveropyge?*' *marokkensis* Schraut, 2000 has small eyes, pygidial spines longer than pleural segments and a terminal spine too narrow and as long as the other pygidial spines.

Coltraneia Lieberman & Kloc, 1997
(Fig. 6Y)

Type species. *Treveropyge celtica* Morzadec, 1969.

Additional species. *Coltraneia effelesa* Chatterton *et al.*, 2006; *C. henryi* (Smeenk, 1983); *C. leunissen* Basse, 2003; *C. oufatenensis* Morzadec, 2001; *C. saourensis* (Morzadec, 1997).

Diagnosis. Frontal lobe rounded; axial furrows curved between S2 and S3; L3 and L2 more elevated than L1; large eyes, anteriormost portion of palpebral lobe opposite intersection of S3 with axial furrows, posterior portion in contact with posterior border furrow, 13–14 lenses per dorsoventral file of visual surface; anterior border arched. Thirteen to 15 pygidial axial rings, axial constriction between 6th and 7th rings; 8–11 pleural segments; 5 pairs of pygidial spines developed from anterior and posterior pleural bands, shorter than pleural width (tr.); wide (tr.); short (sagittal, sag.) terminal medial spine.

Occurrence. *Coltraneia* occurs in the upper Emsian (until lower Eifelian for *C. henryi*) of France (Armorican Massif), Germany (Eifel), Spain (Cantabrian Mountains), Algeria (Ougarta) and Morocco (Anti-Atlas).

Discussion. *Coltraneia* and *Treveropyge* are resolved as sister groups in our cladistic analysis, as is well supported by the jackknife analysis (81%, Fig. 5). They share large eyes, L2 and L3 above L1, axial furrows curved between S2 and S3, and the pygidial spines originating from anterior and posterior pleural bands. *Treveropyge* differs from *Coltraneia* in having eyes not as developed in length and width, an anterior border not arched, a lesser number of pygidial axial rings and pleural segments, and a narrower (tr.) and longer (sag.) terminal pygidial spine.

At a macroevolutionary scale, these genera appear to show a complex pattern of evolutionary mode of ontogenetic modifications (Webster & Zelditch 2005). The supernumerary pygidial axial rings and pleural segments in *Coltraneia* represent either a heterometry compared to *Treveropyge* or an increase of the rate modification occurring in the development of *Coltraneia*. The size difference between the eyes of these genera could correspond to an ontogenetic change too. Such a size difference seems to correspond to an allometric repatterning or a rate

modification pattern, but only a detailed ontogenetic analysis could confirm these assumptions.

***Quadrops* Morzadec, 2001**
(Fig. 6Z)

Type species. *Quadrops flexuosa* Morzadec, 2001.

Additional species. None.

Diagnosis. Frontal lobe rounded; four rather long separate precephalic projections; axial furrows curved between S1 and S3, no contact between S2 and axial furrows; L3 and L2 more elevated than L1; no contact between palpebral lobe and posterior border furrow, maximum of 11 lenses per dorsoventral file of visual surface; subocular platform present; genal spines as long as glabella; long spine on occipital ring; metafixigenal, palpebral and glabellar spines present. Eleven pygidial axial rings with spines; 5 pleural segments with length (tr.) decreasing posteriorly, rounded pleural bands, pleural furrows moderately wide; interpleural furrows clearly incised; 5 pairs of pygidial spines only developed from posterior pleural bands, strongly curved, longer than pleural width (tr.).

Occurrence. Morzadec (2001) assigned a late Emsian age to the Moroccan *Quadrops flexuosa*, but B.D.E. Chatterton (pers. comm.) suggests an occurrence only in the early Eifelian.

Discussion. Although *Quadrops* and *Walliserops* share palpebral and metafixigenal spines, the phylogenetic analysis does not group these genera as sister taxa. The other synapomorphies shared are a genal spine size close to the glabella length and eyes posterior to the junction of the axial furrow and S3.

Phylogenetic relationships are not resolved between the clades *Quadrops*–*Saharops* and *Walliserops*–*Psychopyge* (node 33, Fig. 5), although the four projections of the anterior border of *Quadrops* suggest a close relationship with *Walliserops*. Indeed, the trident of *Walliserops* could be very long as for *W. trifurcatus* but some other species have a strongly reduced trident shaft (*W. tridens* and *W. hammii*), close to the three separate projections as found in *Quadrops*. The discovery of new species or the precise description of the ontogeny of this structure could bring new information on the relationship of these genera. Thus, understanding if the trident was derived from the four projections could help us to understand the role of this unusual structure (Morzadec 2001; Chatterton *et al.* 2006; Chatterton & Gibb 2010). This trident could correspond to the exaptation (Gould & Vrba 1982) of a former structure in *Quadrops*.

***Saharops* Morzadec, 2001**
(Fig. 6A')

Type species. *Saharops bensaidi* Morzadec, 2001.

Additional species. None.

Diagnosis. Frontal lobe rounded; large and very short precephalic projection; axial furrows curved between S1 and S3, contact of S2 with axial furrows; L3 and L2 more elevated than L1; 11 lenses per dorsoventral file of visual surface; genal spines shorter than glabella, contact between posteriormost portion of palpebral lobe and posterior border furrow; subocular platform present; tubercle on occipital ring. Thirteen pygidial axial rings with tubercle; 5 pleural segments with length (tr.) decreasing posteriorly, rounded pleural bands, tubercle on the distal part of each posterior band; pleural furrows moderately wide; interpleural furrows clearly incised; 5 pairs of pygidial spines, only developed from posterior pleural bands, slightly longer than pleural width (tr.).

Occurrence. *Saharops bensaidi* occurs in the upper Emsian of Morocco.

Discussion. Phylogenetic relationships are not resolved between *Quadrops* and *Saharops* and the clade formed by *Walliserops* and *Psychopyge*. *Quadrops* and *Walliserops* appear, at first sight, closely related because of characteristic features such as cephalic spines, anterior projections and metafixigenal spines. However, detailed examination of all the apomorphic characters shared by these different genera explains the relationships found herein.

Saharops and *Quadrops* share the following synapomorphies: moderately incised interpleural furrows, S1 straight, S2 not in contact with axial furrows, a large angle formed by axial furrows, and eyes resting on a narrow horizontal platform.

Saharops and the clade formed by *Walliserops* and *Psychopyge* share only two synapomorphies: a larger pygidium and a frontal lobe less laterally displaced than the posterior tip of the palpebral lobe.

Finally, *Quadrops* and the clade *Walliserops*–*Psychopyge* have the following common synapomorphies: narrow pygidial spines, the anteriormost portion of the facial suture posterior branch opposite L2, contact of lateral margin and the facial suture opposite L1, a long anterior extension of the cranium, a genal spine as long as the glabella, and a narrow cephalon.

***Walliserops* Morzadec, 2001**
(Fig. 6B')

Type species. *Walliserops trifurcatus* Morzadec, 2001.

Additional species. *Walliserops hammii* Chatterton *et al.*, 2006; *W. lindoei* Chatterton & Gibb, 2010; *W. tridens* Chatterton *et al.*, 2006.

Diagnosis. Frontal lobe rounded; long, trident-shaped precephalic projection; axial furrows curved between S1 and S3, contact of S2 with axial furrows; L3 more elevated than L2 and L1; 9 lenses per dorsoventral file of visual surface, no contact between posteriormost portion of palpebral lobe and posterior border furrow, no subocular platform; genal spines as long as glabella; long spine on

occipital ring; metafixigenal and palpebral spines present. Six to 7 pygidial axial rings with long spines; 5 pleural segments with length (tr.) decreasing posteriorly, rounded pleural bands; vertical spines on the distal part of each posterior band; 5 pairs of pygidial spines only developed from posterior pleural bands, slightly longer than pleural width (tr.).

