

THE TRILOBITE FAMILY NILEIDAE: MORPHOLOGY AND CLASSIFICATION

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ABSTRACT. Species of genera currently referred to Nileidae are reviewed, and those of *Hemibarrandia*, *Lakaspis*, *Peraspis* and *Symphysurina* are excluded from the family. Nileidae are united in having a distinctive form of the hypostome, the glabellar organ, in the shallowness or absence of external furrows on the axial and pleural regions, and in the development of strong ventral ridges on the axial region. It is contended that the glabellar organ of nileids and illaenids may not be homologous with the glabellar tubercle of asaphids, that the median ventral suture is not exclusively a character of Asaphina, and doubt is cast on the identification of an asaphoid protaspis as being that of *Nileus*. These arguments provide a case for allying Nileidae with the Illaenidae, rather than with the Asaphina.

KEY WORDS: Trilobita, Nileidae, morphology, Cambro-Ordovician.

IN commenting on the use of characters and the progress made in the classification of trilobites, and in particular on placement of Styginidae and Illaenidae (Whittington 2000), I brought forward new evidence for considering that species of *Nileus* might be better considered as related to Illaenidae than included in Suborder Asaphina. Here this suggestion is explored further in a review of species (particularly the type species) of genera currently placed in the Nileidae. Reasons for excluding *Hemibarrandia*, *Lakaspis*, *Peraspis* and *Symphysurina* from the family are given. Characters common to the restricted Nileidae are summarised, and my doubts are rehearsed regarding the validity of particular characters as sufficiently established to justify including Nileidae (and possibly also Cyclopygidae) in Asaphina. My tentative conclusion is that Nileidae are best regarded as allied to Illaenidae. It is tentative because, while some nileid species are relatively well known from entire exoskeletons, others are known only from incomplete or isolated parts of exoskeletons. Thus critical morphological details of the thorax or doublure are unknown, and isolated cranidia or pygidia lack distinctive features. A more general difficulty in trilobite classification is the lack of understanding of the evolutionary pathways linking Cambrian trilobites to the much more clearly defined families that are present from early post-Cambrian time onwards.

Terminology follows that of the revised Treatise (Whittington and Kelly *in* Kaesler 1997, p. 313). The term *glabellar organ* was introduced (Whittington 2000, pp. 879, 881) for the depression in the visceral surface of the glabellar exoskeleton (seen as a tubercle on the internal mould) lying in a transverse line passing through the posterior portion of the eye lobe. It was described from polished sections (Fortey and Clarkson 1976) in *Nileus armadillo*; because the exoskeleton is thin over the top of the organ these authors considered it may have been light receptive. The term nonfulcrate (Whittington and Kelly *in* Kaesler 1997, p. 51) describes the condition of the thoracic pleura which curves downward and outward from the axial furrow in a smooth curve, so that it lacks the inner, horizontal portion of the fulcrate pleura. When this inner portion is reduced greatly in width (tr.) the pleura may appear nonfulcrate, as in species of *Nileus*, referred to below.

SYSTEMATIC PALAEOLOGY

Family NILEIDAE Angelin, 1854

Discussion. The genera assigned to this family are commented on below, the nominate genus *Nileus* first, others in alphabetical order. Notes on genera excluded from the family follow. Unifying features of the

restricted family include the glabella which may expand forward in front of the eye lobes, the lack of a palpebral rim in the large-eyed species, the presence of the glabellar organ and lack of an occipital furrow, the narrow (tr.) fixed cheek, the hypostome bilobed in outline with a small median posterior projection, the fulcrate thorax with shallow, or no pleural furrows, and the paucity of inter-ring and pleural furrows on the external surface of the pygidium. In addition is the strong ventral ridge developed beneath the articulating furrow of the axial ring or in the corresponding position when the articulating furrow is absent. It was the presence of this latter feature in *Nileus*, together with the glabellar organ and absence of transverse furrows in the axial region, that led me (Whittington 2000) to suggest that *Nileus* was related to Illaenidae rather than to Asaphidae. I now extend this view to considering that Nileidae should be allied with Illaenidae rather than the Asaphina. In addition to *Nileus*, *Platypeltoides* (= *Varvia*), *Poronileus*, *Symphysurus* and also *Aocaspis* show these illaenid-like characters. *Barrandia*, and the similar *Homalopteon*, have the nileid hypostome, but the glabellar organ has not been recognized; they presumably belong in the family. *Illaenopsis* is distinguished from them by the small eye lobe and broader (tr.) fixed cheek. *Kodymaspis* and *Parabarrandia* have the glabellar organ, and the nileid hypostome is known in the type species of the latter genus; both have the genal spine. *Elongatanileus*, *Shenjiawania* and *Troedssonina* are all incompletely known from portions of the exoskeleton, but appear to be nileids.

