The Silurian and Devonian proetid and aulacopleurid trilobites of Japan and their palaeogeographical significance

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FOSSILS AND STRATA

THE LETHAIA FOUNDATION

Stocker, C.P., Siveter, D.J., Lane, P.D., Williams, M., Oji, T., Tanaka, G., Komatsu, T., Wallis, S., Siveter, D.J. & Vandenbroucke, T.R.A. 2019: The Silurian and Devonian proetid and aulacopleurid trilobites of Japan and their palaeogeographical significance. *Fossils and Strata*, No. 64, pp. 205–232.

Trilobites referable to the orders Proetida and Aulacopleurida are geographically widespread in the Silurian and Devonian strata of Japan. They are known from the South Kitakami, Hida-Gaien and Kurosegawa terranes. Revision of other Japanese trilobite groups, most notably the Illaenidae, Scutelluidae and Phacopidae, has extended the palaeobiogeographical ranges of several Japanese trilobite taxa, but has not signalled conclusive evidence of a consistent palaeogeographical affinity. In part, this may relate to the temporally and spatially fragmented Palaeozoic record in Japan, and perhaps also to the different ecological ranges of the trilobites. Here, we present a taxonomic revision of all previously described proetid and aulacopleurid trilobites from Japan, along with descriptions of new material, which comprises thirteen species (one new: *Interproetus mizobuchii* n. sp.) within nine genera, with three species described under open nomenclature. These trilobites show an endemic signal at species level, not just between Japan and other East Asian terranes, but also between individual Japanese terranes. This endemicity may be explicable in terms of facies and ecology, rather than simply being a function of geographical isolation. □ *Aulacopleurida, Devonian, Japan, palaeogeography, Proetida, Silurian.*

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Introduction

Silurian and Devonian marine successions in Japan comprise those of the South Kitakami Terrane of north-eastern Honshu, the Hida-Gaien Terrane of central Honshu and the Kurosegawa Terrane, which extends from the Kii Peninsula in southwest Honshu to the islands of Shikoku and Kyushu (Fig. 1). Strata in each of these terranes contain locally abundant fossil faunas including brachiopods, cephalopods, radiolarians, ostracods and trilobites (see Williams *et al.* 2014 for an overview).

The trilobite Order Proetida, combined with its sister group Aulacopleurida, constitutes the most widely represented and diverse group of trilobites in Japanese Silurian and Devonian rocks. Previous studies have described trilobites referable to twelve species within eight genera and three in open nomenclature (Okubo 1951; Kobayashi 1957, 1985, 1988a,b; Kobayashi & Hamada 1974, 1977, 1985a,b, 1986, 1987; Okazaki 1974; Kaneko 2007). In addition, one new species is described herein and is the first record of its genus from Japan (and indeed eastern Asia). These trilobites have, in general, been considered endemic at the species level, even between separate Japanese terranes. The recent revision of the Illaenidae and Scutelluidae of Japan (Holloway & Lane 1998, 2012, 2016) has nevertheless extended the palaeobiogeographical ranges of several genera and

DOI 10.1002/9781119564232

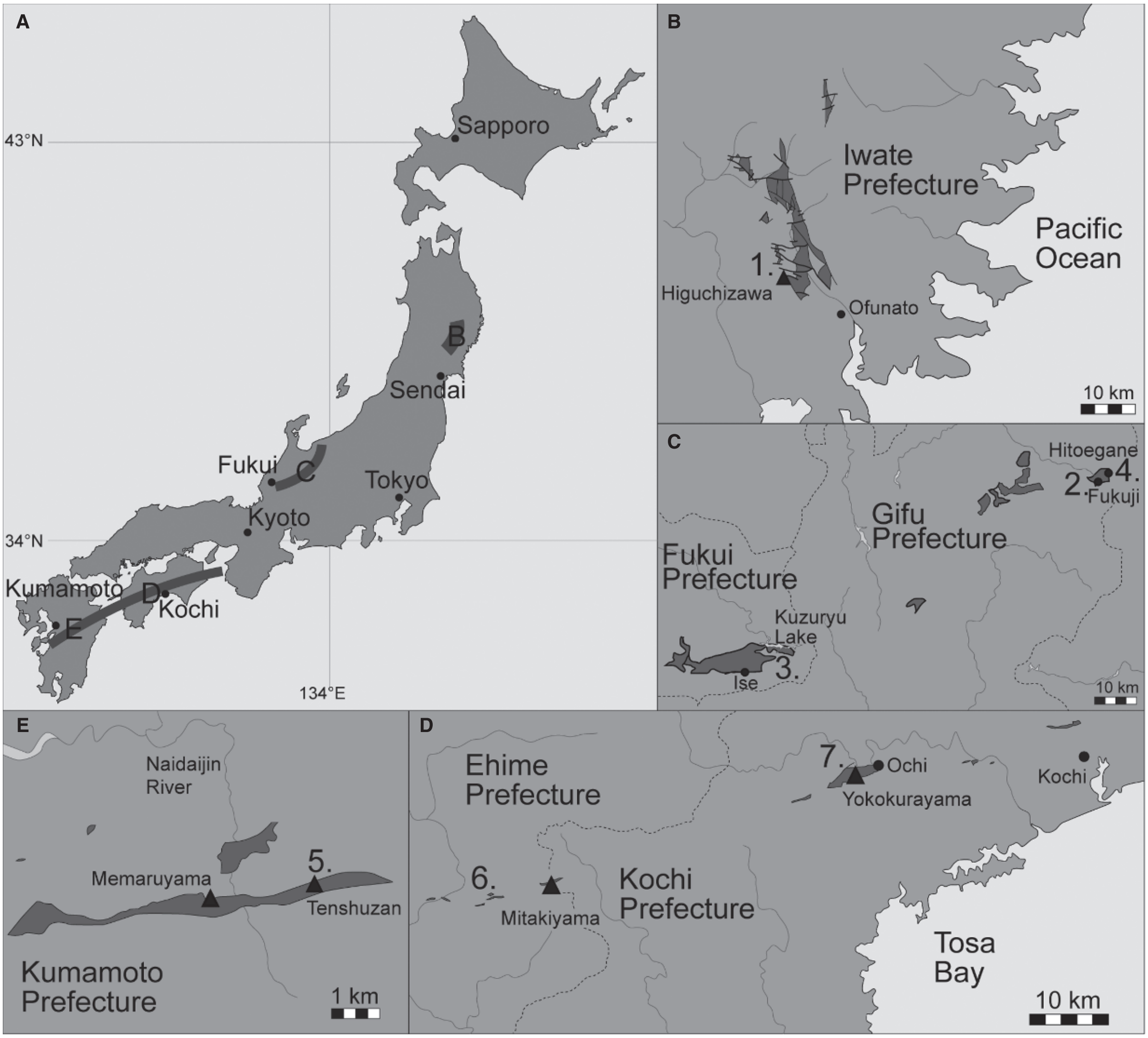


Fig. 1. Geographical location of the three Japanese Palaeozoic terranes investigated for trilobites. The dark grey lines on the main map of Japan (**A**) denote the approximate position of the South Kitakami (**B**), Hida-Gaien (**C**) and Kurosegawa terranes (**D**, **E**), and detailed maps of the outcrops of each are presented in B–E.

species. This study revises the record and taxonomy of Proetida and Aulacopleurida from Japan. As well as describing one new species, we re-examine all previously described species, thereby enabling a comprehensive palaeobiogeographical analysis of Japanese proetid trilobites compared with those of other East Asian and eastern peri-Gondwanan terranes.

Geological background

Silurian and Devonian fossiliferous sedimentary rocks of the South Kitakami Terrane occur in the Hikoroichi and Arisu districts of the Iwate Prefecture (Fig. 1B). These rocks contain invertebrate fossils including brachiopods, corals, crinoids, bryozoans and trilobites, as well as plant fossils and radiolarians. Silurian trilobites are known from the Wenlock and Ludlow age Kawauchi Formation and the Llandovery to Wenlock age Okuhinotsuchi Formation. Although no proetids or aulacopleurids have previously been described from these strata, a single proetid cephalothorax from the Kawauchi Formation is reported herein, but it has not been formally identified. In the Devonian, the Nakazato Formation contains a diverse trilobite fauna that includes one proetid species and additional proetid material noted in open nomenclature (Kaneko 2007).

Fossiliferous Silurian and Devonian rocks of the Hida-Gaien Terrane are found in the Fukuji-Hitoegane area in the Gifu Prefecture and the Kuzuryu Lake-Upper Ise River area in the Fukui Prefecture (Fig. 1C). These strata contain conodonts, corals, radiolarians and trilobites. Strata in the Fukuji-Hitoegane area have previously yielded one Silurian proetid species and material that is herein referred to *Coniproteus* in open nomenclature, in some instances tentatively. Most of the Devonian trilobite record of Japan is from the Hida-Gaien Terrane, including at least two proetid species and one aulacopleurid described from the Fukuji Formation and its lateral equivalent in the Kuzuryu Lake-Upper Ise River areas, the Kamianama Formation.

In the Kurosegawa Terrane of Shikoku, the Yokokura Limestone of the Yokokurayama Group, Yokokurayama, Ochi area, Kochi Prefecture (Fig. 1D) contains a diverse fossil fauna including trilobites. The majority of Silurian proetids that have been described from Japan, with seven species, are from the Yokokurayama Group, Fukata and Gomi formations of the Kochi Prefecture (Kobayashi & Hamada 1974, 1985a,b, 1986). One species was described by Kobayashi & Hamada (1974) from the Okanaru Group (Hirayama *et al.* 1956) of Higashikawa County, Ehime Prefecture (Fig. 1D), which corresponds to the Joryu Formation of the Yokokurayama Group (equivalent to the lowermost 'G4 member' of Hamada (1959)). Trilobites have not been recorded from the overlying Devonian Nakahata and Ochi formations in that terrane.

In Kyushu, the Kurosegawa Terrane is represented by the Silurian to Lower Devonian Gionyama Formation of Gionyama in the Kuraoka area, Miyazaki Prefecture (Fig. 1E). It contains a rich invertebrate fauna of corals, crinoids, bryozoans, stromatoporoids, brachiopods, trilobites, cephalopods, bivalves and gastropods (Kido 2010; Kido & Sugiyama 2011 and references therein). Silurian trilobites, for example *Coronocephalus kobayashii,* were described by Hamada (1959) and Kobayashi & Hamada (1974) from the Gionyama Formation, but neither proetids nor aulacopleurids were recorded; a single proetid pygidium is recorded herein. Trilobites have also been described from the overlying Devonian Naidaijin Formation. Murata *et al.* (1997), and subsequently Kaneko (2007), reported two species of phacopine, and one each of a scutelluid, a lichid, a calymenid and a proetid, from the Lower Member of the formation, as well as several species in open nomenclature. Stocker *et al.* (2018) described a new species of phacopine trilobite from the Lower Member of the Naidaijin Formation, which combined with a radiometric age from detrital zircons suggests a Givetian (Middle Devonian) age for at least part of the Lower Member (Fig. 2).

Material and methods

The bulk of the material analysed here is from collections in Japanese museums: Tokyo University Museum (PA); Kyoto University Museum (KT); Kochi Prefectural Fossil Museum (KPFM); Yokokurayama Natural Forest Museum, Ochi area, Kochi Prefecture (YFM); Sakawa Geology Museum, Kochi Prefecture (SGM, KA); Ofunato City Museum, Iwate Prefecture (OCM.G); and Nagoya University Museum (NUM). The numbering system of Kobayashi & Hamada (1977) is complex, and it is not possible to assign an original number for the specimens from the Kyoto University Museum collection. This collection is on loan to the Tokyo University Museum, and here, we utilize replacement Tokyo University Museum repository numbers with the code 'KT' for these specimens. Silicone moulds and epoxy replicas of all specimens figured and cited herein, as well as one other specimen collected during this study, have been deposited in the Oxford University Museum of Natural History (OUMNH). The majority of the trilobites were reported by Okubo (1951), Kobayashi (1957, 1988b), Okazaki (1974), Kobayashi & Hamada (1974, 1977, 1985b, 1986, 1987) and Kaneko (2007). The specimens of Kaneko are well localized, with accurate stratigraphical logs of at least one of the localities and detailed locality maps for the others. Because the specimens described by Kobayashi (1957, 1988b) and Kobayashi & Hamada (1974, 1977, 1985b, 1986, 1987) were often donated by private collectors, associated locality information is not always precise (Table 1). Fossil preservation varies between formations, but is generally poor, with most specimens disarticulated and/or exfoliated.

Silicone moulds were made from museum specimens using the two-part addition cured polysiloxane dental putty, Provil Novo Putty. Black epoxy resin was poured into the moulds, which were then placed in a pressure chamber at 2 Mbar overnight to harden. Smaller specimens were coated with gold prior to scanning electron microscopy (SEM). Casts were mounted on a black plastic plaque with black plasticine and whitened with ammonium chloride sublimate for photography. Digital images were taken with Leitz 'Aristophot' apparatus mounted with a Canon EOS 5D camera and Leica 12 mm Summar lens. Small specimens were imaged with a Hitachi S-3600N environmental SEM at Leicester University.

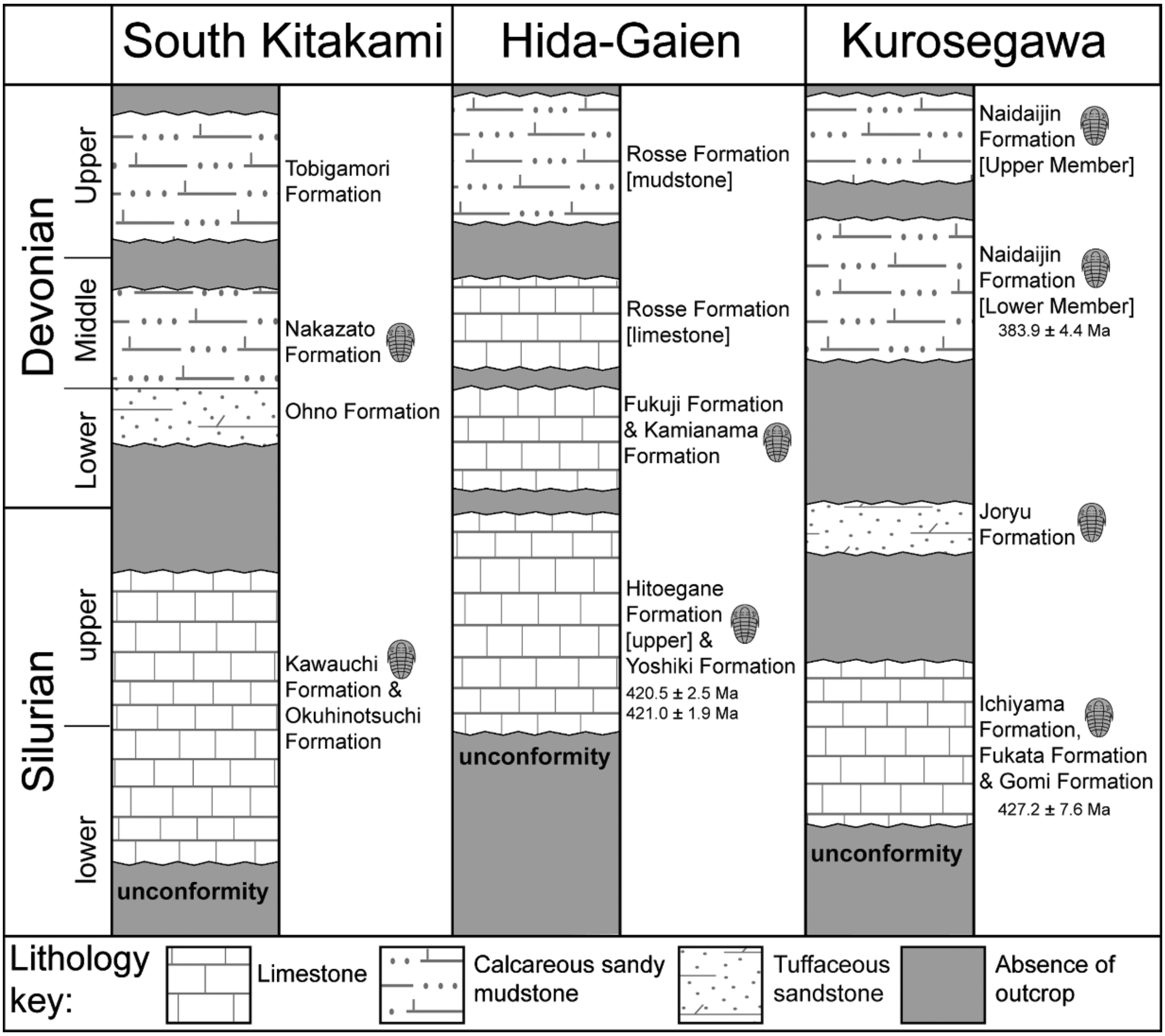


Fig. 2. Generalized lithostratigraphy for Silurian and Devonian strata in the three trilobite-bearing Japanese Palaeozoic terranes investigated here. For the Silurian, 'lower' denotes Llandovery and Wenlock series, whilst 'upper' denotes the Ludlow and Pridoli. For the Devonian, Lower, Middle and Upper are formal series. Radiometric ages are from the following sources: Manchuk *et al.* (2013) for the Yoshiki Formation, Stocker *et al.* (2018) for the Naidaijin Formation and Aitchison *et al.* (1996) for the Gomi Formation.

