Agraulos longicephalus and *Proampyx*? *depressus* (Trilobita) from the Middle Cambrian of Bornholm, Denmark

THOMAS WEIDNER & ARNE THORSHØJ NIELSEN

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The trilobite genus *Agraulos* Hawle & Corda 1847 has within Scandinavia been recorded only from Bornholm, Denmark, where its representatives occur in the Middle Cambrian *Paradoxides paradoxissimus* Superzone of the Alum Shale Formation. Only cranidia have been found so far, representing *Agraulos longicephalus* (Hicks 1872) and the rare "*Agraulos*" *depressus* Grönwall 1902.

The two species from Bornholm are redescribed and discussed based on museum collections in combination with newly collected material from Borggård, Øleå. *Agraulos longicephalus* occurs commonly in the lower and upper part of the *Acidusus atavus* Zone as well as in the *Ptychagnostus punctuosus* Zone. It closely resembles the coeval *Agraulos ceticephalus* (Barrande 1846) known from Bohemia and eastern Newfoundland. A lectotype for "*Agraulos*" *depressus* is designated and re-illustrated; this taxon is hesitantly assigned to *Proampyx*? It is known only from the *Ptychagnostus punctuosus* Zone and may represent an early, atypical *Proampyx* or maybe a precursor that should be separated in a new genus. Emended diagnoses of *Agraulos* Hawle & Corda 1847 and *Proampyx* Frech 1897 are presented.

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The trilobite family Agraulidae is in Scandinavia represented by the genera *Proampyx* Frech 1897 and *Agraulos* Hawle & Corda 1847. *Proampyx* is common and widespread and includes the five species *P. difformis* (Angelin 1851), *P. aculeatus* (Angelin 1851), *P. acuminatus* (Angelin 1851), *P. anceps* (Westergård 1953), and *P. cornutus* Buchholz 1997, all occurring in the Middle Cambrian *Paradoxides forchhammeri* Superzone of Norway, Denmark and Sweden (Brøgger 1878; Grönwall 1902; Westergård 1953) (Fig. 1). Various species have also been reported from glacial erratic boulders of northern Germany (Rudolph 1994; Buchholz 1997). Representatives of *Agraulos* Hawle & Corda 1847 are, on the other hand, rare in Scandinavia and have been recorded solely from Bornholm, Denmark, and from glacial erratic boulders of northern Germany (Grönwall 1902; Rudolph 1994; Buchholz 1997; Weidner & Nielsen 2014). The latter contain a fauna showing that they likely derive from the Bornholm area.

So far, only cranidia of *Agraulos* have been found. Grönwall (1902) reported three cranidia of *A. ceticephalus* (Barrande 1846) and two cranidia of *A. depressus* Grönwall 1902 (here assigned to *Proampyx*?) from the *Ptychagnostus punctuosus* Zone at Borggård, Øleå (Fig. 2). Rudolph (1994) figured one cranidium of *A.* cf. *ceticephalus* (Barrande 1846) from the *P. punctuosus* Zone. There are two further cranidia assigned to *A. ceticephalus* (Barrande 1846) from the same zone in the collection of Buchholz (1997; personal communication 2010). All mentioned material of *A. ceticephalus* is here identified with *A. longicephalus* (Hicks 1872). This species strongly resembles *A. ceticephalus* which occurs in strata of similar age in the Czech Republic (Šnajdr 1958) and eastern Newfoundland, Avalonian Canada (Fletcher *et al*. 2005), and the only conspicuous difference is the outline of the occipital ring (see below). About 25 additional cranidia of *A. longicephalus* were collected during the years 2004–2007 from the older *Acidusus atavus* Zone at Borggård (for details, see

Weidner & Nielsen 2014) and one additional young cranidium of *P.*? *depressus* was collected from the basal layer of the *P. punctuosus* Zone.

The two species presently known from Bornholm, *Agraulos longicephalus* (Hicks 1872) and *Proampyx*? *depressus* (Grönwall 1902), are treated in this paper.

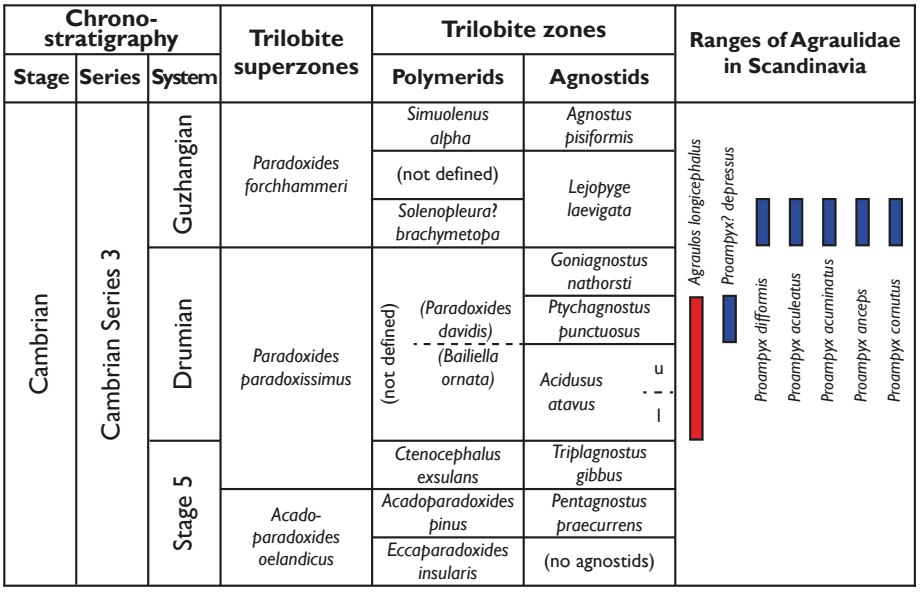


Fig. 1. Biozonation of the Middle Cambrian in Scandinavia. The updated zonation includes data from Axheimer & Ahlberg (2003), Weidner & Nielsen (2014) and Nielsen *et al.* (2014). On the right hand side are shown ranges of Scandinavian taxa. Abbreviations: l: lower part, u: upper part; these units are informal.