Fortey and Chatterton (1988, p. 198) rehearsed their argument for classifying the Nileidae (with the Cyclopygidae) in the Suborder Asaphina. There are characters used in this argument which I question:

1, that the glabellar organ in nileids is homologous with the posterior glabellar tubercle characteristic of many asaphids. The tubercle in asaphids is prominent on the external surface (as well as being visible on the internal mould) and so may not have thin cuticle over the apex, as does that of *Nileus*. The assumption of homology between these distinctive features may be incorrect;

2, an asaphid type of protaspis (Chatterton and Fortey 1988, p. 184) is assigned to nileids. The transition between this protaspis and the early meraspid cranidium and pygidium has yet to be clearly demonstrated. Further, species of *Peraspis*, in addition to those of *Nileus* and *Poronileus*, occur in the strata yielding this protaspis. If, as I suggest below, *Peraspis* is an asaphid and not a nileid, then the protaspis may be that of an asaphid. A keyhole-shaped indentation in the posterior margin of the supposed nileid protaspis is distinctive. I note that the bilobed posterior outline of the early meraspid pygidium of the asaphid *Stegnopsis* (Whittington 1965, pl. 23, figs 6–7, 9–10) could have been inherited from such an indentation in the protaspis;

3, emphasis is placed on the median ventral suture as a unifying feature of Asaphina, and such a suture is present in the early nileid *Platypeltoides* (= *Varvia*, see below) and in the early cyclopygid *Prospectatrix* (now widely known; e.g. Zhou *et al.* 1994). This suture, though so characteristic of Asaphina, is not confined to this group, and is present in quite different Upper Cambrian trilobites. Rasetti (1952), for example, observed its presence in *Leiocoryphe*, *Stenopilus* and *Theodenisia*.

Poulsen (1927, p. 231) proposed the Family Symphysuridae to include the genera *Nileus*, *Symphysurus*, and with question *Symphysurina*, for trilobites which lacked the rostral plate. Because the family Nileidae had been proposed earlier, it became the practice to use Nileidae rather than Symphysuridae to include the first two of these genera and those erected subsequently (e.g. Poulsen *in* Moore 1959). Poulsen (1927, p. 329) remarked on the illaenid-like characters of *Nileus*, and combined with my views expressed above, this might lead to isolating *Nileus* (and probably *Poronileus*) as of illaenid affinity, and placing the other genera in the Symphysuridae. I do not advocate this procedure, because of the characters that *Nileus* shares with the other genera regarded as nileids here. In proposing his new Middle Cambrian genus, *Prosymphysurus*, Poulsen (1927, p. 279) regarded it as a possible ancestor of *Symphysurus*, so relating symphysurids to the Dolichometopidae, a relationship quite different from others proposed subsequently.

Nileids are best known from the Ordovician of Scandinavia, Spitsbergen, the United Kingdom and Ireland, North America and the Czech Republic (probably a reflection of intensive collecting and publication), with *Nileus* being the most widespread (Nielsen 1995, p. 199). In China the earliest record is of *Troedssonina* in the very late Cambrian, with many species of this and other genera recorded from the Ordovician.

Genera included in Nileidae

NILEUS Dalman, 1827

Discussion. Species of this genus, including the type species *N. armadillo* Dalman, 1827, have been described in recent years by Nielsen (1995) and Schrank (1972) from the Ordovician of Scandinavia, by Fortey (1975) from Spitsbergen, and by Whittington (1963, 1965) from Newfoundland. In further comment on these species I drew attention (Whittington 2000, p. 880) to the presence of the glabellar organ in *Nileus*, and to the lack of transverse furrows on the external surface of the axial exoskeleton, and to features on the visceral surface of the thorax. As Nielsen's many photographs show well (e.g. Nielsen 1995, figs 181F, 149F) traces of muscle attachment areas in the glabella, thorax and pygidium, and of inter-ring furrows in the pygidium, may be visible on the visceral surface, as revealed by internal moulds. A feature of *Nileus* on which I did not comment is the apparently non-fulcrate form of the pleurae of the thorax, the even curve outward and downward of the pleurae, in conformity with the curve of the posterior margin of the cephalic cheek. This is clearly exhibited by enrolled specimens (e.g. Whittington 2000, fig. 1.2), which have no inner, horizontal portion of the pleura. These specimens (Whittington 2000, fig. 1.3) also show the main axial articulating process, a large backward-facing boss fitting into a socket in the axis of the following segment, a process common to many different trilobites. However, in certain species of *Nileus* (e.g. Schrank 1972, pl. 10, fig. 1; pl. 11, fig. 1; Nielsen 1995, fig. 182B) a ridge is present on the inner edge of the pleural facet, which immediately outside the axial furrow projects to form an additional, more dorsal articulating process which fits into a small socket on the posterior margin of the cephalic border, or this margin of the pleura in front. In *N. scrutator* a narrow (exs.) horizontal inner portion of the pleura, with an articulating process at the fulcrum, is retained (Whittington 1965, pl. 30, fig. 12; pl. 31, fig. 9). Thus in species of *Nileus* the horizontal, inner portion of the pleura may be narrow (tr.) or reduced almost to disappearance, in the latter case leading to the pleurae appearing nonfulcrate.