Images were processed using Adobe Photoshop CS 2015.5.

Palaeoecology

Proetids inhabited a variety of Silurian and Devonian lithofacies worldwide, representing a range of environments, from shallow to deep marine and including carbonates and siliciclastic sedimentary rocks (e.g. Owens 1973). Hughes & Thomas (2011) suggested that in northern Greenland, proetids utilized sheltered niches (depressions and cavities) within the Silurian reefs. Proetids and aulacopleurids have been interpreted as low-level, epifaunal deposit-feeding detritivores (Fortey & Owens 1999) and their possession of a highly conservative natant hypostome (except for some highly derived post-Devonian forms) suggests a particle-feeding habit (Fortey 1990).

Most Japanese proetids are found in shallow water carbonate lithofacies (Table 2). In the carbonates of the Silurian Fukata Formation, the associated assemblage of trilobites includes those from families that are typical of shallow marine environments such as Scutelluidae, Illaenidae, Encrinuridae and Lichidae. A similar trilobite fauna co-occurs with proetids in the limestones of the Silurian part of the Hitoegane Formation in the Hida-Gaien Terrane. In that terrane too, the proetid-bearing limestones of the Devonian Fukuji Formation also record a shallow marine trilobite fauna of

Table 1. Silurian and Devonian proetids from Japan, with stratigraphical and geographical provenance and palaeoenvironmental information.

Terrane	Formation	Chronostrat.	Geographical location	Locality number	Lithofacies	Fossils	Proetid/ Aulacopleurid taxa	Palaeoenvironment
South Kitakami Terrane	Nakazato Formation	Devonian (Emsian to Eifelian Stage)	Higashizawa, Hikoroichi, Ofunato City, Iwate Prefecture, Honshu Island	1. 'NTL-1' of Kaneko (2007)	Calcareous mudstone, calcareous sandstone	Corals, brachiopods, gastropods, tabulate and rugose corals, cephalopods and plants	*Dechenella minima*	Open shelf with volcaniclastic input
	Kawauchi Formation	Silurian (Wenlock Series)	Gyoninzawa, Hikoroichi, Ofunato City, Iwate Prefecture, Honshu Island	2. Locality of Harashinai (1981)	White to grey limestone	Corals, brachiopods, bryozoans, bivalves, cephalopods, conodonts	*Latiproetus*? sp.	Shallow shelf carbonates with some terrigenous input
Hida-Gaien Terrane	Fukuji Formation	Devonian (Lochkovian to Emsian Stage)	Fukuji, Okuhida-onsen-gou, Takayama City, Gifu Prefecture, Honshu Island	3. 'Sorayama' of Kobayashi & Hamada (1977)	Black-bedded limestone	Corals, cephalopods, conodonts, ostracods, tentaculitids, bivalves	*Ganinella fukujiensis, Ganinella oisensis, Maurotarion megalops*	Shallow water carbonates of possible marginal marine environment
	Kamianama Formation	Devonian (Lochkovian to Emsian Stage)	Kuzuryu Lake-Upper Ise River, Fukui Prefecture, Honshu Island	4. 'Oise-dani' of Kobayashi & Hamada (1977)	Limestone, argillaceous limestone	Corals	*Ganinella oisensis, Ganinella fukujiensis*	Shallow water carbonates
	Hitoegane Formation (upper)	Silurian (Ludlow Series)	Hitoegane, Kamitakara-mura, Yoshiki-gun, Gifu Prefecture, Honshu Island	5. 'Loc. 5.' of Kobayashi & Hamada (1974)	Banded and black limestone	Corals, conodonts	*Ganinella tenuiceps, Coniproetus* sp. A	Carbonate platform
Kurosegawa Terrane	Naidaijin Formation (Lower Member)	Devonian (Emsian to Givetian Stage)	Tenshuzan, near Tomochi Town, Shimomashiki District, Kumamoto Prefecture, Kyushu Island	6. 'NDTL-1' of Kaneko (2007)	Calcareous sandy mudstone	Corals, crinoids, brachiopods	*Dechenella minima*	Open shelf
	Joryu Formation	Silurian (Pridoli Series)	Okanaru, Seiyo City, Ehime Prefecture, Shikoku Island	7. 'Loc. 2.' of Kobayashi & Hamada (1974)	Tuffaceous sandstone	Radiolarians	*Prantlia bilobus*	Open shelf with volcaniclastic input
	Fukata Formation	Silurian (upper Wenlock to lower Ludlow Series)	Yokokurayama, Ochi, Kochi Prefecture, Shikoku Island	8. 'Loc 3.' of Kobayashi & Hamada (1974)	Limestone and limestone conglomerate	Brachiopods, cephalopods, corals, crinoids, conodonts, stromatoporoids	*Interproetus mizobuchii, Eremiproetus? magnicerviculus, Eremiproetus? subcarinatus, Coniproetus subovalis, Gomiites granulatus, Gomiites latiaxis*	High-energy fore-reef Lack of terrigenous material suggests isolation from major landmass

Lists of fossils, lithofacies and chronostratigraphical data are from Williams *et al.* (2014) and references therein.

Table 2. Palaeobiogeographical affinities of Silurian and Devonian proetid species from Japan, China and Australia.

Terrane	Formation*	Proetid species	Relevant biogeographical affinities
Kurosegawa Terrane	Fukata Formation	*Coniproetus subovalis* (Kobayashi & Hamada, 1974)	Different from species of *Coniproetus* from other areas
		Gomiites granulatus (Kobayashi & Hamada, 1974)	*Gomiites* is endemic to the Kurosegawa Terrane of Japan
		Gomiites latiaxis (Kobayashi & Hamada, 1986)	*Gomiites* is endemic to the Kurosegawa Terrane of Japan
		Interproetus mizobuchii n. sp.	Different from species of *Interproetus* from other areas
		Eremiproetus? *magnicerviculus* (Kobayashi & Hamada, 1974)	Uncertain due to poor preservation
		Eremiproetus? *subcarinatus* (Kobayashi & Hamada, 1974)	Uncertain due to poor preservation
		Hedstroemia sugiharensis (Kobayashi & Hamada, 1974)	Different from species of *Hedstroemia* from other areas
	Joryu Formation	*Latiproetus bilobus* (Kobayashi & Hamada 1974)	Genus common and diverse in South China
	Naidaijin Formation	*Dechenella minima* Okubo, 1951	Also occurs in the Nakazato Formation of the South Kitakami Terrane
Hida-Gaien Terrane	Hitoegane Formation	*Ganinella tenuiceps* (Kobayashi & Hamada, 1987)	Different from species of *Ganinella* from other areas
		Coniproetus sp. A	Different from species of *Coniproetus* from other areas
	Fukuji Formation	*Ganinella fukujiensis* (Kobayashi & Hamada, 1977)	Different from species of *Ganinella* from other areas
		Maurotarion megalops (Kobayashi & Hamada, 1977)	No links with other *Maurotarion* species from other areas
	Kamianama Formation	*Ganinella oisensis* (Kobayashi & Hamada, 1977)	No links with *Ganinella* species from other areas
South Kitakami Terrane	Nakazato Formation	*Dechenella minima* Okubo, 1951	Also occurs in the Naidaijin Formation of the Kurosegawa Terrane
Melbourne Terrane, Australia	Mt. Ida Formation, upper Silurian to Lower Devonian	*Coniproetus* sp. nov. of Holloway & Neil 1982	Different from *C. subovalis* from the Fukata Formation of the Kurosegawa Terrane
Benambra Terrane, Australia	Canberra Group, Silurian (Wenlock)	*Prantlia canberrensis* Chatterton & Campbell, 1980	Considered synonymous with *Latiproetus*. Not similar to *L. bilobus*
	Garra Limestone Formation, Lower Devonian (upper Lochkovian to middle Pragian)	*Otarion listron* Chatterton, Johnson & Campbell, 1979	Different from Japanese species of the closely related genus *Maurotarion*
		Coniproetus irroratus Chatterton, Johnson & Campbell, 1979	Different from Japanese species of *Coniproetus*
	Biddabirra Formation, Lower Devonian (Lochkovian to Pragian)	*Cyphaspis mcnamari* Ebach, 2002	Different from Japanese species of the closely related genus *Maurotarion*
	Taemas Formation, Lower Devonian	*Cyphaspis dabrowni* (Chatterton, 1971)	Different from Japanese species of the closely related genus *Maurotarion*
South China Plate	Yujiang Formation, Lower Devonian	*Dechenella*? *liujingensis* Zhang, 1974	Different from *Dechenella minima* found in the Nakazato Formation of the South Kitakami Terrane and the Naidaijin Formation of the Kurosegawa Terrane
	Luojiashan Formation, middle Silurian	*Luojiashania meitanensis* Zhang, 1974	Similar to *Gomiites* in cephalic morphology
North China (Sino-Korean) Plate	Yikewusu Formation, Middle Devonian (Eifelian)	*Ganinella*? *auspicata* Zhou *et al.*, 2000	Different to *Ganinella* species found in the Fukuji and Kamianama formations of the Hida-Gaien Terrane
	Zhusileng Formation, Middle Devonian (Emsian)	*Paradechenella lunata* Zhou *et al.*, 2000	*Paradechenella* represented in the Nakazato Formation (under open nom.)
		Otodechenella convexa Zhou *et al.*, 2000	*Otodechenella* represented in the Nakazato Formation (under open nom.)
		Basidechenella? *exquisita* Zhou *et al.*, 2000	Similar to *Dechenella minima* of the Nakazato Formation
Liaoling Terrane, North China	Zhangjiatun and Erdagou formations, middle upper Silurian	*Otarion sphaericum* (Kuo, 1962)	Different from Japanese species of the closely related genus *Maurotarion*
		Otarion conveximarginatum (Kuo, 1962)	Different from Japanese species of the closely related genus *Maurotarion*

*For stratigraphical ages of Japanese formations, see Table 1.

scutelluids, cheirurids, calymenids, lichids and odontopleurids. The presence of leperditicopid arthropods in a laminated mudstone in the lower part of the Fukuji Formation (Tanaka *et al.* 2012) suggests a shallow marginal marine environment. One specimen of the aulacopleurid *Maurotarion megalops* (Kobayashi & Hamada, 1977) has been found alongside a leperditicopid.

In the open shelf mudstones and sandstones of the Devonian Nakazato Formation in the South Kitakami Terrane, trilobites including proetids occur as a major component of an allochthonous fauna. However, the original ecological setting of the trilobites cannot be determined.

Palaeobiogeography

Table 2 summarizes the palaeobiogeographical affinities of Japanese proetids as determined here.

Intra-Japanese terrane palaeobiogeography

Of the thirteen species and nine genera of Japanese proetids, most are endemic at species level within their individual terranes, especially so in the Silurian. In the Devonian, *Dechenella minima* occurs in the Nakazato Formation of the South Kitakami Terrane and at a comparable stratigraphical level (Eifelian) in the Naidaijin Formation of the Kurosegawa Terrane (Table 2). The overall endemic signal of Japanese proetids may reflect, in part, lithofacies associations. Most taxa (e.g. *Gomiites* and *Ganinella*) are found in shallow marine carbonates, whilst the lithofacies of the Nakazato and Naidaijin formations suggests deeper shelf environments (Table 1). Fortey (1975) concluded that in the Early Ordovician of Spitsbergen and North America (Laurentia), trilobite faunas such as the shallow marine 'illaenid-cheirurid community' were characterized by taxa with a high degree of endemicity, whereas those faunas in outer shelf settings, such as the 'nileid community', had greater potential for dispersal and were more cosmopolitan. Such a depth-related pattern is also suggested in the Devonian of Japan by the wide biogeographical affinities of the trilobites in the Nakazato and Naidaijin formations (Table 2). Other non-proetid components of the Japanese early- and mid-Palaeozoic trilobite fauna, such as scutelluids, illaenids and encrinurids from shallow marine carbonate lithofacies, have different palaeobiogeographical affinities to the proetids, and based on the proposed endemicity of these other groups (see below) may be more informative to palaeogeography.

Connections with Chinese and peri-Gondwanan terranes

In contrast to some of the other trilobite groups, the palaeobiogeographical connections of Japanese proetids with other regions of East Asia are limited (Fig. 3). For example, although illaenids and scutelluids (Holloway & Lane 1998, 2012) from the Silurian Fukata Formation of the Kurosegawa Terrane show multiple species

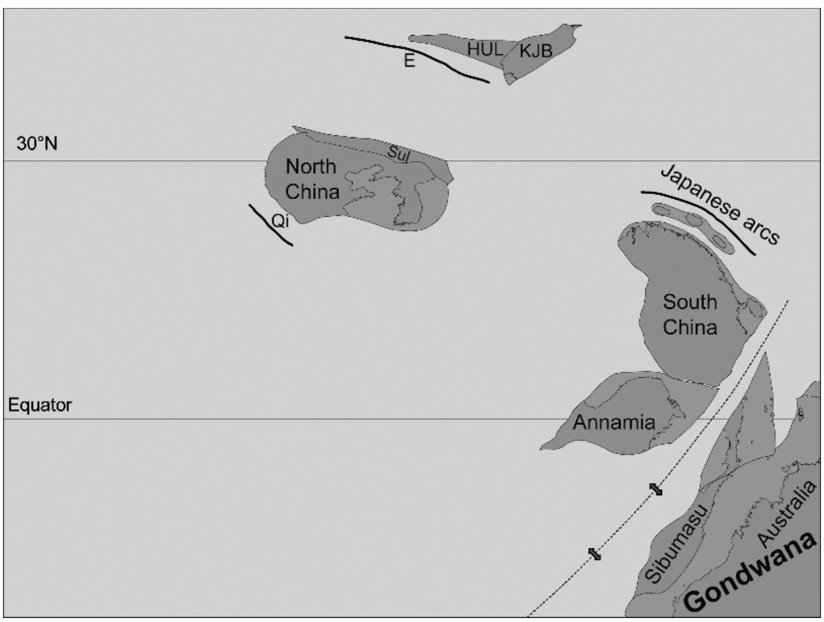


Fig. 3. Palaeogeographical map of part of East Asia and adjacent Gondwana during the late Early Devonian (Emsian) at 400 Ma, after Cocks & Torsvik (2013). E, Enshoo Arc; HUL, Hutag Uul–Songliao; KJB, Khanka-Jiamusu-Bureya; Qi, arcs now in the Qaidam–Qilian Terrane; Sul, Sulinheer. Bold black lines are subduction zones. According to the figures in Cocks & Torsvik (2013), there is no significant change in the configuration of these palaeocontinents between the Silurian and Devonian.

links with the Australian Benambra Terrane, and encrinurids show possible links also with Australia (Strusz 1980), the proetids of the Fukata Formation do not. Similarly, during the Devonian, palaeobiogeographical links have been suggested between the lichid and cheirurid trilobite assemblages of the Fukuji Formation of the Hida-Gaien Terrane and the Xiaoputonggou Formation of Shaanxi Province, China (South China Plate; see Kaneko 2007), but proetids do not demonstrate the same links. However, the Silurian upper Hitoegane Formation and the Devonian Fukuji Formation of the Hida-Gaien Terrane do contain several species of the proetid *Ganinella*, a genus that has been recorded in the Silurian and Devonian of Siberia (Yolkin 1968, 1983), and the Devonian Xipingshan Formation of Inner Mongolia (Zhou *et al.* 2000). A dechenellid fauna has been reported from the Devonian Nakazato Formation of the South Kitakami Terrane by Kaneko (2007), but unlike the phacopids from the same formation (Kaneko 1990, 2007), these do not appear to show links with Inner Mongolia faunas (Zhou *et al.* 2000).

The apparently limited palaeogeographical dispersal of Japanese proetids, compared with scutelluids or encrinurids, might reflect ecology and feeding habits. Proetids in reef limestones of Greenland have been interpreted as having a cryptic habit as outlined above (Hughes & Thomas 2011). In contrast, scutelluids, illaenids and encrinurids are interpreted to have been more active predator/scavenger forms (Fortey & Owens 1999). Scutelluids may have been capable of powerful swimming with their large, flat, 'paddle-like' pygidia, with a large surface area and an exceptionally wide doublure (Selwood 1966; Chatterton 1971; Feist & Lerosey-Aubril 2008), perhaps enabling greater dispersal.

