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

THOMAS WEIDNER & ARNE THORSHØJ NIELSEN

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 paradoxius 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 ceticphalus (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.

Keywords: Agraulos, Proampyx, trilobites, Middle Cambrian, Bornholm, Denmark.

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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. aniceps (Westergård 1953), and P. cornutus Buchholz 1997, all occurring in the Middle Cambrian Paradoxides forchhammeri Superzone of Norway, Denmark and Sweden (Bregger 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. ceticphalus (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. ceticphalus (Barrande 1846) from the P. punctuosus Zone. There are two further cranidia assigned to A. ceticphalus (Barrande 1846) from the same zone in the collection of Buchholz (1997; personal communication 2010). All mentioned material of A. ceticphalus is here identified with A. longicephalus (Hicks 1872). This species strongly resembles A. ceticphalus 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...
The two species presently known from Bornholm, *Agraulos longicephalus* (Hicks 1872) and *Proampyx? depressus* (Grönwall 1902), are treated in this paper.
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, *Micraulodus* 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* and *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 Wuanidae, 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
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 monogenic 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 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).

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); Menever, 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 Læså 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 Øløe 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-rafter 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 Paraalithina 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. cranial 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 rotated. 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 parafacial 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 parafacial 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 cranial 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 when the thick test is intact. The largest specimen (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 cranial 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, and thus they do not form a direct continuation of the ridges commence at midlength of the palpebral lobes upstanding palpebral lobes. We here note that the eye

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 SI; 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)

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 *Catalagnostus 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
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 cranial length (measured from the occipital furrow) and the maximum width corresponds to almost 50 % of the cranial 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 Proampyx? 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 (Trilobita) from the Middle Cambrian of Bornholm. 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
P. difformis
Australian species

...of potentially it offers strong support for an assignment
P. difformis has only been observed in
furrows behind S1 on glabella. So far, this feature

Ptychagnostus punctuosus
Proampyx
Bed), whereas
in the

of the Gondwanan family Wuaniidae.

authors transferred
agra
border” (cit. Bentley & Jago 2004 p. 184). The latter

less tapered glabella and a much less variable anterior
cranidium, not so strongly curved palpebral lobes,
more effaced, having wider fixed cheeks, a more

Proampyx

1961, pl. 12, fig. 5a). However, 
P. agra

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. 5), 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 auxiliary
furrows behind S1 on glabella. So far, this feature has only been observed in P. difformis (Fig. 5i), but potentially it offers strong support for an assignment of depressus to Proampyx.

Öpik (1961) stressed the similarity between the Australian species 
P. agra and the Scandinavian 
P. difformis and P. acuminatus. The Australian species occurs in the 
P. 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 Armnoepikus of the Gondwanan family Wuaniiidae.

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