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Biodiversity, distribution and patterns of extinction of the last odontopleuroid trilobites during the Devonian (Givetian, Frasnian)

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Abstract – Biostratigraphical ranges and palaeogeographical distribution of mid-Givetian to end-Frasnian odontopleurids are investigated. The discovery of *Leonaspis rhenohercynica* sp. nov. in mid-Givetian strata extends this genus unexpectedly up to the late Middle Devonian. New material of *Radiaspis radiata* (Goldfuss, 1843) and the first koneprusiine in Britain, *Koneprusia*? sp., are described from the famous Lummaton shell-bed, Torquay, Devon. New taxa of *Koneprusia*, *K. serrensis*, *K. aboussalamae*, *K. brevispina*, and *K.* sp. A and *K.* sp. B are defined. *Ceratocephala* (*Leonaspis*) *harborti* Richter & Richter, 1926, is revised and reassigned to *Gondwanaspis* Feist, 2002. Two new species of *Gondwanaspis*, *G. dracula* and *G. spinosa*, plus three others left in open nomenclature, are described from the late Frasnian of Western Australia. A further species of *Gondwanaspis, G. prisca*, is described from the early Frasnian of Montagne Noire. Species of *Gondwanaspis* are shown to possess a number of paedomorphic features. A functional analysis suggests that, unlike other odontopleurids, *Gondwanaspis* actively fed and rested with the same cephalic orientation. The sole odontopleurid survivors of the severe terminal mid-Givetian biocrisis ('Taghanic Event') belong to the koneprusiine *Koneprusia* in the late Givetian and Frasnian, and, of cryptogenic origin, the acidaspidine *Gondwanaspis* in the Frasnian. Whereas the former became extinct in the late Frasnian at the Lower Kellwasser Event, the latter disappeared, and with it the entire Odontopleuroidea, at the terminal Frasnian Upper Kellwasser global biocrisis.

Keywords: trilobites, Odontopleuridae, Devonian, biodiversity, extinction.

1. Introduction

The long-lived odontopleuroids were most diversified and widespread during the Silurian but declined thereafter in Devonian times. According to the annotated species lists provided by Ramsköld (1991) and Ramsköld & Chatterton (1991), updated by Basse (1998) and Basse & Müller (2004), only two genera of Odontopleurinae, *Kettneraspis* and *Radiaspis*, and two genera of Koneprusiinae, *Koneprusia* and *Isoprusia*, persisted during the Middle Devonian and were thought to disappear prior to the late Givetian Taghanic Event. Surviving lineages from these Middle Devonian taxa were hitherto unknown both in the late Givetian and early Frasnian. However, rare occurrences of a single odontopleurid species (originally described as *Ceratocephala (Leonaspis) harborti* Richter & Richter, 1926) in the Frasnian have long been known (Harbort, 1903; Richter & Richter, 1926). After recent discoveries of an acidaspidine, *Gondwanaspis*, from below the base of the Upper Kellwasser level (terminal Frasnian), it has become clear that the Odontopleuroidea persisted to the terminal Frasnian Extinction Event, at which point they vanished together with the Corynexochina (McNamara & Feist, 2006), Harpetina and Dalmanitoidea (Feist, 1991). However, our knowledge of these last occurrences of odontopleuroids was restricted to just two incompletely documented species. Recently discovered material from the Canning Basin (NW Australia), Rhenish Slate Mountains (Germany), Tafilalet (SE Morocco) and Montagne Noire (Southern France) enhances considerably our knowledge of the diversity, palaeogeographical distribution and morphological features of the last representatives of the superfamily, from Givetian through Frasnian times. Biostratigraphical correlation of their occurrences with fine-scaled conodont-based biozonations (Feist & Klapper, 1985; Klapper, 1988) enable us to assess how the three major extinction events in the later Devonian, namely the Taghanic, Lower Kellwasser and Upper Kellwasser events, affected the demise of the Odontopleuroidea.

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2. Stratigraphical distribution and palaeogeography

Among odontopleurine taxa present in the middle *varcus* Zone prior to the late Givetian Taghanic extinction events, the long-ranging *Radiaspis* group (including *Charybdaspis* Basse, 1998) is geographically distributed in reefal and peri-reefal biofacies developed in the Torquay area, SW England (Lummaton Shell Bed:

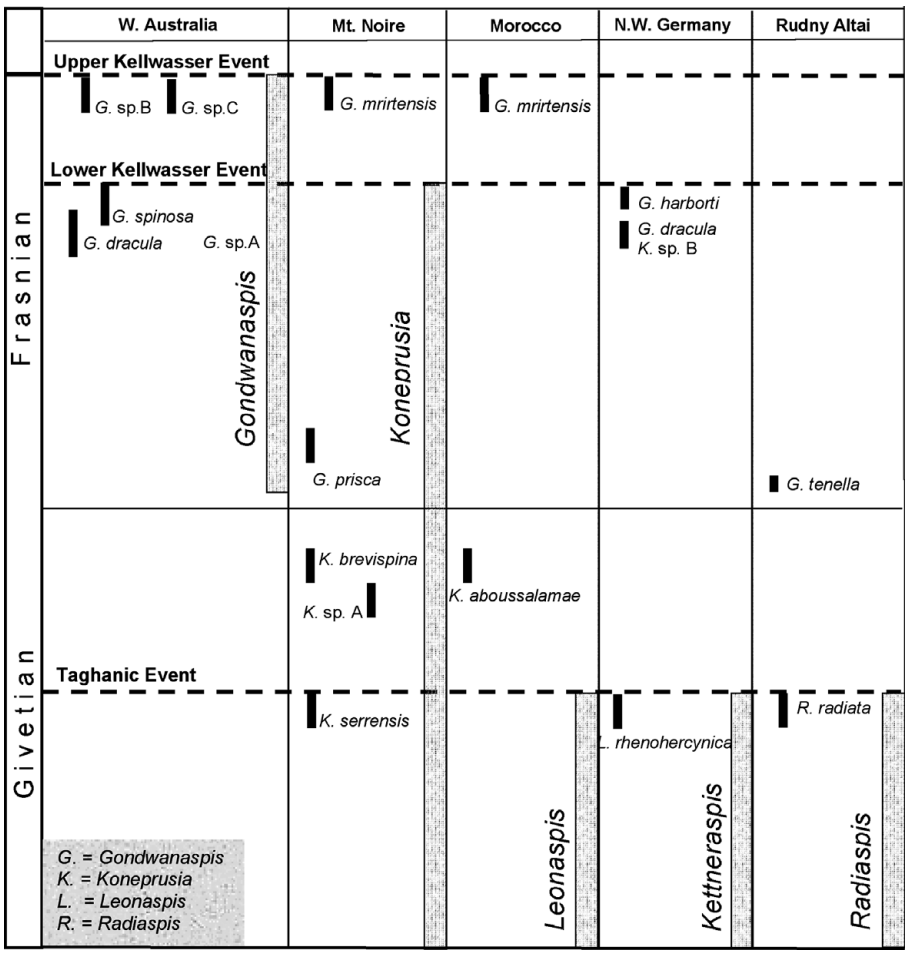

Figure 1. Stratigraphical distribution of the odontopleurids *Gondwanaspis, Koneprusia, Leonaspis, Kettneraspis,* and *Radiaspis* during the Givetian and Frasnian in Western Australia, France (Montagne Noire), Morocco, Germany, Siberia (Rudny Altai) and England (Devon), showing the influence of the Taghanic, and Upper and Lower Kellwasser Events on extinction patterns. Species ranges in geographical provinces. Generic ranges not geographically configured.

Whidborne, 1889), and at Djebel Ziata, NW of Rissani (SE Morocco: Feist & Orth, 2000); it occurs also in various lower Givetian localities in the Rhenish Slate Mountains, some of which might extend into the middle *varcus* Zone (Basse, 1998; Basse & Müller, 2004). Richter & Richter (1926, p. 110) mention its occurrence in dark 'Flinzkalk' from Vollmühle, Mettmannbachtal near Wuppertal (Germany), which was considered mid-Frasnian at that time. As this late Devonian occurrence has not been confirmed since, either by new finds or updated biostratigraphy, we suspect that the age given to this isolated occurrence might be erroneous. Hence we consider that the *Radiaspis* group became extinct at the Taghanic Event. *Kettneraspis* is still present with eight defined species in the Eifelian, where it is widely distributed in the Rhenish and Thuringian Slate Mountains, Harz, Bohemia, Turkey, SE Morocco, southern China and Gorny Altai (see annotated species list in Ramsköld & Chatterton, 1991). By contrast, it is absent in the Middle Devonian, both in the Americas and Australia. Unnamed species of *Kettneraspis* occur in the early Givetian in the eastern Rhenish Slate Mountains (Basse, 1998), and a hypostome assigned to *Kettneraspis* by Basse (1998, p. 92) has been recovered from the middle Givetian *Massenkalk* at Garbeck, northern Rhenish Slate Mountains. The closely related *Leonaspis* was hitherto known no later than the terminal Emsian. We report here on the first occurrence of *Leonaspis* in the middle Givetian, thus unexpectedly extending its range at least as far as that of *Kettneraspis*. Both genera probably became extinct simultaneously, being victims of the Taghanic Event (Fig. 1).

Whereas *Kettneraspis* demonstrably had a world-wide distribution, *Leonaspis* was considered by Ramsköld & Chatterton (1991) to be restricted to the north Gondwana margin and as such never crossed the mid-European (Rheic) oceanic barrier. However, *Leonaspis* species are present from the late Emsian onwards in the Rhenish Slate Mountains (Basse & Müller, 2004), that is, in the Eifel and Eastern Sauerland regions in particular, which are undoubtedly of Avalonian origin (Franke, 1999). Contemporaneously with *Leonaspis* the typical Gondwanan scutelluid *Paralejurus* succeeded in crossing the mid-European

oceanic barriers in late Emsian times (Schraut & Feist, 2004). These cases of dynamic palaeobiogeography reflect the effective approach of European continental margins at the end of Early Devonian times.

The Koneprusiinae are represented by ten taxa: eight in the Eifelian and two in the early and middle Givetian (Ramsköld, 1991; Feist, 1999, and herein; Basse & Müller, 2004). Among them only three species can be assigned with certainty to *Koneprusia* and three others to *Isoprusia*; from the remaining taxa, pygidia are not known, consequently their generic attribution cannot be made with any confidence. As stated by Ramsköld (1991, p. 132), koneprusiines are widely distributed in European/North African Middle Devonian sites. In addition to Ramsköld's data, *Isoprusia* occurs in the early Eifelian at Wolayer See, Carnic Alps, Austria (Feist, 1999), and the discovery of a fragmentary koneprusiine cranidium in the mid-Givetian of Lummerton Quarry near Torquay (described herein) is the first documentation of the subfamily in England. Elsewhere it remains poorly known: mid-Devonian? of Turkestan (Weber, 1932) and early Givetian of Pokrovskoje, eastern slope of Central Urals (Feist, unpub. data; Feist *et al.* 1997); or absent: Americas, Australia, SE Asia. The previously published data on the ranges of koneprusiine species indicate that this subfamily disappeared prior to the Taghanic Event. However, *Koneprusia* sp. was recently reported from the post-Taghanic Late Givetian *disparilis* Zone at Ras el Kebbar, western vicinity of Erfoud, SE Morocco (Aboussalam, 2003). This taxon, together with three others from the late Givetian of the Montagne Noire and one from the middle Frasnian at Sessacker locality, Rhenish Slate Mountains, are all assigned to *Koneprusia*. These discoveries considerably extend the range of the subfamily, such that it is now likely to have become extinct at the base of the terminal Frasnian Kellwasser Extinction, some 12 million years later than previously thought (Fig. 1).

The Acidaspidinae are represented in the Frasnian by forms assigned by us to *Gondwanaspis* Feist, 2002. This taxon has previously only been reported by its type species *G. mrirtensis* from Morocco and a closely related form from southern France. Including '*Ceratocephala* (*Leonaspis*)' *harborti* Richter & Richter, 1926, together with several newly discovered species, the extended range of *Gondwanaspis* now nearly covers the entire Frasnian. It is a cosmopolitan taxon that is known from the Avalonian margin of the Old Red landmass (Rhenish Slate Mountains and Harz, Germany), Kasakhstania (Rudny Altai), NW Gondwana margin (southern France and Morocco) and NE Gondwana (NW Australia) (Fig. 2). As the youngest representative of the Odontopleuridae, its last occurrence is in the terminal Frasnian *linguiformis* Zone (Zone 13b: Girard, Klapper & Feist, 2005) at Mrirt (Morocco) and in the Canning Basin (Western Australia).