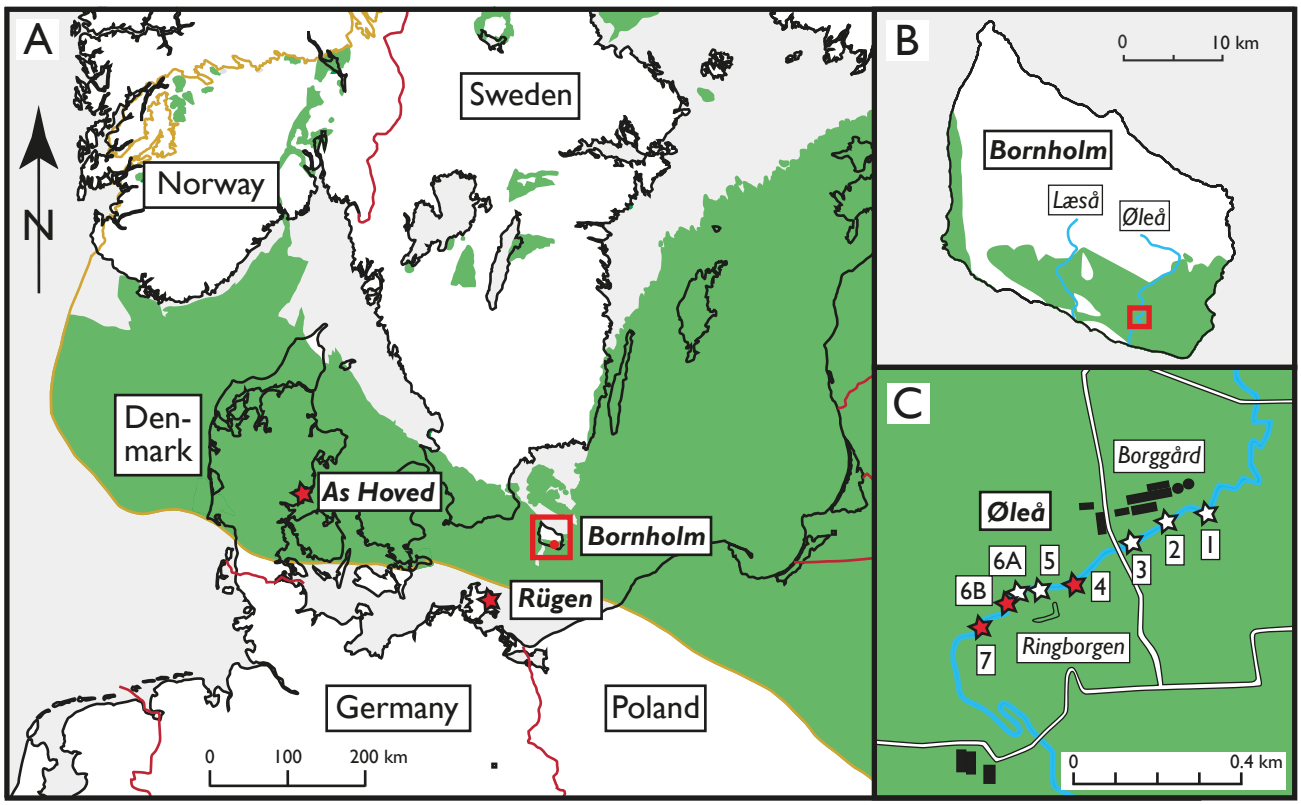


Fig. 2. **A**, map of Scandinavia showing location of Bornholm and the As Hoved locality in Jutland. **B**, map of Bornholm; insert shows location of Borggård. **C**, detailed map of the Øleå rivulet near Borggård showing localities; those marked in red are referred to in the text. (Map modified from Hansen 1945). Areas where Lower Palaeozoic strata are preserved are shown in green; the Caledonian Front is shown in brown.

Taxonomy

The available specimens of *A. longicephalus* and *P.*? *depressus* derive from Borggård, Øleå, Bornholm (for description of exposures, see Weidner & Nielsen 2014). Comparative material of *Proampyx difformis* is from the Andrarum Limestone Bed and the Exporrecta Conglomerate Bed, including material found in glacial erratic boulders at As Hoved, Denmark. Illustrated specimens are deposited at the Natural History Museum of Denmark, University of Copenhagen (MGUH), except for SB-MK 143 from the private collection of A. Buchholz, Stralsund, Germany. A cast of the latter is kept at the Natural History Museum. Measured features are shown in Fig. 3.

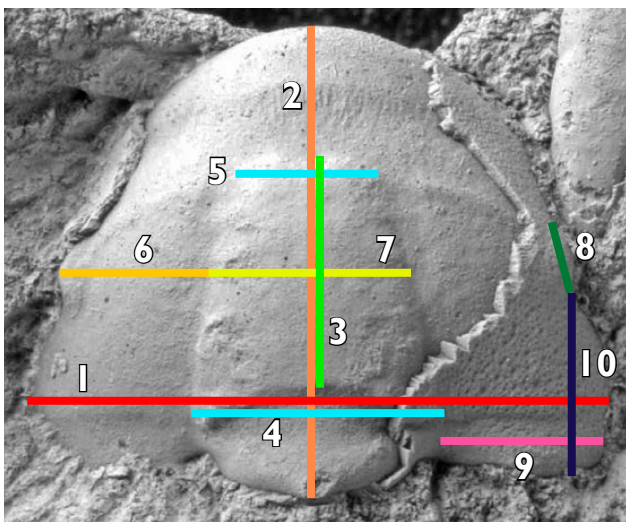


Fig. 3. Measurements referred to in the text (illustrated cranidium, MGUH 30.144, represents *Agraulos longicephalus*). 1: Cranidial width. 2: Cranidial length. 3: Glabellar length. This is the value of the glabella *s. str.* (without occipital ring) on the sagittal line only, due to the forward curvature of the occipital furrow. 4: Posterior glabellar width. 5: Anterior glabellar width. 6: Width of fixigena across palpebral lobe. 7: Width of glabella level width palpebral lobe. 8: Length of palpebral lobe. 9: Width of posterior border. 10: Length of posterior fixigena.

