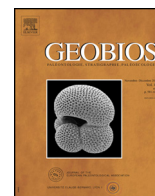




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Original article

## A revision of the first Asteropyginae (Trilobita; Devonian)<sup>☆</sup>



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### ABSTRACT

A recent cladistic analysis of the Asteropyginae led to the recognition of the genus *Minicryphaeus* as one of the most ancestral of this subfamily. A new species, *M. giganteus*, is described here from the Ihandar Formation (Pragian, Lower Devonian) of Jbel El Mrakib, southern part of the Mader Basin (Morocco). Among other characteristic features, it is almost three times larger than the other species of the genus. The description of this new species provides information on the ancestral character states of the subfamily and necessitated a revision of the oldest known representatives. Moreover, this recent analysis identified *Treveropyge* as a derived form of asteropygines, whereas it was traditionally considered as ancestral due to one of its oldest species, now *Ganetops ebbae* nov. comb., which was formerly included in this genus. In order to offer a better view of the ancestral Asteropyginae, the features of *M. giganteus* nov. sp. and *G. ebbae* nov. comb. have been coded following the scheme of the previous cladistic analysis. The updated phylogeny reveals that *M. giganteus* nov. sp. is the sister-group of the other *Minicryphaeus* species; a paedomorphic event explains their decreasing size. The new phylogeny confirms the basal position of *G. ebbae* nov. comb. and distinguishes it clearly from the genus *Treveropyge*, which necessitates the erection of the new genus *Ganetops*. It appears that the association of *G. ebbae* nov. comb. with more derived species within the genus *Treveropyge* disturbed the previous cladistics analysis of the Asteropyginae. Indeed, considering a derived species as root of the subfamily leads necessarily to the formation of two major clades, as it was usually suggested for the Asteropyginae.

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## 1. Introduction

During the last decades, the evolution within the Asteropyginae has been interpreted as based on two separate clades evolving from the genus *Treveropyge* (Haas, 1970; Smeenk, 1983; Morzadec, 1983; Lieberman and Kloc, 1997) or from *Paracryphaeus* (Gandl, 1972; Timm, 1981). A new phylogeny of the subfamily was recently performed (Bignon and Crônier, 2014), suggesting an entirely new pattern with a largely pectinated topology without major clades distinguishable. This work suggests *Destombesina* as the sister-group of all Asteropyginae members. However, the proposition that this genus is the common ancestor remains somewhat debatable since it depends on the affiliation of this genus within this subfamily or within the Acastavinae (Bignon and Crônier, 2014). Consequently, *Minicryphaeus*

was the most ancestral Asteropyginae that they can identify with certainty (Bignon and Crônier, 2014).

In the context of the research project “DEVMAR 2011/10” supported by FOSILART (Corbacho and Kier, 2013; Corbacho and López-Soriano, 2013), the Jbel El Mrakib outcrop (Morocco) was excavated in 2011. Other sections were jointly studied, particularly Jbel El Mrakib, Jbel bou Lachral, El Achana, El Jorf and Tinejda from both Lower and Middle Devonian of the Mader Basin. As a result, a new species of Asteropyginae, *M. giganteus* nov. sp., extracted in the Ihandar Fm. (Pragian, Lower Devonian; Morocco) of the Jbel El Mrakib section is presented here.

The present work constitutes a contribution to the knowledge of the basal members of the Asteropyginae. Both *M. giganteus* nov. sp. and the oldest species formally described within the Asteropyginae, *Ganetops ebbae* nov. comb. (R. and E. Richter, 1954), are included in a data matrix used to solve the phylogeny of the subfamily (Bignon and Crônier, 2014). Such new developments bring pertinent information about the origin of this trilobite subfamily and an explanation of the difference between former phylogenies proposed and the new one (Bignon and Crônier, 2014).

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## 2. Material and methods

### 2.1. Geographical location

The studied site (Fig. 1) belongs to the Ihandar Fm. Originally described by HOLLARD (1974), several sections where this lithostratigraphic unit is exposed have been the subject of recent investigations. JOHNSON and FORTY (2012) described the Proetids of the Oufatene and Jbel El Mrakib sections, from the western and southern parts of the Mader region, respectively. MORZADÉC (2001) focused on the Oufatene asteropygines and from the Jbel Issoumour. The present study adds to this previous work by describing a new Asteropyginae species from the Jbel El Mrakib section.

This section is exposed in the southern slope of Jbel El Mrakib, from the South of the Mader Basin, administrative district of Er Rachidia, approximately 367 km SE of Rabat and 24 km W of Rissani (Eastern Anti-Atlas, Morocco). Coordinates of the excavation are N 30°44.230'–W 4°34.197' and the altitude was 716 m a.s.l. (data recorded in October 2010 by one of us [J.C.] using a Garmin GPS model Foretrex 401).

### 2.2. Stratigraphy

The locality (Fig. 1(C,D)) exposes an alternation of limestones and marly limestones that are included in the Ihandar Fm.,

belonging to the Pragian (Lower Devonian). The outcrop where *M. giganteus* nov. sp. was found is a stratum located in the southern slope of Jbel El Mrakib, at a depth of approximately 0.9 m and with the following lithologic and faunistic composition (Fig. 1(D)):

- **Level I:** 0.35 m of papery light-grey, very fine-grained marly limestones. This level does not contain fossils;
- **Level II:** 0.25 m of brownish-red, very fine-grained limestones, slightly marly and ferruginous, containing *Acanthopyge* (*Belenopyge*) *estevei* Corbacho and Kier, 2013, *Asteropyge* sp., *Leonaspis* sp., *Paralejurus* sp., *Dalejeproetus* sp., *Cyphaspis* sp., and *M. giganteus* nov. sp.;
- **Level III:** 0.30 m papery light-grey, very fine-grained marly limestones. This level does not contain fossils.