Occurrence. *Walliserops* occurs in the upper Emsian of Morocco. Chatterton *et al.* (2006) mentioned the possibility of an early Eifelian age.

Discussion. Chatterton *et al.* (2006) suggested that *Walliserops* is closer to *Comura* than *Psychopyge*. This assumption is not in agreement with our cladistic analysis, in which *Walliserops* is the sister group of *Psychopyge*, supported by the following synapomorphies (jackknife, 57%, node 34; Fig. 5): a short pygidial axis, an acute angle formed by the axial furrows, L2 and L3 width rather close, absence of a vertical wall under the eyes, anteriormost portion of the facial suture posterior branch reaching a transversal line passing through L2, and curve of the cranial posterior border more distal than eye. Potential synapomorphies shared between *Walliserops* and *Comura* are fewer: metafixigenal and palpebral spines, genal spines as long as glabellar length, rather short pygidial spines, and faint interpleural furrows.

Psychopyge Termier & Termier, 1950
(Fig. 6C')

Type species. *Psychopyge elegans* Termier & Termier, 1950.

Additional species. *Psychopyge hammerorum* Chatterton *et al.*, 2006; *P. praestans* Morzadec, 2001; *P. psyche* Basse, 2003; *P. termierorum* Morzadec, 2001.

Diagnosis. Frontal lobe rounded; long sword-shaped precephalic projection; axial furrows curved between S1 and S3, contact of S2 with axial furrows; 9–10 lenses per dorsoventral file of visual surface, no contact between posteriormost portion of palpebral lobe and posterior border furrow, no subocular platform; genal spine longer than glabella; long spine on occipital ring; no metafixigenal spines. Eighteen to 21 pygidial axial rings with median long spines; 5–6 pleural segments with length (tr.) increasing posteriorly, rounded pleural bands, interpleural furrows clearly incised; vertical spines on the distal part of each posterior band; 5 pairs of pygidial spines only developed from posterior pleural bands, longer than pleural width (tr.).

Occurrence. *Psychopyge* occurs mostly in the upper Emsian of Morocco and Germany.

Discussion. Morzadec (1988b) placed *Comura kervezensis* Morzadec, 1983 within the genus *Psychopyge*, due to spines on the axial rings and distal extremities of pleural segments. Nevertheless, this species appears not to belong

to *Psychopyge* because of the pleural segments decreasing in width (tr.) posteriorly, pleural furrows too narrow and pygidial spines too short. Unfortunately, the cephalon of this species is still unknown, preventing a reliable assignment. The shape of the pygidium, size of the spines, the pleural furrows and the number of pygidial axial rings suggest that this species is closer to *Comura*.

Psychopyge psyche from German Eifel (Basse 2003) differs from Moroccan species with no vertical spine on the distal part of pleural segments.

Comura Richter & Richter, 1926
(Fig. 6D')

Type species. *Cryphaeus cometa* Richter, 1909.

Additional species. *Comura bultyncki* Morzadec, 2001; *C. defensor* Richter & Richter, 1952; *C. echinata* Morzadec, 1983; *C. joaquinii* Richter & Richter, 1952; *C. kervezensis* Morzadec, 1983; *C. tuberculata* Morzadec, 1969; *C. philonyx* (Richter & Richter, 1952).

Species doubtfully assigned to the genus. *Comura? eos* Haas, 1970; *C.? inermis* Haas, 1970.

Diagnosis. Frontal lobe rounded; short precephalic projection; axial furrows curved between S1 and S3, contact of S2 with axial furrows, S2 straight; 11–12 lenses in a dorsoventral file on visual surface, subocular platform absent or roughly designed; genal spine longer than glabella; metafixigenal spines present; posteriormost portion of palpebral lobe in contact with posterior border furrow. Seven to 13 pygidial axial rings, 5–6 pleural segments, only developed from posterior pleural bands, length (tr.) decreasing posteriorly; 5 pairs of pygidial spines, longer than pleural width (tr.).

Occurrence. *Comura* occurs in upper Eifelian of Germany (Eifel), France (Armorican Massif), Spain and Morocco. *Comura philonyx* and *C.? inermis* occur in the lower Eifelian of Germany.

Discussion. The type species *Comura cometa* is only partially known from the cephalon while *C. kervezensis*, *C. joaquinii*, *C.? eos* and *C.? inermis* have no described cephalon. This imperfect knowledge of cephalic characters leads to an incomplete diagnosis.

Otherwise, some features are here proposed to distinguish *Comura* from other genera sharing pygidial spines only developed from posterior pleural bands. *Psychopyge* has the length (tr.) of pleural segments decreasing posteriorly and longer pygidial spines. *Quadrops* has longer and curved pygidial spines. *Walliserops* has pygidial spines with the same length as the pleural width (tr.) and vertical spines present on the distal part of posterior bands (as in *Psychopyge* and *Quadrops*). Pleural furrows of *Saharops* are narrow (tr.) compared with those of *Comura*. The posterior medial spine of *Delocare* Struve, 1958 (not included

in our cladistic analysis) is more triangular and pygidial spines are shorter than in *Comura*.

Philonyx was erected by Richter & Richter (1952) from some incomplete cephalae. Haas (1970) considered *Comura philonyx* to be a junior synonym of *C. defensor*. This attribution was accepted by Arbizu (1977) and Morzadec (1983). However, according to Basse (2003), *C. philonyx* is not closer to *C. defensor* or any particular *Comura* species. Indeed, the cephalae of *C. cometa* and *C. defensor* and the pygidia of *C. philonyx* are insufficiently known to determine whether or not these species are synonyms and if they belong to different genera. However, Jell & Adrain (2003) and Chatterton *et al.* (2006) considered *Philonyx* as a valid genus without giving arguments to support this proposition. In the present state of knowledge, we agree with Basse's (2003) assumption.

Comura? inermis is included with uncertainty in *Comura* because of pygidial spines as long as pleural width. Only the discovery of cephalae could confirm this assignment.

Morzadec (2001) suggested that *Comura echinata* may belong to the genus *Quadrops*. Their pygidia are indeed very similar, but without the discovery of better preserved cephalae it is difficult to propose a definite generic attribution. However, the 5th spine pair is not significantly shorter than the 4th as in *Q. flexuosa*. Consequently, we maintain this species in *Comura* awaiting a better description of its cephalon.

Alcaldops Arbizu, 1977
(Fig. 6E')

Type species. *Alcaldops alcaldei* Arbizu, 1977.

Additional species. *Alcaldops camfroutensis* (Morzadec, 1983); *A. troaonensis* (Morzadec, 1983); *A. renaudae* (Morzadec, 1969).

Species doubtfully assigned to the genus. *Alcaldops? argovejensis* Smeenk, 1983.

Diagnosis. Frontal lobe rounded; short precephalic projection; axial furrows curved between S1 and S3, no contact of S2 with axial furrows; S2 proximal tip more distal than S1 and S3 proximal tip; 6–10 lenses per dorsoventral file of visual surface, posteriormost portion of palpebral lobe in contact with posterior border furrow; subocular platform present; genal spine longer than glabella. Twelve to 16 pygidial axial rings; 5 pleural segments with long fenestrae, rounded pleural bands; 5 pairs of pygidial spines only developed from posterior pleural bands, longer than pleural width (tr.).