AOCASPIS Dolambi and Gond, 1992

Discussion. Entire exoskeletons of the type species, *Platypeltis? macrophthalmus* Thoral, 1935, are described from the Ordovician (late Tremadoc–early Arenig) of the Montagne Noire. They resemble specimens of *Platypeltis* and *Varvia*, show the typical nileid type of hypostome, have seven thoracic segments, the inner, horizontal portion of the pleura narrow (tr.) on the anterior segment, becoming wider backward; the broad-based genal spine recalls that of *Kodymaspis*.

BARRANDIA M'Coy, 1849

Discussion. The type species of *Barrandia*, *B. cordai* M'Coy, 1849, was described by Hughes (1979), together with other slightly different species. Earlier work by Whittard (1961, p. 221, pl. 32) on *B. homfrayi* Hicks, 1875, shows such details as the wide (tr.) doublure of the free cheek, the hypostome in place, and the external sculpture; additional material from South Wales was described by Fortey and Owens (1987). These species of *Barrandia* are known only from Shropshire and Wales, in rocks of late Arenig–early Llandeilo age. *Barrandia* is distinguished from the older *Symphysurus* largely by the less prominent eye lobe, deep furrow dividing the middle body of the hypostome, the presence of a genal spine, and the pleural furrow of the thorax. The doublure in *Symphysurus* is not well known, but in the cephalon of *Barrandia* it extends inward close to the eye lobe, and to the fulcrum; internal moulds show that it extends inward to the fulcrum of the thorax and pygidium.

Illaenopsis thomsoni Salter, 1866, type species of the genus from the Llanvirm of Shropshire, was described by Whittard (1961), and a second species, *I. harrisoni*, from the Arenig of the Lake District and South Wales by Fortey and Owens (1987). These species differ from those of *Barrandia* chiefly in that the small eye lobe is situated far forward in the anterolateral portion of the cheek, and the posterior branch of the suture lies close to the outer margin of the cheek; the pygidium has the doublure less extensive beneath

the pleural region, the inner margin parallel to the posterolateral margin. The hypostome is not known. Other species are recorded from the Lower Ordovician of France and Bohemia.

Homalopteon portlockii Salter, 1866, type species of the genus from the Caradoc of southern Ireland, was redescribed by Owen *et al.* (1986), subsequent to the redescription of Welsh Llandeilo material of *H. radians* (M'Coy, 1849) by Hughes (1979). The species differ from the largely older species of *Barrandia* chiefly in showing four shallow pairs of glabellar furrows, and in having a pygidium with inter-ring and pleural furrows, the inner margin of the doublure subparallel to the posterolateral margin.

The species of these three genera are mainly known from flattened exoskeletons; uncommon are the specimens which show the probable original convexity (e.g. Whittard 1961, pl. 33, fig. 1; Fortey and Owens 1987, fig. 68a–b, e). Hence comparisons between them are difficult to make, and rarely (e.g. Fortey and Owens 1987, fig. 68a–b) is reference made to the presence of the glabellar organ. Whether the obvious differences, such as the small eye lobe in species of *Illaeonopsis*, justify the use of three generic names is debatable. Fortey and Owens (1987, pp. 193–194) gave their reasons for considering that *Rokycania* Přibyl and Vaněk, 1965, *Procephalops* Whittard, 1966, *Pseudobarrandia* Courtessole and Pillet, 1976, and *Eurymetopus* Postlethwaite and Goodchild, 1886, are synonymous with *Illaeonopsis*, and that their type species are also like those of *Borthaspidella* Rasetti, 1954, and *Psilocephalinella* Kobayashi, 1951. The type species of these latter two genera are too incompletely known for further assessment of the likeness.