The top of the section is the subaerial surface. JOHNSON and FORTY (2012: 1036) proposed a precise stratigraphical column of the Ihandar Fm. in the southern slope of Jbel El Mrakib.

### 2.3. Cladistic analysis

Two species were added to the cladistic analysis performed by BIGNON and CRÔNIER (2014): *M. giganteus* nov. sp., the new species discovered in Jbel El Mrakib, and *G. ebbae* nov. comb. (R. and E. Richter, 1954), generally accepted as one of the oldest and most

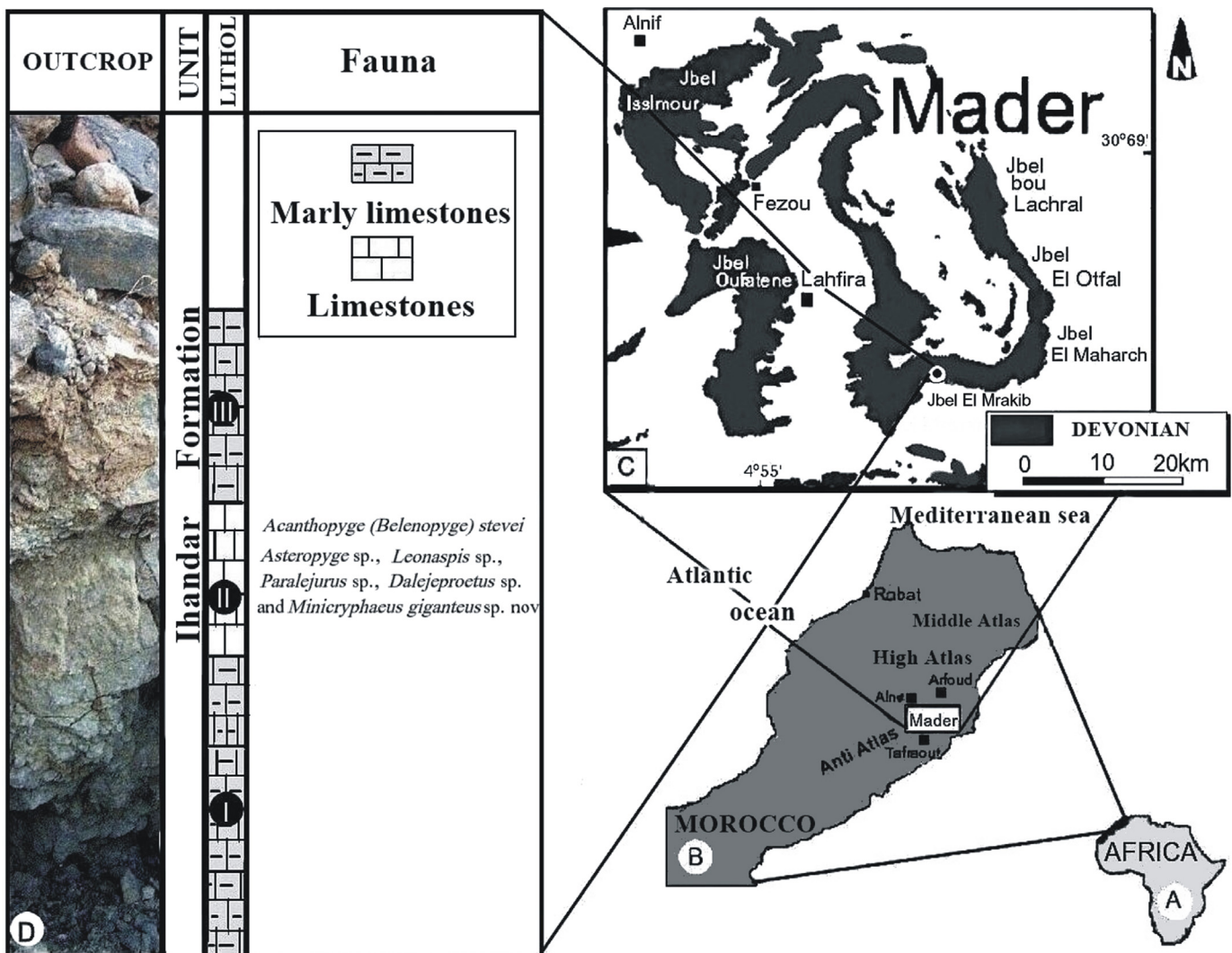


Fig. 1. Studied outcrop, Ihandar Formation, Lower Devonian (Pragian) of Jbel El Mrakib (Morocco). A. Map of Africa with the location of Morocco. B. Map of Morocco with the geographical location of the Mader Basin. C. Map of the Mader Basin (modified after Kaufmann, 2006). D. Studied section of the Ihandar Fm.

**Table 1**

Data matrix of the two taxa added in the phylogenetical analysis.

