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Silurian craniide brachiopods from Gotland

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Typescript received

Abstract: Seven craniide brachiopod genera are described from the Silurian
(Wenlock–Ludlow) of Gotland, including one new genus and five new species. The
new genus and species *Thulecrania septicostata* is unique among Silurian craniides as
it possesses solid spines. The new species *Lepidocrania multilamellosa* is the first
Silurian record of this poorly known Permian genus. The problematic North American
Propatella Grubbs, 1939, was originally described as a gastropod, but the new species
Propatella palmaria from Gotland shows that it is a craniide with sutured hollow
spines of a type not previously recorded from Silurian craniides. The dorsal valves of
the new species *Valdiviathyris? bicornis* are remarkably similar to those of the type
species, and represent the first possible Palaeozoic record of this poorly known extant
craniide. This first systematic study of craniide brachiopods from the Silurian of
Gotland shows that the diversity is relatively high as compared with other known
Silurian craniide faunas, but a more thorough comparison is not possible due to the

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3 lack of data from most parts of the world. The new data from Gotland supports the
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5 view that the craniides were not affected by the end-Ordovician extinction.
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10 **Key words:** Brachiopoda, Craniiformea, Craniidae, Lazarus taxon, Silurian, Gotland.
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14 THE CRANIIDA brachiopods within the Subphylum Craniiformea are not a
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16 taxonomically diverse group, comprising only the extant Family Craniidae that first
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18 appeared in the early Ordovician. Craniids can be regarded as examples of ‘living
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20 fossils’ as they have retained the same anatomical organization since the Ordovician
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22 (Bassett 2000; Popov *et al.* in press). Whilst the Ordovician craniide faunas are
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24 comparatively well studied, in particular from Laurentia and Baltica (Popov *et al.* in
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26 press and references therein), Silurian craniide faunas are very poorly known,
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28 commonly just briefly recorded, usually characterised by *Petrocrania* (e.g. Bassett
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30 1979), and rarely illustrated as representing relatively minor parts of larger faunal
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32 studies (e.g. Cocks 2008).
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36 The well-preserved brachiopod faunas from the Silurian carbonate platform
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38 succession of Gotland have been studied since Linnaeus (1758; see e.g. Bassett and
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40 Cocks 1974; Copper 2004; Bassett 2005 for reviews). However, the last systematic
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42 study including craniides from Gotland was undertaken by Huene (1899), who
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44 described *Philhedra gracilis* from the Eke Formation, but as noted by Bassett (1979,
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46 p. 185), other records of craniides are mentioned in papers dealing with stratigraphic
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48 matters, as faunal lists. Lindström (1861, p. 374) listed *Crania sedgwickii* Davidson,
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50 1848 from Gotland, but Bassett and Yochelson (1979) revised this specimen
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52 originally described from the Much Wenlock Formation of England as a hyolith
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operculum. Although Bassett (1979) recorded craniides from the Wenlock Höglint Formation in the Vattenfallet section, Visby, he did not illustrate them.

The aim of this paper is to provide the first systematic study of craniide brachiopods from the Silurian of Gotland. This work is based on the material of well-preserved craniides isolated from marl samples, investigated by Popov *et al.* (2010, 2012) while studying their ontogeny.

MATERIAL AND METHODS

All studied brachiopod specimens were isolated and picked from residues after washing and sieving soft argillaceous marl samples in water, using standard techniques. The samples are derived from a series of soft marl samples collected by A. Martinsson (prefix MS; see also Martinsson 1962), L. Ramsköld, M. Arup and C. Franzén; the original sample series are stored in Naturhistoriska Riksmuseet, Stockholm.

The exact geographic and stratigraphic location of each of the studied samples can be tied to a Silurian Gotland Reference Locality (*sensu* Laufeld 1974; see also Calner *et al.* 2004*a, b*), and the stratigraphic and geographic distributions of the material are shown in Figure 1. Samples derive from the following Silurian Gotland Reference Localities:

Solklint 1, Wenlock, Slite Group (Larsson 1979) – collected by L. Ramsköld by 1987.

Sunnkyrke 1, Ludlow, Eke Formation (Laufeld 1974) – collected by C. Franzén (sample 85-35).

Snäckgärdsbaden 1, Wenlock, Upper Visby and Högklint formations, unit a (Laufeld 1974) – collected by A. Martinsson (sample MS492).

Hunninge 1, Wenlock, Klinteberg Formation (Laufeld 1974) – collected by C. Franzén (sample 85-17).

Tänglings 1, Ludlow, Hemse Formation (Laufeld 1974) – collected by C. Franzén (sample 85-28).

Follingbo 3, Wenlock, Slite Group (Laufeld 1974) – collected by A. Martinsson (sample MS485).

Olsvenne 3, Ludlow, Eke Formation (Laufeld 1974) – collected by C. Franzén (sample 74-32).