Occurrence. *Alcaldops* is recorded in the Eifelian of France (Brittany) and Spain (Leon). Arbizu (1977) gave a possible Givetian age for the type species *A. alcaldei*.

Discussion. Arbizu (1977) differentiated *Alcaldops* from *Heliopyge* according to the separation of anterior and poste-

rior bands along the pleural width because *Heliopyge* has anterior and posterior bands connected in the distal part just before the beginning of pygidial spines. However, Morzadec (1983) considered this difference insignificant and placed *Alcaldops* in junior synonymy of *Heliopyge*. He was probably misled by Armorican species that he considered as *Heliopyge*. The cladistic analysis clearly separates these species from *H. helios* and they instead appeared close to *A. alcaldei* in sharing pygidial spines only linked with posterior pleural bands.

Following the phylogenetic pattern (Fig. 4), *Alcaldops* is paraphyletic. We propose a definition of this genus unsupported by the tree because this topology seems to be due to intrageneric variation. The differences between the species of this genus come from characters not considered as diagnostic. Indeed, all these species share S2 not contacting the axial furrow, rounded pygidial pleural bands, fenestrae, long pygidial spines of different lengths and only connected to the posterior pleural bands, allowing them to be grouped into the same genus.

According to Smeenk (1983), *Alcaldops? argovejensis* may be included with uncertainty in *Alcaldops*. Indeed, this species shares several diagnostic features of *Hallandclarkeops*, such as a constant and rather short length of pygidial spines. Nevertheless, the large fenestrae, S2 not in contact with the axial furrows, and a posterior decrease in pleural width make this species closer to *Alcaldops*. *Alcaldops? argovejensis* constitutes an intermediate form between *Alcaldops* and *Hallandclarkeops*.

Hallandclarkeops Lieberman & Kloc, 1997
(Fig. 6F')

Type species. *Kayserops? cantarmoricus* Morzadec & Arbizu, 1978.

Additional species. None.

Diagnosis. Frontal lobe rounded; short precephalic projection; axial furrows curved between S1 and S3, contact of S2 with axial furrows; S2 proximal tip on the same exsagittal line as S1 and S3 proximal tip; 9 lenses per dorsoventral file of visual surface, posteriormost portion of palpebral lobe in contact with posterior border furrow; subocular platform present; genal spine longer than glabella. Fifteen axial pygidial rings; 5–6 pleural segments, with the same length (tr.), rounded pleural bands; 5 pairs of pygidial spines with equal length, only developed from posterior pleural bands, as long as pleural width (tr.); narrow terminal spine.

Occurrence. *Hallandclarkeops cantarmorica* occurs in the Eifelian of France (Armorican Massif) and Spain (Cantabrian Mountains and Aragon).

Discussion. Lieberman & Kloc (1997) originally included *Alcaldops renaudae*, *Alcaldops troaonensis* and '*Asteropyge? quelernensis*' Morzadec, 1983 in *Hallandclarkeops*. Although these species are closely related to

H. cantarmoricus, they differ in having no contact of S2 with the axial furrows, no constant width (tr.) of pleural segments, and in the length of pygidial spines. Moreover, '*Asteropyge*' *quelernensis* has bent pleural bands and pygidial spines developed from anterior and posterior pleural bands. *A. renaudae* and *A. troaoensis* have large fenestrae, absent in *H. cantarmoricus*.

Lieberman & Kloc (1997) placed *Hallandclarkeops* as the sister group to *Bellacartwrightia*. The present analysis disagrees with this proposition because these genera have different pygidial and cephalic organization. Axial furrows are curved between S2 and S3 in *Bellacartwrightia*, the frontal lobe is diamond shaped, the subocular platform is absent, eyes are narrower, and the genal spines are shorter and have a rectangular section. Moreover, the pygidia of this genus have the ancestral characters corresponding to pygidial spines developed mainly from posterior pleural bands, pleural and interpleural furrows more incised, and anterior and posterior bands of the same width (exsag.). However, these two genera share a constant length of pygidial spines but this feature is a symplesiomorphy.

Heliopyge Haas & Mensink, 1970
(Fig. 6G')

Type species. *Asteropyge* (*Comura*) *helios* Richter & Richter, 1926.

Additional species. None.

Diagnosis. Frontal lobe rounded; short precephalic projection; axial furrows curved between S1 and S3, S2 not in contact with axial furrows; subocular platform present; genal spine twice as long as glabella. Twelve pygidial axial rings; 6 pleural segments, posteriorly shorter (tr.), bent pleural bands; 5 pairs of very long pygidial spines, mainly developed from the posterior pleural bands, longer posteriorly except the 5th twice as short as the 4th; rather wide terminal spine.

Occurrence. *Heliopyge helios* is endemic to the middle Frasnian of Belgium (Ardenne Massif).

Discussion. According to Van Viersen & Prescher (2007), Lieberman & Kloc (1997) should not have restricted the genus *Heliopyge* to species having the third pygidial spine projecting further posteriorly because the type species, *H. helios*, has the fourth pygidial spine projecting further posteriorly.

Several species were previously assigned to *Heliopyge*. From our cladistic analysis, it appears that they belong either to *Alcaldops* or *Bradocryphaeus* (see discussion of these genera for more details). Consequently, this genus is restricted to the type species *H. helios*.

In spite of differences in fundamental characters, such as the pygidial spine origin, *Heliopyge* appears closely related to *Hallandclarkeops* in the cladistic analysis. This relationship is based on the number of pleural segments (6), curved pygidial and genal spines, wide pleural furrows, and the

anterior tip of the palpebral lobe more proximal than the posterior.

Morzadec (1983) reported *Heliopyge* n. sp. aff. *helios* (Richter & Richter, 1926) in the lower Frasnian of the Armorican Massif (France). This material is too badly preserved to determine the pygidial pattern and a generic determination cannot be reliably proposed.

Bradocryphaeus Haas & Mensink, 1970
(Fig. 6H')

Type species. *Cryphaeus supradevonicus* Frech, 1888.

Additional species. *Bradocryphaeus afghanica* Haas & Mensink, 1970; *B. asturica* (Haas, 1970); *B. briceae* (Morzadec, 1988a); *B. caelata* (Haas & Mensink, 1970); *B. coallajuensis* (Arbizu, 1977); *B. feisti* Morzadec, 1992; *B. fiacrensis* Morzadec, 1976b; *B. hispanica* (Richter & Richter, 1926); *B. iberica* (Haas, 1970); *B. kermanensis* Morzadec in Morzadec *et al.*, 2002; *B. maillieuxi* (Richter & Richter, 1926); *B. mariamae* (Farsan, 1981); *B. mosana* (Richter & Richter, 1926); *B. nasocostata* (Paeckelmann, 1913); *B. neptuni* Van Viersen & Bignon, 2011; *B. nodosa* (Morzadec, 1983); *B. porsguenensis* (Morzadec, 1983); *B. psilus* Haas, 1970; *B. quadratispinosa* (Gandl, 1972); *B. sharudensis* Pillet in Brice *et al.*, 1973; *B. turolensis* Gandl, 1972; *B. vanherlei* Van Viersen & Bignon, 2011; *B. zornensis* (Morzadec, 1983).

Species doubtfully assigned to the genus. *Bradocryphaeus? pentacosta* (Farsan, 1981).

Diagnosis. Frontal lobe rounded; no precephalic projection; S2 proximal tip on the same exsagittal line as S1 and S3 proximal tip; axial furrows forming an angle of mostly 40–50°, curved between S1 and S3; 5–8 lenses per dorsoventral file on visual surface; subocular platform present; genal spine equal to glabellar length or slightly longer. Elliptical pygidium; maximal pygidial width (tr.) greater than axial length (sag.); 9–13 axial rings; 5–6 pleural segments, width (exsag.) increases strongly distally, bent pleural segments; 5 pairs of pygidial spines mainly developed from the posterior pleural bands, with length rather close to pleurae width (tr.); narrow terminal spine; small fenestrae may be present.