Systematic palaeontology

Remarks. – Morphological terminology for the trilobite exoskeleton follows that of Whittington & Kelly (1997) and Owens (1973). Ordinal taxonomy is that of Adrain (2011), whilst the familial-level systematics of Proetida is that of Ivanova & Owens (*in* Ivanova *et al.* 2009). Synonymy lists only contain entries where species have been figured or reassigned, and not merely cited. For localities, see Table 1.

All of the trilobites occur as disarticulated sclerites. For those specimens of Kobayashi & Hamada (1974, 1977) that we have been unable to locate, we cannot always be certain from their illustrations of their degree of exfoliation, and we have noted this where applicable. Christopher Stocker, Derek Siveter and Phil Lane are responsible for the systematic descriptions.

Order Proetida Fortey & Owens, 1975
Family Proetidae Salter, 1864
Subfamily Proetinae Salter, 1864

Genus *Coniproetus* Alberti, 1966

Type species. – *Proetus condensus* Přibyl, 1965 from the Devonian (Pragian Stage), Czech Republic. By original designation.

Stratigraphical and geographical range. – Silurian (Wenlock Series) to Devonian (Emsian Stage), Europe, North Africa, Australia, North America, Japan.

Coniproetus subovalis (Kobayashi & Hamada, 1974)

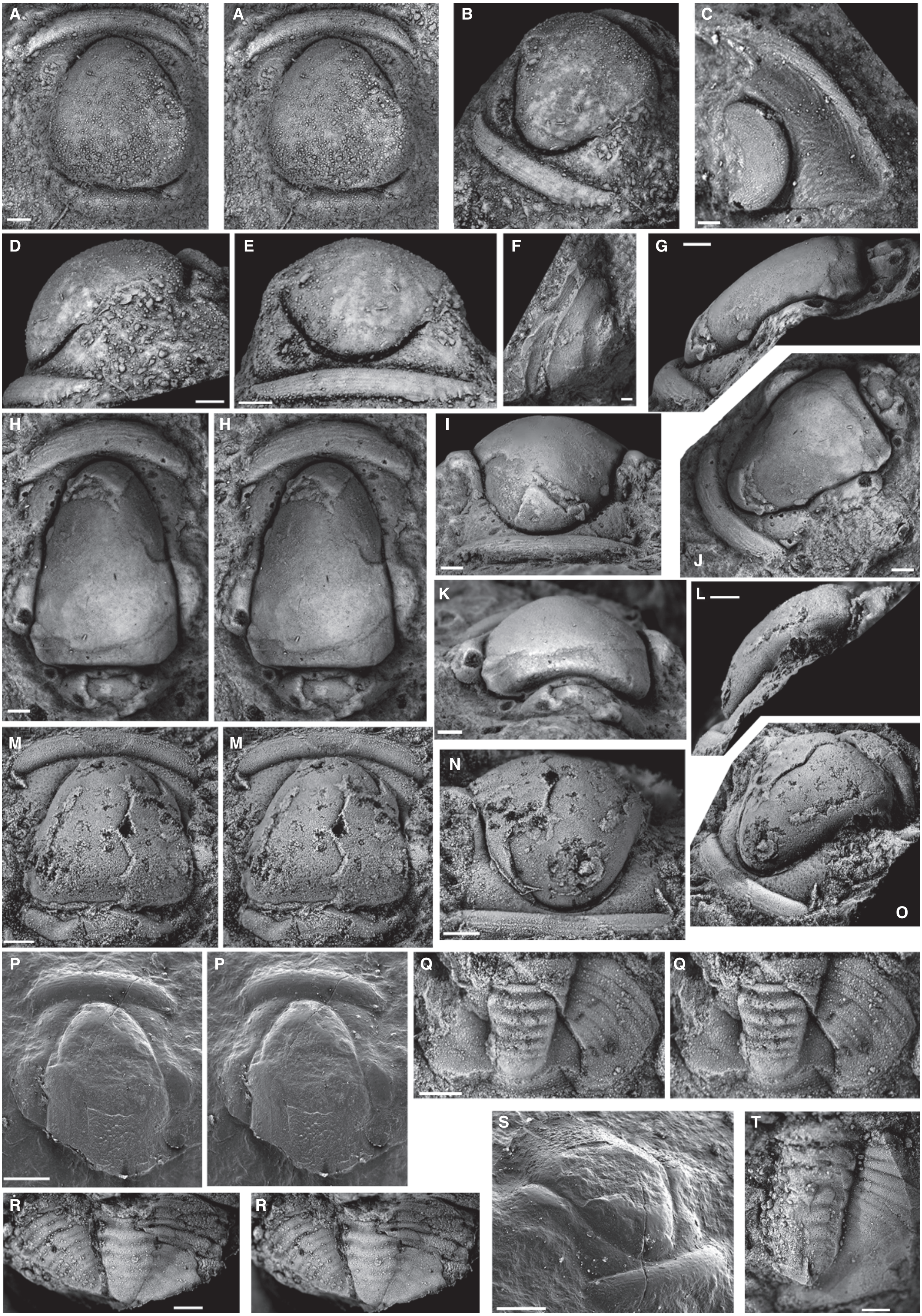
Figure 4A, B, D, E

1974 *Proetus subovalis* Kobayashi and Hamada sp. nov. Kobayashi & Hamada, pp. 113, 114 (*pars*), pl. 12, fig. 1, text-fig. 8A (*sic.*), (*non* fig. 2 = Proetid indet.).

Holotype. – Cranidium (KPFM15188), from Locality 8 (Table 1) (the only specimen).

Diagnosis. – Glabella pyriform; strongly convex (sag.); furrows absent. Occipital ring with large median tubercle and well-formed, small subtriangular lateral lobe. Anterior border 10% of glabellar length with sculpture of strong, parallel terrace ridges.

Fig. 4. Silurian proetids from the Fukata Formation of Yokokurayama, Kochi Prefecture, Shikoku (A–E), and the upper Hitoegane Formation, Fukuji-Hitoegane area, Gifu Prefecture (F–T). **A**, **B**, **D**, **E**, *Coniproetus subovalis* (Kobayashi & Hamada, 1974), partially exfoliated holotype incomplete cranidium (KPFM15188) in dorsal stereo, left anterior oblique, left lateral and anterior views. **C**, proetid indet., incomplete right librigena (PA7372), previously tentatively assigned to *C. subovalis* by Kobayashi & Hamada (1974, p. 113, pl. 12, fig. 1), dorsal view. **F**, **G**–**K**, **P**, **S**, *Ganinella tenuiceps* (Kobayashi & Hamada, 1987); F, internal mould, paratype left librigena (PA18100), dorsal view; G-K, partially exfoliated holotype incomplete cranidium (PA18098), left lateral, dorsal stereo, anterior, left anterior oblique and posterior views; **P**, **S**, internal mould, juvenile incomplete cranidium (PA18099), dorsal stereo and right anterior oblique views, previously assigned to *Proetus* (*Coniproetus*?) *subconicus* by Kobayashi & Hamada (1987, p. 138, figs 1–5a–d). **L**–**O**, *Coniproetus* sp. A., partially exfoliated incomplete cranidium (NUM-Fa214), left lateral, dorsal stereo, anterior and left anterior oblique views. **Q**, **R**, **T**, three specimens tentatively referred to *Coniproteus*; Q, partially exfoliated pygidium (NUM-Fa217), dorsal stereo view. R, partially exfoliated pygidium (NUM-Fa216), dorsal stereo view. T, pygidium (NUM-Fa215), dorsal view. Scale bars = 2 mm.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Description. – Cranidium incomplete, strongly convex sagittally, moderately convex transversely. Palpebral lobe and posterior fixigena not preserved. Glabella 80% as wide as long with maximum width at 30% length from posterior; frontal lobe slightly overhanging preglabellar furrow. Occipital ring 20% as long as wide, slightly longer than anterior border. Lateral occipital lobe well-defined and crescentic, approximately half as wide as long, 20% of occipital width. Preglabellar field short, about 20% as long as anterior border; preglabellar furrow deep. Anterior border moderately convex.

Glabellar surface with granular sculpture posteriorly and on occipital ring anteriorly. Anterior cephalic border with strong, parallel terrace ridges. Fixigenal field smooth.

Discussion. – Kobayashi & Hamada (1974, p. 113) claimed that the holotype bears many characteristics in common with *Proetus concinnus* (Dalman, 1827) from the Silurian Much Wenlock Formation (Wenlock Series) of the UK, but they did not state which they were. They described and illustrated lateral glabellar furrows (1974, p. 114, text-fig. 8A) for which, however, there is no evidence: their S3 furrow is an artefact (it is asymmetrically placed and in an incorrect position for a glabellar furrow). They also questionably assigned an incomplete librigena (PA7372, their pl. 12, fig. 2) to this species, but the librigena has a chevron pattern of fine raised ridges, possibly caecal structures, that are not visible on the holotype fixigena (Fig. 4C). As a result, we regard this specimen as a proetid of indeterminate affinity.

Coniproetus sp. A

Figure 4L–O

Material. – Cranidium (NUM-Fa214) from Locality 5 (Table 1).

Description. – Incomplete cranidium strongly (sag.) and moderately (tr.) convex. Glabella almost as wide as long, maximum width at approximately 25% length from posterior margin, across L1; strongly convex (sag.) with frontal lobe slightly overhanging preglabellar furrow. Occipital ring 20% as long as wide, equal in length to anterior border; wide 'W' in dorsal outline. Occipital tubercle very poorly preserved. Lateral occipital lobe subtriangular, 75% as long as wide and about 20% of occipital ring width, divided by shallow, broad intraoccipital furrow. Occipital furrow deep, moderately wide (exsag.), increasing in width (exsag.) abaxially; convex medially. Glabellar furrows effaced; remnants of S1 and S2 indicated by slight indentations on the lateral glabellar margin at 60% and 40% length from the anterior glabellar margin. Preglabellar field very short; preglabellar furrow moderately deep. Anterior border convex, long, 12% length of cranidium, with relatively narrow, deep border furrow. Palpebral lobe approximately half as wide as long, with anterior margin in line with approximately midglabellar length. Anterior facial suture weakly divergent (36°).

Glabella smooth; anterior border bears coarse terrace ridges parallel to the anterior margin; anterior fixigena with densely packed, large, subcircular pits.

Discussion. – In the only cranidium at hand (NUM-Fa214), the glabella is partially exfoliated on the left-hand side (Fig. 4L–O); the remnants of cuticle, which persist on the right-hand side, lack sculpture. However, it shows sufficient characters to confidently assign this specimen to *Coniproetus*. The glabella is conical, very convex (sag.) with a steep slope anteriorly, and it has a well-developed lateral occipital lobe. *Coniproetus* sp. A also possesses some characters associated with *Ganinella*, such as the long (sag.) glabella and sculpture of pits on the fixigena, so it may well represent a transitional form between these two closely related genera, but there is insufficient material to test this hypothesis.

Coniproetus sp. A differs from *C. subovalis* from the Fukata Formation of the Kurosegawa Terrane (Fig. 4A, B, D, E) in the following characters: the glabella is less convex (sag.), longer (sag.), more conical in dorsal outline, with a wider (trans.) anterior margin; the occipital ring is wider, with larger (sag., trans.) lateral lobe.

An additional three specimens of poorly preserved pygidia (Fig. 4Q, R, T) have been recovered from the Silurian part of the Hitoegane Formation (Locality 5, Table 1), and these have been tentatively assigned to *Coniproetus*, based on their subsemicircular pygidial outline, and weakly developed, short (sag.) pygidial border; it is uncertain how the pygidia relates to *Coniproetus* sp. A.

Genus *Ganinella* Yolkin, 1968 (= *Lophiokephalion* Kobayashi, 1988)

Type species. – *Dechenella batchatensis* Chernysheva, 1951 from the Devonian (Eifelian Stage), Salair, south-western Siberia. By original designation.

Diagnosis. – Glabella elongate and conical to pyriform, with a rounded or slightly pointed anterior margin and three or four pairs of lateral furrows, often strongly incised. Genal ridge is present. Pygidium subsemicircular in outline, with eight to twelve axial rings and five to eight variably defined ribs. Sculpture of distinct pitting on fixigenae and librigenae; cephalon with granular or tubercular sculpture, or smooth. (Emended from Yolkin 1968, to include species described herein).

Discussion. – Owens (1973) considered *Ganinella, Khalfinella* and *Lacunoporaspis* to be congeneric; this was based on the poor material of these genera originally described by Yolkin (1966) from the Lower and Middle Devonian of Siberia. We follow Zhou *et al.* (2000) in considering *Ganinella* distinct from *Lacunoporaspis*, based on differences in glabellar shape and the often coarse cephalic sculpture. Relationships between these closely related genera are difficult to resolve at present and therefore they are kept separate herein, pending a detailed phylogenetic analysis. *Lophiokephalion* Kobayashi, 1988, was based on four species from the Devonian Fukuji Formation (Locality 3, Table 1), the type species *L. antijuba,* and *L. angustus, L. latipolus* and *L. longiconus.* We have been unable to locate the type material of these species (Kobayashi 1988b did not give a museum repository and indicated only that they were part of Hamada's private collection), and although they are poorly illustrated, it is clear they belong to *Ganinella*. The feature Kobayashi (1988b) described in *Lophiokephalion* as a librigenal 'trifurcate keel' is the genal ridge, which is diagnostic of *Ganinella*.

Stratigraphical and geographical range. – Silurian (Ludlow Series) to Devonian (Eifelian and ?Frasnian stages), Russia, North China, Japan.

Ganinella tenuiceps (Kobayashi & Hamada, 1987)

Figure 4F–K, L–P, S

1987 *Proetus* (*Coniproetus*) *tenuiceps* Kobayashi and Hamada, sp. nov. Kobayashi & Hamada, p. 136, figs. 1, 4a–d, fig. 3, 1a, b.

1987 *Proetus* (*Coniproetus*?) *subconicus* Kobayashi and Hamada, sp. nov. Kobayashi & Hamada, p. 138, figs. 1, 5a–d.

Holotype. – Cranidium (PA18098), from Locality 5 (Table 1).

Paratype. – Librigena (PA18100) from Locality 5 (Table 1). The repository number of this specimen in Kobayashi & Hamada (1987) is incorrectly recorded as PA18098.

Other material. – Cranidium (PA18099), a juvenile, from Locality 5 (Table 1) that was originally the holotype of *Proetus* (?*Coniproetus*) *subconicus.*

Diagnosis. – Glabella coniform, with pointed anterior margin; lateral furrows weakly impressed. Preglabellar field very narrow (sag.); anterior border broad and convex. Occipital ring moderately long (sag.), of low relief, with broad, rounded median tubercle and much reduced lateral lobes. Genal ridge low and broad. Anterior part of fixigena with distinct pitting. Anterior border with strong terrace ridges; anterior fixigena with weakly impressed pitting; carapace otherwise smooth.

Description. – Cranidium incomplete. Glabella coniform, twice as long as wide, widest at L1 and 65% the width (at $\delta - \delta$) of the cranidium, moderately convex (sag.) with steep slope anteriorly. Occipital ring 30% as long as wide, slightly longer than anterior border, convex (sag.), subelliptical and less convex (tr.) than the pre-occipital glabella; occipital tubercle broad and weakly convex. Lateral occipital lobe very small and crescentic (may be incomplete), separated by a short, oblique intraoccipital furrow. Occipital furrow deep, narrow, increasing in length (exsag.) abaxially. Remnants of lateral glabellar furrows S1 and S2 visible as slight incisions in lateral margin. Preglabellar field <25% the length of anterior border, with deep anterior border furrow. Anterior border broad (sag.), rounded and convex, with shallow border furrow. Anterior branch of facial suture weakly divergent; posterior branch moderately strongly divergent. Palpebral lobe poorly preserved, narrow, approximately 25% as wide as long, with anterior margin in line with approximately half length of the glabella. Lateral border wide, with narrow border furrow. Subocular furrow broad, with narrow ridge. Genal ridge low and broad (tr.).

Glabellar sculpture uncertain; anterior border with coarse terrace ridges parallel to anterior margin; fixigena with weak pits; librigenal field smooth (but mostly exfoliated); lateral border with coarse, parallel terrace ridges.