Häftingsklint, Wenlock, Upper Visby and Högklint formations (Laufeld 1974) – collected by A. Martinsson (sample MS711).

Storburg 2, Ludlow, Sundre Formation (Laufeld 1974) – collected by M. Arup (sample 89-911).

Bassett (2005), Calner *et al.* (2004a, b) and Copper (2004) have already provided geological summaries, stratigraphical outlines and historical background regarding the Silurian geology of Gotland.

Selected specimens were coated with gold palladium, then studied and photographed under CamScan MaXim 2040S scanning electron microscope (SEM) with variable vacuum chamber. The specimens examined under the SEM were cleaned in an ultrasonic cleaner, and etched in 2% EDTA for five minutes.

CRANIIDS AND THE TERMINAL ORDOVICIAN EXTINCTION

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Craniiforms first emerged and proliferated during the Ordovician. Unlike linguliforms, they constitute a minor component of the Palaeozoic Evolutionary Fauna (Popov *et al.* 1999, in press). In spite of a distinctive morphological diversification, the generic diversity of craniides remained low during all of the Ordovician. By the Late Ordovician their geographical distribution was mainly confined to Laurentia, Baltica, Avalonia and the high latitude peri-Gondwana terranes (e.g. Bohemia) situated on the margins of the Iapetus Ocean (Popov *et al.* 1999, in press; Mergl 2012); however, there are no records of their occurrences in the Late Ordovician of Siberia, North and South China, and the Australian sector of Gondwana.

Rong *et al.* (2006) provided a comprehensive analysis of how the terminal Ordovician extinction affected brachiopod taxonomic diversity, and among the craniide victims *Orthisocrania* only was listed, whereas *Acanthocrania*, *Philhedra*, and *Petrocrania* (= *Philhedrella*) were listed by Bassett (2000) as survivors. However, Bassett (2000) considered *Philhedra* to be a monospecific genus. It is clear that most finely ribbed Palaeozoic craniide species that were previously erroneously identified as *Philhedra* - which is characterised by a smooth shell and hollow spines - are probably assignable to *Deliella* Halamski, 2004. *Acanthocrania* has a long range from the Late Ordovician to the Permian; however, there were no previous records from the Silurian; the occurrences of *Acanthocrania* and *Philhedra* in the Wenlock of Gotland, recorded below, are the first Silurian records of both genera. *Propatella* Grubbs, 1939, was also considered by Rowell (1965) as a junior synonym of *Philhedra*, but it clearly represents a separate taxon, characterised by tubular ribs and sutured marginal spines, which represent morphological novelties among the Silurian craniides. In this paper, we also consider *Philhedra*? sp. from the late Katian (Kráľův

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3 Dvůr Formation) of the Prague basin (Mergl 2012) as being congeneric with
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5 *Propatella palmaria* sp. nov. from Gotland (see below), with *Propatella* being
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7 regarded as a survivor of the end Ordovician extinction.
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10 During most of the pre-Hirnantian, craniides were mainly confined to epeiric
11 seas in warm temperate environments (e.g. Baltica) and low latitudes (e.g. Laurentia),
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13 whereas their diversity in peri-Gondwanan settings declined considerably (Popov *et*
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15 *al.* 1999; Mergl 2012). Craniides represent a minor component of the Palaeozoic
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17 Evolutionary Fauna (Popov *et al.* in press), and were adapted to an encrusting mode
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19 of life in shallow to open marine environments (BA2 – BA4). Their life strategies and
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21 ecologies were ecologies seemed stable throughout the Silurian. However, their exact
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23 bathymetric range cannot be evaluated with confidence due to lack of data.
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27 The core of the Silurian craniide fauna from Gotland described in this paper,
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29 and which includes *Acanthocrania*, *Petrocrania*, *Philhedra* and *Propatella*, represents
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31 extinction survivors. Almost all morphological innovations acquired by the craniides
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33 during the Ordovician radiation - including sutured and hollow spines, radial
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35 ornament of various kind, and an encrusting mode of life - were preserved into the
36
37 Silurian, and only *Orthisocrania* did not survive the extinction event. Almost all these
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39 genera, with the possible exception of *Petrocrania*, represent Lazarus taxa that
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41 disappeared during the Hirnantian-Llandovery, and re-emerged in the Wenlock in the
42
43 advanced stage of post-extinction recovery.
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47 The Wenlock craniide fauna also includes a number of newcomers. Among
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49 them, *Thulecrania*, was with its characteristic lamellose ribs, a short lived taxon;
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51 *Lepidocrania* survived until the Permian (Cooper and Grant 1974), whereas the extant
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53 *Valdiviathyris* possibly remained a Lazarus taxon through the rest of the Phanerozoic
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55 only to re-emerge in the Eocene (Robinson and Lee 2007).
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The high survival rate in the craniides, in combination with the prolific Lazarus effect on the stratigraphical distribution of craniide genera across the Ordovician – Silurian transition, may partly be explained by the fact that this group of brachiopods represented insignificant components of the faunas that often have been neglected in taxonomical studies. The studied Silurian craniides from Gotland are micromorphic adults, not exceeding 3 mm width.