ELONGATANILEUS Ji, 1986

Discussion. The type species, *E. convexus* Ji, 1986, was based on isolated, convex cranidia, having a large palpebral lobe, from the Pagoda Limestone, Upper Ordovician, of south China. Similar material from south Thailand has been described by Fortey (1997), who compared and contrasted its characters with those of *Peraspis* and *Poronileus*.

KODYMASPIS Prantl and Přibyl, 1949a

Discussion. Originally proposed as a subgenus of *Symphysurus* by Prantl and Přibyl, with the type species *S. (K.) puer* (Barrande, 1872) from the Llanvirn of the Czech Republic, differing in having a broad-based genal spine. The specimens figured by Prantl and Přibyl (1949a, pl. 2, figs 1–2) have been refigured respectively by Fortey (1975, pl. 19, fig. 10) and Horný and Bastl (1970, pl. 5, fig. 5). Fortey (1975, p. 51) commented that the supposed occipital furrow is an axial ring of a thoracic segment exposed beneath the broken posterior edge of the glabella. Prantl and Přibyl (1949a, p. 6) commented that the thoracic pleurae are smooth, and the photographs show the absence of the pleural furrow. The hypostome is not known.

PARABARRANDIA Prantl and Přibyl, 1949b

Discussion. Originally proposed by Prantl and Přibyl as a subgenus of *Barrandia*, with the type species *bohémica* Novák, 1884, from the Llanvirn of the Czech Republic (see Horný and Bastl 1970, pl. 5, fig. 3; Chlupáč *et al.* 1998, pl. 15, fig. 2). The forwardly-projecting glabella and apparently flattened pygidial border are distinguishing characters, and Prantl and Přibyl (1949b, figs 1–2) show a tubercle on the glabella, presumably the internal mould of the glabellar organ. Other species from the Tremadoc and Llandeilo of the Czech Republic show the typical nileid hypostome, and have a genal spine.

PLATYPELTOIDES Přibyl, in Prantl and Přibyl 1949b

Discussion. Additional material of the type species, *croftii* Callaway, 1877, from the Tremadoc of South Wales, was described by Fortey and Owens (*in* Owens *et al.* 1982, p. 11). This shows that the dorsal exoskeleton is *Symphysurus*-like, having a large eye lobe, the typical nileid hypostome, and seven fulcrate

thoracic segments. It has a median cephalic suture, which these authors regarded as a primitive feature that was subsequently lost.

PORONILEUS Fortey, 1975

Discussion. A stratigraphical succession of four species of this genus was described by Fortey (1975, p. 51), occurring with species of *Nileus* in the Ordovician of Spitsbergen. They are distinguished from those of *Nileus* by the pitted sculpture of the cephalon, the lateral border of the pygidium, and other minor features; they show that the glabellar organ and the hypostome is typical. In only the type species, *P. fistulosus*, is the fulcrate thorax preserved (Fortey 1975, pl. 12, figs 5, 9). The axial rings are largely exfoliated, showing laterally the smooth external surface, medianly the mould of a strong ventral ridge and the oval areas behind it (see Whittington 2000, p. 881, fig. 1, for these features in a species of *Nileus*). The pleurae are fulcrate, with a shallow pleural furrow and small fulcral process on the anterior margin. There seems no doubt of the close relationship between *Nileus* and *Poronileus*.