| <i>Minicryphaeus giganteus</i> nov. sp. |       | <i>Ganetops ebbae</i> nov. comb. |       |
|---|-------|----------------------------------|-------|
| Character #                             | State | Character #                      | State |
| 1                                       | 1     | 41                               | 1     |
| 2                                       | 0     | 42                               | 1     |
| 3                                       | 0     | 43                               | 1     |
| 4                                       | 1     | 44                               | 1     |
| 5                                       | 0     | 45                               | 1     |
| 6                                       | 1     | 46                               | 0     |
| 7                                       | 1     | 47                               | 1     |
| 8                                       | 1     | 48                               | 1     |
| 9                                       | 0     | 49                               | 1     |
| 10                                      | 1     | 50                               | 1     |
| 11                                      | 1     | 51                               | 0     |
| 12                                      | ?     | 52                               | 1     |
| 13                                      | 0     | 53                               | 0     |
| 14                                      | 2     | 54                               | 0     |
| 15                                      | 1     | 55                               | ?     |
| 16                                      | 0     | 56                               | 0     |
| 17                                      | 0     | 57                               | 1     |
| 18                                      | 0     | 58                               | 1     |
| 19                                      | 1     | 59                               | 1     |
| 20                                      | 0     | 60                               | 1     |
| 21                                      | 0     | 61                               | 0     |
| 22                                      | 0     | 62                               | 1     |
| 23                                      | 0     | 63                               | 1     |
| 24                                      | 1     | 64                               | 0     |
| 25                                      | 1     | 65                               | 0     |
| 26                                      | 0     | 66                               | 0     |
| 27                                      | 0     | 67                               | 1     |
| 28                                      | 2     | 68                               | 0     |
| 29                                      | 2     | 69                               | 0     |
| 30                                      | 1     | 70                               | 0     |
| 31                                      | 0     | 71                               | 1     |
| 32                                      | 2     | 72                               | 0     |
| 33                                      | 0     | 33                               | 0     |
| 34                                      | 1     | 34                               | 0     |
| 35                                      | 1     | 35                               | 1     |
| 36                                      | 0     | 36                               | 0     |
| 37                                      | 1     | 37                               | 1     |
| 38                                      | 1     | 38                               | 1     |
| 39                                      | 0     | 39                               | 0     |
| 40                                      | 1     | 40                               | 1     |

ancestral Asteropyginae (Haas, 1970; Gandl, 1972; Timm, 1981; Morzadec, 1983; Smeenk, 1983). The coding of *G. ebbae* nov. comb. is based on the original description and illustrations of this species (Richter and Richter, 1954) and also on the work of Timm (1981). Unfortunately, we were not able to study directly this material. Data for these two species are given in Table 1.

The 72 characters coded in this analysis are identical to those used by Bignon and Crônier (2014). In the same way, the analytical protocol is rigorously the same as this original work, namely: parsimony analysis performed under PAUP\* 4.0β10 (Swofford, 2002) with unweighted and unordered characters, based on an heuristic search with TBR (tree bisection and reconnection) and 1000 random addition sequence replicates, and synapomorphies optimised with delayed transformation assumption (Deltran). A parsimony jackknife (10,000 replicates, 36% characters deletion) was performed in order to assess the strength of nodes.

### 3. Systematic paleontology

Order PHACOPIDA Salter, 1864  
 Suborder PHACOPINA Struve, 1959  
 Superfamily ACASTACEA Delo, 1935  
 Family ACASTIDAE Delo, 1935  
 Subfamily ASTEROPYGINAE Delo, 1935

#### Genus *Minicryphaeus* Bignon and Crônier, 2014

**Type species:** *M. minimus* (Morzadec, 2001), from the Pragian (Lower Devonian) of Morocco.

**Assigned species:** *M. minimus* (Morzadec, 2001), *M. quaterspinosus* (Morzadec, 2001), *M. sarirus* (Morzadec, 2001), and *M. giganteus* nov. sp.

**Occurrence:** All the species included in this genus come from the Pragian (Lower Devonian) of the Mader Basin (Morocco).

**Diagnosis** (emend. from Bignon and Crônier, 2014): Cephalon may have a prefrontal spine; frontal lobe diamond shaped; axial furrows straight between S1 and S3, no contact between S2 and axial furrows; 5–8 lenses per vertical row on visual surface; genal spine shorter than glabella with narrow proximal portion; narrow anterior border, lateral border very large, poorly or developed on genal spine. Pygidium with anterior pleural bands as wide and elevated as posterior bands, flat pleural bands; axis with 7–10 rings; 4 or 5 pleural segments; 4 or 5 pairs of pygidial spines shorter than pleural width (tr.), mainly developed from posterior pleural bands; terminal pygidial spine wider than axis, roughly triangular, twice or as long as other pygidial spines.

**Remarks:** Morzadec (2001) described from the Ihandar Fm. three species that he attributed to the genus *Pseudocryphaeus*. After the review by Bignon and Crônier (2014), these species (*M. minimus*, *M. quaterspinosus* and *M. sarirus*) were determined as forming a distinct genus: *Minicryphaeus*. Indeed, these two genera are closely related, as obvious from the pleural structure (shape and size of the pleural bands, connexion between pleural bands and pygidial spines), S1 straight, L2 and L3 with similar length and a wide cephalic posterior border furrow. But members of *Minicryphaeus* differ from *Pseudocryphaeus* by having straight glabellar axial furrows between S1 and S3, eyes with fewer lenses per vertical row (max: 8), a triangular terminal spine, and sometimes a prefrontal spine present or only four pygidial spine pairs.

The discovery of this new species confirms that *Minicryphaeus* has variable features (Bignon and Crônier, 2014). Indeed, the three first species described in the genus have different numbers of facets per row on the visual surface, and of pygidial spine pairs or axial rings. However, the size and the terminal pygidial spine length is a shared feature possessed by all of them, excluded the new species *M. giganteus*. Nevertheless, *M. giganteus* nov. sp. shares several characters with the other three species (such as a prefrontal spine and the shape of the terminal part of the pygidium), justifying its attribution to this genus.

The prefrontal spine of the type species of the genus, *M. minimus*, and of *M. giganteus* nov. sp. may support the assignation of the two other species in a new genus. However, this assumption is not supported by the phylogeny and, as said above, the type species shares with *M. sarirus* and *M. quaterspinosus* a similar size as well as the long terminal pygidial spine. In the present state of knowledge, these features appear as an intrageneric variability.

