

Ontogeny of a new cyrtosymboline trilobite from the Famennian of Morocco

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Abundant trilobite remains were recovered from late mid-Famennian marlstones from various sites in Eastern Tafilalet, southeast Morocco. All belong to a single taxon previously identified as *Cyrtosymbole* (*Waribole*) *prima*. This taxon is designated the type species of *Osmolskabole* gen. nov. A redefinition of this species, including the description of newly discovered, disarticulated exuviae both in limestone and silicified state of preservation, is given. In particular, silicified sclerites of various sizes allow the first complete growth series of a cyrtosymboline proetid to be presented. The close morphological resemblance of its protaspis stages to known proetoid larvae emphasizes the homogeneity of the early ontogeny in this superfamily. The Famennian proetoid anaprotaspis is also of comparable size to that of other Devonian proetoid larvae. However, their size-range is much less than that observed in Carboniferous larvae. This suggests that the survival of proetoid trilobites at the Frasnian-Famennian Kellwasser crisis did not result from a modification of the developmental strategy, as it might have been the case at the terminal Devonian extinction event. Moreover, *O. prima* possesses a plectrum from the metaprotaspis to the mid meraspis periods. This implies that the natant hypostomal condition is not steadily acquired early in the ontogeny of the Proetida. Thus we preclude the use of this character in the diagnosis of this order.

Key words: Trilobita, *Proetoidea*, *Cyrtosymbolinae*, ontogeny, protaspis, Famennian, Morocco.

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Introduction

Until recently, the youngest proetoid protaspides known were those described from the Eifelian of Canada (Chatterton et al. 1999). They were attributed to an undetermined species of *Dechenella*. Four older proetoid larvae are known, ranging from the Ordovician to the Lower Devonian. Edgecombe et al. (1997) described the ana- and metaprotaspides of the tropidocoryphid *Stenoblepharum astinii* Edgecombe, Chatterton, Vaccari, and Waisfeld, 1997, from the Ordovician of Argentina. These authors also reassigned Ordovician metaprotaspides previously described by Beecher (1893, 1895) to another tropidocoryphid species, *Decoroproetus beecheri*. Only one specimen of proetoid anaprotaspis is known from the Silurian. It was figured by Chatterton and Speyer (1997: fig. 166.5) as an undetermined anaprotaspis, “possibly of an *Illaenina*”, but was recently reassigned to an undetermined proetoid species (Lerosey-Aubril and Feist 2005). So far, the only known complete growth series of a proetid trilobite was described by Chatterton (1971) from the Lower Devonian of New South Wales (i.e., *Devonoproetus talenti* Chatterton, 1971).

The recent discovery of Lower Carboniferous protaspides (Lerosey-Aubril and Feist 2005) has substantially extended our knowledge of the early growth stages of proetoid

trilobites. Indeed these larvae illustrate that among Proetida, proetoid trilobites may have experienced a particular kind of early life history, which is exceptionally conservative over a long time-span. However, the occurrence of unusually large anaprotaspis specimens led us to speculate on a possible modification of early ontogeny that may have allowed the survival of proetoids during the end-Devonian biocrisis. In order to evaluate whether this hypothesis is well founded, the discovery of Upper Devonian proetoid larvae is of utmost importance. Crônier et al. (1999) described anaprotaspides from the Upper Famennian of Germany that they considered, with some doubt, to be possible proetid larvae. Re-examination of these specimens confirms that they are typical proetoids but also reveals that they have suffered from deformation. In this sample, we subsequently recognized metaprotaspides, as well as additional anaprotaspides, which will be described in a forthcoming work.

In the present contribution we describe the ontogenetic development of a late mid-Famennian cyrtosymboline species from southeastern Morocco, which is conspecific with *Cyrtosymbole* (*Waribole*) *prima* Osmólska, 1962, and which we designate as the type species of the new genus *Osmolskabole*. The recovery of its earliest larval stages enables the first complete growth series of a Famennian pro-

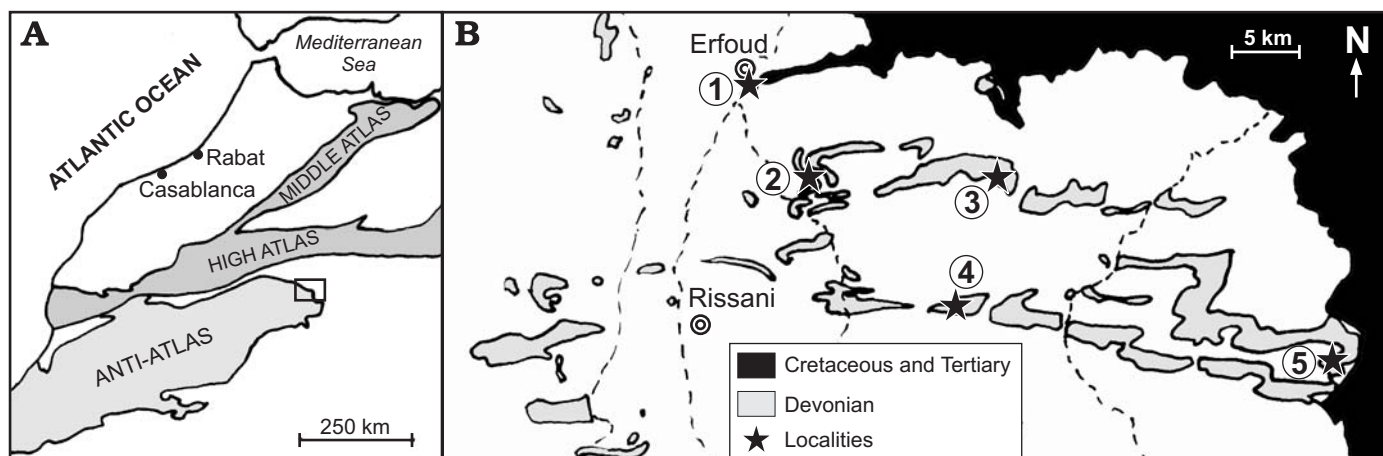


Fig. 1. Location of the considered trilobite localities. **A.** Location of the Tafilalt region, eastern Anti-Atlas, Morocco. **B.** Devonian outcrops southeast of Erfoud, Tafilalt, with considered trilobite localities: 1, Bordj Est; 2, Bou Tcherafine; 3, Hamar Laghdad; 4, Korb-el-Atil; 5, Ouidane Chebbi.

etid to be presented. This is particularly important because the cyrtosymbolines represent a major clade that characterizes latest Devonian proetoid evolution. Indeed, the Late Devonian Kellwasser extinction event led to a profoundly impoverished trilobite community in the basal Famennian (Feist and Becker 1997). Thereafter, the appearance of cyrtosymbolines in the Late *Palmatolepis crepida* Zone and their subsequent radiation was crucial for trilobite recovery in the early Famennian. Despite the description of numerous cyrtosymbolines, their ontogeny has remained poorly known, being restricted to isolated meraspid stages in a few species only (e.g., Osmólska 1962; Chlupáč 1966; Alberti 1975a, b, 1976).

Localities, material, and methods

The occurrence of the Polish species *Osmolskabole prima* (Osmólska, 1962) in southeastern Morocco was first recognized by Alberti (1975a), as *Archegonus (Waribole?) prima* (Osmólska, 1962), at the locality Bordj Est in the immediate vicinity of Erfoud (locality 1 in Fig. 1). Abundant disarticulated sclerites in limestone preservation were recovered by us at this locality, and additionally at Bou Tcherafine, south of Erfoud (locality 2 in Fig. 1) and at Hamar Laghdad, east-southeast of Erfoud (locality 3 in Fig. 1). These occur in the Famennian marlstones where they are associated with clymenids and conodonts indicating a *Protoxyclymenia dunkeri* Zone (= *Palmatolepis postera* Zone) age (i.e., the upper “to IV stuffe” of the ammonoid biozonation). Other co-occurring trilobites are *Phacops (Phacops) tafilaltensis* Crônier and Clarkson, 2001 and *Dianops* sp.

Silicified specimens of *O. prima* were recovered from two different localities to the southeast of Erfoud. The first sample originates from loose limestone blocks collected in the western part of Korb-el-Atil (locality 4 on Fig. 1). These contained remains of arthrodires associated with silicified

sclerites of *Phacops (Phacops) tafilaltensis* Crônier and Clarkson, 2001. Associated conodonts provide only generalised Famennian age, within the span of the *Palmatolepis crepida* and *Palmatolepis postera* Zones.

The second sample is from green-beige argillaceous limestone concretions that were collected in the easternmost part of the Tafilalt, beneath the overlying Cretaceous Hamada, about 2.5 km northeast of Ouidane Chebbi (locality 5 in Fig. 1). It also contains remains of *Phacops (Ph.) tafilaltensis* (Catherine Crônier, personal communication 2004). In addition to a few long-ranging conodonts, associated specimens of *Platyclymenia* sp. (Ammonoidea) suggest a middle Famennian age (“to IV stuffe” of the ammonoid biozonation; Upper *Palmatolepis trachytera* to *Palmatolepis postera* zones) for this trilobite assemblage.

Silicified trilobites were obtained by etching of the carbonate rock with diluted (10 percent) formic acid. In both samples, the material is undistorted and only slightly silicified by extremely fine-grained white recrystallisation. However, the material from Korb-el-Atil is better preserved than the extremely fragile and mostly fragmentary specimens from Ouidane Chebbi. The sclerites of *O. prima* recovered from Korb-el-Atil mostly represent later growth stages, although protaspid larvae also occur. In contrast, the trilobite remains from Ouidane Chebbi consist almost exclusively of early and earliest larval stages, the few associated holaspid sclerites supporting their attribution to *O. prima*. Neither complete specimens nor articulated sclerites were found in any of the samples.

Institutional abbreviations.—The material described and figured in this work is housed in the collection of Invertebrate Palaeontology at the University Montpellier II (silicified specimens: UMC-IP361-422; calcareous specimens: UMC-IP423-432).

Other abbreviations.—exsag., exsagittal; sag., sagittal; tr., transversal.