SHENJIAWANIA Peng, 1984

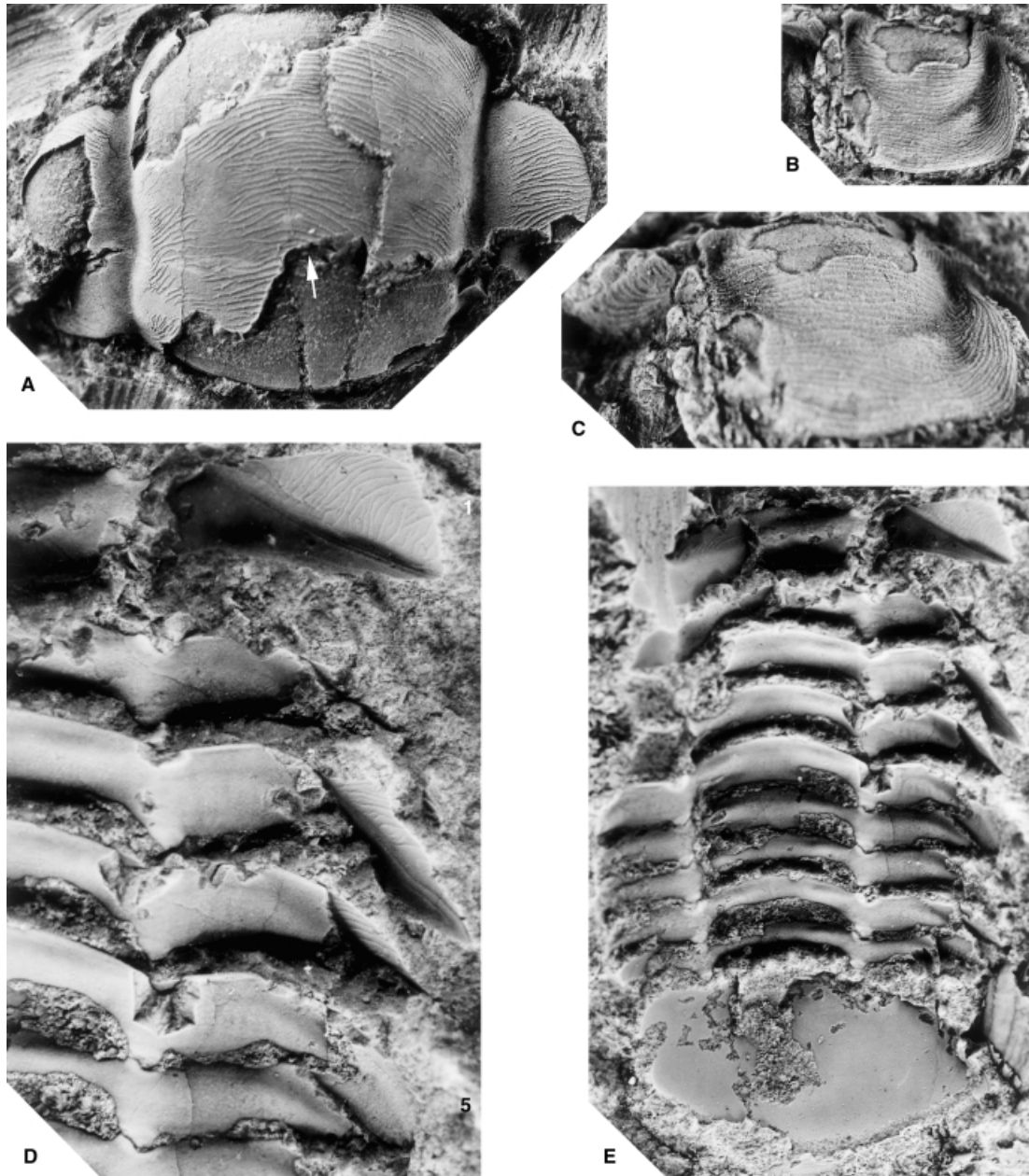
Discussion. The type species, *S. brevia*, is based on isolated cranidia and pygidia from the latest Cambrian strata of north-western Hunan. These specimens are similar to those of species of *Troedssonina* and *Platypeltoides*, and do not show characters that are obviously distinctive.

SYMPHYSURUS Goldfuss, 1843

Discussion. The type species, *S. palpebrosus* (Dalman, 1827), has been described by Fortey (1986); it and other species are present in Tremadoc and Arenig rocks in Scandinavia, Spitsbergen, Bohemia, Poland, southern France, Kazakhstan and China. Coaptative devices that enable close-fitting enrollment include vincular grooves in the cephalic doublure to receive pleural tips and the pygidial margin. The description of *S. angustatus* by Ebbestad (1999) includes a figure (66A) of a cast from an external mould of an exoskeleton. On the left pleural region the cast is of the external surface, and shows no pleural furrow in thorax or pygidium. On the right side of the cast the external surface of the pleural region is preserved only immediately adjacent to the axial furrow; distal to here the cast is of the inner surface of the exoskeleton. The latter shows (as furrows) the broad, shallow, diagonal ventral ridges of the pleural furrow of the thoracic segments and first pygidial segments, and the inner surface of the facets. In the axial region the inner surface of the exoskeleton of the thorax is shown medianly, as the under side of the articulating halfring, the transverse articulating furrow, and doublure of the axial ring; in the pygidium as the under side of some five inter-ring furrows. In this species and in the type species (Fortey 1986, p. 259) pleural furrows are lacking on the external surface, being expressed only as low ventral ridges. Ebbestad's (1999, fig. 66L) illustration of the external surface of the cranidium does not show all the specimen, and has been reversed in printing; the present illustration (Text-fig. 1A) shows the specimen more completely. The smooth patches that interrupt the terrace ridges are, as Ebbestad noted, like the muscle impressions illustrated by Rudolph (1992, pl. 7, figs 2–6). The glabellar organ, preserved as a tubercle on the internal mould (Ebbestad 1999, fig. 66C) is faintly raised on the external surface and interrupts the terrace ridges. The slightly distorted specimens of the hypostome (Ebbestad 1999, fig. 66F, I; Text-fig. 1B–C) show that in *S. angustatus* the median projection of the posterior margin of the hypostome is less prominent than in the type species (Fortey 1986, fig. 2), and that the large anterior wing is also twisted to lie vertical, and bears strong terrace ridges.