SYSTEMATIC PALAEONTOLOGY

Abbreviations used in the text. L, W – maximum sagittal length and width of valves; Al – distance between the apex and posterior margin. Morphological terminology and taxonomic classification follow Bassett (2000). Figured specimens are housed in Naturhistoriska Riksmuseet, Stockholm (RM Br).

Order CRANIIDA Waagen, 1885

Superfamily CRANIOIDEA Menke, 1828

Family CRANIIDAE Menke, 1828

Genus ACANTHOCRANIA Williams, 1943

Type species. By original designation *Crania spiculata* Rowley, 1908; Carboniferous, Mississippian, Louisiana Limestone, Buffalo Creek, Louisiana, USA.

Acanthocrania? sp.

Figure 2F–I

Material. RM Br141143, dorsal valve (L=2.15, W=1.6), Wenlock, Upper Visby and Höglint formations, Snäckgårdsbaden 1.

Description. Dorsal valve high conical, asymmetrical, with steep lateral slopes; posterior margin narrow, almost straight, with umbo situated at about one-quarter valve lengths from the posterior margin (Fig. 2F). Ornamentation of fine, densely spaced pustules, arranged along fine concentric filae. Metamorphic shell about 265 µm across (Fig. 2H), with pustulose micro-ornament appearing immediately outside halo (Fig. 2G).

Dorsal interior with paired muscle scars of large, slightly elongate, suboval anterior adductors situated on callus of secondary shell, directly anterior and lateral of umbo. Pair of small and weakly defined posterior adductor muscle scars situated on inner side of posterior valve slope. Inner valve surface outside muscle scars finely and densely pitted (Fig. 2F). Ventral valve unknown.

Remarks. *Acanthocrania* is relatively common in the Katian (Late Ordovician) of the peri-Iapetus region (Cooper 1956; Wright 1972; Harper 1984; Candela 2003). The unnamed species from Gotland is comparable to the Ordovician *Acanthocrania papillifera* (Roemer, 1861) in the finely pustulose ornamentation, but *Acanthocrania?* sp. lacks hollow spines.

Genus LEPIDOCRANIA Cooper and Grant, 1974

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Type species. By original designation *Lepidocrania tardispinosa* Cooper and Grant, 1974; Lower Permian, Road Canyon Formation, Wolfcampian, western Texas.

Remarks. Previously *Lepidocrania* was known only from a number of species described by Cooper and Grant (1974) from the Permian of Texas. Cooper and Grant (1974) described the silicified Permian forms as having densely packed, very fine spines. The Silurian specimens from Gotland lack spines, but they are closely similar to the Permian species of *Lepidocrania* in all other aspects of shell morphology. Pending restudy of the type material, we suggest that the so-called ‘spines’ may represent an artefact produced by the silicification of the primary layer, with a characteristic craniide surface pattern, with laths (see Popov *et al.* 2012). The ventral valves of the Permian species of *Lepidocrania* are not known, but the Silurian species is provided with a mineralised ventral valve with a large cicatrix attachment.

Lepidocrania multilamellosa sp. nov.

Figures 3, 4A–B, D

2012 *Lepidocrania* sp.; Popov *et al.*, fig. 2F, G.
2012 Craniidae gen. et sp. indet. 1; Popov *et al.*, fig. 2A, B.

Derivation of name. Referring to the characteristic dense lamellose ornamentation.

Holotype. RM Br24288a, dorsal valve (L=2.45, W=1.75, Al=0.5; Fig. 3D), Wenlock, Slite Group, Solklint 1.