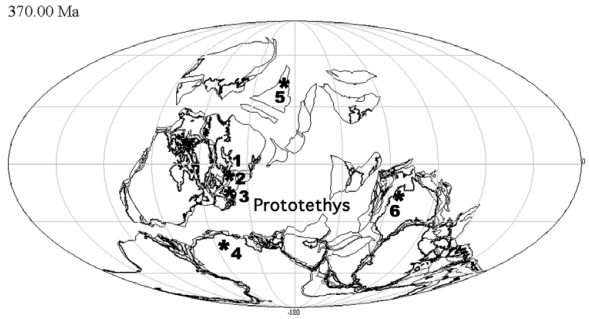

Figure 2. Palaeogeographical distribution of species of *Gondwanaspis* around the Prototethys Ocean during the Late Devonian. Avalonian margin: 1 – Harz Mountains, Germany; 2 – Rhenish Slate Mountains, Germany; Northwestern Gondwana margin: 3 – Montagne Noire, France; 4 – Central Meseta, Morocco; Kasakhstanian plate: 5 – Rudny Altai, Russia; Northeastern Gondwana: 6 – Lawford Range, Western Australia. Map courtesy of Dr A. Smith, University of Cambridge.

3. Systematic palaeontology

Figured and additional material investigated in this study have the following repositories: GZG IN – Collections of the Geowissenschaftliches Zentrum, University Göttingen, Germany; MB – Humboldt Museum für Naturkunde, Berlin; NHM – Natural History Museum, London; NMV – Museum Victoria, Melbourne; SM – Sedgwick Museum, Cambridge; SMF – Forschungsinstitut Senckenberg, Frankfurt; UMC-IP – Collections of the University Montpellier, France, Invertebrate Palaeontology; WAM – Western Australian Museum, Perth

Family ODONTOPLEURIDAE Burmeister, 1843
Subfamily ODONTOPLEURINAE Burmeister, 1843
Genus *Radiaspis* Richter & Richter, 1917 (including *Charybdaspis* Basse, 1998)

Type species. *Arges radiatus* Goldfuss, 1843.

Radiaspis radiata (Goldfuss, 1843)
Figure 3w

Synonymy. See Basse & Müller, 2004, p. 128.

Material. One pygidium, NHM It 27820.

Locality and age. Lummaton Quarry, Torquay (Devon, England), Middle *varcus* Zone, middle Givetian.

Diagnosis. See Bruton, 1968, p. 37.

Remarks. The occurrence of odontopleurid remains in the Lummaton Shell Bed was first documented by Whidborne (1889), based on fragments of a single cephalon and a pygidium assigned to *Acidaspis robertsii* and *Acidaspis pilata*, respectively. These were later synonymized with *Radiaspis radiata* by Bruton (1966). The new pygidium collected by B. Selwood (Exeter) is much better preserved than Whidborne's original (SM H 4080–1) and allows a more comprehensive appraisal of the taxonomic status of the Lummaton form. The overall shape, in particular the large, protruding hemispherical swellings of the second rachial ring and the straight, radially outstreched border spines that curve adaxially at their extreme distal ends are identical to *R. radiata*. However, in contrast to the type species from the

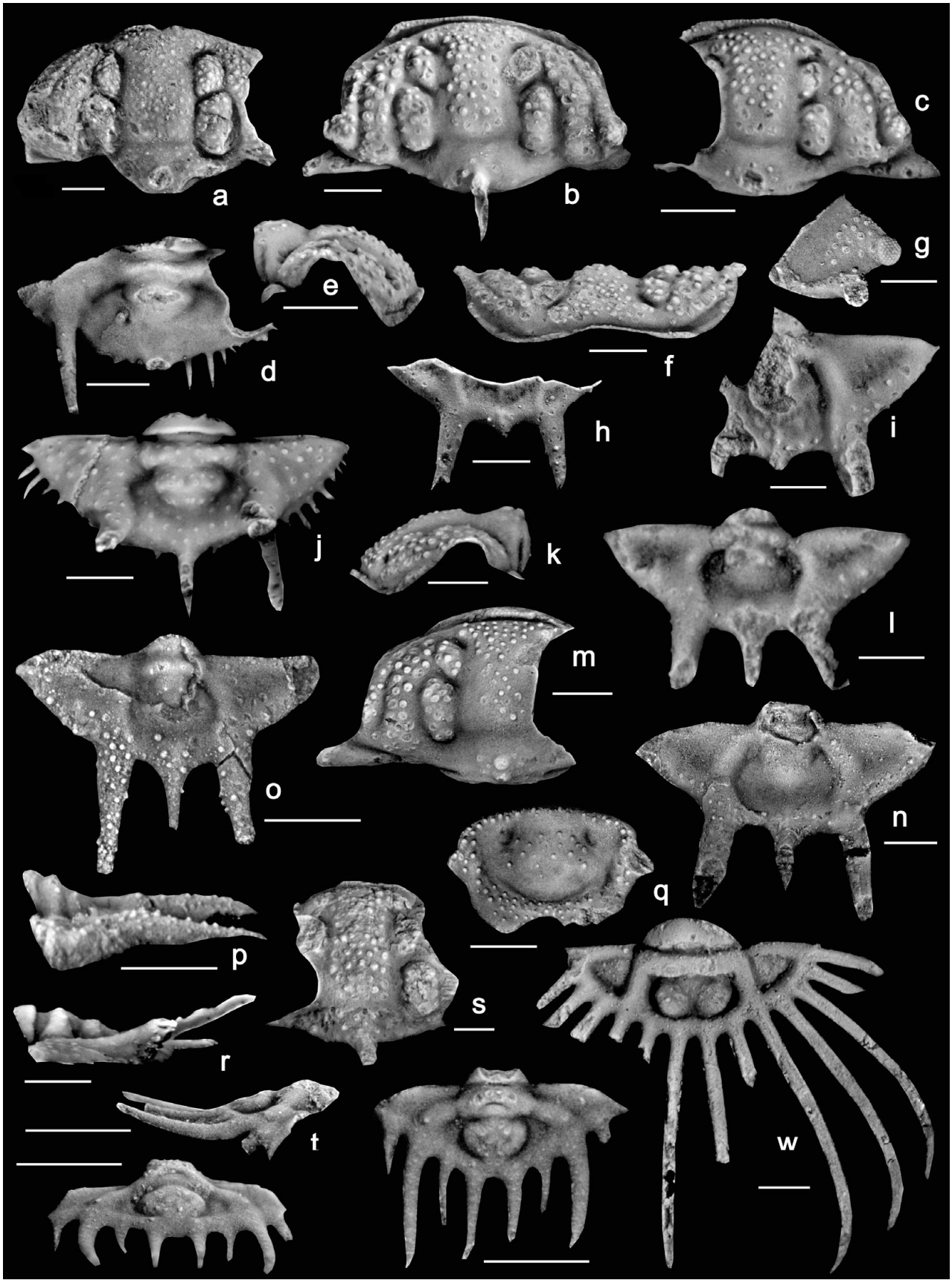

Figure 3. Scale bar = 1 mm. (a, d, j, r) *Koneprusia serrensis* sp. nov., Givetian, Middle *varcus* Zone, La Serre Hill, Cabrières, Montagne Noire, France; (a) UMC-IP 650, cranidium, dorsal view; (d) UMC-IP 652, incomplete pygidium, dorsal view; (j, r) UMC-IP 649, holotype, pygidium, dorsal and lateral views. (c, e, h, i, q) *Koneprusia brevispina* sp. nov., late Givetian, Upper *disparilis* Zone, Mont

Eifelian of the Eifel region, the Lummaton specimen exhibits only 14 border spines instead of 16. Until the ontogenetic development of *radiata* is elucidated we cannot decide whether the reduced number of border spines is a generically fixed character state that would confirm the independent status of *Charybdaspis* Basse, 1998, or whether the number is variable within the same population of *Radiaspis*.

Genus *Leonaspis* Richter & Richter, 1917

Type species. *Odontopleura leonhardi* Barrande, 1846.

Leonaspis rhenohercynica sp. nov.
Figure 3t–v

Material. Holotype, pygidium SMF 76832.

Type locality and horizon. Western border of open quarry on the western flank of Burgberg, within Lethmathe township, northern Rhenish Slate Mountains, Germany. Black *Flinzkalk* at 20 m above *Massenkalk*, associated with *Stringocephalus* and *Scutellum pustulatum* Archinal, 1994; middle Givetian (Basse & Lemke, 1996, p. 8).

Etymology. From Latin *rhenohercynicus* referring to the Rheno-Hercynian region.

Diagnosis. Pygidium long, triangular with a single pair of anterior border spines; rachis with long first ring and ovoid, depressed posterior part composed of second ring, partially fused with end piece; short pleural ridge, not prolonged on to border; closely spaced, slender border spines disposed parallel to axis.

Description. Pygidium considerably less than three times as wide (tr.) as long (sag.) (width/length index without border spines 2.6/1). Adaxial two-thirds of anterior border straight, flexed backwards and downwards abaxially, thickened at fulcrum. Maximum width of rachis attains that of pleural area. First axial ring long (sag.) and modestly elevated. Second axial ring low, poorly defined as it is abaxially fused to remaining terminal piece of rachis with which it forms a depressed ovoid structure of semicircular posterior outline. Axial furrow poorly defined alongside first axial ring but sharply incised and deep around posterior part of rachis, dying out adaxially leaving a broad, axial bridge between this and slightly swollen posterior margin. Crescent-shaped interannular lobes conspicuously impressed on posterior axial regions of both first and second ring. Pleural area relatively narrow, subdivided by short and broad swollen pleural ridge that turns backward with only slight curvature from beside posterior half of first rachial ring; it suddenly diminishes in height before reaching slightly swollen lateral margin from which it remains separated by an inconspicuous marginal furrow formed by the break in slope. Anterior pleural field adaxially as long as pleural ridge (exsag.); ramp-like, inclined backwards from elevated anterior border, without obvious internal structures. Posterior pleural field deeply depressed between pleural ridge and axial furrow, displaying an inconspicuously elevated thin pleural ridge. Lateral and posterior borders remain on same level along margin. Border spines long and slender, narrow at bases, closely spaced and equidistant to each other, not divergent and oriented parallel to axis immediately at their bases; slightly upwardly curved in lateral view. Single anterior border spine shorter than all others. Major border spine opposite to pleural ridge but not connected to it across the border. Paired nodules displayed on first and second axial ring as well as on the distant ends of pleural ridge. Spaced tubercles displayed on terminal piece of rachis, border and border spines. Pleural area smooth.

Remarks. The hitherto youngest known species of *Leonaspis* that possess a single pair of anterior border spines are widely distributed in the Late Emsian. All of them display a much larger and shorter pygidium with a narrower, ridge-like first axial ring. The following species, though similar to the Givetian taxon from Germany, display additional distinct, characteristic traits: *Leonaspis belisarius* Haas, 1968, from Bithynia, Turkey, has a longer and distally backwards curved pleural ridge that runs onto the border, a shorter posterior part of the rachis, and border spines with thicker bases. *Leonaspis brittanica* Morzadec, 1969, from Brittany, has a rachis with a transverse posterior outline and a longer pleural ridge that crosses the border. *Leonaspis issoumourensis* Alberti, 1970, from Maïder, SE Morocco, displays pronounced anterior border ridges and a largely reduced anterior pleural field. In *Leonaspis maura* Alberti, 1969, from the Moroccan Meseta, the border spines are divergent and much thicker at their bases. *Leonaspis heisdorfensis* Basse, 2004 (*in* Basse & Müller, 2004) from the Eifel Hills, Germany, has a strong anterior border ridge, a much shorter posterior part of the rachis, and divergent, thicker border spines. In *Leonaspis kleini* Basse, 2004 (*in* Basse & Müller, 2004), the pleural ridge is narrower and sharply delimited behind, the posterior rachis is not depressed and the border spines are much larger at their base.

Taking into account the particular traits that distinguish the Givetian taxon from all other species of *Leonaspis* and its much younger age, we consider that its attribution to a new species is justified, despite the fact that only a single pygidium is known. Its diagnosis must be completed when more material of the exoskeleton is discovered.

Peyroux, Causses-et-Veyran, Montagne Noire, France; (c, e) UMC-IP 547, cranidium, dorsal and lateral views; (h) UMC-IP 549, fragmentary pygidium, dorsal view showing posterior border and border spines; (i) UMC-IP 546, holotype, incomplete pygidium, dorsal view; (q) UMC-IP 548, hypostome, dorsal view. (b, f, g) *Koneprusia brevispina* sp. nov., late Givetian, Upper *disparilis* Zone, Pic de Bissous, Cabrières, Montagne Noire, France; (b, f) UMC-IP 550, cranidium, dorsal and anterior views, (g) UMC-IP 551, incomplete librigena, dorsal view. (k, m, n) *Koneprusia aboussalamae* sp. nov., late Givetian, Upper *disparilis* Zone, Ras el Kebber Hill, Jorf near Erfoud, SE Morocco; (k, m) MB.T. 4572, cranidium, lateral and dorsal views; (n) MB.T. 4571, holotype, pygidium, dorsal view. (l) *Koneprusia* sp. A, late Givetian, Lower *disparilis* Zone, Col du Puech de la Suque, St Nazaire-de-Ladarez, Montagne Noire, France, UMC-IP 545, pygidium, dorsal view. (o, p) *Koneprusia* sp. B, late Frasnian, Zone 12, Sessacker, Oberscheld, Rhenish Slate Mountains, Germany, SMF 76833, pygidium, dorsal and lateral views. (s) *Koneprusia*? sp., Givetian, Middle *varcus* Zone, Lummaton Quarry, Torquay, England, NHM It 27821, fragmentary cranidium, dorsal view. (t–v) *Leonaspis rhenohercynica* sp. nov., middle Givetian, *Stringocephalus*-bearing Flinzkalk, Lethmate, Rhenish Slate Mountains, Germany, SMF 76832, holotype, lateral, posterior and dorsal views. (w) *Radiaspis radiata* (Goldfuss, 1843), Givetian, Middle *varcus* Zone, Lummaton Quarry, Torquay, England, NHM It 27820, pygidium, dorsal view.

