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Biostratigraphy of Devonian tropidocoryphid trilobites from the Montagne Noire (southern France)

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Abstract. An unbroken trilobite-bearing limestone succession of the Montagne Noire yielded tropidocoryphids from the late Emsian to the latest Frasnian. Their occurrences and biostratigraphical ranges are compared with both the Standard conodont zonation and in particular the Montagne Noire Frasnian conodont zonation. Whereas tropidocoryphids are modestly represented in the Eifelian and absent from early Givetian strata, most of the established conodont zones can be characterized by different taxa of quickly evolving tropidocoryphid lineages. In comparison with taxa from elsewhere, the group is by far the most diversified in the Montagne Noire with 22 different species recognized within the considered time span. One genus (*Chlupaciparia* gen. n.) and 7 species (*Chlupaciparia minutilobus* sp. n., *Erbenicoryphe nazairensis* sp. n., *Longicoryphe anteglabra* sp. n., *L. tenuistriata* sp. n., *L. lanceolata* sp. n., *Astycoryphe planifrons* sp. n. and *Ensecoryphe tumida* sp. n.) are erected. New definitions of Denemarkiinae Hupé 1953 and Pteropariinae Hupé 1953 are given.

Key words: trilobites, tropidocoryphidae, Devonian, Montagne Noire, biostratigraphy

Introduction

The Emsian through Frasnian deposits in Devonian sections of the southeastern Montagne Noire are characterized by continuous sequences of biodetrital trilobite-rich limestones that yield tropidocoryphids in particular abundance. Besides Eremiproetinae, that are not considered in this contribution, 22 tropidocoryphid species (including 6 new and 4 unnamed) have been reported from this area to this date. These are attributed to three subfamilies with 8 genera (including one new genus). Amongst Montagne Noire trilobites, tropidocoryphids are the most diverse and quickly evolving group within the considered time span; they allow, after a comparison with the established conodont biozonations, the first attempt at trilobite-based regional biozonal subdivision of the Middle and early Upper Devonian.

Occurrences and biostratigraphy

The Devonian successions in the southeastern Montagne Noire were described by Feist (1985), and biostratigraphical subdivisions were updated by Feist in Morzadec et al. (2000). The trilobite occurrences have been dated after a comparison with the established conodont-based biozonations in the late Emsian to Eifelian succession (Feist et al. 1985) and in the Givetian through the Frasnian (Feist and Klapper 1985, Klapper 1989, 1997, Klapper et al. 1987, Klapper and Becker 1999, Ziegler and Sandberg 1990).

Tropidocoryphid trilobites were recovered from five sites (Fig. 1):

1. Pic de Bissous 2.5 km NNW of Cabrières village; western slope, crinoidal limestone, late Eifelian *Tropidocoryphe lemniscata* Feist 1976; southern slope, red calcilutite, early Frasnian, *Erbenicoryphe parvula* Feist and Clarkson 1989, pink calcilutite, mid Frasnian: *Chlupaciparia oculata* (Feist and Clarkson 1989).

2. La Serre, western end of La Serre Hill 2 km SSW of Cabrières village; top of hill, light grey calcisparite, late Eifelian: *Astycoryphe planifrons* sp. nov., *Tropidocoryphe* cf. *endorfensis* Basse 1997; southern slope, grey brachiopod–trilobite coquina bed, middle Givetian: *Longicoryphe* aff. *brilonensis* Richter and Richter 1919, grey-brown calcilutite with phacopid coquinas, latest Givetian: *Longicoryphe circumincisa* Feist 1976, dark grey calcilutite, lower Frasnian: *Pterocoryphe languedociana* Feist 1976,

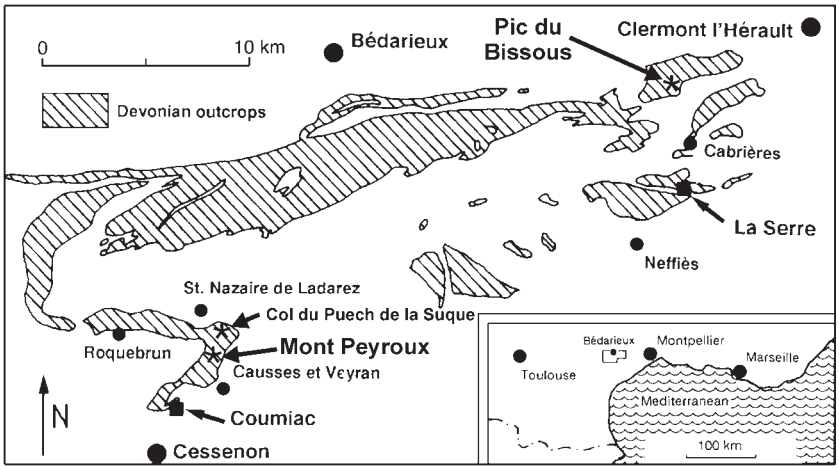

Fig. 1. Location map of trilobite sites with tropidocoryphids in the Devonian outcrops of the southeastern Montagne Noire, southern France.

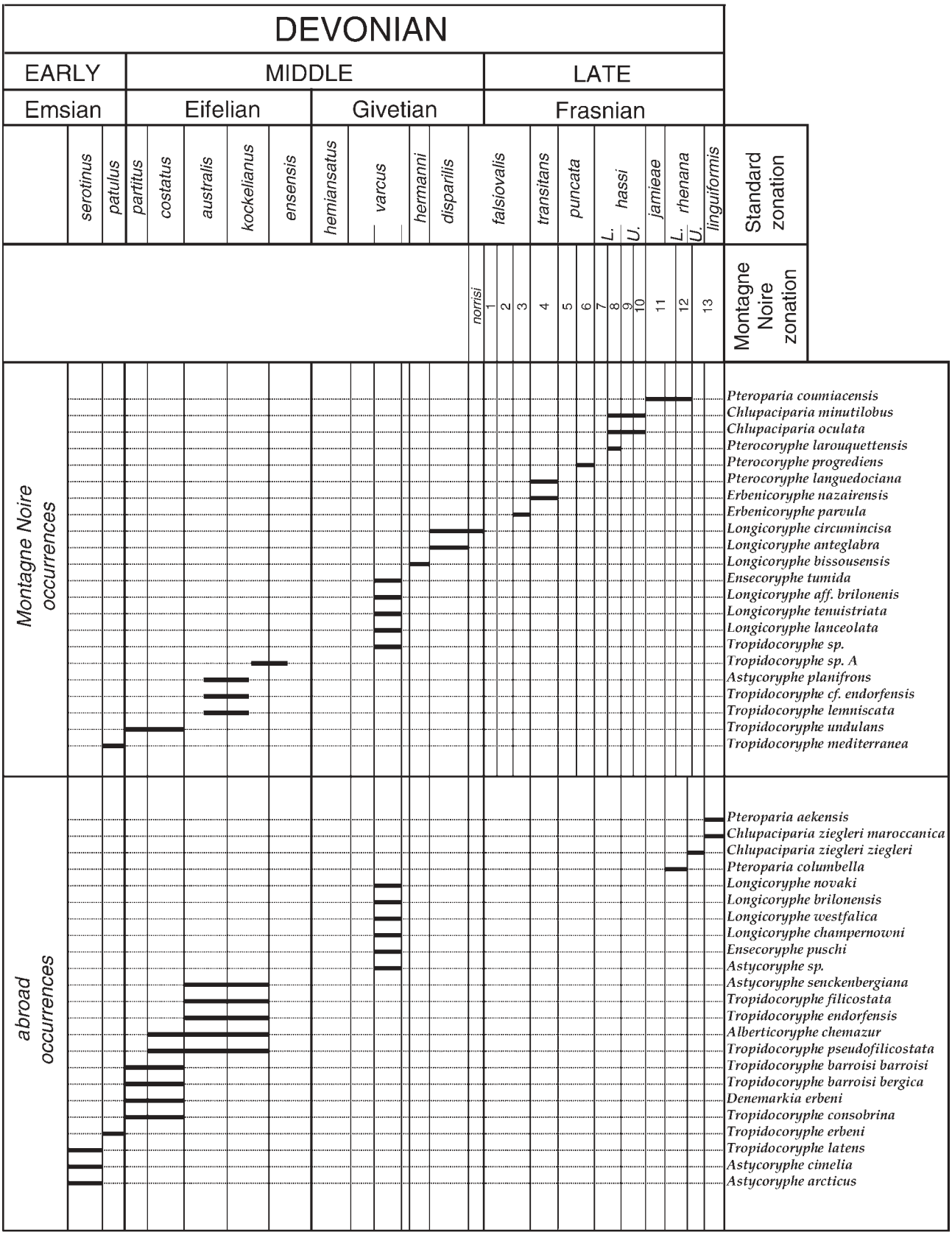

Fig. 2. Range charts of the latest Early, Middle and Late Devonian tropidocoryphid species from the Montagne Noire and from occurrences abroad in comparison with the Standard conodont zonation (Ziegler and Sandberg 1990, Weddige and Ziegler 1996) and the Montagne Noire conodont zonation (Klapper 1988).

Pterocoryphe progrediens Feist and Clarkson 1989, light grey calcisparite with trilobite coquinas, *Pterocoryphe larouquettensis Feist* 1976.

3. Col du Puech de la Suque, white and red calcilutite, Upper Emsian: *Tropidocoryphe mediterranea* Feist 1976, grey-brown calcilutite, early Frasnian: *Erbenicoryphe nazairensis* sp. nov.; western slope of Puech de la Suque Hill, grey pink-spotted calcilutites, mid Frasnian: *Chlupaciparia minutilobus* sp. nov.

4. Mont Peyroux, eastern slope, grey calcilutite, basal Eifelian: *Tropidocoryphe undulans* Feist 1976, grey and pink calcilutite: late Eifelian: *Tropidocoryphe* A aff. *pseudofilicostata* Přibyl 1965, grey-beige calcisparite, mid Givetian: *Longicoryphe tenuistriata* sp. nov., *Tropidocoryphe* sp., *Ensecoryphe tumida* sp. nov., grey calcilutite, mid Givetian: *Longicoryphe lanceolata* sp. nov., light grey *Styliolina* packstone, late Givetian, *Longicoryphe anteglabra* sp. nov.

