

A remarkable Amgan (Middle Cambrian, Stage 5) fauna from the Sauk Tanga, Madygen region, Kyrgyzstan

GERD GEYER, JOHN S. PEEL, MICHAEL STRENG, SEBASTIAN VOIGT, JAN FISCHER & MARVIN PREUßE



Early Middle Cambrian bituminous coquinoid limestones from a tectonically isolated outcrop in southwestern Kyrgyzstan yield a remarkably diverse fauna, with stem-group cnidarians, trilobites, rhynchonelliformean brachiopods, and other shelly fossils. The fossil site is in the northern foothills of the Turkestan Range and thus forms part of the westernmost extension of the South Tien Shan. The fauna includes two fairly well known trilobite species, *Glabrella ventrosa* Lermontova, 1940 and *Dorypyge richthofeniformis* Lermontova, 1940, that provide confident support for an Amgan age of the rocks. New described taxa include the stem-group cnidarian *Cambroctoconus kyrgyzstanicus* Peel sp. nov., the trilobite *Olenoides sagittatus* Geyer sp. nov., and the helcionelloid *Manasoconus bifrons* Peel gen. et sp. nov. Additional fossils within the samples include the trilobites *Olenoides* sp. A, *Kootenia* sp., and *Pseudoeteraspis?* sp.; the rhynchonelliform brachiopods *Narynella* cf. *ferganensis* (Andreeva, 1962), *Narynella?* sp., *Austrohedra?* sp. nov., and two species of uncertain generic affinity; the tomotioid *Tesella* sp.; the hyolithelminth *Hyolithellus* sp.; and the palaeoscolecoid *Hadimopanella oezgueli* Gedik, 1977. Of particular interest is *Cambroctoconus kyrgyzstanicus* with an octagonal corallum and a sparsely septate calyx. • Key words: Middle Cambrian, Cnidaria, Mollusca, Trilobita, Brachiopoda, Tommotiida, Palaeoscolecida, Kyrgyzstan.

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Cambrian rocks from western Kyrgyzstan are known only from rare, scattered occurrences and usually only the trilobite and brachiopod faunas are described. Here, we present preliminary data on a tectonically isolated occurrence of tremendously fossiliferous lower Middle Cambrian bioclastic limestone with a surprisingly complex macrofossil assemblage.

The material was collected between 2007 and 2009 during geological mapping in the stratotype area of the Triassic Madygen Formation. Large-scale geological mapping in this area is part of a research project, which focuses on the palaeoenvironmental reconstruction of the renowned Madygen Lagerstätte (e.g., Voigt *et al.* 2006, Shcherbakov 2008, Berner *et al.* 2009, Voigt *et al.* 2009, Schoch *et al.* 2010, Voigt & Hoppe 2010, Fischer *et al.* 2011, Moisan *et al.* 2011).

Geological setting

All fossils described herein come from a single locality in the Sauk Tanga (or “Sauk Tan’ga”; FG locality 596/III/11; 40° 01’ 33.4” N, 70° 16’ 18.3” E) about 50 km to the west of Batken, the capital of the eponymous district in southwestern Kyrgyzstan, Central Asia (Fig. 1A). The fossil site is situated in the northern foothills of the Turkestan Range and thus part of the westernmost extension of the South Tien Shan. The local name Sauk Tan’ga means “cool ravine” and refers to a deep, dry valley ca 2 km east of Madygen village (Dobruskina 1995; Voigt *et al.* 2006). A fossil sample locality in the Sauk Tanga canyon area, which produced Amgan fossils, is listed in Repina *et al.* (1975, p. 103) under their locality “27”. This locality is possibly

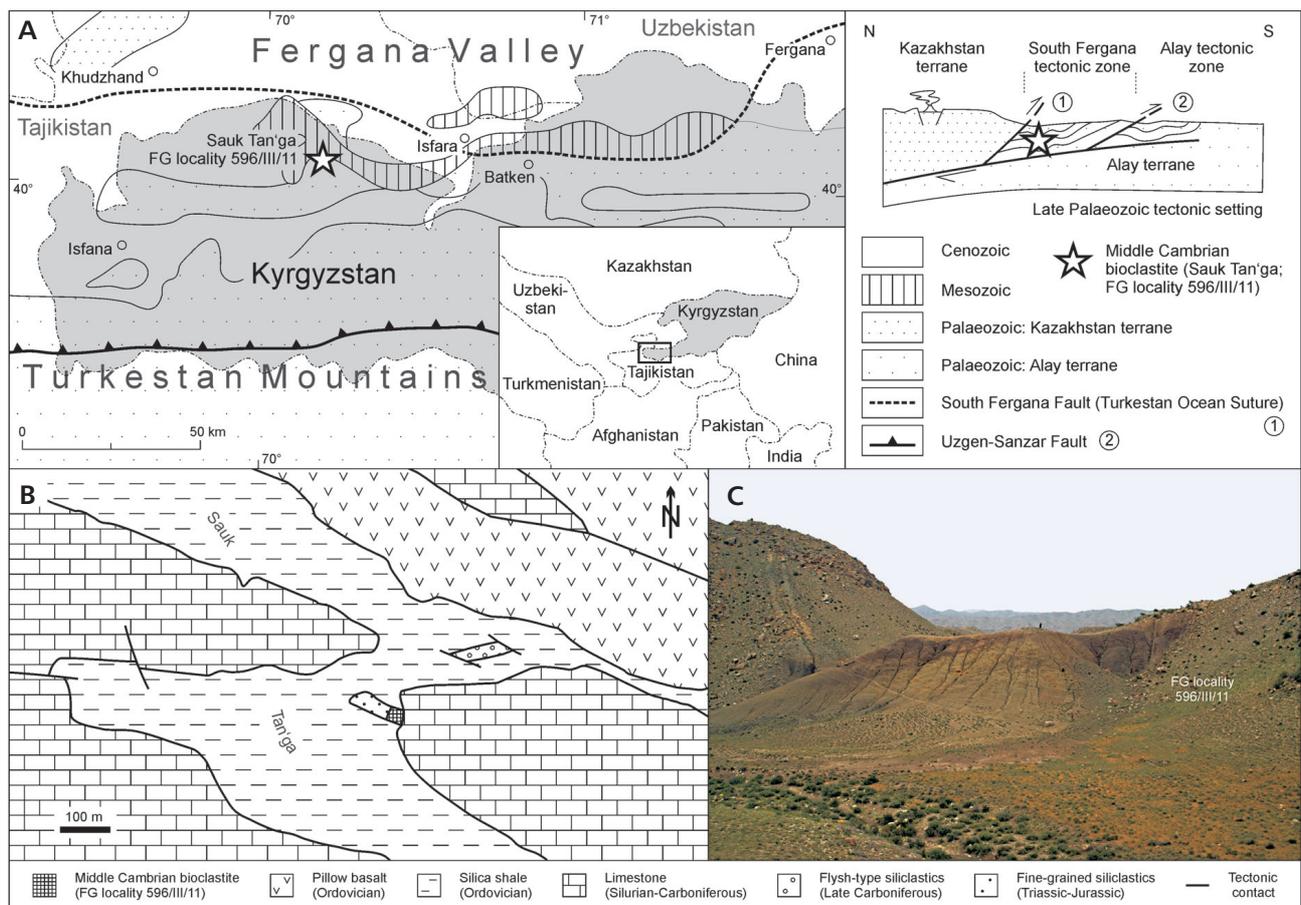


Figure 1. Location and geological overview of the study area. • A – position of Sauk Tanga in southwest Kyrgyzstan and schematic expression of the Late Palaeozoic tectonic setting of the region. • B – geological sketch map of the southern part of the Sauk Tanga valley (modified from Preuße 2011). • C – fossil site seen from south; persons in the centre for scale.

identical with the locality from which the herein described material originated although a symbol in the sketch map points to a slightly different location. However, the information provided by Repina *et al.* (1975) is insufficient for a precise location.

The outcrop area of the Cambrian rocks is an approximately 20 × 30 m large natural exposure of dark brown to greyish-black bituminous limestone on the right bank of the southern part of the Sauk Tanga valley (Fig. 1B, C). The richly fossiliferous, coquinoid rock lacks bedding and breaks down into irregular fragments with uneven surfaces. Tectonic fracturing promotes deep weathering of the limestone so that fallen rock covers most of the slope below the outcrop.

This small occurrence of bituminous limestone is fault-bounded in all directions, juxtaposed against heavily tectonised Ordovician silica shale in the north and south, Silurian–Carboniferous marine limestone in the east, and Triassic–Jurassic continental deposits in the west (Fig. 1C; Berezanskii 1999, Preuße 2011). On account of its detached nature and the biostratigraphically inferred

Middle Cambrian age, which is in contrast to the surrounding rocks, we interpret the fossil-bearing bituminous limestone at this locality as a tectonically emplaced fragment.

The Palaeozoic evolution of the relevant part of Central Asia that includes the study area is mainly the history of the Turkestan Ocean (Burtman 1997, 2008). Throughout the early and mid Palaeozoic, the region has been a shallow to deep marine depositional environment. In the Early Carboniferous, the closure of the Turkestan Ocean started by subduction of oceanic crust beneath the present-day northern Kazakh–Kyrgyz terrane. Crustal shortening culminated in a continent–continent collision with the Alay terrane at the end of this period. The Palaeozoic Turkestan Ocean suture is reflected by the roughly E–W directed South Fergana Fault running a few kilometres to the north of the study area (Fig. 1A). It is suggested that the bituminous limestone of FG locality 596/III/11 originated at an unknown place in the Turkestan Ocean, was transported to the north during the closure of the Turkestan Ocean, and finally became part of the accretionary wedge that formed

in front of the Kazakh-Kyrgyz continent. The present-day position of the Cambrian limestone adjacent to fault-bounded Mesozoic rocks is a result of Cenozoic deformation related to the modern Tien Shan uplift (Bazhenov 1993, Yin 2010).

Age and stratigraphic position

The age of the fossiliferous rock from the Sauk Tanga locality can be deduced with some confidence from the two well-known species of trilobites, which occur in the sample. *Glabrella ventrosa* Lermontova, 1940 and *Dorypyge richthofeniformis* Lermontova, 1940 are both species exclusively known from the Middle Cambrian Amgan Stage and probably from only the upper part termed the *Sdzuyella-Aegunaspis* Zone in the Turkestan and Alay ranges (see Repina et al. 1975). The only exception is a report of immature silicified material of *Dorypyge richthofeniformis* from the eastern Alay Range from the younger *Pseudanomocarina* Zone (Ghobadi Pour & Popov 2009), but this determination remains problematic as long as adult specimens are not known from these beds. Other trilobites as well as the brachiopods in the Sauk Tanga samples do not provide a precise age, but are frequently found in strata of upper Amgan age.

Facial and depositional characteristics

The rocks are generally dark brownish to greyish-black bituminous limestones developed as abundantly fossiliferous coquinas without well recognizable bedding. They break down into irregular fragments with uneven surfaces that, when fresh, emit a slightly sulphuric smell originating from processed organic matter. The primary calcareous matrix is totally recrystallised to sparitic calcite with often large epipedic crystals. Two types of fossil fragments can be distinguished, one being smaller particles of shelly fossils with slightly to well-rounded edges of the fractured faces and thus transported over a considerable distance or reworked; the other consisting of shell or sclerite fragments with sharp edges and thus more or less deposited *in situ*. The presence of these two types of fossil remains with obvious different depositional histories is in accordance with the poorly visible stratification of the rocks, the absence of a preferred orientation of shell fragments and sclerites, and the assemblage of species from systematic groups with different ecological preferences, such as trilobites and helcionelloids as vagile benthic organisms including probable scavengers, and articulate brachiopods and cnidarians as sessile filter feeders with different types of attachment to the substrate.

Systematic palaeontology

The material is deposited in the geological collections of the Technische Universität Bergakademie Freiberg, Germany, under the cumulative collection number FG 596/XII. The additional terminal number refers to individual rock samples (001 through 033) or an electron microscope stub (034), the individual specimens on which are identified by a to [n]; e.g. specimen FG 596/XII/010c is derived from rock sample 10 of the collection.

Stem-group Cnidaria

Genus *Cambroctoconus* Park, Woo, Lee, Lee, Han, Chough & Choi, 2011

Type species (by original designation). – *Cambroctoconus orientalis* Park, Woo, Lee, Lee, Han, Chough & Choi, 2011. Middle Cambrian (Cambrian Series 3, Drumian Stage), Changhia Formation, Shandong Province, China.

Discussion. – Park et al. (2011) focused on the octagonal cross-section of the corallum, the perforated wall and the presence of paired internal septa originating from each of the corners of the calyx when proposing *Cambroctoconus* as a stem-group cnidarian. A similar octagonal cross-section and much shorter, stubby, septa are seen in *Tretocylichne* Engelbretsen (1993) from the Murrawong Creek Formation of New South Wales (Middle Cambrian; Series 3, Stage 5) but the base in the Australian form has a broad basal holdfast-like structure which is perforated centrally (Engelbretsen 1993), unlike the closed tip of *Cambroctoconus*; pores are not reported in *Tretocylichne*. *Cothonion* Jell & Jell, 1976, from the latest early Cambrian (Series 2, Stage 4) of Australia and Greenland, lacks the octagonal form and the pores characteristic of *Cambroctoconus* whilst the conical corallum carries numerous internal short septa or septal grooves (Jell & Jell 1976, Peel 2011).

Cambroctoconus kyrgyzstanicus Peel sp. nov.

Figure 2

Holotype. – FG 596/XII/034a (Fig. 2E, G, I).

