

Ontogeny of *Drevermannia* and the origin of blindness in Late Devonian proetoid trilobites

RUDY LEROSEY-AUBRIL*

Laboratoire de Paléontologie, Institut des Sciences de l'Évolution, Université Montpellier II,
Cc 062, Place E. Bataillon, 34095 Montpellier, France

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Abstract – Numerous silicified and calcareous sclerites of various sizes, recovered from the latest Famennian of Thuringia (Germany), allow the description of the first complete growth series of a blind proetoid trilobite: *Drevermannia richteri*. In addition, the partial ontogenetic development of *Drevermannia antecurvata* sp. nov. and undetermined species, *Drevermannia* sp. 1, are described. The proetoid anaprotaspides, associated with *D. richteri*, illustrate that a marked increase in larval size occurred prior to the terminal Devonian extinction event. Considering the homogeneity of larval size in older Devonian proetoids, it is interpreted as evidence that the developmental strategy of these trilobites was significantly modified. Though largely speculative, two alternative hypotheses are proposed to explain this modification. Finally, all three ontogenetic sequences show that ocular structures never develop externally in *Drevermannia*, but also illustrate that the development of optical nerves is not completely lost in this group. This suggests that blindness in the *Drevermannia* lineage followed a centripetal mode of eye reduction.

Keywords: Trilobita, Proetidae, ontogeny, Famennian, palaeoecology.

1. Introduction

Well-developed compound eyes are a primitive character for trilobites (Fortey & Whittington, 1989). Throughout their evolutionary history, these structures persisted and even in the Late Permian, prior to their final extinction, all trilobite species were normally oculated (Clarkson, 1997). On the other hand, eye loss constitutes a typical and well-documented evolutionary trend in certain independent lineages, appearing repeatedly during the 275 million years of trilobite history (Fortey & Owens, 1990). Though commonly observed, blindness in trilobites remains difficult to explain in terms of adaptation. This probably stems from the fact that the 'loss of a structure is hard to prove as a positive adaptation', as stated by Fortey & Owens (1990, p. 129). However, there is some evidence that eye reduction in trilobites (and *a fortiori* blindness) may have been, in most cases, related to changes in life habits and accordingly, it seems likely that eye regression may have been an adaptive response to modifications of ecological constraints. Thus, Feist (1995) pointed out that the proportion of blind or reduced-eyed trilobite species was positively correlated to sea-level rises in the Late Devonian. In addition, it is noteworthy that the assemblages of Late Devonian blind or reduced-eyed trilobites constantly occur in deeper water outer shelf biofacies of the pelagic cephalopod realm. Feist

(1995) also suggested that the evolution of the visual system in Late Devonian trilobites might have been affected by heterochronic processes (that is, 'changes in relative time of appearance and rate of development of characters already present in ancestors': Gould, 1977, p. 2). Thus, the investigation of the ontogenies of blind species has appeared essential in the search for their origins and, more generally, for understanding the modalities of eye regression in trilobites.

In this contribution, the ontogenetic development of three blind drevermanniine trilobites, including *Drevermannia antecurvata* sp. nov., are presented. The discovery of earliest ontogenetic stages of these late Famennian trilobites sheds light on the modalities of eye regression in the *Drevermannia* lineage. It also increases our knowledge of the evolution of early ontogeny in proetoid trilobites.

2. Material and stratigraphy

Numerous trilobite remains were recovered by K. Bartzsch and D. Weyer in the terminal Famennian Breternitz Member of the Gleitsch Formation, best exposed in sections at Breternitz and Fischersdorf in the southern vicinity of Saalfeld, Thuringia, Germany. The 12 m thick succession consists of dark mudstones that rhythmically alternate with thin nodular limestone layers (Figs 1, 2). This fine-grained sedimentation is a typical deep water biofacies dominated by pelagic nekton such as orthoconic cephalopods, clymenids and

* E-mail: lerosey@isem.univ-montp2.fr

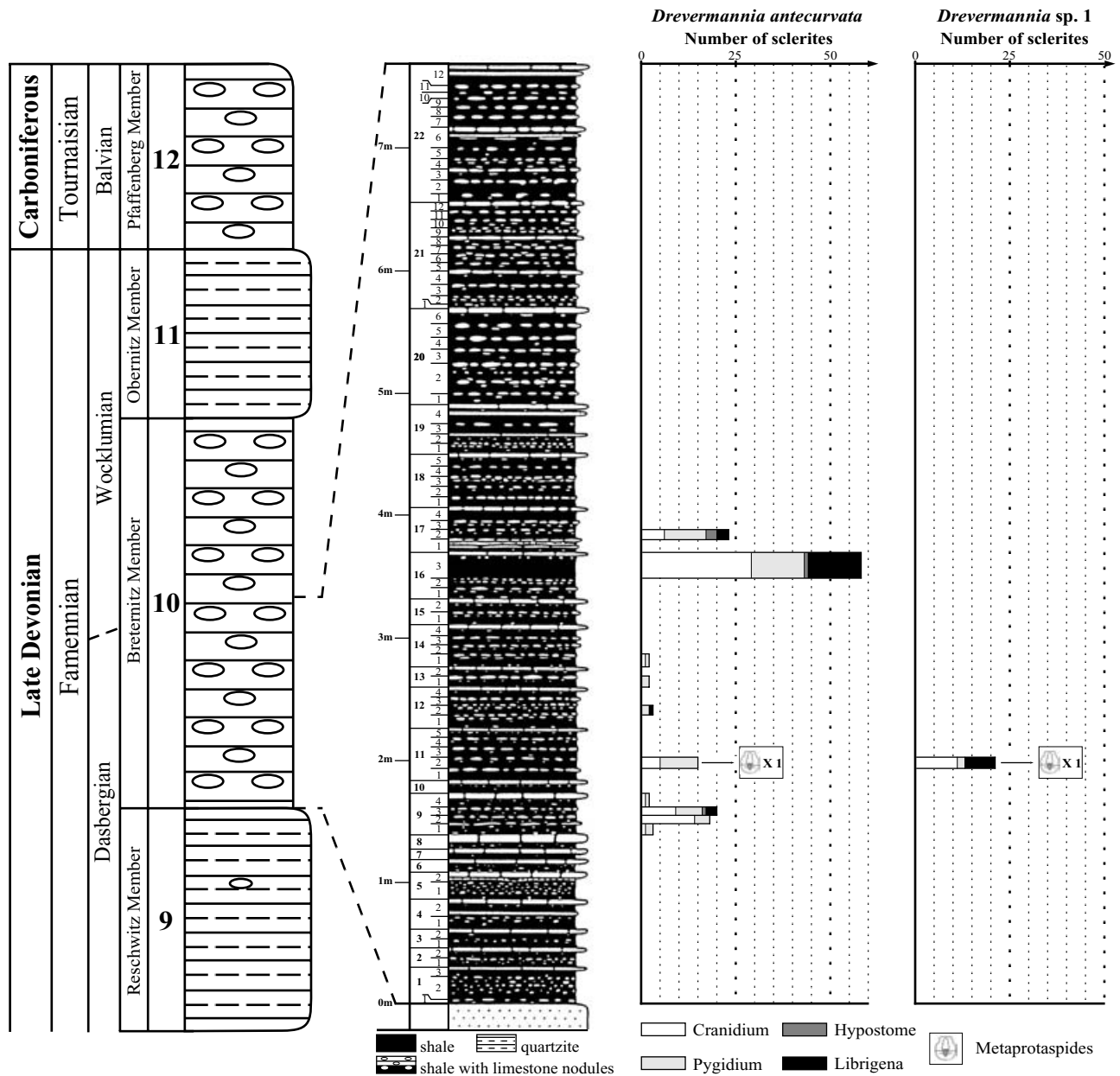


Figure 1. Occurrence and numerical abundance of different sclerites of *Drevermannia antecurvata* and *Drevermannia* sp. 1 in the columnar section representing the lower (Dasbergian) part of the Breternitz Member at Breternitz near Saalfeld, Thuringia.

ostracods of the Thuringian ecotype, as well as rich benthic biotas with small rugosan corals and reduced-eyed trilobites. The depositional environment was one of the deeper continental slope regions beyond the limits of light penetration (200–500 m) that faced open oceanic conditions to the northwest of the Thuringian Schwarzburg Anticline (Bartsch, Blumenstengel & Weyer, 1999).

The trilobite assemblages are mainly composed of the blind proetids *Drevermannia*, *Chaunoproetus* and *Typhloproetus* throughout the upper Dasbergian (to V) and Wocklumian (to VI) parts of the Breternitz Member. Other blind or reduced-eyed proetids, such as *Helioproetus* (see Lerosey-Aubril & Feist, 2005a), ‘*Struveproetus*’ and ‘*Haasia*’ are sporadically associ-

ated as minor elements. In addition, an undetermined phacopid species co-occurs rarely with *Helioproetus costifusus* in the lowest part of the Breternitz section (Lerosey-Aubril & Feist, 2005a) and *Weyerites ensae* (Richter & Richter, 1926) is abundantly found in the upper part of the Breternitz Member both in Breternitz and Fischersdorf (Crônier *et al.* 1999). Generally distorted in mudstones, these trilobites are better preserved in calcilitites where they occur silicified in the form of disarticulated sclerites densely filling body chambers of large cephalopod shells.