5. Causses-et-Veyran and Coumiac, red calcilutite, late mid Frasnian, *Pteroparia coumiacensis* Feist 1976.

The distribution of tropidocoryphid trilobites in the Montagne Noire in comparison with known occurrences from elsewhere is shown in Fig. 2. According to these data, the presence of representatives at the Eifelian/Givetian transition and in the early Givetian remains unknown. Thereafter occurs an unbroken suite of taxa in all conodont biozones of the Standard zonation (Ziegler and Sandberg 1990) from the middle Givetian through the uppermost Frasnian; however, the taxa from Montagne Noire zones 1–2, 5 and 7 (Klapper 1989) are absent to date. It is noteworthy that *Tropidocoryphe* is still represented in the middle Givetian *varcus* Zone in the Montagne Noire whereas the latest representatives of the genus are restricted to the Eifelian elsewhere. By contrast, the latest upper Frasnian pteropariins known from both the Upper *rhenana* and *linguiformis* zones, i.e., from the interval between the Lower and Upper Kellwasser horizon, both in the Rhenish Slate Mountains and Harz (Feist and Schindler 1994) and from Morocco (Feist 2002) are absent from Montagne Noire sequences. Comparing the worldwide distribution of tropidocoryphids, it is striking that the group is so far exclusively represented in the Montagne Noire from the late Givetian to mid Frasnian during a time span of some 5 million years.

Genus and subfamily occurrences are shown in Fig. 3. Besides the terminal Frasnian Upper Kellwasser Horizon

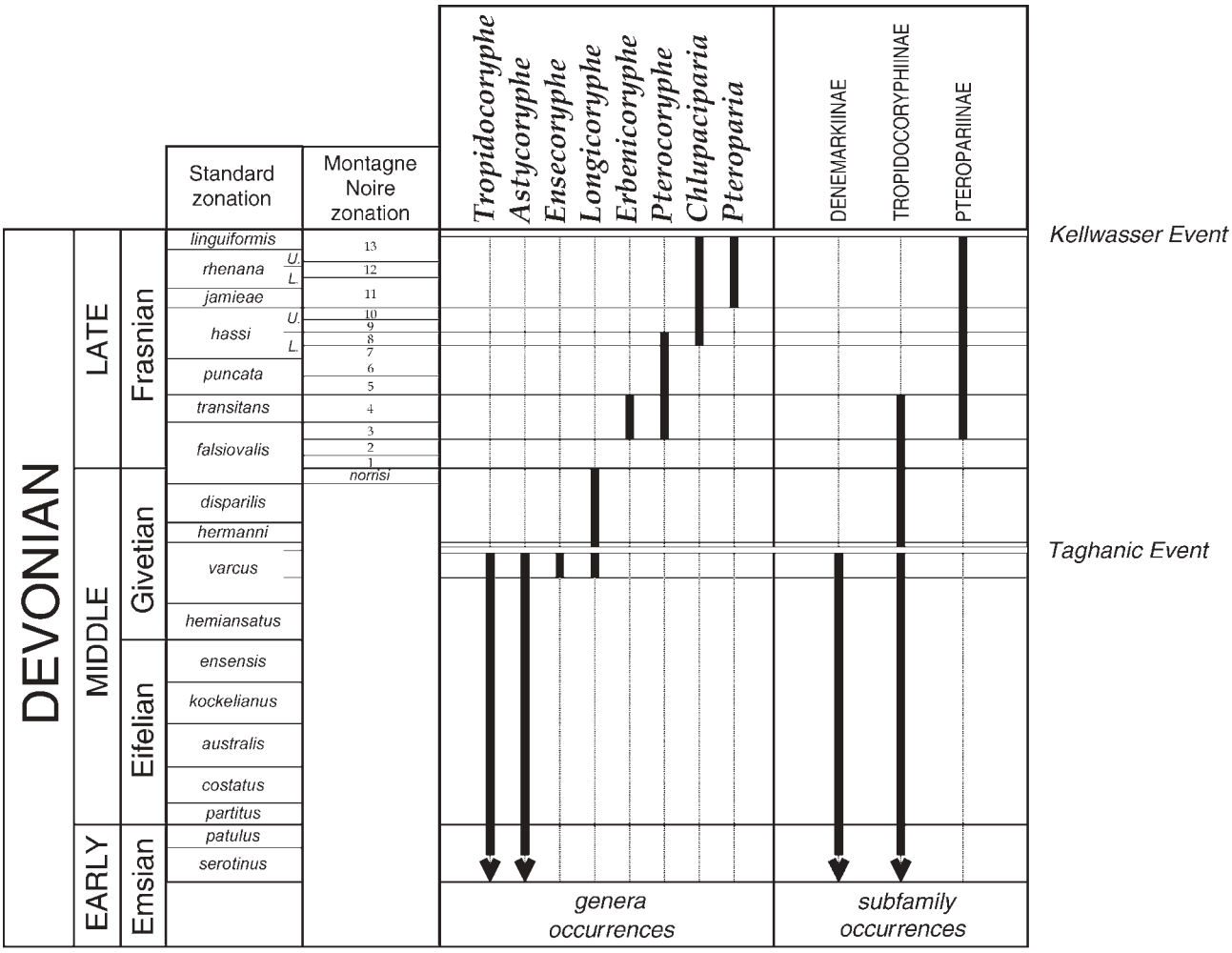

Fig. 3. Range charts of the latest Early, Middle and Late Devonian tropidocoryphid genera and subfamilies in comparison with conodont zonations and the position of major extinction events, i.e., the late Givetian Taghanic Event and the terminal Frasnian Upper Kellwasser Event.

that marks the global mass extinction of benthic communities such as tropidocoryphid trilobites, one major extinction is situated at the beginning of the Taghanic onlap at the Middle/Upper *varcus* Zone boundary. At this level, major clades of the tropidocoryphids disappear, such as *Tropidocoryphe*, *Astycoryphe* and all denemarkiins with *Ensecoryphe*. No less than six initial species of *Longicoryphe* that dominated the tropidocoryphid communities in the Middle *varcus* Zone became extinct during this event. However, *Longicoryphe* radiates with many species in the late Givetian where it is the sole tropidocoryphid taxon present. It virtually disappears at the Givetian/Frasnian boundary, and direct descendants are not known, as the earliest Frasnian MN Zones are devoid of tropidocoryphines and succeeding representatives of the subfamily occur no earlier than in MN Zone 3. The youngest tropidocoryphid subfamily, the Pteropariinae, is supposedly derived from *Longicoryphe* (Feist and Clarkson 1989), but the earliest Frasnian intermediate taxa have not been found yet. Appearing shortly after *Erbenicoryphe*, pterocoryphines radiate during middle and late Frasnian times; their last representatives became extinct in the latest Frasnian *linguiformis* Zone, being victims of the Upper Kellwasser Event.

Systematic palaeontology

Tropidocoryphidae Přibyl 1946
Tropidocoryphinae Přibyl 1946

Tropidocoryphe Novák 1890

Type species: *Tropidocoryphe filicostata* Novák 1890.

Diagnosis: see Harrington H. J. et al. (1959) in Moore R. C. (ed.): Treatise of Invertebrate Paleontology, part O, p. 0397.

Tropidocoryphe sp. A aff. *pseudofilicostata* Přibyl 1965
Plate I, figs 1, 4

aff. *Tropidocoryphe pseudofilicostata*, Přibyl: 96, pl. 2, figs 8–9
aff. *Tropidocoryphe pseudofilicostata pseudofilicostata*, Šnajdr: 1980, pl. XVIII, figs 12–17, pl. LXIII, fig. 4

Material: 1 cranidium, UM2-RF 259; 1 pygidium, UM2-RF 260.

Locality: Eastern slope of Mont Peyroux, 160 m above abandoned marble quarry near Concours-le-Haut, 1.6 km N of Causses-et-Veyran village.

Stratum: Grey and pink biodetrital calcilutite with *Acanthopyge* cf. *haueri* and conodonts of the *kockelianus* Zone, late Eifelian.

Remarks: As far as can be seen based on the fragmentary material (the anterior border and the palpebral areas are damaged and the right side of the pygidium is lacking), this material shares numerous traits with the contemporaneous Bohemian species *pseudofilicostata*. In particular these concern the outline of the glabella and the praeglabellar area (compare cranidia of *pseudofilicostata* figured by Šnajdr 1980, pl. XVIII, fig. 15–16) as well as the general shape of the pygidium. However, the pygidium from the Montagne Noire has a shorter pleural area and a relatively wider and shorter axis. Significantly there are only 7 (+ 1) axial rings and 7 pleural ribs instead of 9 rings and ribs in the Bohemian species. Before defining a possibly new species, additional more complete material must be found.

Tropidocoryphe cf. *endorfensis Basse 1997*
Plate I, fig. 5

cf. 1997 *Tropidocoryphe barroisi endorfensis*, Basse: 101–103, pl. 8, fig.6–12

Material: 1 cranidium, UM2-RF 263.

Locality: Top W of La Serre, 2.2 km SSW of Cabrières village.

Stratum: Massive light grey calcisparite of probably mid to late Eifelian age (no conodont data yet available).

Remarks: The unique cranidium closely resembles the mid Eifelian Rhenish taxon *endorfensis* that Basse (1997) considered a subspecies of the older *T. barroisi* (Maillieux 1904). In my opinion, the longer and less robust glabella together with the sharp continuous tropidial ridges justify an independent specific status for *endorfensis* though its origin in *barroisi* is unquestioned. In *T. lemniscata* Feist 1976 from the lower Eifelian of Pic de Bissous (Montagne Noire), multiple tropidia ridges are also developed but these ridges which start very close to the frontal glabella decrease in size anteriorwards where they become discontinuous, whereas cf. *endorfensis* exhibits three continuous ridges of equal size.

Additional material, and in particular the discovery of the pygidium, is needed in order to complete the comparisons.

Tropidocoryphe sp.
Plate I, figs 2–3

Material: 1 fragmentary cranidium, UM2-RF 262; 1 librigena, UM2-RF 261.

Locality: Eastern slope of Mont Peyroux at 150 m W above abandoned marble quarry at Concours-le-Haut, NNW of Causses-et-Veyran village.

Stratum: Fine-grained beige biodetrital stylioline calcilutites of topmost Middle *varcus* Zone age (middle Givetian).