Family Agraulidae Howell 1937

The authorship of this family is often attributed to Raymond (1913). He published several papers that year but mentioned the family Agraulidae only once (Raymond 1913, p. 64), however, without stating that it is new; neither did he provide authorship, diagnosis etc., the name is just a bare heading. We do not consider that this justifies citing Raymond as the author of Agraulidae. Westergård (1953) and Henningsmoen (1959) attributed the family Agraulidae to Howell (1937) where the taxon was described as new and with diagnosis (Howell 1937, p. 1187). We here follow Westergård and Henningsmoen and consider Howell as the author of Agraulidae.

Diagnosis. See Howell (1937) and Henningsmoen (1959).

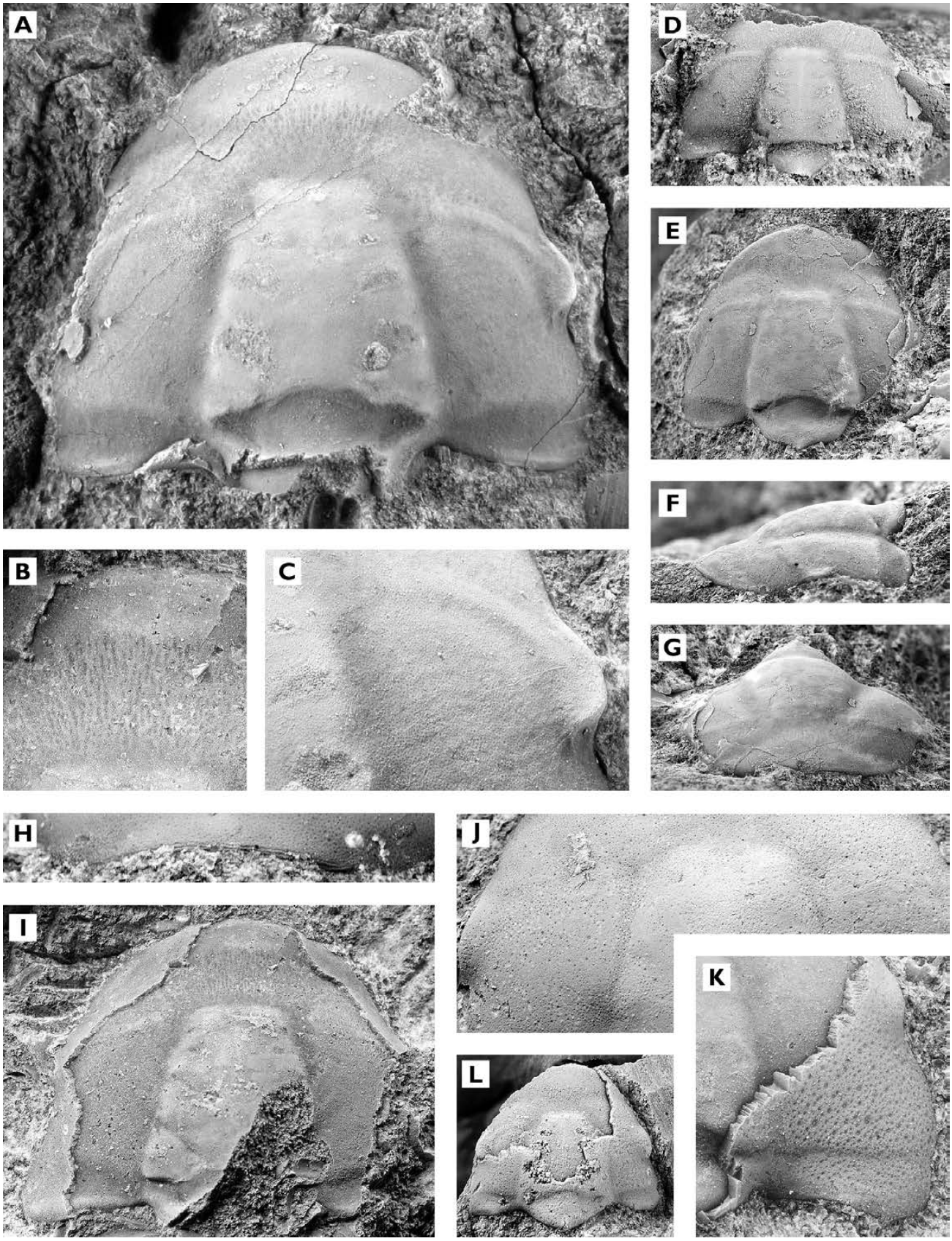
Remarks on diagnosis. Howell's (1937) original diagnosis emphasized that the glabella is almost or quite flush with the fixed cheeks in convexity and that the preglabellar field and border slope evenly towards the anterior margin, in addition to the presence of small eyes and fixed cheeks. He also stated that the posterior fixed cheeks are bluntly triangular, but this is not the case in *A. ceticephalus* or in *A. longicephalus* (Fig. 4). The diagnosis given by Henningsmoen (1959) stresses the forward tapering glabella, the presence of a preglabellar field and the small palpebral lobes situated opposite the anterior half of the glabella.

Geyer & Landing (2001) added as general characters of the cranidium an overall moderate convexity and subtrapezoidal outline. Glabella is also of low to moderate convexity and shows three pairs of short and relatively faint lateral glabellar furrows. However, *A. ceticephalus* and *A. longicephalus* have four pairs of lateral glabellar furrows. Geyer & Landing (2001) further noted that an axial crest tends to be developed and that the cephalic furrows generally are shallow and rather wide, often poorly developed.