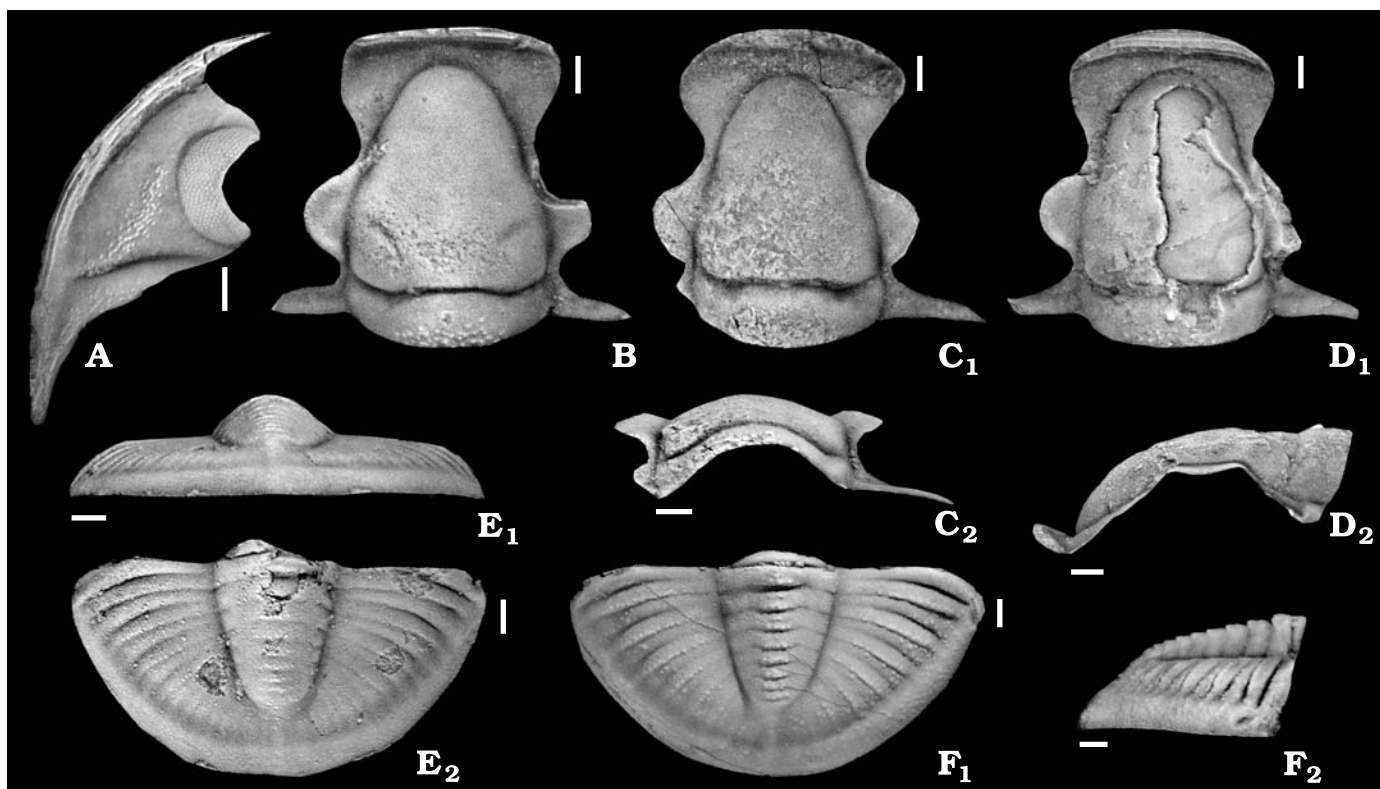


Fig. 2. *Osmolskabole prima*. Middle Famennian (to IV, Upper *Palmatolepis trachytera* to *Palmatolepis postera* Zones). A. Left librigena, Hamar Laghdad, UMC-IP423 in dorsal view (see the small tubercles). B. Cranidium, Hamar Laghdad, UMC-IP424 in dorsal view. C. Cranidium, Hamar Laghdad, UMC-IP425 in dorsal (C₁) and posterior (C₂) views. D. Largest cranidium, Hamar Laghdad, UMC-IP426 in dorsal (D₁) and lateral (D₂) views. E. Pygidium, Ouidane Chebbi, UMC-IP427 in posterior (E₁) and dorsal (E₂) views. F. Pygidium, Hamar Laghdad, UMC-IP428 in dorsal (F₁) and lateral (F₂) views. All figures are digital photographs of calcareous specimens. Scale bars 0.5 mm.

Systematic paleontology

Family Proetidae Hawle and Corda, 1847

Subfamily Cyrtosymbolinae Hupé, 1953

Genus *Osmolskabole* nov.

Type species: *Cyrtosymbole (Waribole) prima* Osmólska, 1962; Gałęźnice, Holy Cross Mountains, Poland, Famennian, Devonian.

Derivation of the name: After professor Halszka Osmólska, Warsaw, in recognition of her fundamental work on cyrtosymboline trilobites.

Assigned species: *Cyrtosymbole (Waribole) prima* Osmólska, 1962, *Cyrtosymbole (Waribole) secunda* Osmólska, 1962, *Cyrtosymbole (Cyrtosymbole) neptis* Chlupáč, 1961.

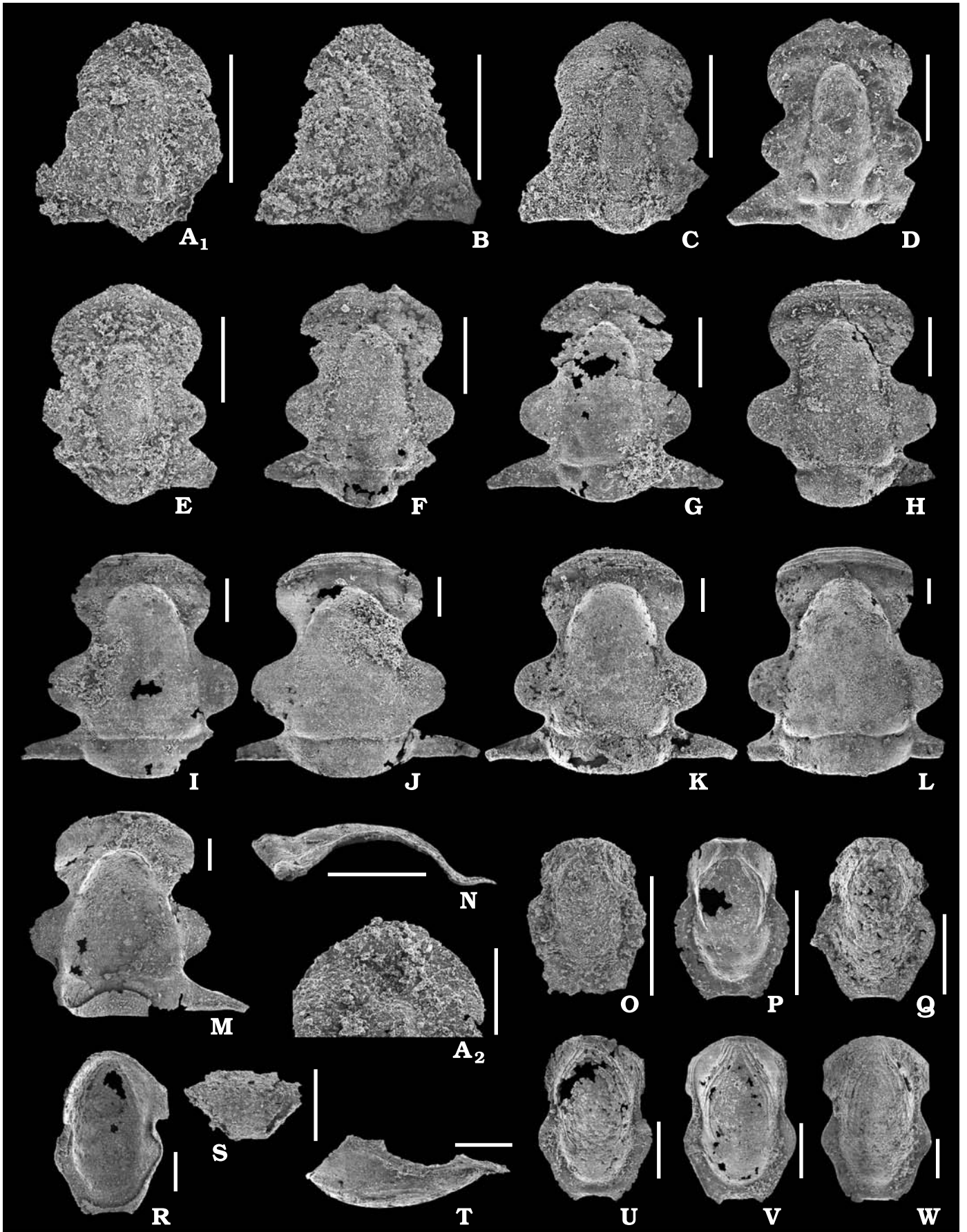
Diagnosis.—*Osmolskabole* differs from all other genera of the subfamily by having the following unique combination of characters: glabella low, with strongly tapering and slightly constricted frontal lobe; preglabellar field short; anterior border medially straight and upraised; glabellar furrows faint; palpebral lobes broad (tr.) and far backwardly placed; visual surface very large and gently sloping abaxially, genal spine short; pygidium semielliptical, with slightly inflated border; pygidial axis high with 8–9 rings; postaxial ridge long; postaxial field short or absent; up to 7 pleural ribs, pleural field horizontal adaxially with abaxially impressed pleural and interpleural furrows.

The major traits that distinguish *Osmolskabole* from *Cyrtosymbole*, as redefined by Feist and Lerosey-Aubril (2005, this volume), are: glabella (tr. and sag.) low, with strongly tapering frontal lobe and faint glabellar furrows, preglabellar field short, palpebral lobes backwardly placed; eyes comparatively larger (bearing almost twice the number of eye-lenses); inner pleural field horizontal, with adaxially effaced pleural and interpleural furrows, and postaxial ridge conspicuously long.

Osmolskabole share the following features with *Pseudowaribole*: glabella conical and slightly constricted antero-laterally, palpebral lobes and eyes large, and glabellar, pleural and interpleural furrows frequently effaced. However, it differs from this genus by having the following characteristics: anterior border upraised and straight, vault of glabella higher, dorsal furrows deeper; pygidial border defined.

Remarks.—Previous authors (Osmólska 1962: 131) were aware of the particularities of the “*neptis–primus–secundus* group” (Alberti 1975b) that share some characters with the older *Cyrtosymbole*, and others with certain species of the younger, late Famennian *Cyrtosymbole (Waribole)* Richter and Richter, 1926 [= *Archegonus (Waribole) sensu* Hahn 1965; = *Pseudowaribole* Hahn and Hahn, 1967].

After having first assigned this group with doubt to *Archegonus (Waribole?)* Alberti (1976) reassigned it to *Cyrtosymbole*. This reflects the hesitation in systematic paleontology



when defining a taxon that apparently takes a phylogenetically intermediate position between the older *Cyrtosymbole* and species of the younger *Pseudowaribole*. However, we consider that it is adequate to recognize the independent generic status of this group, as it is characterized by a combination of ancestral and derived traits within the evolutionary lineage leading from *Cyrtosymbole* (*sensu* Feist and Lerosey-Aubril 2005, this volume) to *Pseudowaribole*.