Remarks: The fragmentary material belongs to the nominate subgenus as is indicated by the anteriorly tapering, slightly constricted glabella and the wide praeglabellar area with its upturned edge without border rim. There is a single prominent tropidial ridge that runs to the posterior part of the librigenal field where it is suddenly interrupted at a point where the distal end of the tropidia generally curves outward and, decreasing in height, runs parallel to the posterior border furrow to the genal angle. Additional

material is necessary before the material can be specifically determined.

Longicoryphe Erben 1966

Type species: *Tropidocoryphe nováki* Beyer 1896.

Remarks: The definition of *Longicoryphe* by Erben (1966) was based on *Tropidocoryphe nováki* Beyer 1896. Erben considered his new taxon a subgenus of *Astycoryphe* especially because it shares the presence of marginal rims in the cephalon and a short pygidium with the latter. Feist (1976) considered *Longicoryphe* descendant from *Tropidocoryphe* in maintaining the pattern of strongly divergent anterior sutures and backward placed palpebral lobes and eyes. With respect to novel features developed in *Longicoryphe*, such as the trend towards the reduction of tropidia that vanishes completely in some late representatives, the high relief of the praeglabellar field along with the reduction in relief of the adaxial and posterior pleural ribs in the pygidium, *Longicoryphe* is here considered an independent genus.

Species assigned: *Longicoryphe nováki* (Beyer 1896), *L. westfalica* (Richter and Richter 1919), *L. brilonensis* (Richter and Richter 1919), *L. champernowni* (Whidborne 1889), *L. circumincisa* Feist 1976, *L. lanceolata* sp. nov., *L.* tenuistriata sp. nov., *L. anteglabra* sp. nov.

Diagnosis: Cephalic margins bordered with rims, glabella unconstricted or slightly constricted anterolaterally, glabella longer than sagittal length of praeglabellar field, anterior sutures widely divergent, palpebral lobes short and modestly wide, pygidial axis narrower than pleural field, postaxial area narrower than half-length of axis, pleural ridges increasing in height abaxially and from rear to front.

Longicoryphe lanceolata sp. nov.
Plate II, figs 1–4

Derivation of name: *lanceolatus* (Lat.) = provided with a small lance.

Holotype: Cranidium, UM2-RF 274, Plate II, fig. 2a, b.

Type locality: Eastern slope of Mont Peyroux, 200 m WSW above the abandoned marble quarry at Concours-le-Haut, NNW of Causses-et-Veyran village.

Stratum: Fine-grained grey biodetrital stylioline calcilutites of topmost Middle *varcus* Zone age (middle Givetian).

Additional material: 1 juvenile cranidium, UM2-RF 275; 2 librigenae, UM2-RF 276-277; tentatively assigned: 2 pygidia, UM2-RF 278-279.

Diagnosis: Cephalon without tropidia, praeglabellar and genal fields with strongly vaulted inner area; plump, anteriorly truncated glabella; occipital spine 2/3 of glabellar length. Pygidium with two anterior ribs bent back at margin.

Description: Cranidium strongly vaulted longitudinally. Glabella highly arched transversely, without keel, wider at base (tr.) than sagittal length, unconstricted anterolaterally with broad, slightly truncated frontal outline. Glabellar furrows inconspicuous, besides S1 that forms shallow depressions parallel to axis. Praeglabellar field subdivided into two parts: the inner, slightly larger part (sag.) is strongly vaulted, merging anteriorly with outer broad depression that is continuous onto librigena as far as to genal angle. Anterior border with thin upturned rim. Occipital furrow shallow, meeting dorsal furrow. Occipital ring considerably wider than base of glabella (tr.), uninflated, of even length (sag., exsag.). Medial posterior margin extends into a rather strong spine that reaches 2/3 of glabellar length. Anterior sutures long and straight, γ situated opposite 2/3 of glabellar length. Palpebral lobe short and narrow, backward shifted with respect to glabella. Librigena with broad inner genal field that is less vaulted than the corresponding praeglabellar area. Lateral furrow inside border depression meets posterior border furrow in genal angle from where a joint furrow is continuous onto long and thin genal spine. Eye prominent, defined against genal field by a deep furrow around the base of the visual surface. Eye platforms absent. Exoskeletal surface of test smooth.

Pygidium wide, with parabolic latero-posterior outline and slightly upturned sharp-edged border. Prominent axis carrying 7 (+1) straight rings that continuously diminish in length (sag.) from front to rear, all provided with backward directed median spines at the posterior margin. Ring furrows shallow, not reaching the axial furrow, relatively broad, the two anterior ones transversely split into two. Posterior end of axis thickened. Axial furrows straight, divergent as far as to fifth axial ring, then curving inward as far as to pointed posterior end of axis. Thin prominent postaxial ridge does not reach border depression. Large, anterolaterally extending pleural fields with seven prominent anterior pleural bands of which the anterior two are slightly backward directed in their inner two thirds, then, at the level of the inner margin of the doublure, bent abruptly backward until turning into the outer edge. Distal ends of anterior pleural bands narrower than proximal portions, provided with prominent crests. The five posterior pleurae do not reach the border and are progressively straighter. The rearmost two ones are convergent, faint, and remain below the level of postaxial ridge. Exoskeleton lacks sculpture.

Remarks: The type species of the family, *L. nováki* Beyer 1896, has similar long occipital spine but is distinguished by a pointed anterior outline of the glabella and the presence of a strong tropidial ridge.

Longicoryphe tenuistriata sp. nov.
Plate II, figs 5–6

Derivation of name: *tenuis* (Lat.) = thin, *striatus* (Lat.) = striated (regards thin tropidial ridges).

Holotype: Cranidium, UM2-RF 280, Plate II, fig. 5a, b.

Type locality: Eastern slope of Mont Peyroux, 160 m above the abandoned marble quarry near Concours-le-Haut, 1.6 km N of Causses-et-Veyran village.

Stratum: Fine-grained beige biodetrital calcisparite of Middle *varcus* Zone age (middle Givetian).

Additional material: 3 cranidia, UM2-RF 281-283; 1 librigena, UM2-RF 284; 2 pygidia, UM2-RF 285-286.

Diagnosis: Broad glabella with sagittal keel, two thin tropidia ridges approaching glabella, vanishing in the anterior third of librigenal field, occipital ring with marginal spine, pygidium with slender axis, straight convergent axial furrows, evenly curved pleurae, anterior three exhibiting elevated inner posterior bands and interpleural furrows.

Description: Glabella length and basal width equal, robust, broadly pear-shaped with widely parabolic anterior outline, modestly constricted anterolaterally, central part prominent with keel-like longitudinal crest. Glabella highest at base. Depressed, little inflated L1 lobes are separated from median lobe by deep, straight, slightly convergent S1 grooves. S2 and S3 furrows in far anterolateral position, very weak, isolated, directed obliquely backward, unconnected with axial furrow. Praeglabellar field laterally extended, relatively narrow (sag.), moderately vaulted, bordered by deep narrow border furrow and prominent cylindrical enrolled border rim carrying continuous terraces. Two thin tropidial ridges situated closer to anterior glabella than to border furrow. Anterior ridge becomes discontinuous abaxially where several tiny secondary ridges appear. Occipital furrow straight, deepest behind medial lobe of glabella. Occipital lobe widest medially (sag.), uninflated, roof-like flexed in posterior view, provided with an occipital spine on its medioposterior margin. Anterior sutures highly divergent, curved outward. Palpebral lobes crescentic, narrow (tr.), shifted forward, leaving a straight portion of posterior suture between ε and ζ that runs parallel to axial furrow, leaving an extremely small posterior fixigenal field. The entire surface is granulated; sculpture becoming slightly coarser on postero-median glabella lobe and occipital lobe. Librigena with small bulbous eye-lobe, large, moderately arched genal field that merges with broad border depression, large based genal spine. Tropidial ridges are restricted to the anterior third of the central genal field. Pygidium with slender axis defined by straight converging dorsal furrows and narrow parabolic posterior end. 7 (+ 1) moderately inflated axial rings provided with backward-directed medio-posterior nodes and separated from each other by narrow ring furrows that reach axial furrows. First axial ring narrowing medially with sigmoidal, medially backward projected posterior margin followed by an enlarged ring furrow. Postaxial ridge faint. Seven pairs of prominent pleural ridges, directed backward, flexed in the middle of pleural field, their distal part narrowing and crest-like elevated, running obliquely towards lateral margin. Only the first two ridges reach the slightly upturned sharp edge. Sculpture granulated.

Longicoryphe anteglabra sp. nov.
Plate II, figs 7–10

Derivation of name: *ante* (Lat.) = in front; *glaber* (Lat.) = smooth (regarding the absence of tropidia).

Holotype: Cranidium, UM2-RF 287, Plate II, fig. 9.

Type locality: Eastern slope of Mont Peyroux, 200 m WSW above the abandoned marble quarry at Concours-le-Haut, NNW of Causses-et-Veyran village.

Stratum: Light grey *Styliolina* carbonate packstone of *disparilis* Zone age (upper Givetian).

Additional material: 3 cranidia, UM2-RF 288-290; 1 librigena, UM2-RF 291; 1 pygidium, UM2-RF 292.

Diagnosis: Glabella pear-shaped, anterolaterally markedly constricted, with narrow anterior outline, deeply impressed glabellar furrows; moderately arched praeglabellar field without tropidia, upturned thin border; pygidium widely parabolic, axis low, with faint rings, pleural ridges outstretched, with low backward curvature.

Description: Glabella as long as wide at base, parallel sided in posterior half, anterolaterally constricted, narrowly semicircular in frontal outline. Median lobe elevated, rounded transversely, without keel, horizontal from base to frontal slope in lateral view. Glabellar furrows conspicuous, S1 broad, groove-like, deeply impressed, converging posteriorly without reaching occipital and axial furrows; S2 and S3 straight, inclined backward, connected with axial furrow; combined L1 and L2 lobes slightly inflated. Praeglabellar area moderately arched, without tropidial structures, merging in the front with a large border depression defined by upturned border with thickened edge bearing terrace lines. Occipital furrow narrow, projected slightly forward behind elevated medial glabellar base, deepest laterally behind L1 lobes, vanishing before reaching axial furrows. Occipital lobe enlarged centrally (sag.), narrowing laterally, with a small occipital spine. Occipital node shifted forward, sitting in a small depression and separated from occipital furrow by slightly inflated anterior occipital margin. Palpebral lobes crescent-like, narrow, flat, slightly inclined. Surface of glabella micro-granular. Librigena with border rim and very long narrow genal spine. Inner genal field vaulted, abaxially separated from broad border depression by marked furrow that runs into posterior border furrow before the latter curves backward to join lateral border furrow in genal angle. Fused furrow continuous into basal genal spine. Pygidium of even, broadely parabolic latero-posterior outline. Axis low, evenly tapering, carrying 7–8 uninflated, rather faint axial rings of which only the anterior are conspicuous, carrying small and low nodes on their medial posterior margins. The first ring is somewhat higher and the first ring-furrow is broader than the following ones. 7–8 pleurae of which the anterior bands remain relatively low and do not carry crests except on the distal ends of the second pleural rib. Pleural ribs outstretched with increasing backward curvature from front to rear.

