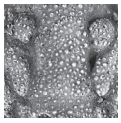
Mid-Silurian odontopleurid trilobites from Roquemaillère, Montagne Noire, Southern France

Raimund Feist & Euan N.K. Clarkson



The Roquemaillère site on the southeastern margin of the French Massif Central is one of the rare localities along the Northern Gondwana margin from which Silurian odontopleurid trilobites have been recovered. Revision of M.-C. Chaubet's collections from this site, presented in her monograph (1937), together with additional new records revealed the presence of *Kettneraspis* Prantl & Přibyl, 1949 with 5 species [*K. acanthifrons* sp. nov., *K.* cf. *juengeri* Santel, 2001, *K. rojanensis* sp. nov., *K. anteflexa* sp. nov., *K.* aff. *parkini* (Siveter, 1989)], *Eoleonaspis* Sheng, 1974 with *E. maeander* sp. nov., *Radiaspis* Richter & Richter, 1917 with *Radiaspis* sp., *Laethoprusia* Ramsköld, 1991 with *L. augur* sp. nov., and *Ceratocephalina* Whittington, 1956 with *C. angustifurcata* sp. nov. Evidence from associated graptolites, brachiopods, bivalves and conodonts assigns the trilobites to the late Wenlock Homerian stage. The diverse fauna is dominated, both in specific diversity and number of individuals by *Kettneraspis*. The absence of the closely related *Leonaspis* regarded as characterising Gondwana-related terranes from the late Silurian onwards, confirms the pre-Ludlow age of the Roquemaillère fauna. • Key words: odontopleurid trilobites, Silurian, Homerian, Montagne Noire, systematics.

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In North Gondwana-related terranes, Silurian odontopleurids have been reported from Bohemia, the Carnic Alps and, more sporadically, from the Spanish Pyrenees, Moroccan Meseta and Montagne Noire, southern France. In the latter, they occur only at Roquemaillère at the external southeastern margin of the French Massif Central, a site that constitutes a gravitationally emplaced olistolithic slab within the mass-flows of the synorogenic flysch sedimentation that characterises the Laurens-Cabrières klippen area (Engel *et al*. 1978). The Roquemaillère site (Fig. 1), situated 3 km NW of Roujan township (Hérault department), was exhaustively investigated by M.-C. Chaubet (1937). Poor outcrop conditions, where only loose blocks and a few isolated limestone beds are available for study, and tectonic complication did not allow an uninterrupted record of strata. Rich faunas gave evidence of the presence of late Llandovery, late Wenlock and early Ludlow rocks at Roquemaillère. Trilobites seemed to be restricted to levels with *Monograptus priodon*, and are thus considered to be Wenlock in age. Besides aulacopleurids and proetids, Chaubet recognised the presence of odontopleurids that she attributed to *Acidaspis* aff. *tricornis* Barrande, 1852, *Acidaspis* aff. *minuta* Barrande, 1852 and *Acidaspis* sp. In his thesis, Feist (1977) revised Chaubet's material and supplemented it with new collections. The data presented in Feist's thesis remained hitherto unpublished, and are presented for publication in this contribution. All odontopleurid remains are undeformed and dissociated; they were recovered from dark marly bioclastic ostracod limestones also yielding numerous small brachiopods and fewer unflattened graptolites. From a few trilobite-bearing beds, associated brachiopods and graptolites were determined by V.G. Walmsley (Swansea) and R.B. Rickards (Cambridge). Among them the presence of *Hircinisca rhynchonelliformis* and *Colonograptus ludensis* indicate a late Homerian age for the fauna (written comm. by V.G. Walmsley, May 1976). This is not in conflict with the scarce record of *Kockelella ortus ortus* and *K. absidata* (Corradini, det.). Associated bivalves belong to the Homerian *Cardiola agna figusi* Community with graptolites of the *Monograptus priodon flemingii* group, *Cyrtograptus lundgreni* Zone (Kříž 1996). According to these data a late Homerian age is confirmed for the Roquemaillère trilobites.

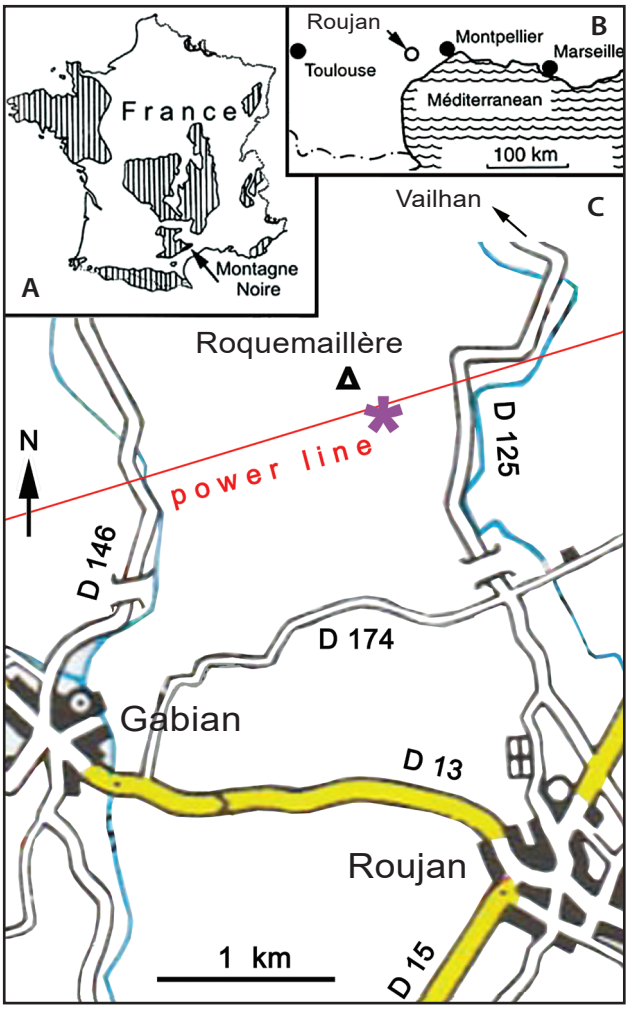


Figure 1. Locality maps. A – location of the Montagne Noire at the southern edge of the French Massif Central. • B – location of Roujan township in the vicinity of Roquemaillère. • C – Roquemaillère Hill (triangle) and trilobite collecting site (star) below electric power line, 3 km NNW of Roujan township.

Systematic palaeontology

Terminology follows Whittington & Kelly (1997). Measurements of pygidial length exclude the articulating half-ring.

Depository. – University of Montpellier, Invertebrate Palaeontology (UM-IP 962–1031).

Order Odontopleurida Whittington, 1959
Family Odontopleuridae Burmeister, 1843
Subfamily Odontopleurinae Burmeister, 1843

Genus *Kettneraspis* Prantl & Přibyl, 1949

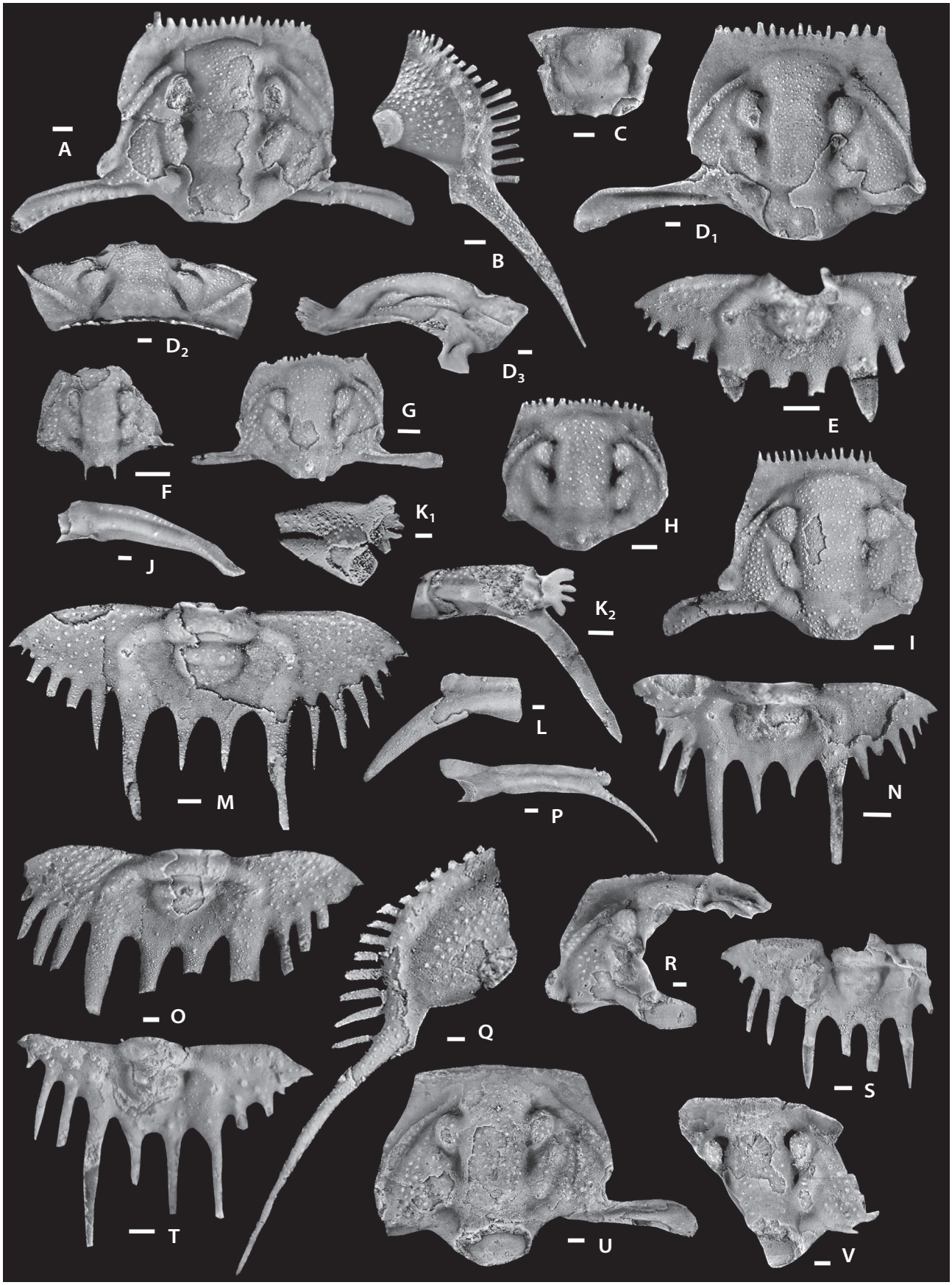
Type species. – *Acidaspis pigra* Barrande, 1872 from the *Acanthopyge* Limestone, lower Eifelian, Bohemia.