Morzadec (2001) suggested a close relationship between *M. minimus* and *Pseudocryphaeus cossensis* Morzadec, 1971. Unfortunately, the cephalon of this species has not been described so far, thus decreasing the number of characteristic features helpful in order to precisely assign a genus to this species. In any case, the pentagonal terminal spine and the distance between the others pygidial spines suggest that this species is closer to *Pseudocryphaeus* than to *Minicryphaeus*.

*M. giganteus* nov. sp. appears to be the most ancestral and largest species of the genus (Fig. 2). Thus, it is highly likely that a pedomorphic event has reduced the size of the common ancestor of the three other species, as already suggested by Morzadec (2001). Unfortunately, *M. sarirus* is not included in the cladistic analysis because the poorly preserved material makes difficult a coding based on the published data. However, the absence of the precephalic spine suggests that this form is the sister species of



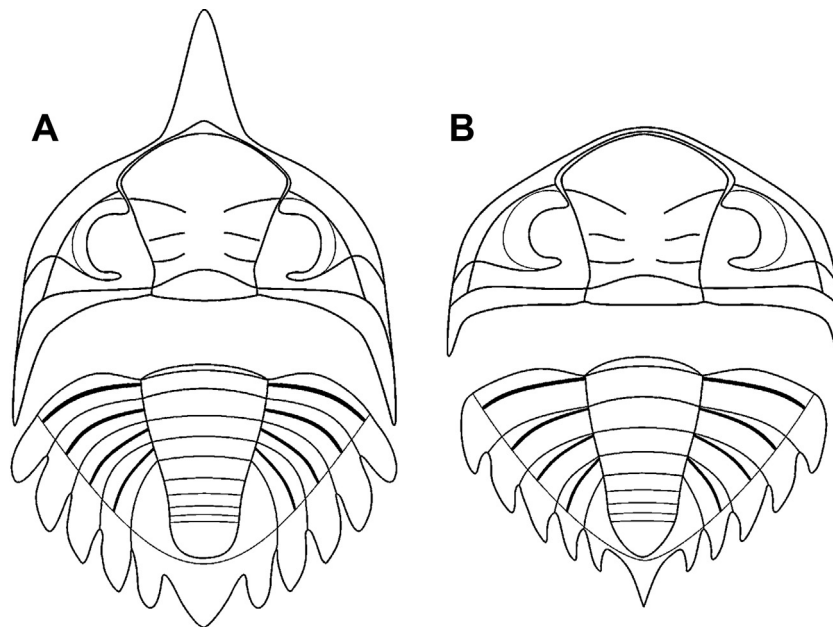


Fig. 2. A. Line drawing of *Minicryphaeus giganteus* nov. sp. B. Line drawing of *Ganetops ebbae* nov. comb.

*M. quaterspinosus*. This assumption would reveal another paedomorph event – a heterometry (Webster and Zelditch, 2005). Indeed, *M. quaterspinosus* is the only species of the genus bearing four pygidial spine pairs whereas the other three have five. However, the longer terminal pygidial spine in *M. minimus*, *M. sarirus* and *M. quaterspinosus* may suggest a peramorphic event as a rate modification (Webster and Zelditch, 2005).

***Minicryphaeus giganteus* nov. sp.**

Figs. 2(A), 3 and 4

**Derivation of the name:** refers to the larger size of this species when compared to the other three species currently included in the genus *Minicryphaeus*.

**Holotype:** a complete and tri-dimensionally well-preserved exoskeleton, with registration number 80202 (Fig. 3(1–3)), housed in the Museo Geológico del Seminario de Barcelona (Spain).

**Paratypes:** three complete specimens (JC101, JC102 and JC103; Joan Corbacho's collection) housed in the Museo Geológico del Seminario de Barcelona (Spain).

**Type locality and horizon:** Ihandar Fm. (Lower Devonian, Pragian) of Jbel El Mrakib, Southern Mader Basin (Morocco).

**Occurrence:** This species is currently known only from its type locality and horizon.

**Measurements:** The whole exoskeleton of the holotype (Fig. 3(1–3)) is either 75 mm (with cephalic spine) or 63 mm (without cephalic spine) in total length. The three paratypes, JC101 (Fig. 3(4–5)), JC102 (Fig. 4(1, 3 and 6)) and JC103 (Fig. 4(2, 4 and 5)), are excellently preserved in three dimensions; their total lengths are: 70 mm/60 mm (JC101), 85 mm/73 mm (JC102), and 75 mm/63 mm (JC103) with and without the cephalic spine, respectively. Table 2 shows the various exoskeletal measurements.

**Diagnosis:** Large holaspide species when compared to the other species included in the genus. Cephalon bearing a strong prefrontal spine. Visual surface with 34 dorsoventral rows of lenses and a maximum of 8 lenses per row. 5 pygidial spines slightly shorter than pleural width (tr.); terminal pygidial spine close to the length of others pygidial spines.

**Description:** Middle-sized Asteropyginae with an exoskeleton of elongated outline. Cephalon with a semi-circular outline, its width is twice its length (without prefrontal spine). Strong and

wide prefrontal spine, as long as the glabella and half as wide as the maximal glabellar width. Pygidium slightly narrower than cephalon and half shorter than thorax. Frontal lobe diamond-shaped. Straight glabellar axial furrows between S1 and S3; S2 straight and oriented towards the front proximally. S1, S2 and S3 proximal tips on the same extrasagittal line. Eye length almost one third of total cephalic length and posterior to the contact between S3 and glabellar axial furrows. Visual surface with 34 dorsoventral rows of facets and a maximum of 8 facets per row. Occipital lobe wider in its middle part. Short and strong genal spines, shorter than glabella and prolonged until the fourth thoracic segment. Narrow anterior border and very wide lateral border, developed in the proximity of the genal spine.