Osmolskabole prima (Osmólska, 1962)

Figs. 2–5.

Cyrtosymbole (*Waribole*) *prima* sp. nov; Osmólska 1962: 129, pl. 7: 1–3, text-pl. 6: 5, 6.

Archegonus (*Waribole*) *primus* (Osmólska, 1962); Hahn 1965: 242.

Archegonus (*Waribole?*) *primus* (Osmólska, 1962); Alberti 1975a: 190, fig. 2: 18–27, fig. 3: 1–7, 9–12.

Pseudowaribole (*Pseudowaribole*) *neptis prima* (Osmólska, 1962); Hahn and Hahn 1975: 52.

Cyrtosymbole (*Cyrtosymbole*) *prima* (Osmólska, 1962); Alberti 1975b: 45.

Material.—Figured silicified material: 14 cranidia (UMC-IP361–374), 8 hypostomes (UMC-IP375–382), 1 rostral plate (UMC-IP383), 10 librigenae (UMC-IP384–393), 2 thoracic segments (UMC-IP394–395), 13 pygidia (UMC-IP396–408), 7 anaprotaspides (UMC-IP409–415), 1 anaprotaspis hypostome (UMC-IP416), 5 metaprotaspides (UMC-IP417–421); Additional silicified material (UMC-IP422): 79 cranidia, 65 hypostomes, 30 librigenae, 27 thoracic segments, 126 pygidia, 49 anaprotaspides, 54 metaprotaspides; Figured calcareous material: 3 cranidia (UMC-IP424–426), 1 librigena (UMC-IP423), 2 pygidia (UMC-IP427–428); Additional calcareous material: 4 cranidia, 4 librigenae, 5 pygidia from Bordj Est (UMC-IP429); 8 cranidia, 5 librigenae, 12 pygidia from Bou Tcherafine (UMC-IP430); 14 cranidia, 1 hypostome, 12 librigenae, 13 pygidia from Hamar Laghdad (UMC-IP431); 1 cranidium from Ouidane Chebbi (UMC-IP432), in association with silicified sclerites.

Remarks.—The abundant new material from Morocco corresponds largely to the description of the species given by Osmólska (1962: 130). A few additional adult features and slight differences that might characterize the Moroccan population of the species are summarized as follows:

In late holaspids rather faint posterior branches of S1 are discernable and more glabellar furrows are discernable on the internal mould (Fig. 2D). The anterior border is ridge-like, upraised and of nearly equal breadth (sag.) as the pre-

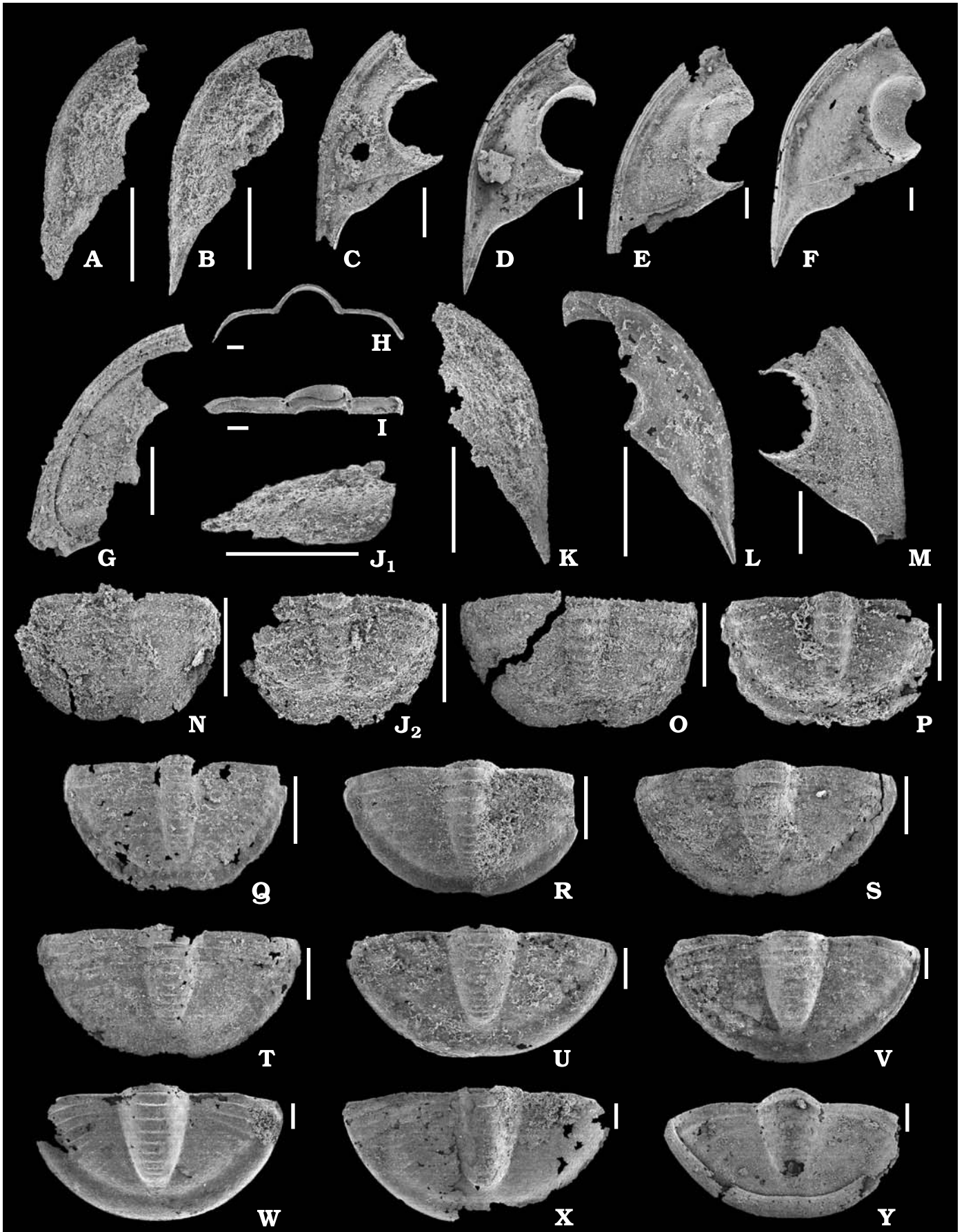
glabellar field. α - α is long and almost straight. γ is defined by a broad adaxially curving arc. The postocular suture is short, diverging in the early holaspis; a very short straight portion ε - ζ may be present in some late holaspids. A few tubercles are grouped on the medio-posterior margins of both the pre-occipital glabella and occipital ring.

Only a single poorly preserved rostral plate was found (Fig. 3S). It is trapezoidal in outline, bearing four, possibly five terrace ridges; connective sutures convergent backwards (~45°).

Hypostome sub-rectangular, with maximum width (tr.) across shoulders about 65 percent of maximum length; middle body strongly inflated, separated from the lateral and posterior border by deep furrows, weakly divided into anterior and posterior lobes by very faint middle furrows; three pairs of terrace ridges fused antero-medially, running from anterior border to shoulders level and slightly curved outward; no maculae visible; narrow, down-curved (ventrally) anterior rim, separated from the anterior lobe by a break in slope that dies out laterally; sub-trapezoidal anterior wings projecting dorso-laterally; lateral notch rather broad, about 10 percent of hypostomal length (exsag.), and angular; three discontinuous terrace ridges running from the posterior border of the anterior wing to the middle of the wide, about one fifth of maximum hypostomal width (tr.), and outwardly rounded posterior shoulder; posterior border almost straight, inflated and delimited laterally by a pair of tiny forks; doublure narrow (half the width of lateral and posterior borders).

Librigena with large, kidney-shaped eye, provided with a particularly broad visual surface, composed of about 275 lenses, sloping moderately abaxially, and surrounded by a narrow eye-socket around the anterior half of the eye that widens posteriorly to form a smooth triangular surface between eye and posterior border furrow; genal field rather wide and of equal size from front to rear, separated from lateral border by a deep, broad lateral border furrow that shallows posteriorly, smooth anteriorly but bearing a group of small tubercles on a narrow elevated area near the boundary between it and the posterior triangular eye socket; lateral border inflated, widening slightly anteriorly, bearing four well-defined terrace ridges; rather short genal spine (less than one-third of the maximum exsagittal length of the librigena) with broad base, flattened roughly dorso-ventrally and bearing four to five terrace ridges; broad posterior border separated from genal field and eye socket by a deep and slightly backwardly curved posterior border furrow. Doublure incurved, thus cre-

← Fig. 3. *Osmolskabole prima*. Middle Famennian (to IV, Upper *Palmatolepis trachytera* to *Palmatolepis postera* Zones). Korb-el-Atil (“West”) and Ouidane Chebbi, southeast of Erfoud, Tafilalt, Morocco. **A–N.** Cranidia. **A.** Smallest meraspis, UMC-IP361 in dorsal view (A_1); A_2 , detail of the preglabellar area (note the plectrum) in dorsal view. **B.** Small meraspis, UMC-IP362 in dorsal view. **C.** Meraspis, UMC-IP363 in dorsal view. **D.** Meraspis, UMC-IP364 in dorsal view. **E.** Meraspis, UMC-IP365 in dorsal view. **F.** Meraspis, UMC-IP366 in dorsal view. **G.** Meraspis (?), UMC-IP367 in dorsal view. **H.** Meraspis (?), UMC-IP368 in dorsal view. **I.** Small holaspis, UMC-IP369 in dorsal view. **J.** Holaspis, UMC-IP370 in dorsal view. **K.** Holaspis, UMC-IP371 in dorsal view. **L.** Holaspis, UMC-IP372 in dorsal view. **M.** Holaspis, UMC-IP373 in ventral view. **N.** Meraspis, UMC-IP374 in lateral view. **O–R, T–W.** Hypostomes. **O.** Smallest specimen, UMC-IP375 in ventral view. **P.** Small specimen, UMC-IP376 in ventral view. **Q.** Small specimen, UMC-IP377 in ventral view. **R.** Large specimen, UMC-IP381 in dorsal view. **U.** Rather large specimen, UMC-IP378 in ventral view. **V.** Rather large specimen, UMC-IP379 in ventral view. **W.** Largest specimen, UMC-IP380 in ventral view. **T.** Rather large specimen, UMC-IP382 in lateral view. **S.** Rostral plate, UMC-IP383 in ventral view. All figures are scanning electron micrographs of silicified specimens. Scale bars 0.5 mm, except A_2 for which is 0.25 mm.



ating a tubular structure in association with lateral border, of equal width with latter except anteriorly, where it widens; four terrace ridges present. In lateral view, relief high.