This contribution deals with three species of *Drevermannia* Richter, 1913. The presence of this genus in Thuringia was first recognized by Pfeiffer who found *D. schmidtii* Richter, 1913 in the Dasbergian

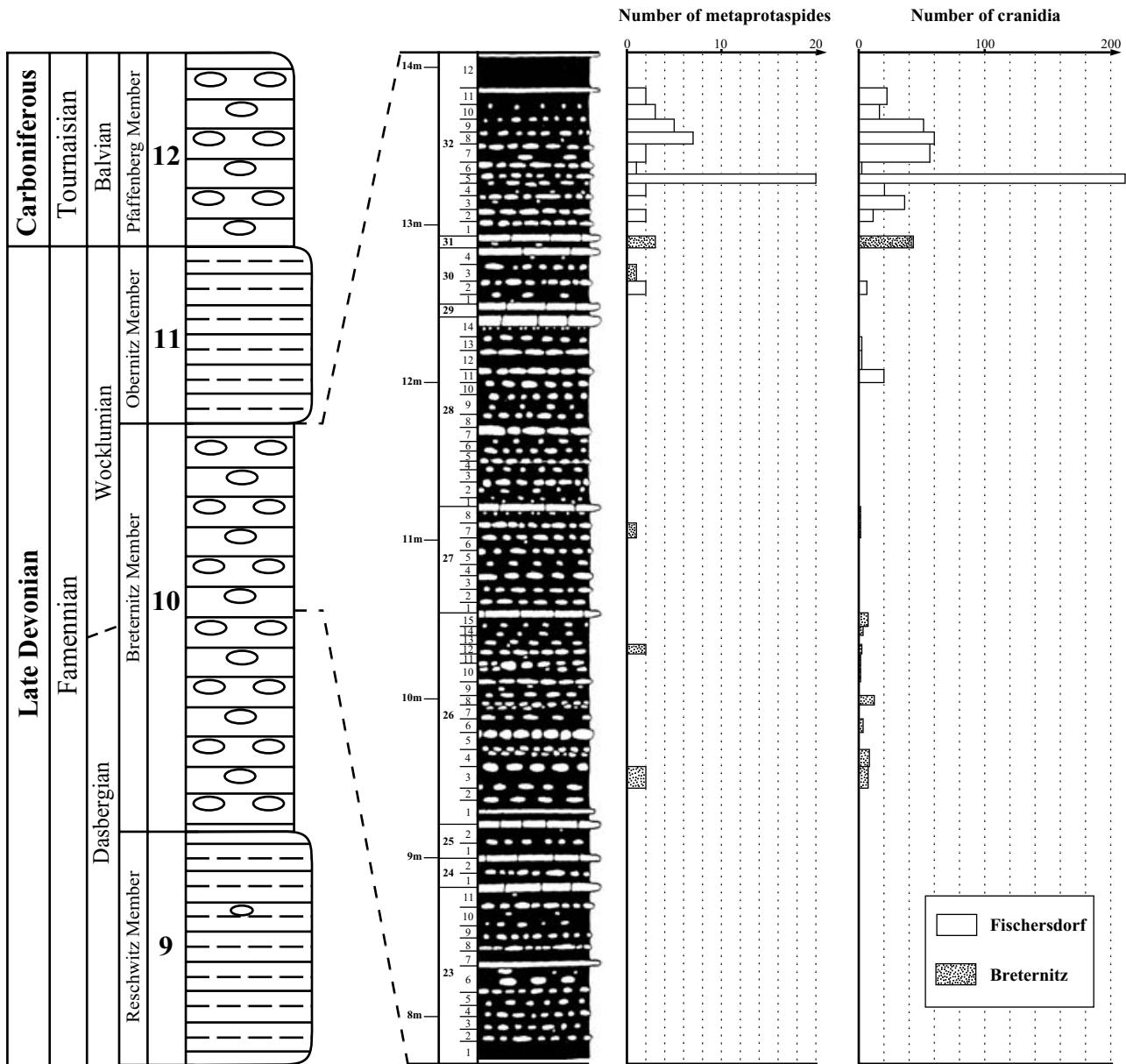


Figure 2. Occurrence and numerical abundance of metaprotaspides and cranidia of *Drevermannia richteri* Pfeiffer, 1959, in the columnar section representing the upper (Wocklumian) part of the Breternitz Member at Breternitz and Fischersdorf near Saalfeld, Thuringia. For stratigraphic legend, see Figure 1.

at Vorderbohlen and *D. richteri* Pfeiffer, 1959 in the Wocklumian at Vorderbohlen and Fischersdorf (Pfeiffer, 1954, 1959). Although two species from the lower (Dasbergian) part of the Breternitz Member at Breternitz are recognized herein, none of them resembles *D. schmidtii*. The rare *Drevermannia* sp. 1 has been found in a single bed in association with *D. antecurvata* sp. nov. (Fig. 1). This latter is more widely distributed in the Breternitz section, occurring from bed 9.1 to bed 17.1. In addition to these species, the trilobite assemblages also yield specimens attributed to *D. richteri*. However, this taxon is found exclusively in the upper part (Wocklumian) of the Breternitz Member, both at Breternitz and Fischersdorf, but

not in older levels (Fig. 2). The rather rich material of *D. richteri* comprises a complete growth series, including protaspis larvae. Accordingly, its ontogeny is hereafter described in detail, before the description of *D. antecurvata* sp. nov. and *D. sp. 1*.

The described and figured material is housed in the collections of the Museum für Naturkunde, Berlin, Germany (no. MB.T.4866.1–39, 4867.1–25 and 4868.1–8). The original material of *Drevermannia richteri* Pfeiffer, 1959 is housed in the collections of the Geological and Palaeontological Institute of the Bergakademie, Freiberg, Germany (no. A10/580–603). The measurements were obtained using a Nikon measuroscope (± 0.001 mm).

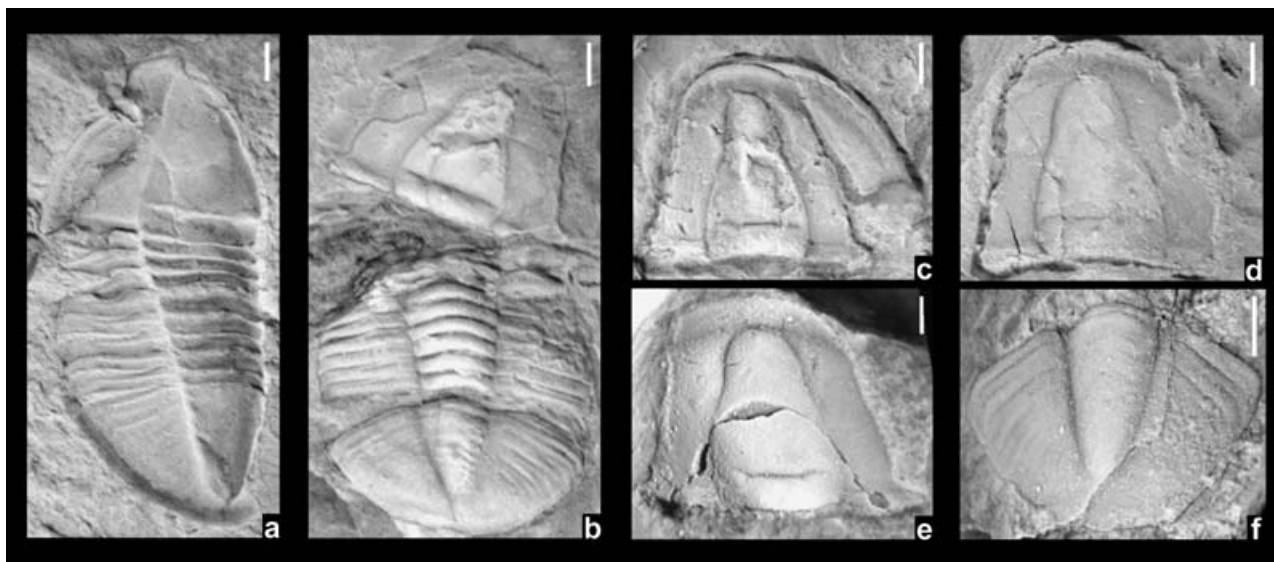


Figure 3. *Drevermannia richteri* Pfeiffer, 1959, upper Famennian (to VI), upper part of the Breternitz Member, Fischersdorf locality, Thuringia, Germany. All figures are digital photographs of calcareous specimens in dorsal views. Scale bars 1 mm. (a) External mould of an almost complete specimen (right side is missing), MB.T.4866.36. (b) Slightly disarticulated specimen (the librigenae and, possibly, the most anterior thoracic segments are missing), MB.T.4866.37. (c) Cranidium with right librigena slightly displaced, MB.T.4866.38. (d) Cranidium, MB.T.4866.39. (e, f) Originals. (e) Holotype, cranidium, A10/586. (f) Paratype, deformed pygidium, A10/596.

3. Systematic palaeontology

Terminology. Morphological terms used herein largely followed those defined by Whittington *et al.* (1997). Taking into account the particular course of the facial suture in *Drevermannia* where ε and ζ are fused, I introduce the term ‘pseudo-palpebral lobe’ to designate the narrow area defined by the portion $\gamma - \delta - (\varepsilon + \zeta)$ of the facial suture and the straight line linking γ and $(\varepsilon + \zeta)$. I maintain in this term the notion of ‘palpebral lobe’ because of the presence of a faint eye ridge in early meraspid cranidia. This latter runs abaxially from the axial furrow toward this area as it generally does toward the palpebral lobe in normally oculated proetids.