Thorax with eleven segments. Thoracic rachis width very similar to thoracic pleurae length. Pleural furrows well-differentiated, extended as far as the pleural tips. Long and strong pleural tips, projected backwards in their distal part.

Pygidium with a triangular outline, almost twice wider than long. First axial ring as wide as adjacent pleural ribs, nine axial rings as well as a terminal piece, separated by deep furrows. 5–5½ well-differentiated pleural ribs with deep pleural furrows and well-defined interpleural furrows. Pleural bands flat; anterior bands as wide and elevated than posteriors. Five pairs of pygidial spines, shorter than adjacent pleural rib. Wide terminal spine with a triangular or a roughly pentagonal outline and with more or less a similar length of the other pygidial spines. Pygidial border present.

Both hypostome and ventral morphology are unknown.

**Remarks:** The main difference between this new species and the three others included in this genus is the size, *M. giganteus* nov. sp. being almost three times larger than the other species. Moreover, the terminal spine, as long as the other pygidial spines, is characteristic of this species. The precephalic spine of the genus type-species, *M. minimus*, has a thinner basis. Moreover, its pygidium can be differentiated from that of the new species thanks to its terminal spine, which is as wide as the terminal tip of the rachis. *M. quaterspinosus* differs in having only four pairs of pygidial spines and seven axial rings. The cephalon of *M. giganteus* nov. sp. is easily differentiated from that of *M. sarirus* and *M. quaterspinosus* by the presence of the prefrontal spine; the eyes of the new species have more lenses (8) per row.



**Fig. 3.** *Minicryphaeus giganteus* nov. sp., Ihandar Fm., Lower Devonian (Pragian) of Jbel El Mrakib (Morocco). 1–3. Holotype 80202. 1: Dorsal view; 2: Cephalon; 3: Thorax and pygidium. 4, 5. Paratype JC101. 4: Cephalon; 5: Pygidium. All specimens coated with ammonium chloride. Scale bars: 10 mm.

Genus *Ganetops* nov. gen.

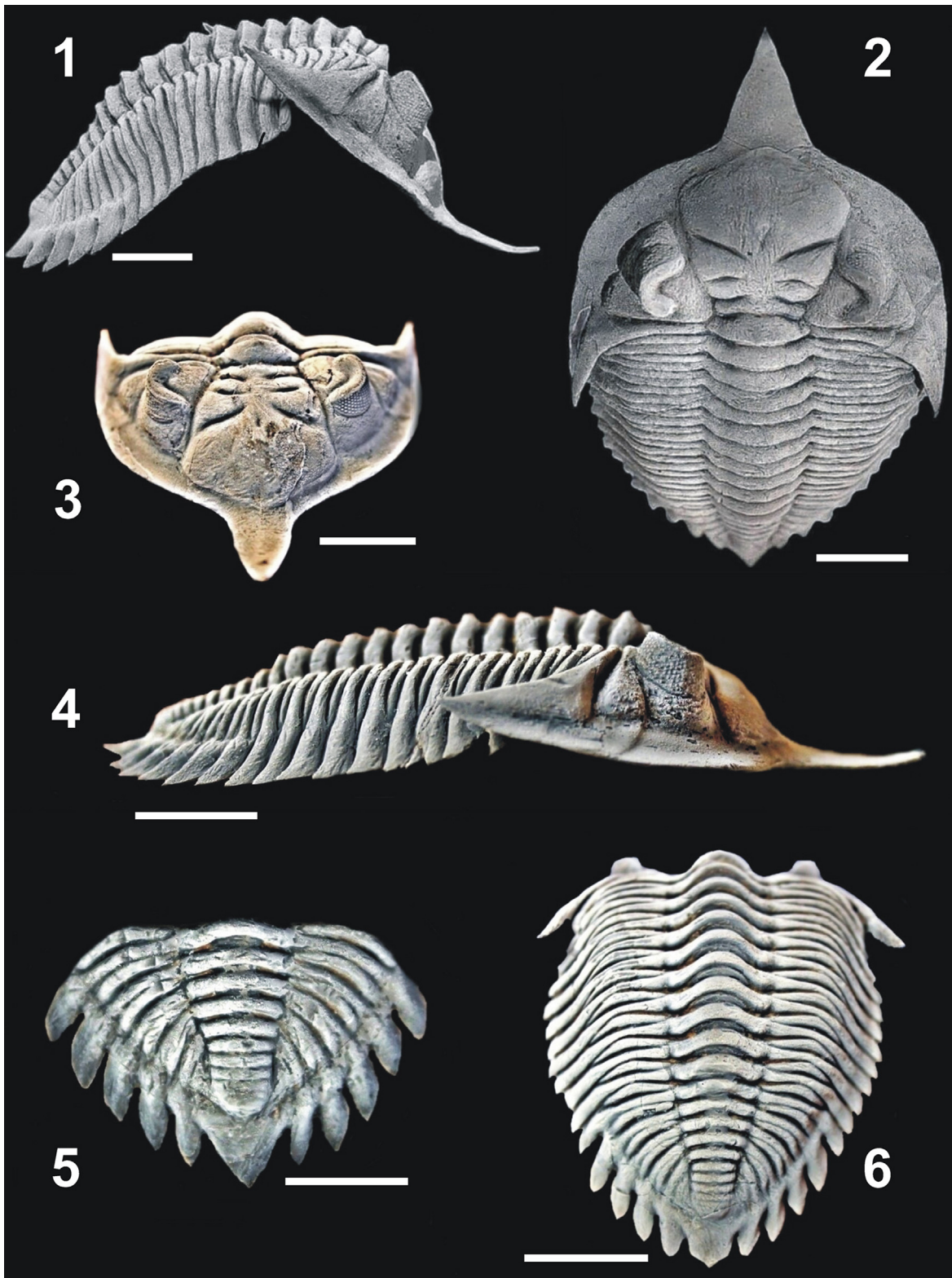
Fig. 2(B)

**Derivation of the name:** from the word “ganet”, meaning first-born in Breton language, since it is the oldest genus so far formally ascribed to the Asteropyginae subfamily.