Remarks. – The genus *Kettneraspis* is outstanding in its longevity (lowermost Llandovery to lower Givetian), its cosmopolitan distribution and its high specific diversity. Some 50 species were assigned to *Kettneraspis* by Ramsköld & Chatterton (1991: p. 357). Among 23 species listed from the Silurian, 5 species were reassigned to *Edgecombeaspis* Adrain & Ramsköld, 1997. Additional Silurian species of *Kettneraspis* that have been described are *K. wrightae* Adrain & Ramsköld, 1997 from the upper Sheinwoodian, *K. lindoei* Adrain & Ramsköld, 1997 from the lower Homerian, *K. caldwelli* Adrain & Ramsköld, 1997 from the Gorstian, all from Arctic Canada; *K. hollowayi* Sandford, 2000 from the lower Ludlow of Australia; *K. juengeri* Santel, 2001 from the upper Wenlock of the Carnic Alps; *K. copelandi* Chatterton & Ludvigsen, 2004, *K. ramskoeldi* Chatterton & Ludvigsen, 2004, both from the lower Silurian of Anticosti Island, Quebec. *Kettneraspis*? *coalescens* (Van Ingen, 1901) and *K.*? *arkansana* (Van Ingen, 1901) from the Wenlock of Oklahoma and Arkansas, recently revised by Holloway (2021), are only known from the cranidia but may belong to the genus. To date, from 25 Silurian species assigned to *Kettneraspis* with confidence nine species are contemporary with those from Roquemaillère. Among them only three, i.e. *K. dormitzeri* (Hawle & Corda, 1847), Motol Formation, Bohemia, *K. leridae* Degardin & Pillet, 1984, Espui, Spanish Pyrenees and *K. juengeri* Santel, 2001, Carnic Alps were reported from North Gondwana-related terranes and as such are palaeogeographically closest to the Montagne Noire material.

***Kettneraspis acanthifrons* sp. nov.**
Figure 2A–O

Holotype. – Cranidium, partially exfoliated, UM-IP 962, Roquemaillère, Montagne Noire, Homerian (Fig. 2D).

Figure 2. Specimens from Roquemaillère, Montagne Noire, S-France, Homerian. • A–O – *Kettneraspis acanthifrons* sp. nov.; A – cranidium UM-IP 963, partly exfoliated; B – librigena UM-IP 969; C – hypostome UM-IP 968; D – holotype cranidium UM-IP 962, partially exfoliated, dorsal (D_1), anterior (D_2), lateral (D_3) views; E – pygidium UM-IP 973; F – cranidium UM-IP 964, early holaspid; G – cranidium UM-IP 965, early holaspid; H – cranidium UM-IP 966, small holaspid; I – cranidium UM-IP 967, small holaspid; J – fragmentary anterior thoracic segment UM-IP 970; K – fragmentary thoracic segment showing quadrifid termination of anterior pleural band UM-IP 971, partially exfoliated (K_1), internal mould (K_2); L – fragmentary mid-thorax segment UM-IP 972; M – pygidium UM-IP 974, partly exfoliated; N – pygidium UM-IP 975, partly exfoliated; O – pygidium UM-IP 976. • P–V – *Kettneraspis* cf. *juengeri* Santel, 2001; P – fragmentary thoracic segment UM-IP 986; Q – librigena UM-IP 985; R – incomplete cranidium UM-IP 982; S – incomplete pygidium UM-IP 987; T – pygidium UM-IP 988; U – cranidium UM-IP 983; V– incomplete cranidium UM-IP 984. Scale bars = 2 mm.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Type horizon and locality. – Solid beds of dark-grey microsparitic brachiopod limestone, slope below lower track, at 300 m SE of Roquemaillère hill-top.

Paratypes. – Cranidia (UM-IP 963–967), hypostome (UM-IP 968), librigena (UM-IP 969), thoracic segments (UM-IP 970–972), pygidia (UM-IP 973–976).

Other material. – Eight cranidia (UM-IP 977), 4 hypostomes (UM-IP 978), 5 librigenae (UM-IP 979), 2 thoracic segments (UM-IP 980), 4 pygidia (UM-IP 981).

Etymology. – After *ακαντα* (Grec.) = spine, and *frons* (Lat.) = front, designating the spiny anterior margin of cranidium.

Diagnosis. – Cranidium with long preglabellar area, anterior glabellar lobe distant from anterior border, projecting spines present on anterior border, eye ridges without straight portion, very wide posterior area of fixigenal field. Thoracic segments with fan-shaped, quadrifid anterior pleural projection distally. Pygidium with pleural ridges extending far from axis, converging posteriorly, 5–6 pairs of lateral border spines.

Description. – Cranidium quadrangular excluding posterior area of fixigena, a little wider (83%) at palpebral lobes than long (sag.). Anterior margin straight, without border, provided with a row of 16 to 18 symmetrically set projecting spines of almost even length. Preglabellar area long (sag.), moderately inclined. Glabellar frontomedian lobe narrow, parallel-sided adjacent to L1 and L2, expanding anteriorly to reach 45% of maximum cranidial width across palpebral lobes, of parabolic anterior outline, delimited against preglabellar area by distinct, uniformly curved preglabellar furrow. In lateral view, profile of median lobe moderately arched, more strongly so transversely, indistinctly separated from median part of occipital ring by a wide and shallow occipital furrow. Longitudinal furrow distinct, wide, rather deep towards inner ends of S1 and S2, not reaching posterior margin of occipital ring, partially defining lateral occipital lobes against median part of occipital ring. Axial furrow shallow, of sigmoid course around lateral glabellar lobes, reaching posterior margin adjacent to lateral occipital lobes. S0 is very deep, straight and narrow distally where separating moderately distinct lateral occipital lobes from L1. Occipital ring wider than remainder of glabella, median portion rectangular, not inflated, with prominent median node. A pair of short spines is set close to posterior margin. Lateral glabellar lobes inflated, distinctly defined. L1 of elongated elliptical outline, with oblique axis at 25° to the sagittal line; axial furrow becoming shallower towards anterior end of lobe. L2 ovoid, 58% as long as L1 and with its long axis parallel to sagittal line, higher than L1, remaining below median lobe in lateral view. S1 oblique at 50° to the sagittal line, deepest adaxially. S2 short and deep, parallel to S1. Eye ridges prominent, semi-cylindrical, defined by deep furrows, slightly narrowing adaxially before merging with distal extensions of anterior glabellar lobe, diverging in an angle of 90°, gently and evenly curved without straight exsagittal portion, meeting anterior facial suture far back slightly in front of γ. Palpebral lobe upraised, extended, flat with central pit opposite posterior one-third of L1, overlapping posterior branch of facial suture in dorsal view. Fixigenal field outside eye ridge is subtriangular, concave, sunken towards the eye ridge, very wide opposite frontal glabellar lobe. Internal fixigena long triangular, moderately vaulted, considerably widening posteriorly where it reaches 1.6 times the width of L1, 33% of cranidial width at γ, and 50% of glabellar width at S0 (tr.). Anterior branches of facial suture converging between γ and α, almost parallel posteriorly, gently curving inwards anteriorly, tending to become concave in outline close to anterior margin. Posterolateral projections very long (tr.), their borders provided with rows of prominent tubercles. Surface sculpture is granulose with numerous, small isolated nodules, present over the whole cranidium with the exception of preglabellar field, palpebral lobes and lateral occipital lobes.

Librigena with large prominent eye, protruding from a moderately vaulted genal field; lateral border pronounced, bearing at least 18 slender, parallel-sided, bluntly-ending marginal spines the posteriormost of which is situated just in front of librigenal spine base; marginal spines long posteriorly, diminishing in size towards the front. Genal spine longer than remainder of librigena, without lateral spines, very slightly curved, pointed at tip. Width of genal spine at base is 20% of spine length. Lateral margin is weakly re-entrant in front of the genal spine. Sculpture: exoskeleton granulose, nodules of various sizes on genal field, evenly distributed, finer-grained and denser on genal spine, a row of 7 short epiborder nodes in addition to tubercles on lateral border.

