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## *Morocconites* Struve, 1989, A Devonian Acastine Trilobite (Calmoniidae: Acastinae)

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### ABSTRACT

A well-preserved dorsal exoskeleton of *Morocconites malladoides* Struve, 1989, from the Devonian of Morocco, allows a complete description of the type species of this monotypic genus. *Morocconites* is most closely related to the acastine *Acas-*

*toides* Delo, 1935, with unique modifications of the cephalic border and pygidium. *Morocconitinae* Struve, 1989, is a subjective synonym of the calmoniid subfamily Acastinae Delo, 1935.

### INTRODUCTION

*Morocconites malladoides* Struve, 1989, was based on a mostly exfoliated dorsal exoskeleton from Devonian strata in the Alnif area, west of Erfoud, Maider, Morocco. The species was interpreted as "possibly rooting in dalmanitine dalmanitaceans" and with "zeliszkelline/dalmanitine descent . . . obvious" (Struve, 1989: 567). An independent genus and subfamily (*Morocconitinae* Struve, 1989) were established with the hypothesis that a "mixture of distinctly divergent characters of different, clearly separated phyletic branches . . . seems to root deep in the early history of the dalmanitids" (p. 568). These ancient (Ordovician) affinities are intriguing, given the Emsian or Eifelian age attributed to *Morocconites*.

Simon Harrison of Bath, England, allowed

me to examine a superbly preserved acastine from Devonian strata at Alnif in the Moroccan North Sahara. It was determined that the outstretched dorsal exoskeleton described in this paper is conspecific with the holotype of *Morocconites malladoides* Struve. The new specimen provides strong evidence for closest relations to taxa classified in the calmoniid subfamily Acastinae (notably *Acastoides* Delo, 1935). Accordingly, the subfamily *Morocconitinae* is removed from the Dalmanitidae, and is regarded as a synonym of Acastinae (Calmoniidae). New morphological information afforded by fine preservation, as well as necessity for differentia from similar acastines, have stimulated a revised diagnosis of *Morocconites*.

Descriptive terminology used herein is

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generally that of Harrington et al. (1959). Points of curvature on the facial suture are lettered as by Richter and Richter (1949: fig. 1). Lateral glabellar lobes and furrows are denoted following Jaanusson (1956: 37), with the prefix L- or S-, numbered 0–4 from rear (occipital) to front. *Pseudo-articulating half ring* is as suggested by Holloway (1981: 695). The term *epipleural furrow* is introduced for transverse grooves on the pygidial pleural ribs between the pleural and interpleural furrows. These are observed in the Acastinae (*Morocconites*), Phacopidellinae (e.g., Chlupáč, 1977: pl. 1, fig. 11), and Dalmanitidae (e.g., Destombes, 1972: pl. 4, fig. 7).

## SYSTEMATIC PALEONTOLOGY

### FAMILY CALMONIIDAE

DELO, 1935

### SUBFAMILY ACASTINAE

DELO, 1935

*Morocconites* Struve, 1989

TYPE SPECIES: *Morocconites malladoides* Struve, 1989. By original designation.

DIAGNOSIS: Acastinae with anterior border having very long, upcurved median spine. Cephalic lateral border broadened against anterior genal region; lateral margins subparallel between border swelling and genal angle. Pygidial margin entire; transverse apodemes in anterior five ring furrows; ring furrows shallow medially. Anterior pleural furrow narrow but moderately deep, succeeding pleural furrows shallow, subequal to interpleural furrows; shallow epipleural furrows bisect anterior and posterior pleural bands.

DISCUSSION: *Morocconites* is maintained as a monotypic genus, but its diagnosis is revised to distinguish it from other genera of Acastinae. The conspicuous cephalic anterior border spine is peculiar for an acastine, although similar to Calmoniinae such as *Schizostylus* Delo and the acastavine *Centauropyge* Haas, 1968. The entire-margined, semicircular pygidium of *Morocconites* with a distinct border furrow is most typically acastine [although, as noted by Struve (1989), pygidial form is superficially similar to that of Phacopidellinae. This applies particularly to species with shallow epipleural furrows, e.g., *Phacopidella glockeri* (Barrande)].