Remarks: Whereas the librigena of *anteglabra* differs from that of the slightly younger *circumincisa* in its much narrower base of the librigenal spine (see Feist 1976: pl. 2, fig. 12), it is virtually identical with the librigena of the older *lanceolata* (Plate II, fig. 1) that has, however, a slightly larger and less bulging inner genal field.

Longicoryphe aff. *brilonensis* Richter and Richter 1919
Plate II, figs 11–12

1976 *Tropidocoryphe* (*Longicoryphe*) aff. *brilonensis*, Feist: 57, pl. 2, fig. 5–8
1989 *Tropidocoryphe* (*Longicoryphe*) aff. *brilonensis*, Feist and Clarkson 1989: fig. 2, 9

Locality: Western end of La Serre Hill, 2 km SSW of Cabrières village.

Stratum: Brachiopod-trilobite limestone coquina ("*Rhynchonella* Bed", Feist 1976), Middle *varcus* Zone (Mid Givetian).

Additional material: 1 cranidium, UM2-RF 293, 1 pygidium, UM2-RF 294.

Remarks: The recovery of larger specimens of aff. *brilonensis* from the same bed that yielded the material figured in Feist (1976) allows additional observations. The cranidium has a broad unconstricted glabella with a widely parabolic anterior outline. Central lobe moderately vaulted transversely, without keel. Glabellar furrows S1 and S2 markedly impressed, the former rather deep, with a shallower connection with occipital furrow. L1 inflated. Occipital ring with medial border spine. The surface is densely covered with elongated tubercles grouped to short lines and wrinkles on the glabella. The pygidium corresponds to the diagnosis of *brilonensis* except that the pygidia from the Montagne Noire exhibit a slightly sigmoidal pattern in the distal course of the third and fourth pleural ridge.

Astycoryphe Richter and Richter 1919

Type species: *Astycoryphe senckenbergiana* Richter and Richter 1919.

Remarks: In the original concept of the genus, Richter and Richter (1919) included features that concern Givetian taxa that are now assigned to *Longicoryphe* Erben 1966. The diagnosis of the genus given by Harrington et al. (1959) in the Treatise on Invertebrate Paleontology corresponds to the type species *A. senckenbergiana* and is followed here. According to this, the main distinctive features of the genus are the only slightly divergent anterior sutures, the narrow praeglabellar field, the short pygidium with throughout pronounced pleural ribs, and the presence of border rims on the cephalon.

Species assigned: *A. senckenbergiana* Richter and Richter 1919, *A. gracilis* (Barrande 1846), *A. cimelia* Ormiston 1967, *A. arcticus* Ormiston 1967, *A. minuta* (Ellermann 1992), *A. austriaca* Ellermann 1992, *A. junius* (Billings 1869), *A. larminiei* Wright and Chatterton 1988, *A. planifrons* sp. nov.

Astycoryphe planifrons sp. nov.
Plate I, figs 6–7

Derivation of name: *planus* (Lat.) = flat, *frons* (Lat.) = frontal area.

Holotype: Cranidium, UM2-RF 265, Plate I, fig. 7a, b.

Type locality: Western end of La Serre Hill, 2 km SSW of Cabrières village.

Stratum: Massive light grey calcisparite of probably mid to late Eifelian age (no conodont data available yet). Associated taxon: *Tropidocoryphe* cf. *endorfensis* Basse 1997.

Additional material: 1 fragmentary librigena, UM2-RF 264, Plate I, fig. 6.

Diagnosis: Traverse and longitudinal vault of cranidium extremely low, glabella longer than wide, low front flush with praeglabellar field bordered with low rim, palpebral lobes extending beyond occipital furrow, posterior ends of axial furrow bent strongly outward to join posterior suture, occipital ring laterally merging with posterior border ridge. Eye very narrow and long. Thin tropidia terminates on anterior third of librigenal field.

Description: The cranidium is remarkable for its rather low vault longitudinally and transversely. The glabella, defined by faint axial furrows, is nearly flush both with the palpebral and the praeglabellar areas. Its central lobe has a very weak keel, visible in posterior view only. The glabella is markedly longer than wide. It is slightly constricted anterolaterally and has a wide parabolic frontal outline. No glabellar furrows and lateral lobes are discernable. The praeglabellar field is flush with the frontal glabella, forming a flat slope to a narrow border furrow that separates it from a low border rim carrying terrace lines. Tropidial ridge single, tiny, lying nearer to glabellar front than to border furrow. Occipital furrow narrow, straight, deepest behind medial glabella lobe, shallowing laterally. Occipital lobe flat, with straight parallel anterior and posterior borders, laterally undefined because axial furrows turn outward immediately behind occipital furrow to join posterior suture. At this point, the lateral extensions of occipital lobe narrow and merge with post-sutural part of uninflated posterior border. Occipital medial node shifted slightly backward from medial position. Anterior sutures straight and modestly divergent. Turning points γ lie anteriorly to constriction of anterolateral glabella. At this point, the adjacent fixigenae are relatively large and nearly equal the rather narrow, flat palpebral lobes. The latter extend far behind, beyond the level of occipital furrow, where ε is situated very near to the out-turning axial furrow. The posterior medial lobe of the glabella is indistinctly covered with tiny low tubercles. The librigena exhibits a very long, narrow upraised eye lobe with extended visual surface. The inner librigenal field is moderately vaulted and is framed by a flattened large border area that merges with a low thickened border carrying continuous terraces. Tropidia continuous onto inner librigenal field, dying out in the anterior third. Inner pleural field granulate.

Remarks: The extremely weak relief exhibited by the new taxon is unique among all hitherto known species of *Astycoryphe* that have generally upraised border rims and a shorter glabella.

Erbenicoryphe Feist and Clarkson 1989

Type species: *Erbenicoryphe parvula* Feist and Clarkson 1989.

Species assigned: *E. parvula* Feist and Clarkson 1989, *E. nazairensis* sp. nov.

Diagnosis: Subtriangular, laterally non-constricted glabella, a short praeglabellar field lacking tropidia, a large border depression and elevated border rim, straightened palpebral sutures, flattened eye-lobes lacking lenses, inner pleural field in pygidium undifferentiated, pleural bands emerging on peripheral pleural field.

Erbenicoryphe parvula Feist and Clarkson 1989

1989 *Erbenicoryphe parvula*, Feist and Clarkson: 372–373, fig. 3 A–D, 8 B

Additional material: 2 fragmentary cranidia, UM2-RF 295-296, fragments of cranidia, librigenae and pygidia, UM2-RF 297 from the type locality (Pic de Bissous section VS-E, Bed 48, Feist and Klapper 1985), MN Zone 3, early Frasnian.

Diagnosis: Cranidium with unbroken curvature in side view, glabella low, smooth, with very faintly curved S1 furrows, slightly broader at base than long, straight palpebral sutures, anterolateral border with a narrow, moderately elevated rim; praeglabellar field evenly vaulted, merging with a broad border depression; pygidium with narrow axis pointed behind and merging with prominent postaxial ridge.

Erbenicoryphe nazairensis sp. nov.
Plate II, figs 13–15

Derivation of name: From St. Nazaire-de-Ladarez village in the vicinity of the type locality.

Holotype: Cranidium, UM2-RF 298, Plate II, fig. 14a, b.

Locus typicus: Col du Puech de la Suque, 1.1 km SE of St. Nazaire-de-Ladarez village, Givetian/Frasnian boundary stratotype section, Bed CPS-E 58 (Klapper et al. 1987).

Stratum: Grey-brown trilobite-rich cephalopod calcilutite, MN Zone 4, early Frasnian.

Additional material: 3 cranidia, UM2-RF 299-301, 1 librigena, UM2-RF 302, 2 pygidia, UM2-RF 303-304, fragments of cranidia, librigenae and pygidia, UM2-RF 305.

Diagnosis: Glabella of equal length and width, moderately upraised with higher longitudinal curvature than overall cranidium; anterior border depression defined by two parallel furrows, anterolateral border rim broadly cylindrical, vertically upraised about border furrow, weakly curved palpebral sutures with tiny relicts of forward shifted palpebral lobes, pygidium with posteriorly well defined short axis separated from lowered postaxial ridge by a faint axial furrow. Surface granulated.