**Type species:** *Asteropyge* (*Asteropyge*?) *ebbae* R. and E. Richter, 1954, from the upper Lochkovian (Lower Devonian) of the Rhenish Massif (Germany).

**Included species:** *Treveropyge djemelensis* Morzadec, 1997; *Treveropyge*? cf. *ebbae* Smeenk, 1983; *Paracryphaeus gerrinensis* Timm, 1978; *Acastella lata* Timm, 1978; *Treveropyge* sp. Morzadec, 1976.





**Fig. 4.** *Minicryphaeus giganteus* nov. sp., Ihandar Fm., Lower Devonian (Pragian) of Jbel El Mrakib (Morocco). **1, 3, 6.** Paratype JC102. 1: lateral view; 3: frontal view; 6: thorax and pygidium. **2, 4, 5.** Paratype JC103. 2: dorsal view; 4: lateral view; 5: pygidium. All specimens coated with ammonium chloride. Scale bars: 10 mm.

**Occurrence:** All the species included in this genus come from the upper Lochkovian (Lower Devonian). *G. ebbae* nov. comb., *G. gerrinensis* nov. comb. and *G. lata* nov. comb. have been described from the Rhenish Massif (Germany), *G. djemelensis* nov. comb. from the Ougarta (Algeria), *G.?* cf. *ebbae* (Smeenk, 1983) from the Cantabrian Mountains (Spain), and *G.* sp. (Morzadec, 1976) from the Armorican Massif (France).

**Diagnosis:** Frontal lobe diamond-shaped; axial furrows straight between S1 and S3, no contact between S2 and axial furrows; 7–8 lenses per row on visual surface; genal spine very much shorter than glabella, with narrow proximal portion; narrow anterior and lateral border, developed on genal spine. Pygidium with anterior pleural bands as wide and elevated as posterior

**Table 2**

Dimensions of *Minicryphaeus giganteus* nov. sp. A. Sagittal cephalic length; B. Sagittal glabellar length; C. Eye length; D. Distance between the posterior eye side and the posterior border furrow; E. Distance between the anterior margin and the posterior side of S3; F. Maximum cephalic width; G. Maximum glabellar width; H. Occipital lobe width; I. Total thorax length; J. Maximum pygidial width; K. Anterior width of pygidial rachis; L. Posterior width of pygidial rachis; M. Sagittal pygidial length (without pygidial spine); N. Terminal pygidial spine length.

| Specimen  | A  | B  | C | D   | E  | F  | G  | H | I  | J  | K | L | M  |
|-----------|----|----|---|-----|----|----|----|---|----|----|---|---|----|
| MGSB80202 | 17 | 14 | 6 | 1   | 10 | 34 | 16 | 8 | 25 | 22 | 7 | 4 | 13 |
| JC101     | 17 | 14 | 6 | 1   | 10 | 35 | 16 | 8 | 25 | 22 | 7 | 4 | 13 |
| JC102     | 20 | 17 | 7 | 1.5 | 11 | 40 | 18 | 9 | 30 | 26 | 9 | 5 | 16 |
| JC103     | 18 | 15 | 6 | 1   | 11 | 36 | 16 | 8 | 28 | 25 | 7 | 4 | 14 |

bands, flat pleural bands; axis with 8–9 rings; 5 pleural segments; 5 pairs of pygidial spines strongly shorter than pleural width (tr.), mainly developed from posterior pleural bands; terminal pygidial spine, triangular, more than twice longer than other pygidial spines.

**Remarks:** Originally described within the genus *Asteropyge* by Richter and Richter (1954), the type species of this new genus, *G. ebbae* nov. comb., has been attributed to various genera by subsequent authors. Indeed, Struve (1958) included this species in the genus *Treveropyge*, and Gandl (1972) considered it as a member of *Paracryphaeus* (see discussion below for implications of this error on the phylogeny of the Asteropyginae). The confusion with *Treveropyge* probably came from the size of genal and pygidial spines and shape of the median terminal spine. However, *Treveropyge* differs from *Ganetops* nov. gen. by having a rounded frontal lobe, axial furrows curved between S2 and S3, very large eyes, very short genal spines, at least 12 axial rings, six pleural segments, and longer pygidial spines developed from anterior and posterior pleural bands. On the other hand, *G. ebbae* nov. comb. has been considered as a member of *Paracryphaeus* because of the long median spine compared to the other pygidial spines. However, *Paracryphaeus* and *G. ebbae* nov. comb. cannot form a clade because *Paracryphaeus* bears features, such as axial furrows curved between S2 and S3, longer genal spines, at least 11 rings, rounded pleural band section, longer pygidial spines, and a pentagonal shape of the pygidial medial spine.

The cephalon of *G. djemelensis* (Morzadec, 1997) nov. comb. is presently unknown but its pygidium has several features highlighting a close relationship with the type species of *Ganetops* nov. gen. These species share the same number of axial (9) and pleural (5) segments, the very short pygidial spines, the triangular shape of the medial spine which is twice as long as the other pygidial spines. The pygidial structure is the same, with pygidial spines mainly

developed from posterior pleural bands, flat anterior and posterior pleural bands similar in width and height, and wide pleural furrows. However, the spines of *G. djemelensis* nov. comb. are slightly longer and the medial spine is wider than *G. ebbae* nov. comb.