Subfamily KONEPRUSIINAE Vaněk & Pek, 1987
Genus *Koneprusia* Prantl & Přibyl, 1949

Type species. *Acidaspis fuscina* Novák, 1883.

Remarks. Cephalic features remain poorly differentiated in koneprusiines, and it is difficult, if not impossible, to confidently assign isolated cephala to any of its genera. However, this is not the case with pygidial features; therefore pygidia are generally chosen as holotypes for koneprusiine taxa. The pygidium of the latest, post-Taghanic taxa share with *Koneprusia* the depressed anterior and posterior pleural fields, and the presence of three major border spines, whereas *Isoprusia* possesses only two major border spines and has a homogeneously, gently vaulted entire pleural region (besides pleural ridges) (Bruton, 1966). We suggest, therefore, that the post-Taghanic new koneprusiine taxa presented here should be assigned to *Koneprusia* rather than to *Isoprusia*. The only feature that they share with *Isoprusia* is the rather narrow and shorter axis with fewer rings. This might result from homeomorphic adaptation to fine-grained substrate conditions in quiet environments and not from any direct phylogenetic relationship.

Koneprusia serrensis sp. nov.
Figure 3a, d, j, r

1977 *Koneprusia angustifrons* n. sp.; Feist, unpub. thesis, p. 144, pl. 9, figs 8, 9.
1991 *Koneprusia* vel *Isoprusia* n. sp.; Ramsköld, p. 132.

Material. Holotype, pygidium UMC-IP 649 (Fig. 3j, r); two cranidia UMC-IP 650 (Fig. 3a), UMC-IP 651; one pygidium UMC-IP 652 (Fig. 3d), from type locality and horizon.

Type locality and horizon. Westernmost summit of La Serre Hill, 2.5 km south of Cabrières, Hérault, southern France. Coquina limestone: '*Rhynchonella* Bed', Middle *varcus* Zone, middle Givetian (Feist & Klapper, 1985).

Etymology. From La Serre, the name of the type locality.

Diagnosis. Anterior outline of frontal glabella with slight medial inflexion; L1 trapezoidal, forwardly extending as far as midline of median glabella; pygidial axis wide, with three axial rings, no end-piece; first ring markedly separated from pleural ridge; inner pleural area undepressed and unpitted; extended posterior margin between diverging major spines.

Description. Cranidium with glabellar lobes moderately inflated. Median glabellar lobe of equal width from its base to laterally extending frontal lobe. Frontal lobe very low and short (sag.), medially reduced by backward inflexion of border furrow, laterally nearly entirely occupied by ovoid swellings of L3 lobes. S2 rather deep, backwards curved adaxially, abruptly terminating abaxially before reaching axial furrow. L2 subrhomboidal, half as wide as median lobe. S1 oblique, straight, deepening adaxially, merging with axial furrow. L1 subtrapezoidal, wider than half the width of median glabellar lobe, extending as far forward as median line (tr.) of the latter. Axial furrow moderately deep, slightly outwardly curved around lateral glabellar lobes, meeting anterior border furrow. Anterior border very narrow, forming a straight transverse rim. Occipital furrow shallow medially, rather deep abaxially behind far backwards extending L1 lobes. Occipital ring not inflated, provided with very strong occipital spine. Adaxial fixigenal field moderately vaulted anteriorwards (exsag.), steeply downwards flexed posteriorly, as high as glabella in frontal view, narrower (tr.) than adjacent medial lobe of glabella opposite eye. Eye ridge swollen, slightly curved. Sculpture comprises spaced tubercles of various sizes on entire prosopon.

Pygidium of crescentic outline with elevated axis that is nearly as wide (tr.) as pleural field. Axial furrow deep, distinctly marked along first axial ring. Furrow of articulating half ring straight, rather deep and large (sag., exsag.), sharply delimited against articulating half ring. Three axial rings clearly defined by continuous, straight ring furrows. Terminal portion of axis lacking end-piece. First axial ring hemispherical in cross-section, sharply defined anteriorly, postero-medially weakly indented by interannular lobe of lower and slightly narrower (sag.) second axial ring. Pleural ridge sigmoidal and continuing into main border spine; anteriorly moderately convex, abaxially merging with pleural field, adaxially sharply defined by deep recess of flat inner pleural area. Anterior pleural field not depressed, nor inflated; downwardly flexed posterolaterally; anteriorly framed by rather narrow flat border that is only adaxially defined by weak border furrow. Lateral and posterior borders not inflated, without border furrows, from front to rear increasingly downwardly curved. Major border spines slender, longer than remaining pygidium, slightly divergent. Distance at base between major border spines greater than width of first axial ring (tr.). Antero-lateral and posterior margins with long and thin secondary border spines. Prosopon of pygidium, including inner pleural area, provided with randomly dispersed tubercles of different sizes.

Remarks. When this new species was assigned by R. Feist (unpub. Ph.D. thesis, Univ. Montpellier, France, 1977) to *Koneprusia* (manuscript name: '*Koneprusia angustifrons*'), only the cranidium and an additional cranidial fragment, both from the '*Rhynchonella* Bed' (Feist & Klapper, 1985), were available. However, this material alone did not allow the generic attribution either to *Koneprusia* or to *Isoprusia*. Subsequently two pygidia of undoubted *Koneprusia* affinity were recovered from the same bed. As this provides more distinctive features than the cranidium it is chosen as the holotype of the newly named species.

Of all known koneprusine cranidia the new species is closest to *Koneprusia*? *laportei* (Hawle & Corda, 1847) from the Bohemian Suchomasty Limestone (Lower Emsian). It differs from this much older Bohemian species by its flatter and anteriorly concave frontal glabellar lobe, the less inflated glabellar lobes, the slightly sigmoidal course of the axial furrow and the narrower inner fixigenal fields. *Koneprusia*? *laportei* was considered by various authors (e.g. Přibyl & Vaněk, 1966; Alberti, 1970) to be a junior synonym of the contemporaneous *Koneprusia subterarmata*, of which it would constitute the cranidium. The similarities of our specimens with both the cranidium of *K. laporteii* and the pygidium of *K. subterarmata* tends to support this viewpoint.

The pygidium differs from *Koneprusia subterarmata* (Barrande, 1846) from the Bohemian Suchomasty Limestone (early Emsian) in that the first axial ring is not confluent with the pleural ridge. It can be further distinguished by the curved outline of its lateral border, the greater distance between the major border spines and the presence of a well-defined third axial ring. It shares these features with *Koneprusia* sp. n. W of Basse (1998), which this author considered as representing a possible new genus because of the presence of a third axial ring. Our taxon is distinguished by the absence of an additional axial end-piece, and a narrower (exsag.), undepressed anterior pleural field lacking any sculptural elements.

Koneprusia aboussalamae sp. nov.
Figure 3k, m, n

2003 *Koneprusia* sp.; Aboussalam, p. 24, plate 27, figs 4, 5.

Material. Holotype, pygidium MB.T. 4571 (Fig. 3n); cranidium MB.T. 4572 (Fig. 3k, m).

Type locality and horizon. Summit of Ras el Kebber Hill, 12 km SSW of Jorf village near Erfoud, Tafilalet, SE Morocco. Beige cephalopod calcilutite, Upper *disparilis* Zone, late Givetian (Th. Becker, pers. comm.).

Etymology. After Sarah Aboussalam, University of Münster, who first figured the specimens in her monograph on the Taghanic Event.

Diagnosis. Anterior outline of glabella moderately convex with truncated central part; medial glabellar lobe wide; occipital lobe with two central-posterior nodes. Pygidium with effaced axis narrowing behind; long median spine; narrow posterior margin; wide posterior pleural field.

Description. Cranidium with short (sag.), uninflated medial lobe that is moderately arched longitudinally and transversely, of slightly convex anterior outline, higher than fixigenal fields in frontal view, separated from L1 and L2 by large longitudinal furrows. Expanding parts of frontal lobe entirely formed by slightly inflated L3 that anteriorly encroaches onto deep border furrow. L1 and L2 half of medial lobe width (tr.). S1 and S2 deepest adaxially, enlarged abaxially to merge with axial furrow that curves around lateral glabellar lobes. Occipital furrow wide (sag.) and shallow. Occipital ring not swollen, posterolaterally sharply incised by deep border furrows, carries two medial nodes, anterior of which is provided with four pits representing occipital organ. Anterior border rim prominent. Inner fixigenal field gently arched (exsag.), of even width from L2 to opposite posterior end of palpebral lobe, where it is as wide as L1 (tr.), enlarging thereafter; steeply sloping towards border furrow. Eye ridge broad, moderately swollen, straight from antero-lateral corners of frontal glabellar lobe to opposite anterior limit of L1 where it is bent backwards to run into palpebral lobe in parallel to sagittal line. Eye lobe and eye ridge delimited against inner pleural field by deep furrow that dies out at posterior end of eye lobe. Eye lobe slightly swollen and moderately upraised. Posterior border furrow oblique, enlarged abaxially. Posterior border large, hemispherical in cross-section. Sparse tuberculation on medial glabellar lobe and occipital lobe, becoming more dense and coarser on lateral and frontal parts of cranidium; a single row of tubercles on anterior border and on ocular ridge.

Pygidium with low, tiny axis, inconspicuously subdivided by two ill-defined axial rings preceding bulged posterior part of semicircular posterior outline. Pleural ridges broad and considerably swollen, straight in adaxial anterior part, posteriorly curved and extending in continuity into major border spines. Inner pleural field large, ovoid, moderately swollen in anterior part, pitted behind junction of first axial ring and pleural ridge, declining rearwards to form a broad transverse depression between axis and elevated posterior border. In prolongation of axis, but without connecting to it, there is a tiny axial ridge inconspicuously marked on anterior slope of medial posterior border. Anterior border of pleural field unswollen, slightly posteriorly flexed abaxially. Outer pleural field with large triangular depression. Lateral border narrow and slightly swollen. Major border spines robust, considerably thicker than pleural ridge, remaining level with pleural ridge and lateral borders, horizontally displayed. Median spine long, thinner and on lower level than major spines, slightly downwardly directed. Sparse nodules on lateral and posterior borders.

Koneprusia brevispina sp. nov.
Figure 3b, c, e–i, q

Etymology. Referring to the rather short median spine on the posterior pygidial border.

Type locality and horizon. Eastern slope of Mont Peyroux Hill above abandoned marble quarry 'Concours-le-Haut', 1.5 km north of Causses-et-Veyran village, Montagne Noire, southern France. Light grey-beige *Styliolina* rich calcilutites with *Longicoryphe anteglabra* Feist, 2003, Upper *disparilis* Zone, late Givetian.

Material. Holotype, pygidium UMC-IP 546 (Fig. 3i), cranidium UMC-IP 547 (Fig. 3c, e), hypostome UMC-IP 548 (Fig. 3q), pygidium UMC-IP 549 (Fig. 3h) from type locality; cranidium UMC-IP 550 (Fig. 3b,f), librigena UMC-IP 551 (Fig. 3g), from southern slope of Pic de Bissous peak, 2.2 km north of Cabrières village, Montagne Noire, southern France, bed VS-E 25, Upper *disparilis* Zone, late Givetian (Feist & Klapper, 1985).

Diagnosis. Cranidium with evenly curved anterior outline of frontal glabella; narrow median glabellar lobe, posteriorly framed by enlarged longitudinal furrows, long occipital spine; pygidium with long axis and prominent post-axial ridge extending into short median border spine; lateral border spines divergent; depression of outer pleural field narrow and deep along lateral border, merging with anterior border.