Type locality and horizon. – Sauk Tanga, FG locality 596/III/11, 40°01' 33.4" N, 70°16' 18.3" E; Alay range, western Kyrgyzstan, upper Amgan Stage.

Paratypes. – FG 596/XII/001c, FG 596/XII/001e, FG 596/XII/001f, FG 596/XII/001g, FG 596/XII/007d, FG 596/XII/007e, FG 596/XII/007f, FG 596/XII/017a, FG 596/XII/019a, FG 596/XII/020c, FG 596/XII/020d,

FG 596/XII/020e, FG 596/XII/021a, FG 596/XII/022a, FG 596/XII/034a.

Etymology. – From Kyrgyzstan, the Kyrgyz Republic.

Diagnosis. – Corallum trochoidal, octagonal in cross-section, with broad longitudinal angulations separated by flat to shallowly concave fields. Calyx deep, without septa or with only isolated septa or short, broad, septal spines, possibly with a basal transverse tabula or apical plug; theca porous, with densely packed, meandering pores.

Description. – The maximum known length of the slightly curved corallum is about 7 mm, with observed width varying between 5 and 8 mm; the tip is blunt. In cross-section the corallum is octagonal, usually with broad, rounded longitudinal angulations separated by shallowly concave longitudinal fields (Fig. 2C–E). The calyx varies from equidimensional (Fig. 2A, C, F) to wider in the plane transverse to the plane of curvature (Fig. 2E, I). The thecal walls are perforated by a tight meshwork of meandering pores composing about one third of the surface area (Fig. 2G, K). The calyx is deep, without observed tabulae, but crystalline spar in some specimens as preserved suggests apical fill or the presence of a tabula. Internally, the calyx preserves infrequent, short, stubby septa or septal spines (Fig. 2F), although one specimen shows a single, thin and parallel-sided septum or septal spine extending about one sixth of the radius of the calyx (Fig. 2A, B). Evidence of budding is shown by a scar in one specimen (Fig. 2E, I) and by buttressing of a second generation individual against the original calyx in cross-section (Fig. 2A).

Discussion. – The scarcity of septa within the calyx serves to delimit the Kyrgyz material from the type species, *C. orientalis*, which has 8 pairs of septa (Park *et al.* 2011). Of four available transverse sections, one shows no septal structures, two show a blunt spine or septum (Fig. 2F) and the fourth shows a single thin septum (Fig. 2A, B). *Cambroctoconus orientalis* also attains twice the height of *C. kyrgyzstanicus*, which may explain why many specimens illustrated by Park *et al.* (2011, fig. 1) become almost parallel-sided in the latest growth stages. The pores in the thecal wall of *C. kyrgyzstanicus* may be obscured by recrystallisation in the material at hand (Fig. 2D, H, J) and have not been detected in cross-sections.

Phylum Mollusca Cuvier, 1797
Class Helcionelloidea Peel, 1991
Order Helcionellida Geyer, 1994
Family Helcionellidae Wenz, 1938

Genus *Manasoconus* Peel gen. nov.

Type species. – *Manasoconus bifrons* Peel gen. et sp. nov.

Etymology. – Named after Manas, hero of the traditional Kyrgyz epic poem.

Diagnosis. – Isostrophic, open-coiled through about three-quarters of a whorl. Whorl cross-section sub-circular in earlier growth stages, uniformly convex, later expanding along the plane of symmetry (“antero-posteriorly”) with little lateral increase. Early stages with prominent, acute, transverse costae separated by concave interareas, becoming restricted to the mid-dorsal area with increased growth. Later growth stages with a reticulation of widely spaced cords and growth lines, appearing first on the umbilico-lateral areas before later spreading across the entire dorsum.

Discussion. – The laterally compressed shell morphology is described but not common amongst helcionelloids (*cf.* Peel 1988, Resser 1939, Gubanov & Peel 2001) where most species show a higher rate of shell expansion. *Manasoconus* is readily distinguished from other described taxa by its distinctive ornamentation. Both the costate and reticulate ornament patterns occur in other helcionelloids (*e.g.*, Geyer 1986, Gubanov *et al.* 2004) but the ontogenetic change from prominent transverse costae to a reticulate pattern after about one third of a whorl is unique.

Manasoconus bifrons Peel sp. nov.

Figure 3A–D

Holotype. – Nearly complete conch under FG 596/XII/017b (Fig. 3A, B).

Type locality and horizon. – Sauk Tanga, FG locality 596/III/11, 40° 01′ 33.4″ N, 70° 16′ 18.3″ E.; Alay range, western Kyrgyzstan, upper Amgan Stage.

Paratype. – Nearly complete conch under FG 596/XII/029a.

Etymology. – From the Latin *bifrons*, with two faces; a reference to the two contrasting styles of ornamentation.

Diagnosis. – As for genus.

Description. – Type species of *Manasoconus* gen. nov. in which the isostrophic shell forms an open coil of about three quarters of a whorl. Maximum length of the present specimens is *ca* 2.1 to 2.6 mm, max. width 0.8 to 1.1 mm.

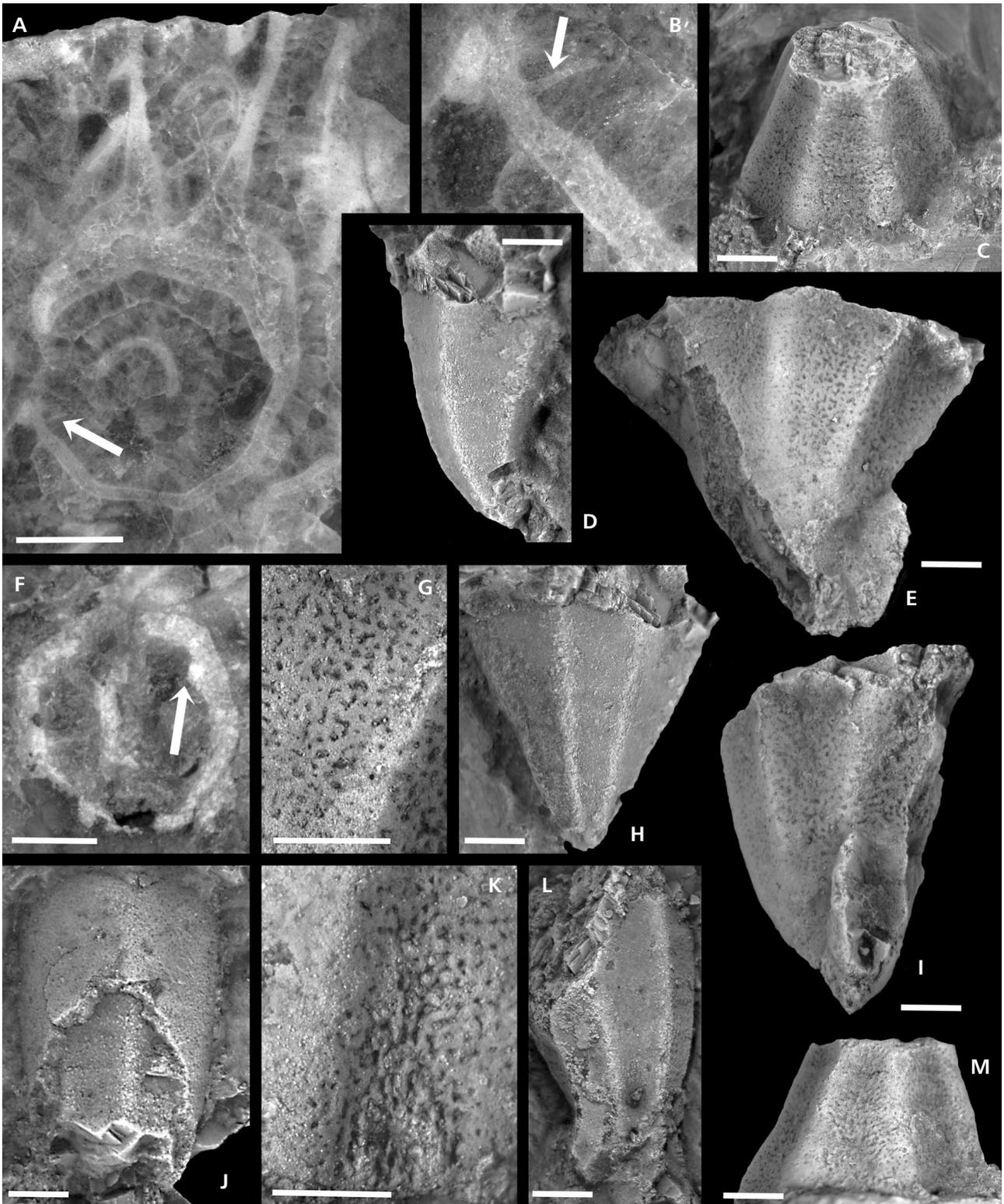


Figure 2. *Cambroctoconus kyrgyzstanicus* Peel sp. nov. • A, B – paratype, transverse polished section with thin septum (arrowed, see also B); a second buttressed calyx (A, top) in long section is seemingly budding from the first calyx, FG 596/XII/19a. • C, M – paratype, inverted calyx with broken early growth stages, in oblique (C) and lateral (M) views, FG 596/XII/007d. • D, H – paratype, FG 596/XII/022a. • E, G, I – holotype, note attachment scar (H) and detail of porous surface (G), FG 596/XII/034a. • F – paratype, transverse section showing blunt spine or septum (arrow), FG 596/XII/001e. • J – paratype, partly exfoliated specimen with shell pores indicated by papillae on internal mould of calyx, FG 596/XII/020d. • K – paratype, detail of pores, FG 596/XII/007d. • L – paratype, FG 596/XII/020c. Scale bars 1 mm.

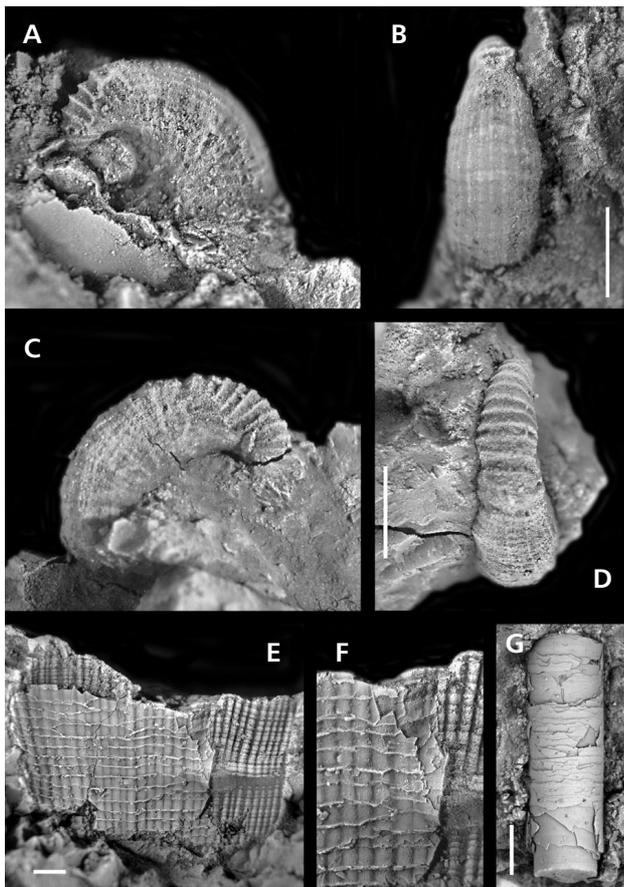


Figure 3. A–D – *Manasoconus bifrons* Peel gen. et sp. nov, Sauk Tanga locality; A, B – conch, internal mould, FG 596/XII/017b, lateral view and view of the abapical side of the whorl; C, D – conch, internal mould, holotype, FG 596/XII/029a, lateral view and view of the abapical side of the whorl. • E, F – *Tesella* sp., FG 596/XII/016b, entire specimen as preserved and detail. • G – *Hyolithellus* sp., FG 596/XII/004b, fragment of tube. All scale bars 1 mm.

In the early growth stages, comprising about one third of a whorl, the cross-section is sub-circular and ornamented by prominent transverse costae separated by broad, concave, intercostal areas. Initially, the costae extend across the lateral and dorsal areas but gradually they become restricted to the dorsum as the aperture is approached, with lateral areas ornamented with the reticulate pattern characteristic of the late growth stage. The intersections of the longitudinal and transverse elements within the reticulate pattern create small and low nodes. A slight transverse constriction separates the two growth stages with the shell in the late growth stage initially continuing the slow expansion in width characteristic of the early growth stage before becoming parallel-sided. In lateral view, however, the whorl profile expands in the plane of symmetry such that the aperture at the latest preserved growth stage forms about four-fifths of the total length. A broad but very shallow median sinus is present in the later growth stages.

Discussion. – *Manasoconus bifrons* is distinguished from *M. reticulata* (Lermontova, 1940) from Shodymir in Fergana in having less prominent longitudinal cords in the reticulate pattern of the late growth stage. In *M. reticulata* the longitudinal cords dominate whereas longitudinal and transverse elements are more equally expressed in *M. bifrons*. Furthermore, the conspicuous transverse costae which are characteristic of the earliest stages of *M. bifrons* are not clearly discernible in the published illustrations of *M. reticulata* (Lermontova 1940, pl. 34, fig. 5; Lermontova 1951, pl. 3, fig. 14).

In terms of its lateral compression, *Manasoconus bifrons* resembles the late Middle Cambrian species from North Greenland described by Peel (1988) as *Latouchella pearylandica* but that species is more open coiled and lacks the characteristic reticulate ornamentation in the late growth stages. Ornamentation in *Tichkaella* Geyer, 1986 from the Middle Cambrian of Morocco is dominated by finer, more closely spaced spiral elements throughout growth, and the costate early growth stage is lacking (Geyer 1986). The Middle Cambrian species described by Resser (1939) from the Middle Cambrian of Idaho, USA, as *Helcionella aequa* is strongly laterally compressed, with a narrow dorsum, but the lateral sides are almost parallel. Its later stages carry a spiral/reticulate ornamentation similar to *Tichkaella* and the late stages of *M. bifrons*.