Discussion. – We agree with Kobayashi & Hamada (1987) that the paratype librigena of *G. tenuiceps* has been correctly associated with the holotype, based on its elongate morphology, broad border and smooth librigena. The juvenile specimen referred to *Proetus* (?*Coniproetus*) *subconicus* by Kobayashi & Hamada (1987) is herein assigned to *G. tenuiceps* based on the proportions of the glabella. They placed *G. tenuiceps* in *Proetus* (*Coniproetus*) Alberti, 1966 based on its cranidial characteristics, one of which is a well-developed lateral occipital lobe; but in the single, partial internal mould cranidium available, these are not well developed: only remnants of cuticle on the frontal lobe and occipital ring being preserved. It is possible that in the holotype cranidium, the occipital ring is incompletely known because it appears to be partially sediment-covered, particularly on the left side. Moreover, glabellar sculpture is unknown. The elongate, conical holotype compares best with *Ganinella* species, but the effacement of its furrows and reduced lateral occipital lobe is unusual, though not unknown in this genus. From the Devonian of southwest Siberia, *G. schebalinoensis* Yolkin, 1968; has a smooth glabella apparently lacking furrows and *G. tchernyshevae* Yolkin, 1968; has a reduced lateral occipital lobe, which however is not as small as that of *G. tenuiceps*. In the overall shape of the glabella and anterior border, the occipital ring with small lateral lobe, and position and size of palpebral lobe, *G. tenuiceps* is similar to *Ejinoproetus leprosus* Zhou *et al.* (2000) from the Emsian and Eifelian of Inner Mongolia although that species has coarse glabellar sculpture, weakly incised glabellar furrows and no median occipital tubercle. Although pygidial characters are important in diagnosing *Ejinoproetus*, none are known in *G. tenuiceps*.

Ganinella fukujiensis (Kobayashi & Hamada, 1977)

Figure 5A–G, J

1974 *Proetus* sp. indet. Okazaki, p. 90, pl. 9, figs 6–9.

1977 *Proetus* (*Coniproetus*) *fukujiensis* Kobayashi and Hamada, sp. nov. Kobayashi & Hamada, p. 133, pl. 13, figs 2–13; text-fig. 3I.

1977 *Unguliproetus oisensis* Kobayashi and Hamada sp. nov. Kobayashi & Hamada, p. 133, pl. 13, fig. 3 (*non* pl. 12, figs 1, 2, 4–25, pl. 13. fig. 1, = *Ganinella oisensis*).

Holotype. – Cranidium (PA8961), from Locality 3 (Table 1).

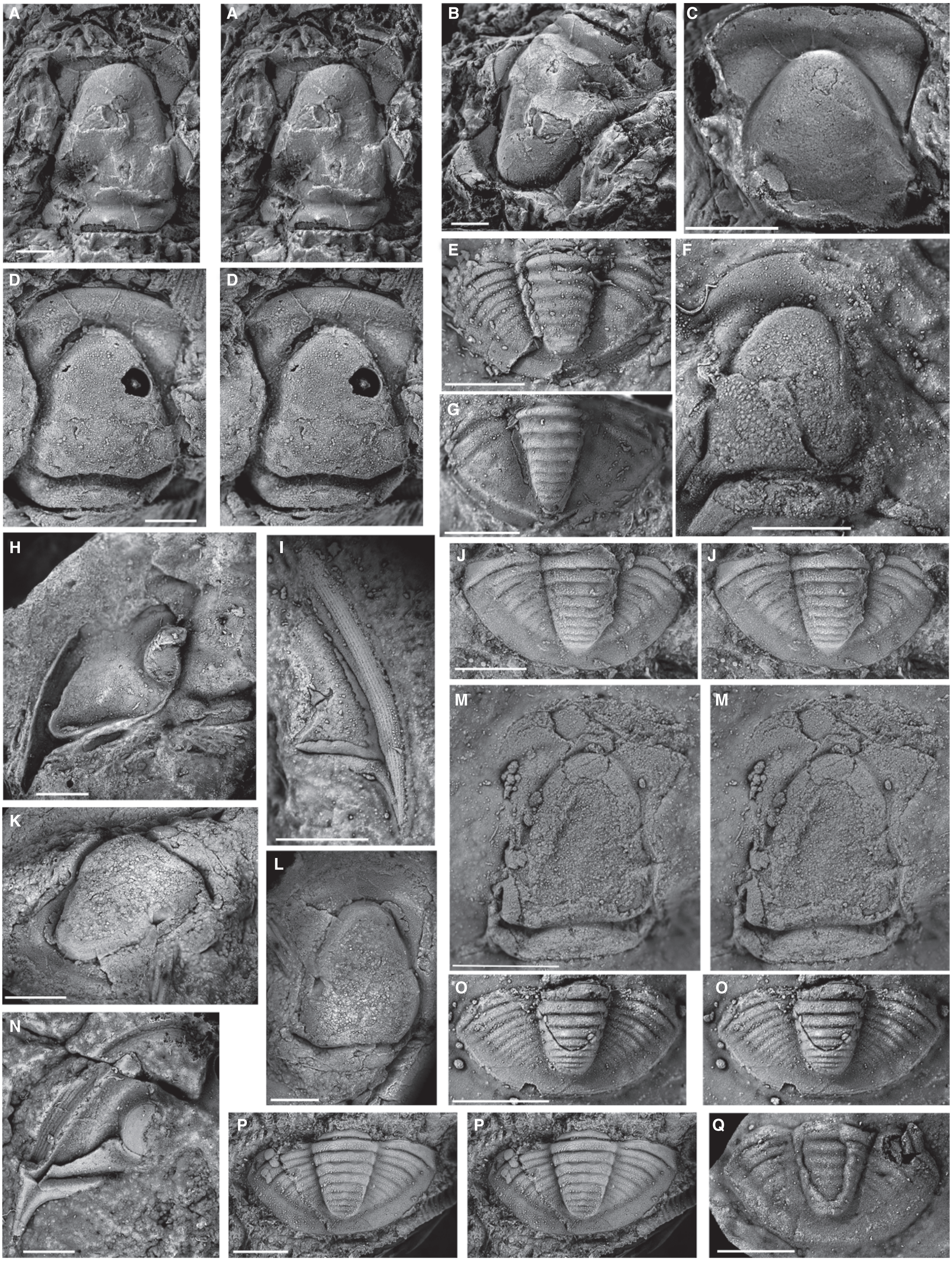
Paratypes. – Cranidia (PA8962-8964); librigenae (PA8959, PA8960), pygidia (PA8957, PA8958). All from Locality 3 (Table 1).

Other material. – Specimens described as *Proetus* sp. by Okazaki (1974): cranidium (KT-20160520-38), librigena (KT-20160520-35) and pygidia (KT-20160520-02, KT-20160520-35); specimens identified during this study: pygidia (NUM-Fa218, NUM-Fa223, NUM-Fa224,). All from Locality 3 (Table 1). A cranidium (PA8933) from Locality 4 (Table 1), originally assigned as a paratype of *G. oisensis* by Kobayashi & Hamada 1977, is here assigned to *G. fukujiensis.*

Diagnosis. – Anterior border 16% length of cranidium. Moderately elongate and subconical glabella, approximately as long as wide, with weakly incised S1 and S2. Occipital ring wider than pre-occipital glabella with moderately sized, triangular lateral lobe. Librigena with short, stout, genal spine. Anterior facial suture weakly divergent (30°). Fixigena with weak pitting; cephalon with pustules; pygidium with granules.

Description. – Cephalon 65% as long as wide, moderately convex (sag. and tr.). Cranidium about 10% wider than long, occupying 60% total width of cephalon at widest point. Glabella moderately convex (sag. and tr.); subconical; as wide as long, with maximum width at occipital ring and is 5% of maximum cranidial width. Occipital ring 25% as long as wide, 10% longer than anterior border; occipital tubercle small, posteriorly positioned. Lateral occipital lobe 80% as wide as long, 20% width of occipital ring, weakly depressed, subtriangular and separated by shallow, broad intraoccipital furrow. Occipital furrow long, deepening abaxially. Lateral glabellar furrows weakly incised; S1 50% from anterior of glabella, and 20% glabellar width, angled posteriorly at about 35°; S2 40% from anterior margin and is about same length as and parallel to S1; S3 absent. Preglabellar field very short (sag.); preglabellar furrow moderately deep and

Fig. 5. Devonian proetids from the Fukuji Formation, Fukuji-Hitoegane area, Gifu Prefecture (A–G, J), and the Kamianama Formation of the Kuzuryu Lake-Upper Ise area, Fukui Prefecture (H, I, K–Q). **A –G**, **J**,*Ganinella fukujiensis* (Kobayashi & Hamada, 1977); A, B, partially exfoliated holotype incomplete cranidium, (PA8961), dorsal stereo and left anterior oblique views; C, internal mould, paratype cranidium (PA8962), dorsal view; D, partially exfoliated paratype incomplete cranidium, (PA8963), dorsal view; E, partially exfoliated pygidium, (KT-20160520-02), dorsal view; F, partially exfoliated incomplete cranidium, (PA8933), dorsal view (note well-preserved granular sculpture and S1); G, internal mould, pygidium (KT-20160520-35), dorsal view; J, pygidium, (NUM-Fa218), dorsal stereo view (note well-preserved granular sculpture). **H**, **I**, **K–Q**, *Ganinella oisensis* (Kobayashi & Hamada, 1977); H, internal mould, paratype left librigena attached to incomplete cranidium, (PA8942), dorsal view; I, paratype right librigena, (PA8943), dorsal view; K, L, partially exfoliated paratype cranidium (PA8935), left anterior oblique and dorsal views; M, partially exfoliated cranidium, (PA8934), dorsal stereo view; N, partially exfoliated paratype librigena, (PA8944), dorsal view; O, partially exfoliated paratype pygidium (PA8950), dorsal stereo view; P, partially exfoliated pygidium (NUM-Fa219), dorsal stereo view (note well-preserved granular sculpture); Q, partially exfoliated paratype juvenile pygidium (PA8954), dorsal view. Scale bars = 2 mm.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broad (sag.). Anterior border convex, 15% length of cranidium, 10% shorter than occipital ring, with shallow and broad (sag.) anterior border furrow. Palpebral lobe narrow, an elongate, semi-elliptical platform 30% as wide as long, occupying 25% length and 7% width of cranidium, anterior margin in line with anterior of S2. Cranidial width at δ is 60% of maximum. Anterior facial suture weakly divergent (30°); posterior facial suture moderately divergent (140°). Eye 40% as wide as long. Lateral and posterior borders approximately as broad as anterior border. Librigena 60% as wide as long and roughly 30% as wide as cranidium. Genal spine 60% as wide as long, with gently rounded point.

Pygidium 65% as long as wide. Axial furrow deep and narrow; axis 30% width of pygidium anteriorly, eight axial rings that become shorter (sag.) posteriorly, and terminal piece; ring furrows deep, shallowing posteriorly. Pleural lobe with five to six pleural ribs that curve moderately posteriorly, separated by deep interpleural furrows; anterior three to four ribs with deep pleural furrows. Axis and pleural lobe of subequal width anteriorly. Posterior border gently convex, 10% pygidial length, with a shallow and long posterior border furrow.

Cephalon bears pustules, and fixigena small shallow pits. Pygidium with granules.

Ontogeny. – Cranidia, measured by posterior glabellar width (the only commonly preserved feature), vary from 3.7 to 7.5 mm; maximum pygidial width ranges from 4.9 mm to 6.5 mm. Small cranidia (<5 mm) have a relatively broader preglabellar field and a transversely wider and longer palpebral lobe than large specimens. Also, the fixigenal pitting is weakly expressed in smaller specimens, but this could be a factor of preservation. The pygidial border becomes more defined as size increases, but the definition of the pleural ribs is variable throughout ontogeny, and this may similarly be a preservational difference.

Discussion. – Glabellar and pygidial sculpture is only visible in those specimens with well-preserved cuticle (e.g. Fig. 5F, J, respectively). Kobayashi & Hamada (1977, p. 150, text-fig. 3.) showed two pairs of glabellar furrows in this species. We have also observed faintly incised S1 and S2 (see Fig. 5D, F; though in exfoliated specimens, furrows are not visible: Fig. 5A, C). As a lack of glabellar furrows is diagnostic of *Coniproetus*, *Proetus* (*Coniproetus*) *fukujiensis* is here reassigned to *Ganinella*. This is supported by other characters, including fixigenal pits and a much more elongate, conical glabella. The occipital ring in *Ganinella fukujiensis* is much wider than in *G. tenuiceps*, with a more prominent lateral occipital lobe. *G. fukujiensis* is similar in its cephalic characters (other than the border), to *Ganinella*? *auspicata* Zhou *et al.* (2000) from the Devonian of Inner Mongolia, though the pygidium of *G. fukujiensis* is different, having fewer axial rings (eight as opposed to eleven). *C. fukujiensis* is also similar in glabellar shape to *Ejinoproetus* species from the Devonian of the same region, but *Ejinoproetus* has a longer and more subtriangular pygidium with a greater number of axial rings and pleural ribs.

Ganinella oisensis (Kobayashi & Hamada, 1977)

Figure 5H, I, K–Q

1974 ?*Cyrtosymbole* sp. Okazaki *et al.*, pl. 1, figs 5–7.

1977 *Unguliproetus oisensis* Kobayashi and Hamada, sp. nov. Kobayashi & Hamada, p. 134, pl. 12, figs 1, 2, 4–25, pl. 13, fig. 1; text-fig. 3H (*non*-pl. 12, fig. 3 = *G. fukujiensis*).

Holotype. – Cranidium (PA8932) from Locality 4 (Table 1).

Paratypes. – Cranidia (PA8931, PA8934, PA8935, PA8937, PA8938); juvenile cranidium (PA8936); librigenae (PA8943-8946); librigena attached to partial cranidium (PA8942); hypostomes (PA8939-8941); pygidia (PA8947-8956). All from Locality 4 (Table 1).

Other material. – Three pygidia (NUM-Fa219, NUM-Fa221, and NUM-Fa222) from Locality 3 (Table 1) were identified during this study.

Diagnosis. – Glabella pyriform, constricted (tr.) anteriorly and abaxially expanded (tr.) posteriorly. Occipital furrow deep. Lateral glabellar furrows weakly incised. Genal ridge low and broad. Moderately long genal spine. Pygidium with seven or eight distinct pleural ribs and dense granular sculpture.

Description. – Cephalon 80% as long as wide, moderately convex (sag. and tr.). Cranidium about as long as wide, 65% width of cephalon. Glabella pyriform, just over 50% as wide as cranidium, maximum width at occipital ring. Occipital ring 25% as long as wide, slightly shorter than anterior border; occipital tubercle small, lenticular, posteriorly positioned. Lateral occipital lobe 60% as wide as long and 20% the width of occipital ring, depressed, subtriangular and separated by moderately shallow, broad intraoccipital furrow. Occipital furrow long (sag.) and deep. Lateral glabellar furrows weak, S1 meets axial furrow at 60% from anterior margin of glabella where it is 30% its total width, angled posteriorly at about 25°; S2 meets axial furrow at 45% length from the anterior margin, parallel to and about half width of S1; S3 absent. Preglabellar field approximately 50% anterior border length, with moderately deep preglabellar furrow. Anterior border weakly convex, 20% cranidial length, slightly longer than occipital ring; anterior border furrow moderately shallow and moderately long. Palpebral lobe a very narrow, elongate, semi-elliptical platform 20% as wide as long, 25% total length and 5% total width of cranidium; anterior margin in line with S2. Cranidial width at *a* is 60% of maximum. Lateral border at genal angle is about as broad as anterior border; posterior border 60% of anterior border length (sag.). Librigena moderately wide, 50% as wide as long and 60% as wide as cranidium. Genal ridge low, broad, extends from midwidth of librigenal field in line with occipital furrow to anterior fixigena slightly posterior of preglabellar furrow. Genal spine sharply pointed, moderately long and narrow, 25% as wide as long; genal angle approximately 65°.

Hypostome poorly preserved and incomplete, elongate, width across anterior wings approximately 85% of length. Posterior wing not preserved. Anterior lobe subparallel sided. Narrow (tr.) maculae, orientated adaxially at 140°. Posterior lobe reniform and with moderate independent convexity. Anterior border poorly preserved, posterior and lateral borders unpreserved. Middle body with poorly preserved, coarse terrace ridges forming a Bertillon pattern.

Pygidium 60% as long as wide. Axial furrow deep and narrow; axis 35% width of pygidium anteriorly, with eight axial rings that become shorter posteriorly, and a short terminal piece; ring furrows are deep, becoming shallower posteriorly. Pleural lobe formed of seven or eight ribs curving moderately strongly backwards, separated by deep interpleural furrows; anterior three to four ribs with deep pleural furrows, shallowing posteriorly; ribs 60% longer in anterior part of pygidium. Posterior border gently convex, 10% of maximum pygidial length, with shallow, long posterior border furrow.

Glabellar and pygidial sculpture is visible in specimens of this species with well-preserved cuticle (e.g. Fig. 5K, L, P). Cephalon bears densely packed pustules and fixigenal pits. Pygidium with dense granular sculpture.

Ontogeny. – Cranidia measured by glabellar width vary from 1.4 to 6.7 mm; cranidia 3 mm or less have a relatively broader preglabellar field and larger palpebral lobes. Maximum pygidial width ranges from 2.0 to 10.3 mm, and the pygidial border is better defined as size increases, but the definition of the pleural ribs is variable throughout ontogeny, perhaps due to differences in preservation.