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5 *Paratypes*. Dorsal valves: RM Br141158 (L=2.5, W=2.3, Al=0.40; Fig. 3A-B), RM
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7 Br141162 (Fig. 3H, J), RM Br141163 (L=1.85, W=2.0; Fig. 3I); RM Br141159
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9 (L=1.9, W=2.0; Fig. 3C), Wenlock, Slite Group, Solklint 1; RM Br141164-85,
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11 Wenlock, Upper Visby and Högklint formations, Häftingsklint; RM Br141160 (Fig.
12
13 3E-F); RM Br141186-201, Wenlock, Slite Group, Solklint 1; ventral valves: RM
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15 Br141161 (Fig. 3G), Wenlock, Slite Group, Follingbo 3; RM Br141202 (L=3.2,
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17 W=2.9; Fig. 4A, B), Wenlock, Upper Visby and Högklint formations,
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19 Snäckgårdsbaden 1; RM Br24286g (L=1.7, W=1.7; Figs 3K-L, 4D), Wenlock, Upper
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21 Visby and Högklint formations, Häftingsklint; total of two ventral and 51 dorsal
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23 valves.
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30 *Diagnosis*. *Lepidocrania* with strongly asymmetrical convexo-planar shell; ventral
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32 valve with large cicatrix attachment, lamellose peripherally; dorsal valve with
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34 submarginal umbo, ornamented by closely overlapping, crowded irregular concentric
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36 lamellae. Dorsal interior with well-defined limbus.
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40 *Description*. Shell convexo-planar, strongly variable in profile and outline, usually
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42 strongly asymmetrical (Figs 3A–E, I, J; 4A, B, D). Ventral valve flat, with large,
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44 circular cicatrix attachment bearing characteristic lath pattern; area outside of cicatrix
45
46 ornamented with regular concentric rugellae and crowded concentric lamellae along
47
48 margins (Fig. 4A, B, D). Dorsal valve gently convex with submarginal apex. Anterior
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50 slope long and gentle. Dorsal metamorphic shell about 175–180 µm across with
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52 inflated central area, somewhat flattened along periphery, and delineated by distinct
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54 halo (Fig. 3F). Dorsal postmetamorphic shell ornamented with closely overlapping,
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crowded irregular concentric lamellae. Ventral interior lacking distinctive characters (Fig. 3K, L). Dorsal interior with flattened limbus and large, elongate suboval, often asymmetrical anterior adductor scars situated on thick callus of secondary shell. Posterior adductor scars small, weakly impressed. Inner shell surface outside the muscle scars coarsely pitted (Fig. 3I).

Remarks. *Lepidocrania multilamellosa* sp. nov. differs from the numerous Permian species referred to the genus by Cooper and Grant (1974) in having a strongly asymmetrical, gently convex dorsal valve with well defined, flattened limbus along the inner margins. The ventral valve of the Permian taxa remains unknown.

Genus PETROCRANIA Raymond, 1911

Type species. By original designation *Craniella meduanensis* Oehlert, 1888; from the upper Lower Devonian of Ferques, France.

Petrocrania gracilis (Huene, 1899)

Figures 4C, E–I, 5

1899 *Philhedra gracilis* Huene, p. 393, pl. 4 (12), fig. 25.

Holotype. By monotypy; dorsal valve illustrated by Huene (1899, pl. 4 (12), fig. 25) from the Ludlow, Eke Formation (most likely Lau Backar); deposited in the Museum of Breslau (now Wrocław, Poland) and lost by the end of World War 2.

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3 *Material.* Dorsal valves: RM Br141203 (L = 3.5, W = 3.3, Al = 0.8; Fig. 4C, E); RM
4 RM Br141204 (Fig. 4F–G); RM Br141205 (Fig. 4H–I), RM Br141206–223, Ludlow,
5 Hemse Formation, Tänglings 1; RM Br87136, Ludlow, Eke Formation, Olsvenne 3;
6 RM Br141231–233 (Fig. 5), Ludlow, Eke Formation, Sunnkyrke 1; total of 70 dorsal
7 valves.
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16 *Description.* Dorsal valve forming low cone with slightly exocentric apex and
17 variably irregular, subquadrate outline. Ornamentation of closely spaced, concentric
18 undulating filae, becoming densely lamellose peripherally (Figs 4E, F, H, 5A–C).
19 Dorsal interior with distinct limbus bounded by angular rim. Anterior adductor muscle
20 scars large, elongate and suboval, situated on callus of secondary shell anterolaterally
21 to the apex. Posterior adductor scars relatively small, subcircular, situated on callus of
22 secondary shell posterolaterally to the apex. Inner shell surface of valve outside of
23 muscle scars finely pitted (Figs 4C, I; 5D–F). Ventral valve unknown.
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36 *Remarks.* *Petrocrania gracilis* (Huene) was previously known from a single dorsal
37 valve from the Ludlow Eke Formation, described and illustrated by Huene (1899).
38 The description by Huene (1899) is brief, but the illustrated dorsal interior characters
39 as well as the size and outline of the shell, closely match the new material described
40 here and it is from the same unit. The specimens from the Eke Formation at
41 Sunnkyrke 1 (Fig. 5) come from the same horizon as the type specimen and they are
42 conspecific with better preserved specimens from the Hemse Formation of Tänglings
43 1 illustrated here. Craniides from both localities form a monotaxic association and
44 belong to the same craniide, which leave little doubt that they are conspecific with the
45 shell described and illustrated by Huene (1899).
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The Wenlock *Petrocrania siluriana* (Davidson, 1848) appears to be somewhat similar in outline and ornamentation; however, this species, like most Silurian forms assigned to *Petrocrania*, is poorly known and requires re-study.

Genus PHILHEDRA Koken, 1889

Type species. By original designation *Philhedra baltica* Koken, 1889, from Ordovician, Sandbian, Kukruse Regional Stage of North Estonia.