Only a few remains of thoracic segments were found (Fig. 4H, I). As far as it is known, axial ring rather large (about one third of the maximum transversal width of the thoracic segment), more convex anteriorly than posteriorly; articulating half ring well developed (less than one third of the maximum sagittal length of the axial ring) and separated from a more or less visible preannulus by a deep (in particular medially) articulating furrow; preannulus, when visible, separated from postannulus by a faint intra-annular furrow; no apodemal pits obvious; axial furrows rather deep; ring sockets very small; pleura divided by a break in slope (about 45°) at its mid-width (tr.) into a backwardly directed inner portion and an outer portion that is rounded at its extremity (with the exception of a tiny rearwardly directed spine) and bearing a small projection at the antero-lateral corner of the flange; deep pleural furrow shallows adaxially and does not reach the distal end of the pleura; doublure of the axial ring wide, extending forward almost as far as the articulating half ring; pleural doublure limited to the posterior and the lateral parts of the outer portion and exhibiting a small panderian notch.

The mean width of Moroccan pygidia is a little larger than that of the holotype. In adult specimens the pygidial axis carries 8 axial rings and a terminal piece. The posterior border furrow is medially interrupted by the postaxial ridge, which continues onto border. Posterior border extends in breadth (sag.) that of the postaxial field (the border furrow included). On the pygidium, a single row of tiny tubercles is aligned along the posterior edge of both posterior pleural bands and the central parts of the axial rings (see Fig. 2F). In addition, other tiny nodules are widely spaced and randomly dispersed on the remaining parts of the pleural fields and the border.

Ontogeny.—The discovery of a wide size-range of cranidia, pygidia and to a lesser degree of librigenae in addition to protaspisid remains of *Osmolskabole prima* enables us to describe the first almost complete growth series of a cyrtosymboline trilobite.

Protaspisid period

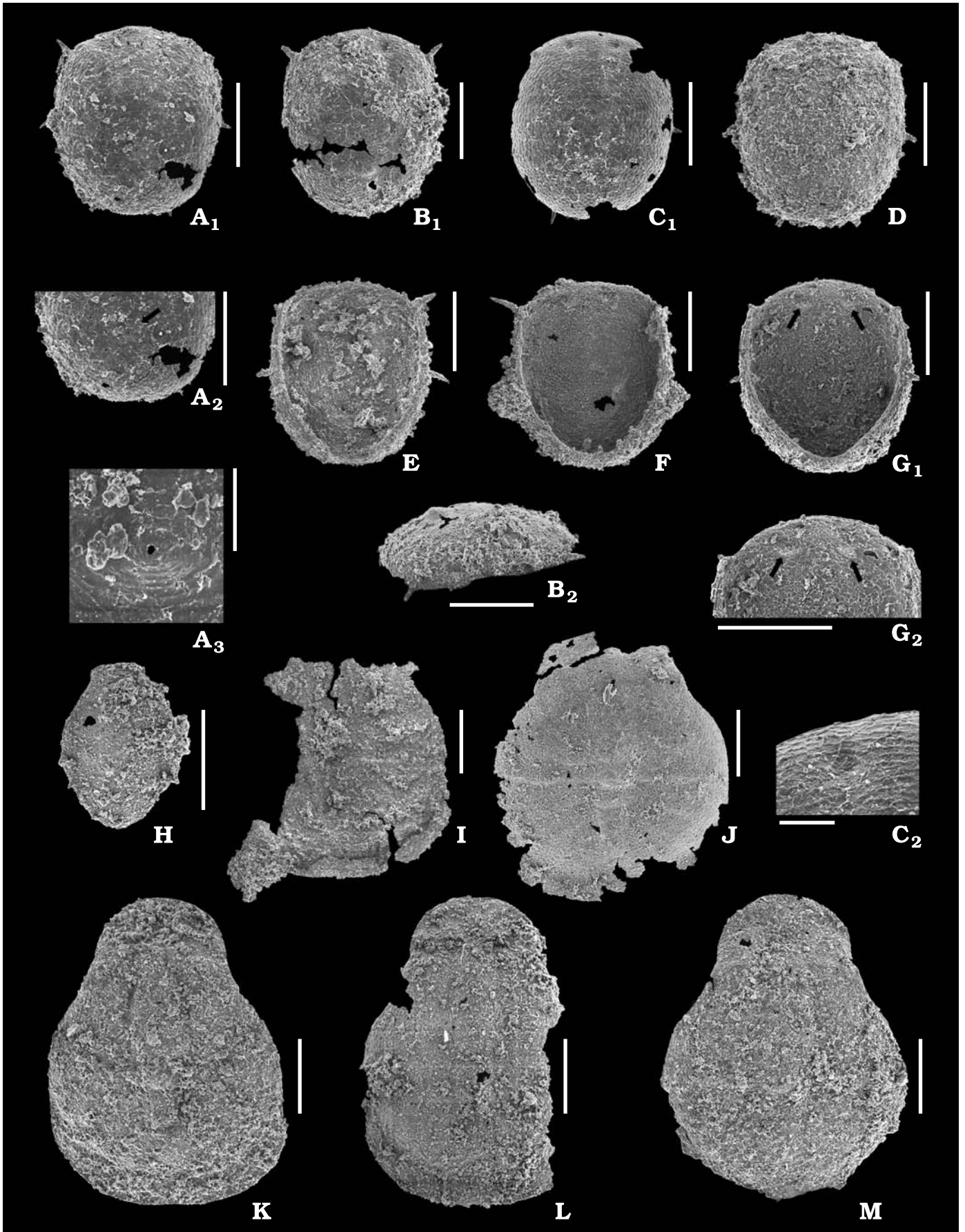
Fig. 5.

Pre-metamorphic stage.—More than 50 anaprotaspisid remains were recovered. The scatter plot of maximum length

(sag.) versus maximum width (tr.) of the well-preserved specimens is shown in Fig. 6. Only one pre-metamorphic stage is recognized. All are bulbous, dorsally sub-ovoid, slightly longer than wide, length (sag.) 0.590–0.661 mm, width (tr.) 0.512–0.568 mm; axis long (about 85 percent of the maximum sagittal length of the larva) and subdivided into a glabella and a protopygidial axis by a faint, often inconspicuous transverse furrow located just posterior to a large node that we suppose to be occipital; glabella expands (tr.) forward in its posterior third (sag.) then tapers anteriorly, reaching a pair of usually obvious anterior pits close to the margin; no preglabellar furrow visible; short triangular protopygidial axis, devoid of transverse furrows and slightly rounded postero-medially; exceptionally the axial transverse furrow seems to continue slightly onto the pleural field partially separating a protocranidium and a protopygidium; three pairs of short, sharp and conical spines project from margin; sub-horizontal anterior pair that projects antero-laterally at about 12 percent length of anaprotaspis, where facial suture crosses doublure; middle pair of spines projects postero-laterally and sometimes slightly dorsally from about mid-length of anaprotaspis; posterior pair of spines slightly laterally, backward and strongly ventrally directed from 90 percent length of anaprotaspis, with spines separated by roughly 30 percent width of the anaprotaspis. Ventrally, incurved doublure, slightly narrower postero-medially and gently decreasing in width anteriorly. Librigena unknown, but it can be supposed with respect to the facial suture that it is sub-marginal, narrow (almost entirely constituted of doublure), lacking a genal spine and restricted to anterior 30 to 40 percent of anaprotaspis. Rostral plate unknown. Hypostome known from a single poorly preserved specimen (Fig. 5H); it is elongate, ovoid in outline except anteriorly where it is sub-rectangular; one (but possibly three) pair of short lateral spines projecting latero-ventrally; postero-median spine broken; no furrows distinct ventrally; dorsally, narrow doublure all around the border except anteriorly where it decreases gradually in width; laterally, hypostome almost flat except anteriorly where it is bent dorsally.

Slight differences are observed in certain larvae. For example, in most of the specimens dorsal features consist only of anterior pits, whereas rare specimens display discernable axial and even a transverse furrow. This seems to be due to different qualities of silicification. It is also possible to observe slight differences in the shape of the larvae that can be

← Fig. 4. *Osmolskabole prima*. Middle Famennian (to IV, Upper *Palmatolepis trachytera* to *Palmatolepis postera* Zones). Korb-el-Atil (“West”) and Ouidane Chebbi, southeast of Erfoud, Tafilalt, Morocco. **A–F.** Left librigenae in dorsal view. **A.** Smallest specimen, UMC-IP384. **B.** Small meraspis, UMC-IP385. **C.** Meraspis (?), UMC-IP386. **D.** Small holaspis, UMC-IP387. **E.** Holaspis, UMC-IP388. **F.** Largest holaspis, UMC-IP389. **G.** Partial right librigena, UMC-IP390 in ventral view. **H, I.** Thoracic segments. **H.** Large specimen, UMC-IP394 in anterior view. **I.** Large specimen, UMC-IP395 in ventral view. **K, L, M.** Right librigenae in dorsal view. **K.** Smallest specimen, UMC-IP391. **L.** Small specimen, UMC-IP392. **M.** Largest specimen, UMC-IP393. **J, N–Y.** Pygidia. **J.** Small meraspis, UMC-IP396 in lateral (J1) and dorsal (J2) views. **N.** Smallest meraspis, UMC-IP397 in dorsal view; **O.** Meraspis, UMC-IP398 in dorsal view. **P.** Meraspis, UMC-IP399 in dorsal view. **Q.** Meraspis, UMC-IP400, dorsal view. **R.** Meraspis, UMC-IP401 in dorsal view. **S.** Large meraspis, UMC-IP402 in dorsal view. **T.** Large meraspis, UMC-IP403 in dorsal view. **U.** Small holaspis, UMC-IP404 in dorsal view. **V.** Holaspis, UMC-IP405 in dorsal view. **W.** Large holaspis, UMC-IP406 in dorsal view. **X.** Largest holaspis, UMC-IP407 in dorsal view. **Y.** Large holaspis, UMC-IP408 in ventral view. All figures are scanning electron micrographs of silicified specimens. Scale bars 0.5 mm.



more or less elongated. The magnitude of these shape differences is so small that it is not possible to know whether they are due to natural inter-individual variations or to some extent to taphonomic influences. In all cases, these minor differences do not warrant any suggestion that more than a single pre-metamorphic stage occurs.

Note that the presence of a transverse furrow on the axis, which in some cases runs abaxially on the pleural field, should preclude the use of the term “anaprotaspis” for this first larval stage. Nevertheless, it seems more judicious to conserve this term in particular for comparative purposes, because the globular first protaspis stage in proetoid trilobite ontogenies is usually referred to as an anaprotaspis. Possession of these features is exceptional and, although it seems improbable, we cannot rule out that their presence or absence may correspond to variation within the population.