Howell (1937) included *Agraulos* Hawle & Corda 1847, *Micragraulos* Howell 1937, *Agrauloides* Howell 1937 and *Conagraulos* Howell 1937 in the Agraulidae. Westergård (1953) assigned only *Agraulos*, but the Scandinavian species he attributed to this genus were later transferred to *Proampyx* Frech 1897 (see Ahlberg & Bergström 1978). Šnajdr (1958) and Henningsmoen (1959) assigned only *Agraulos* and *Skreiaspis* Růžička 1946 to the Agraulidae; Henningsmoen (1959) considered *Agraulos* as a senior synonym of *Proampyx*. Since then, a large number of genera have been assigned to the family; for a summary see Jell & Adrain (2003), who listed more than 35 taxa as a "broad grouping". Geyer & Landing (2001) accepted only *Agraulos* Hawle & Corda 1847, *Skreiaspis* Růžička 1946 and *Proampyx* Frech 1897 in Agraulidae *s.str.*

Bentley & Jago (2004) placed *Agraulos* together with 16 other genera in Agraulidae, whereas *Proampyx* and *Skreiaspis* were transferred to the Gondwanian family Wuaniidae, including 21 genera.

Skreiaspis differs from *Agraulos* and *Proampyx* in having a shorter frontal area, pronounced axial furrows and large eyes (Šnajdr 1958, 1990; Henningsmoen 1959). *Proampyx* differs from both *Agraulos* and *Skreiaspis* by having the frontal area extremely extended or even drawn out into a spine; the palpebral lobes are also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relatively long and strongly curved (Öpik 1961). According to Fletcher *et al*. (2005), details of the type species *Agraulos ceticephalus* exclude *Proampyx* and *Skreiaspis* as close relatives, and the Agraulidae may constitute a monogeneric family.

Genus *Agraulos* Hawle & Corda 1847

Type species. Arion ceticephalus Barrande 1846, designated by Miller (1889); *Eccaparadoxides pusillus* Zone; Skryje, Bohemia, Czech Republic.

Diagnosis (emend. Fletcher & Greene 2013). Test thick, cephalic furrows practically effaced on the outer surface; glabella and fixigenae typically show almost even convexity; glabella forward tapering, often slightly bowed out laterally; four pairs of lateral glabellar furrows, S1 bifurcated; eye ridges start at midpoint of palpebral lobes and meet axial furrows level with front of glabella; internal moulds show indistinct parafrontal band on anterior glabellar lobe; long frontal area; anterior border mesially expanded; no anterior border furrow, border defined by a smooth area on the internal mould devoid of caecal ridges; short palpebral lobes situated anteriorly, centre level with S2; converging anterior branches of facial suture; posterior branch of facial suture meets the posterior border in a gentle curvature; occipital ring backwards extended; spinose librigenae and some pygidial rings; exoskeleton smooth to punctate.

Remarks on diagnosis. Already Lake (1932) observed that the test is thick in *Agraulos* and masks the cephalic furrows and hollows, and specimens with intact test therefore look very different from exfoliated specimens. Lake (1932) also noted that the eye ridge starts at the middle of the palpebral lobe in *A. longicephalus.* This appears to be a salient distinguishing feature of *Agraulos* in comparison with most other trilobites where the eye ridge meets the palpebral lobe at its anterior end. This important feature is often incorrectly shown in drawings of *Agraulos* (e.g. Barrande 1846; Šnajdr 1958; Sdzuy 1961).

***Agraulos longicephalus* (Hicks 1872)**
Fig. 4

1872 *Arionellus longicephalus* Hicks, p. 176, pl. V, figs 20–26.
1902 *Agraulos ceticephalus* BARR., Grönwall, pp. 158–159, pl. 4, fig. 25.
1916 *Agraulos* cf. *holocephalus* Matthew, Nicholas, pp. 461–463, pl. 29, fig. 7.
1932 *Agraulos longicephalus* (Hicks), Lake, pp. 157–159, pl. 19, fig. 10; pl. 20, figs 1–10.
1958 *Agraulos longicephalus* Hicks, Lotze, pp. 731, 737.
1961 *Agraulos longicephalus* (Hicks 1872), Sdzuy, pp. 620–622 (338–340), pl. 23, figs 7–17; text-figs 32, 33.
1988 *Agraulos longicephalus* (Hicks 1872), Martin & Dean, pp. 21–22, pl. 3, figs 9–13.
1988 *Agraulos longicephalus* (Hicks 1872), Morris, p. 13. (Listed).
1994 *Agraulos longicephalus* (Hicks 1872), Young *et al*., p. 343.
1994 *Agraulos* cf. *ceticephalus* (Barrande 1846), Rudolph, p. 217, pl. 24, fig. 5.
1997 *Agraulos ceticephalus* (Barrande 1846), Buchholz, p. 252. (Listed).
2002 *Agraulos longicephalus* Hicks, Young *et al*., p. 17, pl. 4, fig. 5.
2006 *Agraulos longicephalus* (Hicks), Fletcher, pl. 34, fig. 34.
2014 *Agraulos longicephalus* (Hicks 1872), Weidner & Nielsen, pp. 47–48, fig. 41.

Lectotype. Complete specimen SM A3495a, original of Hicks (1872, pl. V, fig. 20), refigured by Lake (1932, pl. 19, fig. 10) and designated as lectotype by Morris (1988); Menevian, St David's, Wales.

Material. Approximately 25 more or less intact cranidia (see also Weidner & Nielsen 2014). Only one of Grönwall's (1902) specimens from Øleå could be identified in the collection of the Natural History Museum, Copenhagen; the whereabouts of the other specimen from Øleå and the single specimen from Læsø are unknown.