Remarks. The diagnostic features of *Philhedra* Koken have remained poorly understood (e.g. Wright, 1972); Huene (1899) included several species that, although lacking spines, have a distinct costellate radial ornament. Bassett (2000) convincingly demonstrated that *Philhedra baltica* Koken, 1889, which is the type species of the genus, lacks a radial ornament but possesses long hollow spines covering the entire surface of the shell. Thus *Philhedra longispina* sp. nov. is the only other species that can be confidently assigned to the genus whereas all other existing records of *Philhedra* in the Silurian and younger deposits are doubtful and in need of revision.

Philhedra longispina sp. nov.

Figure 6

Derivation of name. Referring to the characteristic ornamentation with long, hollow spines.

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3 *Holotype*. RM Br141224 (L=1.7, W=1.7, Al=0.3; Fig. 6A-B), dorsal valve, Wenlock,
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5 Slite Group, Solklint 1.
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10 *Paratypes*. Dorsal valves: RM Br141225 (Fig. 6C, F); RM Br141226 (L=2.2,
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12 W=2.05, Al=0.35; Fig. 6D, G), RM Br141227 (Fig. 6E), RM Br141228 (Fig. 6H-K),
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14 RM Br141229 (L=1.8, W=1.8, Al=0.4; Fig. 6L), all from Solklint 1; RM Br141230,
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16 Follingbo 3; all from Wenlock, Slite Group.
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21 *Diagnosis*. Small *Philhedra* with low subconical dorsal valve, submarginal apex and
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23 hollow spines merging into radial rows peripherally.
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27 *Description*. Dorsal valve low, subconical, almost subquadrate in outline with narrow,
28
29 straight posterior margin; apex located at slightly less than one-fifth of maximum
30
31 valve length from posterior margin. Anterior slope evenly convex; posterior slope
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33 steep and almost straight in sagittal profile. Ornamentation with radially arranged
34
35 hollow spines increasing in diameter and length and merging into radial rows
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37 peripherally (Fig. 6A–C, H–L). Metamorphic shell about 290 µm wide with radial
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39 laths and minor spines originating immediately outside the halo (Fig. 6I, K). Dorsal
40
41 valve interior with large, almost circular anterior adductor scars situated on callus of
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43 secondary shell anterolaterally from apex, and extending to mid-length. Posterior
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45 adductor muscle scars small, situated laterally to umbo (Fig. 6D, E, G).
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52 *Remarks*. *Philhedra longispina* is the first and to date the only known Silurian species
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54 of *Philhedra*. *Philhedra longispina* differs from the type species *Philhedra baltica* in
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56 having a less strongly convex dorsal lateral profile and a more posteriorly placed
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apex. The new species from Gotland also differs from *Philhedra baltica* in having merging spines that form distinctive radial rows in the peripheral part of the shell. Robinson and Lee (2011) described similar types of hollow spines from Holocene *Novocrania*.

Genus PROPATELLA Grubbs, 1939

Type species. By original designation *Propatella magnacostata* Grubbs, 1939, Silurian, Wenlock, Niagara Group, Illinois, USA.

Diagnosis. Craniide with conical shell and central to slightly eccentric umbo; radial ornament of rounded ribs increasing in number by intercalation and terminated by sutured hollow spines. Dorsal interior with large anterior adductor scars on callus of secondary shell, situated laterally to umbonal area. Interior valve surface outside muscle scars finely and densely pitted.

Remarks. *Propatella* can be distinguished from most other known craniides in having hollow sutured marginal spines. However, Robinson and Lee (2011) recently also described similar spines on *Novocrania* and *Danocrania*. This type of spine has previously also been reported from rhynchonelliform brachiopods (e.g. Alvarez and Brunton 2001). *Propatella* was originally described by Grubbs (1939) as a gastropod mollusc. Subsequently, Rowell (1965) recognised the brachiopod nature of the taxon and considered it as junior objective synonym of *Philhedra* Koken, 1889; however, *Propatella* differs from *Philhedra* Koken in having sutured rather than tubular spines that are developed along the shell margin only, whilst in the latter taxon they cover

the entire shell surface. Moreover, Bassett (2000) demonstrated that the type species – *Philhedra baltica* Koken, 1889 – lacks radial ornament. Therefore pending revision, species assigned to *Philhedra* with radial ornament but lacking hollow tubular spines may be assigned to *Deliella* Halamski, 2004.

Mergl (2012) recently described *Philhedra?* sp. from the Katian Králův Dvůr Formation ('Perník bed') at Jezerka, in the Prague basin. This is probably the earliest and yet only known Ordovician representative of *Propatella*. Mergl (2012) illustrated tubercles that are aligned along the rounded ribs on internal moulds; most likely they do not represent spine bases, but represent casts of large punctae that are characteristic also of *Propatella*. *Philhedra?* sp. also has radial ornamentation and prominent marginal spines like *Propatella* but due to preservation it is not possible to assess whether it also possesses sutured spines.

Propatella palmaria sp. nov.

Figure 7

2012 Craniidae gen. et sp. indet. 2; Popov *et al.*, fig. 2C–E.

Derivation of name. Latin, *palmarium*, meaning excellent, outstanding.