Order PROETIDA Fortey & Owens, 1975
 Family PROETIDAE Hawle & Corda, 1847
 Subfamily DREVERMANNIINAE Maximova, 1960
 Genus *Drevermannia* Richter, 1913

Type species. *Drevermannia schmidti* Richter, 1913.

Drevermannia richteri Pfeiffer, 1959
 Figures 3a–f, 4a–u, 6a–n

1954 *Drevermannia* sp. A; Pfeiffer, p. 38, pl. I, fig. 10.

1959 *Drevermannia richteri* Pfeiffer; Pfeiffer, pp. 267–8, pl. II, figs 1–4.

Remarks. In his original description of *Drevermannia richteri*, Pfeiffer (1959) used the term ‘Typus’ for two specimens, a cranidium (specimen A10/585) and a pygidium (specimen A10/596). However, he did not explicitly designate the holotype of the species. Also, I designate herein a large cranidium (specimen A10/

586), figured by Pfeiffer (1959, pl. II, fig. 1) and re-figured herein (Fig. 3e), the holotype of *Drevermannia richteri*. This specimen is on the same block but larger and better preserved than specimen A10/585.

The new specimens considered in this work are assigned to *Drevermannia richteri*, after comparison with the original material of Pfeiffer (1959). This attribution is reinforced by the fact that the considered materials are contemporaneous and that they have been collected at neighbouring localities (Fischersdorf, Vorderbohlen and Breternitz). However, some cranidia (e.g. Fig. 4l) possess a strongly upraised anterior border bearing terrace ridges, whereas that of the holotype is rather low and smooth. Taking into account that the anterior border is preserved in only four distorted cranidia of the original material, I consider that this difference is not significant enough to distinguish two taxa.

Material. 650 cranidia, 680 pygidia, 57 metaprotaspides, 12 anaprotaspides and an undetermined number of librigenae and hypostomes. About four-fifths of the specimens come from Fischersdorf.

Localities and age. Breternitz, Fischersdorf and Vorderbohlen, Thuringia, Germany. Upper part of the Breternitz Member. Late Famennian (to VI; Wocklumian; Late *P. expansa* to *P. praesulcata* biozones).

Additional description. The external mould of a large articulated specimen has been recovered at Fischersdorf (Fig. 3a). It reveals that holaspides of *D. richteri* possessed eight segments in the thorax. A similar number of segments has been observed in the thorax of *D. schmidti* (Richter, 1913), which may

indicate that it is a characteristic of Devonian representatives of the genus. In addition, three cranidia with hypostomes, positioned almost *in situ* (e.g. Fig. 4m, q), have been discovered. They allow the hypostome of *Drevermannia richteri* to be described. Assignment to *Drevermannia* is also supported by the fact that the relative abundance in one bed of this kind of hypostome corresponds to that of other associated sclerites of *Drevermannia richteri*.

The hypostome is subrectangular and elongate; middle furrows faint; neither terrace ridges nor maculae discernible; narrow, slightly down-curved (ventrally) anterior rim that regresses medially and vanishes laterally; anterior margin straight medially; anterior wings narrowing (exs.) abaxially, projecting dorsally and slightly laterally; lateral notches and posterior shoulders poorly differentiated; deep border furrow that shallows posteriorly; posterior margin straight, short and devoid of lateral forks. Doublure narrow, almost vertical, provided with a pair of small, ventrally projecting wing processes. Laterally, anterior margin subhorizontal; middle body inflated anteriorly, gently flattening posteriorly.

Ontogeny. Twelve proetoid anaprotaspides were found associated with *D. richteri*. All are arbitrarily assigned to this species, as there is no means to differentiate the anaprotaspides of the different proetoid species occurring in the sample. Indeed, it has been demonstrated that the morphology of proetoid anaprotaspides has remained practically unchanged from the Ordovician to the Early Carboniferous (Lerosey-Aubril & Feist, 2003, 2005*b,c*). Moreover, the restricted number of found specimens prevents testing whether or not their relative abundance in one bed is positively correlated with that of *D. richteri*.

Crônier *et al.* (1999) studied seven of these specimens and their description is generally in accordance with my observations except for minor features. Firstly, no anterior lobe or eye ridge, even incipient ones, was observed. Secondly, a medial node located at the posterior third (sag.) of the larvae is visible in well-preserved specimens (Fig. 4a, b). The addition of five new specimens extends the size range from 0.68–0.81 to 0.68–0.815 mm in length (sag.) and from 0.60–0.67 to 0.57–0.69 mm in width (tr.). Finally, two newly discovered specimens were associated with their hypostome (Fig. 4c, d). This broad ovoid hypostome is typically that of a proetoid anaprotaspis (Lerosey-Aubril & Feist, 2005*b*).

Fifty-seven metaprotaspis remains are confidently assigned to *D. richteri*. Most of them correspond to almost complete, well-preserved or only slightly deformed larvae. According to Figure 5, a single metaprotaspis stage can be recognized within the growth series of *D. richteri*. It is slightly elongate, 1.206–1.397 mm in sagittal length and 0.867–1.041 mm in maximum width (tr.); glabella long and gently tapering

anteriorly; axial furrows deep; preglabellar furrow faint to inconspicuous; S1 shallow to inconspicuous, strongly curved back defining low L1, no other glabellar furrows visible; occipital furrow deep; occipital node large and especially high (Fig. 4h); preglabellar field narrow; anterior border rather flat; α – β short and diverging; β – γ long, almost straight and diverging backwards; γ – ω more strongly diverging than β – γ ; no palpebral lobes or eye ridges discernible; posterior border furrow almost straight and rapidly shallowing abaxially; posterior border moderately inflated near axial furrow but flattening abaxially; junction between the protocranidium and the protopygidium marked by rather deep furrow that moderately shallows and strongly curves backwards abaxially. Protopygidium semi-circular, devoid of postero-medial notch; axial furrow rather deep; axis short with single axial ring discernible; one, possibly two, backwardly-curved abaxially, pleural furrows visible; post-axial field smooth, at least as wide (sag.) as flat border, from which it is separated by break in slope. Doublure flat, of equal width and in same position as protopygidial border. In lateral view, larvae slightly and almost symmetrically vaulted; glabella and protopygidial axis inflated.

From metaprotaspis protocranidium to largest holaspis cranidia (Fig. 4i–l), the following shape changes can be observed: glabella elongating (sag.) and significantly enlarging (tr.) posteriorly, mostly in late ontogeny; axial and preglabellar furrows initially deepening but shallowing in late stages; early meraspis fixigenal fields moderately inflating to form faint eye ridges that run postero-laterally from axial furrows toward pseudo-palpebral lobes without reaching facial suture, before rapidly vanishing in later stages; glabellar furrows deepening initially (up to three discernible) before shallowing in late ontogeny until complete disappearance in largest specimens; occipital furrow moderately deepening; occipital ring first narrowing (exs.) abaxially but broadening thereafter; occipital node decreasing in diameter throughout ontogeny though becoming high in early meraspides; preglabellar field narrowing (sag.) and faintly depressing medially in late ontogeny; anterior border furrow appearing rapidly in early meraspides and deepening thereafter throughout ontogeny; anterior border slightly protruding forward medially initially, subsequently straightening; α – β divergence increasing; β – γ straightening, elongating and less diverging backward; appearance of narrow (tr.) but long (exs.) pseudo-palpebral lobes that shorten throughout ontogeny, with initially long and moderately diverging γ – δ that progressively shorten, and short and sub-parallel δ – ($\epsilon + \zeta$) that increasingly converge backwards; ($\epsilon + \zeta$) – ω , initially short and slightly divergent, elongate and become strongly divergent; posterior border furrow first deepening but shallowing in late ontogeny; posterior border broadening (exs.) abaxially in late stages due to modification of the posterior margin that abruptly curves backwards at