Phylum Arthropoda Siebold & Stannius, 1848
 Subphylum Trilobita Walch, 1771
 ?Order Redlichiida Richter, 1932
 ?Suborder Redlichiina Richter, 1932
 ?Family Ellipsocephalidae Matthew, 1887

Genus *Glabrella* Lermontova, 1940

Type species (by original designation). – *Glabrella ventrosa* Lermontova, 1940. Middle Cambrian, Amga Stage, Shodymir region, Turkestan Range, southern Fergana Basin.

Nomenclatural note. – The generic name *Glabrella* Lermontova, 1940 for Cambrian trilobites is a junior homonym of *Glabrella* Scudder, 1882, introduced for extant molluscs. However, Scudder’s name is a *nomen nudum* based on an unpublished manuscript by the Austrian scientist Carl Megerle.

Discussion. – Lermontova (1940, 1951) described and figured the fairly smooth and highly convex cranidium of *Glabrella ventrosa* with short, distinctly upturned palpebral lobes. The pygidium from the type material and subsequently described material equate with the specimens presented herein, which have a clearly smaller convexity. Lermontova (1940, p. 120) compared the cranidia with

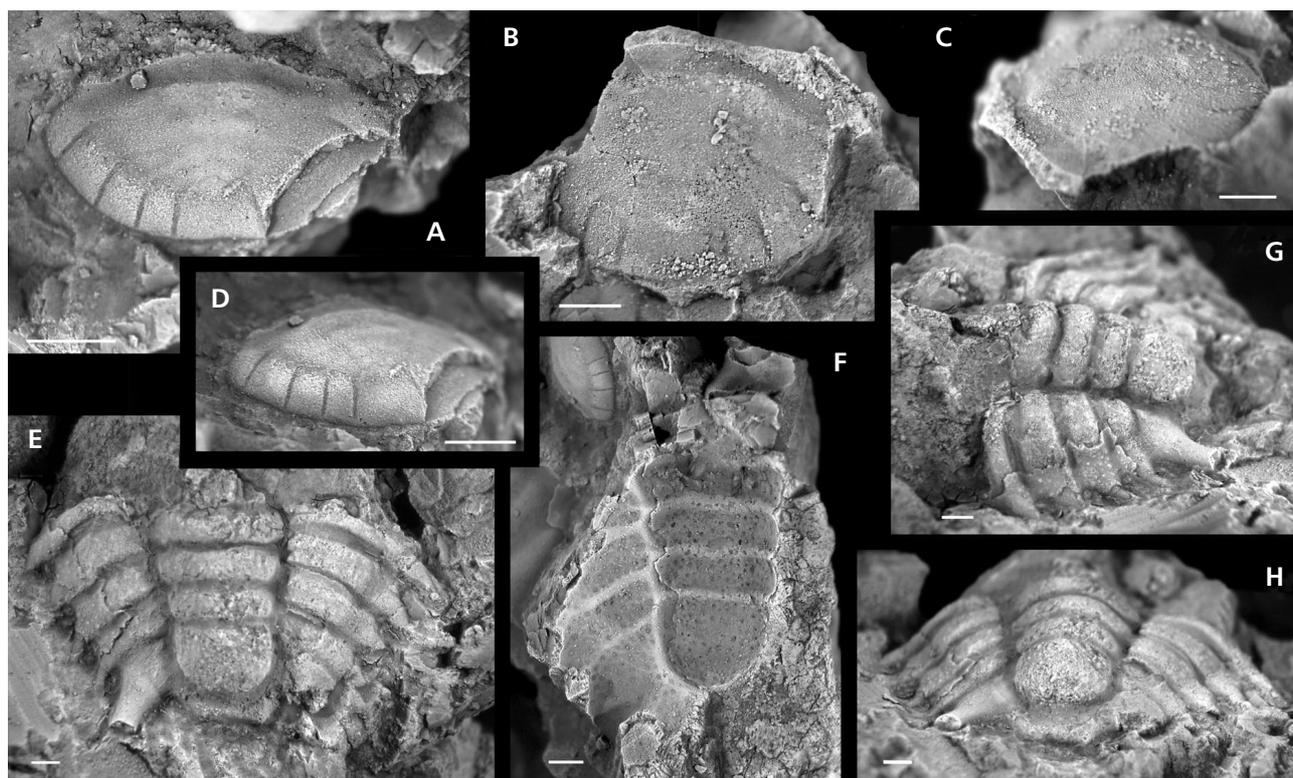


Figure 4. A–D – *Glabrella ventrosa* Lermontova, 1940, Sauk Tanga locality. • A, D – pygidium, internal mould, partly broken and exhibiting ventral doublure, FG 596/XII/018b; A – dorsal view; D – oblique posterior view. • B, C – incomplete pygidium, internal mould, FG 596/XII/014a; B – dorsal view; C – slightly oblique lateral view. Scale bar 1 mm. • E–H – *Dorypyge richthofeniformis* Lermontova, 1940, Sauk Tanga locality; E, G, H – pygidium, partly exfoliated, FG 596/XII/001a. E – dorsal view; G – left lateral view; H – posterior view. • F – incomplete pygidium, partly exfoliated, ventral view external mould, FG 596/XII/018a, together with pygidium of *Glabrella ventrosa* shown in Fig. 4A and 4D. Note infilling of a central canal in the coarse granules. Scale bar 1 mm.

those of *Pagetiellus* Lermontova, 1940 and thus placed the genus among the (at that time appropriate) Family Pagetidae [*sic!*] Kobayashi, 1935. However, the pygidium clearly excludes *Glabrella* from the Hebediscidae Kobayashi, 1944 as now used and the Eodiscoidea in general.

Jell & Adrain (2002) obviously acknowledged the similarity of the cranidium with those known from *Kingaspis* Kobayashi, 1935 and placed *Glabrella* under the Family Ellipsocephalidae Matthew, 1887. The pygidium is clearly distinguished from any pygidium known from unequivocal genera of the Ellipsocephalidae. However, some resemblance can be seen in the pygidium of *Ellipsocephalus hoffi* Schlotheim, 1823 from the lower Middle Cambrian Jince Formation of Bohemia. This species has a pygidium with a poorly subdivided, tapering rhachis reaching nearly to the posterior margin, to probably the position of the obsolescent border furrow, and smooth pleural areas (*e.g.*, Geyer 1990, pl. 14, figs 1b, 2c, 3). The upturned, rope-like palpebral lobes in *Glabrella ventrosa* are clearly different from the palpebral lobes in the superficially similar species of *Kingaspis*, which has transversely weakly convex, blade-like palpebral lobes. However, somewhat upturned, but less rope-like palpebral lobes are again seen in

Ellipsocephalus. For the moment, the placement under the Ellipsocephalidae appears to be poorly constrained by apomorphic characters, but the most parsimonious solution for the systematic relationship of *Glabrella*.

***Glabrella ventrosa* Lermontova, 1940**

Figure 4A–D

- 1940 *Glabrella ventrosa*, Lerm. (MS); Lermontova, p. 120, pl. 35, fig. 9, 9a–9d.
- 1951 *Glabrella ventrosa* Lermontova. – Lermontova, pp. 28–29, 36, pl. 2, figs 1–4.
- 1975 *Glabrella ventrosa* Lermontova, 1940. – Repina *et al.*, pp. 102–103, pl. 8, figs 8–13.
- 2002 *Glabrella ventrosa* Lermontova, 1940. – Jell & Adrain, p. 378.

Type material. – From Shodymir region, Turkestan Range, southern Fergana Basin.

Material. – Two pygidia, FG 596/XII/014a and FG 596/XII/018b.

Description. – Pygidium a shallow convex, lenticular to transversely subelliptical body, ratio length/width *ca* 55 percent (inclusive articulating half-ring), maximum transverse width across anterior axial ring. Axis weakly convex, poorly defined from pleural areas, longitudinally lancet-shaped, with *ca* 45 percent maximum pygidial width across first axial ring, and of *ca* 85 percent pygidial length (including articulating half-ring); consisting of four axial rings and a terminal axial piece. Axial rings separated by feebly imprinted, but broad axial furrows, with slightly more elevated lateral portions resulting in a nearly flat or even somewhat sunken sagittal line. Terminal axial piece a diamond-shaped low pad with subrounded corners, particularly the anterior margin defined by gently curved low and narrow furrow. Posterior rim of terminal axial piece reaches posterior border. Articulating furrow sagittally broad and curved, moderately deep, articulating half-ring sagittally very narrow, merely collar-like, raised from the articulating furrow. Pleural areas barely convex (tr.), slightly sunken between axis and margin, defined by narrow, shallow and with interpleural furrows and obsolescent pleural furrows. Pygidial lateral and posterior border relatively wide, subequal in breadth throughout, defined by a shallow to obsolescent border furrow which is as well a change in convexity. Four well developed, moderately deep, sharply defined furrows perpendicular to the margin mark the segmental boundaries, the posterior-most of which corresponds with the boundary between the terminal axial piece and the adjacent axial ring. Lateral and posterior margins composed of two gentle arches separated by a tr. wide and very shallow median indenture. Ventral doublure a broad and almost flat blade (Fig. 4A, D). Entire surface of pygidium smooth.

Discussion. – The pygidia from Sauk Tanga compare perfectly those from the type lot. For differential diagnosis from *Glabrella babakovica* Repina, 1960 and *G. mrassina* Egorova, 1962 see Repina (1960, p. 157) and Egorova (1962), respectively. *Glabrella? pitans* Palmer & Gatehouse, 1972 shows only superficial similarities and belongs to a separate genus.

The species has already been found in the Sauk Tanga canyon area, listed in Repina *et al.* (1975, p. 103) under their locality 27. This locality is possibly identical with the locality from which the herein described material originated, but the information provided by Repina *et al.* (1975) is insufficient for a precise location.

Order Corynexochida Kobayashi, 1935
Family Dorypygidae Kobayashi, 1935

Genus *Dorypyge* Dames, 1883

Type species (by original designation). – *Dorypyge rich-*

thofeni Dames, 1883 from the Middle Cambrian Changhia Formation, Liaoning Province, North China Platform.

Dorypyge richthofeniformis Lermontova, 1940

Figure 4E–H

- 1940 *Dorypyge richthofeniformis* Lerm. (MS). – Lermontova, p. 141, pl. 44, fig. 2, 2a–2c.
1951 *Dorypyge richthofeniformis* Lermontova. – Lermontova, pp. 11–12, 36, pl. 1, figs 1–5.
1973 *Dorypyge richthofeniformis* Lermontova. – Khayrullina, p. 53, pl. 4, figs 1–3.
1975 *Dorypyge richthofeniformis* Lermontova, 1940. – Repina *et al.*, pp. 142–143, pl. 21, figs 2–7.
? 2009 *Dorypyge richthofeniformis* Lermontova, 1940. – Ghobadi Pour & Popov, pp. 1046–1048, figs 2N–Q, 4A–U.

Type material. – From Shodymir region, Turkestan Range, southern Fergana Basin.

Material. – Two incomplete pygidia, FG 596/XII/001a and FG 596/XII/018a (incomplete external mould); partial thoracic segment attributed to *Dorypyge richthofeniformis* under FG 596/XII/015a.

Description. – Pygidium with maximum transverse width across anterolateral corners. Axis with *ca* 35 percent maximum pygidial width across first axial ring and of more than 80 percent pygidial length (except for articulating half-ring); consisting of three axial rings and a terminal axial piece of *ca* 75 percent tr. width of anteriormost pygidial axial ring. Axial rings distinctly convex (sag. and exsag.) with slightly swollen lateral portions, separated by fairly broad (sag. and exsag.) furrows. Terminal axial piece with semicircular posterior margin, composed of a posterior spherical section and an anterior cylindrical section separated by an obsolescent transverse furrow. Articulating half-ring not entirely preserved in the present material, obviously sag. narrow but distinctly convex, transversely convex and well raised from articulating furrow. Posterior end of rhachis defined by shallow border furrow. Pleural areas moderately convex (tr.), sloping towards border furrow, defined by five well impressed, but progressively somewhat shallower and narrower pleural furrows and with faint interpleural furrows. Pleurae develop across lateral border furrow into fairly long, slender, acute and posterolaterally directed spines. Spines at subterminal segment (corresponding to anterior part of terminal axial piece) conspicuously enlarged, somewhat curved upward, subelliptical in cross-section. Lateral border furrow a broad band creating shallow depressions between pleural areas and bases of the lateral spines, intersected by extensions of pleural furrows. Posterior border a narrow, weakly

convex blade with a pair of stout corners posterior to the axial furrows.

Entire carapace with irregularly spaced low, coarse and moderately coarse granules.

Discussion. – Material assigned to *Dorypyge richthofeniiformis* has recently been described from the Arpatektyr Mountains in the northern foothills of the Akai Range, Kyrgyzstan (Ghobadi Pour & Popov 2009). This material includes silicified sclerites of relatively small specimens with clearly prevailing characters of immature individuals, such as the arrangement of coarse granules into transverse rows on the pygidial axial rings, narrow and weakly convex pleurae and marginal spines separated by acute angles at the lateral margin. Although the preserved features of this material fit into the general set of characters of *Dorypyge richthofeniiformis*, the absence of adult specimens does not allow a confident assignment to this species. In addition, the fauna described by Ghobadi Pour & Popov (2009) appears to belong to the *Pseudanomocarina* Zone and would thus represent a younger age than the specimens described under *D. richthofeniiformis* to date.