Holotype. RM Br24287a, dorsal valve (L = 2.0, W = 1.9; Fig. 7A–C, E–F), Wenlock, Slite Group, Solklint 1.

Paratypes. Dorsal valves: RM Br24287b (Fig. 7D); RM Br141151 (L = 1.5, W = 1.5; Fig. 7G–H), RM Br141152 (Fig. 7I), RM Br141153 (L = 1.35, W = 2.5; Fig. 7J–K),

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RM Br141154 (L = 1.45, W = 1.6; Fig. 7L), RM Br141134–151, all from Solklint 1; RM Br141155–157, Follingbo 3; all specimens from Wenlock, Slite Group; total 26 dorsal valves.

Diagnosis. As for genus, but with 15–22 primary ribs and up to 40 rounded costellae along shell margins of mature individuals.

Description. Shell, subcircular to suboval in outline. Dorsal valve conical with centrally placed or slightly eccentric apex. Posterior margin broadly and evenly rounded. Radial ornament costellate, with up to 40 rounded ribs, increasing by intercalation and separated by interspaces at about equal width as ribs and terminated by sutured hollow spines. Fifteen to twenty-two ribs originated outside smooth umbonal area, which measures about 735–740 µm across, delineated by a distinct halo (Fig. 7B, D, G, H, J–L). Shell inside halo exhibits characteristic lath pattern and encloses metamorphic shell, about 175–180 µm across, bearing mosaic of irregular tablets (Popov *et al.* 2012, fig. 2D, E). Dorsal valve interior with pair of large subcircular anterior adductor scars situated on both lateral sides of apex. Interior of shell outside muscle scars covered by deep pits arranged in radial rows along ribs (Fig. 7A, I). Ventral valve unknown.

Remarks. Grubbs (1939) provided a detailed description of *Propatella*. In particular he mentioned hollow marginal spines, finely pitted inner shell surface and the presence of a pair of large muscle scars laterally from the umbo. Therefore there is no doubt that shells from Gotland are congeneric with the type species of *Propatella*.

Propatella palmaria differs from *Propatella magnacostata* mainly in having a finer radial ornamentation, with 15–22 ribs originating at the umbonal area instead of 12 ribs as in the type species. The most interesting aspect of the morphology of *Propatella palmaria* is the presence of the sutured hollow spines, which are closely comparable with the sutured spines of rhynchonelliform brachiopods described by for example Alvarez and Brunton (2001), and closely similar types of hollow spines have also recently been described from Holocene *Novocrania* and Palaeocene–Eocene *Danocrania* by Robinson and Lee (2011). The early ontogenetic stages of shell growth in *Propatella palmaria* have been recently outlined by Popov *et al.* (2012). The shell shape and outline, as well as position of the umbo in *Propatella palmaria* depend strongly on the nature of the substratum. Individuals that apparently were cemented to an even hard ground surface tend to be almost symmetrical, subcircular in outline and possessed with an almost central to slightly eccentric apex (Fig. 7B, H, L). In contrast individuals that were cemented onto cylindrical objects (e.g. echinoderm stems) show a considerable distortion of the cone (Fig. 7J–K).

Genus THULECRANIA gen. nov.

Derivation of name. Greek, Thule, a region in the far north.

Type and only species. *Thulecrania septicostata* sp. nov. from the Silurian, Wenlock, Upper Visby and Höglint formations of Gotland.

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Diagnosis. Low subconical shell with submarginal apex, ornamented with high, blade-like ribs separated by wide interspaces and terminated with solid, prone spines along growth lamellae.

Remarks. *Thulecrania* differs from *Deliella* Halamski, 2004 and *Propatella* Grubbs, 1939 in having high, blade-like ribs separated by wide interspaces and terminated with solid prone pines along the growth lamellae. *Thulecrania* also differs from these genera in having a more submarginal apex.

Thulecrania septicostata sp. nov.

Figure 2A–E

Derivation of name. Referring to the thin lamellose ribs.

Holotype. RM Br141144, dorsal valve ($L = 2.3$, $W = 3.2$, $Al = 0.3$; Fig. 2A–E), Wenlock, Upper Visby and Höglint formations, Snäckgårdsbaden 1.

Paratypes. RM Br141145–50, six dorsal valves, locality and unit are the same as for the holotype; seven dorsal valves in total.

Diagnosis. As for the genus.