◀ **Fig. 4**. *Agraulos longicephalus* (Hicks 1872), cranidia. All except L are from Borggård, Øleå, Bornholm. **A,** internal mould previously illustrated as *A. ceticephalus* by Grönwall (1902, pl. 4, fig. 25), × 8. *Ptychagnostus punctuosus* Zone, MGUH 200, see also C. **B,** close-up showing caeca on the internal mould illustrated in full in I, × 8. **C,** close-up of the internal mould illustrated in A showing eye ridge and palpebral lobe; note fine threads at rear end of lobe, × 12. **D,** internal mould of small cranidium showing distinct parafrontal band on anterior glabellar lobe, × 6, *A. atavus* Zone, MGUH 31.236. **E–G,** dorsal, side and frontal views of internal mould, × 4, *A. atavus* Zone, MGUH 30.143. **H,** close-up of frontal margin (anterior view) showing terrace lines on test surface, × 12, *A. atavus* Zone, MGUH 31.237. **I,** largest cranidium recorded, partly exfoliated, × 4, *A. atavus* Zone, see also B, MGUH 31.238. **J,** close-up of test surface showing prosopron, × 8, *A. atavus* Zone, MGUH 30.145. Cranidium previously illustrated by Weidner & Nielsen (2014, fig. 41F). **K,** close-up of test surface showing prosopron, × 8, *A. atavus* Zone, MGUH 30.144. Cranidium previously illustrated in full by Weidner & Nielsen (2014, fig. 41E). **L,** partly exfoliated cranidium showing triangular occipital ring. Ice-rafted boulder from Rügen, Mecklenburg, Germany, × 4, *Ptychagnostus punctuosus* Zone, SB-MK 143.

Occurrence. This species occurs commonly in the Øleå section on Bornholm. The material derives from concretions of bituminous limestone in the lower and upper part of the *Acidusus atavus* Zone (localities 6B and 4 on Fig. 2C, respectively); the specimens described by Grönwall (1902) came from the *Ptychagnostus punctuosus* Zone where they are associated with *P. punctuosus*, *Lejopyge elegans* and *Doryagnostus incertus* amongst others. Three cranidia are known from ice-rafted boulders of limestone found in northern Germany; these concretions contained the same agnostids and likely derive from the Bornholm area (Rudolph 1994; Buchholz 1997). The species is also reported from the *Paradoxides hicksii* Zone of eastern Newfoundland, Avalonian Canada (Martin & Dean 1988; Fletcher 2006) and from the *Tomagnostus fissus* Zone to the lower part of the *P. punctuosus* Zone in Avalonian Great Britain (Thomas *et al.* 1984). Outside Baltica and Avalonia it occurs in Spain in the *Pardailhania* and *Solenopleuropsis* substages (Caesaraugustian Stage) (Lotze 1958; Sdzuy 1961, 1972), which correspond to the *A. atavus* and *P. punctuosus* zones of the *Paradoxides paradoxissimus* Superzone in Scandinavia (Geyer & Shergold 2000).

Description. Most of the described features can only be observed in exfoliated specimens and if not otherwise stated the following description is based on internal moulds. In testaceous material many features are masked by the thick test. Cranidium subtriangular in outline, with rounded anterior margin; length corresponds to about 85 % of max. width (n = 8); largest specimen is 14.2 mm long (Fig. 4I). Glabella occupies *c.* 50 % of the total cranidial length and 40 % of max. cranidial width in adult specimens (measured on exfoliated specimens, see Fig. 3:3–4); it tapers evenly and rather strongly, slightly bowed out laterally, front truncate and the anterior width corresponds to only 50 % of glabellar width at the occipital furrow (Fig. 3:4–5). When the exoskeleton is preserved, the axial furrows are shallow, on internal moulds well-impressed, broad; the preglabellar furrow is shallow, on internal moulds mostly very faint. On exfoliated specimens four faint and broad lateral glabellar furrows extend on each side across one-third of the glabellar width (Fig. 4A; see also Weidner & Nielsen 2014, figs 41A–B, D–E). S1 and S2 are relatively large, elongate and directed rearwards-inwards; S1 tends to bifurcate. S3 and S4 are comparatively small, elongate rounded. Anterior and lateral views show the moderate convexity (tr. and sag.) of the cranidium and a glabella distinctly raised above the level of the downsloping fixigenae and preglabellar field (Fig. 4F–G). A faint glabellar crest is commonly present. When the test is preserved, the occipital furrow appears abaxially just as two curved, short and deep lateral impressions (see Weidner & Nielsen 2014, fig. 41F); on internal moulds the occipital furrow is very broad and curving forwards. Occipital ring triangular in testaceous specimens (Fig. 4L; see also Sdzuy 1961, text-fig. 32 and Weidner & Nielsen 2014, fig. 41A); on internal moulds the occipital ring expands into a distinct node at the posterior margin (Fig. 4E; see also Weidner & Nielsen 2014, fig. 41E). The anterior margin of the cranidium is smoothly curved; the border is long (sag.), mesially swollen and projected forward, sloping downwards and separated from the glabella by a preglabellar field which is slightly longer (sag.) than the border. Border furrow not developed. The preglabellar field carries caeca, the anterior border is smooth (Fig. 4A–B, I). Eyes far from glabella; width of fixigena corresponds to *c.* 60 % of the glabellar width across the centre of the palpebral lobe (Fig. 3:6–7). Palpebral lobes are short (corresponding to *c.* one third of glabellar length, Fig. 3:8), gently falcate, widening slightly posteriorly, with its centre level with S2. The anterior and posterior ends of the palpebral lobe divide into thin, short threads which run parallel with the suture and form narrow, tiny grooves between the threads and the suture (Fig. 4C). The eye ridges start at the palpebral lobes just above their midlengths (Fig. 4C; see also Whittington 1992, pl. 51; Fletcher *et al.* 2005, fig. 11–1; Weidner & Nielsen 2014, fig. 41C). This is an important diagnostic feature not seen in the majority of other trilobites. The eye ridges continue gently curved towards anterior lobe of glabella; they meet the axial furrows nearly level with front of glabella and bifurcate just before reaching the axial furrows (Fig. 4A). The anterior thread continues as an indistinct parafrontal band across the anterior lobe, forming a semi-continuous ridge uniting the eye ridges (Fig. 4D–E). In some specimens a small mesial boss is seen centrally on the parafrontal band (Fig. 4A). A distinct furrow, approximately of the same width as the eye ridge, runs parallel to it on its rear side and amalgamates with the palpebral furrow, which continues to the posterior end of the palpebral lobe where it fades out (Fig. 4C). The facial suture is directed inwards in front of and slightly outwards behind the palpebral lobe and generally runs parallel to the axial furrow, forming almost one single gentle curve, just interrupted by the short palpebral lobe (Fig. 4A; see also Weidner & Nielsen 2014, fig. 41B–F). The posterior branch meets the posterior border in a gentle curvature. The posterior border furrows are adaxially weakly curved impressions on the shell exterior; on internal moulds they are wide (exsag.) and deep and broaden abaxially. Length (exsag.) and width (tr.) of posterior fixigena (Fig. 3:9–10) are equivalent to about 70 % of glabellar length and about 60 % of the width of the occipital ring, respectively. Test thick, with three sizes of punctae scattered over a background of