Hypostome is transverse trapezoidal in outline with a slightly undulating anterior margin and short, dorsally directed wings. Width/length ratio = 1.3. Lateral border strongly convex with a small shoulder. Posterior margin is sinuous, with a small median spine. Posterior border almost flat, long (sag.), anteriorly poorly defined against faint posterior border furrow. Posterolateral corners obtusely pointed. Anterior lobe of middle body moderately swollen, defined against short anterior border by thin border furrow, laterally by deep, parallel border furrows; middle furrows oblique, long and straight, vanishing near the mid-line. Posterior lobe transverse, half as long (sag.) as anterior lobe, inflated laterally, defined against lateral border by rather deep border furrows that become progressively shallower posteriorly. External surface with dense, minute pustules.

Thoracic segments with a pair of nodes on axial rings (unfigured) and with well-rounded pleural ridges except on first segment (Fig. 2J), extending into long and robust, backwardly curved posterior pleural spines. Distal extremities of anterior pleural bands with small, platform-like, fan-shaped extensions that display four projecting lobes of different width. This structure is downwardly directed in relation to the posterior pleural spine. Sculpture consists of dense tuberculation on axial ring and pleural spine, a row of tubercles on pleural ridge and sometimes on anterior band, fan-like extremities smooth.

Pygidium four times as broad as it is long, posterior and lateral borders absent, anterior pleural margin straight in its adaxial half, gently turned backward distally, projecting into stout spiny projections at lateral angles. Axis comprising 70% of pygidial length, parabolic in posterior outline, with two (three?) axial rings in addition to terminal piece. First ring robust, highly inflated, 23% of pygidial width, embayed posteromedially (sag.) by pseudo-articulating half ring of following segment. Remainder of rachis 79% of width of first axial ring, ovoid, sunken against first axial ring, circumscribed by deep axial furrows, subdivided into an anterior ring clearly defined by transverse inter-ring furrows that are interrupted medially, and an end-piece in which the anterior part might correspond to a very short (sag.) and weak third axial ring as indicated by transversely aligned sculpture elements defined by faint inter-ring furrow behind them (Fig. 2M, O). Adaxial portion of pleural ridge is semi-cylindrical, clearly narrower than first axial ring (exsag.) at junction. It curves outward to reach a distance equalling half width of first axial ring, before being deflected backwards in a knee-like curve distant from second axial ring, thereafter curving slightly adaxially and enlarging considerably before merging with the major border spine. Depressed area between axis and pleural ridges is as wide (tr.) as postaxial region (sag.), flat, slightly inclined towards axial furrow. Outer pleural field flat, slightly inclined to the rear, anteriorly bordered with thin ridge running parallel and close to anterior margin. Nearly straight major spines and a pair of much shorter, stoutly-based interior spines on the same level as major spines are parallel to each other and slightly raised backwards. Posterolateral margin with 6 secondary border spines (besides pointed extremity of pleural field), that are slightly curved backwards and increase in size rearwards. Entire exoskeleton is granulose. Axis, posterior pleural ridges and outer pleural fields sculptured with moderately spaced nodules that become finer and denser on marginal spines. There is a row of nodules on ridge close to anterior border of pleural field. Nodules are sometimes organized into obliquely backward directed rows on outer pleural fields. Axial rings and points of maximum flexure of pleural ridges provided with a pair of prominent nodes. Adaxial parts of pleural ridges and internal genal fields around axis without sculpture.

Remarks. – Odontopleurids are characterised by the development of prominent spines on their entire skeleton, and the pattern of their size, number and distribution is primarily used for the classification of the family. In accordance with the generally admitted usage to assign taxa of classical *Leonaspis* morphology but with only two interior pygidial border spines to *Kettneraspis*, as proposed by Ramsköld & Chatterton (1991), the new species *acanthifrons* is ascribed to this genus. However, it exhibits a higher number of librigenal border spines than diagnosed for the genus (18 versus 12–16). As pointed out by Holloway (2021: pp. 86, 87) the only irrefutable character that remains to distinguish *Kettneraspis* from *Leonaspis* is the number of interior border spines on the pygidium.

The new species is distinguished from most other *Kettneraspis* by the row of distinctive, closely spaced spines along the anterior edge of the cranidium that are not upraised but flush with the prefrontal area. Such morphology is unknown in other Silurian odontopleurids with the exception of *K. hollowayi*. Unlike *acanthifrons* the frontal spines in *hollowayi* are upraised with respect to the prefrontal area and do not extend forwards as is the case in *acanthifrons*. These spines may constitute enlargements of the row of tubercles present on the anterior border of most species of *Kettneraspis*. Another distinctive feature of spine development concerns the high number of lateral secondary pygidial border spines in *acanthifrons*. It is considerably higher (6 spines) than in all other species of *Kettneraspis* where up to 4 spines at the most are observed such as in the type species *K. pigra* (Barrande, 1872). Small, paired projecting occipital spines are present in juveniles of *acanthifrons* (Fig. 2F) but these are reduced in adults to knob-like nodes similar to those in *K. crenata angelini* (Prantl & Přibyl, 1949) from Gotland but unlike *K. juengeri* where exceptionally very long spines are retained in adults.

Besides spine distribution other particular morphological features characterise the new species. Many of them also occur in *K. juengeri* making it the closest related species. For example, eye ridges without straight exsagittal portions are likewise developed in *K. juengeri* but apparently not in any other species of the genus. Unusually broad posterior fixigenal projections in large specimens that are considerably wider than the glabella across L1 (tr.) are shared with *K. juengeri.* Distally indented fan-like extensions of the anterior bands of some (?all) thoracic pleurae of *acanthifrons* recall similar structures developed in *juengeri*, a feature that is so far exclusive in Silurian *Kettneraspis*. It is however common in Lower Devonian taxa (Santel 2001: p. 145), among them *K. seiberti* Basse in

Basse & Müller, 2004 of which entire specimens illustrated in spectacular ventral views exhibit thoracic segments with indented fan-like extensions identical to those of *acanthifrons* (Basse & Müller 2016: pl. 23, figs 214, 216–218). These structures displayed at the extremities of all anterior bands are ventrally directed and may have had a coaptative function during enrolment.

The pygidium of *K. acanthifrons* resembles that of *K. juengeri* in its general outline and the widely spaced pleural ridges that are distant from the axis. It differs from *K. juengeri* by the slight convergence and considerable enlargement of the posterior ends of the pleural ridges, the presence of slight ridges along the anterior borders, the shorter median secondary spines as well as the higher number of lateral border spines. In addition to the nodular sculpture the exoskeleton of *acanthifrons* is densely granulated whereas it is smooth in *juengeri*.

***Kettneraspis* cf. *juengeri* Santel, 2001**
Figure 2P–V

Material. – Cranidia (UM-IP 982–984), librigena (UM-IP 985), thoracic segment (UM-IP 986), pygidia (UM-IP 987–990).

Remarks. – The material exhibits all detailed features characterising *juengeri*, in particular: absence of preglabellar field, anterior border with a row of nodes, border spines of pygidium narrow-based, slender and long including internal pair, narrow axis, and sparse nodules. The posterior fixigenae seem to be a little narrower than in type material. The identity of the specimens with the Carnic species cannot be assured at this stage due to damage of the occipital ring that prevents observation of the presence of long occipital spines that characterise *juengeri*.

Occurrence. – Loose light-grey crinoid limestone, north of power line between upper and lower track, at 250 m SE of Roquemaillère hill-top.

***Kettneraspis rojanensis* sp. nov.**
Figure 3A–G

Holotype. – Cranidium, UM-IP 991, Roquemaillère, Montagne Noire, Homerian (Fig. 3A).

Type horizon and locality. – Loose blocks of light-beige marly ostracod limestone, slope above lower track, at 200 m SE of Roquemaillère hill.