Description: Subtriangular glabella well defined by narrow axial furrows that are slightly out-curved posteriorly and straight antero-laterally; frontal glabella narrow, parabolic. In side view, the glabella moderately rises above fixigenae anteriorly and more strongly posteriorly. Glabellar furrows distinct, in shallow connection with axial furrows. S1 large, adaxially convex, bent, defining weakly vaulted L1 lobes, S2 and S3 straight, inclined backward, S3 opposite γ turning point. Praeglabellar area subdivided into a larger internal part of individual vault and a large border depression that is separated from vaulted inner area by a distinct furrow. The border depression is framed by a vertically upraised cylindrical border, as long (sag.) as border depression (sag.), carrying strong continuous terrace ridges. Occipital furrow straight, not reaching axial furrows, slightly set backward behind base of lateral glabella lobes (L1). The occipital lobe, slightly swollen medially and broader (sag.) than laterally, rises backward above glabella level. Occipital node shifted forward from medial position. Anterior sutures long, straight or slightly curved in some larger specimens. In holotype cranidium, a shallow depression crosses obliquely anterior fixigenal field from γ to anterolateral frontal glabella. This depression is not seen on larger specimens. The palpebral suture shows a slight outward curvature between points opposite S3 and S1, which constitute remains of a nearly entirely reduced palpebral lobe. The remainder of the palpebral suture runs parallel to axial furrow, leaving a very narrow strip of posterior fixigena before out-curving into posterior border. Librigena with a strong, cylindrical genal spine, inflated inner genal field and a broad border depression delimited against inner genal field by furrow that shallows in genal angle. Pygidium with parabolic posterior outline, truncated anterolaterally. Short conical axis as wide as the adjacent pleural field (tr.), delimited by straight axial furrows that are in connection behind blunt end of axis. In side view, the axis descends slowly and steadily to the rear, sloping abruptly behind above lowered postaxial ridge. 6–7 (+ 1) low, slightly inflated axial rings without medial nodes, the anterior two medially thickened and slightly flexed forward; glabellar furrows rather faint, the anterior two reaching axial furrow. Adaxial pleural field flat, and inclined to a slight degree, inner edge of doublure sloping stronger thereafter as far as to the border. Pleurae inconspicuous, emerging on the peripheral area on the inner pleural field, the anterior bands being more prominent in carrying sharp crest lines. 6–7 anterior pleural ridges present, the anterior 3 reaching the edge. Border flat lying, without rim, but provided with a narrow elevated stripe displayed between the distal ends of the second pleural ridges and enlarging adaxially. All posterior pleural ridges and postaxial ridge extend to this border elevation.

Sculpture: Entire exoskeleton granulate, very tiny dense tuberculation can be distinguished on adaxial parts.

Denemarkiinae Hupé 1953 emend.

Genera: *Denemarkia* Přibyl 1946, *Ensecoryphe* Basse 1997, *?Proetocephalus* Lütke 1977

Diagnosis: Glabella long, subcylindrical, slightly tapering; praeglabellar field narrow, bordered by prominent rim; fixigenae narrow with reduced palpebral lobes shifted far anteriorly; eye-lobe small with reduced visual surface; occipital spine present. Pygidium with long prominent axis, larger than pleural field, postaxial field narrow, border horizontal and without rim.

Remarks: As Lütke (1980: 112) suggested, *Astroproetus* Begg, exhibiting large palpebral lobes and eyes, a tapering glabella and a relatively wide praeglabellar field (tr.), is not related to *Denemarkia* Přibyl and should be excluded from Hupé's (1953) original concept of the subfamily. By contrast, *Proetocephalus* Lütke has very similar traits, especially the course of the facial sutures, the reduced eye, and the narrow praeglabellar field bordered by a prominent rim. The single immature pygidium said to belong to this taxon does not show definite tropidocoryphid traits. I agree with Basse (1997) that *Ensecoryphe* Basse originates in *Denemarkia* from which it differs in the absence of tropidial structures and in significantly lesser differentiation of both glabellar furrows and pygidial segmentation. It is remarkable that the evolutionary trends leading to the disappearance of the tropidia and the poor differentiation of glabellar and pygidial segmentation occur in late Middle and Upper Devonian representatives of different tropidocoryphid lineages.

Ensecoryphe Basse 1997

Type species: *Ensecoryphe puschi* Basse 1997.

Ensecoryphe tumida sp. nov.
Plate I, figs 8–13

Derivation of name: *tumidus* (Lat.) = swollen, designating the swollen genal spines.

Holotype: Cranidium, UM2-RF 268, Plate I, fig. 10 a, b.

Type locality: Eastern slope of Mont Peyroux, 200 m WSW above the abandoned marble quarry at Concours-le-Haut, NNW of Causses-et-Veyran village.

Stratum: Fine-grained beige-grey biodetrital stylioline calcilutites of Middle *varcus* Zone age (middle Givetian).

Additional material: 1 fragmentary cranidium, UM2-RF 270; 10 librigenae, UM2-RF 267, 269, 272; 3 pygidia, UM2-RF 266, 271, 273.

Diagnosis: Glabella broadly conical without anterolateral constriction, slope of praeglabellar field flush with frontal lobe; distal genal spines bulged; pygidial axis voluminous; pleural fields narrow; second pleura does not reach border.

Description: Cranidium elongate and highly arched in lateral view. Glabella widest at base (tr.), gently tapering without lateral constriction as far as to opposite γ, then strongly converging to parabolic frontal outline, gently arched transversely and axially, surrounded by narrow, evenly impressed axial furrows. No glabellar furrows discernible. Slope of frontal lobe continuing without break in praeglabellar field as far as to border depression. Glabella 2 1/3 times longer than entire praeglabellar area. Praeglabellar field gently arched. Anterior margin with sharply upturned cylindrical border rim carrying terrace ridges. Occipital furrow narrow and faint, laterally shallowing. Occipital lobe unswollen, slightly enlarged anteromedially, narrowing laterally, provided with a strong occipital spine situated posteromedially, no additional median tubercle. Fixigenae extremely narrow with anteriorly shifted, slightly enlarged palpebral area. Anterior sutures very short and curved from α to γ. The latter is situated opposite to base of glabellar frontal lobe and its distance from axial furrow is twice that of ε. The palpebral area remains far inside the projection of β (exsag.). Posterior portion of suture comprises a very long straight portion that runs parallel to the sagittal line before turning abruptly outward at ζ opposite to occipital furrow. Librigenae narrow, framed with narrow upturned border rim carrying continuous terrace ridges. Genal field gently arched, sloping to broad border depression. Eye lobe small and low, carrying numerous densely packed lenses; eye accompanied by two slightly swollen platforms, the anterior ellipsoidal in outline, the posterior more elongated, both well defined by surrounding furrows. Posterior deep border furrow and cylindrical border merging with lateral border rim and furrow at a narrow angle emphasized by the continuation of the fused furrows into the basal genal spine. Genal spine long, cylindrical at base, thicker than border rim, increasing distally to form an elongate bulge-like swelling that quickly decreases to its distal end, being provided with a tiny spine there. Pygidium subtriangular in outline, with a large prominent axis, narrow postaxial field and narrow triangular pleural fields. Slightly upturned narrow latero-posterior edge without border rim. Axis conical, highly vaulted transversely, rather prominent in side view, slightly diminishing in height from front to rear, abruptly descending behind to low postaxial field without postaxial ridge. Six (+ 1) indistinct axial rings forming low, unswollen, straight bands continuously decreasing in width (sag.) to the rear. Pleural field moderately vaulted. Five rather faint pleural segments discernible, of which the distal portions of the anterior bands are prominent in the form of short elevated crests that are bent backward and vanish shortly before reaching border depression. The latter is defined by a change in slope between pleural field and narrow upturned edge. Sculpture: the test of the entire exoskeleton is smooth.

Discussion: Among the few traits that distinguish the new species from the contemporaneous type species *E. puschi*, the following are the most obvious: laterally unconstricted, anteriorly more pointed glabella, medially enlarged occipital lobe provided with a much stronger spine, narrower triangular pygidium with more effaced ring and pleural furrows, and the second anterior pleural band that does not reach the border.

The most spectacular and characteristic feature of the new species, apparently not developed in *E. puschi*, concerns the inflated distal ends of the librigenal spines. This feature – so far unique among tropidocoryphids – has been

observed in Early Carboniferous phillipsiids which accordingly were grouped under the subfamily Cystispininae Hahn and Hahn 1982.

The discovery of inflated genal spines in a proetid family that is not related to phillipsiids must bring the definition of cystispinines into question. However, the necessary reconsideration of the taxonomic status of the Cystispininae and allies is beyond the scope of the present contribution.

Pteropariinae Hupé 1953 emend.

Genera: *Pteroparia* Richter 1913, *Pterocoryphe* Feist 1976, *Chlupaciparia* nov. g.

Diagnosis: Cephalon evenly high vaulted, no tropidia, lateral anterior fixigenae extended postero-laterally, anterior facial sutures subtending an angle of more than 180°. Eyes reduced or obsolete, ring-furrows on pygidial axis and relief of adaxial pleural fields faint.

Pterocoryphe Feist 1976

Pterocoryphe larouquettensis Feist 1976
Plate III, figs 1–2

1976 *Pterocoryphe larouquettensis*, Feist: 61, pl. 3, fig. 8–9

Additional material: 1 cranidium, UM2-RF 306, 2 pygidia, UM2-RF 307-308 from type locality and stratum, MN Zone 8, mid Frasnian.

Remarks: The preservation of the lateral wings of the anterior fixigenal fields allows to recognize that the β turning points lie opposite to each other subtending an angle of about 180° as seen in the type species *languedociana*.

Pterocoryphe progrediens Feist and Clarkson 1989
Plate III, figs 3–4

1989 *Pterocoryphe progrediens*, Feist and Clarkson: 373, fig. 4 G-I, 6 B, 9

Material: 1 cranidium, coll. Feist and Clarkson 1989, USTM 35; 1 pygidium, UM2-RF 309 from type locality and stratum, MN Zone 6, mid Frasnian.

Remarks: This species contrasts with the type species and with *larouquettensis* in the position of turning points β that sustain an angle of more than 180° (about 190°). The pygidium that was only known from a juvenile specimen is rather large, with a posteriorly truncated outline. The axis is slender and high, exhibiting 7 + 1 faint axial rings that are only distinguished centrally by their backward directed medial nodes and weakly impressed ring furrows. There are 7 + 1 pleurae of which the anterior bands become sharp-edged and prominent distally. Significantly, also the posterior pleural bands are clearly discernible; they are much shorter than the anterior bands and vanish well before reaching the border.

Chlupaciparia gen. nov.

Derivation of name: For the late Prof. Ivo Chlupáč, formerly head of Geology and Palaeontology of Charles University in Prague, author of outstanding works on trilobites and biostratigraphy of Bohemia.

Type species: *Pteroparia oculata* Feist and Clarkson 1989.

Species assigned: *Ch. oculata* (Feist and Clarkson 1989), *Ch. ziegleri ziegleri* (Feist and Schindler 1994), *Ch. ziegleri maroccanica* (Feist 2002), *Ch. minutilobus* sp. nov.

Diagnosis: Cephalon bordered with broad cylindrical rim, praeglabellar field narrower than half glabellar length, large groove-like border furrow mostly delimited by parallel furrows, palpebral suture straight or with slight palpebral excursion, presence of individualized eye-lobes and visual surfaces displaying lenses, pygidial axis wider than pleural field, axial rings without median nodes.