tiny granules. A few terrace lines are seen along the anterior margin (Fig. 4H).

Remarks. The cranidium of *Agraulos longicephalus* strongly resembles that of *A. ceticephalus*, and the two species are likely closely related (see also Fletcher *et al.* 2005). Various width/length ratios and other parameters of *A. ceticephalus* are similar to those discussed above for *A. longicephalus*. The only conspicuous difference is a "short (sag.) occipital ring strongly curved backward into a blunt point" in *A. ceticephalus* (cit. Fletcher *et al.* 2005, fig. 11:4) versus the massive triangular occipital ring in *A. longicephalus* (Fig. 4L) and the latter is considered a possible early variant of *A. ceticephalus*.

The cranidium figured by Grönwall (1902, pl. 4, fig. 25) as *A. ceticephalus* was shown with an intact occipital ring. However, re-investigation of the specimen revealed that the occipital ring is not preserved (see Fig. 4A), except that the base of a broad extension of the occipital ring can be observed on the right side of the cranidium, suggesting that this specimen represents *A. longicephalus*.

In their description of topotype material of *A. ceticephalus* from the *Eccaparadoxides pusillus* Zone of Bohemia, Fletcher *et al.* (2005) showed details not noted previously: the ornament consists of three sizes of punctae scattered over a background of tiny granules with fine terrace ridges along the anterior cranidial margin and the posterior edge of the occipital ring; four pairs of lateral glabellar furrows arching backwards; weakly impressed anterior border furrow; upstanding palpebral lobes. We here note that the eye ridges commence at midlength of the palpebral lobes and thus they do not form a direct continuation of the palpebral lobes as often reconstructed (Barrande 1852, pl. 10, figs 6, 14; Šnajdr 1958, fig. 37; Henningsmoen 1959, fig. 205, 1; Sdzuy 1961, text-fig. 32).

Genus *Proampyx* Frech 1897

Type species. Proetus? *difformis* var. *acuminatus* Angelin 1851, by original designation; from the Andrarum Limestone Bed of the *Lejopyge laevigata* Zone at Andrarum, Scania, Sweden.

Diagnosis (emend. Öpik 1961 and Ahlberg & Bergström 1978). Test thick, cephalic furrows practically effaced on the outer surface; forward tapering glabella elevated above fixigenae and frontal area; glabella parallel-sided, rarely bowed out laterally; three to four pairs of lateral glabellar furrows, S1 bifurcated; median keel on glabella comparatively well marked; eye ridges start at front of palpebral lobes and meet axial furrows slightly behind front of glabella; long to very long flat frontal area, some species with extended cusp; anterior border mesially expanded forwards, rarely backwards; no anterior border furrow, and border is poorly separated from preglabellar field; long palpebral lobes situated posteriorly, centre level with S1; diverging anterior branches of facial suture in front of palpebral lobes; posterior fixigena short (exsag.), distinctly triangular; occipital ring expanded backwards, carrying node or spine on anterior margin; posterior margin evenly rounded; spinose librigenae and thorax; exoskeleton punctate; comparatively large pygidium.

Remarks. Ahlberg & Bergström (1978) assigned several Lower Cambrian species to *Proampyx*; they would now be allocated to various other genera (e.g. Geyer 1990; Geyer & Landing 2004; Geyer *et al*. 2004).