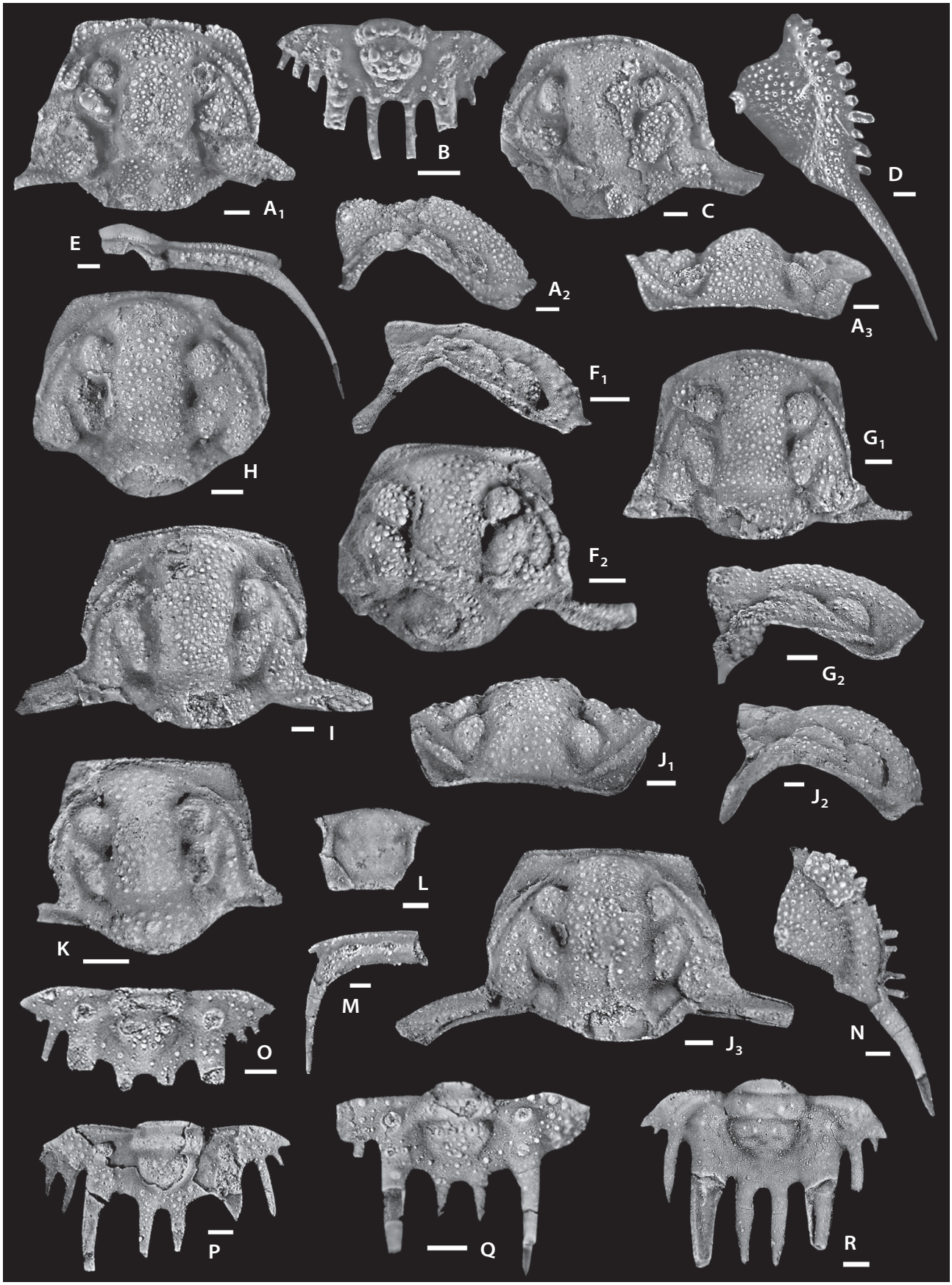
Paratypes. – Cranidia (UM-IP 992–995), librigena (UM-IP 996), thoracic segment (UM-IP 997), pygidium (UM-IP 998).

Etymology. – After Roujan township in the vicinity of the type locality.

Diagnosis. – Cranidium with inflated, abaxially broadening anterior border with a row of prominent tubercles that continue alongside straight anterior sutures. Intersection of anterior border and anterior sutures blunt. Median glabellar lobe moderately sloping anteriorly, posteriorly much higher than lateral glabellar lobes and horizontal fixigenae. Librigena with very small eye, very long, slender genal spine. Pygidium with robust axis, as wide as long, with postaxial triangular swell, subparallel internal border spines converging, three pairs of lateral border spines.

Description. – Cranidium subquadrate excluding posterior fixigenal prolongations (length/width across palpebral lobes = 0.89), with anterior margin slightly curved forwards medially. Anterior border swollen, enlarged abaxially before meeting anterior sutures in a blunt angle. Width of glabellar median lobe opposite palpebral lobes equals one-third of the width of the cranidium at palpebral lobes, rectangular apart from markedly expanded frontal lobe, slightly expanding posteriorly (tr.). Frontal lobe markedly separated from anterior border by continuously deep preglabellar furrow. Occipital furrow is a wide shallow depression. Occipital ring broad with posterior margin regularly curved, projecting backwards, slightly raised, bearing a median nodule flanked by a pair of nodes on the posterior slope. Lateral occipital lobes insignificant. Lateral glabellar lobes separated from fixigenae by shallow axial furrows; L1 obliquely elongated, L2 globular, more strongly inflated than L1. Anterior branches of facial suture weakly curved in outline and slightly converging anteriorly, Anterior triangles of fixigenae depressed, flush with preglabellar furrow, framed by a row of prominent tubercles along anterior suture. Palpebral lobe small. Eye

Figure 3. Specimens from Roquemaillère, Montagne Noire, S-France, Homerian. • A–G – *Kettneraspis rojanensis* sp. nov.; A – holotype cranidium UM-IP 991, dorsal (A_1), lateral (A_2), anterior (A_3) views; B – pygidium UM-IP 998; C – cranidium UM-IP 992, partially exfoliated; D – librigena UM-IP 996, latex cast of external mould; E – fragmentary thoracic segment UM-IP 997; F– cranidium UM-IP 993, partially exfoliated, lateral (F_1), dorsal (F_2) views; G – cranidium UM-IP 994, internal mould, dorsal (G_1), lateral (G_2) views. • H–Q – *Kettneraspis anteflexa* sp. nov.; H – cranidium UM-IP 1000, internal mould; I – cranidium UM-IP 1001, internal mould; J – holotype cranidium UM-IP 999, internal mould, anterior (J_1), lateral (J_2), dorsal (J_3) views; K – cranidium UM-IP 1002, internal mould; L – hypostome UM-IP 1003, mostly exfoliated; M – fragmentary thoracic segment UM-IP 1005, mostly exfoliated; N – librigena UM-IP 1004, partially exfoliated; O – pygidium UM-IP 1006; P – pygidium UM-IP 1007, partially exfoliated; Q – pygidium UM-IP 1008. • R – *Kettneraspis* aff. *parkini* (Siveter, 1989); pygidium UM-IP 1012. Scale bars = 2 mm.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ridges rather stout throughout, with even and moderate curvature. Posterior triangle of fixigenae narrow (tr.), slightly swollen. Profile of glabella in lateral view moderately curved with slow anterior slope. Transverse profile of cranidium with high- vaulted posterior glabella, lateral glabellar lobes and fixigenae much lower than glabella, horizontal at palpebral lobes. Librigena with small, globular eye, set high on the triangular genal field, with a very strong, raised lateral border broadening posteriorly. Genal spine longer than distance α–ω, slim, divergent and weakly curving, much narrower at base than lateral border and carrying a row of 11–12 stout marginal spines that diminish in size anteriorly. Cephalic exoskeleton except in furrows and anterior angle of fixigena with prominent nodules of various sizes. Blister-like individual larger nodules are dispersed within a dense groundmass of finer tubercles especially displayed on thick librigenal border and on the genal spine. Thoracic segment provided with semi-cylindrical pleural ridge that extends into a slim, very long, evenly curved and divergent posterior pleural spine. Anterior pleural band ends bluntly in front of base of spine. Anterior band and pleural ridge densely sculptured with nodules of various sizes that become tiny on pleural spine. Pygidium subtriangular (length/width ratio without spines = 0.36). Axis is prominent and robust, as wide across first ring as pleural field and attaining 75% of pygidial length. It has a wide parabolic posterior outline, well defined continuous axial furrows, and two rings besides undifferentiated terminal piece. First ring curves forwards medially disclosing a wide pseudo-articulating half-ring in front of second ring. Swollen, triangular postaxial field reaches posterior margin. Pleural ridges are poorly differentiated. Pleural fields short subtriangular, not inflated, devoid of borders. Stout major border spines and much thinner internal spine pair are positioned close to each other, running backwards parallel to the sagittal axis. There are three pairs of robust external border spines. Axial rings and swollen postaxial area, pleural fields and base of border spines carry blister-like inflated nodules of various sizes.

Remarks. – The new species shares a large number of features with the contemporaneous *Kettneraspis leridae* Degardin & Pillet, 1984 from the neighbouring Spanish Pyrenees, and it is tempting to evaluate whether they could be possibly conspecific. Unfortunately, we have only a single though complete negative impression of *leridae*, of which C. Crônier provided a cast that seems slightly compressed. Both taxa share the rather prominent tubercular sculpture, the curved anterior cranidial outline, the low anterior glabellar profile, the palpebral lobe that is situated far backwards, and, in the pygidia, the transverse outline, the robust axis with wide posterior contour, the absence of borders, and the three pairs of lateral border spines. The cranidia differ in the median glabella lobe, parallel-sided in *rojanensis* but wider and slightly expanding opposite S2 in *leridae*. The librigenae share a very long, slender genal spine, longer than the remainder of the librigena, but *rojanensis* has a much smaller eye, fewer border spines (11–12 *vs* 14) and a more re-entrant marginal curvature in front of the spine-base. Significantly the librigenal border of *leridae* has a row of epi-border spines that is lacking in *rojanensis*. The pygidia differ in the much shorter, conical, main and secondary border spines, and the absence of a postaxial swelling in *leridae*.

***Kettneraspis anteflexa* sp. nov.**
Figure 3H–Q

Holotype. – Cranidium, UM-IP 999, Roquemaillère, Montagne Noire, Homerian (Fig. 3J).