Chlupaciparia oculata (Feist and Clarkson 1989)
Plate III, figs 6–8

1989 *Pteroparia oculata*, Feist and Clarkson 1998: 373, fig. 4D–F, 5B, 9

Additional material: 2 cranidia, coll. Feist and Clarkson 1989, USTM 29-30, 1 pygidium, UM2-RF 310 from type locality and stratum.

Remarks: The additional material reveals that the generally straight palpebral suture exhibits a slightly outcurved course in its anterior part in some specimens. However, no palpebral lobe can be defined. The β turning points subtend an angle of 240°. The pygidium is slightly longer than a half of its width and has a robust axis that is wider than one pleural field. The elevation of distal ends of anterior pleural bands decreases behind the second pleura.

Chlupaciparia minutilobus sp. nov.
Plate III, fig. 5

Derivation of name: *minutus* (Lat.) = minute, *lobus* (Lat.) = lobe (regards the presence of tiny palpebral lobes).

Holotype: Cephalon, UM2-RF 311, Plate III, fig. 5 a, b.

Type locality: Western slope of Puech de la Suque Hill, 1.4 km SE of St. Nazaire-de-Ladarez village.

Stratum: Thick-bedded grey pink-spotted calcilutites of mid Frasnian age (MN Zones 8–10 undifferentiated).

Material: Only holotype cephalon.

Diagnosis: Praeglabellar field and fixigenae evenly vaulted and wide, anterior border furrow narrow, enlarging laterally, palpebral suture with anteriorly situated small palpebral lobe.

Description: Glabella as long as wide, subtriangular, with narrow parabolic frontal outline, laterally defined by evenly deep incised axial furrows that slightly curve out-

ward behind mid-length of glabella. Praeglabellar field of half glabellar length (sag.), evenly arched in continuation with slope of frontal glabella. Border furrow deep, narrowest adaxially, enlarging laterally. Border with high relief in the form of broad cylindrical rim markedly rising above border furrow and anterior praeglabellar field. It is throughout sculptured with numerous continuous terrace ridges. Glabellar furrows and lobes inconspicuous. Occipital furrow straight, set forward behind medial glabellar base where it is deepest and widest, shallowing laterally behind backward-projected lateral glabellar base, in shallow connection with axial furrow. Occipital ring wider than glabellar base (tr.), of equal length (sag.-exsag.), slightly inclined forward, laterally flat, medially thickened posteriorly and of higher elevation than glabella. Occipital node situated on triangular elevation adjacent to medial occipital furrow, directed backward and surrounded by a furrow that is in connection with occipital furrow. Lateral anterior fixigenae wing-like, moderately wide. Anterior sutures from β to γ straight, subtending an angle of 230°. Remnant of a short, crescent-like, slightly elevated palpebral lobe in anterior position. Projection δ-δ crosses glabella slightly behind mid-length. Posterior suture long, with steady inward curvature approaching axial furrow opposite to occipital furrow, curving outward thereafter to posterior border. Exoskeleton smooth, except for minute granulation of median part of basal glabella and occipital ring. Attached librigena framed with continuous broad marginal rim and elevated posterior border that merge with the base of librigenal spine. Lateral border depression larger and shallower than in postero-lateral fixigenal wings, extending adaxially along anterior suture that runs on a minute ridge. Adaxial librigenal field vaulted. Eye-lobe with a narrow, kidney-shaped visual surface carrying lenses of different sizes.

Remarks: The new species differs from *Ch. oculata* in the narrower border depression that widens abaxially, the much wider praeglabellar field and the presence of a minute palpebral lobe.

Pteroparia Richter 1913

Type species: *Pteroparia columbella* Richter 1913

Species assigned: *Pteroparia columbella* Richter 1913, *Proetus aekensis* Born 1912, *Pteroparia coumiacensis* Feist 1976

Diagnosis: Praeglabellar field half as wide (sag.) as glabella length, narrow frontal furrow pitted, low border rim, anterior sutures subtending an angle of more than 240°, librigena with flattened visual field lacking lenses, pygidial axis without axial nodes.

Pteroparia coumiacensis Feist 1976
Plate III, figs 9–11

1976 *Pteroparia coumiacencis*, Feist: 62, pl. 3, fig.10–12
1989 *Pteroparia coumiacensis*, Feist and Clarkson: fig. 3A–C, 6C, 8A

Additional material: 2 cranidia, UM2-RF 312-313, 3 librigenae, UM2-RF 314-316, 2 pygidia, UM2-RF 317-318, cranidia, librigenae and pygidia, UM2-RF 319 from locality CV-S 350 m NW of Causses-et-Veyran village, recovered from well-bedded dark red calcilutites, MN Zones 11–12, late Frasnian.

Remarks: The new material permits observing particular traits regarding the librigenal spine and the disposition of pleural bands in the pygidium. The genal spine has a cylindrical section from its base to the distal end. The spine decreases only slowly in thickness and, shortly before its distal end, enlarges to form a slightly swollen bulge before terminating into a short spine. In the pygidial pleural field, both anterior and posterior pleural bands are conspicuous from front to rear. The anterior ones markedly predominate in elevation and length only in the first two segments where they are distally upraised, forming sharp crests before reaching the lateral edge. By contrast, they do not reach the axial furrow as they are adaxially obliquely cut off by the straight interpleural furrow of the preceding segment. In the posterior segments the anterior bands are much lower, lacking crests and not reaching the latero-posterior edge of the pygidium.

Conclusions

Based on enhanced knowledge on the development of late tropidocoryphids, several main, quickly evolving trends can be observed prior to the extinction of the family at the end of Frasnian Upper Kellwasser Event. From the long-lived ancestral stock represented by *Tropidocoryphe*, the mid Givetian descendant *Longicoryphe* is of smaller size, develops cephalic border rims and, related to this, a narrower praeglabellar field whereas the pygidium reduces in post-axial length. As shown by Feist and Clarkson (1989), *Longicoryphe* gave rise to two different descending lines: first, the youngest tropidocoryphine *Erbenicoryphe* lineage with straight palpebral sutures and secondly, the *Pterocoryphe-Pteroparia* lineage that, together with the new genus *Chlupaciparia*, is essentially distinguished by the backward migration of the β turning points of the anterior suture. Other trends concern the increase in cephalic vault, the effacement of sculptures including tropidia ridges, the development of large groove-like border depressions, the reduction of ring furrows and axial nodes in the pygidium as well as the reduction of pleural relief giving emphasis to the sole elevation of abaxial anterior pleural bands. The most spectacular evolutionary trend that can be followed in both lines concerns eye reduction until final blindness in both *Erbenicoryphe* and *Pteroparia*. Within the *Pterocoryphe-Pteroparia* lineage, the reduced-eyed *Chlupaciparia* branched off in mid Frasnian times and the last representatives retained a small visual field with lenses until the final extinction of the group at the Upper Kellwasser level. Evolutionary trends to eye reduction are also seen in *Ensecoryphe* that is considered here the last representative of the Denemar-

kiinae becoming extinct at the end of the Givetian Taghanic Event.

Short-ranged evolutionary steps that characterise late tropidocoryphids from offshore habitats (Feist and Clarkson 1989) make this group particularly suited for refined biostratigraphical subdivisions and alignment with conodont-based zonations of the Middle Devonian, especially Givetian, and Frasnian offshore limestone sequences such as those developed in the Montagne Noire successions.

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References

Barrande, J. (1846): Nouveaux Trilobites. Supplément à la notice préliminaire sur le Système Silurien et les trilobites de Bohême. I-IV, 1–40, Prague.

Basse M. (1997): Trilobiten aus Mittlerem Devon des Rhenohercynicums: II. Proetida (2), Ptychopariida, Phacopida (1). Palaeontographica, Abt. A 246, 3–6, 53–142.

Beyer E. (1896): Beitrag zur Kenntnis der Fauna des Kalkes von Haina bei Waldgirmes (Wetzlar). Verh. Naturhist. Ver. Rheinl. Westf. 53, 56–102.

Billings E. (1869): Description of some new species of fossils with remarks on others already known, from the Silurian and Devonian rocks of Maine. Proc. Portland Soc. Natur. Hist. 1, 2, 104–126.

Born A. (1912): Die geologischen Verhältnisse des Oberdevons im Aeketal (Oberharz). N. Jb. Mineral. Beil.-Bd. 34, 553–632.

Chlupáč I., Feist R., Morzadee P. (2000): Trilobites and standard Devonian stage boundaries. In: Bultynck P. (ed.) Subcommission on Devonian Stratigraphy, Fossil groups important for boundary definition. Cour. Forsch.-Inst. Senckenberg 220, 87–98.

Erben H. K. (1966): Über die Tropidocoryphinae, Liefg. I. N. Jb. Geol. Paläont. Abh. 125, 170–211.

Ellermann I. (1992): Trilobiten aus dem Unterdevon der Karnischen Alpen / Österreich. Palaeontographica A, 221, 1–3, 1–62.

Feist R. (1976): Systématique, Phylogénie et Biostratigraphie de quelques Tropidocoryphinae (Trilobita) du Dévonien français. Géobios 9, 1, 47–80.

Feist R. (1985): Devonian Stratigraphy of the southeastern Montagne Noire (France). In: Ziegler W., Werner R. (eds) Devonian Series Boundaries – Results of world-wide Studies. Cour. Forsch.-Inst. Senckenberg 75, 331–352.

Feist R. (2002): Trilobites from the latest Frasnian Kellwasser Crisis in North Africa (Mrirt, central Moroccan Meseta). Acta Pal. Pol. 47, 2, 203–210.

Feist R., Clarkson E. N. K. (1989): Environmentally controlled phyletic evolution, blindness and extinction in Late Devonian tropidocoryphine trilobites. Lethaia 22, 359–373.

Feist R., Klapper G. (1985): Stratigraphy and conodonts in pelagic sequences across the Middle-Upper Devonian boundary, Montagne Noire, France. Palaeontographica A, 188, 1–3, 1–18.

Feist R., Schindler E. (1994): Trilobites during the Frasnian Kellwasser Crisis in European Late Devonian cephalopod limestones. Cour. Forsch.-Inst. Senckenberg 169, 195–223.

Feist R., Schönlaub H.-P., Bultynck P. (1985): Faciès et biostratigraphie (conodonts) du passage Dévonien inférieur-moyen dans la Montagne Noire (France). Hercynica 1, 2, 81–97.