Description. Cranidium with narrow medial lobe, strongly downwardly curved anteriorly, separated from lateral lobes L1 and L2 by rather wide longitudinal furrows. Frontal lobe of evenly curved anterior outline. Anterior border upraised, becoming wider (exsag.) abaxially. Occipital ring evenly vaulted (sag. and tr.); extending far forwards it is distinctly separated from base of medial glabeller lobe by narrow occipital furrow. Occipital spine very long and slender. Posterior band of occipital lobe demarcated by continuous groove-like furrows. Eye lobe, fixigenae and glabellar lobes of equal height in frontal view (Fig. 3f). Adaxial fixigenae delimited against prominent eye ridges and inflated eye lobe by deep furrow of sigmoidal curvature that dies out abruptly behind eye lobe without reaching posterior furrow. Coarse tuberculation on glabellar lobes and fixigenae; a row of distinct drop-like nodules along frontal border. Librigena with rounded genal angle and inflated posterior margin that extends into adaxially placed strong genal spine. Distance between genal angle and genal spine twice that between the latter and eye. Eye hemispherical, elevated above uninflated conical librigenal field. Coarse tuberculation on adaxial genal field and on posterior border.

Hypostome short, subrectangular with slightly convex anterior margin and medially concave margin forming wide incursion between flattened posterior extensions of large, slightly vaulted posterior border. Lateral margin with elevated outwardly curved, short (exsag.) shoulders. Deep lateral and posterior furrows join to form a convex backward curvature; middle body moderately inflated with two anteriorly positioned, deep longitudinal grooves. Anterior margin and lateral and posterior borders carrying prominent, drop-like tubercles; middle body with sparse nodules.

Pygidium with rectilinear anterior margin, forming sharp angle where meets gently curved lateral margin. Axis with broad end-piece. Anterior axial ring indistinctly separated from pleural ridge. Pleural ridge straight from axis to postero-lateral border, broadly inflated, abruptly thinning though remaining prominent, crossing border parallel to axial line to reach margin at adaxial base of major border spine. Postaxial ridge distinct, crossing wide inner pleural field to develop into rather short median border spine. Major border spines divergent, posterior border of moderate width (tr.). Lateral borders inflated. Antero-lateral pleural field wide, deeply depressed postero-laterally, merging anteriorly with uninflated anterior border. Sparse granules on lateral and posterior borders. Inner pleural field pitted.

Remarks. The new species can be distinguished from the contemporaneous *K. aboussalamae* by its wider inner fixigenal field and the presence of a long occipital spine on the cranidium and a much shorter median spine and a well-developed axial ridge in the pygidium.

Koneprusia sp. A
Figure 3l

Material. Pygidium UMC-IP 545.

Locality and horizon. Col du Puech de la Suque at 1.1 km SE of St Nazaire-de-Ladarez village, Montagne Noire, southern France. Grey-pink speckled calcilutites, bed CPS-F 19 in Feist & Klapper, 1985, Lower *disparilis* Zone, late Givetian.

Description. Anterior and lateral borders largely inflated; axis cylindrical, broadly rounded behind; axial rings marked with prominent tubercles; pleural ridges adaxially strongly bent; posterior pleural field narrow and deeply depressed anteriorly.

Remarks. The single small specimen is very similar to *K. aboussalamae*, in particular with regards to the general outline and the strength and disposition of the border spines. By contrast, the axial rings are more clearly distinct and sculptured with nodules, the anterior and lateral borders are more broadly swollen, framing a deep depression in the anterior pleural field, and the major border spines are closer to each other that results in a shorter posterior margin. Finally, the shape of the posterior pleural field, deeper in front and merging with the border behind, is narrower behind.

Koneprusia sp. B
Figure 3o, p

Material. Pygidium SMF 76833.

Locality and horizon. Trench VI at Sessacker, Oberscheld village, southeastern Rhenisch Slate Mountains, Germany, brick red calcilutite, bed 4a (Feist & Schindler, 1994, text-fig. 3), Zone 12, late Frasnian.

Description. Pygidial axis rather narrow reaching merely 2/5 of width of pleural field, anteriorly rather prominent in side view, strongly sloping behind first axial ring; high and short (sag.), clearly separated from pleural ridge by deep dorsal furrow; second axial ring low, carrying two prominent tubercles; end-piece of axis narrow. Pleural ridge of moderate outward curvature defining a relatively narrow, slightly depressed posterior pleural field. Posterior border large (sag.), slightly inflated very narrow (tr.), merging with enlarged base of long median spine that protrudes anteriorly across central posterior border. Main border spines very long and straight, disposed nearly parallel to axial line. All border spines slightly downwardly inclined, the median spine stronger than the main ones. Interior two-thirds of anterior border rectilinear, lateral borders moderately curved, large, slightly inflated. Anterior pleural field excavated by rather large triangular depression devoid of sculptural elements. With the exception of depressed parts of pleural fields, prosopon is covered by numerous coarse tubercles that increase in size on anterior axial ring, posterior borders and border spines.

Remarks. This species differs from *K. aboussalamae* by possessing a shorter, well-differentiated axis, a narrower (tr.) posterior margin and much coarser tuberculation. It can be distinguished from *K.* sp. A by its narrower and finer axis and wider depression of the outer pleural field, and from *K. brevispina* not only by the rather different disposition of the border spines, but also by the absence of the axial ridge which might be obscured by the protruding base of the median spine.

The pygidium is particular in the disposition of the closely spaced border spines that are nearly parallel to the axial line. This feature has not previously been observed in any other koneprusiine and might ultimately justify the assignment of this pygidium to a new species. The occurrence of this last representative of the subfamily in the late Frasnian is considerably later than the other taxa of *Koneprusia*.

Koneprusia? sp.
Figure 3s

Material. A single, fragmentary cranidium NHM It 27821.

Locality and horizon. Lummaton Quarry, Torquay (Devon, UK), Middle *varcus* Zone, middle Givetian.

Remarks. This koneprusiine cranidium is tentatively assigned to the genus *Koneprusia* until complete material, especially a pygidium, is found. The cranidium is characterized by its relatively long (sag.), anteriorly rounded glabellar frontal lobe and the outwardly placed L1 lobes separated from both the median lobe and L2 by a rather large S1 furrow. The prosopon is sculptured with coarse tubercles throughout.

Subfamily ACIDASPIDINAE Salter, 1864
Genus *Gondwanaspis* Feist, 2002

Type species. Gondwanaspis mrirtensis Feist, 2002, by original designation.

Assigned species. G. mrirtensis Feist, 2002, *G. dracula* sp. nov., *G. spinosa* sp. nov., *G. prisca* sp. nov., *G. harborti* (Richter & Richter, 1926), *G. tenella* (Maximova, 1960), *G.* sp. A., *G.* sp. B and *G.* sp. C.

Emended diagnosis. Cephalon of low convexity, with downward flexed anterior border; glabellar lobes often weakly inflated; L3 very small or absent; rectangular central lobe; relatively deep, wide (sag.) preglabellar furrow; almost straight eye ridges with large angle of convergence; sutural ridges weakly developed or absent; eye located in centre of wide genal field; genal angle advanced; straight, outward directed librigenal spine; margin of librigenae with 12 long, straight spines; up to four pointed protuberances or exsagittally directed spines on anterior border of cranidium; no occipital spines. Hypostome subquadrangular, with anteriorly narrowing central lobe. Pygidium wide and short, with long, divergent major pair of border spines; axis relatively narrow.

Remarks. Feist (2002) proposed the genus *Gondwanaspis* on the basis of a late Frasnian form from Morocco that he characterized by the possession of a rectangular central glabellar lobe, lateral glabellar lobes that are not swollen, the anterior-most being inconspicuous, absence of sutural ridges, straight border spines that are also present on the anterior margin of the cranidium, and the very advanced, not posteriorly curved, librigenal spine. The discovery of further acidaspinine species with these morphological characteristics and the reinterpretation of other species from the Frasnian of the Canning Basin (Western Australia), Montagne Noire (France), the Rhenish Slate Mountains (Germany) and the Rudny Altai (Russia) that are morphologically close to the Moroccan *G. mrirtensis*, allows us to define *Gondwanaspis* more rigorously and assess the extent of its biodiversity and palaeobiogeographical distribution. This is particularly significant, given that this is the last known odontopleuroid genus. Our study of these species has enabled the recognition of further diagnostic characters of *Gondwanaspis*, especially the downward-flexed anterior border of the cranidium, a character unique in odontopleurids, and also its low convexity, very wide genal areas and deep, wide (sag.) preglabellar furrow.

Despite the apparently large number of distinctive features for this last surviving member of the Odontopleuroidea, Adrain (*in* Jell & Adrain, 2003) was of the opinion that *Gondwanaspis* should be considered a junior subjective synonym of *Taemasaspis*. Unfortunately no justification was given for this action. Chatterton (1971) had originally proposed *Taemasaspis* as a subgenus of *Primaspis* for a form from the late Silurian to early Devonian of New South Wales in which lateral glabellar lobes L1 and L2 were not as inflated as in *Primaspis* s.s.; the base of the genal spine was positioned further forward; the genal spines projected more transversely, being strongly curved and shorter; and lack of paired occipital spines. Although placing it within *Primaspis*, Chatterton (1971) was of the view that it was close to *Dudleyaspis*, suggesting an evolutionary lineage of *Primaspis–Taemasaspis–Dudleyaspis*.

Adrain's actions in placing *Gondwanaspis* in synonymy with *Taemasaspis* are surprising, given that a number of authors have previously considered *Taemasaspis* to be a synonym of other odontopleurids. Přibyl & Vaněk (1973) believed it to be a junior subjective synonym of *Primaspis (Meadowtownella)*. Shortly thereafter, Šnajdr (1975), ignoring the action of Přibyl & Vaněk (1973), raised *Taemasaspis* to generic status, although he failed to justify his actions. The species that he described as a new species of *Taemasaspis, T. llandoveryana*, Ramsköld (1984) later considered to fall somewhere between *Primaspis* and *Odontopleura*. In a subsequent publication, Šnajdr (1978) provided some justification for his actions in raising *Taemasaspis* to generic level, but declined to follow Přibyl & Vaněk (1973) in synonymizing the taxon, considering that *Primaspis (Meadowtownella*) was too poorly defined to allow *Taemasaspis* to be considered synonymous with it. Chatterton *et al.* (1979) argued for the retention of *Taemaspasis* as a subgenus of *Primaspis*.

However, in his review of the Wenlock odontopleurids, Thomas (1981) proposed that *Taemasaspis* should be regarded as a junior subjective synonym of *Dudleyaspis*. Chatterton & Perry (1983, pp. 44–5), while suggesting that *Taemasaspis* could only really be distinguished from *Dudleyaspis* on the presence or absence of posterior spines on the posterior margin of the cephalon, followed Thomas's recommendation, as did Chatterton & Wright (1986). Ramsköld (1984) accepted that *Taemasaspis* was closer to *Dudleyaspis* than to *Primaspis* and also followed Thomas's recommendation, as do we. However, Adrain (*in* Jell & Adrain, 2003) apparently prefers to accept Šnajdr's (1986) view that considers *Taemasaspis* to be a valid genus and to encompass within it the late Frasnian form that Feist (2002) described as *Gondwanaspis*. However, if one accepts the view of Thomas (1981), Chatterton & Perry (1983) and Ramsköld (1984) that *Taemasaspis* is synonymous with *Dudleyaspis*, then *Gondwanaspis*, following this line of argument, should also be regarded as synonymous with *Dudleyaspis*.

However, for the following reasons we consider that *Gondwanaspis* is a valid taxon and therefore synonymous with neither *Taemasaspis* nor *Dudleyaspis*. Unlike *Taemasaspis campbelli*, in which all the glabellar lobes are quite distinct (Chatterton, 1971, pl. 11, figs 25, 28), in *Gondwanaspis* S1 is very shallow and L1 is generally of particularly low tumidity. Moreover, L3 is either very small or absent. In late forms the axial furrows are very weak. The central glabellar area is narrower and more rectangular in *Gondwanaspis*, with a more transverse anterior margin to the frontal lobe. In addition, it has a deeper and longer (sag.) preglabellar furrow and centrally a much thicker (sag.) border. The eye lobe is set close to the prominently raised narrow fixigena in *Taemasaspis*, but is more distally positioned in *Gondwanaspis*, both from the axial furrow and the posterior border furrow. As a consequence the eye ridges converge anteriorly at between about 130 and 155° in *Gondwanaspis*, but at only 110° in *Taemasaspis*. *Gondwanaspis* possesses a much wider (tr.) and flatter posterior fixigena. The pronounced occipital node in *Taemasaspis* is absent in *Gondwanaspis*, the occipital organ being flush with the surface. The anterior border of the cranidium in *Gondwanaspis* characteristically possesses up to four protuberances or anteriorly projecting spines. These are absent in *Taemasaspis*. Moreover, all species that can be assigned to *Gondwanaspis* have a downwardly flexed anterior border. In *Taemasaspis* this border is straight (see Chatterton, 1971, pl. 18, fig. 11). The short spines on the librigena increase in size posteriorly in *Taemasaspis*, but are of more constant length and are longer and straight in *Gondwanaspis*. The librigenal spine is more anteriorly positioned in *Gondwanaspis* and stretches outward without a strong backward curvature. The pygidium of *Gondwanaspis*, which is described herein for the first time, is quite distinct from that of *Taemasaspis*, being much wider and possessing divergent, rather than exsagittal major border spines, a relatively much smaller axis and wider inner pleural areas.