Type horizon and locality. – Various loose blocks of light beige marly limestone with *Aulacopleura* lumachelles, slope above lower track, 250 m SE of Roquemaillère hill-top.

Paratypes. – Cranidia (UM-IP 1000–1002), hypostome (UM-IP 1003), librigena (UM-IP 1004), thoracic segment (UM-IP 1005), pygidia (UM-IP 1006–1008).

Other material. – Eleven cranidia (UM-IP 1009), 7 librigenae (UM-IP 1010), 1 pygidium (UM-IP 1011).

Etymology. – *Anteflexus* (lat.): downwardly-flexed anteriorly (profile of glabella).

Diagnosis. – Cranidium with transverse profile sloping laterally; anterior glabella strongly curved downward anteriorly, anterior border straight, thin, sharply angular; anterior branch of facial suture curving inward anteriorly. Genal spine stout, a little longer than librigenal field. Pygidium has low axis devoid of pseudo-intercalating half-ring, and short and closely spaced interior border spines.

Description. – Cranidium considerably shorter than wide across palpebral lobes (length/width ratio = 0.87). Anterior margin straight or slightly curved, meeting anterior suture in an obtuse angle; anterior border very short sagittally, flat, sharply edged, provided with small nodules. Preglabellar furrow distinct. Fronto-median glabellar lobe is almost parallel-sided for most of its length, anteriorly expanded. Occipital furrow narrow (sag.) and shallow, much deeper behind L1. Occipital ring transverse, short, protruding backwards adaxially, with median node and barely visible paired posterior nodes, provided with well

defined, moderately inflated lateral lobes. Lateral glabellar lobes moderately inflated, well defined by undulating axial furrows. Anterior branches of facial suture inwardly curved. Anterior triangles of fixigenae wide, concave. Eye ridges thin, narrowing anteriorly. Fixigenae adaxial to eye ridge and palpebral lobe narrow, about as wide as maximum width of L1, inflated. Profile of glabella in lateral view exhibits a moderately elevated occipital ring and a strong longitudinal vault of remainder of glabella that is markedly downwardly flexed to the front. In transverse profile cranidium slopes outwards abaxial to rather low vault of median glabellar lobe.

Librigena with a moderately vaulted triangular genal field, with a very wide, semi-cylindrical border of even width from front to rear and with a row of 15–16 stout, marginal spines diminishing in size anteriorly. Genal spine stout, slightly curved, a little shorter than distance α–ω, at its base almost equal in width to lateral border and forming an open angle with it. Hypostome subrectangular, shorter than wide, with an evenly curved anterior suture. Lateral borders slightly convex with small shoulders midway between anterior margin and obtuse posterior corners. Posterior margin slightly embayed. Middle body very wide and swollen, poorly subdivided into a shorter anterior lobe and a longer posterior one that almost reaches the posterior margin. Surface granulose.

Anterior pleural bands of thoracic segments have short distal spines; posterior pleural bands convex, with a stout distal spine directed exsagittally backwards. Pygidium short subtriangular (length/width ratio without spines = 0.31), without borders. Axis tiny, narrow; width across first ring is about equal to that of pleural region, with prominent, straight first axial ring, a second ring without pseudo-articulating half ring, and a depressed terminal piece with narrow parabolic posterior outline; axial furrow incomplete medially behind axis. Pleural ridges thick, enlarging beyond their point of backward deflection and extended into stout major border spines that are slightly divergent proximally and curve backwards to become slightly convergent distally. These remain markedly distant from a closely set pair of short, inner secondary border spines. There are two pairs of outer border spines behind the spinose anterolateral corners of pleural field. Axis, pleural fields and border spines with spaced nodules of various sizes, axial rings and pleural ridges carrying pairs of larger nodes.

Remarks. – The new species is close to *rojanensis* in general features but differs mainly in the straight un-swollen anterior edge, the markedly downwardly-curved profile of the anterior glabella, the wider internal fixigenae and the wider pygidium with shorter (exsag.) pleural fields and more widely spaced major border spines. Among species with straight-sided, anteriorly down-curved median glabellar lobe and transverse pygidium *K. anteflexa* is closest to *K. wrightae* Adrain & Ramsköld, 1997 from the Sheinwoodian of the Cape Phillips Formation, Canadian Arctic. The outline and shape of the hypostomes and of the pygidial axis and are also very similar. The French taxon differs in having a sagittally very narrow anterior border which is not upturned and less arcuate (tr.), wider, downwardly sloping inner fixigenae, a more forwardly placed and lower palpebral lobe, longer librigenal border spines, a markedly wider pygidium with more outer border spines, and a much denser sculpture of closely set nodules that are not aligned in rows on the fixigenae and librigenal border. The contemporaneous Bohemian species *K. dormitzeri* Hawle & Corda, 1847 (= '*Acidaspis*' *roemeri* Barrande, 1852; see Bruton 1968), figured by Šnajdr (1990: p. 249), has a transverse pygidium with similar configuration of axis and number of border spines, but the pleural fields lateral to the pleural ridges are flat and larger, the pleural ridges are deflected more strongly backwards from the axial furrow, their prominent tubercles are situated much further back, and the border spines are much thinner. The median glabellar lobe is narrower and not parallel-sided but expands slightly at S2. The eye ridge is deflected more strongly backward and the fixigena between it and L1 is extremely narrow. As such the Bohemian and French representatives of *Kettneraspis* are less closely related.

***Kettneraspis* aff. *parkini* (Siveter, 1989)**
Figure 3R

Material. – Pygidium (UM-IP 1012).

Remarks. – The single well-preserved pygidium is very close to *parkini* from the Annascaul Formation in south-west Ireland. This is surprising as the Leinster Terrane of southern Ireland was part of Avalonia (Torsvik & Cocks 2017: p. 51, fig. 3.5), unrelated to North Gondwana. Identical features are, in particular: same length/width ratio, strongly backwardly turned outer anterolateral margin, small lateral pleural area, presence of a marked pseudo-articulating half-ring in front of first axial ring, marked medially interrupted second axial ring, wide (sag.) postaxial pleural field, immediate backward deflection of the pleural ridge adaxially, presence of a small second spine pair on the outer posterolateral margin, scarcity of isolated nodules and the extremely fine and dense granulation of the exoskeleton. Different features in the French species include a slightly more tapering axis, and longer internal spines that are more slender proximally and taper less strongly distally. The possible assignment of the specimen to a new species must await the discovery of more material and in particular sclerites of the cephalon.

Occurrence. – Homogenous dark grey, fine-grained, poorly fossiliferous marlstone on slope above lower track, SE of Roquemaillère hill.

Genus *Eoleonaspis* Sheng, 1974

Type species. – *Acidaspis shanensis* Reed, 1915 from Hirnantian strata of the lower Panghsapye Formation, Myanmar (see Aye Ko Aung & Cocks 2017: p. 322).

Remarks. – Curtis & Lane (1998: pp. 80, 81) provided an emended diagnosis of the genus and gave detailed comparisons between the odontopleurine genera *Eoleonaspis*, *Primaspis* Richter & Richter, 1917 and *Leonaspis* Richter & Richter, 1917 that share nine thoracic segments and the presence of four posterior border spines between the major border spines in the pygidium. They considered that the overall morphological similarities of *Eoleonaspis* and *Primaspis* may indicate direct phyletic relationship. *Primaspis* is now restricted to its Bohemian type species and the allied *P. tremeda* (Barrande, 1852), and as such is exclusively Ordovician after the reassignment of the Silurian species '*P.*' *mackenziensis* Chatterton & Perry, 1983 to the acidaspidine *Anacaenaspis* Bruton, 1967 (Holloway & Sandford 1993), and '*P.*' *mendica* Siveter, 1989 to *Eoleonaspis* (Curtis & Lane 1998). Whittington 1956 considered *Leonaspis* a descendant of *Primaspis* but no representative of *Leonaspis* as that genus is now understood is known prior to the Ludlow leaving a gap of knowledge of intermediate forms between the Late Ordovician and the late Silurian. It is tentative to consider the Late Ordovician–Silurian *Eoleonaspis* as intermediate between *Primaspis* and *Leonaspis* as it has characteristic traits in commun with each of them (Curtis & Lane 1998). However, *Leonaspis* was exclusively Gondwanan since its first appearance in the Ludlow (Ramsköld & Chatterton 1991) in the Bohemian Kopanina Formation (Bruton 1968), and it did not cross mid-European oceanic barriers (Franke *et al.* 2017) prior to the late Early Devonian. (*e.g.* Basse & Müller 2004 for earliest occurrences in the Rheno-Hercynian Zone). By contrast *Eoleonaspis*, though wide-spread in the Latest Ordovician and early Silurian in Gondwanan East Asia, and, on the northern Gondwana margin, in the Ashgill of Bohemia and in the Wenlock of Southern France (herein), was present on the Avalonia–Baltica side of the Rheic Ocean since the Late Ordovician (Ashgill in Scandia, Ashgill and Llandovery in England, Wenlock in Ireland). The origin of Leonaspis remains unexplained; it might speculatively derive from isolated mid-Silurian North Gondwanan populations of *Eoleonaspis*.

***Eoleonaspis maeander* sp. nov.**
Figure 4A–H

1937 *Acidaspis minuta* (?). – Chaubet, p. 204, pl. 7, fig. 15.