Genus *Olenoides* Meek, 1877

Type species (by original designation). – *Paradoxides? nevadensis* Meek, 1877 from the Middle Cambrian Wheeler Formation, Utah, U.S.A.

Discussion. – The primary features for specific identification within the genus *Olenoides* are the number of axial rings and pairs of marginal spine pairs in the pygidium. In addition, the development of interpleural furrows of the pygidium is a helpful criterion.

Olenoides sagittatus Geyer sp. nov.

Figure 5A–Q

Holotype. – Fairly complete pygidium, FG 596/XII/010a (Fig. 5C, F, I).

Type locality and horizon. – Sauk Tanga, FG locality 596/III/11, 40° 01' 33.4" N, 70° 16' 18.3" E.; Alay range, western Kyrgyzstan, upper Amgan Stage.

Paratypes. – Three incomplete cranidia and cranidial fragments under FG 596/XII/005a, FG 596/XII/011b and FG 596/XII/019a (external mould); librigena under FG 596/XII/012a; eight incomplete pygidia and pygidial fragments under FG 596/XII/002a, FG 596/XII/005b, FG 596/XII/006c, FG 596/XII/007a, FG 596/XII/008a, FG 596/XII/011a, FG 596/XII/013d, and FG 596/XII/016a;

partial thoracic segments attributed to *Olenoides sagittatus* under FG 596/XII/002b, FG 596/XII/008b, and FG 596/XII/012f.

Etymology. – From Latin *sagitta*, arrow, and *sagittatus*, with arrows; a reference to the characteristic shape of the pygidial pleural ribs.

Diagnosis. – Species of *Olenoides* with narrow anterior border swinging around frontal lobe, nearly pinches out medially; lateral glabellar furrows S1 clearly bifurcate, S2 less so. Pygidium with considerably tapering rhachis, terminal axial piece narrow (sag.); four pairs of long, fairly slender marginal spines the terminal pair of which is separated by a considerable distance; interpleural furrows form triangular areas with a posteriorly shallowing margin, extending as an almost thread-like narrow band towards the base of the corresponding marginal spine.

Description. – Cephalon and glabella with typical dorypygid shape. Glabella more than 95 percent cephalic length, with subparallel sides or faintly growing in width from the occipital furrow to S3; with moderately well developed kootenoid constriction in front of S3; frontal lobe with moderate curvature anteriorly, reaching to the anterior border furrow, with faint anterolateral corners, from which the eye ridges originate as shallow backwardly crooked lobes; three pairs of lateral glabellar furrows developed, all characterised by the absence of the surface prosopon: S1 formed by transverse and then strongly backwardly arched shallow furrows, commence distant from axial furrows, a faint bifurcation indicated at the backward curvature; S2 a shallow, moderately long and faintly backwards curved depression commencing distant from axial furrow; S3 short and faint, transversely directed depressions well distant from axial furrow; S4 apparently indicated as small, obsolescent and poorly defined depressions. Occipital furrow consists of deeply incised distal portions connected by a moderately deep median section. Occipital ring of *ca* 18–19 percent cephalic length, tr. gently convex, with shallow sagittal curvature, lenticular in outline with moderately curved lateral sections and a almost straight median section of the posterior margin, expanding laterally into anterolaterally pointing projections that have a faint connection with the posteroproximal corners of the fixigenae.

Eye lobe moderately long, exsagittal length *ca* 28 percent cephalic length, nearly parallel to axis, located with centre in transverse line with posterior half of L2, palpebral furrow shallow, but well visible, with faint curvature; eye ridge almost straight, low, but forming posterior margin of steeply sloping preocular areas, defined from eye lobes by shallow and poorly defined depression, directed strongly forward to axial furrow opposite posteriormost part of L4 to extend into narrower and low, s-shaped lobes towards

anterolateral corners of the glabella. Fixigenae with shallow to moderate convexity in transverse section, moderately convex exsagittally, with steep slope towards posterior border furrow, subtrapezoidal in outline, extended into acute, strongly deflected posterolateral projections.

Anterior border very narrow (sag.) and thread-like in front of the glabella, moderately curved, broadening anterior to axial furrows and faintly growing in exsag. width towards facial sutures. Anterior border furrow a very narrow (sag. and exsag.) incision anterior to the glabella, moderately wide and relatively shallow in front of the preocular fields. Genal field steeply inclined and thus narrow in dorsal view. Posterior border convex, narrow proximally, broadening distally from a narrow section at axial furrows to a maximum just proximal to the line of the palpebral furrow, then less convex and with a slight forward curvature of the posterior margin. Posterior border furrow well-defined, moderately broad and moderately deep, more-or-less straight in the proximal portion, with a slight broadening anteriorly close to the facial suture. Anterior branch of facial suture almost straight and slightly adaxially directed from the anterior ends of the visual surface, curved slightly inward when reaching anterior border. Posterior branch of the suture long, directed obliquely outward, rapidly swinging backward to create large posterolateral projections.

Librigena with fairly wide (tr.), weakly to moderately raising ocular platform with very narrow, collar-like and nearly vertical basal strip of eye platform; lateral border relatively narrow anteriorly, growing to moderate width (tr.) rearward; lateral border furrow shallow, weakly defined; lateral border extends into moderately long genal spine with broad base. Doublure corresponds to the lateral border in the rearward growing width.

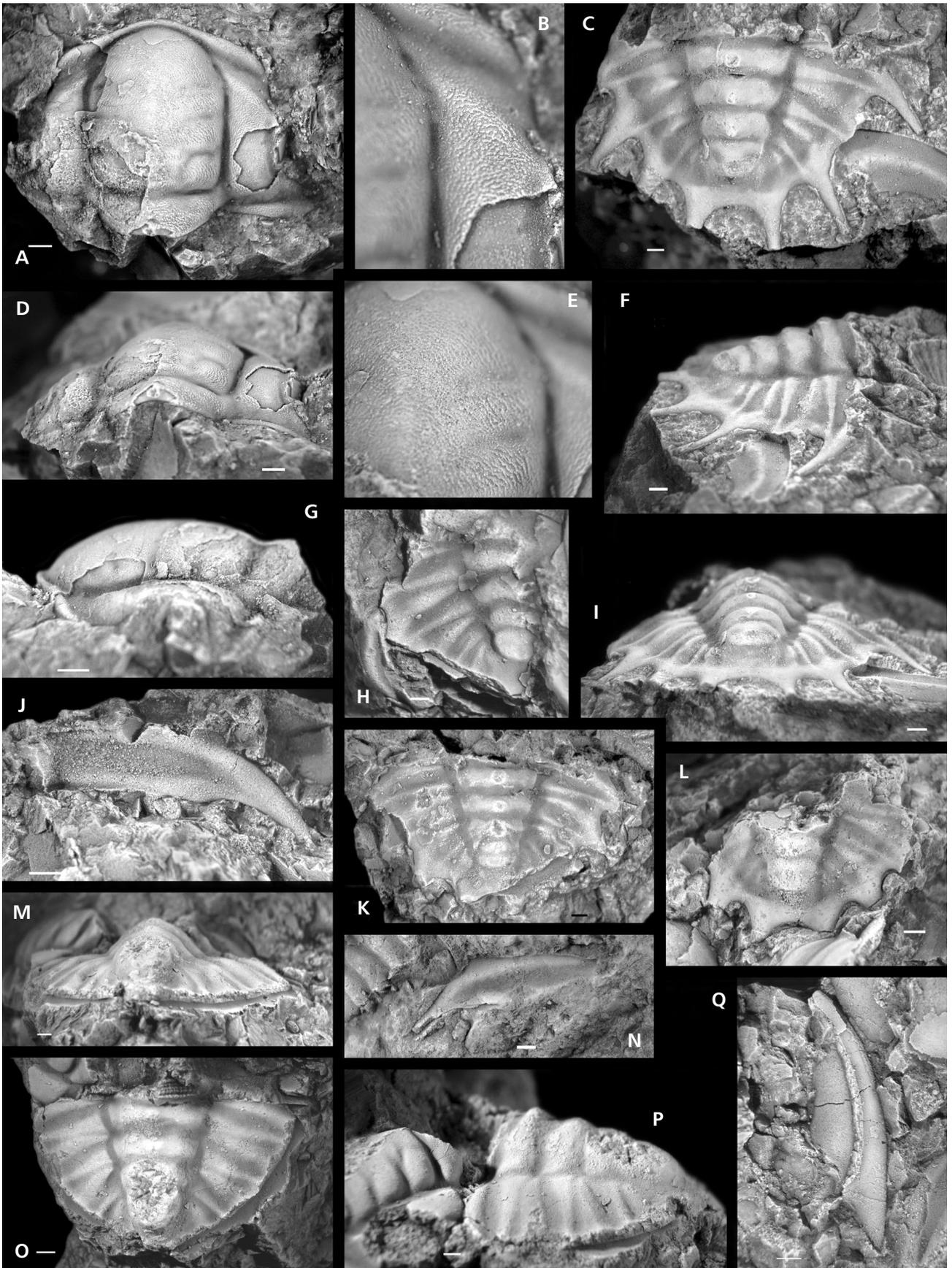
Thorax known only from fragments of thoracic segments. Pleurae subequal in exsag. breadth along their course, with a faint geniculation at about midlength and with large ventrally deflected facet. Pleural furrows moderately deep, deepest near axial furrow, slightly backward directed from there, with a slight curvature, fading at the base of the pleural spines. Pleural spines long, falcate, gently curved posterolaterally, clearly separated from pleural base by the termination of the anterolateral facet and a small swelling at the posterior margin.

Pygidium subsemicircular with four pairs of strong

marginal spines. Rhachis moderately to strongly convex in transverse section, composed of three axial rings and a composite terminal axial piece plus a narrow articulating half-ring. Axial rings distinctly convex (sag. and exsag.) with lateral swollen portions defined from middle portion by shallow furrows obsolete in the central (exsag.) part of its course and a slight change in convexity, each ring with a strong node in a slightly posteromedian position; terminal axial piece with sag. narrow section with gently curved posterior margin, and an anterior cylindrical section separated by a pair of elongate shallow depressions, with median node on the posterior section; axis (except for articulating half-ring and spines) of ca 82 percent pygidial length; width across anterior axial ring ca 38 percent pygidial width at anterolateral corners; width across terminal axial piece almost 60 percent width across anterior axial ring. Articulating half-ring sag. narrow, well raised above articulating furrow. Articulating furrow well incised, moderately wide; furrow between axial ring 1 and 2 similar to articulating furrow, moderately wide and moderately deep, furrow between axial ring 2 and 3 moderately wide, slightly narrower and shallower than anterior furrow, furrow between axial ring 3 and terminal axial piece narrow and relatively shallow. Posterior end of rhachis defined by slightly sunken area in front of posterior border.

Pleural areas moderately convex (tr.), sloping towards border furrow, defined by well impressed, but progressively narrower pleural and interpleural furrows; interpleural furrows developed as triangular areas with a posteriorly shallowing margin. This triangular shape, which is particularly well developed in the anterior two segments, creates the characteristic arrow-shape of the posterior ribs on each segment, extending as an almost thread-like narrow band towards the posterior base of the corresponding marginal spine. Anterior ribs form roughly lancet-shaped areas, which are nearly separated from the lateral border on internal moulds. Four pairs of marginal spines, each long, slender, acute, posterolaterally directed. Terminal pair of spines commences almost posterior to axial furrows, strongly backward directed, separated by a considerable distance and forming a broadly parabolic course of the posterior margin. Posterior border moderately broad (sag.) and moderately convex, slightly broader than lateral border and thus with a faint forward curvature behind the terminal

Figure 5. *Olenoides sagittatus* Geyer sp. nov., Sauk Tanga locality. • A, B, D, E, G – paratype, incomplete cranium, partly exfoliated, FG 596/XII/011b. A – dorsal view; B – dorsal view, detail of fixigena and eye ridge showing pattern of terrace ridges; D – posterior view; E – dorsal view, detail of anterior part of glabella with pattern of terrace ridges; G – left lateral view. • C, F, I – holotype, incomplete pygidium, FG 596/XII/010a, internal mould, dorsal, lateral and posterior views. • H – paratype, fragment of pygidium, internal mould, FG 596/XII/016a. • J – paratype, fragment of thoracic segment, internal mould, FG 596/XII/008b. • K – paratype, incomplete pygidium, internal mould, FG 596/XII/011a. • L – paratype, incomplete pygidium, FG 596/XII/008a. • M, O, P – paratype, incomplete pygidium, internal mould, FG 596/XII/007a; M – posterior view; O – dorsal view with exposed mould of ventral doublure; P – lateral view, together with cranium of *Olenoides* sp. A. • N – paratype, fragment of thoracic segment, internal mould, FG 596/XII/002b. • Q – paratype, librigena, FG 596/XII/012a, ventral view, together with fragment of thoracic pleura. Scale bar 1 mm. Dorsal views unless otherwise stated.



axial piece. Lateral border moderately convex, strongly rhythmic due to the intersection from the pleural areas; lateral border furrow consisting of separated depressions in continuation of the pleural and interpleural furrows. Double more-or-less corresponding to the lateral border (Fig. 5O).

Cranidial external surface except for furrows entirely covered by fingerprint-type terrace ridges which are modified to small elliptical crests on the lateral portions of the occipital ring, on the posterior border and on the anterior and posterior convex parts of the fixigenae.