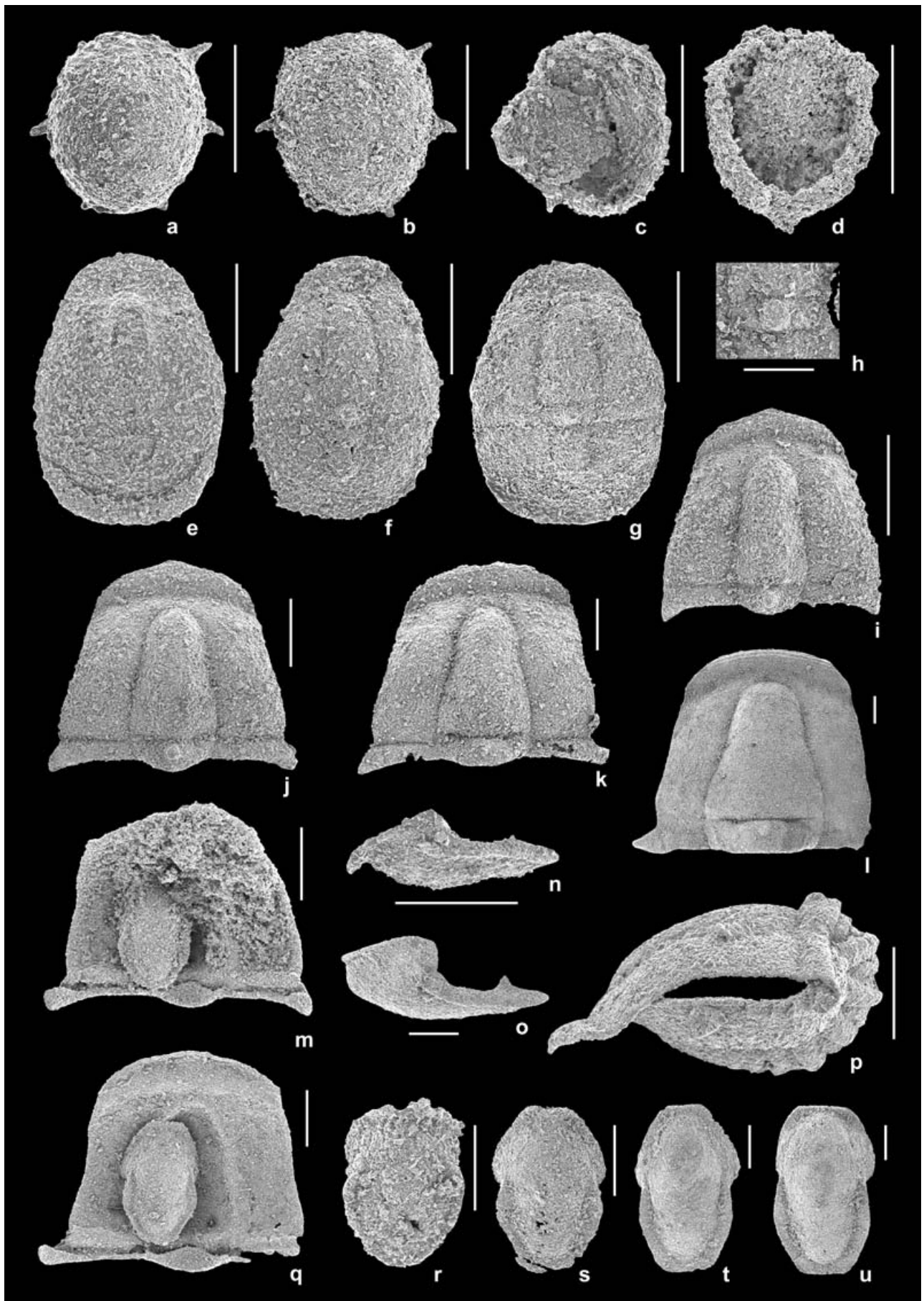


Figure 4. For legend see facing page.

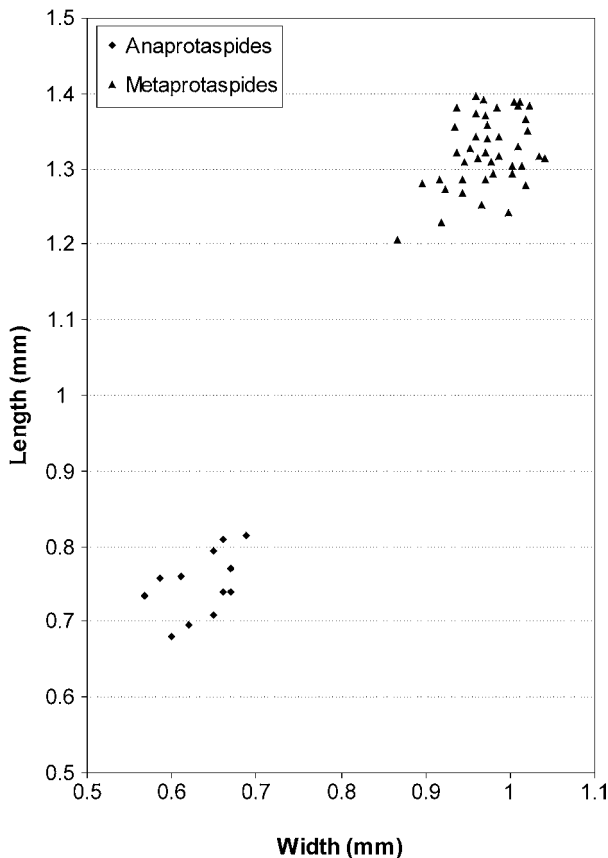


Figure 5. Scatter plot of length versus width for protaspides of *Drevermannia richteri* Pfeiffer, 1959. Measurements were obtained using a Nikon measuroscope (± 0.001 mm).

its mid-length. In lateral view, cranidium significantly flattening in late ontogeny; glabella substantially inflating initially but strongly flattening in late stages, whereas anterior border inflates throughout ontogeny; posterior border initially inflating while flattening thereafter, and becoming decreasingly ventrally flexed abaxially.

Developmental traits concerning the hypostome are as follows: anterior and posterior lobes less and less separated due to inflation of middle body posteriorly; anterior rim, initially broad medially and strongly curved ventrally, substantially narrows (Fig. 4n–o); anterior margin straightening medially; anterior wings

broadening (exs.); posterior border, initially convex, straightening. Doublure moderately broadening. In lateral view, anterior margin rocks forward to become subhorizontal.

The smallest librigenae found (Fig. 6a) exhibit the following features: no ocular structures discernible; librigenal field especially narrow in dorsal view and poorly separated from particularly broad and smooth lateral border that flattens laterally; genal spine short; posterior border poorly separated from genal field by faint posterior border furrow. Doublure broad, widening (exs.) near connective sutures, flat except adaxially where it curves dorsally, bearing one or possibly two terrace ridges. In lateral view, librigena rather high and librigenal field subvertical. The following ontogenetic changes can be described in subsequent stages (Fig. 6b–f): librigenal field broadening (tr.); lateral border furrow appears in early ontogeny but is rapidly replaced by break in slope thereafter; lateral border inflating; genal spine first substantially elongating but rapidly shortening in late ontogeny; posterior border furrow deepening and posterior border inflating before respectively shallowing and flattening in latest stages. Librigenal field progressively flattens throughout ontogeny in lateral view. Doublure incurving and bearing two obvious terrace ridges.

From the metaprotaspid stage to the holaspid period (Fig. 6i–n), the following shape changes can be observed in the pygidium: it substantially widens (tr.), progressively becoming elliptical in outline; faint postero-medial notch appears in early meraspides, gradually regressing until vanishing in rather late ontogeny; axis broadening (tr.) anteriorly, thus increasingly tapering posteriorly; axial, inter-ring, pleural and interpleural furrows deepening, except in late stages where they secondarily shallow; post-axial field narrowing (sag.); border rapidly narrowing (exs.), gradually rocking outward until forming an almost continuous slope with the pleural fields. In lateral view, axis substantially heightening mainly in early meraspid stages; pleural field, initially subdivided into subhorizontal inner part and outer part that strongly slopes ventrally, significantly flattening. Doublure narrowing and strongly incurving; up to four low terrace ridges progressively appear.

Figure 4. *Drevermannia richteri* Pfeiffer, 1959, upper Famennian (to VI), upper part of the Breternitz Member, Breternitz and Fischersdorf localities, Thuringia, Germany. All figures are scanning electron micrographs of silicified specimens. Scale bars 0.5 mm for all figures except (h) and (r) where they represent 0.25 mm. (a–d) Anaprotaspides. (a) Dorsal view, MB.T.4866.1. (b) Dorsal view, MB.T.4866.2. (c) Ventral view (note the associated hypostome), MB.T.4866.3. (d) Ventral view (note the associated hypostome), MB.T.4866.4. (e–h) Metaprotaspides. (e) Ventral view, MB.T.4866.5. (f) Dorsal view, MB.T.4866.6. (g) Dorsal view, MB.T.4866.7. (h) Detail of the occipital ring showing the large occipital node, MB.T.4866.8. (i–l) Cranidia, dorsal views. (i) Smallest meraspid specimen, MB.T.4866.9. (j) Meraspis, MB.T.4866.10. (k) Meraspis (?), MB.T.4866.11. (l) Large holaspis, MB.T.4866.12. (m, q) Cranidia with associated hypostomes, ventral views. (m) MB.T.4866.13. (q) MB.T.4866.14. (n, o) Hypostomes, left lateral views. (n) Small specimen (note the large anterior rim strongly curved ventrally), MB.T.4866.15. (o) Large specimen, MB.T.4866.16. (p) Complete and enrolled specimen (meraspid degree 4), left lateral view, MB.T.4866.21. (r–u) Hypostomes, ventral views. (r) Smallest specimen, MB.T.4866.17. (s) Small specimen, MB.T.4866.18. (t) Large specimen, MB.T.4866.19. (u) Largest specimen, MB.T.4866.20.



Figure 6. *Drevermannia richteri* Pfeiffer, 1959, upper Famennian (to VI), upper part of the Breternitz Member, Breternitz and Fischersdorf localities, Thuringia, Germany. All figures are scanning electron micrographs of silicified specimens. Scale bars 0.5 mm. (a–f) Librigenae, dorsal views. (a) Smallest specimen, MB.T.4866.22. (b) MB.T.4866.23. (c) MB.T.4866.24. (d) MB.T.4866.25. (e) MB.T.4866.26. (f) Largest specimen, MB.T.4866.27. (g) Left librigena, ventral view, MB.T.4866.28. (h) Left librigena, lateral view, MB.T.4866.29. (i) Large pygidium, ventral view, MB.T.4866.30. (j–n) Transitory pygidia and pygidia, dorsal views. (j) Small meraspis, MB.T.4866.31. (k) Meraspis, MB.T.4866.32. (l) Meraspis (?), MB.T.4866.33. (m) Holaspis, MB.T.4866.34. (n) Largest holaspis, MB.T.4866.35.