Holotype. – Pygidium, UM-IP 1013, Roquemaillère, Montagne Noire, Homerian (Fig. 4D).

Type horizon and locality. – Dark-grey microsparitic limestone, slope below lower track, 300 m SE of Roquemaillère hill-top.

Paratypes. – Cranidia (UM-IP 1014–1017), hypostome (UM-IP 1018), librigena (UM-IP 1019), pygidium (UM-IP 1020).

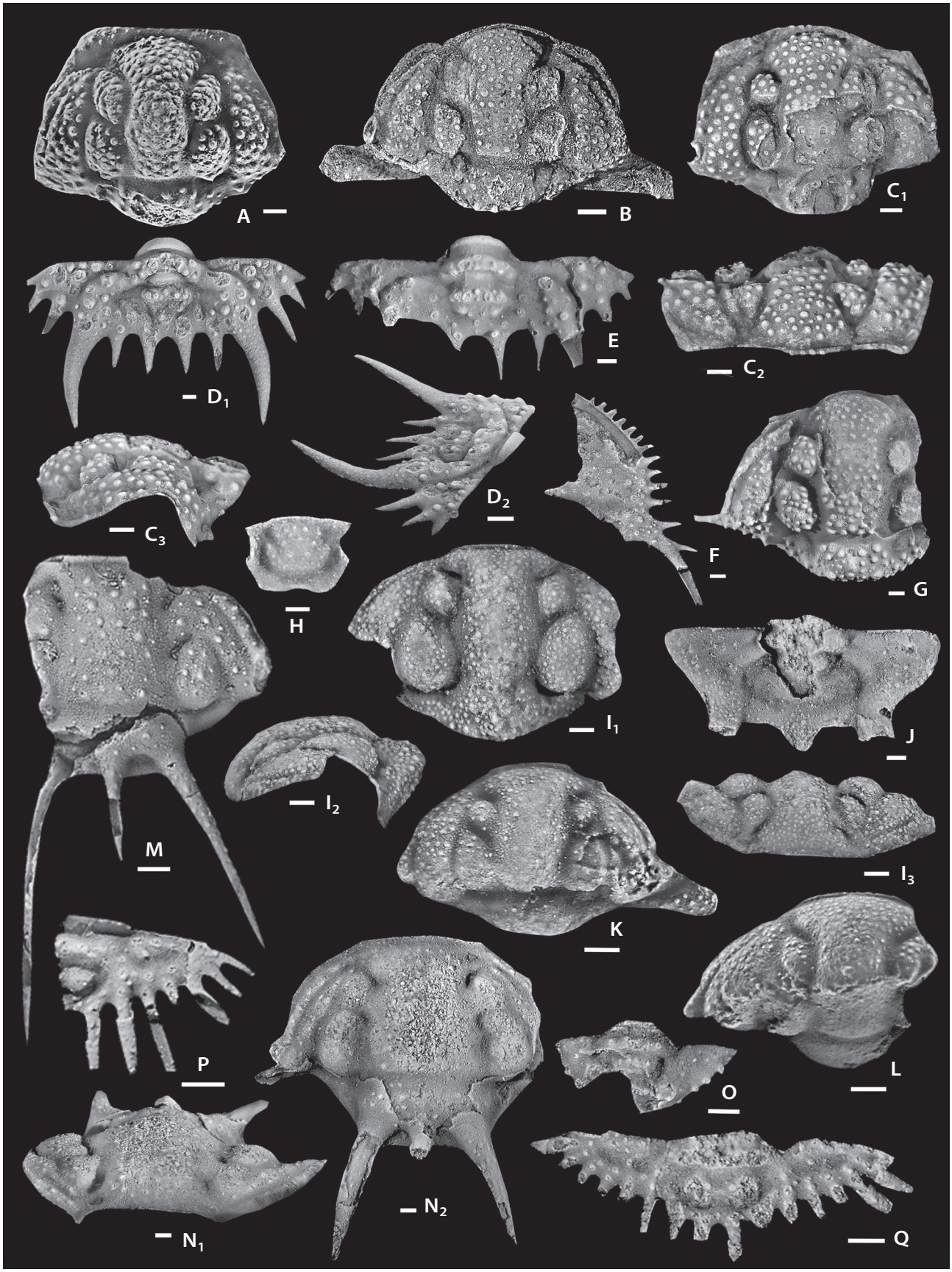
Other material. – Cranidium (UM-IP 1021), pygidium (UM-IP 1022).

Etymology. – *Maeander* (lat.): sinuosity, refers to meandering furrows along median glabellar lobe.

Diagnosis. – Glabella excluding occipital ring as wide as long, with expanding frontal lobe of rounded, protruding outline; median glabellar lobe narrow, defined alongside by undulating longitudinal furrows; inner fixigenae wide, widening posteriorly; eye-lobe small, located opposite posterior third of L1; librigenal spine narrow-based, short; hypostome narrow subrectangular with tubercles on anterior middle body; pygidium a little more than three times wider than long, without borders; two pairs of outer border spines; pleural field convex with pleural ridges. Sculpture: coarse blister-like tubercles.

Description. – Cranidium subtrapezoidal, width across palpebral lobes being markedly wider than length (length/width ratio = 0.72). Glabella narrow parabolic, 0.76 times as wide across L1 lobes as sagittal length, surrounded

Figure 4. Specimens from Roquemaillère, Montagne Noire, S-France, Homerian. • A–H – *Eoleonaspis maeander* sp. nov.; A – cranidium UM-IP 1014; B – cranidium UM-IP 1015, exfoliated; C – cranidium UM-IP 1016, partially exfoliated, dorsal (C_1), anterior (C_2), lateral (C_3) views; D – holotype pygidium UM-IP 1013, dorsal (D_1), oblique anterolateral (D_2) views; E – pygidium UM-IP 1020, latex cast of external mould; F– fragmentary librigena IM-IP 1019; G – fragmentary cranidium UM-IP 1017, partially exfoliated; H – hypostome UM-IP 1018. • I–L – *Laethoprusia augur* sp. nov.; I – cranidium IM-IP 1026, dorsal (I_1), lateral (I_2), anterior (I_3) views; J – holotype pygidium UM-IP 1025; K – cranidium UM-IP 1027; L – cranidium UM-IP 1028. • M–O – *Ceratocephalina angustifurcata* sp. nov.; M – fragmentary cranidium UM-IP 1030; N – holotype cranidium, mostly exfoliated, anterior (N_1), dorsal (N_2) views; O – fragmentary pygidium UM-IP 1031. • P, Q – *Radiaspis* sp.; P – fragmentary pygidium UM-IP 1023, latex cast of external mould; Q – pygidium UM-IP 1024, mostly exfoliated. Scale bars = 2 mm.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by continuously deep, outwardly convex axial furrows. Fronto-median glabellar lobe defined against isolated lateral glabellar lobes by continuously deep, markedly sinuous longitudinal furrows, widest across strongly outwardly projecting frontal lobe, constricted at lateral glabellar lobes, widens between S1, narrowest at base along occipital furrow. Frontal lobe long (sag.), projecting forward, of strongly curved anterior outline, steeply falling anteriorly. Vaulted median lobe is considerably higher than adjacent lateral lobes and fixigenae in frontal view and has a moderately curved longitudinal profile. L1 narrow, a fourth to one-third of glabellar width, suboval, pointed anterolaterally, convex abaxially. L2 oval, slightly inflated, separated from L1 and frontal lobe by straight, deeply impressed, oblique glabellar furrows. L3 barely perceptible behind lateral extensions of frontal lobe (Fig 4B). Preglabellar field being absent, preglabellar furrow coincides with border furrow. Anterior border narrow medially where it is straight or moderately curved in outline, slightly inflated and enlarged abaxially with blunt anterolateral corners. Occipital furrow straight, of moderate width and depth medially, deep behind L1. Length of occipital ring reaches 21% of total glabellar length (sag.). It is convex backward, diminishing considerably in length abaxially (exsag.). Pitted median tubercle is present, posterior spines are absent. Anterior edge of occipital ring notched abaxially to separate small slightly swollen lateral lobes. Fixigenal lobe adaxial to eye is strongly swollen, reaching as far forward as junction of eye ridge and lateral extension of frontal lobe, curving rearwards and attaining 22% of cranidial width at occipital furrow where it is about the same width as L1 (tr.). Eye ridge is moderately distinct, separated from lateral extensions of frontal glabella by thin axial furrow, curving backwards to reach facial suture in front of eye lobe. Anterior branches of facial suture run inward with slight curvature to meet blunt angle of anterior border. Outer triangle of fixigenae narrow, slightly depressed. Palpebral lobe short and tiny, steeply raised, positioned far back opposite posterior third of L1. Posterolateral projections of fixigenae long abaxially (exsag.) with enlarged posterior border and oblique border furrow.

Lateral border of librigena moderately swollen, not broadening posteriorly before meeting much larger posterior border. Lateral margin weekly re-entrant in front of genal spine, in an open angle of 140°. Genal spine slender, narrow-based, gently curved, attaining half-length of cheek from back to front of facial suture. Lateral margin with 13–14 radiating, slender and pointed border spines that remain moderate in length though slightly increasing from front to rear, the last one sited on base of genal spine and slightly posteriorly inclined. Librigenal field moderately vaulted, posterior border furrow wide (exsag.) and shallow.