Hahn G., Hahn R. (1982): Einige seltene Trilobiten-Taxa aus dem deutschen Kulm (Unter-Karbon). Senckenberg. lethaea 63, 5–6, 429–449.

Harrington H. J. et al. (1959): Tropidocoryphinae. In: Moore R. C. (ed.) Treatise on Invertebrate Palaeontology, part O, 0397–0398.

Hupé P. (1953): Classe des Trilobites. In: Piveteau J. (ed.) Traité de Paléontologie III. Masson, Paris, pp. 44–246.

Klapper G. (1988): The Montagne Noire Frasnian (Upper Devonian) conodont succession. In: McMillan N. J., Embry A. F., Glass D. J. (eds) Devonian of the World. Canad. Soc. Petrol. Geol. 14, 3, 449–459.

Klapper G., Becker R. T. (1999): Comparison of Frasnian (Upper Devonian) Conodont Zonations. Boll. Soc. Paleont. Ital. 37, 2–3, 339–348.

Klapper G, Feist R., House M. R. (1987): Decision on the boundary stratotype for the Middle/Upper Devonian Series boundary. Episodes 16, 4, 433–441.

Lütke F. (1977): Neue Proetidae (Trilobita) aus dem herzynischen Unter-Devon des Harzes. Senckenberg. lethaea 58, 1/3, 99–111.

Lütke F. (1980): Zur Evolution der altpaläozoischen Proetina (Trilobita). Senck. Leth. 61, 1–2, 73–144.

Maillieux E. (1904): Quelques mots sur les trilobites du Couvinien des environs de Couvin. Bull. Soc. Belge Géol., Dal., Hydr. 17, année 1903, 579–582.

Morzadec P., Brice D., Cygan C., Feist R., Majesté-Menjoulas C., Paris F., Racheboeuf P. R. (2000): The Devonian of France: a tentative tie with the GSSP of the Devonian stages. Cour. Forsch.-Inst. Senckenberg 225, 115–129.

Novák O. (1890): Vergleichende Studien an einigen Trilobiten aus dem Hercyn von Bicken, Wildungen, Greifenstein und Böhmen. Paläont. Abh. N. F. 1,3, 1–46.

Ormiston A.R. (1967): Lower and Middle Devonian Trilobites of the Canadian Arctic Islands. Geol. Survey. Can. Bull. 153, 1–148.

Přibyl A. (1945): Příspěvek k poznání českých Proetidů (Trilobitae). Rozpr. Čes. Akad. Věd Umění, Tř. II. 55, 10, 1–37.

Přibyl A. (1965): Proetidní trilobiti z nových sběrů v českém siluru a devonu – I. část. Proetiden aus neueren Aufsammlungen im böhmischen Silur und Devon (Trilobitae) – I. Čas. Nár. Muz., Odd. přírodověd. 134, 2, 91–98 (in German).

Richter R. (1913): Beiträge zur Kenntnis devonischer Trilobiten. Oberdevonische Trilobiten. Abh. Senckenberg. naturforsch. Gesell. 31, 341–423.

Richter R., Richter E. (1919): Der Proetidenzweig *Astycoryphe-Tropidocoryphe-Pteroparia*. Senckenbergiana 1, 1–17, 25–51.

Šnajdr M. (1980): Bohemian Silurian and Devonian Proetidae (Trilobita). Rozpr. Ústř. Úst. geol. 45, 5–324.

Whidborne G. F. (1889): A Monograph of the Devonian Fauna of the South of England. Part I. The Fauna of the Limestones of Lummaton, Wolborough, Chircombe Bridge and Chudleigh. Palaeontograph. Soc. 42, 1–46.

Weddige K., Ziegler W. (1996) in Weddige K. (ed.): Devon – Korrelationstabellen. Conodonten-Zonen des Mitteldevon. Senckenberg. lethaea 76, 1–2, 278.

Wright A. J., Chatterton B. D. E. (1988): Early Devonian Trilobites from the Jesse Limestone, New South Wales, Australia. J. Paleont. 62, 93–103.

Ziegler W., Sandberg C. A. (1990): The Late Devonian Standard Conodont Zonation. Cour. Forsch.-Inst. Senckenberg 121, 1–115.

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Plate explanations
All specimens are external moulds if not otherwise stated. The objects were whitened with MgO before processing with a digital camera Olympus DP12.

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Plate I
1, 4 – *Tropidocoryphe* (*Tropidocoryphe*) sp. A aff. *pseudofilicostata* Přibyl 1965; 1 – cranidium, UM2-RF 259, a – dorsal view, × 10.6, b – lateral view, × 10.6; 4 – fragmentary pygidium, UM2-RF 260, ×11,9. 2–3 – *Tropidocoryphe* (*Tropidocoryphe*) sp.; 2 – librigena, UM2-RF 261, × 9.2; 3 – fragmentary cranidium, UM2-RF 262, × 10.3. 5 – *Tropidocoryphe* (*Tropidocoryphe*) cf. *endorfensis* Basse 1997, cranidium, UM2-RF 263, a – dorsal view, × 12, b – lateral view, × 13.1. 6–7 – *Astycoryphe planifrons* sp. nov.; 6 – librigena, genal spine broken, UM2-RF 264, × 10.6; 7 – cranidium, holotype, UM2-RF 265, a – dorsal view, × 12.4, b – lateral view, × 12.2. 8–3 – *Ensecoryphe tumida* sp. nov.; 8 – fragmentary pygidium, UM2-RF 266, × 11,7; 9 – librigena, UM2-RF 267, × 13.3; 10 – cranidium, holotype, UM2-RF 268, a – dorsal view, × 21.7, b – lateral view, × 21; 11 – librigena, UM2-RF 269, × 16.6; 12 – fragment of anterior cranidium, UM2-RF 270, × 15.5; 13 – pygidium, UM2-RF 271, a – dorsal view, × 12, b – lateral view, × 11.4.

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Plate II
1–4 – *Longicoryphe lanceolata* sp.nov.; 1 – librigena, UM2-RF 276, × 11.8; 2 – cranidium, holotype, UM2-RF 274, a – dorsal view, × 10, b – lateral view, × 10; 3 – juvenile cranidium, UM2-RF 275, × 15.7; 4 – pygidium, UM2-RF 278, × 14.6. 5–6 – *Longicoryphe tenuistriata* sp. nov.; 5 – cranidium, holotype, UM2-RF 280, a – dorsal view, × 14.7, b – lateral view, × 16.3; 6 – pygidium, UM2-RF 285, × 14.8. 7–10 – *Longicoryphe anteglabra* sp. nov.; 7 – librigena, UM2-RF 291, × 11.4; 8 – fragmentary cranidium, UM2-RF 288, × 11.9; 9 – cranidium, holotype, UM2-RF 287, × 13.9; 10 – pygidium, UM2-RF 292, × 6.1. 11–12 – *Longicoryphe* aff. *brilonensis* Richter and Richter 1919; 11 – cranidium, UM2-RF 293, × 11.2; 12 – incomplete pygidium, latex cast of external mould, UM2-RF 294, × 11.9. 13–15 – *Erbenicoryphe nazairensis* sp. nov.; 13 – pygidium, UM2-RF 303, ×15.4; 14 – cranidium, holotype, UM2-RF 298, a – dorsal view, × 16.7, b – lateral view, × 17.5; 15 – cranidium, UM2-RF 299, × 12.1.

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Plate III
1–2 – *Pterocoryphe larouquettensis* Feist 1976; 1 – cranidium, UM2-RF 306, exfoliated, partly with test, a – dorsal view, × 11, b – lateral view, × 11.3; 2 – pygidium, UM2-RF 307, a – dorsal view, × 14.6, b – lateral view, × 15.4. 3–4 – *Pterocoryphe progrediens* Feist and Clarkson 1989; 3 – cranidium, coll. Feist and Clarkson 1989, USTM 35, exfoliated, × 13.2; 4 – pygidium, UM2-RF 309, incomplete, a – lateral view, × 10, b – dorsal view, × 10. 5 – *Chlupaciparia minutilobus* sp. nov., cephalon lacking right librigena, holotypus, UM2-RF 311, a – dorsal view, × 11.1, b – lateral view, × 10.3. 6–8 – *Chlupaciparia oculata* (Feist and Clarkson 1989); 6 – incomplete cranidium, coll. Feist and Clarkson 1989, USTM 29, a – lateral view, × 14.1, b– dorsal view, × 13.1; 7 – pygidium, UM2-RF 310, a – lateral view, × 11.4, b – dorsal view, × 12.1; 8 – cranidium, coll. Feist and Clarkson 1989, USTM 30, × 12.1. 9–11 – *Pteroparia coumiacensis* Feist 1976; 9 – cranidium, UM2-RF 312, a – lateral view, × 13.5, b – dorsal view, × 13.2; 10 – incomplete librigena with inflated distal end of spine, UM2-RF 314, × 13.2; 11 – pygidium, UM2-RF 317, a – lateral view, × 13.5, b – dorsal view, × 12.7.