Form and incision of the lateral glabellar furrows (e.g., evenly curved S3) are very similar in *Morocconites malladoides* and *Acastoides paeckelmanni* (cf. Richter and Richter, 1952: pl. 2) and in *A. constricta* (Salter) (Richter and Richter, 1954: pl. 3, fig. 42). A shortened (exsag.) L1 groups *Morocconites* with the clade Acastinae + Acastavinae + Asteroptyginae (Destombes and Henry, 1987: 136), in contrast to primitive Dalmanitidae and Calmoniinae. This synapomorphy excludes certain taxa previously assigned to Acastinae, which have plesiomorphic conditions of longer (exsag.) L1, with S1 inclined abaxially, and bifurcate proximally (e.g., *Andinacaste* Eldredge and Braniša, 1980; “*Acaste*” *birninghamensis* Norford, 1972; *Juyuyops* Baldis and Blasco in Baldis et al., 1976). Acastinae s.s. (e.g., *Acaste* Goldfuss; *Acastoides* Delo + *Morocconites* Struve; *Acastocephala* Shergold) have S2 approximately transverse (although distinctly convex forward). *Andinacaste* and “*Acaste*” *birninghamensis* retain the primitive state of S2 inclined abaxially (shared with primitive Calmoniinae and *Baniaspis* Destombes, 1972).

Likewise, the auxilliary impression system in the frontal glabellar lobe of *Morocconites* is that diagnostic of post-Llandovery Acastacea (Eldredge, 1979), a triangular pattern of discrete radiating rows of pits (fig. 1). Llandovery “*Acaste*” *birninghamensis* Norford resembles Ordovician Acastacea (*Kloucekia* Delo; *Phacopidina* Bancroft; *Baniaspis* Destombes) in the presence of muscle scars in the median region of the impression system (Norford, 1972: pl. 1, fig. 13). Glabellar morphology of *Morocconites* bears resemblance to that of the Emsian asteropygine *Kayserops kerfornei* (Pichard) (see Morzadec, 1983: pls. 12, 13), as does the long cephalic antero-median spine; however, the smooth-margined pygidium and rounded genal angle of *Morocconites* are acastine features which preclude assignment to Asteroptyginae. Structure of the thoracic pleurae is also comparable to that of Acastinae, e.g., the gently sinuous epifacetal pleural furrow, and blunt distal projection from behind the articulating facet. In addition to similarities in glabellar furrows, *Acastoides* Delo, 1935, is most comparable to *Morocconites* in the relatively short (exsag.) eye with a low visual field, and strong arching

(tr.) of the cephalon, i.e., steep librigenal field. Shergold (1966: 200) cited a subpentagonal cephalic outline and eyes set high up on the genae as characteristic of *Acastoides*; both of these features are shared with *Morocconites*. The relatively deep incision of the cephalic lateral border furrow in Devonian species such as *Acastoides paeckelmanni* (see Haas, 1968: pl. 32) is peculiar among Acastinae, but is shared with *Morocconites*. Among species assigned to *Acastoides*, the pygidium of *A. (?Acastoides) aspidium* Haas, 1968, most closely resembles that of *Morocconites malladoides*. This species likewise has the axis elongated behind the anterior three rings, with less marked anteroposterior differentiation than other *Acastoides*. Devonian species from the Malvinokaffric Realm formerly assigned to *Acastoides* are regarded as Calmoniinae (cf. Eldredge and Braniša, 1980), and have been reassigned to *Pennaia* Clarke (see Edgecombe, in press).