Hypostome subrectangular, 1.36 times as wide as long, embayed posteriorly, with broadly convex anterior outline. Anterior border is absent. Posterior border wide besides embayed median part, flat, scarcely narrowing around bluntly rounded posterolateral angles, diverging thereafter until pointed shoulder posterior to midlength. Middle body widely subquadrate (length/width ratio = 1.14), moderately convex, surrounded by large border furrows that are deepest posterolaterally and become shallower posteriorly. Anterior lobe narrower than posterior, with slightly convex anterior outline running parallel to hypostomal suture, anterolaterally bounded by blunt angles. Posterior lobe crescentic, inflated anterolaterally, of semicircular posterior outline. Middle furrows straight converging, very wide abaxially, narrowing posteromedially before fading out at a third of way across middle body.

Pygidium transverse, 3.3 to 3.4 times as wide as it is long, of wide-parabolic posterior outline (without spines). Axis attains 29% of total width (tr.), remains at a considerable distance from posterior margin, and is composed of two narrow (sag.) axial rings. The presence of an additional third ring is indicated by a paired node on the terminal piece. First axial ring prominent, slightly curved, narrows medially; remaining axis sunken behind first ring. Second axial ring is straight, of even length transversely, provided with a pseudo-articulating half ring that is 1.5 times as long as second ring medially. Axial furrows moderately deep, with incomplete posterior closure. Pleural ridges backwardly curved, strongly convex, increasing in strength abaxially, most swollen at posterior margin before continuing into curved, stout major border spines. These are upraised, not very long, and take the shape of bull horns. Posterior and posterolateral margins lack border. There are two pairs of stout, inner marginal spines that are straight, conical and of equal length, reaching scarcely one-third of length of major spines. Among the two pairs of outer spines the posterior one is slender and twice as long as the anterior. Outer pleural field is subtriangular, slightly convex.

Surface sculpture consists of isolated, large dome-like nodules of various sizes, pervasive over the whole surface, close together on the cranidium, more spaciously set on librigena and pygidium. They are more widely spaced on the middle body of the hypostome. Additionally, smaller, more densely set nodules occur on genal spines of librigenae and marginal spines of pygidium.

Remarks. – Among the few Silurian representatives of *Eoleonaspis* the new species is closest to the contemporaneous *E. mendica* Siveter, 1989 from the Annascaul Formation, southwestern Ireland. The pygidia are almost identical in general features, besides the shorter internal secondary spines in *maeander.* The hypostomes of both

species are also very similar, and they share the same sculpture restricted to the anterior part of the middle body. They differ in the posterior margin which is embayed in *maeander*. The cranidia are less similar: in *mendica* the eye lobe is situated more anteriorly, and the glabella is considerably wider including the fronto-median lobe, but, significantly, undulating, posteriorly converging longitudinal glabellar furrows are also present in *mendica*. Undulation of the longitudinal furrow occurs to a greater or lesser degree in many odontopleurines such as *Odontopleura* (*Sinespinaspis*) *nehedensis* Chatterton & Perry, 1983 from the Llandovery of the Mackenzie Mountains, Canada, and *O*. (*S*.) *llandoveryana* (Šnajdr, 1975) from the middle Llandovery of Bohemia. It constitutes a common but not exclusive trait of the family as it also occurs in many acidaspidines such as *Exallaspis varbolensis* (Bruton, 1967) from the earliest Llandovery of Estonia and *Anacaenaspis mackenziensis* (Chatterton & Perry, 1983) from the early Llandovery of the Mackenzie Mountains (NW Canada). This character may be regarded as homeomorphic.

Genus *Radiaspis* Richter & Richter, 1917

Type species. – *Arges radiatus* Goldfuss, 1843 from Gees near Gerolstein, Eifel Mountains, Germany (Eifelian).

***Radiaspis* sp.**
Figure 4P–Q

Material. – Pygidia (UM-IP 1023–1024) from Roquemaillère, dark-grey limestone, Homerian.

Remarks. – Two fragmentary pygidia are assigned to *Radiaspis* as they exhibit typical features such as 16 long border spines of similar diameter proximally with the pleural ridge being connected with the 6th border spine from the exterior, and a pair of bulge-like swellings posterior to the first axial ring. The poorly preserved material from Roquemaillière resembles *Radiaspis* aff. *nauseola* of Kříž & Pek (1974) from the Wenlock of Bohemia, sharing in particular the presence of spaced nodules on pleural fields and axial rings as well as on bases of marginal spines.

Subfamily Koneprusiinae Vaněk & Pek, 1987

Genus *Laethoprusia* Ramsköld, 1991

Type species. – *Laethoprusia salax* Ramsköld, 1991, from the Wenlock of Gotland.

***Laethoprusia augur* sp. nov.**
Figure 4I–L

1937 *Acidaspis* sp. − Chaubet, p. 207, pl. 7, fig. 11.
1977 *Koneprusia augur* n. sp. – Feist, unpublished thesis.
1991 *Laethoprusia* sp. of Feist. – Ramsköld, p. 134.

Holotype. – Pygidium, UM-IP 1025 (original of Chaubet 1937, pl. VII, fig. 11), Roquemaillère, Montagne Noire, Homerian (Fig. 4J).

Type horizon and locality. – Dark-grey microsparitic limestone, southern bank of Roquemaillère brook (Chaubet's locality), 300 m S of Roquemaillère hill-top.

Paratypes. – Cranidia (UM-IP 1026–1028).

Etymology. – *Augur* (lat.): prophet, announcing descendant relations.

Diagnosis. – Cranidium with very short anterior border that is curved in outline, slightly sigmoidal longitudinal furrows alongside median glabellar lobe, swollen fixigenae considerably widening from front to rear inside eye ridge. Pygidium transverse trapezoidal, obtusely truncated between anterior and lateral margins, with straight transverse posterior outline between major and median spine, slightly inflated lateral and posterior borders, broad-based short median spine.

Description. – Cranidium semicircular in anterior outline, uniformly convex in longitudinal profile in front of occipital furrow, almost horizontal transversely, slightly down-curved distally. Anterior border curved in outline, extremely narrow, separated from glabella by coinciding preglabellar and anterior border furrows. Glabella trapezoidal, convex (tr. and sag.), as long as wide, widest across middle of L1. Fronto-median glabellar lobe broad (tr.), enlarged in axe shape anteriorly. Longitudinal furrows deep throughout, slightly sigmoidal due to outward curvature between lateral glabella lobes. Axial furrows convex outward, narrower and shallower than longitudinal furrows, Lateral glabellar lobes very strongly inflated, as high as median lobe in frontal view. L1 obliquely ovoid, bluntly pointed anteriorly, slightly narrower than median lobe (tr.), 0.7 times as wide as long, twice as long as L2. L2 subrhomboidal, defined by oblique, straight, very deep S1 and S2 furrows connected to both longitudinal and axial furrows. L3 slightly inflated, merged with lateral expansion of frontal glabella, lacking separation by any clearly defined S3 (Fig. 4I$_1$) Occipital furrow fading medially in larger specimens, being situated further forward than the much deeper lateral part. Occipital ring convex medially, strongly narrowing abaxially, without lateral lobes. Median occipital node inconspicuous. Fixigenae inflated, curving to embrace the glabellar lobes, as wide posteriorly as L1 (tr.), diminishing in width anteriorly from

S1, very narrow in front of L2. Eye ridges unconnected to anterolateral expansion of frontal glabella, thin, of even strength, moderately curving, defined against inner fixigenae by deep furrow. Palpebral lobes tear-shaped, convex, remaining below level of glabella. Posterior border furrow deep, widens considerably as it curves forward abaxially; posterior border distally enlarging (exsag.) and swollen. Cranidial exoskeleton entirely covered with nodules.

Pygidium trapezoidal, with obtuse, rounded anterior angles. Straight anterior border slightly convex (exsag.). Lateral and posterior contour excluding spines widely parabolic, slightly truncated behind. Posterolateral borders broad, swollen and rounded at edge. Axis conical, defined by deep, straight axial furrows, as wide across first ring as pleural area, bearing 2+1 axial rings. Anterior axial rings convex, defined by straight, deep inter-ring furrows. Pleural ridge narrower (exsag.) than first axial ring, directed posterolaterally from first ring and flexed more strongly backwards as it approaches base of paired border spines, slightly swollen, poorly defined against lateral pleural field by very shallow furrow that fades posteriorly. Pleural ridges merge with much wider bases of major border spines that are flush with lateral borders and considerably elevated against posterior border. Major border spines stout, upraised, divergent. Postaxial pleural area between pleural ridges and posterior border sunken, elliptical in outline, slightly vaulted, surrounded by deep and broad furrows. No fenestral structures are present in depressed areas adjacent to inner edges of pleural ridges, as occur in the type species. Posterior border gently curved (tr.), projecting medially into a broad-based, short, conical spine. Posterior edges between major border spines and median spine straight, parallel to anterior margin. Lateral border without secondary border spines. Pygidial exoskeleton bears a few isolated nodules on lateral pleural fields, increasing in number on axial rings, posterolateral borders and spines; postaxial pleural field smooth.