Drevermannia antecurvata sp. nov.

Figure 7a–y

Material. 66 cranidia, 54 pygidia, 5 hypostomes and 29 librigenae.

Etymology. From latin *ante*, anterior and *curvatus*, curved, referring to the curved anterior margin of the cranidium.

Type locality and horizon. Breternitz, Thuringia, Germany. Lower part of the Breternitz Member. Micritic limestone nodules intercalated within dark-coloured argillites. Late Famennian (to V; Dasbergian; *P. expansa* Biozone).

Holotype. Large holaspisid cranidium, MB.T.4867.8, Figure 7h.

Figure 7. *Drevermannia antecurvata* sp. nov., upper Famennian (to V), lower part of the Breternitz Member, Breternitz locality, Thuringia, Germany. All figures are scanning electron micrographs of silicified specimens. Scale bars 0.5 mm. (a–h) Cranidia, dorsal views. (a) Smallest meraspis, MB.T.4867.1. (b) Meraspis, MB.T.4867.2. (c) Meraspis, MB.T.4867.3. (d) Meraspis, MB.T.4867.4. (e) Meraspis, MB.T.4867.5. (f) Holaspis (?), MB.T.4867.6. (g) Large holaspis, MB.T.4867.7. (h) Holotype, large holaspis, MB.T.4867.8. (i) Right librigena, ventral view, MB.T.4867.9. (j–n) Librigenae, dorsal views. (j) Smallest specimen, MB.T.4867.10. (k) MB.T.4867.11. (l) MB.T.4867.12. (m) MB.T.4867.13. (n) Largest specimen, MB.T.4867.14. (o, p) Hypostomes, ventral views. (o) Small specimen, MB.T.4867.15. (p) Large specimen, MB.T.4867.16. (q–w) Transitory pygidia and pygidia, dorsal views. (q) Smallest meraspis, MB.T.4867.17. (r) Meraspis, MB.T.4867.18. (s) Meraspis, MB.T.4867.19. (t) Meraspis (?), MB.T.4867.20. (u) Holaspis, MB.T.4867.21. (v) Holaspis (right side broken), MB.T.4867.22. (w) Largest holaspis (left anterior part broken), MB.T.4867.23. (x, y) Transitory pygidium and pygidium, ventral views. (x) Meraspis, MB.T.4867.24. (y) Holaspis, MB.T.4867.25.

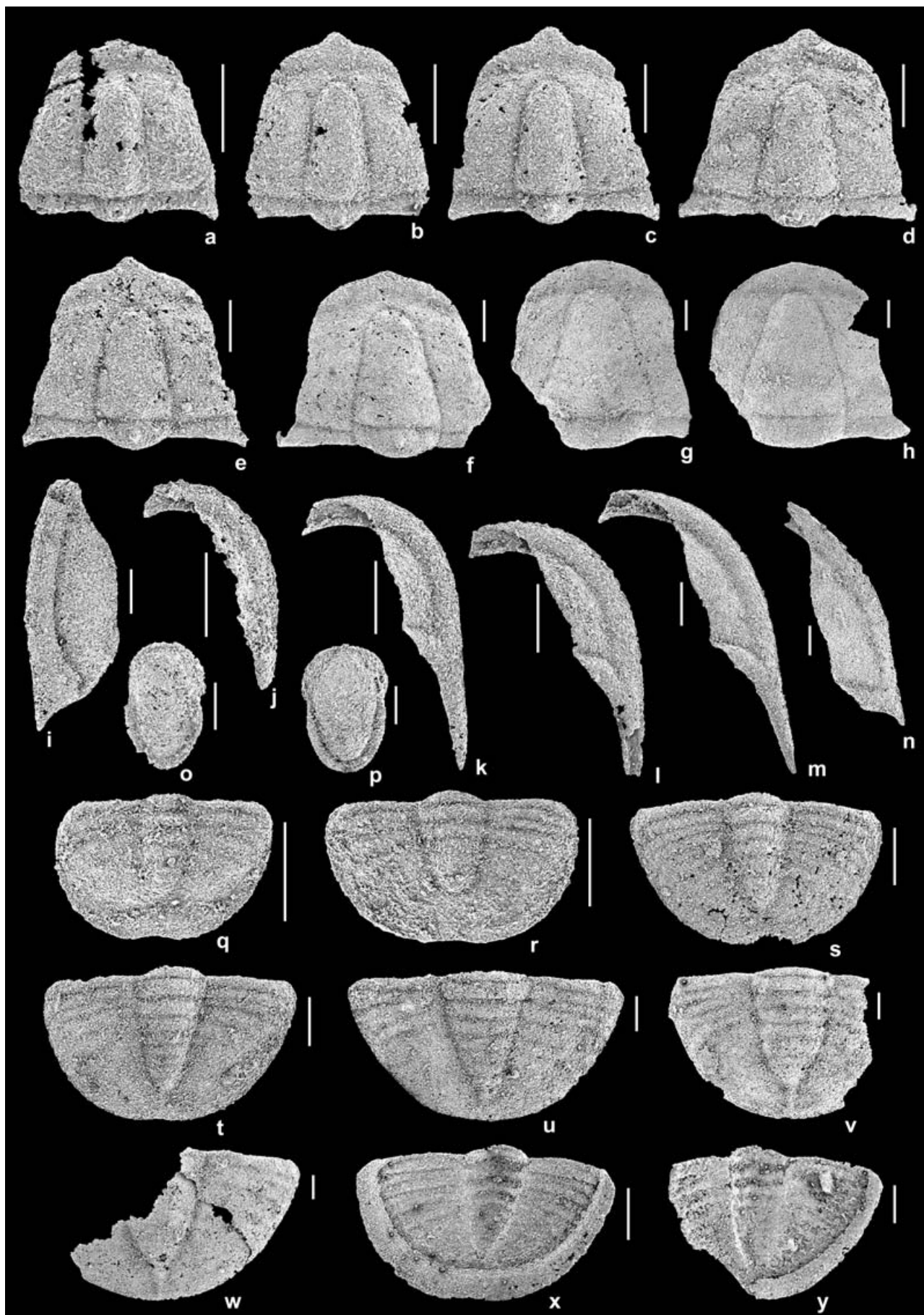


Figure 7. For legend see facing page.

Diagnosis. Species of *Drevermannia* with the following particular features: glabella tapering anteriorly, long (sag.), particularly wide (tr.) posteriorly and only slightly constricted laterally; no glabellar furrows discernible; preglabellar field extremely narrow or absent; anterior border poorly differentiated, smooth and flat; anterior margin convex forwards; β - γ sub-parallel; pseudo-palpebral lobe long (exs.) but narrow (tr.); genal spine short; pygidium semi-circular in outline; axis broad (tr.); low post-axial ridge.

Description. Glabella long (sag.), particularly wide (tr.) posteriorly, tapering anteriorly, and slightly constricted laterally; axial furrows rather shallow; no glabellar furrows discernible; SO rather deep medially but shallowing abaxially; occipital ring only slightly narrowing (exs.) abaxially and bearing a tiny median node; preglabellar field extremely narrow or absent; anterior border poorly differentiated, smooth, flat, narrowing (exs.) and curving backwards abaxially; anterior margin convex forwards; β - γ sub-parallel; pseudo-palpebral lobe long (exs.) but narrow (tr.) with short and diverging γ - δ and sub-parallel δ - ($\varepsilon + \zeta$); ($\varepsilon + \zeta$) - ω short and strongly diverging. Posterior border furrow shallow and moderately curved forwards abaxially; posterior border narrow (exs.) adaxially, inflates, widens (exs.) and moderately slopes down abaxially. In lateral view, cranium rather flat; glabella modestly inflated. Occipital doublure broad medially but strongly narrowing abaxially. External surface smooth.

Rostral plate unknown. Only a single hypostome attributed to *D. antecurvata* is of sufficiently substantial size to be assigned to a young holaspis (Fig. 7p). It is elongate, subrectangular anteriorly but rounded posteriorly, with maximum width (tr.) across anterior wings; middle body strongly inflated, only faintly divided into anterior and posterior lobes by simple curvatures of rather deep lateral furrows, and devoid of discernible terrace ridges or maculae; anterior rim narrow, slightly down-curved (ventrally) and separated from anterior lobe by break in slope that rapidly dies out laterally; anterior wings strongly narrowing (exs.) abaxially, projecting dorsally and moderately laterally; lateral notches and posterior shoulders undefined and replaced by continuous, rather narrow postero-lateral border; postero-lateral forks absent. Doublure narrow, almost vertical and only present on each side of posterior half of hypostome, where it forms a pair of small, ventrally projecting wing processes. Laterally, middle body continuously inflates from rear to front without separating anterior and posterior lobes.

Librigena devoid of ocular structure; librigenal field relatively narrow (tr.) and only separated from lateral border by faint break in slope; lateral border inflated and lacking terrace ridges; genal spine short, flattened laterally, without terrace ridges; broad (exs.) posterior border separated from genal field by shallow posterior

border furrow. Doublure strongly incurved, of equal width (tr.) with lateral border but more expanding anteriorly, no terrace ridges discernible. In lateral view, relief low.