Description. Dorsal valve moderately convex to low subconical, and variable outline, transverse to suboval. Sagittal profile of valve evenly convex anterior to apex, short and steep posteriorly (Fig. 2A–E). Metamorphic shell about 70 μm wide, button-

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3 shaped, delineated by distinct halo and surrounded by smooth area of densely
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5 punctuate shell about 300 μm wide. Radial ornamentation costellate with 11–14
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7 primary ribs originating in umbonal area, and with up to 21 ribs along shell margin of
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9 large specimens. Ribs high, blade-like, increasing in number by intercalation and
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11 separated by interspaces significantly wider than ribs. Concentric ornament of faint
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13 regular filae and growth lamellae bearing prone, solid spines at intersection with ribs
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15 (Fig. 2A–E). Dorsal interior with large, elongate, suboval anterior adductor scars
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17 situated on callus of secondary shell anterior to apex and extending anteriorly slightly
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19 beyond mid length. Inner shell surface outside the muscle scars densely punctate (Fig.
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21 2D). Ventral valve unknown.
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27 Genus VALDIVIATHYRIS Helmcke, 1940
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32 *Type species.* By original designation *Valdiviathyris quenstedti* Helmcke, 1940,
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34 Recent, Southern Indian Ocean.
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38 *Remarks.* Smooth Palaeozoic craniides are usually assigned to *Petrocrania* Raymond,
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40 1911, which effectively has become a ‘waste basket’ taxon; however, the craniide
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42 shells described below are almost undistinguishable from the Recent craniide
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44 *Valdiviathyris* (Bassett 2000; Robinson and Lee 2007) in having smooth dorsal valve
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46 with posteriorly placed apex; moreover the arrangement of the dorsal anterior and
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48 posterior adductors, as well as the presence of a pair ventrally directed interior
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50 processes means that in spite of the considerable stratigraphic separation of the
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52 Silurian and Recent taxa, they cannot be distinguished. The ventral valve of the extant
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54 type species differs somewhat from the Silurian species, and the generic identification
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of the Silurian species to the recent genus is tentative. Paired dorsal processes are rather common in post-Palaeozoic craniides (Bassett 2000), but they have not been documented in any known Palaeozoic genera yet. The only exception is a single dorsal valve briefly described and illustrated by Cooper (1956, p. 290, pl. 25C, figs 8–10) as *Petrocrania?* sp. This specimen possesses a single, ventrally directed process in the central part of the dorsal valve.

Valdiviathyris? bicornis sp. nov.

Figure 8

Derivation of name. Latin, *cornu* = horn. Referring to the two-pronged processes in this species,

Holotype. RM Br141232, dorsal valve (L = 2.7; W = 2.9; Al = 0.5; Fig. 8A–D), Wenlock, Slite Group, Solklint 1.

Paratypes. Dorsal valves: Br141234 (L = 1.2; W = 1.5; Al = 0.2; Fig. 8G); RM Br141235 (Fig. 8H–J); RM Br141236 (Fig. 8K–L); Ventral valve: RM Br141233 (Fig. 8E–F); locality and unit are the same as for the holotype; total of 3 dorsal and 1 ventral valves.

Diagnosis. Like *Valdiviathyris*, with dorsal anterior adductor muscle scars extending almost to mid valve, and paired processes situated anterior to mid valve.

Description. Shell convexoplanar, transverse, suboval, with narrow, almost straight posterior margin, cementing by entire ventral valve surface (Fig. 8). Ventral valve of irregular shape with poorly mineralised umbonal area that may have been occupied by organic attachment structure (Fig. 8E, F). Dorsal valve subconical, with apex situated at about one-fifth of valve length from the posterior margin. Sagittal profile with maximum height at apex; anterior slope almost straight, gently inclined towards shell margin; posterior slope steep. Metamorphic shell button shaped, about 210 μm , delineated by distinct halo and covered by mosaic of radiating elongated tablets (Fig. 8I, L). Postmetamorphic shell smooth, densely punctate, with characteristic lath pattern of primary shell layer (Fig. 8J). Concentric ornamentation of very fine filae.

Ventral interior with central perforation (Fig. 8F). Dorsal interior with elongate suboval anterior adductor scars situated on callus of secondary shell, extending almost to mid-valve; smaller, subcircular muscle fields situated close to posterolateral margins of valve and occupied by posterior adductor and oblique internal muscle scars; pair of oblique ventrally directed processes situated slightly anterior to mid valve. Valve interior outside of muscle scars finely punctate.

Remarks. *Valdiviathyris? bicornis* differs from *Valdiviathyris quenstedti* in the more closely placed, subparallel dorsal anterior adductor muscle scars extending to the centre of the valve and in the more anteriorly placed paired dorsal processes. The ventral valve of *Valdiviathyris? bicornis* differs from that of *Valdiviathyris quenstedti* (see Robinson and Lee 2007) in the lack of thickened muscle field and median ridge.

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FIGURE CAPTIONS

Fig. 1. Geographical and stratigraphical position of Silurian localities on Gotland.

Fig. 2. A–E, *Thulecrania septicostata* gen. et sp. nov., Wenlock, Upper Visby and Högklint formations, Snäckgårdsbaden 1; RM Br141144, holotype, dorsal valve exterior, enlarged umbonal area, oblique lateral view, dorsal interior, and enlarged view of solid marginal spine. F–I, *Acanthocrania?* sp., Wenlock, Upper Visby and Högklint formations, Snäckgårdsbaden 1; RM Br141143, dorsal valve interior, exterior, enlargement of densely pustulose ornament of adult shell, and umbonal area showing metamorphic shell. A, C–D, E–G, scale bars represent 200 µm; B, H, scale bars represent 50 µm.