With this hypothesis of relationships, the recognition of a monotypic subfamily Morocconitinae would render Acastinae a paraphyletic group (since *Morocconites* is, cladistically, a modified acastine). The genus is accordingly classified in Acastinae, with which Morocconitinae is placed in subjective synonymy. Affinities to Siluro-Devonian *Acastoides* are also more compatible with the stratigraphic occurrence of *Morocconites* than Struve's (1989) contention that the genus signals early (i.e., Ordovician) dalmanitid history.

*Morocconites malladoides*

Struve, 1989

Figures 1, 2

*Morocconites malladoides* Struve, 1989: 568–569, pl. 8, fig. 44.

**MATERIAL:** A testiferous, outstretched dorsal exoskeleton, collection of Simon Harrison, from gray, sparitic limestone, Devonian, Alnif, 80 km west of Erfoud, Errachidia Province, Morocco.

**DESCRIPTION:** Cephalon subpentagonal in outline (excluding anteromedian spine). Anteroventral margin with gentle anterior arch. Cranidial length (sag.) 60 percent of width. Axial furrow diverging forward at 40° between distal ends of S1 and S3, convex out-



Fig. 1. Camera lucida drawing of glabella in anterodorsal view, with auxiliary impression system (shallow pits in cuticular surface) illustrated on left side of frontal lobe. pgf, preglabellar furrow.

ward opposite L3; axial furrow shallowest opposite L2 and posterior part of L3, narrow but distinctly incised opposite anterior part of L3/posterolateral edge of frontal lobe and L1/L0. Preglabellar furrow moderately deep (sag.), shallowing abaxially; cranidial anterior border short, moderately declined forward, longest sagittally in dorsal orientation but visible across width. Cephalic anterior border spine gently curved, tip steepened slightly beyond vertical, raised strongly above glabella; spine triangular, gently tapering in dorsal view. Anterior branch of facial suture with nearly straight anteroventral course between  $\gamma$  and just outside anterolateral region of frontal glabellar lobe; cranidial anteromedian margin arched (tr.) dorsally. Posterior branch of facial suture gently curved, convex forward (in dorsal orientation) between  $\epsilon$  and  $\omega$ , set in shallow, narrow genal sulcus; suture sharply flexed backward on outer part of lateral border,  $\omega$  behind  $\epsilon$ . Glabellar length 95 percent of width across frontal lobe. Glabella raised above palpebral lobe, tallest on faintly convex (tr.) median region of L3. L3 lateral lobe raised well above posterolateral region of frontal lobe, gently convex (exsag., tr.), declined abaxially. Frontal lobe mushroom-shaped, 53 percent of glabellar length, flattened (sag.) for most of length, declined anteriorly at 30°; dense, raised granules concentrated anteriorly, anterolaterally. Auxiliary impression system of coarse, shallow pits;

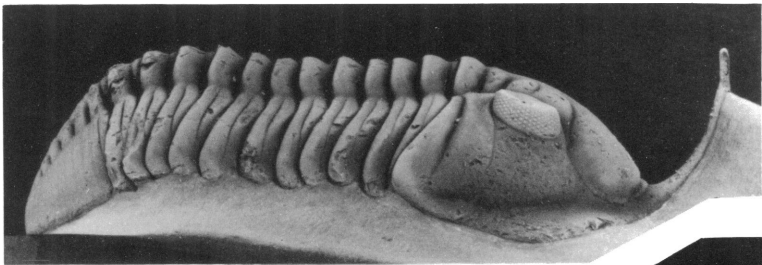
"acastid triangular" pattern, two closely spaced radiating rows, with linear series of pits converging anteromedially toward preglabellar furrow. S3 narrow (exsag.), of even, moderate depth, nonapodemal, evenly convex forward. L3-L2 lateral lobes weakly isolated by shallow longitudinal furrow. L3 widest (tr.) at midlength (exsag.), 82 percent of width across frontal lobe. S2 faintly convex forward, gently inclined anteromedially, narrow, moderately deep, shallowing distally, weakly continuous to axial furrow. S1 deep exsagittally, nearly straight, inclined anteromedially, faintly impressed medially. L1 shortened abaxially, 42 percent length (exsag.) of L2. L1-L0 of moderate, even convexity (tr.). S0 of moderate depth, short (sag.), weakly convex forward, incised as deep, narrow (tr.), apodemal grooves distally. L0 65 percent width of frontal lobe, 110 percent width of L1, longest sagittally, length 22 percent of width, L0 gently arched forward medially, with low convexity (sag.), raised equal to anterior part of L1. Exsagittal length of eye 41 percent of glabellar length (sag.). Palpebral furrow of rounded V-shape, shallow, narrow. Palpebral lobe crescentic, flattened, gently declined outward at midlength (exsag.), set slightly below interocular fixigena. Visual surface with 26 dorsoventral lens files with maximum of 6 lenses per file. Subocular groove shallow, narrow. Librigenal field faintly convex, tall, steeply declined. Extraocular genae with pervasive coarse, shallow pits, subdued granulation; raised granules concentrated distally. Cephalic anterior border narrowest against anterolateral region of frontal glabellar lobe, gradually widening posterolaterally, flattened, gently declined outward; cephalic border, cranial anterior border densely, coarsely granulate; cephalic anterolateral margin weakly convex outward. Lateral border sharply narrowing posteriorly;