Pygidium semi-circular; axis triangular, long and especially wide anteriorly; six inter-ring furrows particularly faint; post-axial region rather narrow, bearing low post-axial ridge that progressively vanishes rearward; pleural region gradually sloping outward and undivided into pleural field and border; two to three pleural furrows well-marked and slightly curved backward abaxially that shallow adaxially; one or two especially faint interpleural furrows only discernible adaxially. Doublure incurved, narrow, gently decreasing in size anteriorly, and bearing at least two low terrace ridges. In lateral view, pygidium of moderate vaulting; axis high but composed of low axial rings except for first one that is higher. Sculpture: entirely smooth.

Remarks. The hypostome described above is assigned to *Drevermannia antecurvata* because it resembles the hypostome attributed to *D. richteri*. This assignment is reinforced by the fact that it consistently co-occurs with other remains of *D. antecurvata*.

Comparisons. The absence of an inflated anterior border and deep anterior border furrow in the cranium of *D. antecurvata* distinguishes this new species from *D. schmidtii*, *D. sp. 1*, *D. pruvosti* Richter & Richter, 1939 and *D. calamicensis* Hahn, Hahn & Brauckmann, 1997. In addition, *D. antecurvata* differs from *D. richteri*, *D. schmidtii*, *D. calamicensis* and *D. pruvosti* by having a less laterally constricted glabella. This latter substantially broadens posteriorly and tapers anteriorly, unlike that of *D. calamicensis* and *D. pruvosti*. Also, *D. calamicensis* does not exhibit pseudo-palpebral lobes. Regarding librigenae, *D. antecurvata* is easily distinguished from *D. pruvosti* by having a short genal spine. The pygidium of *D. antecurvata* differs from those of *D. schmidtii*, *D. pruvosti* and possibly *D. richteri* by its semi-circular outline, and from that of *D. calamicensis* by having a shorter (sag.), broader (tr.) and posteriorly less pointed axis. Finally, I do not consider '*Drevermannia asperula* Chlupáč, 1961 to be correctly assigned. In my opinion, this species is closer to *Typhloproetus* and, in particular, closely resembles *Typhloproetus (Silesiops) korni* Feist, 1992.

Ontogeny. Anaprotaspis unknown. A single metaprotaspis specimen was attributed to *Drevermannia antecurvata*. Unfortunately, this unique specimen was destroyed during preparation for scanning electron micrography. However, the specimen had been precisely observed and no features distinguished it from the metaprotaspis of *D. richteri*. Likewise, it was of similar size (sagittal length: 1.382 mm; maximum width: 0.991 mm).

The post-protaspis development of the cranium is very similar to that of *D. richteri* (Fig. 7a-h). In particular, the overall vaulting in lateral view,

the glabella, the occipital ring, the eye ridges, the $(\epsilon + \zeta) - \omega$ portions and the posterior border undergo the changes observed in the ontogeny of *D. richteri*. Likewise, the axial, preglabellar, glabellar, occipital and posterior border furrows alter in the same way in both ontogenies. However, some developmental traits are slightly different in the ontogeny of *D. antecurvata*. For example, the occipital node and the preglabellar field are almost absent in the latest stages (Fig. 7h). Though initially elongating, the $\beta - \gamma$ portion of the facial suture shortens and becomes subparallel in late ontogeny of *D. antecurvata*. In addition, the pseudo-palpebral lobes do not only shorten (exs.) as in *D. richteri*, but also become narrow (tr.). Lastly, the anterior part of the cranium develops differently in *D. antecurvata* and *D. richteri*. The anterior border is depressed medially and particularly protrudes forwards in early meraspid stages of *D. antecurvata*. Thereafter, the medial depression rapidly disappears, whereas the anterior protrusion persists for a long time before vanishing (e.g. Fig. 7f). Also, the anterior border increasingly curves backwards abaxially. Finally, a faint anterior border furrow appears in early meraspides but is rapidly replaced by a break in slope.

As for the hypostome, the smallest specimen is deformed but may represent the hypostome of a late meraspis (Fig. 7o). The only developmental traits observable in the sample are a narrowing (sag.) of the anterior rim and a decreasing of the convexity of the posterior border, two ontogenetic changes also observed in *D. richteri*.

The smallest librigenae correspond to the smallest cranidia of *D. antecurvata* found in the sample. Moreover, nothing distinguishes them from *D. richteri* librigenae of comparable sizes. Likewise, the librigena develops similarly in both ontogenies. The only minor difference is the number of terrace ridges present on the doublure, as up to three are observed rarely in *D. antecurvata*. However, it is likely that this dissimilarity stems from a difference in the quality of preservation.

The smallest transitory pygidium closely resembles small specimens of *D. richteri* (Fig. 7q). Once again, the ontogenetic changes affecting the pygidium in *D. antecurvata* are particularly similar to those observed in *D. richteri*. For example, there are no differences in the development of the postero-medial notch, the axial furrows, the border, the pleural field and the doublure. Moreover, the inter-ring furrows initially deepen (up to seven, possibly eight, axial rings visible) before shallowing in late ontogeny as in *D. richteri*. Likewise, up to five pleural and four interpleural furrows can be observed prior to their subsequent shallowing in late stages. The axis undergoes comparable changes in both ontogenies, but it is moderately flattened in late holaspides of *D. antecurvata* while a faint post-axial ridge appears. The most significant difference concerns the pygidial outline. Though the pygidium initially broadens (tr.) in both ontogenies, it secondarily

narrows (tr.) in the development of *D. antecurvata*. Thus, in the latter, the pygidial outline is successively semi-circular, elliptical and again semi-circular.

Drevermannia sp. 1

Figure 8a–h

Remarks. All specimens assigned to *Drevermannia* sp. 1 were recovered from a single bed (Fig. 1) in Breternitz. The same bed also yielded pygidia belonging to *Drevermannia*, but they cannot be differentiated from those of *D. antecurvata*. The largest cranium is poorly preserved and, according to its size, may represent a young holaspis. Accordingly, the material does not allow a confident assignment to a particular species and even less the description of a new species. Lastly, 'sp. 1' has been preferred to 'sp. A' to avoid any confusion with *Drevermannia* sp. a described by Richter (1913) and *Drevermannia* sp. A described by Pfeiffer (1954).

Material. 13 cranidia, 8 librigenae and 1 metaprotaspis.

Locality and age. Breternitz, Thuringia, Germany. Lower part of the Breternitz Member. Late Famennian (to V; Dasbergian; *P. expansa* Zone).

Comparison. The largest cranium of *Drevermannia* sp. 1 is particularly similar to specimens of comparable size of *D. antecurvata* and *D. richteri*. The main differences concern the anterior part and the relative overall proportions of the cranium. Indeed, compared to the two other species, *Drevermannia* sp. 1 possesses: significantly broader (tr.) cranium as well as moderately broader (tr.) occipital ring; $\alpha - \alpha$ section, anterior border and border furrow substantially longer; anterior fixigenal fields particularly broader (tr.). In addition, $\beta - \gamma$ is more convergent backwards (especially when compared to *D. richteri*) and the pseudo-palpebral lobes are better differentiated due to more convergent $\delta - (\epsilon + \zeta)$ (especially when compared to *D. antecurvata*). Finally, in *Drevermannia* sp. 1, the anterior border is more inflated and protrudes moderately less medially and the anterior border furrow is deeper than in *D. antecurvata*.

No rostral plate was found, but the shape of the connective sutures on the librigenae suggests that it is of trapezoidal outline. Hypostome unknown.

The librigena in *Drevermannia* sp. 1 is also similar to those of *D. antecurvata* and *D. richteri*. The few minor differences between specimens of similar sizes are: slightly narrower librigenal field (tr.), absence of lateral furrow (still present in the two other species at this stage) and more incurved doublure.

Ontogeny. Anaprotaspis unknown. A single metaprotaspis specimen (Fig. 8a) is assigned to *Drevermannia* sp. 1 because of the great resemblance of its protocranidium to the smallest cranidia of this undetermined species. The specimen is elongate, 1.379 mm sagittal length and 0.963 mm maximum width, and