Discussion. – Kobayashi & Hamada (1977) assigned this species to *Unguliproetus* but nevertheless claimed that because in that genus the preglabellar field is typically short and the pleural field relatively distinct, the species was closely related to *Coniproetus*. However, the species shows the following differences from *Coniproetus*: a much more elongate and pyriform glabellar outline, more incised glabellar furrows and a narrower pygidial axis. Therefore, it is here assigned to *Ganinella*.

Ganinella oisensis is similar to *Ganinella elegantula* (Yolkin, 1968) from the Devonian of southwest Siberia, but the latter has a shorter preglabellar field and differs in possessing a longer cephalon, pyriform glabella with a narrow, rounded anterior margin, deeper occipital furrow, better defined and larger occipital lobe, more incised glabellar furrows, larger eye, longer preglabellar field, much more pronounced genal ridge, longer genal spine, more convex pygidial axis and less distinct pygidial pleural field.

Genus *Gomiites* Přibyl & Vaněk, 1978

Type species. – *Decoroproetus granulatus* Kobayashi & Hamada, 1974 from the Silurian Fukata Formation of Gomi, Yokokurayama, Kôchi Prefecture, Shikoku, Japan (Locality 8, Table 1). By original designation.

Other species. – *Gomiites latiaxis* (Kobayashi & Hamada, 1986) from the Fukata Formation of Gomi, Yokokurayama, Japan (Locality 8, Table 1).

Diagnosis. – Cephalon strongly convex (sag. and tr.); S1 deep defining a prominent L1; occipital ring with lateral lobes. Short preglabellar field may be present. Pygidium with five axial rings and four to five pleural ribs with a flat-topped profile; pygidial border short and weakly convex with broad border furrow. Sculpture of fine to coarse granules on cephalon, thorax and pygidium, but variable throughout.

Discussion. – Přibyl & Vaněk (1978) assigned their monospecific *Gomiites* to the Tropidocoryphinae, which is characterized by a broad preglabellar field, often with tropidial ridge, and an absence of or reduction in the lateral occipital lobes. *Gomiites* is here placed in the Proetinae, based on well-developed S1 and S2 and lateral occipital lobes, and the absence of a tropidium. It is most similar to *Cyphoproetus*, but differs notably in its strongly sagittally and transversely convex cephalon and the presence of a pygidial border. Several characters, for example its flat-topped pygidial ribs, are shared with members of the Warburgellinae (though it should be noted that it is difficult to determine the pygidial rib cross-section in many *Gomiites* species due to indifferent preservation), but differences, such as the lack of a preglabellar ridge or tropidium, suggest *Gomiites* is better placed in Proetinae. *Gomiites* resembles *Luojiashania* Zhang, 1974 from the Silurian of Sichuan and Hubei provinces, China, in glabellar outline, short preglabellar field and broad anterior border. The main differences are that in *Luojiashania,* L1 is more poorly defined and the pygidial axis is narrow and long. There are some similarities between *Gomiites* and *Latiproetus* in the deeply incised S1 glabellar furrow and the broad pygidial border, but the former is more tuberculate, S1 is deeper and the preglabellar field is much shorter. Several juvenile pygidia (KA007.6, KA007.13 to KA007.15, KA007.17, KA007.19, KA007.22, KA-009.2 to KA-009.4, KA-010.2 to KA-010.4), all from Locality 8 (Table 1), are herein tentatively assigned to *Gomiites*.

Stratigraphical and geographical range. – Known only from the Fukata Formation (Silurian), Japan.

Gomiites granulatus (Kobayashi & Hamada, 1974)

Figure 6A–F, J, M

1974 *Decoroproetus granulatus* Kobayashi and Hamada, sp. nov. Kobayashi & Hamada, pp. 114, 119, pl. 12, figs 10–13; text-fig. 8G.

1978 *Gomiites granulatus* (Kobayashi & Hamada, 1974); Přibyl & Vaněk, p. 179, pl. 2, figs 6–8.

Holotype. – Cranidium (PA7377), from Locality 8 (Table 1).

Paratypes. – Left librigena (PA7378), thoracopygon (KPFM15465); pygidium (KPFM15230). All from Locality 8 (Table 1).

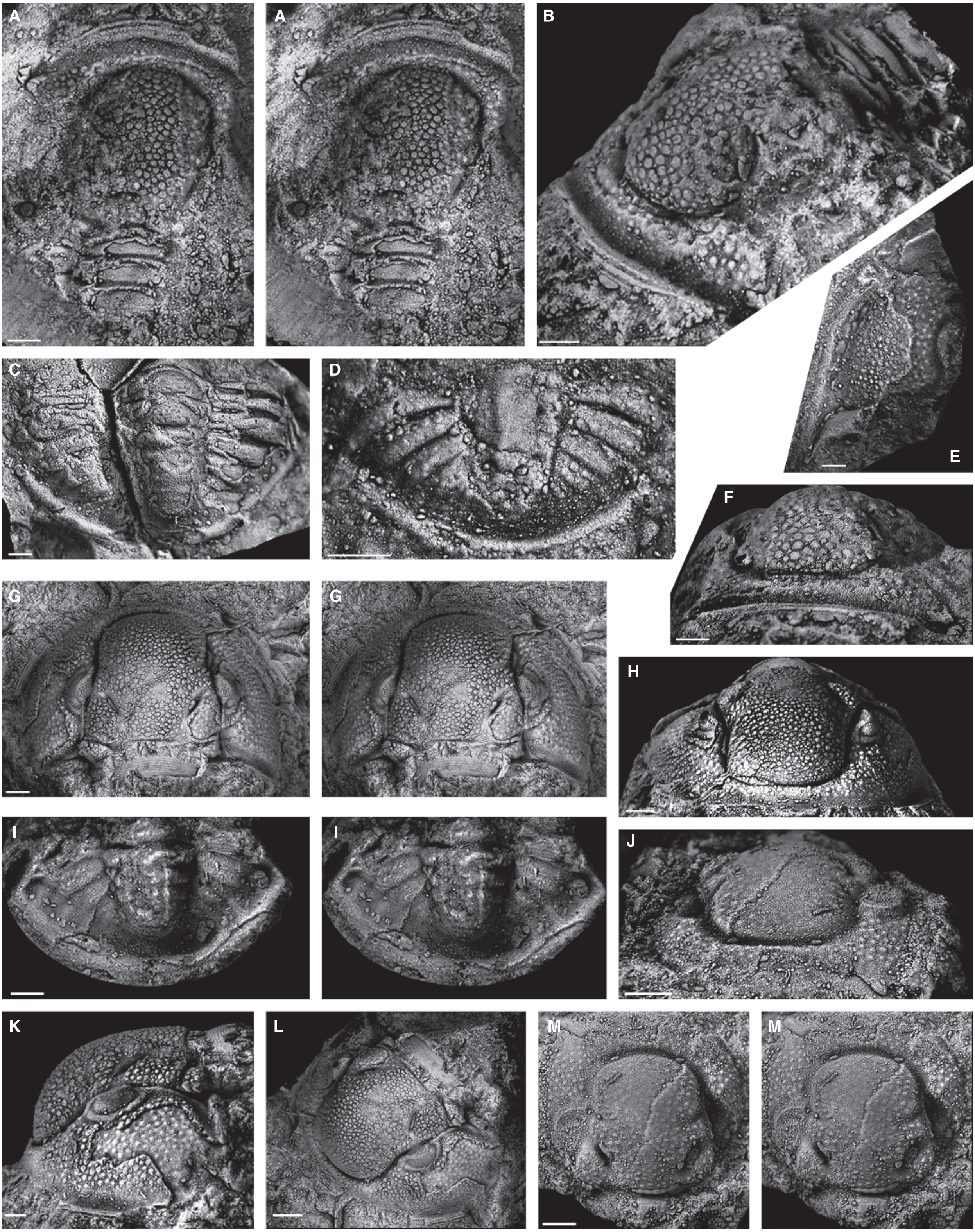
Other material. – Juvenile cranidium (YFM-1101007), and two juvenile cephalothoraces (KA-008, KA-010.1), both from Locality 8 (Table 1), identified during this study.

Diagnosis. – Anterior border furrow long. Pygidium with five axial rings and four pleural ribs; posterior pygidial border furrow broad and deep, with weakly convex border. Glabella with coarsely granular sculpture, finer granules on preglabellar field and librigena. Thoracic segments with pits on the surface of axial rings and pleural ribs; moderately fine granules on anterior two pygidial axial rings and pleural ribs.

Description. – Glabella subquadrate in outline, rounded frontally, about 70% as wide (at L1) as long and 70% width of cranidium; moderately strongly convex (sag. and tr.). Occipital ring 30% as long as wide, about twice the length (sag.) of anterior border, with small, triangular lateral occipital lobe (see left side of holotype, Fig. 6A) and deep intraoccipital furrow. S1 meets axial furrow at about midlength of glabella and occupies 20% of total glabellar width, forming a moderately deep incision trending posteriorly at about 150°. S2 meets axial furrow at 25% glabellar length from anterior margin, and occupies 17% of glabellar width, trending posteriorly at about 135°. Preglabellar field short, approximately as long as anterior border, with deep, short preglabellar furrow. Anterior border flat, upturned and 8% of cranidial length, with long, deep anterior border furrow twice as long as anterior border. Anterior facial suture moderately divergent (33°); indistinct posteriorly. Anterior margin of palpebral lobe opposite anterior of S1. Librigena 62% as wide as long and approximately 30% as wide as cranidium. Eye 40% as wide as long; eye socle absent, ocular furrow deep and broad with a ridge comprising two concentric rows of granules. Posterior border broader than lateral and anterior borders, and due to carapace exfoliation border furrow narrower than lateral and anterior border furrows. Genal spine as long as posterior border, slightly wider than lateral border; genal angle 65°. Holotype cranidium has parts of two exfoliated thoracic axial rings attached.

Pygidium semicircular, about twice as wide as long; moderately convex (tr.). Axial furrow shallow. Axis 24% of pygidial width anteriorly, with seven axial rings that become shorter posteriorly, with a short terminal piece; ring furrows shallow and

Fig. 6. Silurian proetids from the Fukata Formation of Yokokurayama, Kochi Prefecture, Shikoku. **A–F**, **J**, **M**, *Gomiites granulatus* (Kobayashi & Hamada, 1974); A, B, F, partially exfoliated holotype incomplete cranidium, (PA7377), dorsal stereo and left anterior oblique and anterior views; C, partially exfoliated paratype pygidium with thoracic segments attached, (KPFM15465), dorsal view; D, partially exfoliated paratype pygidium, (KPFM15230), dorsal view; E, partially exfoliated paratype left librigena, (PA7378), dorsal view; J, M, partially exfoliated juvenile incomplete cranidium (YFM-1101007), anterior and dorsal stereo views. **G–I**, *Gomiites latiaxis* (Kobayashi & Hamada, 1986); G, H, K, L, partially exfoliated holotype incomplete cephalon (PA18078), dorsal stereo, anterior, left lateral and left anterior oblique views; I, paratype pygidium (PA18079), dorsal stereo view. Scale bars = 2 mm.



narrow. Pleural lobe 33% of pygidial width anteriorly, with four, flat-topped ribs which curve gently backward, more strongly so and shorter posteriorly. Pleural furrows deep, shallowing anteriorly; interpleural furrows indistinct. Pleural lobe 20% wider than axis anteriorly. Posterior border with low convexity is 8% of pygidial length, with deep posterior border furrow almost twice as long.

Glabella is coarsely granulose; preglabellar field with finer granules; fine granules on axial rings and thoracic pleurae and least first two pygidial pleural ribs.

Ontogeny. – A juvenile cephalothorax is assigned to this species based on similarities with adults in the glabellar outline, glabellar furrows, broad anterior border furrow, flat anterior border and coarse tuberculation on the glabella and preglabellar field. The major difference between juvenile and adult is in the preglabellar field length, which is relatively shorter in mature individuals of *G. granulatus*. However, this feature has been shown to undergo reduction during ontogeny in different proetid groups (e.g. Cyrtosymbolinae; Lerosey-Aubril & Feist 2005).

Discussion. – Kobayashi & Hamada (1974) compared *Decoroproetus granulatus* to the type species of *Decoroproetus*: *Decoroproetus decorus* (Barrande, 1846) from the Liteň Formation (Wenlock Series) of the Prague District and claimed that the 'frontal border' of their new Japanese species was considerably broader and the pygidium shorter with a broader and longer axis. Also, they suggested a tropidial ridge was present, but our examination indicates it is absent. Further, they indicated that the preglabellar field in *D. granulatus* is divided into a smooth inner and a granulose outer band separated by a furrow, but this difference simply represents exfoliation. Přibyl & Vaněk (1978) described the same features as Kobayashi & Hamada (1974), but they did not figure the holotype, and their illustrations appear to be borrowed from that paper. Nevertheless, they reassigned *D. granulatus*, making it the type species of their new genus *Gomiites*.

Kobayashi & Hamada (1974) described only the S2 furrow in *D. granulatus*, yet in their text figure, the posterior part of the glabella is straight-sided with no furrow. There is, however, evidence for an S1 on the right side of the holotype (Fig. 6A), although it is poorly preserved. *D. granulatus* is maintained in *Gomiites* based on its deep, well-developed lateral occipital lobe, the absence of a tropidium and pygidial ribs with a flat-topped profile. It is similar to *G. latiaxis* in its deeply incised S1 glabellar furrow; sagittally narrow preglabellar field with granular sculpture; sagittally wide anterior border furrow; small eye; broad posterior pygidial border furrow; and flat-topped pygidial pleural ribs. Differences in *G. granulatus* from *G. latiaxis* include a less sagittally and transversely convex cephalon, better-rounded glabella and better developed S2.

A juvenile specimen (Fig. 6J, M) has been assigned to this species based on its glabellar outline, deeply incised and diagonal S1, weakly incised S2, position of the palpebral lobe, deep preglabellar furrow, glabellar and preglabellar field sculpture of coarse granules. The only major differences are that this juvenile shows a less convex glabella and a larger palpebral lobe. Also, there is a poorly preserved median occipital tubercle on this specimen, which is not preserved in any other *Gomiites* specimen, probably due to incomplete cuticle preservation.

***Gomiites latiaxis* (Kobayashi & Hamada, 1986)**

Figure 6G–I, K, L

1986 *Cyphoproetus latiaxis* Kobayashi and Hamada, sp. nov. Kobayashi & Hamada, p. 453, pl. 91, figs 1a–g, 2a–c.

Holotype. – Cephalon (PA18078), from Locality 8 (Table 1).

Paratypes. – Pygidium (PA18079), from Locality 8 (Table 1).

Diagnosis. – Cephalon with wide, subtrapezoidal glabella with deep, short S1 furrow that shallows abaxially and posteriorly. Small, triangular lateral occipital lobe. Very small eye situated at midglabellar length. Small pygidium with long, broad, concave posterior border furrow; pygidial pleural ribs with flat-topped profile. Cephalon with coarse granules.

Description. – Cephalon 65% as long as wide, strongly convex (sag. and tr.). Cranidium approximately as long as wide, 70% width of cephalon, maximum at ω. Glabella subtrapezoidal, 70% width of cranidium, 55% as long as wide with maximum width across occipital ring, tapers gently forwards to a weakly convex, subtransverse anterior margin. Occipital ring 35% as long as wide, about twice as long as anterior border; the exfoliated cuticle reveals a striated doublure of the median lobe (Fig. 6G, K, L); lateral lobe small, triangular, anteriorly sited, comprising 20% of width of ring, defined by deep intraoccipital furrow. S1 deep and wide medially, shallows abaxially and posteriorly, meets axial furrow at midglabellar length, occupies 30% of glabellar width, angled posteriorly at 35°; S2 weakly incised, 30% from anterior margin of glabella, occupying 18% of glabellar width, subparallel to S1. Narrow preglabellar field 50% length of anterior border, with deep, narrow preglabellar furrow. Anterior border flat, narrow, approximately 10% length of cranidium, with shallow, moderately broad anterior border furrow, approximately half as broad as anterior border.

Cranidial width at δ is 83% of maximum. Anterior facial suture strongly divergent (125°). Palpebral lobe semi-elliptical, very small, as long as lateral occipital lobe, with anterior margin in line with anterior of S2; eye very small, eye socle narrow and convex (tr.). Lateral and anterior borders similar, posterior border unpreserved; posterior border furrow broad and deep.

Pygidium semi-elliptical in outline, about half as long as wide. Axial furrow shallow; axis approximately 35% pygidial width anteriorly, comprises five axial rings and short terminal piece 10% of axial length; ring furrows moderately deep, shallowing posteriorly. Pleural lobe with five ribs, straight, separated by deep pleural furrows; interpleural furrows moderately deep; ribs with flat-topped profile. Pleural lobe 10% narrower than axis at maximum width. Posterior border weakly convex, 10% of pygidial length; border furrow long and broad, slightly longer than border.

Cephalon with coarse granules; pygidial axis and first two pleural ribs with sparse granules.