Timm (1981) suggested *G. lata* (Timm, 1978) nov. comb. as a transitional form between *Acastella tiro* R. and E. Richter, 1954 and *G. ebbae* nov. comb. For him, only a determination at the population level was reliable, the specimen level remaining uncertain. The most obvious character to distinguish them is, of course, the only four pygidial spine pairs of *A. tiro*. These spines are smaller in length and width. The ratios axis on pleural widths, width on length of the pygidium and L2 on L3 lengths are more similar between *G. ebbae* nov. comb. and *G. lata* nov. comb. Moreover, these species have L3 slightly more elevated than L2 and L1. However, *G. lata* nov. comb. is similar to *A. tiro* concerning the posterior branch of the facial suture in front of L2.

According to Timm (1981), *G. gerrinensis* (Timm, 1978) nov. comb. is very similar to *G. ebbae* nov. comb. However, if the cephalon are difficult to distinguish, the pygidia of *G. gerrinensis* nov. comb. are more characteristic, with longer spines and a thinner terminal spine.

Smeenk (1983) described a pygidium, *G. cf. ebbae* nov. comb., that he referred to the type species of the genus. Only a clearly longer terminal pygidial spine for the Spanish form allows the differentiation with *G. ebbae* nov. comb.

The taxon described under the name *Treveropyge* sp. by Morzadec (1976) has to be assigned to the new genus *Ganetops*. If the cephalon of this species is presently unknown, the pygidium only differs from the type species *G. ebbae* nov. comb. by the presence of 8 pygidial rings and a more robust terminal spine.

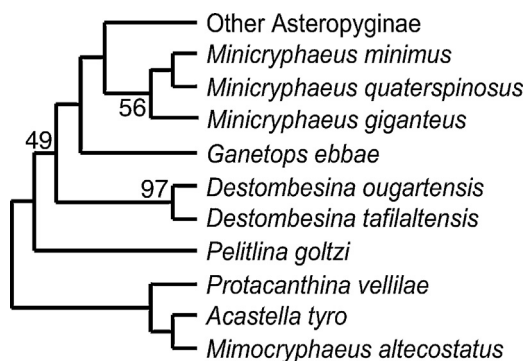
#### 4. Phylogenetic analysis

The parsimony analysis of our data matrix (see Bignon and Crônier, 2014; Table 1) produced 48 most parsimonious trees of 496 steps (consistency index CI = 0.218; retention index RI = 0.740). As no conflict appears between these 48 trees for taxa considered in this work, the basal part of the strict consensus tree shown in Fig. 5 appears fully resolved (all conflicts are located within the group “other Asteropyginae”).

The new species *M. giganteus* appears in a basal position within the genus *Minicryphaeus*. *G. ebbae* nov. comb. is clearly separated from the *Treveropyge* members. Therefore, this species can no longer be considered as a member of the genus *Treveropyge*, thus implying the erection of a new genus: *Ganetops*. It is worth noting that the genus *Destombesina* still appears as the sister group of all others Asteropyginae. As the phylogenetical relationships of the other species in this subfamily are rigorously the same as proposed in Bignon and Crônier (2014), we do not redraw and discuss them here. The jackknife analysis suggests a strong support of the genus *Destombesina* (97%). The genus *Minicryphaeus* (56%) and the node separating the outgroup from the ingroup (49%) are often retrieved. However, the node supporting the position of *G. ebbae* nov. comb. is weakly supported (< 40%).

The addition of two new taxa to the parsimony analysis performed by Bignon and Crônier (2014) highlights the apomorphies developed from or within *Minicryphaeus*. This information illustrates the morphology of the first Asteropyginae and thus the description made by Bignon and Crônier (2014) must be emended for the following features:

- the glabellar axial furrows form an angle more acute (between 20 and 29°; character 43), this angle being more opened in



**Fig. 5.** Basal part of the strict consensus tree of 48 most parsimonious trees (496 steps, CI = 0.218, RI = 0.740); see Bignon and Crônier (2014) for the relationships among other Asteropyginae. Values at nodes were retrieved through a Parsimony jackknife analysis (10,000 replicates, 36% characters deletion; node values < 40% not reported).



derived Asteropyginae than in *Minicryphaeus* (between 30 and 39°) as the anterior border of the cephalon becomes narrower (character 56);

- starting from *Minicryphaeus*, a motion of the cranial posterior border curvature can be observed to the symmetry axis (character 60);
- the cranial lateral border of the first Asteropyginae is not developed on the genal spine (character 66).

The following character states are apomorphies shared by all or some representatives of the genus *Minicryphaeus*, and not features common to the first Asteropyginae as they appeared in the previous version of the phylogeny (Bignon and Crônier, 2014):

- the smooth glabella (character 32) and the tuberculated occipital ring (character 34) are synapomorphies shared by all the members this genus;
- the increase of the number of pygidial axial rings (character 1) is a synapomorphy exclusively shared by *M. sarirus*, *M. minimus* and *M. quaterspinosus*;
- *M. minimus* and *M. quaterspinosus* share the decrease of optical lenses by file (character 49);
- the four pygidial pleural segments (character 6) and spine pairs (character 16) are only intrageneric variability, the most ancestral Asteropyginae having already five pygidial pleural segments and spine pairs.

Because of these changes in the definition of the first asteropygines, the following features support the exclusion of *Destombesina* from this subfamily:

- only up to 8 pygidial axial rings (character 1);
- only four pygidial pleural segments (character 6) and spine pairs (character 16);
- the anterior and posterior pleural bands are not on the same level (character 8);
- S2 are not in contact with the axial furrows (character 42);
- L3 is significantly much wider than L2 (character 44);
- S2 proximal tips are more distal than the one of S1 and S3 (character 45);
- anterior and posterior tips of the palpebral lobe are on the same sagittal line (character 47);
- less lenses by file on the eye (character 49);
- longer glabellar length compared to the width (character 70).