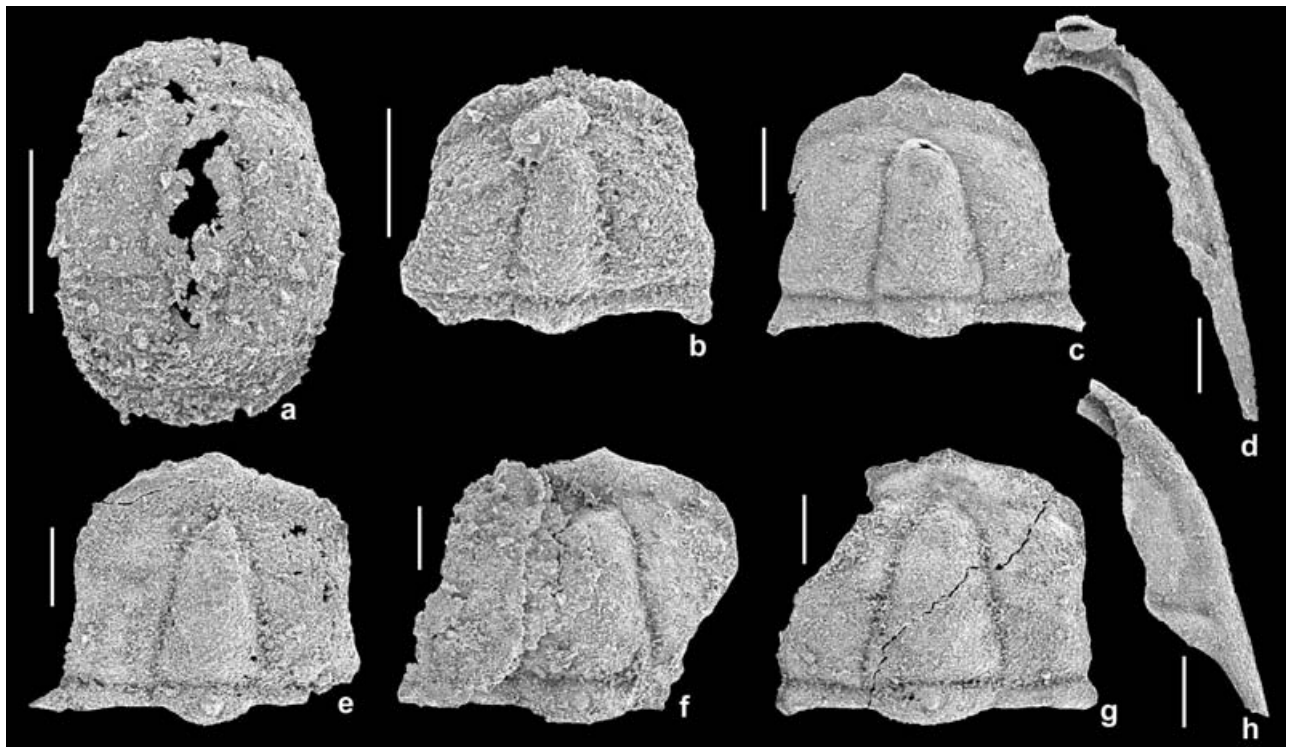


Figure 8. *Drevermannia* sp. 1, upper Famennian (to V), lower part of the Breternitz Member, Breternitz locality, Thuringia, Germany. All figures are scanning electron micrographs of silicified specimens. Scale bars 0.5 mm. (a) Metaprotaspis, dorsal view, MB.T.4868.1. (b, c, e–g) Cranidia, dorsal views. (b) Small meraspis, MB.T.4868.2. (c) Meraspis, MB.T.4868.3. (e) Meraspis, MB.T.4868.4. (f) Holaspis (?), MB.T.4868.5. (g) Holaspis (?), MB.T.4868.6. (d, h) Librigenae, dorsal views. (d) Small specimen, MB.T.4868.7. (h) Large specimen, MB.T.4868.8.

rather similar to the metaprotaspides of *D. antecurvata* and *D. richteri*. The main differences concern the general effacement of furrows, the development of the larval structures dorsally and the shape of the anterior part of the protocranidium. Indeed, the metaprotaspis of *Drevermannia* sp. 1 possesses shallow axial furrows on the whole dorsal shield, a shallow occipital furrow, a faint posterior border furrow on the protocranidium, and a moderately marked junction between protocranidium and protopygidium. Also, the preglabellar furrow and pleural furrows are not discernible. As to relief, the posterior border of the protocranidium is flat, and the glabella as well as the protopygidial axis is only slightly inflated. Overall, the larva is less vaulted in lateral view. Finally, the metaprotaspis of *Drevermannia* sp. 1 exhibits a particularly broad (tr.) anterior part of the protocranidium, as illustrated by the long α – α section and the adaxial locations of β turning points resulting in a subparallel course of β – γ .

The post-protaspis development of the cranium corresponds to that observed in *D. richteri* (Fig. 8b, c, e–g). Indeed, the overall vaulting in lateral view, the glabella, the axial furrows, the occipital ring, the occipital node, the anterior border furrow and the $(\epsilon + \zeta) - \omega$ portions are all features that alter in exactly the same way in both ontogenies. In addition, some features change similarly but with minor variations in both developments. Thus the eye ridges undergo

the same modifications during ontogeny but they are better differentiated in early meraspides. Likewise, three glabellar furrows appear in early meraspides, first deepening and shallowing thereafter in the ontogeny of *Drevermannia* sp. 1, but all are still discernible in some large specimens. The preglabellar field slightly narrows but is never sunken in the ontogeny of *Drevermannia* sp. 1. Also, the anterior border evolves similarly in both ontogenies but it is still protruding and devoid of terrace ridges in the largest cranidia of *Drevermannia* sp. 1. Though straightening and elongating, β – γ are already subparallel in early meraspides and subsequently increasingly converge in *Drevermannia* sp. 1. It is likely that such differences stem from the fact that the absence of large cranidia in the sample prevents the investigation of the latest ontogenetic changes in *Drevermannia* sp. 1. However, there are also a few features that change differently in both ontogenies. These are: pseudo-palpebral lobes not shortening (exs.) but narrowing (tr.); $\delta - (\epsilon + \zeta)$ already convergent in early meraspides, decreasingly convergent in subsequent stages and posterior border broadening (exs.).

The smallest librigena is very similar to the largest specimen and its size corresponds to that of the smallest cranium. The only minor shape changes during ontogeny concern the widening (tr.) of the librigenal field and its separation from the lateral border

by appearance of a faint break in slope. The genal spine, initially circular in section, becomes shorter and flattens. The doublure slightly narrows and curves inwards. In lateral view, the librigenal field moderately flattens, whereas the lateral border inflates.

4. Discussion

4.a. Evolution of proetoid anaprotaspis size through time

Recently, an attempt was made broadly to depict the evolution of anaprotaspis size in proetoid trilobites from the Ordovician to the Early Carboniferous (Lerosey-Aubril & Feist, 2005c). Accordingly, it has been shown that the anaprotaspis larvae of early proetoids may have been rather small, whereas Devonian anaprotaspides illustrate that a marked increase in larval size occurred around the Silurian/Devonian boundary. It is noteworthy that comparable larval sizes are observed in representatives of three distinct sub-families (Proetinae: Chatterton, 1971; Dechenellinae: Chatterton *et al.* 1999; Cyrtosymbolinae: Lerosey-Aubril & Feist, 2005c), living in three different epochs (Early, Middle and Late Devonian, respectively), and that these larval proportions seem to be independent of sizes reached in adulthood. Also, the discovery of larger proetoid anaprotaspides in the upper Famennian of Thuringia significantly contrasts with this homogeneity of larval size, observed in older proetoids from the Devonian. Accordingly, it seems important to propose hypotheses that could explain this increase in larval size, as the latter may denote a significant modification of the early development of some Late Devonian proetoids. In my opinion, two scenarios can be suggested to explicate this increase in larval size, although I recognize the speculative nature of these assumptions, especially with regard to the limited data available on late Famennian proetoid anaprotaspides.

4.a.1. Acquisition of a two-stage planktonic period

The size increase observed in late Famennian proetoid anaprotaspides can be explained by the possibility that these larvae may represent the second stage of a two-stage planktonic period and not, as in the development of older proetoids, a unique planktonic stage. Considering that the first post-embryonic stage in modern crustaceans rarely reaches 0.4 mm (G. Scholtz, pers. comm. 2005), it seems reasonable to assume these large larvae did not represent the first stage that immediately followed hatching. Moreover, similar sizes have been observed in some Early Carboniferous proetoid anaprotaspides from France (Lerosey-Aubril & Feist, 2005b), which were associated with specimens significantly smaller than previously known Devonian larvae. This enabled Lerosey-Aubril & Feist (2005b) to suggest that some Early Carboniferous proetoids may have acquired an extended planktonic period, composed of two successive larval stages. Though

regrettable, the absence of smaller anaprotaspides in the sample (Fig. 5), which might have represented a first planktonic stage, does not imply that the latter did not occur in the development of late Famennian proetoids. Indeed, this absence can be due to the fact that, as planktonic, they might have not lived in the same place as the meraspis and holaspis stages. This would explain why only a restricted number of anaprotaspis specimens (only twelve among several hundred trilobite remains), all corresponding to the larval stage just preceding metamorphosis, have been found in the sample. Also, it cannot be ruled out that this first planktonic stage did not possess a calcified exoskeleton, which may explain why it has not been fossilized. Thus, the assumptions proposed by Lerosey-Aubril & Feist (2005b,c), that some proetoids might have already possessed an extended planktonic period prior to the terminal Devonian Hangenberg biocrisis, and that this modified developmental strategy may have influenced their survivorship during this extinction event, are neither weakened nor reinforced by the new data provided by the discovery of late Famennian proetoid larvae.

4.a.2. Acquisition of a lecithotrophic planktonic larva

As an alternative, the enlargement of these anaprotaspides may be explained by the possibility that, contrary to older Devonian proetoid larvae, they were lecithotrophic (non-feeding). Indeed, it can be demonstrated that lecithotrophic larvae in modern crustaceans are notably larger than planktotrophic (feeding) ones (numerous examples are presented in Anger, 2001). This is particularly obvious if the comparison involves larvae of closely related species, but it is still visible when the concerned taxa belong to the same family (Anger, pers. comm. 2005). Lecithotrophy, especially in crustaceans, is thought to be related to life in habitats with limited food resources or a strong seasonality of food abundance (Thorson, 1950; Anger, 2001). According to Bartzsch, Blummenstengel & Weyer (1999), trilobites and rugosan corals, found in the upper Famennian of Thuringia, were living in a particularly deep (200–500 m) benthic habitat. However, data concerning the abundance of food and its degree of seasonality, in comparable environments in modern seas, are scarce and somewhat ambiguous (e.g. Cartes *et al.* 2002; Danovaro *et al.* 1999). Consequently, it is difficult to explore further the possibility that lecithotrophy might have been acquired in these late Famennian trilobites, in response to the colonization of particularly deep benthic habitats.