Discussion. – Kobayashi & Hamada (1986, p. 454) claimed that this species belonged to 'a *Cyphoproetus* group with a narrow preglabellar area and granulose sculpture, as in *Cyphoproetus strabismus*, but with coarser granulation, a broader cranidium and glabella, and smaller eyes'. The holotype of *C. strabismus* Owens, 1973 (Owens 1973, pl. 6, fig. 15a–d), from the Liteň Formation (Wenlock Series) of the Czech Republic, has a much broader preglabellar field (although the specimen of Owens 1973, pl. 6, fig. 13 has a narrow preglabellar field similar to that in *G. latiaxis*), and the lateral occipital lobe is much larger in *C. strabismus*. *G. latiaxis* is similar to *Cyphoproetus facetus* Tripp, 1954, from the Upper Ordovician Craighead Limestone Formation, Girvan, Scotland, in its narrow preglabellar field and small lateral occipital lobe. However, the cephalon of *G. latiaxis* is significantly more convex than that of any *Cyphoproetus* species.

G. latiaxis is also similar to the type species of *Gomiites*, *G. granulatus*, in its deeply incised S1 glabellar furrow, short preglabellar field with granular sculpture, long anterior border furrow, small eye and broad posterior border furrow. Differences from *G. granulatus* include a more sagittally and transversely convex cephalon, more flattened anterior margin to the glabella, the outline of which is constricted opposite the anterior margin of the eye. The possible eye socle that Kobayashi & Hamada (1986) described may be an indeterminate cuticle fragment, with this feature being the narrow indistinct ridge that they described behind the left eye.

Subfamily Crassiproetinae Osmólska, 1970

Genus *Hedstroemia* Přibyl & Vaněk, 1978

Type species. – *Proetus delicatus* Hedström, 1923, from the Halla Formation, Silurian (Wenlock Series), Horsne Canal, Gotland, Sweden. By original designation.

Stratigraphical and geographical range. – Silurian (Llandovery to Pridoli series), Europe, North America, central Asia, Australia and Japan.

Hedstroemia sugiharensis (Kobayashi & Hamada, 1974)

Figure 7A–C

1974 *Proetus* (*Gerastos*) *sugiharensis* Kobayashi and Hamada, sp. nov. Kobayashi & Hamada, p. 116, pl. 12, figs 5, 6; text-fig. 8C.

1985 *Proetus* (*Gerastos*) *sugiharensis* Kobayashi & Hamada, 1974; Kobayashi & Hamada, p. 208, pl. 29, fig. 1a-c.

1990 *Hedstroemia*? *sugiharensis* (Kobayashi & Hamada, 1974); Lütke, p. 49.

2006 *Hedstroemia sugiharensis* (Kobayashi & Hamada, 1974); Owens, p. 126, fig. 5.4.

Holotype. – Pygidium (PA7375), from Locality 8 (Table 1).

Paratypes. – Pygidium (KPFM809), from Locality 8 (Table 1).

Other material. – Pygidium figured in Kobayashi & Hamada (1985b, pl. 29, fig. 1), from Locality 8 (Table 1). No repository number was given for this specimen.

*Diagnosis (*emended from Owens 2006). – Pygidium strongly convex (tr.) with long (sag.), convex border and broad, gently tapering axis with ten rings plus terminal piece. Pleural lobe with seven ribs with a scalloped profile and distinct pleural furrows. Pygidial sculpture finely granulose.

Description. – Pygidium 75% as long as wide, strongly convex (sag. and tr.). Axial furrow moderately shallow and narrow; axis with seven rings, 45% of pygidial width anteriorly, becoming gradually less well-defined posteriorly, with a poorly defined terminal piece; ring furrows shallow and narrow, becoming less distinct posteriorly. Pleural lobe strongly convex (tr.), comprising seven ribs that curve moderately strongly backwards, separated by distinct pleural furrows that become poorly defined posteriorly; interpleural furrows weaker, broaden (sag.) slightly abaxially and terminate at border furrow; ribs with scalloped profile; postaxial field is 6% pygidial length (sag.); border strongly convex with moderately shallow and moderately broad border furrow. Pygidium bears fine granules on pleural ribs.

Discussion. – In referring this species to *Proetus* (*Gerastos*), Kobayashi & Hamada (1974) indicated that its pygidium had 'about 10' axial rings, which however exceeds that in the diagnosis for *Gerastos* (a maximum of eight). In addition, there are no prominent subparallel terrace ridges on the pygidial border, and no evidence of single rows of small perforations there as noted in *Gerastos* by Adrain (1997). The holotype pygidium however has only seven rings, which places it within the diagnosis of *Hedstroemia* Přibyl & Vaněk, 1978. Other characters in line with this generic position include the nine pleural ribs with well-defined pleural and interpleural furrows, the clavate swellings at the distal ends of pleural ribs and a distinct pygidial border. Therefore, we agree with Lütke (1990) and Owens (2006) that this species better belongs in *Hedstroemia*.

Subfamily Cornuproetinae Richter *et al. in* Moore, 1959

Genus *Interproetus* Šnajdr, 1977

Type species. – *Proetus intermedius* Barrande, 1846, p. 63, from the Kopanina Formation (Silurian, Ludlow Series), Dlouhá Hora, Prague Basin, Czech Republic. By original designation.

Stratigraphical and geographical range. – Silurian (Wenlock and Ludlow series), Ireland, Czech Republic, Uzbekistan and Japan.

Interproetus mizobuchii n. sp.

Figure 7D–H, K

Derivation of name. – Named for Mr Mizobuchi, Curator of Sakawa Geology Museum, Kochi Prefecture, Shikoku, collector of the holotype.

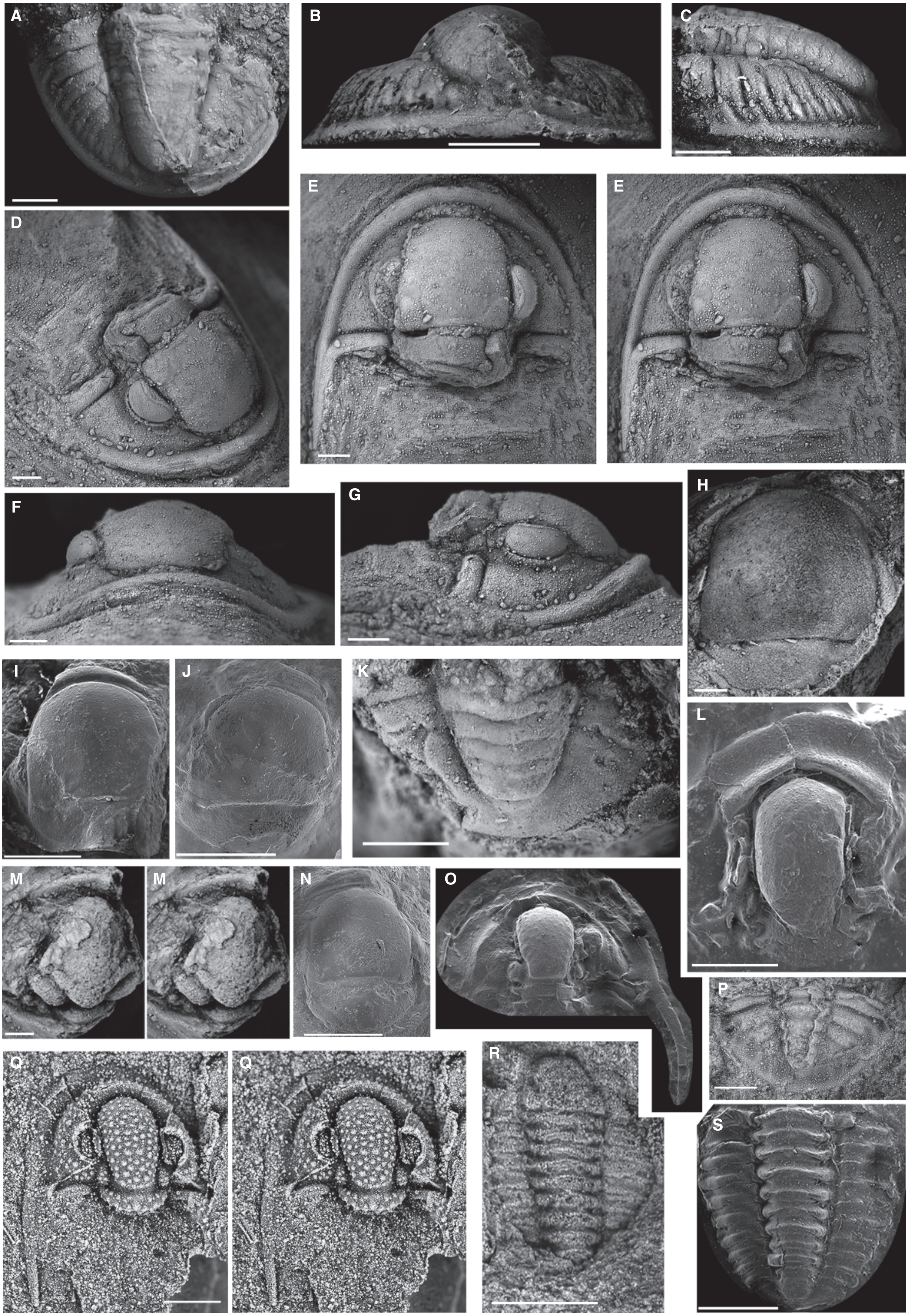
Holotype. – A cephalon (SGM1301), from Locality 8 (Table 1).

Other material. – Cranidium (KA-019) and pygidium (KA-002) from Locality 8 (Table 1), identified during this study.

Diagnosis. – Cephalon with moderately long (3 mm) genal spines. Cranidium narrow, with short palpebral lobe. Glabella with very long occipital ring and weakly impressed lateral furrows. Anterior border long and convex with short, deep border furrow. Preglabellar field less than 50% length of anterior border. Eye large.

Description. – Cephalon moderately strongly convex (sag. and tr.). Cranidium 15% longer than wide and 75% width of cephalon, with 65% cranidial width at δ and maximum width at ω. Glabella weakly convex (sag. and tr.), subquadrate, 75% as long as wide with maximum width across anterior of occipital ring and 55% width of cranidium; Occipital ring 25% as long as wide, twice as long as anterior border; occipital tubercle small, anteriorly placed, weak; lateral occipital lobe small and weak. Lateral glabellar furrows weakly incised. S1 meets axial furrow at midglabellar length and expands adaxially posteriorly to a point opposite posterior margin of

Fig. 7. Silurian proetids from the Fukata Formation (A–K, -N), Nakazato Formation (M), Gionyama Formation (P), and Kawauchi Formation (R) and a Devonian aulacopleurid from the Fukuji Formation (L, O, Q, S). **A–C**, *Hedstroemia sugiharensis* (Kobayashi & Hamada, 1974), holotype pygidium, (PA7375), dorsal, posterior and left lateral views. **D–H**, *Interproetus mizobuchii* n. sp.; **D-G**, holotype, (SGM1301), right anterior oblique, dorsal stereo, anterior and right lateral views, H, incomplete cranidium (KA-019), dorsal view. **I**, **J**, *Eremiproetus*? *subcarinatus* (Kobayashi & Hamada, 1974); I, partially exfoliated holotype incomplete cranidium (PA7373), dorsal view; J, partially exfoliated paratype incomplete cranidium (PA07374), dorsal view. K, *Interproetus mizobuchii* n. sp., incomplete pygidium (KA-002), dorsal view. **L**, **O**, **Q**, **S**, *Maurotarion megalops* (Kobayashi & Hamada, 1977); L, internal mould, paratype cranidium (KT-20160520-03C), dorsal view; O, internal mould, holotype cephalon (KT-20160520-03A), dorsal view; Q, cephalon, silicone cast of external mould, (OUMNH DY.15), dorsal stereo view; S, partially exfoliated paratype thoracopygon (KT-20160520-03B), dorsal view. **M**, *Dechenella minima* (Okubo, 1951), holotype cranidium (PA08006), dorsal stereo view. **N**, *Eremiproetus*? *magnicerviculus* (Kobayashi & Hamada, 1974), internal mould, holotype cranidium, (PA7376), dorsal view. P, partially exfoliated pygidium possibly referable to *Latiproetus* (NUM-Fa220), dorsal view. **R**, incomplete cephalothorax possibly referable to *Latiproetus* (OCM.G.000647), dorsal view. Scale bars = 2 mm.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eye; S2 meets axial furrow 30% from anterior glabella margin, and S3 15% from anterior margin. Preglabellar field <50% length of anterior border, with short, moderately shallow preglabellar furrow. Anterior border strongly convex (sag.), 10% of cranidial length, 50% as long as occipital ring, with deep, broad anterior border furrow. Palpebral lobe very narrow and semi-elliptical, posteriorly placed, with posterior margin adjacent to posterior of L1, 25% as wide as long and occupying 35% length and 7% width of cranidium. Facial suture divergent anteriorly at 40° and divergent posteriorly at 125°. Librigena narrow, 20% as wide as long. Lateral and posterior borders approximately as broad as the anterior border. Genal spine 15% as wide as long. Eye large; eye socle narrow (tr.) with deep, narrow (tr.) furrow and broader subocular furrow lacking an abaxial ridge.

Sculpture of granules on glabella; fine terrace ridges on anterior border.

Discussion. – This species is assigned here to *Interproetus* based on its subquadrate glabella, long occipital ring with reduced lateral lobe and moderately long genal spines. The genus is commonly represented in Europe, in particular the Czech Republic, with numerous species described from Wenlock to Ludlow strata (Šnajdr 1980). The only other non-European occurrence of this genus is *Interproetus pentaxus* Ivanova & Owens, 2009 (*in* Ivanova *et al.* 2009) from Uzbekistan, which differs from *I. mizobuchii* in its shorter glabella, narrower occipital ring, wider and more rounded adaxially S1, slightly longer genal spine and coarser terrace ridges on the cephalic border.

Subfamily Eremiproetinae Alberti, 1967

Genus *Eremiproetus* Richter & Richter, 1919

Type species. – *Proetus eremita* Barrande, 1852 from the Devonian (Eifelian Stage), of the Czech Republic. By original designation.

Stratigraphical and geographical range. – Ordovician to Devonian, Sweden, Czech Republic, Germany, Morocco, and possibly Inner Mongolia and Japan.

Eremiproetus? subcarinatus (Kobayashi & Hamada, 1974)

Figure 7I, J

1974 *Proetus* (*Gerastos*) *subcarinatus* Kobayashi and Hamada, sp. nov. Kobayashi & Hamada, 1974, p. 115, pl. 12, figs 3, 4; text-fig. 8D.

Holotype. – Cranidium (PA7373), from Locality 8 (Table 1).

Paratypes. – Cranidium (PA07374), from Locality 8 (Table 1).

Diagnosis. – Cranidium with wide subquadrate glabella, long (sag.) occipital ring, long (sag.) convex anterior border and deep anterior border furrow.

Description. – Cranidium incomplete. Glabella weakly convex (sag. and tr.), subquadrate with rounded anterior margin, 70% as wide as long with maximum width across L1. Occipital ring 25% length of glabella; weakly convex (sag. and tr.). Occipital tubercle weak and anteriorly placed; occipital lobe absent; occipital furrow shallow and broad. Glabellar furrows effaced except for very poorly defined S1 marked by a slight impression in the lateral glabellar margin. Preglabellar field very short, with moderately deep preglabellar furrow. Anterior border longer medially, representing 10% length of the cranidium, with deep furrow. Fixigenae absent from both specimens, except for slight remnant on left side of holotype at just posterior of midlength. Carapace smooth.

Discussion. – Kobayashi & Hamada (1974) based this species on two incomplete specimens that are mostly internal moulds with otherwise poorly preserved cuticle. The holotype is a small juvenile with an incompletely preserved occipital ring; the paratype has a glabella with the same outline and a similarly short (sag.) preglabellar field and long border. Kobayashi & Hamada (1974) compared *E.*? *subcarinatus* to the type species of *Gerastos*, whilst indicating that in the former the glabella is larger, less convex, subparallel sided and subcarinate axially, and lacks lateral furrows and with a longer occipital ring. The weak convexity of the glabella is possibly a result of tectonic deformation, this also leading to a subcarinate appearance. However, the long (sag. exsag.) occipital ring, glabellar shape and longer median anterior border are all characters found in *Eremiproetus*. Nevertheless, there is no occipital spine preserved, and without a pygidium, it is difficult to make a firm generic assignation. This Japanese species does not belong to *Gerastos* but, based on the characters available, is closer to *Eremiproetus* and we tentatively assign it to that genus. In comparison with *E.*? *magnicerviculus*, which is also from the Fukata Formation of Shikoku, the glabella of

E.? *subcarinatus* is much less convex and marginally wider, with a shorter occipital ring.

Eremiproetus? magnicerviculus (Kobayashi & Hamada, 1974)

Figure 7N

1974 *Proetus* (*Bohemiproetus*) *magnicerviculus* Kobayashi and Hamada, sp. nov. Kobayashi & Hamada, p. 117, pl. 12, fig. 7; text-fig. 8E.