TROEDSSONIA Poletaeva, in Khalfin 1960

Discussion. The type species (originally designated by Poletaeva in Khalfin 1960, p. 418), is *Symphysurus* (?) *wimani* Troedsson, 1937, which was based on two cranidia, two pygidia being doubtfully associated with them. In this species the anterior portion of the glabella expands less than in the second species, *S.?*



TEXT-FIG. 1. A-C, *Symphysurus angustatus* (Sars and Boeck, in Boeck 1838) Tremadoc Bjørkåsholmen Formation, Oslo Region, Norway. A, PMO 1442b, incomplete cranidium partially exfoliated, external surface with terrace ridges and intervening smooth areas; arrow points to external surface of glabellar organ; $\times 5$. B-C, PMO H2688/2, hypostome partially exfoliated, ventral and oblique postero-ventral views; respectively, $\times 5$, $\times 10$. D-E, *Symphysurina brevis* Fortey, 1983, Tremadoc, *Symphysurina*-Zone conglomerate (B1), Broom Point South, western Newfoundland; ROM 42314, thorax having exoskeleton attached and showing visceral surface except where exfoliated, pygidium exfoliated and showing external mould. D, enlargement of partially exfoliated thorax of specimen in E, segments 1, 5, numbered; $\times 10$. E, entire specimen; $\times 4$.

anderssoni, described by Troedsson, and the palpebral lobe is smaller. Hence the criteria of greater expansion of the anterior portion of the glabella, and smaller eye, than in *Symphysurus*, as used to define *Troedssonia* by Lu and Zhou (1990, p. 39), are open to question. These authors discussed many Chinese and European species, and also how species of *Troedssonia* differ from those of *Platypeltoides*. All these species are *Symphysurus*-like, and *Troedssonia* has been regarded as a subgenus of *Symphysurus* (e.g. Zhou and Zhang 1984, p. 134) or of *Platypeltoides* (Peng 1991, p. 158); they occur in rocks of latest Cambrian–Early Ordovician age.

VARVIA Tjernvik, 1956

Discussion. Tjernvik (1956) described the type species *Symphysurus breviceps* Angelin, 1854, and two additional species from Tremadoc and Arenig strata in Sweden. He noted how similar these species were to those of *Symphysurus*, but that they were distinguished by the median cephalic suture; they show the glabellar organ and the nileid type of hypostome. Material from the Tremadoc of Norway of *V. longicauda* Tjernvik was described by Ebbestad (1992, p. 92) and confirmed these opinions. The cast of the counterpart of the holotype of this latter species (Text-fig. 2B–C) shows the external surface of the glabella only on the right anterior area, the steep slope bearing terrace ridges. A faint convexity marks the position of the glabellar organ on the internal mould; at the posterior end of the axial furrow is a deep pit, the mould of the axial articulating process. The eight thoracic segments are most clearly shown by the pleurae on the left side of the part (Text-fig. 2A), those of the first two segments revealed where the cranium is broken. Exoskeleton is present on the outer portions of these pleurae, which show terrace ridges directed parallel to the posterior edge. Exoskeleton is also preserved in the inner portion of the pleura of segment 7, and shows that the pleural furrow was absent. On segment 8 the same portion is exfoliated to show the mould of a low ventral ridge. The axial rings of segments 7 and 8 are exfoliated to show a strong ventral ridge; on the extreme left of ring 7 where the exoskeleton is preserved there does not appear to be a corresponding articulating furrow. The pygidium shows on the external surface (Text-fig. 2B) and the mould of the visceral surface (Text-fig. 2A), features identical to those illustrated by Ebbestad (1999, fig. 69H–I). These include the shallow articulating furrow underlain by a strong ventral ridge, and the absence of pleural furrows. The Scandinavian material of *Varvia* retains much of its original convexity, hence is not readily comparable with the flattened material of *Platypeltoides croftii* from the Tremadoc shale of South Wales (Fortey and Owens in Owens *et al.* 1982, pl. 3, figs a–f). The latter species has seven thoracic segments which show distinct articulating and pleural furrows, but is otherwise very like species of *Varvia*; both have a median suture and the hypostomes are similar. Thus *Varvia* may be regarded as a synonym of the older *Platypeltoides*.