4.b. Post-metamorphic development and systematics

In terms of size and absence of ornamentation, the metaprotaspides of *Drevermannia* are typically of proetoid type. Including anaprotaspides and anaprotaspis

hypostomes, these proetoids possess a particular early ontogeny, which supports the view that the Proetida may comprise two different clades, as already suggested by Lerosey-Aubril & Feist (2005b). The discovery of metaprotaspid specimens also represents a unique opportunity to compare the early ontogenies of closely related species. Although the metaprotaspides of *D. richteri* and *D. antecurvata* cannot be distinguished from one another, that of *Drevermannia* sp. 1., with its particularly broad (tr.) anterior part of the protocranidium, demonstrates that differences between closely related species can be acquired in the earliest ontogenetic stages. However, subsequent shape changes occurring during the meraspis period are limited and very similar in different species. It is relatively late in the ontogeny (probably around the meraspis/holaspis boundary) that evident morphological differences appear between *D. richteri* and *D. antecurvata*. Unfortunately, the absence of large specimens of *Drevermannia* sp. 1 prevents investigation of possible significant shape modifications in the late ontogenetic stages of this species. Thus, two periods of major changes can be identified in the ontogeny of *Drevermannia*. The earliest one is probably linked to the metamorphosis separating anaprotaspid and metaprotaspid stages, whereas the second phase occurs in late ontogenetic stages. The absence of significant shape changes during almost all the meraspis period is also distinctive in the ontogeny of *Drevermannia*, as this period is generally one of important modifications (e.g. Chatterton, 1971; Lerosey-Aubril & Feist, 2005c).

So far, Feist and I have been cautious when considering metaprotaspid features for establishing phyletic relationships between proetid subfamilies (Lerosey-Aubril & Feist, 2005b,c). Indeed, we showed that some Early Carboniferous metaprotaspides more closely resemble Ordovician ones than all other proetoid larvae (Lerosey-Aubril & Feist, 2005b). Considering that these metaprotaspides belong to two phylogenetically distant clades, separated by at least 90 Myr, we were concerned by the fact that proetoid metaprotaspides may be subjected to convergence. That two closely related species of *Drevermannia* exhibit such distinct metaprotaspid stages emphasizes this point of view.

4.c. Eye loss in the *Drevermannia* lineage

Among the trilobites abundantly found in the late Famennian association of Thuringia, *Drevermannia* is the only taxon that has no direct ancestry to forms with normal or even reduced eyes. This may indicate that this group, more so than other blind forms, constitutes highly derived trilobites. In this regard, the elucidation of the ontogeny in *Drevermannia* gives some insight into the phenomenon of eye loss in this group. The three growth sequences described reveal that *Drevermannia* never develops ocular structures externally. Indeed, no lenses occur at any stage. Likewise, the visual areas

never develop in these species, although they can be present as smooth surfaces in other blind proetoids (e.g. *Erbenicoryphe*: see Feist & Clarkson, 1989). Finally, only pseudo-palpebral lobes develop. Incipient but true palpebral lobes do not occur even in the earliest ontogenetic stages that would have indicated a possible origin from a normally oculated ancestor as has been demonstrated recently in *Helioproetus*, another late Famennian blind proetide (Lerosey-Aubril & Feist, 2005a). The absence of external ocular structures throughout development may suggest that blindness has been acquired very early in the evolution of the *Drevermannia* lineage. On the other hand, it may also be regarded as evidence of a drastic modification of eye formation due to mutation of a few genes that have coded for proteins actively involved in the development of this feature (e.g. regulatory factors). In that case, the obsolescence of eye formation may have been attained instantaneously. This challenging hypothesis, however, is hard to support in terms of adaptation acquired under control of natural selection. Moreover, the eye loss in other Late Devonian proetoids and phacopids has proved to be a gradual phenomenon (Yuan, 1988; Feist & Clarkson, 1989; Feist, 1995). Therefore, it seems more likely that blindness in *Drevermannia* has been attained by gradual evolution well before the appearance of these late Famennian representatives.

Nevertheless, there is some evidence that structures related to the eye still developed in early growth of *Drevermannia*. Indeed, short eye ridges are discernible in the early meraspis cranidia of all three species (especially in *Drevermannia* sp. 1, see Fig. 8b). These structures, observed in many trilobites, are thought to reveal the course of the optical nerve (Bergström & Hou, 2003). According to Erben (1961), there are two tendencies of eye reduction in modern arthropods. Centrifugal reduction implies an initial degeneration of internal eye structures (e.g. nerves) while external ones (e.g. lenses) are unaltered. By contrast, centripetal reduction is a degeneration that affects first the external structures while the optical nerves remain unaffected. The presence of eye ridges in early ontogenetic stages suggests that eye loss in *Drevermannia* may have been attained by centripetal reduction. This may also be the case in the *Helioproetus* lineage, as similar structures have been described on small cranidia of *H. costifusus* (Lerosey-Aubril & Feist, 2005a). More generally, eye ridges can be observed in adults of several Late Devonian trilobites with reduced or even absent eyes, including the early Famennian *Pontipalpebralia* (Lütke, 1968) and the late Frasnian *Palpebralia* (Feist, 1995). In the latter lineage, however, the eye ridges have completely vanished in the latest stage, represented by the blind *Palpebralia brecciae*. This may indicate that the process of centripetal reduction has reached a particularly advanced state. In this regard, it is noteworthy that eye ridges in the initial stage of the *Palpebralia* lineage, as well as in early

ontogenetic stages of *Drevermannia* and *Helioproetus*, do not reach the facial suture. This suggests that the development of optical nerves may have also been altered, at least partially. Presumably, eye degeneration and blindness in Late Devonian (and probably also in Early Carboniferous) proetoids must have been attained principally by centripetal reduction. To what extent this evolutionary trend toward eye reduction could have been reversible is unknown. However, in cases where both external and internal ocular structures became obsolete, the eye loss was probably irreversible.

An interesting question is whether other sensory organs may not have developed in *Drevermannia* to compensate for eye loss, as has been claimed for other blind trilobites such as trinucleoids (Clarkson, 1997). Feist and I recently suggested that the occipital node in proetoid larvae might have functioned as a sensory organ, possibly a light sensor (Lerosey-Aubril & Feist, 2005b,c). This hypothesis is supported by its peculiar structure and its relatively large size in larvae in comparison to that of adults of the same species. The *Drevermannia* metaprotaspides exhibit such a particularly large occipital node (Fig. 4h), which supports this assumption. Moreover, some of the anaprotaspides, arbitrarily assigned to *Drevermannia*, display a medial node, as has been illustrated in cyrtosymboline larvae (Lerosey-Aubril & Feist, 2005c). However, the occipital node decreases in diameter in the three ontogenetic sequences described herein, and even almost vanishes in the late ontogeny of *D. antecurvata*. This indicates that the occipital node may not have been a sensory organ in adults of *Drevermannia* although it may have had this function in its larvae. Thus, there is no evidence that eye loss in *Drevermannia* has been compensated for by any particular development of another sensory organ.

5. Conclusions

The discovery of large anaprotaspides in the upper Famennian of Thuringia reveals that the developmental strategy of proetoid trilobites might have significantly changed prior to the Hangenberg extinction event. However, the nature of this modification and, *a fortiori*, its implications on the survivorship of proetoids during the biocrisis remain unclear. In this regard, the discovery of anaprotaspides of late Famennian proetoids living in shallower environments would be of particular interest. Indeed, it may reveal if only proetoids living in deep benthic habitats had a modified developmental strategy or if, on the contrary, the latter occurred in all late Famennian representatives of the group.

Description of the ontogenetic changes in three species of *Drevermannia* illustrates that post-metamorphic development may vary in highly derived proetoids. (1) It exemplifies that the metaprotaspid stage can be significantly different between closely related

species. (2) It illustrates that the main morphological modifications can happen particularly late in the ontogeny of these blind forms and consequently, that the meraspid period is not consistently a period of important shape changes in proetoids. (3) These three ontogenetic sequences show that ocular structures never develop externally in *Drevermannia*. However, the presence of transient eye ridges suggests that development of optical nerves is not completely lost in this group. This suggests that blindness in the *Drevermannia* lineage has followed a centripetal mode of eye reduction. The presence of partially or fully developed eye ridges in early ontogenetic stages as well as in adults of other blind proetoids indicates that the centripetal mode may have been the main mode of eye reduction in Late Devonian proetoids. A first step to test this hypothesis would be to estimate the proportion of proetoid trilobites with reduced or lost eyes that display eye ridges in adults or in early ontogenetic stages. Understanding the modalities of eye reduction in trilobites is of utmost importance as it may reveal if this particular evolutionary trend has implied mutations of genes specialized in the eye development (in the centripetal mode) or of more important genes, also involved in the segmentation of the nervous system (in the centrifugal mode). Thus, it may enable us to estimate grossly the importance of the genetic reorganization implied by this particular evolution and consequently, the potential reversibility of eye loss in trilobites.

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