Occurrence. *Bradocryphaeus* occurs in the Givetian of France (Armorican massif), Spain (Cantabrian Mountains), eastern Iran and western Afghanistan (6 species), and in the Frasnian of France (Armorican massif and Boulonnais), Belgium (Ardenne massif), Germany (Eifel), Spain (Cantabrian Mountains) and eastern Iran (18 species).

Discussion. Considering the results of our cladistic analysis, *Bradocryphaeus* appears paraphyletic (Fig. 4). However, most of the characters discriminating its constituent lineages seem to be particular to a species and/or correspond to slight differences in quantitative features. Thus, the numerous species included in this genus

constitute a homogeneous group based on common glabellar and pygidial organization, with five pairs of rather small and wide pygidial spines.

Bradocryphaeus was defined originally as a subgenus of *Neocalmonia* (Haas & Mensink 1970). The original and short diagnosis, referring to “a subgenus of *Neocalmonia* with narrow interpleural furrows without fenestrae and five pygidial spine pairs”, has produced much confusion between *Bradocryphaeus* and *Heliopyge*. Indeed, the presence/absence of fenestrae was a diagnostic character to discriminate these genera. This diagnosis assigns specimens to *Heliopyge* even if fenestrae were very small. The type species *H. helios* has large fenestrae developed on the entire width (tr.) of the pleural field and pygidial spines twice as long as pleural width. All other species described as *Heliopyge* (except the species attributed to *Alcaldops* in this paper) do not have such large fenestrae and pygidial spines, and their size is not as important. The cephalon of *H. helios* was known only from a juvenile and incomplete specimen figured in the original description. Recently, Van Viersen & Bignon (2011) described new and more complete cephalons of this species. This species has very long genal spines reaching the pygidium, a large angle between the genal spines and an exsagittal line, a slight forward expansion of the precephalic field, and S2 proximal tips more distal than S1 and S3 proximal tips. These new cephalic features differentiate *Heliopyge* from *Bradocryphaeus* and consequently their associated pygidia. Thus, it appears that in *Bradocryphaeus* pygidia the presence of small fenestrae is possible.

In addition of the original diagnosis of *Bradocryphaeus* (Haas & Mensink 1970), Lieberman & Kloc (1997) provided several diagnostic characters, restricting *Bradocryphaeus* to the type species *B. supradevonicus* and *B. afghanica*. These authors claimed that the third pair of pygidial spines projects furthest posteriorly. However, *B. supradevonicus* has the fourth pair of pygidial spines projecting furthest posteriorly. The other diagnostic features are: a prominent axis constriction between the fifth and sixth rings, a narrow pygidial terminal spine, a fifth pair of pygidial spines merging with pygidial axis, S3 straight, S2 anteriorly curved, and rounded posteromedian impressions. Nevertheless, these features are present in other *Bradocryphaeus* species and thus could not be considered as diagnostic.

Gandl (1972) erected the subgenus *Neocalmonia* (*Quadratispina*), grouping mainly species with keeled pygidial spines. Arbizu (1977) rejected this subgenus on the assumption that this keel is only a diagnostic character at a specific level. Lieberman & Kloc (1997) validated this genus based upon the pygidial axis being constricted between the sixth and the seventh rings, a narrow terminal spine, and the third spine pair projected further posteriorly and parallel to the axis. Several species bear one or several of these features. For example, *B. hispanicus*, included previously in *Quadratispina* (Gandl 1972), has its pygidial

axis constricted between the fifth and the sixth rings. Moreover, the long third spine pair could not be considered as a diagnostic character because as for *B. turolensis* this feature presents intraspecific variation (Gandl 1972, pl. 14, figs 7, 8). *Bradocryphaeus quadrispinosa*, *B. hispanica* and *B. asturica*, previously attributed to *Quadratispina*, share median tubercles on pygidial axial rings. We consider that this feature has only a specific importance. This assumption is supported in our cladistic analysis: *B. hispanicus* is well integrated within *Bradocryphaeus*.

Van Viersen & Bignon (2011) explained the problem of the badly preserved type specimen of *B. mosanus*. Without redescription of material coming from the type locality, comparisons with this species are difficult. *Bradocryphaeus* sp. cf. *mosanus* is attributed to specimens from Hotton (Belgium) mentioned by Asselbergs (1912) as *Cryphaeus valleeanus*. This material is close to *B. mosanus* but presently it is not possible to compare them.

Complementary information about *Bradocryphaeus afghanica* and *B. sharudensis* is presented under discussion of *Neocalmonia*.

Jaylopygiella Basse, 2003

(Fig. 6I')

Type species. *Jaylopygiella medusa* Basse, 2003.

Additional species. *Jaylopygiella circe* Basse, 2003; *J. jungheimi* (Struve, 1992).

Diagnosis. Frontal lobe rounded; axial furrows forming a 30–40° angle, curved between S1 and S3; S2 transverse; subocular platform. Triangular pygidium; 11–15 axial rings; 5 pleural segments with width (exsag.) slightly increased distally, bent pleural bands, anterior bands rather wide; 5 pairs of very narrow pygidial spines, mainly developed from the posterior pleural bands, at least as long as pleural width (tr.); terminal spine as wide as axis.

Occurrence. Middle Eifelian of Germany (Eifel).

Discussion. *Jaylopygiella* forms a clade rather well supported by the jackknife analysis (64%, node 45; Fig. 5) with the genera *Radiopyge* and *Neocalmonia*. This clade is based on a medial slope of pleurae in posterior view, glabellar axial furrows parallel posteriorly to S1, a wide posterior border, a narrow posterior border furrow, and narrow genal spines.

The pygidium of *Jaylopygiella* differs from that of *Bradocryphaeus* by narrow pygidial spines, a shape more compressed laterally, anterior pleural bands slightly wider compared to the posterior pleural bands, some species have more axial rings, and a sharper posterior medial spine. No character is presently known to allow a clear discrimination of their cephalons.

Bradocryphaeus sp. 20 Van Viersen & Bignon, 2011, from the lower Frasnian of Belgium, shares some features of *Jaylopygiella*, such as very narrow pygidial spines and anterior pleural bands rather large compared to posterior

bands. However, the laterally developed shape of the pygidium and the low number of axial rings (10) make it closer to *Bradocryphaeus*. Presently, this species is only known from one slightly deformed specimen and new specimens are needed for a better identification.

The cephalae of *Jaylopygiella* are also difficult to differentiate from *Neocalmonia* and *Radiopyge*, the most obvious feature being the posterior branch of the facial suture which is most anteriorly positioned in these genera. The pygidia can be more easily discriminated based upon the number of pygidial spine pairs (six for *Radiopyge* and four for *Neocalmonia*), these spines being wider and shorter, and pleural segments narrower distally.

Radiopyge Farsan, 1981
(Fig. 6J')

Type species. *Neocalmonia (Radiopyge) heratensis* Farsan, 1981.

Additional species. *Radiopyge hamedii* Morzadec in Morzadec *et al.*, 2002; *R. sardarensis* Morzadec, 2002; *R. zendadjanensis* (Farsan, 1981).