Post-metamorphic stage.—About 60 metaprotaspis remains were found in our sample. Most of them consist of broken specimens, where only the protopygidium and the posterior part of the protocranidium can be observed. Nevertheless, eight specimens are sufficiently well preserved to permit the recognition of a single metaprotaspis stage in *O. prima* (Fig. 6). It is slightly elongate, 1.05–1.21 mm in sagittal length, maximum width (located at the mid-length of the protopygidium) 0.84–0.90 mm; glabella rather long (about three quarters of the protocranial sagittal length), maximum width across L1, very gently tapering anteriorly and moderately rounded antero-medially; axial furrow large and shallow, mostly weakly impressed against L1; S1 shallow to inconspicuous, strongly curved back to meet S0 and defining low L1; possible shallow and short S2; occipital furrow deep and wide; occipital ring narrowing abaxially and bearing a large (about one half of the maximum transversal width of the occipital ring and almost equal to occipital sagittal length) and rather high occipital node; faint anterior border furrow curved back abaxially but also medially where it merges with the small depression occurring immediately in front of the glabella in a plectrum; anterior border smooth; α - α short (roughly equal to the transversal width of the anterior glabella) and slightly backwardly-curved abaxially; α - β rather long and strongly diverging backward ($\sim 40^\circ$); β - γ short (about half α - β length) and sub-parallel; γ (+ undefined δ)- ε straight, short and diverging backward ($\sim 25^\circ$); no eye ridge discernable; ε (+undefined ζ)- η diverging backward

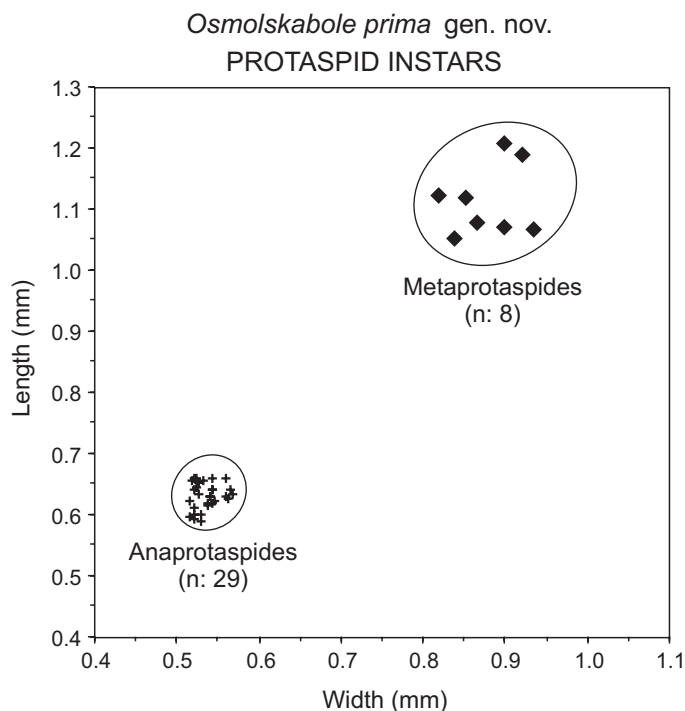


Fig. 6. Scatter plot of length versus width for protaspides of *Osmolskabole prima*. Single anaprotaspis and metaprotaspis stages are recognised. “n” is the number of specimens in each group. Measurements of the 37 specimens were obtained using a Nikon measuroscope (± 0.001 mm).

($\sim 30^\circ$); η - ω less divergent posteriorly; posterior border furrow wide, shallow and almost straight; posterior border moderately inflated; junction between the protocranidium and the protopygidium marked by a deep furrow (especially on the pleurae), the inner two thirds of which is almost straight whereas the outer third strongly curves backward abaxially. Protopygidium elliptical, margins entire with a faint posterior notch; axial furrow deep; axis short (about one half of the maximum sagittal length of the pygidium), one or two axial rings distinct; one pleural and interpleural furrow sometimes visible; post-axial field short (one third of the sagittal length of the post-axial region); flat border, separated from pleural field by an abrupt break in slope, rather broad (two thirds of the sagittal length of the post-axial region), but narrowing antero-laterally. Doublure flat, of equal width and corresponding to the pygidial border. In lateral view, larvae asymmetrically vaulted with the anterior third strongly sloping

← Fig. 5. *Osmolskabole prima*. Middle Famennian (to IV, Upper *Palmatolepis trachytera* to *Palmatolepis postera* Zones). Korb-el-Atil (“West”) and Ouidane Chebbi, southeast of Erfoud, Tafilalt, Morocco. A–G. Anaprotaspides. A. Well-preserved specimen, UMC-IP409 in dorsal view (A₁); A₂, detail of the posterior half showing the occipital node (arrow); A₃, detail of the occipital node (apex broken?). B. Well-preserved specimen, UMC-IP410 in dorsal (B₁) (note the pair of anterior pits, the dorsal furrows and the occipital node) and lateral (B₂) views (posterior on the left, note the occipital node). C. Specimen showing deep anterior pits, UMC-IP411 in dorsal view (C₁); C₂, detail of the left anterior pit. D. UMC-IP412 in dorsal view. E. UMC-IP413 in ventral view. F. UMC-IP414 in ventral view. G. Specimen showing a pair of swollen areas (arrows), UMC-IP415 in ventral view (G₁); G₂, detail of the swollen areas. H. Anaprotaspis hypostome, UMC-IP416 in ventral view. I–M. Metaprotaspides. I. Specimen UMC-IP417 in ventral view (anterior and right parts broken) showing the protopygidial doublure. J. Specimen UMC-IP418 in dorsal view (anterior part of the protocranidium and protopygidial border broken). K. Complete specimen (see the large occipital node), UMC-IP419 in dorsal view. L. Specimen UMC-IP420 in dorsal view (right side partially broken). M. Specimen UMC-IP421 in dorsal view (protopygidial border broken; note the anterior border furrow that merges medially in a plectrum). All figures are scanning electron micrographs of silicified specimens. Scale bars 0.25 mm, except A₃ and C₂ for which are 50 μ m.

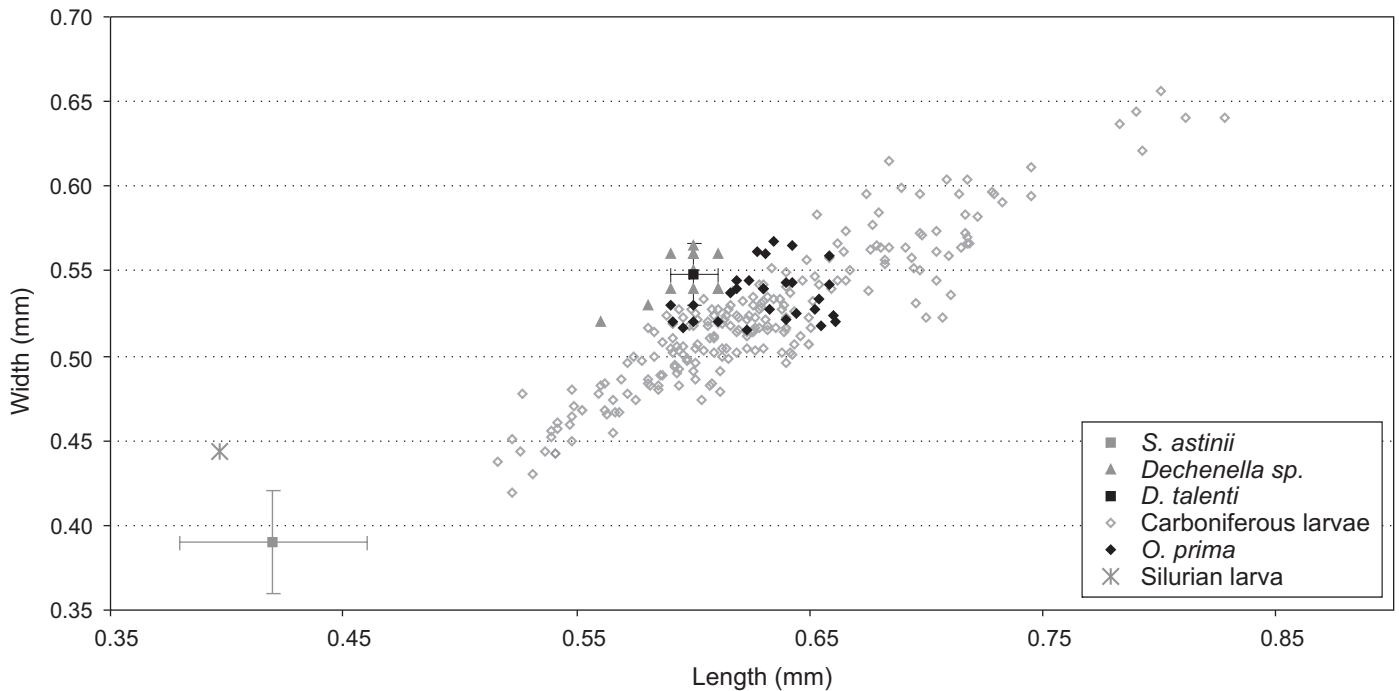


Fig. 7. Scatter plot of width *versus* length for all the proetoid anaptospides known so far. *Stenoblepharum astinii* (early Caradocian, Late Ordovician), data from Edgecombe et al. 1997 (note that the dot represents only the middle of the size-range for width and length); *Dechenella* sp. (Eifelian, Middle Devonian), data from Brian D.E. Chatterton (personal communication 2004); *Devonoproetus talenti* (Emsian, Early Devonian), data from Chatterton 1971 (estimations of the mean anaptospid width and length calculated from pl. 21: 8–11, and magnifications given); Carboniferous larvae, data from Lerosey-Aubril and Feist (2005); *Osmolskabole prima* (middle Famennian, Late Devonian), data provided herein; Silurian larva, data from Chatterton and Speyer 1997 (estimation of the size calculated from fig. 166.5, p. 212 and the magnification given).

downward anteriorly and posterior two thirds more gently flexed rearward.

Meraspid and holaspid period.—The smallest meraspid cranidium found is 0.83 mm long (sag.) (Fig. 3A). Although it is almost impossible to determine which meraspid degree it represents, we speculate that it belongs to the very early meraspid period. When compared to metaprotaspid specimens, it exhibits the following shape changes: glabella rather long (about three quarters of the protocranial sagittal length); axial furrow narrower, deeper and more convergent forward; S1 deeper; L1 more inflated; occipital furrow deeper; occipital ring broader (tr.); plectrum better defined (deeper and narrower transversally); anterior border narrower (sag.), slightly more inflated and protruding anteriorly; α - α moderately longer and becoming straight; α - β divergence increased ($\sim 45^\circ$); β - γ more elongated and curved outward; appearance of δ defining a narrow (tr.) but rather long (exsag.) palpebral lobe with backwardly diverging ($\sim 35^\circ$) γ - δ and moderately backwardly converging ($\sim 5^\circ$) δ - ε of equal length; ε (+undefined ζ)- η more strongly divergent backwards ($\sim 40^\circ$); ν - ω less divergent backwards ($\sim 15^\circ$).