We concur with Thomas (1981), Chatterton & Perry (1983), Ramsköld (1984) and Chatterton & Wright (1986) in regarding *Taemasaspis* as a junior subjective synonym of *Dudleyaspis*, consequently the features that distinguish *Gondwanaspis* from *Taemasaspis* are similar to those that distinguish *Gondwanaspis* from *Dudleyaspis (Dudleyaspis)*. Ramsköld (1984) erected the subgenus *Dudleyaspis (Snoderaspis*) for forms with very anterolaterally positioned eyes, amongst other features. It may be for this reason that Adrain (*in* Jell & Adrain, 2003) chose also to place *Snoderaspis* in synonymy with *Dudleyaspis s.s.* along with *Gondwanaspis*. However, apart from this ocular feature, *Gondwanaspis* and *Snoderaspis* have little in common. Unlike *Gondwanaspis*, *Snoderaspis* has a very much narrower, semicircular cephalon; genal angle posterior (tr.) to the posterior margin of the occipital ring; genal spine that extends posteriorly almost exsagittally; pronounced glabellar lobes, with S1 well incised anteriorly; and broad central glabellar area with rounded

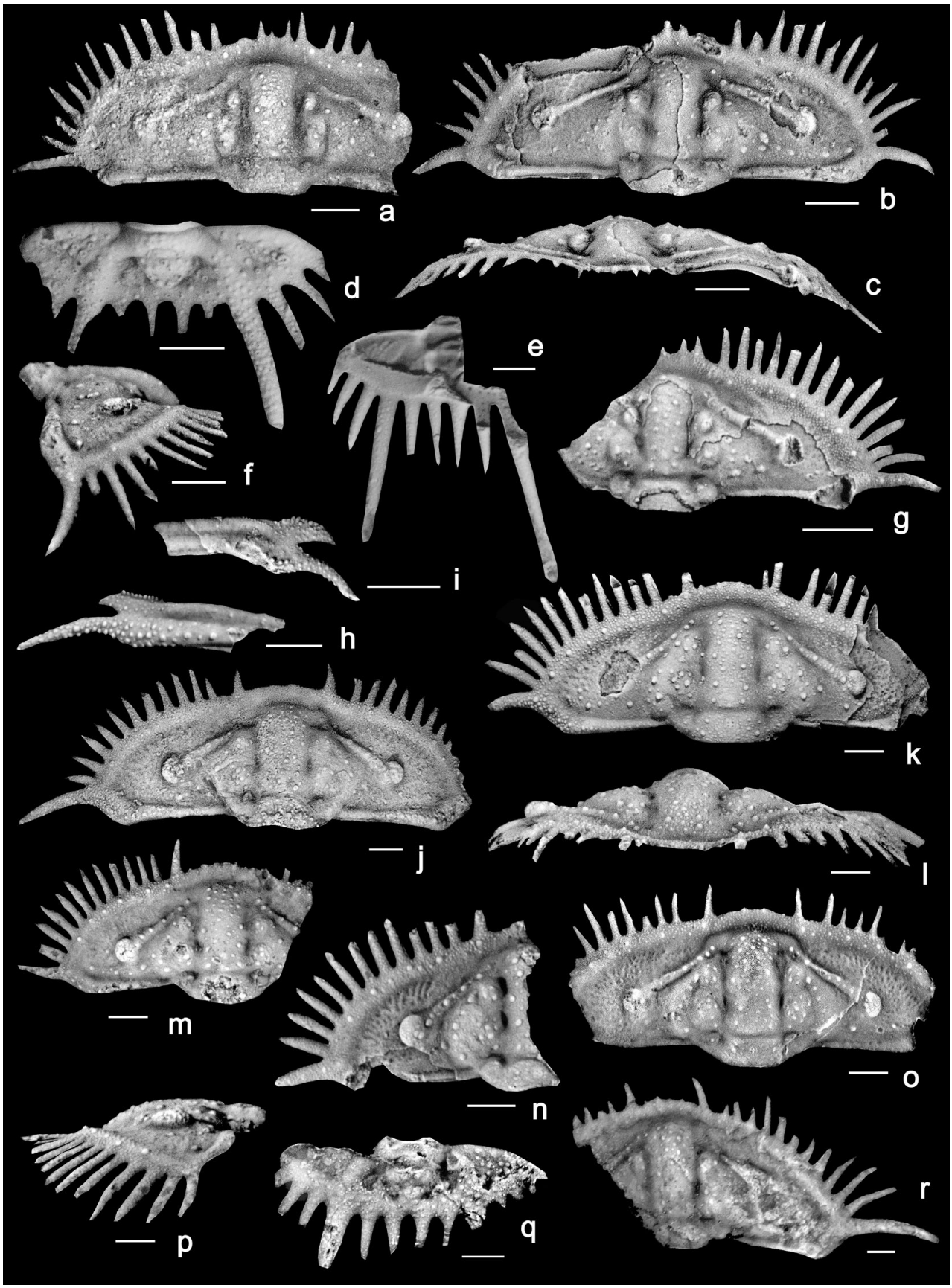

Figure 4. Scale bar = 1 mm. (a–g) *Gondwanaspis spinosa* sp. nov., late Frasnian (Zones 11 and 12), Virgin Hills Formation, Lawford Range, Canning Basin, Western Australia; (a) WAM 07.94, holotype, cephalon, dorsal view; (b, c, f) WAM 07.95, cephalon, dorsal, anterior and lateral views; (d) WAM 07.96, pygidium, dorsal view; (e) WAM 07.97, pygidium, ventral view; (g) WAM 07.98, cephalon,

frontal lobe. Placing *Gondwanaspis* and *Snoderaspis* as synonyms of *Dudleyaspis* would therefore be inappropriate. Whether the distinctive combination of the distal position of the eyes, shape of the cephalon, position of the genal angle and orientation of the genal spines in *Snoderaspis* is sufficient to justify separate generic status for this form is open to question. However, these features would seem sufficiently characteristic to warrant at least subgeneric status for this form.

Gondwanaspis dracula sp. nov.
Figure 4h–r

1927 *Ceratocephala (Leonaspis) harborti* (Richter & Richter); Matern, p. 254.

Type material. Holotype, cephalon WAM 07.99 (Fig. 4j), McWhae Ridge, Lawford Range, Canning Basin, Western Australia; Virgin Hills Formation, Zone 12, late Frasnian. Paratypes NMV P313912 (Fig. 4k, l), P313913 (Fig. 4m, p), WAM 07.103 (Fig. 4o), WAM 07.102 (Fig. 4n), all cephala; WAM 07.100 (Fig. 4h), WAM 07.101 (Fig. 4i), both thoracic segments, and WAM 07.104 (Fig. 4q), pygidium. All paratypes from Bugle Gap, 10 km NNW of McWhae Ridge, Lawford Range, Western Australia; Virgin Hills Formation, Zone 11, late Frasnian.

Other material. Fifteen incomplete cephala, two incomplete thoracic segments and one incomplete pygidium; Bugle Gap, 10 km NNW of McWhae Ridge, Lawford Range, Western Australia; Virgin Hills Formation, Zone 11, late Frasnian; one incomplete cephalon (Figure 4r), SMF 58550 from Sessacker, Oberscheld village, southeastern Rhenisch Slate Mountains, Germany, Zone 12, late Frasnian.

Etymology. After the Transylvanian vampire in Bram Stoker's (1897) novel *Dracula*, in allusion to the prominent pair of fang-like spines on the anterior border of the cephalon.

Diagnosis. Cephalon with gently convex anterior margin; eye ridges expanding distally; glabellar lobes very poorly defined; L3 very weakly developed; anterior margin of cranidium with pair of spines distally, a pair of weak protruberances sagittally; relatively dense concentration of secondary tubercles, particularly on glabella and eye ridges, set in groundmass of relatively coarse, granular tubercles.

Description. Cephalon very broad; width, excluding genal spines, nearly three times sagittal length; gently convex. Glabella with only weakly inflated glabellar lobes. Dorsal furrows very shallow, mostly expressed only laterally and behind L1. Lateral glabellar lobes L1 and L2 circular, widely separated from each other; surrounded by poorly defined, circular furrows. L3 not present or very tiny and deeply depressed. Median glabellar lobe separated from lateral lobes by straight, rectilinear furrows that develop as deeper impressions behind junctions of eye ridges with anterior median lobe, at level of L2 and anteriorly to L1; shallow and widen posterior to L0; present on anterior occipital lobe, then die out after having crossed anterior half of occipital ring. L1 almost as high as median lobe. Frontal part of median lobe laterally extended by somewhat lower swellings at junction with adaxial ends of eye ridges. In lateral view profile of of median lobe very slightly higher than occipital ring; horizontal until anterior limit of L2, gently downcurving anteriorly. Front of glabella abruptly truncated by deep and straight transverse preglabellar furrow that encroaches on relatively large border. Anterior border not inflated; slightly raised (sag.), downwardly flexed medially (tr.). Anterior edge rounded with short protuberances or spines. Axial furrow very shallow, interrupted between L1 and L2. Occipital ring rectangular, medial part transversely rectangular with straight occipital furrow and posterior edge; not inflated; occipital organ situated on highest point anteriorly to middle; not prominent; circular, unornamented area with four pits; flush with surface of occipital ring. Lateral occipital lobes relatively small and weak; not inflated; incompletely separated from median occipital lobe. Eyes lobes globular, set midway between anterolateral and posterior furrow (exsag.), equidistant from axial furrow to posterolateral border furrow. Eye ridges nearly straight; widest at eye lobes, continuously thinning anteriorly, converging at an angle of about 125 to 130°. Slightly more convergent as they approach L2. Anterior fixigenae narrow, depressed between border furrow and eye ridge. Posterior fixigenae very wide, the adaxial half inflated to level of weak lateral glabellar lobes, posterolaterally merging with lateral occipital lobes. Anterior sutural ridges not discernable or extremely weak. Genal field of librigenae sculptured by elongate grooves separated by network of anastomosing ?caecal ridges (Fig. 4n). Posterior border hemi-cylindrical, narrowest adaxially, progressively widening abaxially; extends transversely to fulcrum, set two-thirds distance to genal angle, from where angles forward at about 50° to blunt advanced genal angle. Lateral border adjacent to genal angle broad and low, continuing into genal spine that extends transversely; gently recurved posteriorly and moderately declined. Narrow posterior and anterolateral border furrows of even depths, meeting with blunt angle opposite genal spine. Anterolateral border wide, slightly swollen; extending from bottom of anterior slope of each anterolateral border 12 thick, straight cylindrical spines of nearly equal length that are outstretched perpendicular to border and slightly declined. Distal border spines decline at steeper angle than genal spine. Between most adaxially positioned spine and adjacent (11th) border spine there is a spine-free interval. Prosopon comprises widely spaced scattering of secondary tubercles on borders, eye ridges, glabellar lobes, posterior fixigenae and occipital lobe, set in a groundmass of smaller, dense, relatively coarse tuberculation. Outer parts of posterior fixigenae smooth.

Thoracic segments with moderately convex pleural ridges that expand abaxially beyond fulcrum, where steeply declined. Anterior spine short, flat, spatulate, slightly recurved and bordered anteriorly by closely spaced, short, denticulate spines. Posterior spine longer than anterior; convex, recurving more strongly than anterior spine and

dorsal view. (h–q) *Gondwanaspis dracula* sp. nov., late Frasnian (Zones 11 and 12), Virgin Hills Formation, Lawford Range, Canning Basin, Western Australia; (h) WAM 07.100, incomplete thoracic segment, dorsal view; (i) WAM 07.101, incomplete thoracic segment, dorsal view; (j) WAM 07.99, holotype, cephalon, dorsal view; (k, l) NMV P313912, cephalon, dorsal and anterior views; (m, p) NMV P313913, cephalon, dorsal and lateral views; (n) WAM 07.102, cephalon, dorsal view; (o) WAM 07.103, cephalon, dorsal view; (q) WAM 07.104, pygidium, dorsal view. (r) *Gondwanaspis dracula* sp. nov., late Frasnian, Sessacker, Oberscheld village, southeastern Rhenish Slate Mountains, Germany, SMF 58550, cephalon, dorsal view.

gently tapering distally. Pleural ridge with moderately dense covering of prominent tubercles. Anterior spine sparsely tuberculated.