Discussion. – *Olenoides sagittatus* is best characterised by its delicate furrow pattern of the pleural fields, by its four pairs of slender, obliquely outward and rearward directed spines with the broad paraboloid shape of the margin between the terminal pair of spines, and the distinctly tapering pygidial axis with the narrow terminal axial piece. No other species of *Olenoides* has this combination of characters. The cephalon is only known from fragmentary material and is incompletely recorded. However, the swinging course of the narrow and medially nearly fading anterior border is also an unusual character among the species of *Olenoides*.

A somewhat similar species of *Olenoides* has been briefly described from the Shodymir section of the southern Fergana area under the name “*Neolenus* (= *Olenoides*) *inexpectans* Lerm. (MS)” (Lermontova 1940, p. 138, pl. XLII, fig. 6, 6a–6c). The three figured cranidia and the only figured pygidium are more or less complete, but relatively unfavourably preserved, and the smallest of the three cranidia appears to belong to a different species. In any case, among the recognisable characters the cranidia appear to have a flatter anterior margin of the glabella and a less swinging anterior border; the pygidium of *O. inexpectans* is clearly differentiated by a broader and less tapering rhachis, more stout and more strongly rearward directed marginal spines, and a shorter distance between the terminal pair of marginal spines.

The cranidium of *Olenoides sagittatus* shows some resemblance to *Olenoides procerus* Tomashpolskaya, 1971 (in Chernysheva 1971, pl. 13, figs 4–6) from the lower Middle Cambrian Suyarik “horizon” of the Batenev range of the Altay-Sayan fold-belt. It has a similar pattern of the lateral glabellar furrows and the course of the anterior border. However, the anterolateral grooves in the glabella are more distinct in *O. procerus*, and the fixigenae are slightly wider. In addition, pygidia are unknown from *O. procerus*. Another similar species, described as *Olenoides erbiensis* Tomashpolskaya, 1971 (in Chernysheva 1971, pl. 13, figs 1–3), also from the Suyarik “horizon” of the Batenev range, has S1 as more strongly developed depressions, shorter palpebral lobes in a slightly more anterior position, a less arched anterior margin and a shallower curvature of the frontal lobe. Pygidia are also undescribed from this species.

The characteristic pattern of pleural furrows and the rhachis in the pygidium of *Olenoides sagittatus* is comparable to those on the pygidia of *O. optimus* Lazarenko, 1954. However, the cranidia are easily distinguished by the shape of the glabella, the pattern of lateral glabellar furrows, the length of the eye lobes and a large occipital spine.

Olenoides sp. A

Figure 6A–E

Locality. – Sauk Tanga, FG locality 596/III/11; 40° 01′ 33.4″ N, 70° 16′ 18.3″ E.

Material. – Two incomplete cranidia and cranidial fragments under FG 596/XII/007b and FG 596/XII/033a; incomplete pygidium under FG 596/XII/013c.

Description. – Cephalon and glabella with typical dorypygid shape. Glabella *ca* 95 percent cephalic length, sides faintly growing in width from the occipital furrow to S3; with weakly developed kootenioid constriction in front of S3; frontal lobe with moderate curvature anteriorly, reaching to the anterior border furrow, with faint anterolateral corners; three pairs of lateral glabellar furrows developed: S1 with nearly transverse well impressed lateral section, then with bifurcation into a narrow and shallow, but relatively extended posterior branch and an obliquely anteriorly directed, fairly wide but short anterior branch, commences at axial furrows; S2 a shallow, moderately long and slightly backwards curved furrow commencing at axial furrow, with faint and very short bifurcation adaxially; S3 a shallow but well visible, transversely directed furrow commencing at axial furrow and extending nearly to axis; close to the base of S3 starts a faint to obsolescent fairly broad furrow, which is obliquely forward directed. Occipital furrow consists of deeply incised and long distal portions connected by a slightly shallower, short median section. Occipital ring of probably *ca* 18 percent cephalic length, tr. gently convex, with considerable sagittal curvature, lenticular in outline with moderately curved lateral sections; median section of the posterior margin not preserved in the present material.

Eye lobe, palpebral furrow, and anterior part of fixigena not preserved in the present material; base of eye ridge indicates steeply backward directed course from just anterior to S3, extends from there into very thin and low, s-shaped lobes which traverse axial furrow and fuse with anterolateral corners of the glabella. Fixigenae with shallow to moderate convexity in transverse section and with steep slope towards posterior border furrow, apparently subtrapezoidal in outline.

Anterior border extremely narrow (sag.) and blade-like

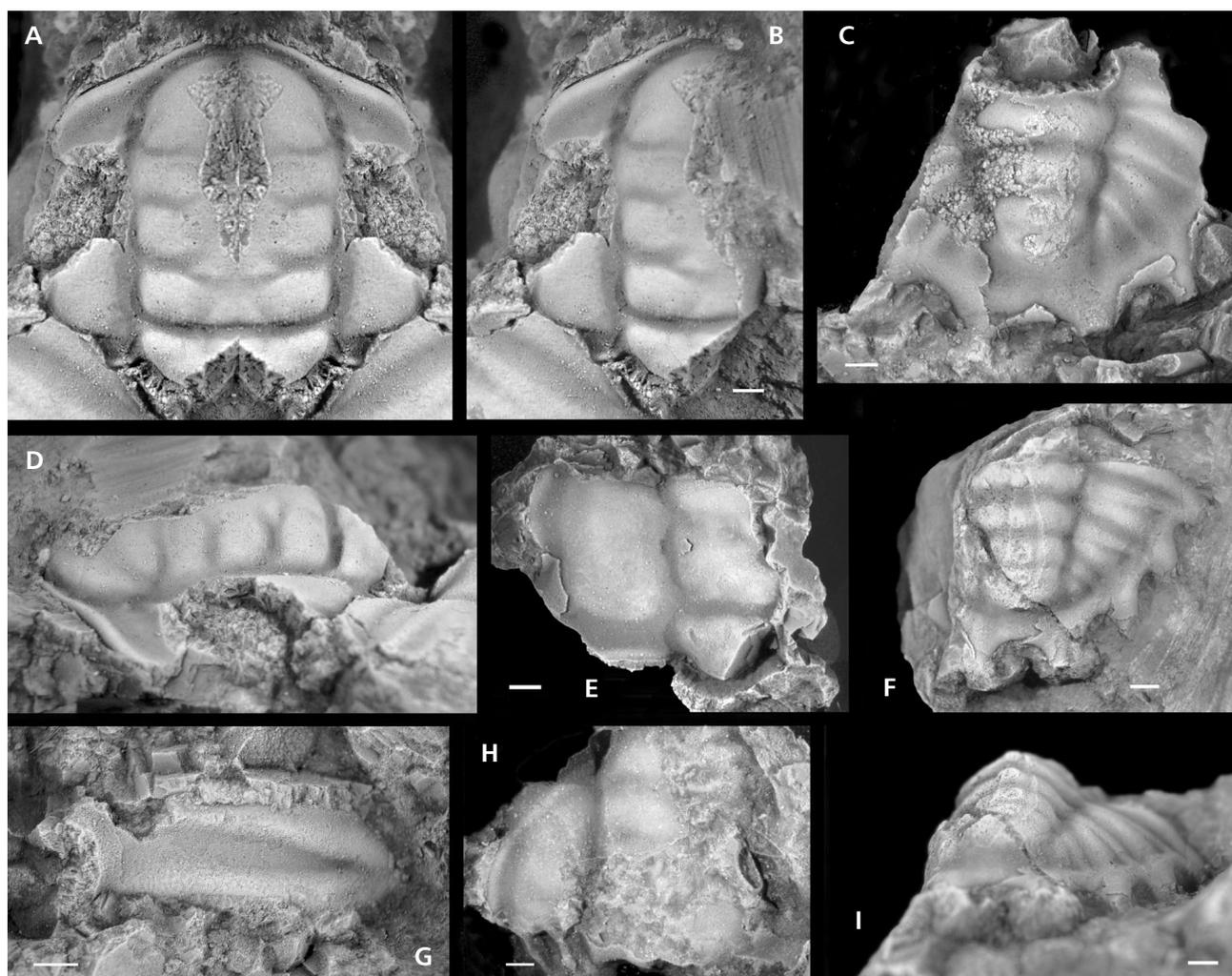


Figure 6. A–E – *Olenoides* sp. A, Sauk Tanga locality. • A, B, D – partial cranium, exfoliated, FG 596/XII/007b; A – dorsal view; B – electronically mirrored and merged to exemplify the morphology of the glabella; D – lateral view. • C – partial pygidium, FG 596/XII/013c, dorsal view. • E – fragment of cranium, largely exfoliated, FG 596/XII/033a, dorsal view. • F–I – *Kootenia* sp. A, Sauk Tanga locality. • F, I – incomplete pygidium, FG 596/XII/003a, dorsal and posterior views. • G – fragment of thoracic segment, FG 596/XII/010b, dorsal view. • H – incomplete cranium, latex cast of shell interior, FG 596/XII/001h, dorsal view. Scale bar 1 mm.

in front of the glabella, moderately curved, broadening and with a change in the curvature of the anterior margin anterior to axial furrows and almost constant in exsag. breadth towards facial sutures. Anterior border furrow a narrow (sag. and exsag.) incision anterior to the glabella, a moderately wide and shallow depression abaxially and poorly defined from preocular fields. Genal field steeply inclined and thus relatively narrow in dorsal view. Posterior border convex, narrow proximally, not visible in the distant portions in the present material. Posterior border furrow well-defined, moderately broad and moderately deep. Anterior branch of facial suture known only for the anteriormost part, curved slightly adaxially when reaching anterior border and cutting the border for a considerable distance. Posterior branch not visible in the present material.

Pygidium apparently subsemicircular, with four pairs of marginal spines. Rhachis strongly convex in transverse section, composed of four axial rings and a small terminal axial piece. Axial rings distinctly convex (sag. and exsag.), each ring with a strong node in a slightly posteromedian position; terminal axial piece sag. very narrow with gently curved posterior margin, forms a posterior appendage of the axial ring posterior to it, separated by a shallow, poorly defined slightly curved furrow with a pair of weak depressions; width across terminal axial piece roughly half width across anterior axial ring. Furrow between axial ring 1 and 2 moderately wide and moderately deep, furrow between axial ring 2 and 3 similar to anterior furrow, furrow between axial ring 3 and axial ring 4 narrow and relatively shallow. Posterior end of rhachis defined by very shallow, poorly defined posterior border furrow.

Pleural areas moderately convex (tr.), sloping towards border furrow, defined by well impressed, but progressively narrower pleural furrows and interpleural furrows; interpleural furrows developed as triangular areas the shape of which creates narrow, posterolaterally narrowing posterior ribs on each segment, extending in thread-like narrow bands towards the posterior base of the marginal spines. Anterior ribs form broader, elongate and slightly curved areas extending into the marginal spines. Marginal spines apparently long, slender, acute, posterolaterally directed. Terminal pair of spines broader (tr.) at base, located posterior to axial furrows, well separated and forming a broadly parabolic course of the posterior margin. Posterior border moderately broad (sag.) and weakly convex, tends to form an obsolescent plectrum posterior to the rhachis. Lateral border low, rhythmic due to the intersection from the pleural areas; lateral border furrow merely depicted as a change in slope, consisting of separated depressions in continuation of the pleural and interpleural furrows.

Entire carapace smooth.

Discussion. – The sparse material in the sample does not allow a precise determination. Characters of the cranidium in particular indicate distinct differences from *Olenoides sagittatus* sp. nov. These characters include (i) the pattern of the lateral glabellar furrows; (ii) the connection between eye ridges and frontal lobe; (iii) the course of the anterior border; and (iv) the shape of the occipital ring and its connection with the fixigenae. In additions, the pygidium is distinguished from that of *O. sagittatus* mainly by differences in the pleural furrows and the shape and course of the posterior border.

The specimens described herein show some resemblance to *Olenoides calvus* Lazarenko, 1954, but can be easily distinguished by tr. wider fixigenae.

Genus *Kootenia* Walcott, 1889

Type species (by original designation). – *Kootenia dawsoni* Walcott, 1889 from the Middle Cambrian Stephen Formation of British Columbia, Canada.

Kootenia sp. A

Figure 6F–I

Locality. – Sauk Tanga, FG locality 596/III/11; 40° 01' 33.4" N, 70° 16' 18.3" E.

Material. – Incomplete cranidia (external moulds) under FG 596/XII/001h and FG 596/XII/033a; incomplete pygidium under FG 596/XII/003a; fragment of thoracic segment under FG 596/XII/010b.

Description. – Cranidium only represented by a fragment of an internal mould showing part of the glabella, a partial fixigena, eye ridge and palpebral lobe. The visible details display the middle part of a typical glabella with the slight constriction at S3 and three pairs of lateral glabellar furrows. The fixigena is moderately convex and of a relatively narrow subcircular outline. The eye ridges have short transverse section near the axial furrow and then directed obliquely backward from a small node to proceed into the palpebral lobe, distinguished from them by a very shallow depression. Palpebral lobe narrow, weakly elevated above the broad and shallow palpebral furrow, which is poorly defined from the fixigena.

Pygidium subsemicircular with four pairs of strong marginal spines. Rhachis moderately to strongly convex in transverse section, composed of three axial rings and a composite terminal axial piece plus a very narrow articulating half-ring; each axial ring with a strong node in a slightly posteromedian position; terminal axial piece with sag. narrow section with gently curved posterior margin, and an anterior cylindrical section separated by an obsolescent transverse furrow, the anterior section with median node; axis (except for articulating half-ring and spines) of ca 80 percent pygidial length; width across anterior axial ring ca 35 percent pygidial width at anterolateral corners; width across terminal axial piece ca 68 percent width across anterior axial ring. Articulating half-ring not entirely preserved in the present material, sag. very narrow and blade-like, well raised above articulating furrow. Articulating furrow well incised, moderately wide, furrow between axial ring 1 and 2 broad and moderately deep, furrow between axial ring 2 and three moderately wide, slightly shallower than anterior furrow, furrow between axial ring 3 and terminal axial piece narrow and shallow. Posterior end of rhachis defined by shallow border furrow.