Fig. 3. A–L, *Lepidocrania multilamellosa* sp. nov. A–B, RM Br141158, dorsal valve exterior, and oblique lateral view, Wenlock, Upper Visby and Högklint formations, Häftingsklint. C, RM Br141159, dorsal valve exterior, Wenlock, Slite Group, Solklint 1. D, RM Br24288a, holotype, dorsal valve, Wenlock, Slite Group, Solklint 1. E–F, RM Br141160, dorsal valve oblique lateral view and umbonal area showing metamorphic shell, Wenlock, Upper Visby and Högklint formations, Häftingsklint. G, RM Br141161, ventral valve exterior, Wenlock, Slite Group, Follingbo 3; H, J, RM Br141162, dorsal valve exterior (J) and detail of dorsal umbonal area (H), Wenlock, Slite Group, Solklint 1. I, RM Br141163, dorsal valve interior, Wenlock, Slite Group, Solklint 1. K–L, RM Br24286g, ventral valve interior, and oblique lateral view of ventral interior, Wenlock, Upper Visby and Högklint formations, Häftingsklint. A–G, I–L, scale bars represent 200 µm. H, scale bar represents 100 µm.

Fig. 4. A–B, D, *Lepidocrania multilamellosa* sp. nov. A–B, RM Br141202, ventral valve exterior, and oblique lateral view, Wenlock, Upper Visby and Högklint formations, Snäckgårdsbaden 1. D, RM Br24286g, ventral valve exterior, Wenlock,

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Upper Visby and Höglint formations, Häftingsklint. C, E–I, *Petrocrania gracilis* (Huene, 1899), Ludlow, Hemse Formation, Tänglings l. C, E, RM Br141203, dorsal valve interior, and exterior. F–G, RM Br141204, dorsal valve exterior, interior. H–I, RM Br141205, dorsal valve exterior, and interior. Scale bars represent 200 µm.

Fig. 5. *Petrocrania gracilis* (Huene, 1899), Ludlow, Eke Formation, Sunnkyrke l. A–C, RM Br141231, dorsal valve exterior, oblique lateral, and oblique posterior views. D, E, RM Br141232, dorsal valve interior, and oblique lateral view. F, RM Br141233, oblique lateral view of dorsal valve interior. Scale bars represent 200 µm.

Fig. 6. *Philhedra longispina* sp. nov., Wenlock, Slite Group, Solklint l. A–B, RM Br141224, holotype, dorsal valve exterior, and oblique lateral view. C, F, RM Br141225, dorsal valve in oblique lateral and dorsal views. D, G, RM Br141226, dorsal valve interior, and oblique lateral view. E, RM Br141227, interior of incomplete dorsal valve. H–K, RM Br141228, radial rows of hollow spines at the distal part of the dorsal valve, metamorphic shell, oblique side view, and oblique anterior view of the umbonal area. L, RM Br141229, dorsal valve exterior. Scale bars represent 200 µm.

Fig. 7. *Propatella palmaria* sp. nov., Wenlock, Slite Group, Solklint l. A–C, E–F, RM Br24287a, holotype, dorsal valve interior, exterior, oblique lateral view of interior, row of marginal spines, and enlarged view of hollow, sutured marginal spines. D, RM Br24287b, dorsal valve, oblique lateral view of exterior. G–H, RM Br141151, oblique lateral and exterior views of a dorsal valve. I, RM Br141152, dorsal valve interior. J–K, RM Br141153, oblique lateral and exterior views of a

dorsal valve. L, RM Br141154, dorsal valve exterior. A–D, F–H, scale bars represent 200 μm . E, I, scale bars represent 100 μm and 50 μm respectively.

Fig. 8. *Valdiviathyris? bicornis* sp. nov., Wenlock, Slite Group, Solklint 1. A–D, RM Br141232, holotype, dorsal valve, exterior, side view of exterior, interior, side view of interior. E–F, RM Br141233, ventral valve exterior, interior. G, RM Br141234, dorsal valve exterior. H–J, RM Br141235, dorsal valve oblique lateral view, umbonal area showing metamorphic shell, lath pattern of external surface and endopunctuation of postmetamorphic shell. K–L, RM Br141236, dorsal valve exterior, umbonal area showing metamorphic shell. A–H, K, scale bars represent 200 μm . I, L, scale bars represent 100 μm . J, scale bar represents 50 μm .

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160x152mm (300 x 300 DPI)

219x288mm (300 x 300 DPI)

168x168mm (300 x 300 DPI)

101x61mm (300 x 300 DPI)

197x233mm (300 x 300 DPI)

214x272mm (300 x 300 DPI)

207x256mm (300 x 300 DPI)