From this early meraspid stage to the oldest holaspid one, the following developmental traits can be observed: glabella elongating (sag.), greatly enlarging (tr.), rounding anteromedially and becoming constricted at the level of γ ; axial furrows deepening at first, but shallowing in the latest stages; S1

deepening in the earliest stages but rapidly shallowing thereafter, brief appearance of a short anterior branch running adaxially; L1 initially inflating greatly, then flattening in the second half of the ontogeny; brief appearance of short straight S2 and S3; S0 slightly shallows; occipital ring continues to widen (tr.) medially but still more laterally (exsag.) thus becoming less narrowed abaxially; occipital node strongly decreasing in relative size and height; plectrum shortens (sag.) but also narrows (tr.), and shallows before being substituted rather late in ontogeny by a short preglabellar field (e.g., it is reduced but still present on specimen of the Fig. 3G); anterior border furrow deepening but remaining still broad throughout ontogeny; anterior border progressively inflating, rapidly developing one then successively two, three, four and even five terrace ridges; α - α continues to extend in length (tr.) throughout almost all the ontogenetic development; α - β shortening slightly and becoming more divergent, subdivided into a strongly divergent anterior part and a less divergent posterior one; β - γ still elongating in early ontogeny, and becoming progressively more convergent; palpebral lobe enlarges (tr.) due to outward migration of δ and inward migration of γ , and to a lesser degree of ε , and shifts backward in the late ontogenetic stages; γ - δ more diverging and moderately elongating; δ - ε more converging; appearance of ζ ; ε - ζ less diverging, becoming almost straight in latest stages, and slightly elongating; ζ - η more diverging backward; posterior border furrow shallowing. In lateral

view, cranidia increasingly arched; glabella flattening dorso-ventrally (especially the occipital ring) but expanding forward; anterior border greatly inflating.

The smallest meraspid hypostome found is 0.65 mm long (sag.) (Fig. 3O). Few shape changes can be observed during ontogeny: posterior part of the middle body inflating; lateral and posterior furrows initially represented by evident breaks in slope that narrow and deepen; initially two short terrace ridges, then appearance of a third, all of which extend progressively farther backwards; anterior rim narrows especially medially, less and less down-curved (ventrally); anterior wings enlarging (exsag.) and projecting more laterally; lateral notch more differentiated, especially from the anterior wings; appearance of third discontinuous terrace ridges on the anterior wings, all of which running farther backwards; posterior shoulder differentiating from the lateral border by the appearance of an increasingly well marked lateral constriction; lateral borders, initially converging backward become sub-parallel; posterior border narrowing (sag.), inflating and straightening (initially posteriorly concave); postero-lateral spines initially elongated, shortening slightly in the latest stages; doublure narrowing medially.

Concerning librigenae, the following shape changes can be observed during meraspid and holaspid periods: genal field enlarging (tr.) and expanding backwardly posterior to the eye; genal spine becoming progressively flattened dorso-ventrally (initially flattened laterally) and shortening; doublure initially bearing two, then three and four terrace ridges. The general trend during ontogeny is a flattening of the librigena, giving rise to the relative enlargement of the librigenal field and the shift in the orientation of the flattening genal spine.

The smallest transitory pygidium is only 0.65 mm long (sag.) (Fig. 4N). It differs from the protopygidium in the following features: sub-parabolic due to the great enlargement of the postero-medial pygidial border; postero-medial notch enlarged (sag.); axial furrows deepened; axis elongated (sag.) and becoming pointed posteriorly (initially rounded); five axial rings visible; four pairs of obvious ribs, defined by five pairs of broad pleural furrows; only one pair of shallow to inconspicuous interpleural furrows. Doublure shape changes reflect that of the pygidial border. In lateral view, axis and pleurae higher, axial rings also become particularly high.

From this smallest specimen to adults, the following trends can be noticed: pygidial outline evolves from sub-parabolic to semi-elliptical; postero-medial notch progressively disappearing; axis enlarging (tr.) and becoming rounded posteriorly; eight inter-ring furrows in meraspid specimens that moderately shallow in largest specimens; post-axial field slightly decreasing in width (sag.); border furrow deepens except in the latest stages where it secondarily shallows; narrow and low post-axial ridge progressively appearing in late ontogeny; pleural field decreasing in width (tr.) posteriorly but greatly enlarging anteriorly, its distal part becoming less and less declined; eight to nine apparent ribs in youngest

meraspid; pleural and interpleural furrows shallowing and enlarging in particular in the largest specimens; border enlarging in early ontogeny but secondarily narrows in later stages, inflating until the almost fading-away of the border furrow. Doublure becomes enrolled and bears progressively more terrace ridges. In lateral view, axis, pleural field and, to a lesser degree, axial rings and post-axial field flatten. In summary, the major ontogenetic changes in the pygidia result in a general flattening of the exoskeleton.

Discussion

Protaspid larvae and systematics of the order Proetida.—

The status of the order Proetida introduced by Fortey and Owens (1975) was questioned by Bergström (1977), who pointed out that many characters used for the original definition of the order Proetida were general characters seen in many other trilobite taxa. Consequently, Fortey (1990) reduced the number of characters diagnostic of this order. More recently some doubts have emerged concerning the relationships of the different superfamilies included in the Proetida. Although close phyletic relationships between the Aulacopleuroidea and Bathyroidea are still supported, the case of the superfamily Proetoidea raises more and more problems. Evidence from new silicified material emphasizes that the early ontogeny of this group is unique among the Proetida. This particular ontogeny is characterized by bubble-shaped and almost smooth anaprotaspides bearing three pairs of marginal spines, associated with a particularly broad ovoid hypostome provided with at least one prominent postero-medial spine, and followed by a maximum of two almost smooth adult-like metaprotaspid stages. Following several authors (Chatterton et al. 1999; Fortey 2001; Jonathan M. Adrain, personal communication 2003), we recently suggested that proetoid trilobites (i.e., proetids, tropidocoryphids and phillipsiids) should be separated from the other superfamilies belonging to the order Proetida (Lerosey-Aubril and Feist 2005). The larvae described in this work support the hypothesis that proetoid trilobites possess a unique early ontogeny that is conservative through time. Indeed, all proetoid protaspides known from Ordovician to early Carboniferous times share the characteristic features mentioned above.

Globular anaprotaspides occur in the ontogenies of a wide range of trilobite taxa but as stated by Chatterton et al. (1999: 223) “they may be derived for the Proetida”. Following Speyer and Chatterton (1989), they have been interpreted as planktonic larvae, and are considered to be separated from the subsequent benthic adult-like forms by a metamorphosis. Likewise a broad larval hypostome is a common ontogenetic feature in many trilobites, but the anaprotaspid hypostomes of proetoid trilobites are of remarkably large size so that they almost fully cover the ventral opening of the larva without the prominent spines displayed by larval hypostomes of other taxa (Lerosey-Aubril and Feist 2005). Moreover, the

proetoid larval hypostome possesses a peculiar morphology characterized by an ovoid outline and a prominent postero-medial spine that extends beyond the doublure in *in situ* hypostomes (Lerosey-Aubril and Feist 2005). Finally proetoid metaprotaspides possess more heterogeneous morphologies but these are all very much “adult like” (in the sense of Fortey 2001). More important is the fact that proetoid metaprotaspides are devoid of complex patterns of tuberculation as seen in many aulacopleuroid taxa, and they never represent more than two stages during ontogeny.

Even if the problem of the origin of the Proetoidea remains unresolved (Fortey 2001), we can speculate that changes in early ontogeny have been of major significance in the emergence of this group. Indeed, it is reasonable to consider that proetoid trilobites differentiated, probably from an Upper Cambrian group among ptychoparioids (Fortey 2001), by the acquisition of a planktonic calcified stage prior to a drastic metamorphosis.

Comparison of sizes of proetoid anaprotaspides.— Though proetoid anaprotaspides are morphologically very conservative through time, they exhibit important differences with regard to their sizes. Fig. 7 is a scatter plot of width *versus* length (in mm) of most of the proetoid anaprotaspides described so far. The undetermined Famennian larvae from Germany described by Crônier et al. (1999) have been excluded, pending a re-examination of this material (work in progress). Indeed, there is some evidence that deformation might have not been sufficiently taken into account in the previous measurements of Crônier et al. (1999).

This scatter plot reveals significant differences that may reflect a specific kind of evolution in the early ontogeny of proetoid trilobites through geological time. Whereas the anaprotaspis larvae described in this work are similar in size to those of *Devonoproetus talenti* Chatterton, 1971 and *Dechenella* sp., those of the Ordovician *Stenoblepharum astinii* Edgecombe, Chatterton, Vaccari, and Waisfeld, 1997 in contrast are distinctly smaller as they do not exceed 0.46 mm in length (sag.) and 0.42 mm in width (Fig. 7). The Silurian larva figured by Chatterton and Speyer (1997) is also significantly smaller (roughly 0.4 mm in sagittal length and 0.45 mm in transversal width). Finally Lower Carboniferous larvae exhibit an unexpectedly wide size-range, with some almost reaching 0.83 mm in length (sag.) whereas others hardly exceed 0.51 mm. To what extent anaprotaspis size can be correlated with adult size remains unknown but it is generally accepted that this correlation is rather low. This assumption is confirmed by Fig. 7 as anaprotaspides from *O. prima* (Osmólska, 1962), *Dechenella* sp., and *D. talenti* are of comparable sizes whereas adults of these species exhibit obvious size differences. Considering this, the differences observed on the scatter plot may permit the evolution of larval size in proetoid trilobites through time to be broadly depicted. Thus we speculate that the first typical proetoid anaprotaspides were rather small, as exemplified by *Stenoblepharum astinii*, although the difficulties of proving this assumption without

new Ordovician material (e.g., of Proetoidea) are appreciated. Later proetoid anaprotaspides did not change significantly until the Devonian, that is, if we take into account the proportions of the unique larva known from the Silurian. In contrast, Devonian anaprotaspides illustrate that a marked increase in larval size occurred in the Upper Silurian or early Lower Devonian. More interesting is the fact that comparable sizes are observed in Devonian representatives of three different subfamilies (i.e., Cyrtosymbolinae, Proetinae, and Dechenellinae). This observation leads us to speculate that whatever the group concerned, the size of proetoid anaprotaspides at this time may have been particularly homogeneous and rather important, ranging from 0.56 to 0.66 mm in length (sag.) and 0.51 to 0.57 mm in width (tr.). The association of Carboniferous anaprotaspides comprises probably several species (Lerosey-Aubril and Feist 2005). The surprisingly wide size-range observed can be interpreted in at least two different ways. Firstly, Carboniferous proetoid species could possess a single anaprotaspis stage during ontogenetic growth, and then there is a spectacular increase of the inter-specific variability of larval proportions. However, it may be noted that even in this case, an extended uncalcified period may occur in species with large anaprotaspides, as it is doubtful that larvae hatch directly at such a size. On the other hand, some of them may have retained the typical single anaprotaspis stage of medium size (i.e., roughly 0.62 mm in sagittal length) whereas others acquired a two-stage anaprotaspis period, the first being of moderate size and the second of unusually large dimensions. The absence of reliable data concerning the number of proetoid trilobite species associated with these Carboniferous larvae leaves open a preference for either of these hypotheses. But whichever hypothesis is considered, it seems necessary to advocate an extension of the planktonic period (represented by uncalcified or calcified larvae) in early ontogenies of some Carboniferous species.