Pleural areas moderately convex (tr.), sloping considerably towards border furrow, defined by five well impressed, but progressively narrower pleural furrows and with shallow, weakly defined oblique interpleural furrows. Pleurae develop across lateral border furrow into fairly long, stout, acute and posterolaterally directed spines. Terminal pair of spines posterior to axial furrows steeply backward directed, well separated, forming a broadly parabolic course of the posterior margin. Posterior border a fairly broad (sag.) moderately convex pad with a faint forward curvature behind the terminal axial piece so that the posterior border furrow is slightly narrower behind the axis' tip. Lateral border moderately convex; lateral border furrow a moderately broad and wavy band with depressions between pleural areas and bases of the lateral spines, intersected by extensions of pleural furrows.

Entire carapace smooth.

Discussion. – The fragments of a single cranidium and a single pygidium of a species of *Kootenia* are too incomplete

to allow a precise determination. Remarkably, all of the *Kootenia* species reported from the Turkestan and Alay ranges (*Kootenia asiatica* Kobayashi, 1935; *Kootenia ontoensis* Chernysheva, 1961; *Kootenia bolgovae* Repina, 1975) are clearly distinguished from the form from Sauk Tanga by at least five segments visible in the pygidial rhachis and none of them appears to have a close relationship with it.

Order Ptychopariida Swinnerton, 1915
?Family Agrauidae Raymond, 1913

Genus *Pseudoeteraspis* Chernysheva, 1950

Type species (by original designation). – *Pseudoeteraspis angarensis* Chernysheva, 1950 from the Middle Cambrian of the Priabar region, Siberia.

Pseudoeteraspis? sp. A

Figure 7A, B

Locality. – Sauk Tanga, FG locality 596/III/11; 40° 01' 33.4" N, 70° 16' 18.3" E.

Material. – Single incomplete cranidium (external mould) under FG 596/XII/031b.

Description and discussion. – This trilobite species is only present in the sample as a very incomplete fragment of a cranidium preserved as an external mould. The specimen is too brittle to reliably allow the preparation of a cast so that the photo (Fig. 7B) is electronically inverted from that of the external mould. Visible are the anterior two-thirds of a forward tapering glabella with a slight change in the course of the lateral sides and the axial furrow. It also displays the relatively weak convexity and the absence of well recognizable lateral glabellar furrows together with a shallow curvature of the frontal lobe. The glabellar front reaches to the anterior border furrow in front of which part of a raised and padded anterior border of considerable sag. breadth can be seen. The preserved parts of the fixigenae show raised smooth and moderately convex areas, which do not show clear signs of eye ridges in front.

Discussion. – These visible characters indicate a high degree of similarity with species described under the genus *Pseudoeteraspis*, such as *P. aldanensis* Chernysheva, 1950. This species was described from the Priabar region and the Aldan Anticline of Siberia and used as an index fossil of the *Pseudoeteraspis*-*Parapoliella*-*Namanoia* Zone, which would be considerably older than the upper Amgan age indicated by well determinable fossils. However, distinct differences exist, e.g., in the lower convexity of the glabella of the Sauk Tanga specimen.

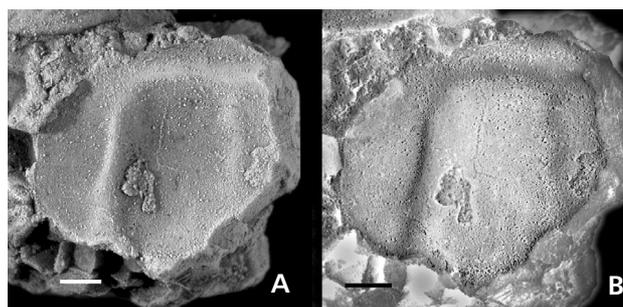


Figure 7. *Pseudoeteraspis?* sp. A, Sauk Tanga locality. • A – partial cranidium, external mould, FG 596/XII/031b. • B – same specimen, electronically inverted photo, slightly enhanced. Scale bar 1 mm.

Phylum Brachiopoda Dumeril, 1806
Subphylum Rynchonelliformea Williams, Carlson, Brunton, Holmer & Popov, 1996
Class Kutorginata Williams, Carlson, Brunton, Holmer & Popov, 1996
Order Kutorginida Kuhn, 1949
Family Nisusiidae Walcott & Schuchert in Walcott, 1908

Genus *Narynella* Andreeva, 1987

Type species (by original designation). – *Nisusia ferganensis* Andreeva, 1962, Middle? Cambrian (see Remarks below), Fergana Basin, Kyrgyzstan.

Discussion. – The family Nisusiidae as defined by Popov & Williams (2000) includes five genera of which *Nisusia* Walcott is by far the most common and diverse. Bell (1941) recognised two morphotypes within *Nisusia* defined by the shape of its ventral valve and the external ornamentation of the shell. The first type is represented by spinose costellate species of *Nisusia* with a conical ventral valve [e.g., the type species *N. festinata* (Billings, 1861)], the second type by costellate species lacking spines and having a ventral valve that is convex in lateral profile (e.g., *N. montanaensis* Bell, 1941). Bell (1941) suggested that the two morphotypes might represent separate genera.

Andreeva (1987) described new genus *Narynella*, with *Nisusia ferganensis* Andreeva 1962 from the Lenan of Kyrgyzstan as the type species. According to Andreeva (1987, p. 24), *Narynella* is distinguished from the similar *Nisusia* by a costellate external ornamentation lacking spines and the development of a ventral fold and a dorsal sulcus, i.e., a unisulcate commissure. The ventral valve of *Narynella ferganensis* is conical in lateral profile, whereas that of *Nisusia sulcata* Rowell & Caruso, 1985 (a species tentatively assigned to *Narynella* by Andreeva 1987) is convex. As a result, two morphotypes distinguished by the shape of the ventral valve are also present within *Narynella*. *Narynella* is

currently distinguished from *Nisusia* by the nature of the commissure only, which is rectimarginate or emarginate in *Nisusia*.

Remarks. – Popov & Williams (2000) and Holmer *et al.* (2001) described, probably erroneously, *Narynella* as having a ventral sulcus and a dorsal fold, rather than a ventral fold and a dorsal sulcus.

There seems to be some confusion about the age and origin of the type material of *Nisusia ferganensis*, the type species of *Narynella*. In the protologue, Andreeva (1962, p. 89-90) described the material as originating from the Madygen area (“урочище Мадьген”) of the southern Fergana Basin, which is located in the Batken district of present-day Kyrgyzstan (see *Geological setting* above). The age of the material was referred to the “Lenan”, a stratigraphical equivalent to the Botoman and Toyonian stages. In her introduction of the genus *Narynella*, Andreeva (1987, p. 34) listed the type material as from the Lenan Stage of the Fergana Basin, Uzbekistan [sic]. In their description of *Narynella cf. ferganensis* from Kazakhstan, Holmer *et al.* (2001, p. 150) referred to the type material as being of Amgan age and to originate from the “Fergana valley, Uzbekistan”. The precise age of the type material remains uncertain because no specific information was provided by Andreeva (1962, 1987) nor details of the associated fauna. Based on the age of other occurrences of *Narynella ferganensis*, *i.e.*, the *Ptychagnostus atavus* Biozone of the Malyi Karatau, Kazakhstan (Holmer *et al.* 2001), and the *Sdzuyella-Aegunaspis* Zone of the southern Fergana Basin, Kyrgyzstan (Aksarina 1975; data presented herein), an Amgan age appears to be more likely for the type material.

***Narynella cf. ferganensis* (Andreeva, 1962)**

Figure 8A–J

- 1962 *Nisusia ferganensis* sp. nov.; Andreeva, pp. 89–90, fig. 2.
- 1975 *Nisusia nasuta* var. *ramosa* Nikitin, 1956. – Aksarina, pp. 97–98, pl. 5, figs 10–15.
- ? 2001 *Narynella cf. ferganensis* (Andreeva, 1962). – Holmer *et al.*, pp. 152, 154, pl. 48, figs 1–7.

Type material. – From the Madygen area (урочище Мадьген), Fergana Basin, Kyrgyzstan.

Material. – Fifteen valves, of which eight are ventral (FG 596/XII/005c, FG 596/XII/006a, FG 596/XII/009b, FG 596/XII/010c, FG 596/XII/025a, FG 596/XII/028a, FG 596/XII/030a, FG 596/XII/032a), and seven are dorsal (FG 596/XII/013a, FG 596/XII/013b, FG 596/XII/020a,

FG 596/XII/020b, FG 596/XII/023a, FG 596/XII/026a, FG 596/XII/027a).

Description. – Shell markedly ventribiconvex, transversely subrectangular in outline, reaching its maximum width at about midlength; cardinal extremities obtuse. External shell surface costellate with most apical area typically smooth. Ventral valve conical, with straight lateral slopes and a straight to concave anterior slope; maximum height at pointed umbo, which is perforated by a relatively large foramen. Ventral interarea smooth, catacline, divided by strongly convex, long pseudodeltidium. Sharp flexures between propareas and pseudodeltidium accentuate pseudodeltidium and posterior margin. Delthyrium not clearly seen but probably low, rounded triangular, measuring less than one third of valve height. Dorsal valve convex, with straight to gently convex lateral slopes and an anterior slope that is initially convex but straightens out towards the anterior margin; maximum height at about one third of valve length from umbo. A shallow, broad median sulcus can only be seen in large specimens (Fig. 8H). Dorsal interarea broad, anacline. Internal characters of both valves not observed except for the costellate ornamentation that is also faintly visible on internal shell surfaces (Fig. 8A). Specimens measure 4.4 to 8.4 mm in length and 6.6 to 11.0 mm in width. Seemingly complete specimens (Fig. 8D, G) suggest a length-width ratio of about 0.75.

Discussion. – Specimens described as *Narynella cf. ferganensis* by Holmer *et al.* (2001) from the Amgan (*Ptychagnostus atavus* Biozone) of the Malyi Karatau, Jambyl (earlier: Dzhambul) Province, south-east Kazakhstan, are questionably referred to *N. ferganensis* as ventral valves from this locality were described as moderately convex rather than conical.

Andreeva (1962) measured lengths and widths of *N. ferganensis* reaching 14 and 17 mm, respectively. The specimens from Sauk Tanga are smaller suggesting that they result from juvenile individuals. This assumption is supported by the general absence of a fold and sulcus in the studied specimens except for the largest valve. This matches the ontogeny described for *Narynella sulcata*, in which a rectimarginate commissure was observed in juvenile and a unisulcate one in adult valves (Rowell & Caruso 1985).

***Narynella?* sp.**

Figure 9E–G

Material. – Two dorsal valves, FG 596/XII/024a and FG 596/XII/031a.

Description. – Both dorsal valves are strongly convex in

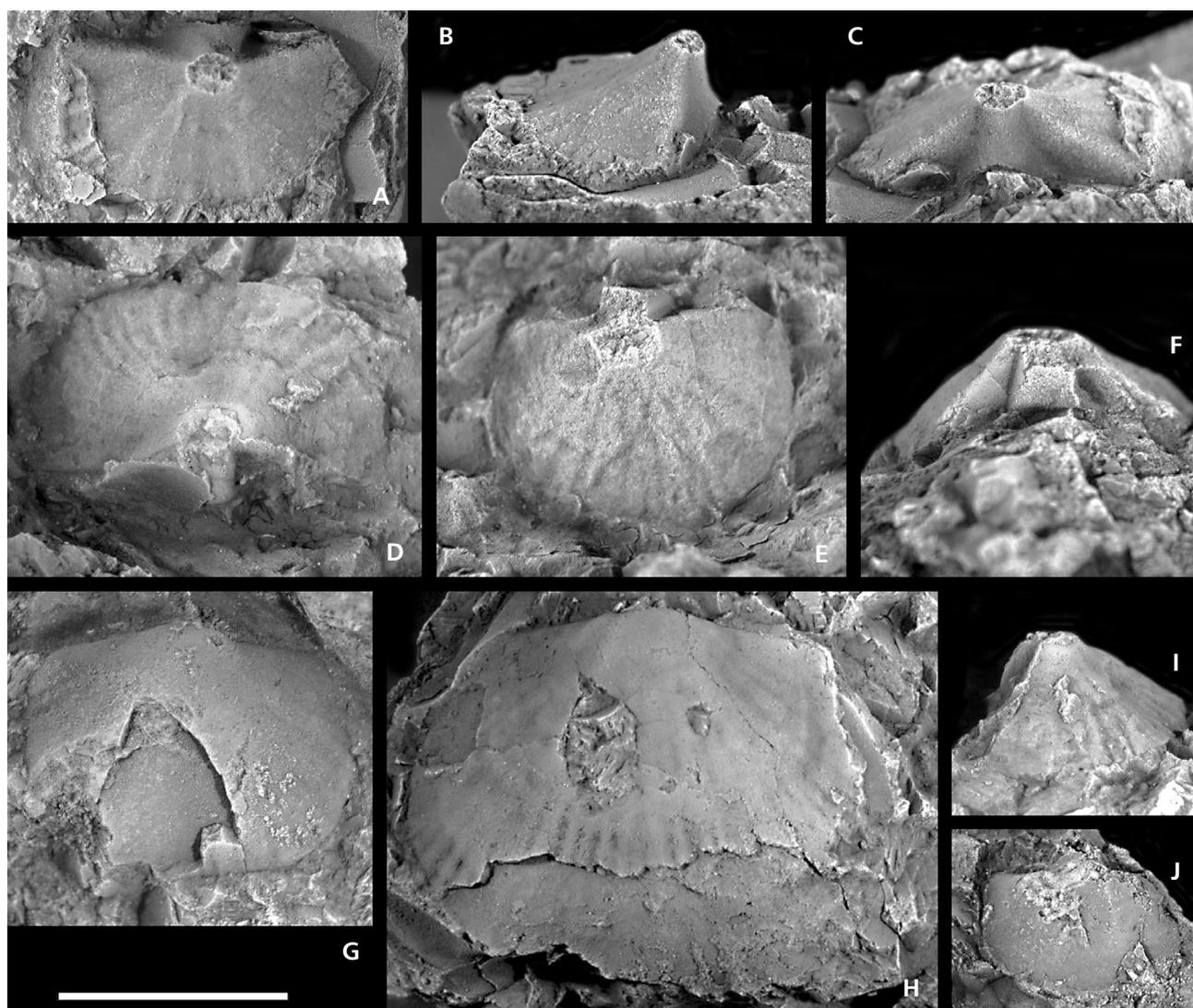


Figure 8. *Narynella* cf. *ferganensis* (Andreeva, 1962), Sauk Tanga locality. • A–C – internal mould of ventral valve FG 596/XII/025a; A – ventral view with remains of costellate shell to the left; B – lateral view showing concave anterior slope; C – posterior view with distinct pseudodeltidium. • D, I – ventral valve in ventral and lateral views, FG 596/XII/032a. • E, F – ventral valve in ventral and posterior views, FG 596/XII/025a. • G – relatively smooth dorsal valve, FG 596/XII/020a. • H – large costellate dorsal valve with shallow sinus, FG 596/XII/027a. • J – latex cast of interior of small ventral valve, FG 596/XII/009b. Scale bar 5 mm.