Diagnosis. Frontal lobe rounded; 5–6 lenses per dorsoventral file of visual surface; S2 anteriorly converging; axial furrows forming a 30–40° angle, curved between S1 and S3; subocular platform; wide posterior border and narrow posterior border furrows; genal spines shorter than glabella. Nine to 11 pygidial axial rings; axis constricted between 5th and 6th rings; 6 pleural segments, width (exsag.) slightly expanded distally, bent pleural bands; 6–7 pairs of pygidial spines mainly developed from the posterior pleural bands, mostly narrower than pleural width (tr.); narrow terminal spine; small fenestrae variably present.

Occurrence. *Radiopyge* is recorded exclusively in the Givetian of Afghanistan–Iran area.

Discussion. Farsan (1981) erected the subgenus *Neocalmonia (Hexacostata)* for species with six pygidial spines, no fenestrae and narrow interpleural furrows. We think that *Hexacostata* is a synonym of *Radiopyge*. Indeed, as demonstrated for *Bradocryphaeus*, the presence of small fenestrae can be considered diagnostic only at the specific level and the large interpleural furrows (Farsan 1981) are strongly associated with the presence of fenestrae. Moreover, *R. zendadjanensis*, the type species of *Hexacostata*, bears several autapomorphic features of *Radiopyge*, such as S2 anteriorly converging, a large posterior border, and an axis constricted between the 5th and 6th rings.

Farsan (1981) proposed an evolutionary scenario (Fig. 1C) involving *Bradocryphaeus* as the sister group of a clade including *Radiopyge* and *Heliopyge*. In the present study, our cladistic analysis shows that *Neocalmonia* and *Radiopyge* constitute a clade (node 46, Fig. 5) in spite of the great difference in the number of pygidial spine pairs. The synapomorphies supporting this clade are a large ante-

rior border, a narrow posterior border furrow, short genal and pygidial spines, and a slight abaxial increase of the pleural segment width (tr.).

Neocalmonia Pillet, 1969
(Fig. 6K')

Type species. *Neocalmonia quadricosta* Pillet, 1969.

Additional species. *Neocalmonia batillifera batillifera* Haas & Mensink, 1970; *N. batillifera orientalis* Feist *et al.*, 2001; *N. brinkmanni* Haas & Mensink, 1970; *N. chitralensis* Feist *et al.*, 2001; *N. erbeni* Farsan, 1981; *N. imperfecta* Pillet, 1969; *N. kakari* Haas & Mensink, 1970; *N. lutenensis* Morzadec, 2002; *N. malistana* Haas & Mensink, 1970; *N. thaumata* Haas & Mensink, 1970; *N. yazdii* Morzadec, 2002.

Species doubtfully assigned. *Neocalmonia? cantabrica* Smeenk, 1983.

Diagnosis. Frontal lobe rounded; 5–8 lenses per dorsoventral file of visual surface; axial furrows forming a 30–40° angle, curved between S1 and S3; S2 transverse; subocular platform; genal spine shorter than glabella; narrow posterior border furrows. Eight to 13 pygidial axial rings; 4–5 pleural segments, width (exsag.) slightly expanded distally; pleural bands bent; 4 pairs of pygidial spines mainly developed from the posterior pleural bands, mostly narrower than pleurae width (tr.); wide terminal spine.

Occurrence. *Neocalmonia* occurs in the Middle Devonian–Frasnian of Afghanistan–Iran–Pakistan area. Unfortunately, Farsan (1981) could not be more precise than the Middle Devonian period. *Neocalmonia? cantabrica*, from the lower Givetian of Spain, would be the oldest and the only European representative of the genus.

Discussion. *Bradocryphaeus afghanica* and *B. sharudensis*, from the Givetian of Iran and Afghanistan, seem to correspond to intermediate forms between the morphology of *Bradocryphaeus* and *Neocalmonia*. These two species bear five pairs of pygidial spines, like *Bradocryphaeus* (four for *Neocalmonia*), but the fifth is almost completely reduced combined with the terminal spine. They are closely related to *Neocalmonia* in having short genal spines, axial furrows forming a 30–40° angle (40–50° for *Bradocryphaeus*), rather short pygidial spines and a slight distal increase in pleural segment width. Nevertheless, these features are also present in some *Bradocryphaeus* species that have a long fifth pair of pygidial spines. Thus, the number of pygidial spines remains fundamental in the determination of these genera. Additionally, the very small pygidial fenestrae of *B. sharudensis*, a character presently unknown in *Neocalmonia*, confirm this assumption.

Neocalmonia? cantabrica from the lower Givetian of the Cantabrian Mountains (Spain) has four or five pairs of pygidial spines. We agree with Morzadec (2002) who

placed this species within *Neocalmonia* with uncertainty, based upon the short pygidial and genal spines and cephalic axial furrows forming an acute angle. Nevertheless, this species is close to *Bradocryphaeus* according to the significant abaxial widening (exsag.) of pleural segments and the smaller occipital ring width (sag.).

Compared to *Bradocryphaeus*, *Neocalmonia* bears several paedomorphic features. Indeed, features such as small genal and pygidial spines, a reduced number of pygidial spines and pleural segments may result from a reduction of modification rate during ontogeny or to a heterometry (*sensu* Webster & Zelditch 2005). Indeed, the very small fifth pair of pygidial spines of *B. afghanica* and *B. sharudensis* may be an argument for a progressive reduction in the length of the fifth pair of pygidial spines until its complete disappearance in *Neocalmonia*. Moreover, cephalic differences between *Bradocryphaeus* and *Neocalmonia*, such as occipital ring and posterior border width and the angle of the axial furrows, may correspond to an allometric repatterning or to a rate modification. A precise study of the ontogeny of these two genera must be performed to test these assumptions.

Remarks on the genus *Erbenochile*

As the systematic position of this monospecific genus has been debated since the redescription of Alberti (1981), it appeared important to clarify the situation. Alberti (1981) assigned the species *Erbenochile erbeni* to the subgenus *Odontochile* based upon the original material described by Le Maître (1952). Morzadec (1995) prepared this pygidium and illustrated 11 pygidial spine pairs, unknown to the previous workers. He rejected membership of *Erbenochile* in the Odontochilinae because this subfamily does not include any members bearing pygidial spines. Moreover the short genal spines and the posterior pleural bands wider and more elevated than the anterior ones make the genus closer to the Asteropyginae. The cephalon, with its famous elevated eyes, was first described by Chatterton *et al.* (2006) and these authors maintained this genus within the Asteropyginae. Subsequently, Chatterton & Gibbs (2010) objected that the number of pygidial spines is stable within the Asteropyginae, varying only between four and six pairs. Thus they reassigned *Erbenochile* to the Odontochilinae based on speculation that adding marginal spines may require fewer genetic modifications than adding numerous pygidial spines. However, Budil *et al.* (2009) suggested Odontochilinae to be a junior synonym of Dalmanitinae because most of the diagnostic features of that subfamily are shared with other dalmanitid groups or seem to have only a generic importance. Consequently, the short genal spines and the developed posterior pleural bands can no longer sustain the placement of *Erbenochile* within the Asteropyginae.

We agree with the proposal by Chatterton & Gibbs (2010) to transfer *Erbenochile* from the Asteropyginae. The

pygidial spine pairs are limited to six in the subfamily and the vestigial terminal spine has no relative among Asteropyginae. Also, the connection of the pleural bands with spines is subtle, producing a smooth pygidial border, whereas in the Asteropyginae this feature has more relief. *Erbenochile* additionally has deep excavations at the proximal extremity of S1 and S2 that could make it closer to the Dalmanitinae.