lateral border furrow strong. Postocular fixigenal field 36 percent length (exsag.) of eye, gently convex (tr.), turned down abaxially. Posterior border furrow narrow, moderately deep, shallowing distally but distinctly continuous with lateral border furrow; border furrow approximately straight, weakly directed backward distally. Posterior border short (exsag.) proximally, set below fixigena, evenly and rather strongly lengthening abaxial to midwidth (tr.) of fixigena, with posterior margin curved backward; genal angle rounded.

Thorax of 11 segments. Axis about 42 percent of thoracic width. Axial ring of even length (sag., exsag.), gently arched forward sagittally and adjacent to narrow, shallow axial furrow; ring gently convex (sag.), moderately convex (tr.) in anterior segments, convexity gently decreasing posteriorly. Articulating half ring raised to crest of axial ring, set off by sharp, moderately incised furrow. Pleural field set well below crest of axial ring, especially in anterior segments. Pleurae of moderate convexity (tr.), inner part weakly convex, declined abaxially; outer part rather straight (tr.), moderately turned down and back. Pleural furrow narrow, moderately incised; shallow immediately adjacent to axial furrow; pleural furrow weakly sinuous, straight and gently oblique backward across inner part of rib, continuing across most of articulating facet with shallow to moderate incision near midlength (exsag.) of facet; posterior band lengthening distally around articulating facet. Articulating facet curving backward across most of distal region of pleura in anterior segments, relatively shorter (exsag.) in posterior segments, with dense granulation. Posterior margin of pleurae flexed forward distal to fulcrum, terminating in short, blunt point, most prominent in anterior segments.

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Fig. 2. *Morocconites malladoides* Struve, 1989, undetermined Devonian strata, Alnif, 80 km west of Erfoud, Errachidia Province, Morocco; private collection of S. Harrison, Bath, UK. Specimen coated with ammonium chloride prior to photography. A. Right lateral view,  $\times 1.5$ . B. Left lateral view of cephalon,  $\times 4$ . C. Dorsal view of cephalon and thorax,  $\times 1.5$ . D. Oblique right anterolateral view of cephalon and thorax,  $\times 1.5$ . E. Dorsal view of pygidium and posterior region of thorax,  $\times 1.75$ . F. Left lateral view of thorax,  $\times 4$ .