lateral profile with the strongest convexity at the umbo; convexity decreases anteriorly. Lateral slopes are concave resulting in a prominent umbonal area and a more straightened appearance of the posterior margin of the valve in dorsal view (Fig. 9E). Smooth umbo overhangs a seemingly broad but short anacline interarea. Cardinal extremities obtuse. External shell surface costellate, except for umbonal area; individual costae and intercalated costellae strong, rounded in cross-section. Origin of costellae (by intercalation or branching) not determinable. A faint median depression at the anterior shell margin might indicate the development of a sulcus (Fig. 9F). A single, prominent growth lamella is developed close to the margin of one valve. The larger of the two valves (Fig. 9E–G) is 5.4 mm

long and 7.2 mm wide, its maximum width at about mid-length.

Discussion. – The described dorsal valves are similar to juvenile dorsal valves of *Narynella* cf. *ferganensis* with respect to size, proportions, and general outline as well as ornamentation of the shell exterior. The umbo, however, is more pronounced in *Narynella?* sp. resulting in a more strophic appearance of the valves. In addition, growth lamellae have not yet been noticed for *Narynella*, but are not uncommon for nisusiids (e.g., Bell 1941, Benedetto & Foglia 2012). However, internal characters and the morphology of the interarea are needed for a confident placement under *Narynella*.

Class Rhynchonellata Williams, Carlson, Brunton,
Holmer & Popov, 1996
Order Orthida Schuchert & Cooper, 1932
Suborder Orthidina Schuchert & Cooper, 1932
Superfamily Plectorthoidea Schuchert & LeVene, 1929
Family Eoorthidae Walcott, 1908

Genus *Austrohedra* Roberts & Jell, 1990

Discussion. – The genus *Austrohedra* was described by Roberts & Jell (1990) from the Middle Cambrian (Ordian) Coonigan Formation of New South Wales and placed in the family Eoorthidae Walcott, which was followed by Williams & Harper (2000b). The type species, *A. mimica* Roberts & Jell, 1990, is currently the only recognised species of this genus, but the two valves described below might represent a new species of *Austrohedra* or a new, closely related taxon.

Austrohedra? sp. nov.

Figure 9A–C

Material. – Internal mould of a single ventral valve, FG 596/XII/019b, and one dorsal valve, FG 596/XII/009a.

Description. – Shell strophic, ventribiconvex, transversely rectangular to semicircular in outline with maximum width at hinge line or slightly anterior to it. Cardinal extremities not clearly visible, acute to rectangular or somewhat obtuse. No fold or sinus observed in either valve suggesting a rectimarginate commissure. External shell surface costellate with prominent, rounded costae and costellae of subequal thickness; number of costellae increases by intercalation. Ventral valve high, hemi-conical with greatest height at apex. Lateral slopes and anterior slope gently convex. Steep, procline to catacline interarea divided by wide, seemingly open, high delthyrium. Internally with low, short platform in the umbonal apex (muscle platform?); platform transversely rectangular in outline, broadens slightly anteriorly before it merges with the valve floor. Mould of ventral valve 7.5 mm wide, 3.8 mm long, and 2 mm high.

Dorsal valve convex, with straight lateral slopes and convex anterior slope; maximum height at about one-third of valve length from umbo. Umbo slightly overhangs short, anacline interarea featuring a low notothyrium. Internal features of dorsal valve not known. Valve is about 7.6 mm wide (reconstructed width based on the complete left half of the valve) and 4.4 mm long.

Discussion. – The observed characters of the two valves described above match best with the monotypic Australian genus *Austrohedra* Roberts & Jell and its type species

A. minima. However, a few differences qualify this assignment. Shells of *A. minima* and *Austrohedra?* sp. nov. share the same outline and external ornamentation, are ventribiconvex, and have a rectimarginate commissure. Their ventral valves are hemiconical with a broad and steep, flat interarea divided by an open delthyrium, and their dorsal valves are convex with a broad, open notothyrium. Distinct differences between the two taxa exist in: 1) the inclination of the ventral interarea, which has been described as catacline to slightly apsacline in *A. minima* (Roberts & Jell, 1990) rather than steeply procline to catacline as in *Austrohedra?* sp. nov.; and 2) the development of a broad and shallow dorsal sulcus in *A. minima*, which is not seen in *Austrohedra?* sp. nov. While such differences could be explained as intrageneric variation, observed discrepancies among internal characters are more significant. The apex of *Austrohedra?* sp. nov. bears a rectangular platform, which appears to be unknown from other Cambrian rhynchonelliform brachiopods. In contrast, the apex of *Austrohedra* is characterised by an apically elevated pseudospondylium (Roberts & Jell 1990). We interpret the platform observed in *Austrohedra?* sp. nov. to be formed of secondary shell, analogous to a pseudospondylium. The actual pseudospondylium and dental plates might be rudimentary and not preserved on the internal mould of *Austrohedra?* sp. nov. Potentially comparable platforms are present in various Furongian to Ordovician orthids such as the eoorthid genus *Apheoorthis* Ulrich & Cooper, 1938 or the archaeorthid *Archaeoorthis* Schuchert & Cooper, 1931. There, the platform presents the anterior support of the pseudospondylium (e.g., Ulrich & Cooper 1938, pl. 10, figs 5, 17 or pl. 13, figs 9–12).

Austrohedra? sp. nov. is also similar to the genus *Arctohedra* Cooper, 1936, a genus previously accommodated within the protorthids (Williams & Harper 2000a), but now considered to be a basal clitambonitoid (Rubel 2007, Topper *et al.* 2013). The genera *Austrohedra* and *Arctohedra* are almost identical externally, except for the cardinal extremities, which are acute in *Arctohedra* rather than obtuse, and the ventral valve, which may be procline to catacline in *Arctohedra* (Cooper 1936, Roberts & Jell 1990, Brock 1998), quite similar to that of *Austrohedra?* sp. nov. However, ventral valves of *Arctohedra* are characterised by a free spondylium growing from the inner ventral margins of the delthyrium (Cooper 1936, Roberts & Jell 1990, Williams & Harper 2000a). No such structure appears to be developed in *Austrohedra?* sp. nov. Nevertheless, the apical platform of the ventral valve from Sauk Tanga is reminiscent of configurations described from other basal clitambonitoids. Such genera include the early Ordovician *Apomatella* Schuchert & Cooper, 1931 and the late Cambrian *Roanella* Brock & Talent, 1999. Both genera show an apical shell thickening in their ventral valves that is reminiscent of the platform

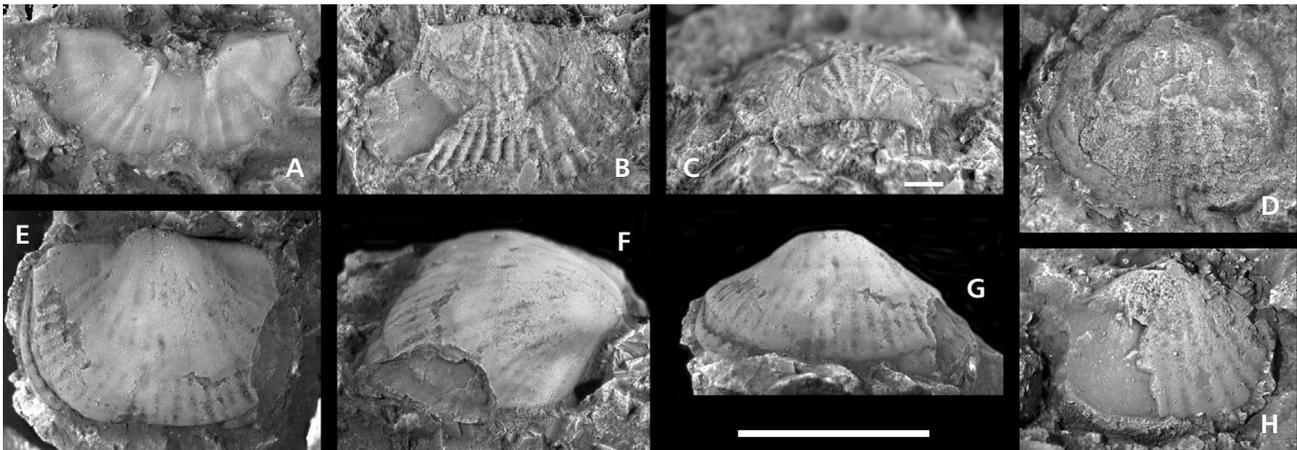


Figure 9. A–C – *Austrohedra?* sp. nov.; A – internal mould of procline ventral valve showing impression of apical rectangular platform, FG 596/XII/019b; B, C – dorsal valve in dorsal and posterior views, FG 596/XII/009a. • D – gen. and sp. indet. 1, corroded shell exterior of presumed ventral valve with shallow sulcus near anterior margin, FG 596/XII/007c. • E–G – *Narynella?* sp., dorsal valve with distinct growth lamella in dorsal, oblique lateral, and anterior view, FG 596/XII/024a. • H – gen. and sp. indet. 2, partly exfoliated exterior of presumed dorsal valve, FG 596/XII/012b. Scale bar 5 mm.

of *Austrohedra?* sp. nov. In *Apomatella*, this thickening is a short, anteriorly broadening ridge, which is the support of a rudimentary, short spondylium. *Roanella* lacks a spondylium but has a similar thickening, which defines the anterior border of its ventral apical muscle field (Brock & Talent 1999, Topper *et al.* 2013). According to the cladistic analysis of Topper *et al.* (2013), *Arctohedra*, *Roanella*, and *Apomatella* all belong at the base of the clitambonitoid branch. Based on the similarities of *Austrohedra?* sp. nov. with these taxa and the observed variability in basal clitambonitoids, the two valves from Sauk Tanga may be interpreted to represent a taxon in a similar position. However, the lack of information concerning the dorsal interior of *Austrohedra?* sp. nov., in particular the configuration of the cardinalia, makes a clitambonitoid affinity conjectural. The same is true for the suggested eoarthid affinity. Nevertheless, an eoarthid affinity of *Austrohedra?* sp. nov. appears to be the most parsimonious interpretation at present.

Class, order, and family indet.

Gen. and sp. indet. 1

Figure 9D

Material. – One partly exfoliated ventral? valve, FG 596/XII/007c.

Description. – The single valve is subspherical to transversely ovaloid in outline, about 5.0 mm long and 6.3 mm wide with the maximum width slightly anterior to midlength. Poorly visible hinge line is either astrophic or extremely narrow. Valve is evenly convex in lateral and posterior view. An external ornamentation of seemingly fine costellae is only pre-

served within a shallow sulcus at the anterior margin. Apex appears pronounced, suggesting a ventral valve.

Discussion. – See Discussion of Gen. and sp. indet. 2.

Gen. and sp. indet. 2

Figure 9H

Material. – One partly exfoliated probable dorsal valve, FG 596/XII/012b.

Description. – The single valve is subspherical to subtriangular in outline, about 4.2 mm long and 5.8 mm wide with the maximum width at about 60% of length from posterior margin. Poorly visible hinge line is either astrophic or narrow. Valve is convex in lateral profile with the maximal convexity at the umbo; lateral and anterior slopes are straight and no signs of a sulcus or fold are visible. External ornamentation consist of strong rounded costae and costellae. Apex inconspicuous at convex posterior margin, suggesting a dorsal valve.

Discussion. – Narrowly strophic or astrophic, costellate shells with a potential uniplicate or rectimarginate commissure are not common among Cambrian rhynchonelli-form brachiopods. Taxa superficially resembling gen. and sp. indet. 1 and 2 belong to the obolellate Family Naukatidae (*e.g.*, *Naukat* Popov & Tikhonov, 1990 or the poorly understood *Swantonina* Walcott, 1905) and the pentameride family Tetralobulidae (subfamily Syntrophopsinae). However, due to the lack of information on any internal characters and the poor state of preservation of both valves that might also comprise the observed shell outlines, we refrain from a systematic assignment of the two specimens.