## 5. Discussion

Morzadec (1992) provided the most recent discussion about the first Asteropyginae. Since the last two decades, the systematics of this subfamily have undergone many significant advances and several taxa considered as basal Asteropyginae have been removed from the group. Accordingly, our knowledge of the most ancestral representatives of this group requires to be updated.

The genus *Protacanthina* was considered as one of the oldest genera of the subfamily (base of the upper Lochkovian of Algeria, France and Spain; Morzadec, 1990, 1997; Loydell, 2012). However, in the phylogenetic analysis performed by Bignon and Crônier (2014), this genus was removed from the asteropygines because the study highlighted a closer relationship with members of the Acastavinae. This re-assignment implies a more restrictive definition of the typical Asteropyginae pygidial segmentation and spine morphology. Consequently, Bignon and Crônier (2014) suggested that *Destombesina* (appearing as the sister genus of all other Asteropyginae in their phylogeny) might not belong to this

subfamily. The present update of the group supports this assumption, though without strictly attesting it. Indeed, in the present phylogeny, *Destombesina* still remains the sister genus of all the other subfamily members. However, the addition of the two taxa *M. giganteus* nov. sp. and *G. ebbae* nov. comb. brings new information on the first asteropygine morphology and 10 synapomorphic characters support the hypothesis. *Destombesina* differs from the Asteropyginae by a more reduced number of pygidial segments (axial rings, pleural segments and spines pairs), distinct pygidial pleurae and glabellar furrows organisations, and different eyes (see above for details).

Hollard (1963, 1974, 1977) reported other occurrences of Asteropyginae, of which *G. ebbae* nov. comb., in the lower Lochkovian of Morocco. Unfortunately, in his review of Moroccan Asteropyginae, Morzadec (2001) was not able to check these specimens or to sample new ones. Consequently, this material must be carefully considered, as a formal description and an attribution to the subfamily is still required.

*Cryphina? gdoumontensis* (Asselberghs, 1930) from the lower Lochkovian was reported as probably the oldest asteropygine (Haas, 1968; Morzadec, 1992). Unfortunately, due to the poor preservation of the material, it is currently not possible to formally assess its generic identity. The pygidial segmentation and the connection with pygidial spines are difficult to observe either for the same reason. However, anterior pleural bands seem to have a very faint connection with the spines or no connection at all, making this species close to the genus *Protacanthina*. Moreover, Morzadec (1990) described this species as having 10 axial rings, 6 pleural segments and 7 spine pairs on pygidium. This metamery seems to be too developed when compared to the first Asteropyginae. Indeed, Bignon and Crônier (2014) and the present improvement of the phylogeny show that the number of pleural segments and spine pairs are quite stable within the most ancestral representatives of this subfamily. A decrease in metamery exists within these trilobites (e.g., *M. quaterspinosus*) but there is no example for such increase. This characteristic suggests that the Belgian species is closer to the genus *Protacanthina* where several species have seven pygidial spine pairs and pleural segments. Until the discovery of better-preserved specimens and a precise description of their segmentation, we strongly doubt that this taxon belongs to the Asteropyginae.

Following the work of Bignon and Crônier (2014), the genus *Minicryphaeus* was one of the most ancestral of the subfamily based on the features of *M. minimus* and *M. quaterspinosus*. This result gave the erroneous idea that the firsts Asteropyginae have a reduced size compared to the derived taxa. Thanks to the new material analysed here and particularly to *M. giganteus* nov. sp., this feature appears as a synapomorphy within the genus.

From the seventies, *G. ebbae* nov. comb. started to be considered as the most ancestral species of the subfamily, although associated to distinct genera (*Treveropyge* fide Haas, 1970; *Paracryphaeus* fide Gandl, 1972). This assumption was sustained by workers of the next decade as Timm (1981), Morzadec (1983) and Smeenk (1983). Lieberman and Kloc (1997) did not consider longer *G. ebbae* nov. comb. as a member of *Treveropyge* or *Paracryphaeus* but they did not include this species in their analysis. Nevertheless, they kept the idea that *Treveropyge* was one of the most ancestral genera of the subfamily by using an assumed close relative of this genus as ancestral character bearer. Indeed, the species they called "*Pelitlina*" *smeenki* appears to be much closer to *Treveropyge* than to the Acastavinae *Pelitlina*. The main issue in considering *G. ebbae* nov. comb. within this genus is that it was associated with younger and more derived species. This misunderstanding led to consider some apomorphic state characters as ancestral. Thus, the root of the Asteropyginae tree was taken on too derived taxa, which artificially created two major clades following the conservative



and progressive pygidial pattern of Haas (1970) in a topology which actually appears as multi-pectinated (Bignon and Crônier, 2014).

## 6. Conclusion

The erroneous ascription of the wrong genus as the ancestral Asteropyginae explains why the phylogeny proposed by Bignon and Crônier (2014) appears so different from previous ones. Actually, the generic relationships are rather similar; it was only the root that has been considered differently.

The future studies on the Asteropyginae origins will have to solve its relationships with genera, such as *Destombesina* and *Gourdonia*. Indeed, in the present phylogeny, *Destombesina* appears to be the sister group of all Asteropyginae, but the present topology may be interpreted in two different ways: this genus may be included either within the subfamily or considered as belonging to another clade. Developing such question now appears fundamental to solve the phylogenetic relationships among the subfamilies included in the family Acastidae (Chatterton and Gibb, 2010; Bignon and Crônier, 2014).

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