Holotype. – Incomplete cranidium (PA7376), from Locality 8 (Table 1) (the only specimen).

Diagnosis. – Glabella with very long occipital ring, 40% of its length and with both median and posterior median tubercle. Anterior border slightly inflated (sag.) medially and occupies 10% of length of cranidium.

Description. – Glabella subovate with straight lateral margins, moderately convex (sag. and tr.), 70% as wide as long with maximum width posteriorly. Long occipital ring, moderately convex (sag. and tr.) with a shallow, gentle slope on the anterior margin to form a long occipital furrow; median tubercle small and central; another tubercle may be present on the median posterior margin; occipital lobe absent. S1 very weak, other glabellar furrows effaced. Anterior border furrow moderately deep and short. Preglabellar field short, approximately 25% as long as anterior border, with short, shallow preglabellar furrow.

Discussion. – The diagnosis and description are based only on the holotype – an internal mould of an incomplete cranidium. Kobayashi & Hamada (1974) placed *E. magnicerviculus* in *Bohemiproetus* Pillet, 1969, while Owens (1973) considered *Bohemiproetus* to be a junior synonym of *Proetus* (*Coniproetus*) Alberti, 1966; which has subsequently been elevated to generic status (Šnajdr 1980).

E.? *magnicerviculus* differs from *Coniproetus* species in that the glabella is roughly parallel sided and subquadrate, the lateral furrows are not effaced, S1 is poorly expressed and isolates a small L1 and the occipital ring is very long and bears a median tubercle anteriorly. Based on its subquadrate glabella with long occipital ring, and medially long anterior border, *E.*? *magnicerviculus* is very similar to *Eremiproetus* species, but it is not clear in the Japanese specimen if there is an occipital spine at the posterior, and it is not possible to confidently place it in this genus.

In comparison with *E.*? *subcarinatus,* from the same formation, the glabella of *E.*? *magnicerviculus* is much less convex and marginally wider, with a shorter occipital ring.

Subfamily Dechenellinae Přibyl, 1946

Genus *Dechenella* Kayser, 1880

Type species. – *Phillipsia verneuili* Barrande, 1852 from the Devonian (Givetian) of Germany. By original designation.

Stratigraphical and geographical range. – Devonian (Emsian to Givetian stages), Europe, North America, and Morocco.

Dechenella minima Okubo, 1951

Figure 7M

1951 *Dechenella minima*, sp. nov. Okubo, p. 136, pl. 1, fig. 6a–c.

1957 *Dechenella* (*Dechenella*) *minima* Okubo; Kobayashi, p. 7, pl. 1, figs 1a, b, 2a, b.

1977 *Dechenella* (*Dechenella*) *minima* Okubo; Kobayashi & Hamada, p. 143, pl. 8, fig. 8; text-fig 3F.

2007 *Dechenella minima* Okubo, 1951; Kaneko, pl. 3, figs 12, 13.

Holotype. – Cranidium (PA08006), from Locality 1 (Table 1).

Other material. – A pygidium figured by Kaneko (2007, pl. 3, fig. 13) from Locality 1 (Table 1).

Diagnosis. – Glabella short, subtriangular, strongly convex (sag.) with deeply incised S1 and S2; L1 and L2 independently convex. Preglabellar field short, anterior border long. Pygidium with narrow axis of twelve rings, and nine pleural ribs, interpleural furrows lacking.

Description. – Cranidium almost as long as wide, moderately convex (sag. and tr.). Glabella moderately convex (tr.); 15% longer than wide, constricted in anterior half with maximum width over L1; 70% length and 75% width of cranidium. Occipital ring weak and low; 20% as long as wide, occupying 15% glabellar length and 65% glabellar width; median third slightly wider than lateral third, median occipital tubercle anteriorly placed; lateral occipital lobe absent. Lateral glabellar lobes have distinct independent convexity, separated by furrows trending adaxially forwards at about 45°. S1 meets axial furrow at approximately 70% from anterior glabellar margin, and occupies 40% of glabellar width, meeting occipital furrow at 30% of its width; S2 meets axial furrow at 55% length from anterior margin and occupies 25% of glabellar width; S3 meets axial furrow at 40% length from anterior margin and occupies 5% of glabellar width. Preglabellar field absent. Anterior border long, convex (sag.), strongly upturned and 15% cranidial length, with long shallow anterior border furrow. Palpebral lobe large, 45% as wide as long, occupying 25% cranidial length and 10% cranidial width; posterior margin adjacent to posterior of L1.

Pygidium conical, long and narrow, 15% longer than wide. Axis long and narrow, 40% pygidial width anteriorly, comprising twelve (possibly thirteen) axial rings separated by narrow, deep ring furrows. Pleural lobe about 40% of pygidial width anteriorly; much wider than axis, with at least nine ribs separated by narrow, deep interpleural furrows; ribs narrow, lacking pleural furrows.

Carapace lacks sculpture.

Discussion. – In the only figured pygidium (Kaneko 2007, pl. 3, fig. 13), it is impossible to count the number of rings and ribs and to determine the presence or absence of a posterior border. This pygidium may be distorted, as it is unusually narrow and elongate, with a very narrow axis; we have been unable to locate this specimen in any museum collection. *D. minima* resembles *Dechenella ormistoni* Yolkin, 1979 from the Devonian of south-west Siberia, in its short glabella with deeply incised lateral furrows, but *D. ormistoni* has coarse granular sculpture and a more convex anterior border with a deeper border furrow. The broad, flat anterior border with a broad, shallow anterior border furrow of *D. minima* is a diagnostic character of *Basidechenella* Yolkin, 1968, and in this character, it especially resembles *Basidechenella arctica* Maximova, 1977, but in the latter species, the occipital lobe is well developed, and the frontal lobe is more elongate. Of the dechenellids described by Zhou *et al.* (2000) from the Devonian of Inner Mongolia, the most similar to *D. minima* is *Basidechenella*? *exquisita* which has a glabella with a similar dorsal outline, but is much less convex, with poorly incised furrows; in addition, the anterior cephalic border of *B.*? *exquisita* is much longer, the lateral occipital lobe better developed and the pygidium much shorter and wider.

Subfamily Warburgellinae Owens, 1973

Genus *Latiproetus* Lu, 1962

Type species. – *Proetus latilimbatus* Grabau, 1924; from the Silurian of western Hubei, China (see Lu 1962).

Stratigraphical and geographical range. – Silurian (Llandovery to Ludlow series), China, Australia, Canada.

Discussion. – We follow Sun (1990) in considering *Latiproetus* distinct from *Astroproetus* (see Lane & Wu 2002), based on the sigmoidal profile of the preglabellar field and differences in lateral occipital lobes. A single pygidium (Fig. 7P) from the Silurian Gionyama Formation of the Kurosegawa Terrane (Locality 7) may belong to *Latiproetus*. A single, incomplete cephalothorax (Fig. 7R) from the Silurian Kawauchi Formation of the South Kitakami Terrane (Locality 2, Table 1) is similar to *Latiproetus* in the shape of the glabella and the deeply incised S1. Furthermore, it is possible that some juvenile pygidia (KA-006.1 – KA-006.5, KA-007.1, KA-007.5, KA-007.7, KA-007.18, KA009.5 and KA-010.1) from the Silurian Fukata Formation (Locality 8) may belong to *Latiproetus*, particularly those lacking a broad pygidial border furrow and border.

Latiproetus bilobus (Kobayashi & Hamada, 1974)

1974 *Prantlia biloba* Kobayashi and Hamada, sp. nov. Kobayashi & Hamada, pp. 114, 118, pl. 12, figs 8, 9; text-fig. 8F.

1985b *Latiproetus biloba* (Kobayashi & Hamada, 1974); Kobayashi, p. 422.

Holotype. – Cranidium (OCU PA0006), from Locality 7 (Table 1).

Paratype. – Pygidium (OCU PA0002), from Locality 7 (Table 1).

Diagnosis. – Glabella with deeply incised S1; preglabellar field and anterior border short.

Pygidium narrow, subtriangular, with anterior two ribs expanding abaxially.

Description. – Cranidium almost as long as wide, moderately convex (sag. and tr.). Maximum width at ω, with 83% at δ. Glabella subquadrate, widens slightly anteriorly, moderately convex (tr.); 80% as long as wide, maximum width across occipital ring, and 75% length and 67% width of cranidium. Occipital ring is 25% as long as wide, forms 20% of glabellar length and is 5% longer than anterior border; occipital tubercle posteriorly placed. Lateral occipital lobe large, narrowly triangular, 45% as long as wide, occupies 30% width of occipital ring; intraoccipital furrow deep. S1 deep, trends at about 25°, meets axial furrow at midglabellar length, occupies 40% of glabellar width; S2 meets axial furrow at 35% length from anterior glabellar margin, occupies 12% of glabellar width; S3 is absent. Palpebral lobe long and narrow, 35% as wide as long, occupies 30% cranidial length and 12% cranidial width, posterior margin in line with occipital furrow. Preglabellar field gently convex, 11% cranidial length. Anterior border 15% cranidial length, flat and strongly upturned.

Pygidium narrow and subtriangular. Axis approximately 30% pygidial width anteriorly comprises eight rings and a terminal piece that is 12% of axial length; ring furrows narrow. Pleural lobe with five ribs that widen abaxially and are separated by narrow, deep pleural furrows that reach posterior border; pleural furrows incised abaxially on first two ribs which are flat-topped in profile. Posterior border long, weakly convex, 15% of pygidial length sagittally and about 50% this laterally.

Cephalon and pygidium smooth.

Discussion. – We have been unable to locate the type specimens of *Prantlia biloba*, and this description is based on the original illustrations of Kobayashi & Hamada (1974, p. 114, text-fig. 8F; pl. 12, figs 8, 9). Kobayashi (1985) reassigned *P. biloba* to *Latiproetus*, due to difference from *Prantlia* in the size and position of the palpebral lobes. Sun (1990) considered these characters to have no generic value, but highlighted the following differences of *Latiproetus* from *Prantlia*: a shorter preglabellar field, the presence of an anterior and lateral cephalic border furrow (and not an epiborder furrow), a longer and wider glabella, a less pronounced S1, a shorter occipital ring, weaker pleural and interpleural pygidial furrows and the lack of a broad pygidial border furrow and border. Based on its possession of these characters, we retain this species in *Latiproetus*.

Order Aulacopleurida Adrain, 2011
Family Aulacopleuridae Angelin, 1854
Subfamily Otarioninae Richter & Richter, 1926

Genus *Maurotarion* Alberti, 1969

Type species. – *Harpidella maura* Alberti, 1967, from the Ludlow of Morocco.

Stratigraphical and geographical range. – Silurian of the USA, Canada, Europe, Morocco and Australia; Devonian of the USA, Europe, Morocco, Turkey, Australia, Bolivia and Japan.

Maurotarion megalops (Kobayashi & Hamada, 1977)

Figure 7L, O, Q, S

1974 *Otarion* sp. Okazaki, pl. 9, figs 10, 11.

1977 *Otarion megalops*, Kobayashi and Hamada, sp. nov. Kobayashi & Hamada, pl. 3, figs 2–4; text-fig 3K

Holotype. – A cephalon (both internal and external moulds, KT-20160520-03A), from Locality 3 (Table 1).

Paratypes. – Thoracopygon (KT-20160520-03B) and cephalon (KT-20160520-03C), from Locality 3.

Other material. – External mould of a juvenile cranidium (OUMNH DY.15), from Locality 3, identified during this study.

Diagnosis. – Cephalon with broad, gently convex anterior and lateral borders, and long robust genal spine. Interocular fixigenae very narrow. Glabella moderately inflated, not overhanging the preglabellar field. L1 small, approximately 15% of total glabellar width; S1 meets axial furrow at 62% length from anterior margin of glabella and 30% of its maximum width. S2 very short (tr.); S3 absent. Thorax lacks axial spine on sixth segment. Pygidium very small with two axial rings and two pleural ribs.

Description. – Cephalon 60% wider than long, moderately convex (tr. and sag.). Cranidial width at ω approximately 75% total width of cephalon. Glabella subquadrate to subovate with well-rounded anterior margin, moderately convex (tr.), 55% width of cranidium with maximum width across anterior of L1. Occipital ring moderately convex, 15% glabellar length; slightly longer medially than laterally; median tubercle about twice as coarse as other tuberculation on the occipital ring, posteriorly positioned. The central area of the pre-occipital glabella is subpyriform and strongly convex (sag. and tr.). S1 deep, diagonal, meets axial furrow at approximately 62% from anterior margin of glabella; L1 represents approximately 15% of total glabellar width, with moderate lateral protrusion from outline of glabella. Preglabellar field moderately short; preglabellar furrow incised. S2 very short (sag.), in line with anterior margin of eye. Anterior border weakly convex, about as long as preglabellar field; anterior border furrow shallow and broad. Interocular fixigenae very narrow. Lateral and anterior borders of equal breadth; posterior border half as broad as anterior border. Eye platform large; eye socle narrow (tr.). Librigenal spine long, curved.

Thorax has 11 segments. Axis roughly 70% wider than pleural field and moderately convex (tr.). Axial rings essentially exfoliated except for ninth ring on left side; axial furrow shallow. Pleurae widening (exsag.) abaxially from about 50% width of segment. Pleural furrows broad (exsag.), moderately shallow; weak boss on anterior pleural band at adaxial edge of articulating facet.

Pygidium very small, subovate in dorsal view, 25% as long as wide. Axis with two axial rings, moderately convex (tr.), approximately 50% as long as wide and approximately 40% of maximum pygidial width. Pleural lobe slightly wider than axis, with two poorly preserved ribs; furrows not discernible on the internal mould. Posterior border not preserved.

Pre-occipital glabella with dense, moderately coarse tubercles, coarsening medially; occipital ring with two transverse rows of five coarse tubercles, coarsening medially. Librigena and fixigena with sparse, coarse, rounded tubercles with interspersed fine tubercles.

Discussion. – We agree with Kobayashi & Hamada (1977) that the cephalothorax and thoracopygon on the same block which they described and which they assigned to *O. megalops* belong to one individual. In this specimen, the detached thoracopygon has ten segments whilst the cephalothorax has one attached thoracic segment. This species was assigned to *Otarion*, without any supporting reasons. However, based on the following characters, it is herein reassigned to *Maurotarion*: moderately convex (tr.) glabella; prominent L1 with moderate protrusion from lateral glabellar margin; broad anterior border; large palpebral lobe and eye; and the absence of an axial spine on the sixth thoracic segment (present only in some species of *Maurotarion* – see Adrain & Chatterton 1994).

Maurotarion megalops has a more sculptured cephalon and slightly more convex (sag.) glabella than most species of *Maurotarion* (see Adrain & Chatterton 1994; Adrain 2009). In the sculpture of coarse granules, it is similar to *M. struszi* (Chatterton, 1971) from the Emsian Waroo Limestone of the Yass Basin of New South Wales, Australia, but *M. struszi* has a much longer and more curved genal spine and a thoracic axial spine.

Acknowledgements

We are grateful to The Leverhulme Trust (International Network) Grant IN-2014-025, ‘Assembling the Early Palaeozoic terranes of Japan’, awarded to Williams, for funding this research. We thank Allaart Van Viersen (Natuurhistorisch Museum Maastricht) for discussion on aulacopleurid systematics; Yujing Lin (Yunnan University) for translating Chinese literature; the curators of Tokyo University Museum, Kyoto University Museum, Yokokurayama National Forest Museum, Sakawa Geology Museum, Iwate Prefectural Museum and Ofunato City Museum, for help and access to specimens; Mr Yoshiaki Mizuno of the Tokai Fossil Society for the donation of his trilobite specimens to the University Museum, Nagoya University. We also thank James Mawson, Aqqid Saparin, Thomas Gray, Harrison Bush and Michael Sekula for technical assistance at Leicester University. We are very grateful to Bob Owens and Alan Thomas for their very thorough reviews of an earlier version of this manuscript.

References

Adrain, J.M. 1997: Proetid trilobites from the Silurian (Wenlock-Ludlow) of the Cape Phillips Formation, Canadian Arctic Archipelago. *Palaeontographia Italica 84*, 21–111.

Adrain, J.M. 2009: New and revised species of the aulacopleurid trilobite Maurotarion from the lower Devonian (Pragian) of Nevada. *Zootaxa 2215*, 1–23.

Adrain, J.M. 2011: Class Trilobita Walch, 1771. *In* Zhang, Z.-Q. (ed.): *Animal Biodiversity: An Outline of Higher-Level Classification and Survey of Taxonomic Richness*, *Zootaxa*, volume *3140*, 104–109.