Lerosey-Aubril and Feist (2005) proposed that this extended planktonic period might have been of utmost importance for the survivorship of proetoid trilobites during the end-Devonian biocrises. In the light of the new data presented herein, this hypothesis must be reconsidered. Indeed the observation that Famennian proetoid anaprotaspides display sizes comparable to those of Lower (i.e., *Devonoproetus talenti*) and Middle Devonian (*Dechenella* sp.) proetoids clearly indicates that a potentially extended planktonic period did not appear before the Late Famennian or even the earliest Carboniferous. Consequently this could not explain why proetoids were the only trilobites along with aulacopleuroids and phacopids to survive the Late Devonian Kellwasser mass extinction event. Nevertheless, nothing excludes the acquisition of an extended planktonic period in the early ontogeny of proetoid trilobites still having been crucial to their survival of the end Devonian Hangenberg event (Lerosey-Aubril and Feist 2003). It seems reasonable to speculate that this particular developmental strategy would increase the capacity for migration during the earliest stages

of growth. To some extent, it is no more than a supplement to Chatterton and Speyer's view (1990: 131) on the possible differences of dispersal in trilobites with or without a calcified planktonic stage in their early ontogenies. As a consequence we admit that the ability to reach neighboring and normally oxygenated habitats would also be enhanced.

Anaprotaspis/metaprotaspis transition, metamorphosis and Dyar's coefficient.—As the protaspis period of proetoid trilobites is composed of two morphologically distinct stages (i.e., nonadult-like anaprotaspides *versus* adult-like metaprotaspides) associated with two different ecologies (planktonic *versus* benthic), it is evident that some kind of metamorphosis must occur. According to Chatterton et al. (1999) this boundary in the ontogeny of proetoids is considered a radical change.

Apart from morphological dissimilarities, a metamorphosis may also be indicated by an abnormal size difference between these two successive stages as previously suggested by Fortey and Chatterton (1988) and Chatterton and Speyer (1997). If we calculate Dyar's coefficient for the maximum length (sag.) of our larvae, we obtain a value of 1.75. This is higher than the expected value (1.26) of Dyar's coefficient according to Przibram's rule (for more details on the different growth formulas, see Chatterton and Speyer 1997: 208). Although our larvae tend to support the hypothesis that a metamorphosis is indicated by a greater size difference between molts, we are doubtful about the validity of this intuitive assumption, as were Chatterton and Speyer (1997). The difficulties for quantifying size (and indirectly volume) differences between these two stages are crucial since the larvae are of completely different shapes. Indeed, a single dimension (for example maximum length) is not equally representative of volume (and indirectly the weight) in an ovoid as compared to a discoid shape. Moreover the length of the dorsal shield measured in dorsal view may not reflect the real length of an anaprotaspis larva as there is some evidence that the posterior part of its body was flexed ventrally (see for example the reconstruction of the nonadult-like protaspis of *Isotelus* in Speyer and Chatterton 1989). In general terms, length (and as a consequence the volume) is underestimated in the nonadult-like protaspis stage and therefore the Dyar's coefficient is over-estimated. With regard to that, and to other more general critiques on growth formulae (see Chatterton and Speyer 1997), we do not advocate the use of size-differences between successive molts for detecting potential metamorphosis in the early ontogeny of trilobites.

Discussion on the occipital node.—Recently (Lerosey-Aubril and Feist 2005), we took the view that the occipital node of proetoid trilobites might consist of a larval sensory organ, possibly a light sensor. This hypothesis is supported by its peculiar structure (at least in proetid and phillipsiid trilobites, see Fortey and Clarkson 1976; Wilmot 1991; Whittington and Wilmot 1997) and its relatively large size in larvae in comparison to that of adults of the same species. In *Osmolskabole prima* (Osmólska, 1962), the metaprotaspis

possesses a large "dome-like" (in the sense of Fortey and Clarkson 1976) occipital node (Fig. 5K). It decreases in size progressively until it represents no more than a tiny structure on the adult occipital ring. These new data are in accordance with observations made on other proetoid metaprotaspides. Interestingly a rather large and prominent node is also visible on the best-preserved anaprotaspis specimens (Fig. 5A, B). To the authors' knowledge, it is the first time that this structure can be distinguished at such an early stage of development in proetoids. Regarding its location, we think that this node is homologous to the metaprotaspis occipital tubercle. Thus, whatever the purpose of this possible sensory organ, it may have already been functional during the planktonic larval period of this species.

Comparison with previously described proetoid metaprotaspides.—In terms of size and absence of ornamentation, the metaprotaspis of *Osmolskabole prima* is typically of proetoid type. In particular, it closely resembles the second metaprotaspis stage of *Devonoproetus talenti* (Chatterton 1971) with respect to overall shape. However, the glabella and, to a lesser degree, the protopygidial axis are much broader (tr.) in *D. talenti* than in *O. prima*. Moreover the proetine metaprotaspis exhibits a glabella that almost reaches the anterior border. These differences are particularly interesting as they are probably the most obvious dissimilarities that can also be observed in adult specimens of both subfamilies.

To a lesser degree, the cyrtosymboline metaprotaspis shares common features with that of *Dechenella* sp. (Chatterton et al. 1999) and the Lower Carboniferous type 1 (Lerosey-Aubril and Feist 2005). In particular, they are widest across the protopygidium, they display a rather broad and well-defined protopygidial border, and a rather similar shape of the glabella. The broad preglabellar areas and the shape of their anterior margins, however, distinguish them from larvae of *Osmolskabole prima*. The metaprotaspis of *Stenoblepharum astinii* also exhibits a well-defined and rather wide protopygidial border as well as a depression between the preglabellar furrow and the anterior border that can be considered as a plectrum (see discussion below). However, its small size, its overall outline and the shape of its glabella easily differentiate it from the metaprotaspis of *O. prima*. Finally the Lower Carboniferous metaprotaspis types 2, 3, and 4 (Lerosey-Aubril and Feist 2005) are not very similar to *O. prima* metaprotaspis. The most important differences are: their overall outlines, the shape of their glabellae, the maximum width located across their protocranidium and their poorly defined protopygidial border (except in type 4).

Recently we emphasized the difficulties of interpreting morphological differences between proetoid metaprotaspides and even question the extent to which they are effective in resolving taxonomic problems (Lerosey-Aubril and Feist 2005). Moreover the poor state of preservation of *Dechenella* sp. and *Devonoproetus talenti* larvae does not permit reliable comparisons to be made with the other lar-

vae. At this stage of our knowledge, it seems unreasonable to speculate on the taxonomic implications of differences observed between proetoid metaprotaspides.

Discussion on the ontogeny of Cyrtosymbolinae.—To compare in detail the ontogeny of *Osmolskabole prima* with all of the more or less complete previously described growth series of cyrtosymbolines is beyond the scope of this work. Nevertheless the general observations on the ontogeny of Cyrtosymbolinae made by Osmólska (1962) and Chlupáč (1966) can be compared with those described herein. Most of the specimens studied by these authors are meraspides (generally late meraspides) or young holaspides. Many evolving traits during ontogeny observed by Osmólska (1962) are also described by Chlupáč and in our own work. On the cranium, these are: the broadening (tr.) and elongation (sag.) of the glabella at the expense of the preglabellar and fixigenal fields, the general shallowing of the furrows (axial, glabellar and occipital), the lengthening (sag.) of the occipital ring abaxially and the elongation of α - α . Both authors also emphasize that the occipital ring and more generally the glabella flatten in late ontogeny as seen in *O. prima*. However they both describe a narrowing of the palpebral lobes that cannot be observed in the ontogeny of *O. prima*. Chlupáč also noticed that γ and ε are less and less sharply bent adaxially, as also seen in the ontogeny of *O. prima*. Interestingly, Chlupáč also mentioned that in some cyrtosymbolines (e.g., *Cyrtosymbole nana* Richter, 1913) the glabella can also narrow (tr.). Our data do not support this observation.

With regards to the pygidium, both authors noticed, as we do, that the border inflates and the postero-medial notch disappears in late ontogeny. Chlupáč pointed out that the furrows generally shallow during ontogeny, again as observed in our species. However our specimens show a general broadening (tr.) of the pygidium whereas Chlupáč indicated a narrowing. Together with Osmólska we observe the flattening of the pleurae.

Preglabellar field, plectrum, and hypostomal condition.—In the metaprotaspis of *Osmolskabole prima*, the preglabellar field is depressed medially and merges with the faint anterior furrow in a plectrum. This latter progressively rises to the level of the adjacent fixigenal fields and then becomes a simple preglabellar field. The transition between the two states is gradual and it is therefore somewhat difficult, in some intermediate stages to determine whether there is still a plectrum or the simple preglabellar field has already originated. However, this transition occurs rather late in the ontogeny, as illustrated by the presence of an obvious plectrum in rather large specimens (e.g., Fig. 3G).