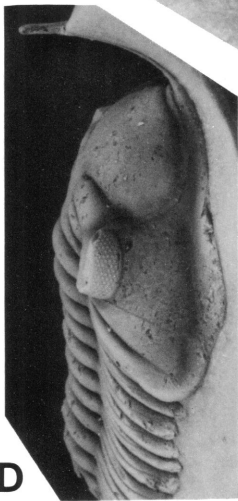
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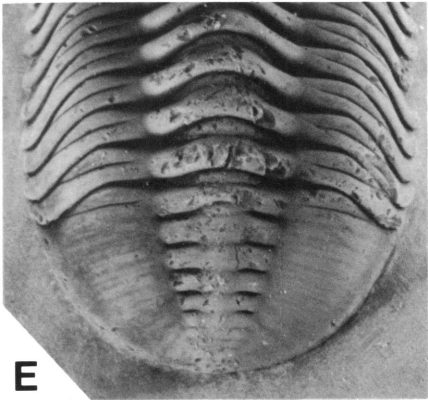
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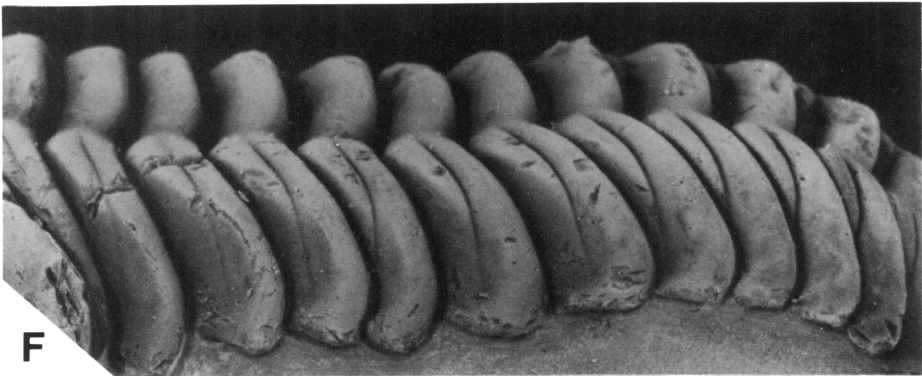
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D



E



F

Pygidium semicircular, length (sag.) 50 percent of width. Axis 38 percent of pygidial width anteriorly. Eight complete axial rings and blunt, indistinctly segmented terminal piece bounded by very shallow axial furrow. Anterior ring moderately arched (tr.), third gently convex, postapodemal segments six through terminal piece nearly flat. Apodemal grooves relatively shallower and narrower (tr.) in rearward ring furrows, grading from 31–27 percent of width of ring furrow from first to fifth furrow. Pseudo-articulating half ring prominent on second axial ring. Postaxial region 8 percent of length (sag.) of pygidium. Pleurae gently, evenly convex (tr.). Anterior pleural furrow extends onto articulating facet distally. Anterior and posterior bands of about even length (exsag.) across pleura to border furrow in second through fifth segments, indistinctly defined in posterior segments. Epipleural furrows parallel to pleural furrows, at about midlength (exsag.) of anterior and posterior bands. Border narrow, of even width, distinctly less declined outward than furrowed pleural region, densely granulate.

DISCUSSION: The preserved details of the holotype of *Moroccanites malladoides* precisely correspond with the specimen described above, allowing little question that they are conspecifics. Struve's specimen retains no evidence of the cephalic anterior border spine, but clearly displays the broadening of the lateral border, unique among acastines. Based on the presence of 26 dorsoventral lens files in the eyes of the new specimen, Struve's guess of 10 to 15 files is regarded as an underestimate (the visual surfaces are not preserved in the holotype). Complete preservation of the pygidial axis (exfoliated posteriorly in the holotype) allows eight axial rings to be identified. Cuticular preservation also reveals a distinctive prosopon of raised granules concentrated toward the external regions of the exoskeleton. This is most conspicuous on the cephalic border, but also well developed on the thoracic articulating facets and pygidial border. Granulation is of lower relief on the extraocular genae, and even more subdued on other (more adaxial) regions of the exoskeleton. Preferential "roughening" of the articulating facet relative to the remainder of the thoracic pleura is evidently a coaptation (cf. Speyer, 1988) for minimizing pleural slippage during enrollment.

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