Adrain, J.M. & Chatterton, B.D.E. 1994: The aulacopleurid trilobite Otarion, with new species from the Silurian of Northwestern Canada. *Journal of Paleontology 68*, 305–323.
Aitchison, J.C., Hada, S., Ireland, T. & Yoshikura, S.-I. 1996: Ages of Silurian radiolarians from the Kurosegawa Terrane, southwest Japan constrained by U/Pb SHRIMP data. *Journal of Southeast Asian Earth Sciences 14*, 53–70.
Alberti, G.K.B. 1966: Über einige neue Trilobiten aus dem Silurium und Devon, besonders von Marokko. *Senckenbergiana Lethaea 47*, 111–121.
Alberti, G.K.B. 1967: Neue obersilurische sowie unter- und mitteldevonische Trilobiten aus Marokko, Deutschland und einigen anderen europäischen Gebieten. 2. *Senckenbergiana Lethaea 48*, 481–509, pl. 481.
Angelin, N.P. 1854: I, Crustacea formationis transitionis. *Palaeontologica Scandinavica Fascicule 2*, 21–92, pls 25–41.
Barrande, J. 1846: *Notice préliminaire sur le systême Silurien et les Trilobites de Bohême*, 97 pp. Hirschfeld, Leipzig.
Barrande, J. 1852: *Système silurien du centre de la Bohême*. 1, 935 pp. Trilobites, Prague, Paris.
Chatterton, B.D.E. 1971: Taxonomy and ontogeny of Siluro-Devonian trilobites from near Yass, New South Wales. *Palaeontographica, Abteilung A 137*, 1–108.
Chatterton, B.D.E. & Campbell, K.S.W. 1980: Silurian Trilobites from near Canberra and some related forms from the Yass Basin. *Palaeontographica Abteilung A167*, 77–119.
Chatterton, B.D.E., Johnson, B.D. & Campbell, K.S.W. 1979: Silicified Lower Devonian trilobites from New South Wales. *Palaeontology 22*, 799–837.
Chernysheva, N.E. 1951: *Upper Silurian and Devonian Trilobites from the Kuznetsk Basin*, 72 pp. Gosgeolizdat, Moscow.
Cocks, L.R.M. & Torsvik, T.H. 2013: The dynamic evolution of the Palaeozoic geography of eastern Asia. *Earth-Science Reviews 117*, 40–79.
Dalman, J.W. 1827: Om Palaeaderna eller de så kallade Trilobiterna. *Kongliga Svenska Vetenskaps-Akademiens Handlingar 1826*, 113–152, 226–294, pls 111–116.
Feist, R. & Lerosey-Aubril, R. 2008: Assessing the hypothesis of a third tagma in scutelluid trilobites: arguments from ontogenetic, functional, and evolutionary perspectives, 127–133. *In* Rábano, R., Gozalo, R. & Garda-Bellido, D. (eds): *Advances in Trilobite Research*, 448 pp. Instituto Geológico y Minero de España, Madrid.
Fortey, R.A. 1975: The Ordovician trilobites of Spitsbergen. 2. Asaphidae, Nileidae and Telephinidae of the Valkhallfonna Formation. *Skrifter Norsk Polarinstitutt 162*, 1–125.
Fortey, R.A. 1990: Ontogeny, hypostome attachment and trilobite classification. *Palaeontology 33*, 529–576.
Fortey, R.A. & Owens, R.M. 1975: Proetida—a new order of trilobites. *Fossils and Strata 4*, 227–239.
Fortey, R.A. & Owens, R.M. 1999: Feeding habits in trilobites. *Palaeontology 42*, 429–465.
Grabau, A.W. 1924: *Stratigraphy of China, Part 1, Palaeozoic and Older*, 528 pp. Geological Survey of China, Beijing.
Hamada, T. 1959: The Gotlandian stratigraphy of the outer zone of Japan. *Journal of the Geological Society of Japan 65*, 688–700.
Harashinai, M. 1981: Discovery of Silurian conodonts in the vicinity of Gyoninzawa, Hikoroichi-machi, Ofunato City, Northeast Japan. *The Journal of the Geological Society of Japan 87*, 841–843.
Hedström, H. 1923: Contributions to the fossil fauna of Gotland. I. *Sveriges Geologiska Undersökning C 1–316*, 311–325.
Hirayama, K., Yamashiya, N., Suyari, K. & Nakagawa, C. 1956: *Geological map of Tokushima, 1: 75,000 Tsurugisan with Explanatory Text*., Tokushima Prefecture.
Holloway, D.J. & Lane, P.D. 1998: Effaced styginid trilobites from the Silurian of New South Wales. *Palaeontology 41*, 853–896.
Holloway, D.J. & Lane, P.D. 2012: Scutelluid trilobites from the Silurian of New South Wales. *Palaeontology 55*, 413–490.
Holloway, D.J. & Lane, P.D. 2016: Trilobites of the suborder Illaenina from the Silurian of north Queensland, Australia. *Journal of Paleontology 90*, 433–471.
Holloway, D.J. & Neil, J.V. 1982: Trilobites from the Mount Ida Formation (Late Silurian – Early Devonian), Victoria. *Proceedings of the Royal Society of Victoria 94*, 133–154.
Hughes, H.E. & Thomas, A.T. 2011: Trilobite associations, taphonomy, lithofacies and environments of the Silurian reefs of North Greenland. *Palaeogeography, Palaeoclimatology, Palaeoecology 302*, 142–155.
Ivanova, O., Owens, R.M., Kim, I. & Popov, L.E. 2009: Late Silurian trilobites from the Nuratau and Turkestan ranges, Uzbekistan and Tajikistan. *Geobios 42*, 715–737.
Kaneko, A. 1990: A new trilobite genus *Rhinophacops*. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series 157*, 360–365.
Kaneko, A. 2007: Nakazato Trilobite Fauna (Early to Middle Devonian). *Jubilee Publication in Commemoration of Professor Tadao Kamei's 80th birthday, Commemorative Association of Professor Kamei Tadao's 80th birthday*, Tokyo, 231–250 [in Japanese with English abstract].
Kayser, E. 1880: *Dechenella*, eine devonische Gruppe der Gattung *Phillipsia*. *Zeitschrift der Deutschen Geologischen Gesellschaft 32*, 703–704.
Kido, E. 2010: Silurian Rugose Corals from the Kurosegawa Terrane, Southwest Japan, and the First Occurrence of *Neobrachyelasma*. *Journal of Paleontology 84*, 466–476.
Kido, E. & Sugiyama, T. 2011: Silurian rugose corals from the Kurosegawa Terrane, Southwest Japan, and their paleobiogeographic implications. *Bulletin of Geosciences 86*, 49–61.
Kobayashi, T. 1957: Notes on two Devonian trilobites from the Kitakami Mountains in Japan. *Journal of the Faculty of Science University of Tokyo, Section 2 11*, 1–10.
Kobayashi, T. 1985: On two Silurian trilobite genera, *Prantlia* and *Latiproetus*. *Proceedings of the Japan Academy, Series B 61*, 419–421.
Kobayashi, T. 1988a: The Devonian trilobites from the Fukuji and other formations in Japan. *Proceedings of the Japan Academy Series B-Physical and Biological Sciences 64*, 103–105.
Kobayashi, T. 1988b: New trilobites of the Devonian Fukuji fauna. *Proceedings of the Japan Academy Series B-Physical and Biological Sciences 64*, 106–108.
Kobayashi, T. & Hamada, T. 1974: Silurian trilobites of Japan in comparison with Asian, Pacific and other faunas. *Special Papers of the Palaeontological Society of Japan 18*, 1–155, 112 pls.
Kobayashi, T. & Hamada, T. 1977: Devonian trilobites of Japan: in comparison with Asian, Pacific and other faunas. *Special Papers of the Palaeontological Society of Japan 20*, 1–202, 213 pls.
Kobayashi, T. & Hamada, T. 1985a: Additional Silurian trilobites to the Yokokura-yama fauna from Shikoku, Japan. *Transactions and Proceedings of the Palaeontological Society of Japan 139*, 206–217.
Kobayashi, T. & Hamada, T. 1985b: Studies on Japanese trilobites and associated fossils. 41. On the Silurian trilobites and cephalopods of Mt. Yokokura, Shikoku, Japan. *Proceedings of the Japan Academy Series B-Physical and Biological Sciences 61*, 345–347.
Kobayashi, T. & Hamada, T. 1986: The second addition to the Silurian trilobite fauna of Yokokura-yama, Shikoku, Japan. *Transactions and Proceedings of the Palaeontological Society of Japan 143*, 447–462.
Kobayashi, T. & Hamada, T. 1987: On the Silurian trilobite faunule of Hitoegane near Fukuji in the Hida Plateau, Japan. *Transactions and Proceedings of the Palaeontological Society of Japan 147*, 131–145.
Kuo, H.-T. 1962: Some Silurian trilobites from the Er-tao-gou group of Jilin. *Acta Palaeontologica Sinica 10*, 377–381.
Lane, P.D. & Wu, H.-J. 2002: Trilobites. *In* Holland, C.H. & Bassett, M.G. (eds): *Telychian rocks of the British Isles and China (Silurian, Llandovery Series): An Experiment to Test Precision*

on Stratigraphy, National Museum of Wales Geological Series, volume 21, Cardiff, 142–150.

Lerosey-Aubril, R. & Feist, R. 2005: Ontogeny of a new cyrtosymboline trilobite from the Famennian of Morocco. *Acta Palaeontologica Polonica 50*, 449–464.

Lu, Y. 1962: Restudy of Grabau's types of three Silurian trilobites from Hupeh. *Acta Palaeontologica Sinica 10*, 158–173 (in Chinese with English summary).

Lütke, F. 1990: Contributions to a phylogenetical classification of the subfamily Proetinae Salter, 1864 (Trilobita). *Senckenbergiana Lethaea 71*, 1–83.

Manchuk, N., Horie, K. & Tsukada, K. 2013: SHRIMP U-Pb age of the radiolarian-bearing Yoshiki Formation in Japan. *Bulletin of Geosciences 88*, 223–240.

Maximova, Z. 1977: Devonian trilobites from Novaya Zemlya and other regions of the Soviet Arctic. *Ezhegodnik Vsesoyuznogo Paleontologischeskogo Obshchestva 20*, 140–185.

Moore, R.C. 1959: *Treatise on Invertebrate Paleontology*, *Part O, Arthropoda 1*, 560 pp. Geological Society of America and University of Kansas Press, Boulder, and Lawrence, Kansas.

Murata, M., Tomooka, M. & Kaneko, A. 1997: Early-Middle Devonian fauna from the middle part of the Naidaijin Formation. In: Abstracts, the 104th Meeting, the Geological Society of Japan, p. 343. [in Japanese].

Okazaki, Y. 1974: Devonian trilobites from the Fukuji Formation in the Hida Massif, Central Japan. *Memoirs of the Faculty of Science Kyoto University, Series Geology & Mineralogy 11*, 83–94, pls. 88, 89.

Okazaki, Y., Tanaka, K. & Tanaka, Y. 1974: A discovery of the Devonian trilobites from Fukui Prefecture. *The Journal of the Geological Society of Japan 80*, 563 [in Japanese].

Okubo, M. 1951: Trilobites from Japan *Chikyu Kagaku* 4 133–139, pl. 131 [in Japanese with English description of species].

Osmólska, H. 1970: Revision of non-cyrtosymbolinid trilobites from the Tournaisian-Namurian of Eurasia. *Palaeontologica Polonica 23*, 1–165, 161-122 pl.

Owens, R.M. 1973: British Ordovician and Silurian Proetidae (Trilobita). *Palaeontographical Society Monographs 127*, 1–98, 15 pls.

Owens, R.M. 2006: The proetid trilobite *Hedstroemia* and related Ordovician to Carboniferous taxa. *In* Bassett, M.G. & Deisler, V.K. (eds): *Studies in Palaeozoic Palaeontology*. National Museum of Wales Geological Series No. 25, Cardiff, 119–143.

Pillet, J. 1969: La classification des Proetidae (Trilobites). *Bulletin de la Société d'études scientifiques de l'Anjou 7*, 53–85, pls 51-56.

Přibyl, A. 1946: Notes on the recognition of the Bohemian Proetidae (Trilobitae). *Bulletin International, Académie tchèque des Sciences 46*, 1–41.

Přibyl, A. 1965: Proetidní trilobiti z nových sběru v českém siluru a devonu. *Casopis Narodniho Muzea 134*, 91–98.

Přibyl, A. & Vaněk, J. 1978: Studie zu einigen neuen Trilobiten der Proetidae-Familie. *Acta Universitatis Carolinae, Geologica 1*, 163–182.

Richter, R. & Richter, E. 1919: Proetiden aus neueren Aufsammlungen im vogtländischen und sudetischen Oberdevon. *Senckenbergiana 1*, 97–130.

Richter, R. & Richter, E. 1926: Die Trilobiten des Oberdevons. Beiträge zur Kenntnis devonischer Trilobiten. IV. *Abhandlungen der Preußischen Geologischen Landesanstalt, Neue Folge 99*, 1–314.

Richter, R., Richter, E. & Struve, W. 1959: Subfamily Cornuproetinae, O385 pp. *In* H. J. Harrington, Classification. *In* Moore, R.C. (ed.): *Treatise on Invertebrate Paleontology*. *Pt. O. Arthropoda 1. Trilobita 1*. 560 pp. The Geological Society of America and University of Kansas Press, Boulder, and Lawrence, Kansas.

Salter, J.W. 1864: A monograph of British trilobites, part 1. *Palaeontographical Society Monograph 16*, 1–80.

Selwood, E.B. 1966: Thysanopeltidae (Trilobita) from the British Devonian. *Bulletin of the British Museum (Natural History) Geology 13*, 117–190.

Šnajdr, M. 1977: New genera of Proetidae (Trilobita) from the Barrandian, Bohemia. *Věstník ústředního ústavu geologického 52*, 293–297.

Šnajdr, M. 1980: Bohemian Silurian and Devonian Proetidae (Trilobita). *Rozpravy Ústredního Ústavu geologického 45*, 1–172.

Stocker, C.P., Tanaka, G., Siveter, D.J., Lane, P.D., Tsutsumi, Y., Komatsu, T., Wallis, S., Oji, T., Siveter, D.J. & Williams, M. 2018: Biogeographical and biostratigraphical significance of a new Middle Devonian phacopid trilobite from the Naidaijin Formation, Kurosegawa Terrane, Kyushu, southwest Japan. *Paleontological Research 22*, 1–16.

Strusz, D.L. 1980: The Encrinuridae and related families, with a description of Silurian species from southeastern Australia. *Palaeontographica Abteilung A 168*, 1–68.

Sun, X. 1990: Proetacean trilobites from the Ludlow of the Yass Basin, New South Wales (Australia). *Geobios 23*, 95–109.

Tanaka, G., Ono, T. & Maeda, H. 2012: A new Early Devonian leperditicopid arthropod: *Sinoleperditia hamadai* sp. nov., from Fukuji District, Gifu Prefecture, central Japan. *Paleontological Research 16*, 260–263.

Tripp, R.P. 1954: Caradocian trilobites from mudstones at Craighead Quarry, near Girvan, Ayrshire. *Transactions of the Royal Society of Edinburgh 62*, 655–693.

Whittington, H.B. & Kelly, S.R.A. 1997: Morphological terms applied to Trilobita. *In* Kaesler, R.L. (ed.): *Treatise on Invertebrate Paleontology*. *Part O Arthropoda, 1. Trilobita, Revised*, Vol. 1, 309 pp. Geological Society of America & University of Kansas Press, Lawrence.

Williams, M., Wallis, S., Oji, T. & Lane, P.D. 2014: Ambiguous biogeographical patterns mask a more complete understanding of the Ordovician to Devonian evolution of Japan. *Island Arc 23*, 76–101.

Yolkin, E.A. 1966: Novyy rod i novye vidy nizhnedevonskikh i eyfelskikh dekhenellid (trilobity). *Geologiya i geofizika 2*, 25–30.

Yolkin, E.A. 1968: *Trilobity (dekhenellidy) i stratigrafiya nizhnego i srednego devona yuga zapadnoy Sibiri*. 1968 Akademiya Nauk SSSR, Sibirskoe otdelenie, Institut geologi i geofizikii, Nauka, Moscow, 156 pp.

Yolkin, E.A. 1979: The new representatives of genus *Dechenella* from Lower Devonian of Taymyr and northeast USSR. In: *The fauna and stratigraphy of Middle and Upper Paleozoic Era of Siberia*, Novosibirsk, Science, Novosibirsk, 82–90.

Yolkin, E.A. 1983: *Regular Patterns in Dechenellid Evolution and Biochronology of the Silurian and Devonian*, 571 pp. Nauka, Moskva.

Zhang, W. 1974: Silurian trilobites. *Handbook of the Stratigraphy and Paleontology of Southwest China*. Science Press, Beijing, 173–187.

Zhou, Z., Siveter, D.J. & Owens, R.M. 2000: Devonian proetid trilobites from Inner Mongolia, China. *Senckenbergiana Lethaea 79*, 459–499.