***Proampyx*? *depressus* (Grönwall 1902)**
Fig. 5A–I

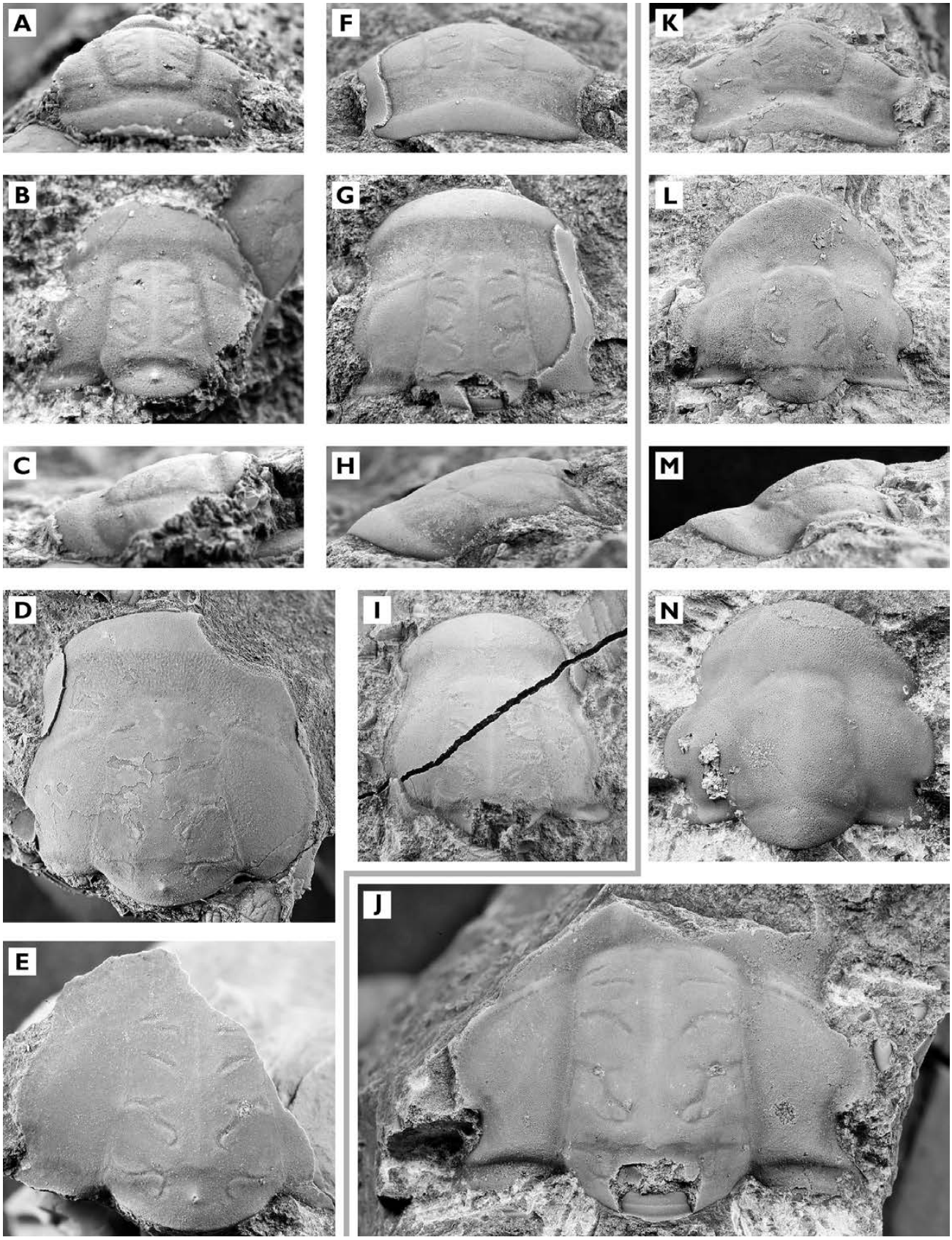
1902 *Agraulos depressus* n. sp. Grönwall, pp. 159–160, pl. 4, fig. 24.

Lectotype. Cranidium MGUH 199, original of Grönwall (1902, pl. 4, fig. 24); here designated as lectotype and re-illustrated in Fig. 5F–H; *Ptychagnostus punctuosus* Zone at Borggård, Øleå, Bornholm.

Material. In addition to the lectotype specimen figured by Grönwall (1902), three more cranidia were located in the collection of the Natural History Museum of Denmark. A young cranidium was further collected from bituminous limestone in the basal part of the *Ptychagnostus punctuosus* Zone at Borggård, Øleå (locality 7, Fig. 2C). It is associated with abundant *Cotalagnostus lens,* rare specimens of *Acidusus atavus* and *P. punctuosus*, as well as *Onymagnostus ciceroides*, *Hypagnostus mammillatus*, *Diplorrhina depressa* and *Diplagnostus planicauda bilobatus.*

Occurrence. The species occurs in the *Ptychagnostus punctuosus* Zone and is only known from Borggård, Øleå, Bornholm.

Description. The cranidia are of low convexity and show one common curvature for glabella and fixigenae (Fig. 5F). The available material is largely exfoliated, allowing the study of details which are masked when the thick test is intact. The largest specimen is 13.3 mm long. The cranidium is almost quadrate in outline, the length corresponds to 90 % of max. width, with a broadly rounded anterior margin. The glabella is not inflated and is defined by shallow and narrow axial furrows; the preglabellar furrow is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very faint to absent, but the gently rounded glabellar front is slightly raised and outlines the anterior delimitation of glabella. The glabella occupies *c.* 60 % of the cranidial length (measured from the occipital furrow) and the maximum width corresponds to almost 50 % of the cranidial width (measured across posterior fixigenae). The glabella tapers to midway between S1 and S2, where glabella is narrowest, then expands faintly forwards; width of the frontal lobe corresponds to *c.* 77 % of the max. glabellar width. Four pairs of lateral glabellar furrows are developed. A fifth pair of furrows is located immediately in front of the occipital furrow and runs in a sinuous course across the entire glabella. The furrows are fairly narrow and well incised and obviously represent a pair of auxiliary furrows not homologous to S1. S1 in front of the auxiliary furrow is biramous, with a fairly long posterior branch directed inwards-backwards, ending in a pair of faintly raised apodemes. Approximately at midlength of the posterior branch, a short anterior branch commences directed inwards-forwards. S2 is composed of simple, faintly curved furrows, starting distant from axial furrows; they are slightly narrower and shorter than the posterior branches of S1 and directed inwards-backwards. S3 is a pair of short, slightly curved, transversely directed furrows located close to glabellar midline. S4 is also short and narrow, but comparatively deep, almost comma-shaped furrows starting close to axial furrows and running slightly anteriorly. The occipital ring shows a small mesial node. In the lectotype specimen a small portion is broken off from the posterior edge of the occipital ring, exposing the ventral doublure. It shows two shallow furrows that may have functioned as stopping devices for the anterior thoracic segment.