Fortey (1990: 546–547) describes the plectrum stage as an intermediate stage between conterminant and natant stages in the ontogeny of typical ptychoparioids. According to this author (Fortey 1990: 546, text-fig. 9), the dorsal occurrence of a plectrum mirrors the presence of a backwardly extended rostral plate in contact with the anterior edge of the hypostome. Consequently, the plectrum stage should corre-

spond to a conterminant hypostomal condition and the modifications of the preglabellar field observed in *O. prima* may indicate that the hypostomal condition changes rather late in the ontogeny from conterminant to natant. This is particularly interesting as it illustrates that the natant hypostomal condition is not steadily acquired early in the ontogeny of the Proetida as claimed by Fortey (1990). In fact, the transition from conterminant to natant hypostomal condition may happen at different times in the development of proetid trilobites. It can be as early as the first post-metamorphic stage (i.e., the first metaprotaspis stage) as supposed by Fortey (1990) in *Scharyia*. A preglabellar field is absent in the metaprotaspides of *Devonoproetus talenti* but appears in the earliest meraspis stages (Chatterton 1971) showing that the shift in the hypostomal condition can correspond to the protaspis / meraspis period boundary. Finally, the ontogeny of *O. prima* demonstrates that the transition can occur in the middle of the meraspis period. It has to be noted that the case of *O. prima* may not be an exception. Indeed, *Stenoblepharum astinii* also exhibits a depressed preglabellar field (i.e., a plectrum) in the metaprotaspis stage and this feature lasts until mid or possibly late meraspis period (see Edgecombe et al. 1997: figs. 4-3, 4-12, and 4-14). Thus, we believe that the time of the acquisition of a natant hypostomal condition in ontogeny should be used cautiously when considering the systematics of the Proetida and in particular, we cast some doubts that this character could be diagnostic of this order. It is also possible that the dorsal exoskeleton might not definitely indicate the hypostomal condition as was previously thought.

Conclusions

This work increases our knowledge of early ontogenetic development of the Proetoidea in two major ways. Firstly it illustrates the first known complete growth series of a cyrtosymboline. Accordingly, proetid larvae are now known from the Proetinae, the Dechenellinae, and the Cyrtosymbolinae. As tropidocoryphid and probable phillipsiid protaspides have been also described, larval stages are known from a broad range of taxa within the Proetoidea. The typical early ontogeny of proetid trilobites is now becoming rather well known, even if only few protaspis specimens have been found. We note, however, that tropidocoryphid and phillipsiid protaspides remain poorly known in comparison with those of proetids. In this respect, it would be particularly interesting to recover larvae of late tropidocoryphid and phillipsid representatives.

Our discovery of cyrtosymboline protaspides provides also important information on the evolution through time of the early ontogeny of proetid trilobites, especially since we have been able to describe the first complete growth series of a Famennian representative of this group. Interestingly, the new anaprotaspis larvae are roughly similar in size to the others from the Devonian. In one sense this may partially call into question our previous statement that the

life history strategy of proetoid trilobites may have been of utmost importance for surviving the end-Devonian biocrisis (Lerosey-Aubril and Feist 2005). It is almost certain that, although a modified early ontogeny may well be related to the survival of proetoids during the latest Famennian Hangenberg event, such could not be the case at the Frasnian-Famennian Kellwasser event where other, and so far unknown criteria must have been of prime importance. Our current work on proetoid larvae from the Upper Famennian of Germany may provide a good opportunity for understanding the survivorship of proetoid trilobites at the Hangenberg biocrisis.

Finally, the overall evolutionary history of the early ontogeny of proetoid trilobites that we depict herein obviously suffers from lack of data. In this respect we need additional proetoid larvae, especially from the Upper Silurian or early Lower Devonian. Such may bring more information about the first increase in larval size that probably occurred at this time. Likewise nothing is known about the evolution of early ontogeny in the youngest proetoids. As long as late Carboniferous and Permian proetoid larvae remain undiscovered, it will not be possible to supplement our current knowledge about the evolution of the early ontogeny in this group. It is highly probable that the final and exceptional adaptive radiation of proetoid trilobites in the Late Paleozoic may relate to modifications in their early larval stages. Such discoveries may then provide a unique opportunity to study the relationship between evolution and development in the longest-lived trilobite taxon.

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References

Alberti, H. 1975a. Neue Trilobiten (*Waribole*) aus dem Ober-Devon IV–VI (Nord-Afrika und Mittel-Europa) – Beitrag 3. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 149: 180–210.

Alberti, H. 1975b. Neue Trilobiten (*Waribole*) aus dem Ober-Devon IV–V (Nord-Afrika und Mittel-Europa) – Beitrag 4 – Revision einiger Typus-Spezies der Proetidae Salter, 1864, aus dem Ober-Devon II–V. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 150: 207–226.

Alberti, H. 1976. Neue Trilobiten (*Cyrtosymbole*) aus dem Ober-Devon II (Nord-Afrika und Mittel-Europa) – Beitrag 5. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 152: 19–50.

Beecher, C.E. 1893. A larval form of *Triarthrus*. *American Journal of Science* 46: 361–362.

Beecher, C.E. 1895. The larval stages of Trilobites. *The American Geologist* 16: 166–197.

Bergström, J. 1977. Proetida—a disorderly order of trilobites. *Lethaia* 10: 95–105.

Chatterton, B.D.E. 1971. Taxonomy and ontogeny of Siluro-Devonian trilobites from near Yass, New South Wales. *Palaeontographica A* 137: 1–108.

Chatterton, B.D.E., Edgecombe, G.D., Vaccari, N.E., and Waisfeld, B.G. 1999. Ontogenies of some Ordovician Telephiniidae from Argentina, and larval patterns in the Proetida (Trilobita). *Journal of Paleontology* 73: 219–239.

Chatterton, B.D.E. and Speyer, S.E. 1990. Applications of the study of trilobite ontogeny. In: D.G. Mikulic (ed.), *Short Courses in Paleontology N°3: Arthropod Paleobiology*, 116–136. Paleontological Society, Knoxville.

Chatterton, B.D.E. and Speyer, S.E. 1997. Ontogeny. In: R.L. Kaessler (ed.), *Treatise on Invertebrate Paleontology, Part O, Arthropoda 1, Trilobita, Revised*, 173–247. Geological Society of America and University of Kansas Press, Lawrence, Kansas.

Chlupáč, I. 1961. Preliminary report on some new Upper Devonian Trilobites from the Moravian Karst. *Věstník Ústřední ústav geologický* 36 (6): 477–481.

Chlupáč, I. 1966. The Upper Devonian and Lower Carboniferous trilobites of the Moravian karst. *Sborník Geologických Věd – Paleontologie* 7: 1–143.

Crônier, C., Bartzch, K., Weyer, D., and Feist, R. 1999. Larval morphology and ontogeny of a Late Devonian phacopid with reduced sight from Thuringia, Germany. *Journal of Paleontology* 73: 240–255.

Crônier, C. and Clarkson, E.N.K. 2001. Variation of eye-lens distribution in a new late Devonian phacopid trilobite. *Transactions of the Royal Society of Edinburgh* 92: 103–113.

Edgecombe, G.D., Chatterton, B.D.E., Vaccari, N.E., and Waisfeld, B.G. 1997. Ontogeny of the proetoid trilobite *Stenoblepharum*, and relationships of a new species from the Upper Ordovician of Argentina. *Journal of Paleontology* 71: 419–433.

Feist, R. and Becker, T. 1997. Discovery of Famennian trilobites in Australia (Late Devonian, Canning Basin, NW Australia). *Geobios* 20: 231–242.

Feist, R. and Lerosey-Aubril, R. 2005. The type species of *Cyrtosymbole* and the oldest (Famennian) cyrtosymboline trilobites. *Acta Palaeontologica Polonica* 50: 465–475.

Fortey, R.A. 1990. Ontogeny, hypostome attachment and trilobite classification. *Palaeontology* 33: 529–576.

Fortey, R.A. 2001. Trilobite systematics: the last 75 years. *Journal of Paleontology* 6: 1141–1151.

Fortey, R.A. and Chatterton, B.D.E. 1988. Classification of the trilobite suborder Asaphina. *Palaeontology* 31: 165–222.

Fortey, R.A. and Clarkson, E.N.K. 1976. The function of the glabella “tubercule” in *Nileus* and other trilobites. *Lethaia* 9: 101–106.

Fortey, R.A. and Owens, R.M. 1975. Proetida—a new order of trilobites. *Fossils & Strata* 4: 227–239.

Hahn, G. 1965. Revision der Gattung *Archegonus* Burmeister, 1843 (Trilobita). *Seckenbergiana lethaea* 46 (4/6): 229–262.

Hahn, G. and Hahn, R. 1967. Zur Phylogenie der Proetidae (Trilobita) des Karbons und Perms. *Zoologische Beiträge, neue Folge* 13 (2/3): 303–349.

Hahn, G. and Hahn, R. 1975. Die Trilobiten des Ober-Devon, Karbon und

- Perm. In: K. Krömmelbein (ed.), *Leitfossilien 1*, 1–127. Gebrüder Borntraeger, Berlin.
- Hawle, I. and Corda, A.J.C. 1847. Prodrum einer Monographie der böhmischen Trilobiten. *Abhandlungen Koeniglichen Boehmischen Gesellschaft der Wissenschaften* 5: 1–176.
- Hupé, P. 1953. Classe des trilobites. In: J. Piveteau (ed.), *Traité de Paléontologie. Vol. 3, Les formes ultimes d'Invertébrés: Morphologie et évolution: Onychophores–Arthropodes–Echinodermes–Stomocordés*, 44–246. Masson, Paris.
- Koenen, A. v. 1886. Über Clymenienkalk und Mitteldevon resp. Hercynkalk (?) bei Montpellier. *Neues Jahrbuch für Mineralogie* 1: 163–167.
- Lerosey-Aubril, R. and Feist, R. 2003. Early ontogeny of trilobites: implications for selectivity of survivorship at the End-Devonian crisis. *Abstract with Programs—Geological Society of America* 6: 385.
- Lerosey-Aubril, R. and Feist, R. 2005. First Carboniferous protaspid larvae (Trilobita). *Journal of Paleontology* 79: 702–718.
- Osmólska, H. 1962. Famennian and Lower Carboniferous Cyrtosymbolinae (Trilobita) from the Holy Cross Mountains, Poland. *Acta Palaeontologica Polonica* 7: 53–222.
- Richter, R. 1913. Beiträge zur Kenntnis devonischer Trilobiten. Zweiter Beitrag. Oberdevonische Proetiden. *Abhandlungen der Senckenbergischen naturforschenden Gesellschaft* 31: 341–423.
- Richter, R. and Richter, E. 1926. Die Trilobiten des Oberdevons, Beiträge zur Kenntnis devonischer trilobiten, IV. *Abhandlungen der Preussischen Geologischen Landesanstalt* 99: 1–314.
- Speyer, S.E. and Chatterton, B.D.E. 1989. Trilobite larvae and larval ecology. *Historical Biology* 3: 27–60.
- Whittington, H.B. and Wilmot, N.V. 1997. Microstructure and sculpture of the exoskeletal cuticle. In: R.L. Kaessler (ed.), *Treatise on Invertebrate Paleontology, Part O, Arthropoda 1, Trilobita, Revised*, 74–84. Geological Society of America and University of Kansas Press, Lawrence, Kansas.
- Wilmot, N.V. 1991. Sensory field maps of proetide trilobites. *Transactions of the Royal Society of Edinburgh, Earth Sciences* 82: 183–193.