Pygidium over three times wider than long, excluding spines; short, with elevated, triangular axis that is slightly narrower (tr.) than pleural field. Axial furrow deep posteriorly, distinctly marked along second axial ring; anteriorly ill defined. Two axial rings and small terminal end-piece defined by continuous, straight shallow ring furrows. First axial ring, well defined, almost twice width (sag.) of more ill-defined second axial ring. Pleural ridges very short, gently convex, slightly curved, extending continuously into wider main border spines, swelling at junction with posterolateral border; abaxially merging with pleural field; adaxially pleural ridges more sharply defined by deeper recess of flat inner pleural areas. Outer pleural areas slightly depressed, flat; anteriorly bounded by narrow rolled border. Inner pleural areas deeper and relatively wide (tr.). Lateral and posterior borders broad, gently convex, border furrow shallow but well defined. Major border spines short, wide, equal in length to axis, moderately divergent. Distance at base between major border spines greater than width of first axial ring (tr.). Antero-lateral and posterior margins with short, thinner secondary border spines, the four between the primary spines extending almost exsagittally. Prosopon on borders and spines consists of moderate concentration of small tubercles. Less concentrated and slightly larger on inner pleural areas.

Remarks. One of the characteristic features of *Gondwanaspis dracula* is its possession of a pair of proximal, slightly curved, fang-like spines on the anterolateral border. Because of the indistinct nature of the anterior course of the facial suture it is not clear whether this 12th pair of spines belongs on the cranidium or on the librigenae. On one specimen (NMV P313912) one of the paired 'fangs' has an extra, slightly shorter adjacent spine developed adaxially (Fig. 4k). An incomplete cephalon of *Gondwanaspis* (Fig. 4r) from the late Frasnian, Zone 12, at Sessacker, Germany (Matern, 1927, SMF X 559b–SMF 58550) appears indistinguishable from the Western Australian Canning Basin *G. dracula*. It shares the characteristic paired 'fang-like' anterior spines; extra space between these spines and adjacent librigenal spine; protuberances on the anterior cranidial margin; and narrow median glabella lobe. Consequently we regard this form as being conspecific with *G. dracula*, demonstrating that this species had a wide biogeographical distribution across the northern margin of Gondwana during the Frasnian (see Fig. 2).

G. dracula is very similar to the type species, *G. mrirtensis* from Morocco. However, the Canning Basin form can be distinguished by the development of the pair of 'fang-like' curved spines on the anterior border; eye ridges that expand distally; narrower median glabellar lobe; and presence of protuberances, rather than spines, on the anterior cranidial margin.

Gondwanaspis spinosa sp. nov.
Figure 4a–g

Type material. Holotype, cephalon WAM 07.94 (Fig. 4a), McWhae Ridge, Lawford Range, Canning Basin, Western Australia; Virgin Hills Formation, Zone 12, late Frasnian. Paratypes, cephala WAM 07.95 (Fig. 4b, c, f), WAM 07.98 (Fig. 4g) from Bugle Gap, 10 km NNW of McWhae Ridge, Lawford Range, Western Australia; Virgin Hills Formation, Zone 12, late Frasnian; pygidia WAM 07.96 (Fig. 4d), WAM 07.97 (Fig. 4e) from Bugle Gap, 10 km NNW of McWhae Ridge, Lawford Range, Western Australia; Virgin Hills Formation, Zone 11, late Frasnian.

Other material. Two cephala from Bugle Gap locality, Zone 11; three cephala from McWhae Ridge locality, Zone 12, late Frasnian.

Etymology. In allusion to the spinose nature of the cephalic border, in particular the presence of prominent spines on the anterior border of the cranidium.

Diagnosis. Cephalon with almost transverse anterior margin; eye lobes anterolaterally positioned; eye ridges long, thin, straight, widely divergent; glabellar lobes reasonably well defined; small L3 present, four long spines on anterior margin of cranidium; sparse secondary tubercles set in groundmass of very small, granular tubercles. Pygidium very wide; with long, slender, divergent major border spines and axis equal in width to pleural field.

Description. Cephalon broad; width, excluding genal spines, about two and a half times sagittal length; gently convex. Lateral glabellar lobes moderately inflated for genus. Dorsal furrows shallow, more incised laterally and behind L1. Lateral glabellar lobes L1 and L2 subovate, separated from each other by shallow, relatively narrow, subcircular furrows. L3 very small. Median lobe separated from lateral lobes by straight, relatively well-incised rectilinear furrows that deepen behind junctions of eye ridges with anterior median lobe, opposite L2 and anterior part of L1; shallow markedly and widen posterior to L1; present on anterior of occipital lobe, then diminish posteriorly. L1 almost as high as median lobe. Frontal part of median lobe extended laterally in line (exsag.) with distal extent of L2 as somewhat lower swellings at junction with adaxial ends of eye ridges. In lateral view profile of median lobe horizontal until anterior limit of L2, gently downcurving anteriorly. Front of glabella abruptly truncated by broad, incised, transverse preglabellar furrow that encroaches on relatively large border. Anterior border weakly inflated, downwardly flexed medially (tr.). Anterior edge bears four prominent spines, outer pair of which longer than inner pair. Axial furrow shallow, deepening and widening slightly posteriorly. Occipital ring weakly inflated; medial part transversely rectangular with straight, well-incised occipital furrow. Lateral glabellar lobes weakly developed, gently inflated, incompletely separated from median occipital lobe. Eye lobes globular, advanced, set closer to anterolateral border furrow than to posterior border furrow (exsag.); set closer to genal angle than to axial furrow; positioned in line with posterior of L1 and anterior of L2. Eye ridges straight, narrow, converging at an angle of about 150°. Anterior fixigenae narrow, depressed between border furrow and eye ridge. Posterior fixigenae very wide, the adaxial half moderately inflated but not as high as lateral glabellar lobes; posterolaterally merging with lateral occipital lobes. Anterior sutural ridges weakly developed (Fig. 4g). Posterior border straight, narrowest adaxially, progressively widening abaxially to fulcrum, which is set three-quarters distance to genal angle, from where angles forward at about 35° to blunt advanced genal angle. Posterolateral border broad and low, continuing into genal spine that extends transversely; slightly recurved posteriorly but moderately declined. Posterior border furrow narrow and moderately incised; anterolateral border furrow shallow, broad. Anterolateral border wide, gently rounded; extending from bottom of anterior slope of each anterolateral librigenal border are 12 long, slender, cylindrical spines of nearly

equal length that are outstretched perpendicular to border and gently declined. Distal border spines decline at a steeper angle than main genal spine. Prosopon comprises sparse scattering of secondary tubercles on eye ridges, glabellar lobes, posterior fixigenae and occipital lobe, set in a dense groundmass of small, granular tubercles that extend onto the borders and spines; anterolateral border also bearing a row of evenly spaced secondary tubercles (Fig. 4g).

Pygidium short, four times wider than long, excluding spines; triangular axis elevated and of similar width (tr.) to pleural field (Fig. 4d). Axial furrow deep posteriorly behind first axial ring, distinctly incised along second axial ring; anteriorly shallows as it passes first axial ring. Axis comprises two axial rings and very small terminal end-piece; axial rings separated by continuous, straight, shallow ring furrows. First axial ring, prominent, half as wide again (sag.) as less prominent second axial ring. Pleural ridges short, gently convex, slightly curved, extending continuously into wider main border spines, swelling at junction with posterolateral border; abaxially separated from pleural field by shallow furrows; adaxially pleural ridges sharply defined by deeper recess of small, flat inner pleural areas. Outer pleural areas slightly depressed, bearing three weakly developed, very small, curving pleural ridges, corresponding to smaller anterolateral spines; anteriorly bounded by narrow rolled border that widens abaxially. Inner pleural areas deeper and narrower (tr.). Lateral and posterior borders broad, gently convex, border furrow shallow but well defined. Major border spines long, slender and almost straight; more than twice sagittal pygidial length; moderately divergent. Distance at base between major border spines twice width of first axial ring (tr.). Anterolateral and posterior margins with more slender secondary border spines, up to almost half length of major spines; the four between the primary spines extending almost exsagittally. Prosopon on borders and spines consists of dense concentration of coarse tubercles, especially on spines. Small anterior pleural ridges carrying single rows of tubercles. Tubercles more widely scattered on anterior border.

Remarks. Gondwanaspis spinosa from the Canning Basin, Western Australia, can be distinguished from the type species, *G. mrirtensis*, by its longer eye ridges that are less anteriorly convergent; larger eye lobes, which are set further from the glabella and closer to the anterolateral border; narrower median glabellar lobe; more well-defined lateral glabellar lobes; presence of very small L3 and deeper S2; more incised axial furrows; less advanced genal angle; and finer granular tuberculation.

G. spinosa differs from the slightly older *G. dracula*, also from the Canning Basin, in having a cephalon with a slightly more transverse anterior margin and in having four spines on the anterior border of the cranidium. The cephalon is less densely tuberculated, with a groundmass of smaller, granular tuberculation. The eye ridges are narrower and of more even width. They converge anteriorly at a wider angle, 150° rather than 130°, due to the more anterolateral position of the eye. The genal angle is less advanced in *G. spinosa*, the preglabellar furrow is shallower and the fixigenae are less inflated adaxially. The pygidial border spines of *G. spinosa* are longer than those of G. *dracula*, especially the major pair.

Gondwanaspis sp. A
Figure 5a

Material. WAM 07.105, incomplete cephalon from Bugle Gap, 10 km NNW of McWhae Ridge, Lawford Range, Western Australia; Virgin Hills Formation, Zone 11, late Frasnian.

Remarks. This form occurs at the same horizon as *G. dracula*, but differs in having a smaller eye lobe; a straighter eye ridge that becomes ill defined distally; lateral glabellar and occipital lobes that are even more ill defined than in *G. dracula*; and a far more coarsely tuberculate prosopon. It shows even fewer similarities to *G. spinosa*, which is a weakly tuberculate species with relatively well-defined lateral glabellar and occipital lobes. Not only does *G.* sp. A. have a smaller eye, but it is set closer to the glabella. *G.* sp. A has more in common with the type species, *G. mrirtensis*, in particular the tuberculate prosopon shows some similarities, although it is still more coarsely developed in *G.* sp. A. Both forms have relatively small eye lobes, but the eye ridge in *G. mrirtensis* is more prominent, as are the lateral glabellar and occipital lobes.

Gondwanaspis sp. B
Figure 5b, c

Material. WAM 96.483 (Fig. 5c), incomplete cephalon, McWhae Ridge, Lawford Range, Canning Basin, Western Australia; Virgin Hills Formation, Zone 13b, late Frasnian. A small, poorly preserved cephalon, WAM 07.106 (Fig. 5b), from the same locality and horizon may also be conspecific.

Remarks. Of the forms of *Gondwanaspis* from the Canning Basin in Western Australia, *G*. sp. B compares most closely with *G*. sp. A in having coarse tuberculation. However, it differs in having a larger eye set in a more advanced position, closer to the anterolateral border than to the posterior border. Only the distal part of the eye ridge is preserved, but this is sufficient to show that this form can be differentiated from *G.* sp. A as the eye ridge is well defined distally.

The poorly preserved complete cephalon from the same locality and horizon as *G*. sp. B is considered more likely to be conspecific with this form rather than with the contemporaneous *G*. sp. A because it has a relatively advanced eye lobe and lateral glabellar lobes that are more defined than in *G*. sp. A. Of the other species of *Gondwanaspis* from the Canning Basin, *G*. sp. B most closely resembles *G. spinosa* in having an anteriorly positioned eye lobe and not very advanced genal angle. However, the younger form differs in its possession of a more tuberculate prosopon and eye lobe that, although anteriorly positioned, is not set as close to the genal angle. *G*. sp. B is similar to *G. mrirtensis* but its eye is set in a more advanced position; its genal angle is less advanced; and its posterolateral border is wider.

Gondwanaspis sp. C
Figure 5e

Material. WAM 07.107 (Fig. 5e), an incomplete cephalon and WAM 07.108, a genal spine and adjacent border, McWhae Ridge, Lawford Range, Canning Basin, Western Australia; Virgin Hills Formation, Zone 13b, late Frasnian.