The anterior margin of the cranidium is smoothly curved. The anterior border slopes gently downwards; it is long (sag., exsag.) and slightly projected backwards medially; border furrow lacking, the preglabellar field is of same length (sag.) as the border. In the lectotype specimen the posterior border furrow is broad and shallow on the internal mould (left hand side), but shallow to nearly effaced on the exterior (right hand side). The width of fixigena across palpebral lobe corresponds to *c.* 66 % of the glabellar width at the same level (Fig. 3:6–7) and the eyes are thus far from glabella. The palpebral lobe is long, corresponding to *c.* 50 % of glabellar length, narrow, gently curved, posteriorly slightly wider than at the anterior end, stretching from mid-part of L1 to almost the level of S3. Eye ridges distinct, forming a continuous arc with palpebral lobes, adaxial end located slightly behind anterolateral corners of frontal glabellar lobe. The anterior branch of the facial suture consists of a faintly diverging posterior section and an anterior section turning towards sagittal line where the anterior branches meet smoothly. The posterior branch runs backwards-outwards from the posterior end of the eye at an angle of *c.* 45° from sagittal line, and the posterior fixigena is distinctly triangular in outline. Length (exsag.) of posterior fixigena corresponds to about one third of glabellar length. Width (tr.) of posterior border corresponds to about 50 % of occipital ring. The few patches of intact test show a prosopon of very fine, densely spaced pits.

A small specimen, only 4.5 mm long, is interpreted as a juvenile specimen of *P.*? *depressus,* despite some morphological differences (Fig. 5A–C). We especially emphasize that the pattern of lateral glabellar furrows is identical. Besides, the anterior cranidial margin is also smoothly rounded, and the glabella and fixigenae form one smooth convexity. The juvenile cranidium differs from the adult specimen by having a parallel-sided glabella, which is a little inflated and bounded by deeper axial furrows, the fixed cheeks are relatively narrower, the eyes are shorter and more strongly falcate, and the preglabellar field is distinctly shorter.

Remarks. Agraulos depressus Grönwall 1902 is here allocated to *Proampyx*? because

1) eye ridges spring from the anterior end of palpebral lobes
2) palpebral lobes are long, centre situated level with S1
3) diverging anterior branch of facial suture
4) occipital ring carries a node, situated anteriorly

◀ **Fig. 5**. **A–I:** Cranidia of *Proampyx*? *depressus* (Grönwall 1902), all from the *Ptychagnostus punctuosus* Zone at Borggård, Øleå, Bornholm. **A–C,** anterior, dorsal and side views of exfoliated juvenile specimen; note that the side view (C) is shown reversed in order to facilitate comparison with the other specimens, × 8, MGUH 31.239. **D,** largest specimen recorded, largely exfoliated, × 4. MGUH 31.240. **E,** internal mould showing distinct lateral glabellar furrows; note sinuous auxillary furrows just in front of the occipital furrow, × 5, MGUH 31.241. **F–H**, anterior, dorsal and side view of partly exfoliated lectotype cranidium, previously illustrated by Grönwall (1902, pl. 4, fig. 24), × 4, MGUH 199. **I,** internal mould showing distinct lateral glabellar furrows, × 5, MGUH 31.242. **J–N**: Cranidia of *Proampyx difformis* (Angelin 1851), all from the Andrarum Limestone Bed, *Lejopyge laevigata* Zone. **J,** internal mould showing distinct lateral glabellar furrows; note small auxillary furrows just in front of the occipital furrow, × 4, Borggård, Øleå, Bornholm, MGUH 31.243. **K–M,** anterior, dorsal and side views of exfoliated cranidium, × 4, found in glacial erratic boulder, As Hoved, Jutland, Denmark, MGUH 31.244. **N,** cranidium showing finely pitted test, × 5, Borggård, Øleå, Bornholm, MGUH 31.245.

5) posterior fixigena triangular
6) four pairs of lateral glabellar furrows arranged in virtually the same pattern are shared with *P. difformis* (see e.g. Fig. 5J, N; Álvaro *et al*. 2013, fig. 5c–e). Another *Proampyx* species showing constantly four pairs of lateral glabellar furrows is *Proampyx aculeatus* (see Westergård 1953, pl. 1, figs 9, 10a).

However, *Proampyx*? *depressus* differs from the Scandinavian species of *Proampyx* in the following features:
1) a non-inflated glabella (adult condition)
2) very faint to effaced preglabellar furrow
3) comparatively short, downsloping frontal area
4) the palpebral lobes are only gently curved, narrow
For these reasons the generic assignment is uncertain.

All specimens at hand of *P.*? *depressus* show a laterally waisted glabella; this feature is only occasionally observed in *Proampyx* species e.g. *P. difformis* (Fig. 5J, N) and *P. anceps* (Westergård 1953, pl. 2, fig. 2a). Most *Proampyx* species show a laterally bowed out glabellar shape. *P.*? *depressus* also shows a fifth pair of auxillary furrows behind S1 on glabella. So far, this feature has only been observed in *P. difformis* (Fig. 5J), but potentially it offers strong support for an assignment of *depressus* to *Proampyx*.

Öpik (1961) stressed the similarity between the Australian species *Proampyx agra* and the Scandinavian *P. difformis* and *P. acuminatus*. The Australian species occurs in the *Proampyx agra* Zone of the Selwyn Range, Queensland, Australia (Öpik 1961, pp. 146–148, pl. 12, figs 1–6), which corresponds to the *Lejopyge laevigata* Zone of Scandinavia. Some of the features found in *P.*? *depressus* are also reminiscent of *P. agra*. The two species thus share an almost quadrate shape of the cranidium, not so strongly curved palpebral lobes, shallow palpebral furrows and deeply incised auxiliary furrows on the posterior glabella (Fig. 5G; Öpik 1961, pl. 12, fig. 5a). However, *P. agra* differs from the Scandinavian species of *Proampyx* by "being much more effaced, having wider fixed cheeks, a more evenly rounded anterior margin of the cranidium, a less tapered glabella and a much less variable anterior border" (cit. Bentley & Jago 2004 p. 184). The latter authors transferred *agra* to their genus *Arminoepikus* of the Gondwanan family Wuaniidae.

Typical species of *Proampyx* occur in Scandinavia in the *Lejopyge laevigata* Zone (Andrarum Limestone Bed), whereas *Proampyx*? *depressus* occurs in the older *Ptychagnostus punctuosus* Zone. *P.*? *depressus* may represent an early, atypical form of *Proampyx* or maybe even a precursor that should be separated in a genus of its own.

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