Conclusions

Our cladistic analysis presents a new vision of the evolution of Asteropyginae. This phylogeny differs from the traditional subdivisions of the subfamily in its highly pectinate topology. In fact, this proposal is not so different from previous evolutionary scenarios (Haas 1970; Gandl 1972; Arbizu 1977; Smeenk 1983; Morzadec 1983). Indeed, the relationships between the genera are rather similar to these former studies. The main difference concerns the ancestral genera of the group. Traditionally, *Treveropyge* was suggested as the ancestor. In the present work, the group would emerge from *Destombesina*, a genus rather close to *Pseudocryphaeus*. Such results are important clues to better understand the phylogenetic relationships within the Acastidae.

Reliable phylogenies need to be established for trilobite clades, and character distributions mapped onto these, to test evolutionary hypotheses about trilobite development and their diversification. We have highlighted, in this work, unresolved questions about evolutionary modifications of ontogeny for several asteropygine genera. Thus, this phylogeny is a prerequisite for exploring this subject. Indeed, detailed studies of trilobite ontogeny may yield insights into mechanisms controlling the evolution of major aspects of trilobite body patterning (Hughes 2007).

Acknowledgements

The authors thank S. Regnault (Muséum d'Histoire Naturelle de Nantes, France), A. Folie (Royal Belgian Institute of Natural Sciences, Belgium) and S. Butts (Yale Peabody Museum of Natural History, USA) who kindly offered access to their collections. This work benefited from the helpful improvement of the English and constructive suggestions made by G. Edgecombe (Natural History Museum, UK), P. Morzadec (Rennes, France), B. Chatterton (Alberta, Canada) and an anonymous reviewer. This paper is a contribution to UMR 8217 Géosystèmes du CNRS and to IGCP 596 'Climate change and biodiversity patterns in the Mid-Palaeozoic (Early Devonian to Early Carboniferous)'. This study was also supported by the Synthesys Project (<http://www.synthesys.info>) which is funded by the European Community Research Infrastructure Action under the FP6 'Structuring the European Research Area Programme'.

Supplemental material

Supplemental material is available online DOI: 10.1080/14772019.2013.804008

References

- Agnarsson, I. & Miller, J. A.** 2008. Is ACCTRAN better than DELTRAN? *Cladistics*, **24**, 1032–1038.
- Alberti, G. K. B.** 1981. Beziehungen zwischen “herzynischen” Trilobitenfauna aus NW-Marokko und Deutschland (Unter- und Mittel-Devon). *Natur und Museum*, **111**, 362–369.
- Arbizu, M.** 1977. Asteropyginae (Trilobita) du Dévonien des Montagnes Cantabriques (Espagne). *Bulletin de la Société géologique et minéralogique, Bretagne*, **9**(2), 59–102, pls 1–10.
- Asselbergs, E.** 1912. Description d’une faune frasnienne inférieure du bord nord du Bassin de Namur. *Bulletin de la Société belge de Géologie, de Paléontologie et d’Hydrologie*, **36**(1), 1–47.
- Basse, M.** 1998. Trilobiten aus mittlerem Devon des Rhenohercynikums: I. Corynexochida und Proetida (1). *Paleontographica Abteilung A*, **239**(1–6), 1–162, pls 1–15.
- Basse, M.** 2003. *Eifel-Trilobiten 2. Phacopida 1*. Goldschneck-Verlag, Korb, 198 pp.
- Basse, M. & Franke, C.** 2006. Marine Faunen aus dem frühen Unteremsium (Unterdevon) des Givonne-Oesling-Antiklinoriums (Luxemburg). *Ferrantia*, **46**, 7–41.
- Basse, M., Müller, P. & Francke, C.** 2006. Neue Daten zu den Trilobiten aus dem frühen Unteremsium (Ulmen-Unterstufe; Unterdevon) vom Reideschbaach (Luxemburg; Givonne-Oesling-Antiklinorium; Rhenohercynikum). *Senckenbergiana lethaea*, **86**, 243–259.
- Becker, G. & Jansen, U.** 1998. Solle’s “Hunsrück-Insel”: eine kustennahe Fauna (Ostracoden, Brachiopoden, Trilobiten) aus Rotsedimenten des Ober-Emsium (Unterdevon) der Moselmulde (Linksrheinisches Schiefergebirge). *Senckenbergiana lethaea*, **77**, 195–221.
- Brice, D., Lafuste, J., de Lapparent, A. F., Pillet, J. & Yassini, I.** 1973. Etude de deux gisements paléozoïques (Silurien et Dévonien) de l’Elbourz oriental (Iran). *Annales de la Société Géologique du Nord*, **93**(3), 177–218, pls 20–25.
- Budil, P., Hörbinger, F. & Mencl, R.** 2009. Lower Devonian dalmanitid trilobites of the Prague Basin (Czech Republic). *Earth and Environmental Science Transaction of the Royal Society of Edinburgh*, **99**, 61–100.
- Burmeister, H.** 1843. *Die Organization der Trilobiten*. Georg Reimer, Berlin, 147 pp.
- Chatterton, B. & Gibb, S.** 2010. Latest Early to early Middle Devonian trilobites from the *Erbenochile* bed, Jbel Issoumour, southeastern Morocco. *Journal of Paleontology*, **84**, 1188–1205.
- Chatterton, B., Fortey, R., Brett, K., Gibb, S. & McKellar, R.** 2006. Trilobites from the upper Lower to Middle Devonian Timrhannhart Formation, Jbel Gara el Zguilma southern Morocco. *Paleontographica Canadiana*, **25**, 1–177.
- De Carvalho, M. & Moody, J.** 2000. A Middle Devonian trilobite assemblage from Venezuela. *American Museum Novitates*, **3292**, 1–15.
- Delo, D. M.** 1935. A revision of the Phacopid trilobites. *Journal of Paleontology*, **9**, 402–420.
- De Tromelin, G. & Lebesconte, P.** 1876. Observations sur les terrains primaires du Nord du département d’Ille-et-Vilaine et de quelques parties du Massif Breton. *Bulletin de la Société Géologique de France*, **4**(3), 583–623.
- Edgecombe, G. D.** 1993. Silurian Acastacean trilobites of the Americas. *Journal of Paleontology*, **67**, 535–548.
- Eldredge, N.** 1971. Patterns of cephalic musculature in the Phacopina (Trilobita) and their phylogenetic significance. *Journal of Paleontology*, **45**, 52–67.
- Eldredge, N.** 1979. Cladism and common sense. Pp. 165–198 in J. Cracraft & N. Eldredge (eds) *Phylogenetic analysis and Paleontology*. Columbia University Press, New York.
- Eldredge, N. & Ormiston, A. R.** 1979. Biogeography of Silurian and Devonian trilobites of the Malvinokaffric Realm. Pp. 147–167 in J. Gray & A. J. Boucot (eds) *Historical biogeography, plate tectonics, and the changing environment*. Oregon State University Press, Corvallis.
- Emmrich, H. F.** 1839. *De trilobitis*. Dissertation petrefactologica quam consensu et auctoritate amplissimi philosophorum ordinis, Berlinis, 56 pp.
- Farris, J. S., Albert, V. A., Källersjö, M., Lipscomb, D. & Kluge, A. G.** 1996. Parsimony jackknifing outperforms neighbor-joining. *Cladistics*, **12**, 99–124.
- Farsan, N. M.** 1981. New Asteropyginae (Trilobita) from the Devonian of Afghanistan. *Palaeontographica Abteilung A*, **176**(4–6), 158–171, 1 pl.
- Feist, R.** 1991. The Late Devonian trilobite crisis. *Historical Biology*, **5**, 197–214.
- Feist, R., Talent, J. A. & Mawson, R.** 2001. Devonian trilobites from the Shogrām Formation Kurgāh, Chitral (NW Pakistan). *Alcheringa*, **25**, 107–115.
- Frech, F.** 1888. Geologie der Umgegend von Haiger bei Dillenberg (Nassau). Nebst einem palaeontologischen Anhang. *Abhandlungen zur Geologischen Special Karte von Preussen und den Thüringischen Staaten*, **8**, 1–36.
- Gandl, J.** 1972. Die Acastavinae und Asteropyginae (Trilobita) Keltiberiens (NE-Spanien). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, **530**, 1–183.
- Gould, S. J. & Vrba, E. S.** 1982. Exaptation; a missing term in the science of form. *Paleobiology*, **8**, 4–15.
- Green, J. M.** 1837. Description of two new species of trilobites. *Journal of the Academy of Natural Sciences of Philadelphia*, **7**(2), 217–226.
- Haas, W.** 1968. Trilobiten aus dem Silur und Devon von Bithynien (NW-Türkei). *Palaeontographica Abteilung A*, **130**(1–6), 60–207, pls 26–37.
- Haas, W.** 1970. Zur Phylogenie und Systematik der Asteropyginae und Beschreibung einiger neuer Arten (Phacopacea, Trilobita). *Senckenbergiana lethaea*, **51**, 97–131.
- Haas, W. & Mensink, H.** 1970. Asteropyginae aus Afghanistan (Triobita). *Abhandlungen der Akademie der Wissenschaften und der Literatur, mathematisch-naturwissenschaftlichen Klasse*, **6**, 1–62, pls 1–5.
- Hall, J.** 1861. Description of new species of fossils from the upper Helderberg, Hamilton and Chemung groups. *Fifteenth Annual Report of the Regents of the University of the State of New York*, 29–114.
- Hawle, I. & Corda, A. J. C.** 1847. Prodrum einer Monographie der böhmischen Trilobiten. *Abhandlungen Konglisch-böhmischen Gesellschaft der Wissenschaften*, **5**(5), 1–176.
- Hughes, N. C.** 2007. The evolution of trilobite body patterning. *Annual Reviews in Earth and Planetary Sciences*, **35**, 401–434.
- Jell, P. A. & Adrain, J. M.** 2003. Available generic names for trilobites. *Memoirs of the Queensland Museum*, **48**(2), 331–553.