Incertae sedis

Order Tommotiida Missarzhevskiy, 1970

Genus *Tesella* Missarzhevskiy & Grigor'yeva, 1981

Type species (by original designation). – *Tesella deplanata* Missarzhevskiy & Grigor'yeva, 1981, from the early part of the Amgan Stage of Mt. Sladkiye Koren'ya, Kuznetsk Alatau Range, Russia.

Discussion. – Missarzhevskiy & Grigor'yeva (1981) described 5 tommotiid sclerite-types from the Amgan Stage of Mt. Sladkiye Koren'ya, which they attributed to new species of *Sonella* Missarzhevskiy & Grigor'yeva, 1981 and *Tesella*. No discussion of the reconstruction of these sclerite-types into a scleritome was given. Yuan & Zhang (1983) did not accept *Sonella* and *Tesella* in their description of early (Tommotian-Atdabanian) tommotiids from south-west China, although Qian (1989) did (with *Tesella* given as "*Tessella*"). Schopf & Klein (1992) synonymised *Sonella* with *Tesella*.

***Tesella* sp.**

Figure 3E, F

Material. – The illustrated fragmentary specimen, FG 596/XII/016b, and several other minute fragments.

Discussion. – The figured fragment shows traces of the transverse septa on the inner wall and behind this, the coarse, corded, ornament of the outer surface (Fig. 3F). The overall shape of the sclerite cannot be accurately ascertained; it most closely resembles *T. deplanata*, the holotype (Missarzhevskiy & Grigor'yeva 1981, pl. XI, figs 5, 6), but this has coarser, more widely spaced cords on the outer surface. A similar association of sclerites to that described by Missarzhevskiy & Grigor'yeva (1981) from Mt. Sladkiye Koren'ya occurs in the Henson Gletscher Formation of North Greenland (C.B. Skovsted and J.S. Peel, unpublished observations) in strata yielding *Ovatoryctocara granulata* Chernysheva, 1961 and thus of similar age to the Russian occurrence (Geyer & Peel 2011).

Incertae sedis

Order Hyolithelminthida Fischer, 1962

Family Hyolithellidae Walcott, 1886

Genus *Hyolithellus* Billings, 1871

Type species (by original designation). – *Hyolithus micans* Billings, 1871, from the *Bonnia-Olenellus* Zone, Dyeran Stage; Troy, New York State, U.S.A.

***Hyolithellus* sp.**

Figure 3G

Material. – Several small fragments and fragmentary specimen, FG 596/XII/004b.

Discussion. – The largest of several small fragments assigned to *Hyolithellus* sp. is illustrated here. Maximum preserved length is 5 mm with a diameter of 1.5 mm. The shell is largely exfoliated, showing the imbrication of growth lamellae, the succession of which forms the fine transverse ornamentation on the tube exterior. Most described *Hyolithellus* are considerably narrower than the current specimen although Skovsted & Peel (2011) figured even larger specimens, with unusually thick walls, that occur *in situ* in the lower Cambrian of North Greenland.

Incertae sedis

Class Palaeoscolecida Conway Morris & Robison, 1986

Family Palaeoscolecidae Whittard, 1953

Genus *Hadimopanella* Gedik, 1977

Type species (by original designation). – *Hadimopanella oezgueli* Gedik, 1977, from the Middle Cambrian (assigned to the Upper Cambrian in the protologue) of the Central Taurus, north of Bađbađy, Konya Province, Turkey.

Discussion. – *Hadimopanella* Gedik is a form genus for button-shaped palaeoscolecoid sclerites that are commonly found in Cambrian sediments. They are known since the lower Cambrian (upper Atdabanian, Cambrian Stage 3; Bengtson 1977) and might reach into the Middle Ordovician (Van den Boogaard 1989). Intraspecific variability of palaeoscolecoid sclerites can be quite extensive as it has been observed in sclerite rich sediments (*e.g.*, Van den Boogaard 1983, Peel & Larsen 1984, Streng & Ebbestad 2007) or in specimens with partly preserved articulated scleritomes (*e.g.*, Ivantsov & Wrona 2004). Thus, it is important to have a sufficient number of specimens when describing disarticulated material to critically assess the potential morphological variability of a taxon. Studies of palaeoscolecoid scleritomes have, however, also revealed that the same morphotype of a sclerite may occur in apparently different species and genera (*e.g.*, Ivantsov & Zhuravlev 2005, Topper *et al.* 2010).

Sclerites of *Hadimopanella* are button or disc-shaped with one side of the discus being smooth and generally gently convex (the so called "proximal", "lower", or "smooth surface"), whereas the other side ("distal" or "upper surface") is elevated centrally and ornamented by nodes of variable sizes and numbers. The distal surface can be subdivided into a marginal area without nodes (the so

called “brim”) and a central area bearing the nodes (also termed the “crown”). The brim is typically ornamented by fine radial grooves and clearly delineated from the crown by a suture (basal suture). The crown itself can be further subdivided in some taxa into a marginal, typically smooth and node-free zone (termed the “girdle”), and the crown *sensu stricto*, *i.e.*, the innermost area bearing the nodes (also called “nodular face”) (for terminology see, *e.g.*, Bengtson 1977 and Wrona 1982).

Hadimopanella oezgueli Gedik, 1977

Figure 10A–F

- 1977 *Hadimopanella oezgueli* n. sp.; Gedik, pp. 46–47, pl. 5, figs 1–5.
 1983 *Hadimopanella oezgueli* Gedik, 1977. – Van den Boogaard, pp. 337, 339, 340, figs 3–5.
 1988 *Hadimopanella oezgueli* Gedik, 1977. – Märss, pp. 14–15, pl. 1, figs 1–8.
 n 2001 *Hadimopanella oezgueli* Gedik, 1977. – Wrona & Hamdi, pp. 104–105, pl. 1, figs 1–5, pl. 2, figs 1–8, pl. 3, figs 1–6.
 ? 2003 *Hadimopanella* sp. – Elicki *et al.*, pl. 5, figs 12–23.
 2011 *Hadimopanella knappologica* (Bengtson, 1977). – Kouchinsky *et al.*, pp. 43–44, fig. 32.
 [selective synonymy that summarises the regional and stratigraphic distribution of the taxon]

Type material. – Middle Cambrian of the central Taurids, Konya Province, Turkey.

Material. – Five individual sclerites, FG 596/XII/034a–e.

Description. – Individual sclerites are circular to somewhat ovaloid in outline, measuring 147 to 187 μm in maximum diameter ($n = 5$). An about 18 μm broad brim is preserved in four of the specimens, ornamented by fine radiating grooves; brim width appears to be constant and independent of sclerite size. Brim concave, straight or slightly convex in lateral profile, typically somewhat less inclined than the girdle. One specimen shows a brim that is additionally ornamented by adjoining circular shallow depressions, with the diameter of the depressions matching the brim width (Fig. 10A). Girdle variably developed among observed specimens; either fully expressed, *i.e.*, surrounding central noded area (Fig. 10C), or partially developed only, *i.e.*, partly surrounding center (Fig. 10A), or reduced to one sector of crown (Fig. 10B). Nodes in centre of crown measure about 13 to 28 μm in diameter and are arranged in two concentric to slightly eccentric rings around a centre. In the centre of the ring, which does not have to be the centre of the sclerite, a single node may be developed (Fig. 10A, C). Observed number of nodes in crown

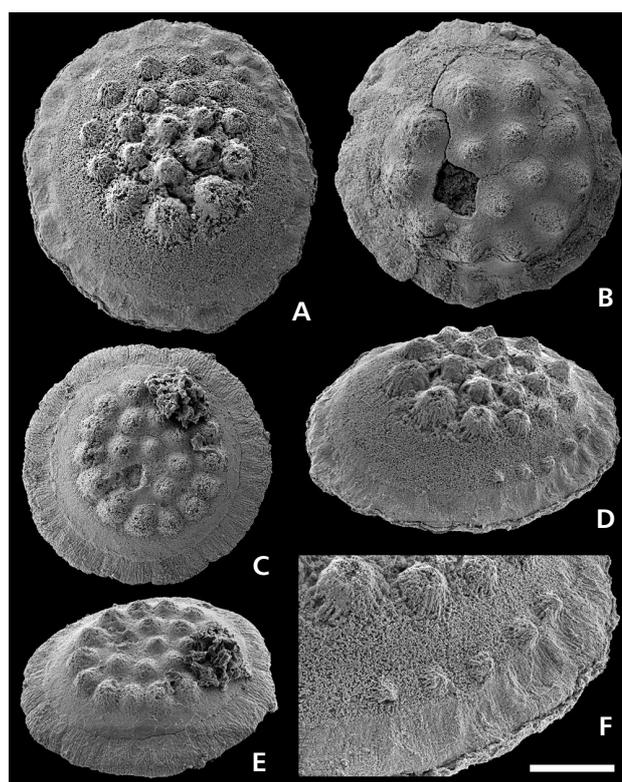


Figure 10. *Hadimopanella oezgueli* Gedik, 1977, Sauk Tanga locality. • A, D, F – specimen with 19 nodes ($19 = 11 + 7 + 1$; see text for further explanation) and five accessory nodes on girdle, in distal (A), lateral (D), and close-up view (F), FG 596/XII/034a. • B – specimen with 15 nodes ($15 = 10 + 5 + 0$), FG 596/XII/034b; note that the girdle is only developed in the upper left sector. • C, E – specimen with 22 nodes ($22 = 14 + 7 + 1$) in distal and lateral view, FG 596/XII/034c. Scale bar 50 μm , except F (25 μm).

centre varies between 15 and 22 ($n = 4$), with ten to 14 nodes in outer ring, and five or seven in the inner ring. Two specimens have a single node in the middle of the second ring (Fig. 10A, C). One specimen bears five small, accessory nodes on the girdle (Fig. 10F) measuring 7.5 to 9.5 μm in basal diameter.

Discussion. – The arrangement of nodes in concentric rings, with the nodes being of similar sizes, is herein considered to be the characteristic feature of *Hadimopanella oezgueli*. Published data on the species shows that nodes can be arranged in three iterations, of which only one or all three can be expressed. Iteration one would be the presence of only one ring of nodes, iteration two is characterised by the presence of one ring of nodes with another ring in its centre. This second “ring” might also comprise only one or two nodes and can be of somewhat irregular shape. The third iteration defines the presence of nodes central to the second ring (see also Van den Boogaard 1983). Only a single node for the third iteration has been reported or depicted. Thus, nodes of *H. oezgueli* can be expressed in the formula

$n = i_1 + i_2 + i_3$, with n being the total number of crown nodes and i_1 to i_3 , the number of nodes in each iteration with i_1 being the outermost. According to literature data on *H. oezgueli* (see Synonymy), the variation ranges from 5 or 4 nodes ($5 = 5 + 0 + 0$, Van den Boogaard 1983, fig. 3f; $4 = 4 + 0 + 0$, Märss 1988, pl. 1, fig. 1) over 8 nodes ($8 = 7 + 1 + 0$; holotype of Gedik 1977, pl. 5, fig. 1) to specimens with two fully developed iterations (see e.g., Fig. 10B, $15 = 10 + 5 + 0$; Märss 1988, pl. 1, figs 5–8; Kouchinsky *et al.* 2011, fig. 32), to three expressed iterations with up to 22 nodes (Fig. 10C, $22 = 14 + 7 + 1$; Van den Boogaard 1983, fig. 3a). The presence of up to 30 nodes has been reported (Van den Boogaard 1983); their arrangement, however, has not been depicted or described in detail. Accessory nodes on the girdle might increase the total number of nodes (Fig. 10F), but have here not been considered within the formula.

The specimens from Sauk Tanga are almost identical to specimens of *H. oezgueli* described from the upper Lancara Formation of Spain (Van den Boogaard 1983) with respect to size, the arrangement and number of nodes, and general sclerite topology. Furthermore, they are of similar age, with the Spanish specimens being slightly younger (*Badulesia* Biozone, lower Caesar-Augustian/lower Drumian). Specimens from Kyrgyzstan (southeastern Fergana Basin) previously reported by Märss (1988) are somewhat smaller and bear a lower number of nodes. Wrona & Hamdi (2001) described a rich association of isolated palaeoscolecid sclerites from a Furongian member of the Mila Group of Iran as *H. oezgueli*. These sclerites are, as also stated by Wrona & Hamdi (2001), on average smaller and have a lower number of nodes than the Turkish, Spanish, or Kyrgyz specimens. In addition, the individual nodes appear to be more pointed. We consider the Iranian sclerites to fall outside the morphological variability of *H. oezgueli*. Specimens from the Amgan of the Siberian Platform described by Kouchinsky *et al.* (2011) as *H. knappologica* (Bengtson, 1977) show a distinct brim, a broad girdle, and an arrangement of the crown nodes in two iteration. The combination of these characters as well as their age suggest an affiliation with *H. oezgueli* rather than *H. knappologica*.

Palaeoscolecid sclerites from the Middle Cambrian Campo Pisano Formation of Sardinia have been described as *Hadimopanella* cf. *oezgueli* (Cherchi & Schroeder, 1985) and *Hadimopanella* sp. (e.g., Elicki *et al.* 2003), respectively. These sclerites resemble *H. oezgueli* in size and general morphology, but their nodular faces are too poorly preserved to describe their morphological variability. As defined herein, *H. oezgueli* occurs in the Middle Cambrian Stages 5 and 6 and is known from Turkey, Spain, Kyrgyzstan, Siberia, and possibly Sardinia.

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