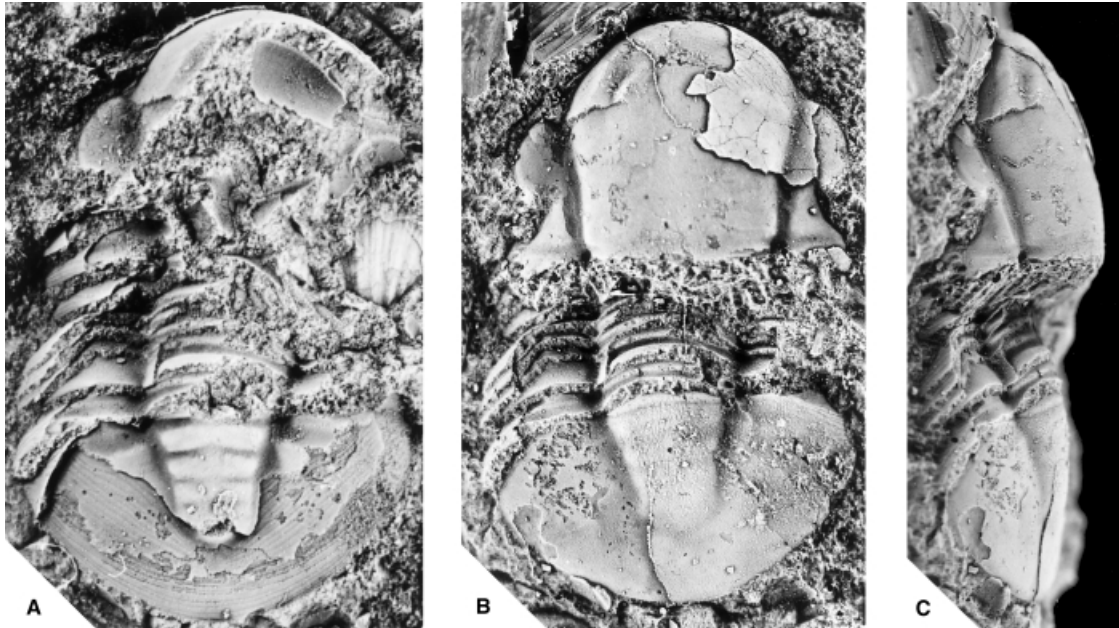
Genera excluded from Nileidae

HEMIBARRANDIA Prantl and Přibyl, 1949a

Discussion. Mergl (1994) has redescribed the type and additional material of *H. holoubkovensis* (Růžička, 1926), giving a restoration of the cephalon and noting the eight thoracic segments of this early Tremadoc type species from the Czech Republic. He suggested that *Hemibarrandia* may be an illaenid related to the Panderiinae Bruton, 1968, a subfamily which I (Whittington 1997, p. 884) included in the Illaenidae, as originally proposed by Bruton.

LAKASPIS Kobayashi, 1937

Discussion. The type species, *Symphysurus apolonista* Lake, 1906, is known only from a small cranium and pygidium collected from loose blocks of sandstone in northern Bolivia, the age of which is given as undifferentiated Ordovician by Hughes and Branisa (1985, p. 324). The original drawings (Lake 1906, pl. 11, figs 2–3) show a cranium having the eye far forward beside a forward-tapering glabella, a wide post-ocular cheek, and occipital and border furrows. The triangular pygidium lacks inter-ring and pleural



TEXT-FIG. 2. A–C, *Varvia longicauda* Tjernvik, 1956, Tremadoc Björkåsholmen Formation, Stenbrottet, Västergötland, Sweden; PMU Vg 248, original of Tjernvik, 1956, pl. 3, fig. 11. A, internal mould of incomplete specimen lacking free cheeks, dorsal view; $\times 5$. B–C, cast from external mould which has exoskeleton clinging to much of the cranidium and thorax, but not the pygidium, dorsal and left lateral views; $\times 5$.

furrows. There is no reason to regard these specimens as nileids; they resemble species of the Ordovician homalonotid *Brongniartella*, and were only doubtfully included in nileids by Poulsen (*in* Moore 1959, p. 358).