- Kayser, E.** 1883. Mittel- und Obersilurische Versteinerungen aus dem Gebirgsland von Tschau-tien im nord-östlichen Teil der Provinz Sz'tshwan. Pp. 37–49 in F. F. Richtofen (ed.) *Beiträge zur Paläontologie von China*. De Gruyter.
- Kayser, E.** 1889. Die fauna des Hauptquartzits und der Zorger Schiefer des Unterharzes. *Abhandlungen Preussischen Geologischen Landesanstalt*, **1**, 1–139.
- Kielan, Z.** 1954. Les trilobites mésodévonien des Monts de Sainte-Croix. *Palaeontologica Polonica*, **6**, 1–50, pls 1–7.
- Lee, M. S. Y.** 1999. Circularity, evolution, systematics... and circularity. *Journal of Evolutionary Biology*, **12**, 724–734.
- Le Maître, D.** 1952. La faune du Dévonien inférieur et moyen de la Saoura et des abords de l'Erg El Djemel (Sud-Oranais). *Mémoire de la Carte géologique de l'Algérie*, **12**, 1–171.
- Lieberman, B. S. & Kloc, G. J.** 1997. Evolutionary and biogeographic patterns in the Asteropyginae (Trilobita, Devonian) Delo, 1935. *Bulletin of the American Museum of Natural History*, **232**, 1–127.
- Morzadec, P.** 1969. Le Dévonien de la rive nord de la rivière du Faou (Finistère). Etude stratigraphique, étude des trilobites. *Bulletin de la Société Géologique et Minéralogique de Bretagne*, 1969, 1–58, 9 pls.
- Morzadec, P.** 1971. Quelques Asteropyginae (Trilobites, Phacopacea) des schistes et calcaires à *Athyris undata* (Dévonien inférieur) du Massif Armoricain. *Palaeontographica Abteilung A*, **138**(5–6), 166–184, pls 15–19.
- Morzadec, P.** 1976a. Les Trilobites. Pp. 285–294, pls 54–58 in C. Babin, F. Bigey, J. Drot, D. Goujet, H. Lardeux, J. Le Menn, J. L'Hottellier, M. Melou, A. Moreau-Benoit, P. Morzadec, F. Paris, Y. Plusquellec, J. Poncet, P. Racheboeuf, P. Taugourdeau & M. Weyant (eds) Les schistes et calcaires Eodévonien de Saint-Cénére (Massif Armoricain, France). *Mémoires de la Société géologique et minéralogique de Bretagne*, **19**.
- Morzadec, P.** 1976b. Les Trilobites. Pp. 35–45, pls 3–7 in J. Le Menn, Y. Plusquellec, P. Morzadec & H. Lardeux (eds) Incursion hercynienne dans les faunes rhénanes du Dévonien Inférieur de la rade de Brest (Massif Armoricain). *Palaeontographica Abteilung A*, **153**.
- Morzadec, P.** 1981. Les Trilobites. Pp. 279–287, pls 34–35 in P. Morzadec, F. Paris & P. Racheboeuf (eds) La tranchée de la Lezais Emsien supérieur du Massif Armoricain, sédimentologie, paléontologie, stratigraphie. *Mémoires de la Société géologique et minéralogique de Bretagne*, **24**.
- Morzadec, P.** 1983. Trilobites du Dévonien (Emsien-Famennien) de la Rade de Brest (Massif Armoricain). *Palaeontographica Abteilung A*, **181**, 103–184, pls 1–32.
- Morzadec, P.** 1988a. Trilobites du Givétien et du Frasnien de Ferques (Boulonnais-France). *Biostratigraphie du Paléozoïque*, **7**, 493–501, pls 57–58.
- Morzadec, P.** 1988b. Le genre *Psychopyge* (Trilobita) dans le Dévonien Inférieur du Nord de l'Afrique et de l'Ouest de l'Europe. *Palaeontographica Abteilung A*, **200**(4–6), 153–161, pls 1–2.
- Morzadec, P.** 1990. Evolution, biozonation, et biogéographie de *Protacanthina* Gandl, trilobite du Dévonien inférieur nord-gondwanien. *Geobios*, **23**, 719–735.
- Morzadec, P.** 1992. Evolution des Asteropyginae (Trilobita) et variations eustatiques au Dévonien. *Lethaia*, **25**, 85–96.
- Morzadec, P.** 1994. Révision de *Gourdonia*, trilobite du Dévonien des Pyrénées Centrales: Morphologie, evolution, environnement. *Geobios*, **27**, 243–253.
- Morzadec, P.** 1995. *Erbenochile erbeni* (Alberti), Trilobite du Dévonien inférieur de l'Ougarta (Algérie). *Neues Jahrbuch für geologie und Paläontologie Monatshefte*, 1995, 614–621.
- Morzadec, P.** 1997. Les trilobites Asteropyginae du Dévonien de l'Ougarta (Algérie). *Palaeontographica Abteilung A*, **244**(4–6), 143–158, pls 1–8.
- Morzadec, P.** 2001. Les trilobites Asteropyginae du Dévonien de l'Anti-Atlas (Maroc). *Palaeontographica Abteilung A*, **262**(1–3), 53–85, pls 1–15.
- Morzadec, P.** 2002. Trilobites Asteropyginae dévonien d'Iran. *Geobios*, **35**, 411–427.
- Morzadec, P. & Arbizu, M.** 1978. *Kayserops? Cantarmoricus* nov. sp., Trilobite Asteropyginae du Dévonien moyen armoricain et cantabrique. *Geobios*, **11**, 925–931.
- Morzadec, P., Dastanpour, M. & Wright, A. J.** 2002. Asteropyginae Trilobites from the Upper Devonian of Kerman region, Iran. *Alcheringa*, **26**, 143–149.
- Oehlert, D.** 1877. Sur les fossiles dévonien du département de la Mayenne. *Bulletin de la Société géologique de France*, **5**, 578–603.
- Oehlert, D.** 1889. Sur le Dévonien des environs d'Angers. *Bulletin de la Société Géologique de France*, **17**(3), 742–791.
- Paackelmann, W.** 1913. Das oberdevon des Bergischen Landes. *Abhandlungen der Preußischen Geologischen Landesanstalt, Neue Folge*, **70**, 1–356.
- Pichard, P.** 1930. Contribution à l'étude du sous-genre *Cryphaeus* dans le Massif Armoricain. *Bulletin de la Société Géologique et Minéralogique de Bretagne*, **9**(1–4), 70–118, pls 1–8.
- Pillet, J.** 1950. Contribution à l'étude des schistes, calcischistes et grauwaques d'Angers. III. *Bulletin de la Société Géologique de France*, **20**(5), 39–48.
- Pillet, J.** 1954. La classification des Phacopacea (Trilobites). *Bulletin de la Société Géologique de France*, **6**(3), 817–839.
- Pillet, J.** 1958. Contribution à l'étude de quelques Asteropyginae (Trilobites). *Bulletin de la Société Géologique de France*, **8**(6), 3–20, pls 1–2.
- Pillet, J.** 1969. Un nouveau genre de Trilobite dévonien en Afghanistan (*Neocalmonia* nov. gen., Calmoniinae, Trilobite). *Compte-rendu sommaire de la Société géologique de France*, **5**, 144–145.
- Pillet, J.** 1972. Les Trilobites du Dévonien inférieur et du Dévonien moyen du Sud-Est du Massif armoricain. *Mémoire de la Société d'études scientifiques de l'Anjou*, **1**, 307 pp., pls 1–64.
- Ramsköld, L. & Edgecombe, G. D.** 1993. Silurian (Ludlow) acastid trilobites from Gotland and Sweden. *Paläontologische Zeitschrift*, **67**, 261–285.
- Reed, F. R. C.** 1925. Some new Silurian trilobites. *Geological Magazine*, **62**, 67–76.
- Richter, R.** 1909. Beiträge zur Kenntnis devonischer Trilobiten aus dem Rheinischen Schiefergebirge. Marburg, 96 pp.
- Richter, R.** 1916. Die Entstehung der abgerollten "Daleider Versteinerungen" und das Alter ihrer Mutterschichten. *Jahrbuch der Kongligen der Preussischen. Geologischen Landesanstalt für*, **37**, 247–259.
- Richter, R. & Richter, E.** 1926. Die Trilobiten des Oberdevon. Beiträge zur Kenntnis devonischer Trilobiten. IV. *Abhandlungen der Preußischen Geologischen Landesanstalt, Neue Folge*, **99**, 1–314, pls 1–12.
- Richter, R. & Richter, E.** 1943. Trilobiten aus dem Devon von Marokko. *Senckenbergiana*, **26**(1–3), 116–199.
- Richter, R. & Richter, E.** 1948. *Neometacanthus* n. nom. (pro *Metacanthus* Corda, 1847) Tril. *Senckenbergiana*, **29**, 107.
- Richter, R. & Richter, E.** 1952. Phacopacea von der Grenze Emsium/Eiflium. (Tril.). *Senckenbergiana*, **33**(1–3), 79–107, pls 1–4.