Remarks. – The pygidium from Roquemaillère was first described and figured by Chaubet (1937: p. 207) under the name *Acidaspis* sp. Subsequently, the specimen, in association with three cranidia from the same locality, was considered to constitute a new koneprusiine taxon by Feist (1977) who named it '*Koneprusia augur*' but this name remained hitherto unpublished and thus a *nomen nudum*. Ramsköld (1991: p. 134) assigned it to his new genus *Laethoprusia*, as '*Laethoprusia* sp. of Feist'.

As noted by Ramsköld (1991, p. 138), *L. augur* is closer to *L. brikelos* (Chatterton *et al.*, 1979) from the Lower Devonian of New South Wales than to the contemporaneous type species *L. salax* from Gotland. In particular, it shares with *brikelos* the relatively broad median glabellar lobe and the proportions of the glabella (length/width ratio = 0.89 in *brikelos* versus 0.95 in *augur*). This ratio is much higher in the type species (1.25) as well as in the Lochkovian species *L. graffhami* Adrain *et al.*, 2008 from the Bois d'Arc Formation, Coal County, Oklahoma and in *L. cozarti* Adrain *et al.*, 2008 from the Ross Formation, Benton County, Tennessee (1.04 and 1.17 respectively). The markedly enlarged posterior fixigenae, as wide as L1 in the new species, contrast significantly with both *brikelos* and *salax* where these are narrower. Similarly broad interocular fixigenae are present in silicified material from the Cape Phillips Formation (Sheinwoodian), northwestern Cornwallis Island, Arctic Canada, representing an unnamed new species of *Laethoprusia* ('*Laethoprusia* n. sp. A' of Adrain *et al.* 2008). This feature is also present in the odontopleurid cranidium figured by Chatterton & Perry (1983: pl. 29, fig. 17 and in additional material from the upper Wenlock of the Delorme Range, Mackenzie Mountains, Canada, assigned to '*Laethoprusia* n. sp. A?' by Adrain *et al*. (2008). Whereas in the Laurentian taxa, as well as in *salax* and *brikelos*, the longitudinal furrows alongside the median glabellar lobe are straight and parallel (or divergent posteriorly in *graffhami*), these furrows are sigmoidal in *L. augur* due to slight outward curvature between L1 and L2.

In contrast to the other taxa assigned to *Laethoprusia* the pygidium of *augur* is wider transversely (length/width index = 0.36) and has a straight posterior margin adjacent to the median spine. The border spines are similar in shape as in the type species whereas they are slender in the other species. The most significant feature is the absence of fenestrae in *augur*, a feature that characterises the type species and the Laurentian species. It is generally absent in *brikelos* but was said by Ramsköld (1991: p. 137) to be present in just one of the pygidia illustrated by Chatterton *et al.* (1979: pl. 111, fig. 14). Unfortunately, only a single pygidium of *augur*, the holotype, has been recovered and the possible presence of fenestrae within a virtual population cannot be tested.

Subfamily Selenopeltinae Hawle & Corda, 1847

Genus *Ceratocephalina* Whittington, 1956

Type species. – *Ceratocephala* (*Ceratocephalina*) *tridens* Whittington, 1956 from the Upper Ordovician Edinburg Limestone, northern Virginia.

***Ceratocephalina angustifurcata* sp. nov.**
Figure 4M–O

1937 *Acidaspis* aff. *tricornis.* − Chaubet, p. 204, pl. 7, fig. 14.

1977 *Ceratocephalina* aff. *tricornis*. – Feist, unpublished thesis.

Holotype. – Cranidium, UM-IP 1029 (original of Chaubet 1937, pl. 7, fig. 14), Roquemaillère, Montagne Noire, Homerian (Fig. 4N).

Type horizon and locality. – Loose dark-grey microsparitic ostracod-rich limestone, slope below lower track, 250 m SE of Roquemaillère hill.

Paratypes. – Cranidium (UM-IP 1030), pygidium (UM-IP 1031).

Etymology. – *Angustus* (lat.) = *narrow*, *furcatus* (lat.) = forked, concerning the major occipital spines.

Diagnosis. – Cranidium subhexagonal in outline, about 1.6 times as wide across posterior border as long (sag., excluding median occipital spine), median glabellar lobe almost as wide posteriorly as median part of occipital ring, major occipital spine pair moderately divergent; pygidium wider than long, triangular with axis markedly wider than pleural field.

Description. – Cranidium weakly convex (sag. and tr.), hexagonal in outline, length = 0.6 of width across posterior border. Glabella lowly vaulted transversely, moderately convex in longitudinal profile, with occipital ring remaining below posterior part of median lobe, and frontal lobe slightly sloping down to narrow anterior border. Glabella in front of occipital ring trapezoidal, widest across middle of L1, 1.6 times wider than long, tapers forward to two-thirds of maximum width at frontal lobe, with shallow axial furrows subtending an angle of 60°. Axial furrows gently curving around L1 and L2, more strongly impressed in posterior half than anteriorly. Fronto-median glabellar lobe tapering forwards before slight lateral expansion of frontal lobe. Three pairs of lateral glabellar lobes, L1 and L2 being moderately inflated. L1 are sub-oval with long axis almost parallel to sagittal line, steeply sloping downward posteriorly. L2 about half size of L1, well defined by straight, oblique S1 and S2. L3 is a short (exsag), somewhat depressed transverse swelling separated from frontal lobe by small, groove-like S3 (Fig 4M, left side; Fig $4N_2$, right side). Eye ridge is prominent, bordered adaxially by deep eye ridge furrow, in uniform curvature from lateral expansion of frontal lobe to palpebral lobe. The latter is positioned opposite the posterior half of L1. Inner fixed cheek moderately curving, slightly convex, narrow, scarcely widening posteriorly. Anterior branch of facial suture runs almost parallel to eye ridge, leaving a very narrow strip of outer fixigena. Occipital furrow long (sag.) and shallow medially, considerably deepening behind L1. Occipital ring half as long as remainder of glabella, composed of a prominent median part and peripheral, sunken, abaxial and posterior parts. Raised, convex median portion of occipital ring slightly wider than base of pre-occipital median glabellar lobe, projecting behind into three slightly downwardly curving occipital spines. Paired major spines diverge at 40°, remain almost straight, and are long and slender in the smaller cranidium, shorter and stout in the larger holotype. Median spine reaches about one-third length of paired spines. Besides the lower, flat posterior and lateral parts of the occipital ring that remain smooth, the entire cranidial exoskeleton is randomly covered with spaced tubercles that become larger on median glabellar lobe and finer on occipital spines.

Pygidium subtriangular in outline, two and a half times as wide as long, with convex axis considerably wider than pleural field (4:3), defined by straight backwardly converging axial furrows, composed of two narrow convex rings and faint end piece, separated by deep inter-ring furrows. Pleural ridge faint, ending in base of upraised major spines situated inside the posterior border. Pleural field triangular, flat, with slightly curved lateral edge carrying at least five secondary border spines. Axial rings sculptured with a row of medium-sized nodules, pleural fields with a few isolated smaller nodules.

Remarks. – As Chaubet (1937) noted, there are only minor differences between the Roquemaillere material and *C. tricornis* (Barrande, 1846) from Bohemia. In the specimens from Languedoc, the cranidium is relatively longer; the median occipital lobe is broader than the width of the median glabellar lobe; the major occipital spines diverge to a markedly lesser degree (40° *versus* 70°); the palpebral lobe is set a little forward, opposite the posterior half of L1; and the lateral glabellar lobes are clearly separated by deep S1. The tuberculation of the median glabellar lobe resembles *tricornis* in size and distribution. The pygidium is narrower with a relatively wider axis carrying rows of tubercles on the axial rings, whereas in the Bohemian species there are only two median tubercles present. *Ceratocephalina tokina* Šnajdr, 1988 (see Bruton 1968: pl. 9, figs 4, 9) and *C. komura* Šnajdr, 1988 (his pl. 2, figs 1, 2) are both closely related to *tricornis* in the shape and divergence of the occipital major spines, but are distinguished from *angustifurcata* by their rather coarse tubercles on the cephalon. Outside Bohemia, Silurian representatives of *Ceratocephalina* were described by Chatterton & Perry (1983) from the Wenlock Delorme Formation, Mackenzie Mountains, north-western Canada. In both of their *C. sevastopuloi* and *C. charlesworthi* the cranidia are shorter, the median part of the occipital furrow situated further forward in relation to L1, the occipital major spines more divergent, and the pygidia more transverse than in *angustifurcata*.

Discussion

The Roquemaillère odontopleurid fauna is characterised by a great variety of taxa (5 genera with 9 species) and as such is representative of the North Gondwana margin along with Bohemia and the Carnic Alps. Generally represented by merely a few dissociated sclerites, the associations are by far dominated, both in number of specimens and specific variation, by *Kettneraspis* whereas, unlike Bohemia and the Carnic Alps, *Diacanthaspis* and *Odontopleura* are absent. Additionally, the closely related *Leonaspis* which is exclusively reported from Gondwana (Ramsköld & Chatterton 1991) has not been found at Roquemaillère. As this taxon has its earliest occurrence in the Ludlow, its absence may constitute an argument for a pre-Ludlow age of the fauna. At generic level all taxa from Roquemaillère occur in Bohemia but both regions do not share any taxon at specific level. There are closer relations to the Carnic Alps and to western Ireland with probably one species in common with each of these regions.

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