Remarks. Gondwanaspis sp. C is a very distinctive form, quite unlike other species from the Virgin Hills Formation in the Canning Basin, demonstrating that, even in the very last beds of the Frasnian, *Gondwanaspis* showed high levels of diversity and disparity. It compares with *G.* sp. A and the contemporaneous *G.* sp. B in having a coarser tuberculation than either *G. spinosa* or *G. dracula*. Both *G.* sp. B and *G.* sp. C also share the very distinctive presence of equi-spaced, large tubercles arranged along the anterolateral border, a

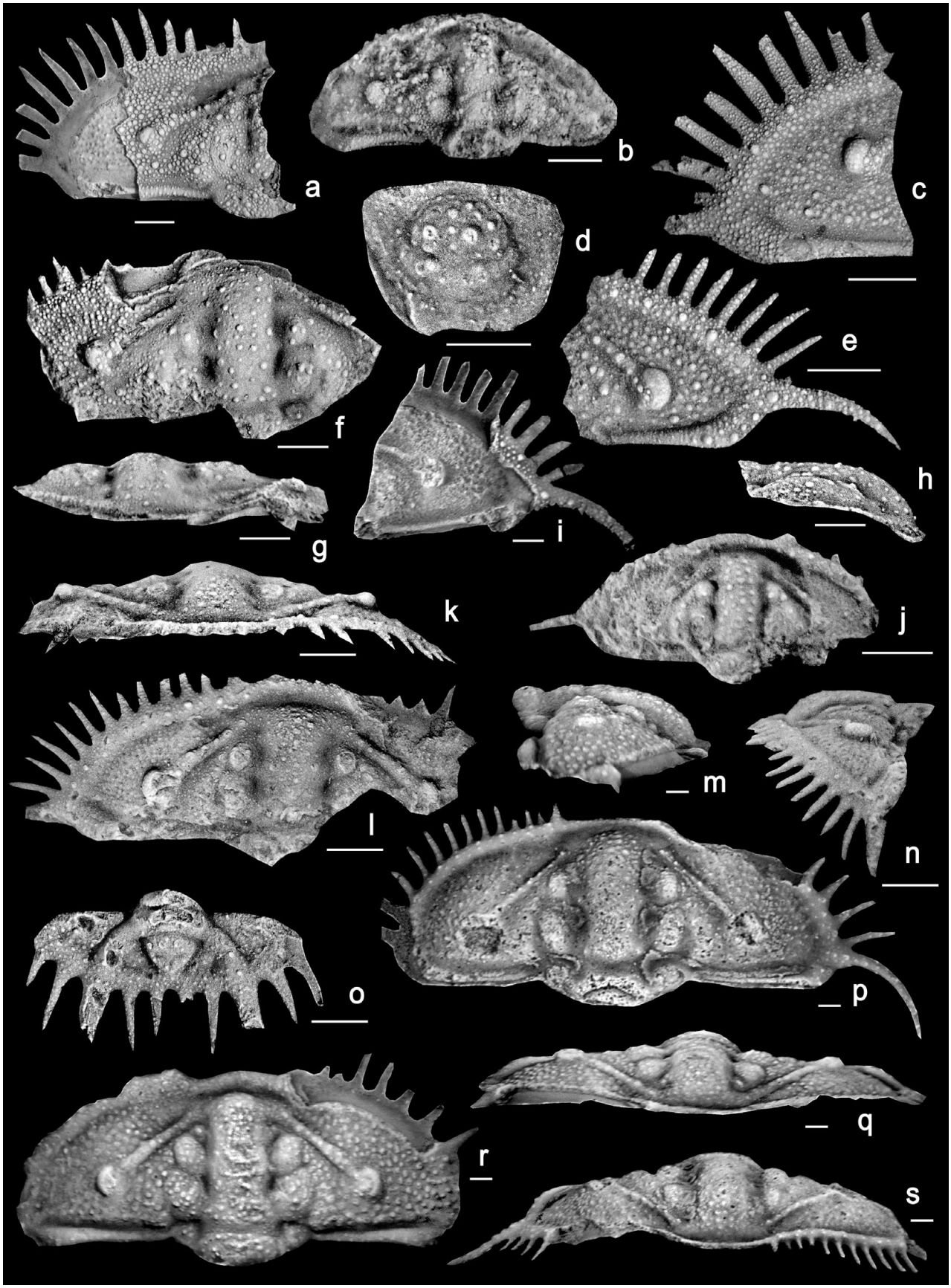

Figure 5. Scale bar = 1 mm. (a) *Gondwanaspis* sp. A, late Frasnian (Zone 11), Virgin Hills Formation, Lawford Range, Canning Basin, Western Australia, WAM 07.105, incomplete cephalon, dorsal view. (b, c) *Gondwanaspis* sp. B, late Frasnian (Zone 13b), Virgin Hills Formation, Lawford Range, Canning Basin, Western Australia; (b) WAM 07.106, cephalon, dorsal view; (c) WAM 96.483, incomplete

feature also seen in *G. spinosa*. In *G.* sp. C they also occur on the distal posterior border between the fulcrum and the genal spine, with the largest tubercle at the adaxial end of the genal spine. Interestingly, this same feature occurs in *G. tenella* from Siberia (compare Fig. 5e and 5i).

G. sp. C differs from both *G*. sp. A and sp. B in having a larger eye lobe that is set relatively close to the posterior margin. Moreover, it has a denser concentration of coarser tubercles than either of these forms. In this regard it compares with *G. harborti* from the Rhenish Slate Mountains in Germany. Like *G*. sp. C, *G . harborti* also has eye lobes located closer to the posterior border than to the anterolateral border (Fig. 5r). *G*. sp. C can also be characterized by its genal spines, which are longer and more curved than in any of the other forms of *Gondwanaspis* from the Virgin Hills Formation. In this regard it again compares with *G. harborti*, which has similar-shaped long genal spines (Fig. 5p). Another feature shared between the Canning Basin and German forms is the possession of relatively deep posterior and anterolateral border furrows. The left side of a cephalon from the Upper Devonian of Wuppertal, Germany, figured by Basse & Müller (2004, fig. 662) was assigned by them to *G.*? cf. *harborti*. This form is very similar to *G*. sp. C in sharing the tubercular prosopon; deep border furrows; large, and posteriorly positioned eye lobe. The only appreciable differences between the two forms are the more slender eye ridges of *G.* sp. C and wider (tr.) librigenae.

Although recognizing that *G*. sp. A, *G*. sp. B and *G*. sp. C are probably specifically distinct from each other, and from the other species of *Gondwanaspis*, they are left in open nomenclature due to the paucity of material.

Gondwanaspis aff. *mrirtensis* Feist, 2002
Figure 5f–h

Material. UMC-IP 552 (Fig. 5f–h), an incomplete cephalon and UMC-IP 553, a fragmentary pygidium from southeastern flank of Mont Peyroux hill at 500 m NW of Causses-et-Veyran village, Montagne Noire, Southern France, Coumiac Formation, Zone 12, late Frasnian.

Remarks. This incomplete cephalon shows a number of features in common with the type species, *G. mrirtensis*. It shares similar tuberculation, poorly defined lateral glabellar lobes, same orientation and width of the eye ridges and comparable size and position of the eye lobes. However, it differs in the presence of deeper exsagittal furrows between L1 and L2 and the median glabellar lobe and in possessing a slightly narrower median glabellar lobe than the type species.

Compared with contemporaneous species from the Canning Basin it certainly has appreciably coarser tuberculation than both *G. dracula* and *G. spinosa*. Like these species it has a relatively small eye lobe but an angle of convergence of the eye ridges that is closer to *G. spinosa* than it is to *G. dracula*. It is comparable with *G. dracula* in having poorly defined lateral glabellar lobes.

Gondwanaspis prisca sp. nov.
Fig. 5d, j–l, n, o

Type material. Holotype, cephalon UMC-IP 554 (Fig. 5k, l, n); paratypes, a small cephalon UMC-IP 555 (Fig. 5j), hypostome UMC-IP 556 (Fig. 5d) and a pygidium UMC-IP 557 (Fig. 5o), from Puech de la Suque, bed CPS-E 58 (Feist & Klapper, 1985), 1.1 km SE of St Nazaire-de-Ladarez village, Montagne Noire, southern France; Coumiac Formation, Zone 4, early Frasnian.

Other material. Six incomplete cephala and three hypostomes from same locality and horizon as type material (UMC-IP 558).

Etymology. From the Latin '*priscus'* meaning 'ancient', alluding to the stratigraphically early occurrence of this species.

Diagnosis. Glabellar relatively broad, with truncate anterior; preglabellar furrow short (sag.) and deep; lateral glabellar lobes relatively well defined and higher than adjacent narrow fixigenae; eye lobes positioned relatively close to posterior margin; eye ridges convergent at relatively low angle; genal angle only slightly advanced. Pygidium with axis wider than pleural field.

Description. Cephalon broad, with gently downwardly flexed anterior margin; gently convex. Glabella with moderately inflated glabellar lobes. Dorsal furrows shallow, more incised adaxially between median and lateral lobes. Lateral glabellar lobes L1 and L2 almost circular; separated from each other by shallow, narrow furrows. L3 very small. Median lobe broad, separated from lateral lobes by straight, relatively well-incised rectilinear furrows that deepen appreciably behind junctions of eye ridges with anterior median lobe, and opposite L2, and adjacent to anterior part of L1; very shallow opposite posterior of lobe. L1 almost as high as median lobe, but higher than adjacent fixigena. Frontal part of median lobe transverse; abaxially merging with adaxial ends of eye ridges. Narrow, relatively deep, straight preglabellar furrow encroaches on relatively well-defined border. Anterior border weakly inflated, broad; slightly downwardly flexed medially (tr.). Axial furrow shallow. Details of occipital ring unknown. Eye lobes relatively large, set closer to posterior border furrow than to anterolateral furrow (exsag.); equidistant between genal angle and axial furrow; positioned in line with L1. Eye ridges straight, narrow, widening slightly abaxially; converging at an angle of about 120°. Posterior border relatively broad; widens abaxially to fulcrum, which is three-quarters distance to genal angle, from where angles

cephalon, dorsal view. (e) *Gondwanaspis* sp. C, late Frasnian (Zone 13b), Virgin Hills Formation, Lawford Range, Canning Basin, Western Australia, WAM 07.107, right genal area, dorsal view. (f–h) *Gondwanaspis* aff. *mrirtensis* Feist, 2002, late Frasnian, Coumiac Formation, Causses-et-Veyran, Montagne Noire, France, UMC-IP 552, cephalon, dorsal, anterior and lateral views. (i) *Gondwanaspis tenella* Maximova, 1960, early Frasnian (Zone 2), Zolotukh brook near former Goryunovo village, Rudny Altai, Siberia, Russia, UMC-IP 559, incomplete cephalon, dorsal view. (d, j–l, n, o) *Gondwanaspis prisca* sp. nov., early Frasnian, Coumiac Formation, Col du Puech de la Suque, Montagne Noire, France; (d) UMC-IP 556, hypostome, ventral view; (j) UMC-IP 555, cephalon, dorsal view; (k, l, n) UMC-IP 554, holotype cephalon, anterior, dorsal and lateral views; (o) UMC-IP 557 pygidium, dorsal view. (m, p–s) *Gondwanaspis harborti* (Richter & Richter, 1926), late Frasnian; (m, q, r) GZG IN 010098, holotype, cephalon, lateral, anterior and dorsal views, latex cast of external mould, Winterberg, Harz, Germany, Iberger Kalk; (p, s) GZG IN 01009, cephalon, dorsal and lateral views, Dorp near Wuppertal, Germany, Dorper Kalk.

forward at about 30° to slightly advanced genal angle. Genal spine short, extending transversely. Details of posterior border furrow unknown; anterolateral border furrow shallow. Anterolateral border wide, gently rounded, carrying row of equi-spaced secondary tubercles; anterolateral librigenal border with 12 long, slender, cylindrical spines perpendicular to border and gently declined. Surface sculpture comprises sparse scattering of secondary tubercles on eye ridges and glabellar lobes, becoming more concentrated on librigenae.

Hypostome wider than long, narrowing posteriorly; middle body wider than long, swollen and coarsely tuberculate; median furrow weakly incised, fading out sagitally; lateral borders weakly convex, with ill-defined border furrows; posterior border and furrow even more indistinct; unlike median lobe, borders have a fine, sparsely distributed tuberculation.

Pygidium three times wider than long, excluding spines; triangular axis elevated and wider (tr.) than pleural field. Axial furrow deep posteriorly behind first axial ring; anteriorly shallow as it passes first axial ring. Axis comprises two axial rings and terminal end-piece, which is almost as long as second axial ring. Axial ring furrows continuous, almost straight. First axial ring prominent. Pleural ridges short, convex, curved, extending continuously into wider main border spines, slightly swelling at junction with posterolateral border; abaxially separated from pleural field by well-incised furrows; adaxially pleural ridges less well defined from small, recessed inner pleural areas. Outer pleural areas slightly depressed; anteriorly bounded by border that widens abaxially. Lateral and posterior borders broad, gently convex; border furrow shallow. Major border spines slender; length unknown; moderately divergent. Distance at base between major border spines less than twice width of first axial ring (tr.). Anterolateral and posterior margins with more slender secondary border spines; the four between the primary spines extending almost exsagittally, outer pair sightly recurved adaxially. Prosopon on borders and spines consists of dense concentration of relatively fine tubercles; small number of larger tubercles scattered on pleural ridges and major spines.

Remarks. Although it is not known whether this acidaspidine possessed spines or protuberances on its anterior border, it possesses sufficient other features to warrant its emplacement within *Gondwanaspis,* including the downwardly flexed anterior border. It is one of the earliest known species of the genus, occurring in the early Frasnian. It shows a number of significant differences to *G. mrirtensis*, which is one of the last species of the genus, having been recorded from the latest Frasnian (Zone 13b), just prior to the Upper Kellwasser Event, in both Morocco and the Montagne Noire (Feist, 2002, p. 205; Feist & Schindler, 1994, p. 211, pl. 4, figs 1, 2). *G. prisca* possesses a relatively wider median glabellar lobe, more convergent eye ridges, more posteriorly positioned eye that is set closer to the posterior border than to the anterolateral border; less advanced genal angle; shorter genal spine; more truncated anterior margin of the median glabellar lobe; more defined lateral glabellar lobes; and eye ridge that is distally wider. In many of these features it approaches *G. harborti* (see below).