- Richter, R. & Richter, E.** 1954. Die Trilobiten des Ebbe-Sattels und zu vergleichende Arten (Ordovizium, Gotlandium/Devon). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, **488**, 1–75.
- Rouault, M.** 1851. Mémoire sur les terrains paléozoïques des environs de Rennes. *Bulletin de la Société Géologique de France*, **8**, 358–399.
- Schraut, G.** 2000. Trilobiten aus dem Unter-Devon des südöstlichen Anti-Atlas, Süd-Marokko. *Senckenbergiana lethaea*, **79**, 361–433.
- Smeenk, Z.** 1983. Devonian trilobites of the southern Cantabrian Mountains (northern Spain) with a systematic description of the Asteropyginae. *Leidse Geologische Mededelingen*, **52**(2), 383–511.
- Steininger, J.** 1831. Observation sur les fossiles du calcaire intermédiaire de l'Eifel. *Mémoires de la Société Géologique de France*, **1**, 331–371.
- Stumm, E. C.** 1953. Trilobites of the Devonian Traverse group of Michigan. *Contributions from the Museum of Paleontology, University of Michigan*, **10**(6), 101–157, pls 1–12.
- Stumm, E. C.** 1965. Two new species of trilobites from the Middle Devonian Silica Shale of northwestern Ohio. *Contribution from the Museum of Paleontology, the University of Michigan*, **19**(13), 163–166, pl. 1.
- Struve, W.** 1958. Beiträge zur Kenntnis der Phacopacea (Trilobita), 3: *Treveropyge* n. gen. und *Comura* (*Delocare*) n. subgen. *Senckenbergiana lethaea*, **39**, 227–234.
- Struve, W.** 1959. Asteropyginae. Pp. 477–483 in R. C. Moore (ed.) *Treatise on Invertebrate Paleontology, O. Arthropoda 1*. University of Kansas Press, Lawrence, Kansas.
- Struve, W.** 1992. Neues zur Stratigraphie und Fauna des rheno-typen Mittel-Devon. *Senckenbergiana lethaea*, **71**, 503–624.
- Swofford, D. L.** 2002. *PAUP*. Phylogenetic analysis using parsimony (*and other methods)*. Version 4. Sinauer Associates, Sunderland.
- Termier, G. & Termier, H.** 1950. Paléontologie marocaine, t. II, Invertébrés de l'Ere primaire: Annélides, Arthropodes, Echinodermes, Conularides et Graptolithes. *Notes et Mémoires du service géologique du Maroc*, **79**(4), 1–279.
- Timm, J.** 1981. Zur trilobiten Stratigraphie des silur/devon Grenzbereiches im Ebbe-Antiklinorium (Rheinisches Schiefergebirge). *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, **50**, 91–108.
- Tomczykowa, E.** 1991. Upper Silurian and Lower Devonian trilobites of Poland. *Prace Panstwowego Instytutu Geologicznego*, **134**, 1–62.
- van Viersen, A. P. & Bignon, A.** 2011. Late Devonian (Frasnian) Asteropygine trilobites from the Frasnes area, southern border of Dinant Synclinorium, Belgium. *Geologica Belgica*, **14**(3–4), 109–128.
- van Viersen, A. P. & Prescher, H.** 2007. Note on *Cyphaspis* Burmeister 1843 (Trilobita, Aulacopleuridae), with a review of several species mainly from the Devonian of Belgium and Germany. *Senckenbergiana lethaea*, **87**, 157–170.
- Verneuil, E. de**, 1867. Liste des fossiles recueillis dans le terrain dévonien de Chagey (Haut-Saône). *Bulletin de la Société géologique de France*, **24**, 127–129.
- Webster, M. & Zelditch, M. L.** 2005. Evolutionary modifications of ontogeny: heterochrony and beyond. *Paleobiology*, **31**, 354–372.