PERASPIS Whittington, 1965

Discussion. In describing (Whittington 1965, p. 363) new and old material of the type species, I assigned the genus to the Nileidae, primarily because of the lack of the median suture in the cephalic doublure. I stated that the thorax was of seven segments, but this is based on a single specimen (pl. 34, figs 1–2) in which some displacement has taken place. The hypostome I assigned to the type species (pl. 35, figs 6, 8) is isolated and from a different locality. I remarked on the asaphid-like pygidium of *P. lineolata*, and recently (Whittington 2000, p. 881) have noted that the glabellar tubercle, prominent on the external surface, is of the asaphid type, and that the thorax has the articulating furrow and halfring typical of asaphids. Thus *Peraspis lineolata* may be an asaphid that lacked the median suture, rather than a nileid.

Ross (1970), Dean (1973), and Fortey (1975) have described additional species of similar age to *Peraspis lineolata*, and referred them to this genus. The cranidia and the hypostome appear to be like that illustrated in place from Spitsbergen (Fortey 1975, pl. 19, figs 4, 8). Whether or not these species are truly asaphids remains uncertain, for they are not known sufficiently completely. If, for example, the thoracic pleurae of *P. lineolata* were known to show the characteristic doublure and panderian opening (e.g. Siegfried 1936) of asaphids, then I should be more certain of its relationships.

SYMPHYSURINA Ulrich, *in* Walcott 1924

Discussion. Fortey (1983), Dean (1990), Westrop *et al.* (1993) and Westrop (1995) have described old and new material of species, and discussed their affinities; all are of Ibexian age (Early Ordovician), and from

North America and Greenland. The glabella is parallel-sided and lacks occipital or lateral furrows, the glabellar organ situated in line with the posterior end of the eye lobe, which was close to the glabella. Internal moulds show a sagittal ridge, and Westrop (1995, pl. 4, figs 1–2) illustrated such moulds showing three pairs of raised, lateral oval areas, presumably muscle attachment areas. With its short (sag. and exs.) preglabellar area, rounded genal angle (in some species), and lack of well-defined borders, the cephalon of *Symphysurina* is, hence, like that of *Symphysurus*. Species of the former with genal spines are distinctive, as also is the row of vincular notches in the cheek doublure (e.g. Hintze 1953, pls 1–3); also shown by Hintze is the inward extension of the cheek doublure to the median ventral suture. The hypostome attributed to particular species by Poulsen (1937, pl. 2, figs 15, 19), Fortey (1983, pl. 26, fig. 6) and Westrop (1995, pl. 4, fig. 12) is in each case isolated, elongate in outline with large anterior wings and a convex middle body; it is unlike that of nileids. The fulcrate thorax of eight segments, with no, or only a shallow, pleural furrow, was shown by Hintze (1953, pl. 1, fig. 17). The pygidium of some species has a terminal axial spine.

The counterpart of the thorax and pygidium attributed to *Symphysurina brevis* (Fortey 1983, pl. 27, fig. 5) largely retains the exoskeleton, so that his illustration of a cast shows a mould of the visceral surface of the exoskeleton. On this surface (Text-fig. 1D–E) the ventral ridge of the axial rings is strongest laterally, and the axial articulating processes at the posterior edge, and sockets at the anterior edge, are prominent. The fulcrate pleurae have a low ventral ridge on the inner portion that becomes conspicuous below the fulcrum. On the left side (Text-fig. 1D), where the pleurae are most completely preserved, the outer portions of segments one, three and four have the exoskeleton broken away so that the external mould of the facet, bearing terrace ridges, is exposed. On the outer portion of the fifth pleura the doublure is preserved, the inner margin a deep V. The detached pygidium appears to be exfoliated and is featureless.

Symphysurina species have features in common with those of nileids, but are distinguished by the form of the hypostome (not known in place); only *Platypeltoides* and its synonym *Varvia* among Nileidae have a median suture. Further, *Symphysurina* is characteristic of Lower Ordovician rocks of Laurentia, while Nileidae are common in the contemporaneous strata of Baltica and Gondwana, the trilobite faunas having little in common. It may be that *Symphysurina* has a different ancestry from that of the Nileidae. Kobayashi (1955, p. 426), in proposing the Symphysurininae, regarded *Symphysurina* as an asaphid because it had a median suture, and this view was followed by Jaanusson (*in* Moore 1959, p. O353), Hupé (1955, p. 210) and Westrop *et al.* (1993, p. 1624). However, Westrop (1995, p. 19) departed from this classification, placing *Symphysurina* in the family Symphysurinidae of uncertain superfamilial relations. Fortey and Chatterton (1988, p. 200) were uncertain how to classify the genus, placing it alone in the subfamily Symphysurininae.

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