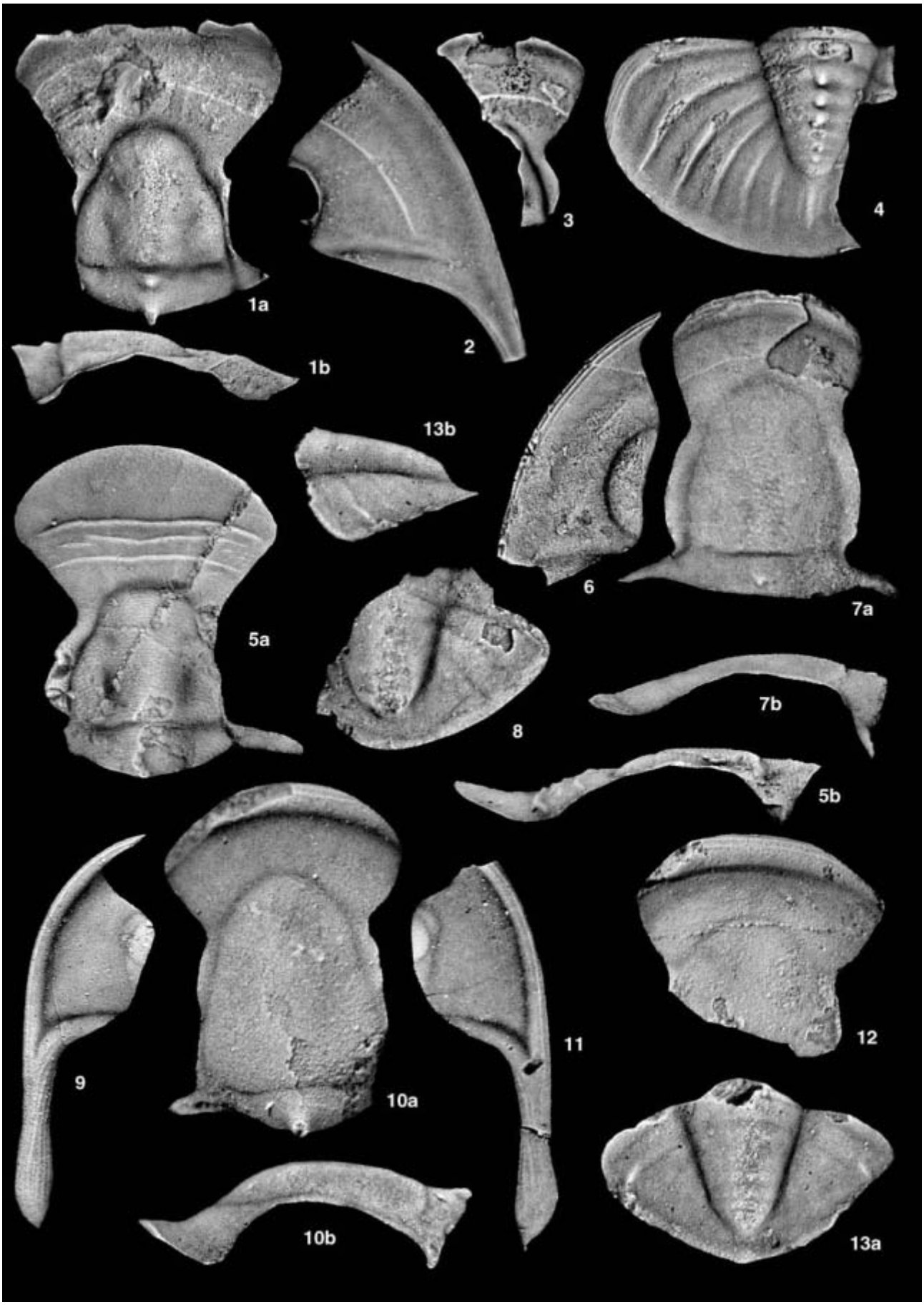

Plate I

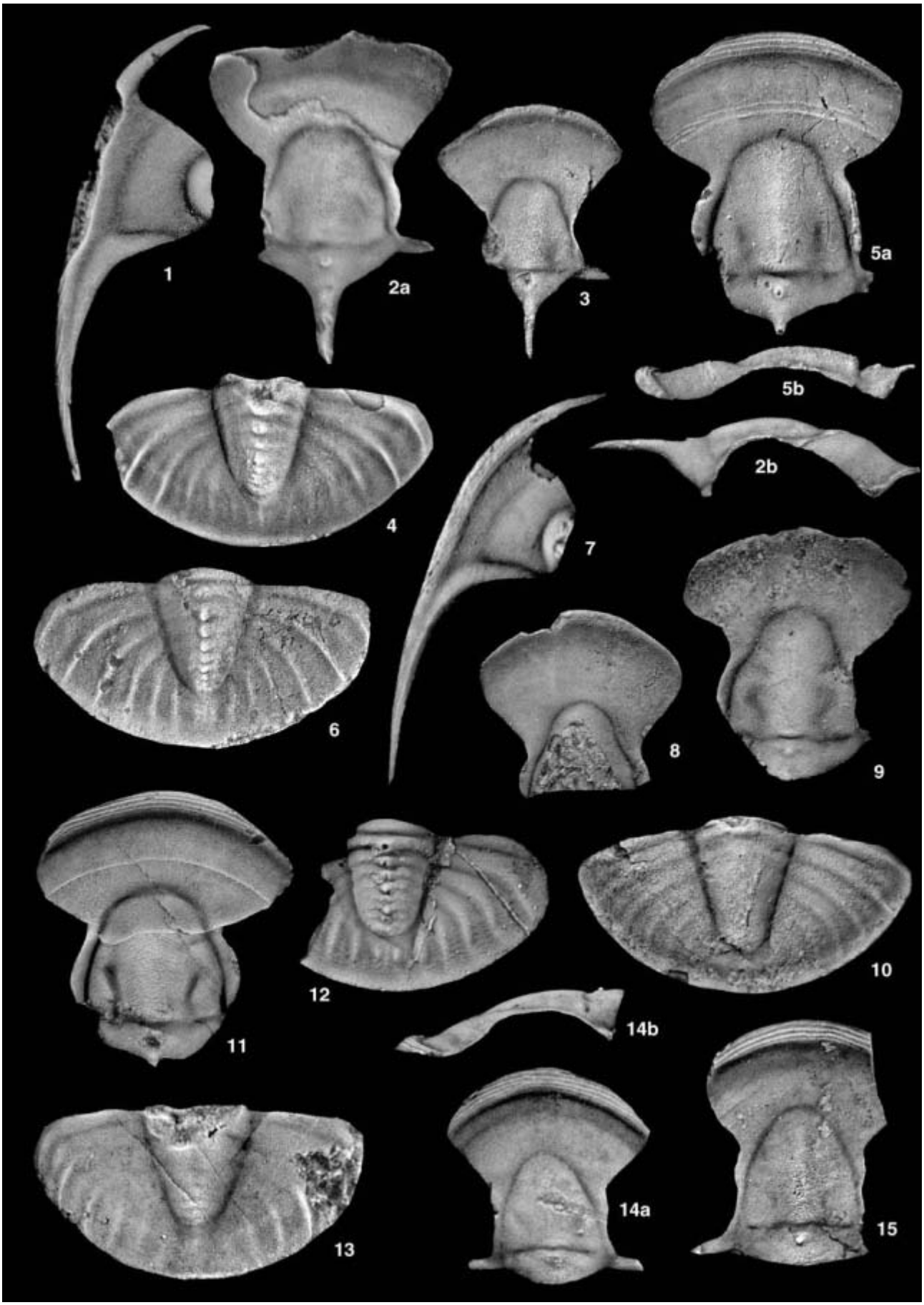

Plate II

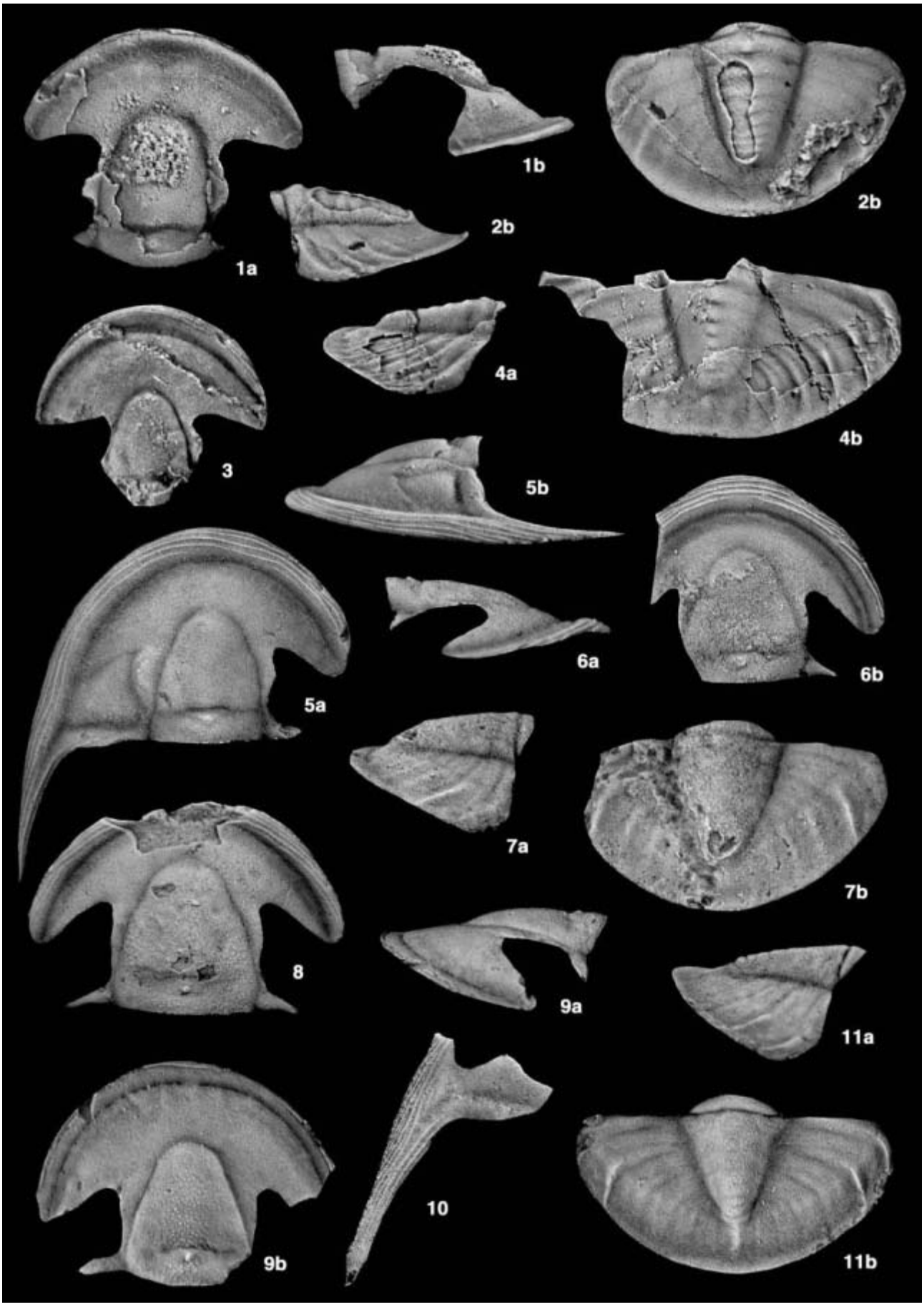

Plate III