Of the Canning Basin forms it most closely resembles *G. spinosa* in terms of its weakly developed tuberculation and more well-defined lateral glabellar lobes. However, *G. prisca* differs in its possession of a wider median glabellar lobe, broader eye ridges that are more convergent due to the more posteriorly positioned eye lobe. Of all the different forms of *Gondwanaspis*, this one has eye lobes closest to the glabella. The pygidia of *G. prisca* and *G. spinosa* are similar, but the Montagne Noire pygidium is narrower, with a broader axis anteriorly and larger terminal end-piece.

G. prisca differs from *G.* aff. *mrirtensis* from younger strata in the Montagne Noire in its weaker tuberculation, broader glabella with more well-defined lateral glabellar lobes and more anteriorly truncate median glabellar lobe and larger, more posteriorly positioned eye lobes.

Gondwanaspis harborti (Richter & Richter, 1926)
Figure 5m, p–s

1926 *Ceratocephala (Leonaspis) harborti* Richter & Richter, pp. 107–9, pl. 7, fig. 17.
1960 *Acanthaloma harborti* (Richter & Richter); Maximova, p. 69.
1968 *Dudleyaspis harborti* (Richter & Richter); Bruton, pp. 35, 37.
1975 *Dudleyaspis harborti* (Richter & Richter); Hahn & Hahn, p. 73, pl. 1, fig. 3.
1983 *Dudleyaspis harborti* (Richter & Richter); Chatterton & Perry, p. 44.
1984 *Dudleyaspis*? *harborti* (Richter & Richter); Ramsköld, p. 246.
2002 *Gondwanaspis*? *harborti* (Richter & Richter); Feist, pp. 204–5.
2004 *Gondwanaspis*? *harborti* (Richter & Richter); Basse & Müller, p. 140, *non* pl. 51, fig. 662.

Material. Holotype, GZG IN 010098 (Fig. 5m, r, q) from Winterberg near Bad Grund, Harz Mountain, Germany, Iberger Kalk. Additional cephalon, GZG IN 010099 (Fig. 5p, s) from Dorp village near Wuppertal, Germany, Dorper Kalk. Zone 11/12, late Frasnian.

Diagnosis. Lateral glabellar lobes relatively well defined for genus; 3p small; eye lobes set closer to posterior border than to anterolateral border; eye ridges converge at relatively low angle; posterior border furrow deep; genal angle weakly advanced; genal spine is moderately recurved; prosopon of dense, relatively coarse tuberculation.

Remarks. This species has had a chequered history in terms of its generic assignment, having been placed at various times in *Leonaspis*, *Acanthaloma* and *Dudleyaspis*. More recently Feist (2002) and Basse & Müller (2004) have suggested that it could possibly be accommodated within *Gondwanaspis*. Revision of this genus, and provision of more morphological information from another specimen from Wuppertal (Fig. 5p, s) confirm that this species belongs in *Gondwanaspis*. Like other species in this genus it possesses a deep and wide preglabellar field (Fig. 5r); rectangular central glabellar lobe with transverse anterior margin; downwardly flexed anterior border (Fig. 5s); weakly swollen posterior fixigenae; straight eye ridges; and broad librigenae. It is not clear whether or not spines are present on the anterior border of the cranidium.

G. harborti differs from the type species, *G. mrirtensis*, in its narrower cephalon; more well-defined lateral glabellar lobes, including L3; more posteriorly positioned eye lobes and more convergent eye ridges; less advanced genal angle and coarser tuberculation. G. *harborti* most closely resembles *G. prisca* from the early Frasnian of Montagne Noire. However, *G. harborti* has a less truncate anterior glabellar margin; distinctly developed L3 and more defined L1 and L2; smaller eye lobes; deeper posterior border furrow and coarser

tuberculation. Similarities to the late Frasnian form *G.* sp. C from Western Australia have been noted above. However, *G. harborti* can be distinguished by having a slightly less advanced, more recurved genal spine and smaller eye lobes. The form from Wuppertal-Elberfeld, Germany that Basse & Müller (2004) assigned to *G.* cf. *harborti* is not conspecific. Unlike *G. harborti* it has narrower posterior fixigenae and librigenae and more ill-defined lateral glabellar lobes.

Gondwanaspis tenella (Maximova, 1960)
Figure 5i

1960 *Acanthaloma (Acanthaloma) tenella* Maximova, pp. 68–9, pl. 8, fig. 14.

Material. An incomplete cephalon, UMC-IP 559, from Rudny Altai, southern Siberia, Russia; right bank of Zolotukh brook near former Goryunovo village, locality 0320 (Yolkin *et al.* 2005), Zone 2, early Frasnian.

Remarks. Maximova (1960) described this species on the basis of a single, complete cephalon. More recently an incomplete right genal area has been found at the type area and is figured herein (Fig. 5i). Although Maximova assigned this species to *Acanthaloma*, the broad cephalon, wide genal areas, downwardly flexed anterior border, long, narrow marginal spines and weakly developed lateral glabellar lobes all indicate this species should be included within *Gondwanaspis*. It shows some similarities to *G. harborti*, but differs in having a wider median glabellar lobe, less defined lateral glabellar lobes, and more anteriorly positioned eye lobe. It compares with *G.* sp. C from Western Australia, particularly in the prosopon, but it has a smaller, more advanced eye lobe. *G. tenella* is also similar to *G. dracula*, but it lacks the fang-like anterior spines and appears to have a slightly more convex cephalon and less advanced genal angle. Unlike *G. mrirtensis*, *G. tenella* has a less truncate anterior margin of the glabella, more swollen lateral glabellar lobes; deeper border furrows and a less advanced genal angle.

4. Heterochrony and functional morphology in *Gondwanaspis*

4.a. Heterochrony

The ontogenetic development of *Gondwanaspis* is not known. However, the ontogenies of a number of odontopleurids have been described in detail, such as by Whittington (1956*b*), Chatterton (1971) and Chatterton & Perry (1983). These show, as these authors have noted, a number of consistent patterns of ontogenetic change from protaspids to holaspids between a variety of odontopleurid genera, such as *Leonaspis, Dudleyaspis, Diacanthaspis* and *Acidaspis*. These include the following:

(1) Lateral glabellar lobes L1 and L2 appear and increase in size to become well defined in holaspids.
(2) Eye lobes move back from opposite L2 to L1. Consequently the angle of convergence of the eye ridges decreases. The eyes also move closer to the glabella, thus the fixigena becomes narrow.
(3) Tubercles increase in abundance as the primary spines disappear, except for the occipital spine.
(4) Glabella expands anteriorly so the anterior margin changes from being transversely truncate to convex forward.
(5) The occipital spines decrease in size.
(6) There is a loss of fixigenal spines.

On the basis of these ontogenetic changes it can be argued that a number of features that characterize *Gondwanaspis* holaspids are the product of evolution by paedomorphosis. These relate to the first four ontogenetic characters listed above. This is reflected by *Gondwanaspis* holaspids possessing features characteristic of other odontopleurid meraspids, such as weakly swollen lateral glabellar lobes; eye lobes that in some species are anteriorly positioned opposite, in part, L2; paucity of tubercle development in many, although not all, species; and frontal lobe of the glabella that is truncate or barely convex forwards. Absence of an occipital spine, however, is a peramorphic feature, as its absence in *Gondwanaspis* holaspids continues and extends the trend seen in odontopleurid ontogenetic development.

4.b. Functional morphology

As with many other odontopleurids the anterolateral margin of the cephalon of *Gondwanaspis* carries a series of border spines. Anterior to the genal spines there are 12 pairs of librigenal spines, and in the case of some species of *Gondwanaspis*, a further two pairs are carried on the anterior margin of the cranidium. Compared with other morphologically similar odontopleurids, such as *Leonaspis, Primaspis, Dudleyaspis* and *Acidaspis*, these spines are particularly long (Fig. 4g, k, p). Most authors have argued that the function of such border spines in odontopleurids was to enable the trilobite to rest upon the substrate (Whittington, 1956*a*,*b*; Clarkson, 1969). In a detailed study of *Leonaspis deflexa* (Lake, 1896), Clarkson (1969) proposed that the cephalon could have been orientated in two attitudes during life. In one, the 'resting' phase, the thoracic spines, genal spines and the tips of the posterior few lateral border spines were in contact with the substrate. In this attitude the anterior margin was raised off the level of the substrate (Clarkson, 1969, figs 5B, 6B).

Clarkson further argued that the trilobite could also have adopted an 'active' attitude, in which the cephalon was tilted forward, and the cephalon was only in contact with the substrate on the tips of the anterior-most few pairs of lateral border spines (Clarkson, 1969, figs 5A, 6A). The effect of this attitude was to bring the anterior margin in close contact with the substrate, thus effectively closing the anterior arch. As a result, the hypostome would have been brought close to the substrate, perhaps into a feeding position.

One of the characteristic features of *Gondwanaspis* that distinguishes it from *Leonaspis*, and from similar forms such as *Primaspis, Dudleyaspis* and *Acidaspis*,

is the absence of an anterior arch. This is due to the downward flexure of the anterior border (Figs 4c, l, 5q, s). When the cephalon of *Gondwanaspis* was orientated into a position where the animal would have been resting on its outwardly stretched, albeit short, genal spines, in a 'resting' attitude, the lateral border spines would have spread out such that the outer tips of almost all of the librigenal spines would have been in contact with the substrate (Fig. 4l). In this attitude the anterior margin would have been curved down close to the substrate and the tips of the four spines that issue from the anterior margin in some species would also have rested on the substrate, providing enhanced cephalic stability. Thus the trilobite would simultaneously have been in the 'resting' and 'active' attitudes.

It would therefore seem that the last of the odontopleurids had evolved the ability to combine the 'resting' and 'active' attitudes that are thought to have been separate behaviours in *Leonaspis* and other odontopleurids. Thus *Gondwanaspis* could, at the same time, have rested upon its genal spines, all of its librigenal spines, and have a closed anterior arch, with further support being provided in some forms, by the spines on the anterior cranidial margin. Attainment of this stance was also enhanced by the presence in *Gondwanaspis* of broad genal areas and low convexity. As a consequence it was functionally imperative for the eye to be positioned in a distal position to reduce what otherwise would have been an appreciable lateral blind spot.

5. Odontopleuroid extinction patterns

Odontopleurids were severely affected by the end of the mid-Givetian when the Taghanic onlap (Johnson, 1970) caused worldwide deepening of neritic habitats to which these trilobites had been adapted during early and mid-Devonian times. On the basis of the material described herein we have been able to show that the Odontopleurinae reached the Taghanic Event, with three genera, *Radiaspis*, *Leonaspis* and *Kettneraspis*, becoming extinct at this event. By contrast to previous knowledge, the Koneprusiinae, in the form of new species of *Koneprusia*, survived into the late Givetian when, adapting successfully to deeper water conditions, it radiated into outer platform, open-shelf environments during the Frasnian. The last representative currently known of this subfamily occurred in late Frasnian times in equivalent off-shore conditions. It probably fell victim to the destabilizing Lower Kellwasser Event when the sea floors of outer shelf margins of northwestern Gondwana and southern Laurussia were invaded by a short period of oxygen-depleted waters.

The only other post-Taghanic odontopleurid of the outer shelf realm, the acidaspidine *Gondwanaspis*, is of cryptogenic origin. Not yet known from the late Givetian, it occurs throughout the Frasnian around the margins of the Prototethys (Fig. 2), to which it remained restricted. In contrast to *Koneprusia*, *Gondwanaspis* seems not to have been affected by the Lower Kellwasser Event at the generic level, but became extinct shortly thereafter when major eustatic perturbations initiated the global end-Frasnian mass extinction (Upper Kellwasser Event). However, of the five species described from the late Frasnian in the Canning Basin, three became extinct at the Lower Kellwasser Event. Two species post-date this event, but became extinct at the Upper Kellwasser level. Interestingly, these two forms, though rare, show relatively wide disparity. Similarly, the scutelluine *Telopeltis* was affected at the species level by the Lower Kellwasser Event in the Canning Basin, and at the generic level by the Upper Kellwasser Event (McNamara & Feist, 2006).

The final demise of *Gondwanaspis*, and thus of the entire Odontopleuroidea, apparently resulted from the extreme impoverishment of its diversity during the late Devonian, both in number of taxa and contraction in its geographical distribution (Fig. 2). All the final representatives were adapted to deeper water level-bottom conditions of the open cephalopod realm. They became trapped in this environment when extrinsic constraints, such as oxygen and bathymetric conditions, suddenly changed, leaving insufficient time for new adaptations and the establishment of new evolutionary pathways.

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