The Early Ordovician (late Tremadocian; Stairsian) dimeropygid trilobite *Pseudohystricurus* Ross

JONATHAN M. ADRAIN, TALIA S. KARIM & STEPHEN R. WESTROP

ADRAIN, J.M., KARIM, T.S. & WESTROP, S.R., 2014:04:25. The Early Ordovician (late Tremadocian; Stairsian) dimeropygid trilobite *Pseudohystricurus* Ross. *Memoirs of the Association of Australasian Palaeontologists 45*, 215-232. ISSN 0810-8889.

The Early Ordovician genus *Pseudohystricurus* Ross has been treated as a minor taxonomic wastebasket for poorly known species featuring small, dorsally convex cranidia and tuberculate sculpture. No previously assigned species apart from the type species appear to belong to the genus. The type species, *P. obesus* Ross, has been known in its type area from only a single cranidium. New collections demonstrate that it is confined to the recently proposed *P. obesus* Zone, the uppermost trilobite zone of the Stairsian Stage. The species is revised on the basis of new collections from the type locality in the Garden City Formation, southeastern Idaho, and from the Fillmore Formation, western Utah. The genus is known from the underlying *Pseudoclelandia cornupsittaca* Zone from a species described in open nomenclature from the Fillmore Formation. The oldest known species is *P. wigglesorum* sp. nov., from the *Bearriverops alsacharovi* Zone of the Garden City Formation. Details of developmental morphology revealed by silicified specimens offer compelling evidence that *Pseudohystricurus* is closely related to the Middle–Late Ordovician *Dimeropyge* Öpik.

Jonathan M. Adrain (jonathan-adrain@uiowa.edu), Department of Earth and Environmental Sciences, University of Iowa, 121 Trowbridge Hall, Iowa City, Iowa 52242, USA; Talia S. Karim, University of Colorado Museum of Natural History, 265 UCB, University of Colorado, Boulder, CO 80309, USA; Stephen R. Westrop, Oklahoma Museum of Natural History and School of Geology and Geophysics, University of Oklahoma, Norman, Oklahoma 73072, USA. *Received 26 September 2013.*

Keywords: Silicified, Utah, Idaho, taxonomy, Dimeropygidae, *Pseudohystricurus.*

THE GENUS *Pseudohystricurus* Ross 1951, has been cited frequently, and has had several taxa assigned to it (e.g., Ross 1953; Wilson 1954; Ross 1970). It has been compared with putatively related genera (Adrain *et al*. 2001; Yuan *et al*. 2006), and has even had several of its (previously) assigned species included in a cladistic analysis (Adrain *et al*. 2001). Despite this, its type species has been documented from its type area only by tiny photographs of a single cranidium (Ross 1951, pl. 16, figs 25, 30, 34). This has been an inadequate basis of comparison, as emphasised by the fact that no previously assigned species aside from the type are considered herein to belong to the genus.

The Stairsian Stage of northern Laurentia (in Ordovician palaeocoordinates) has traditionally been subdivided into the lettered zones D–F of Ross (1949) and Hintze (1951), which were given formal names by Ross *et al*. (1997). This scheme has been significantly modified in recent work. Taylor *et al*. (2012) moved the position of the base of the Stairsian to the base of the Ross-Hintze Zone C ("*Paraplethopeltis* Zone"). Adrain *et al*. (this volume) replaced the more than half century old scheme with a new species-based trilobite zonation founded on new data from recent field sampling, and including 11 Stairsian zones. The new zonation in the latter work is followed herein.

Pseudohystricurus obesus, the type species, is also the zonal namebearer of the highest zone of the Stairsian. As outlined by Adrain *et al*. (this volume), the two highest Stairsian zones, the *Pseudoclelandia cornupsittaca* Zone and the *Pseudohystricurus obesus* Zone, are unusual in that they feature substantial faunal differentiation between horizons in the Garden City Formation in southeastern Idaho and stratigraphically equivalent horizons in the Fillmore Formation of western Utah. In general through the Stairsian, and also in the overlying Tulean, as documented by Adrain *et al*. (2009), the faunal content of a given zone is very similar between the regions, with only modest exceptions. The upper two zones of the Stairsian are different in that they feature multiple genera represented by clearly different species in either region. Hence, it is essential to demonstrate that the occurrences of *P. obesus* in either region are genuinely conspecific.

The goals of this work are: 1) to document the occurrence of *P. obesus* both at its type horizon in the Garden City Formation, Idaho, and in the Fillmore Formation, Utah, and to revise it on the basis of many more specimens than previously known, including librigenae and pygidia; 2) to describe two new species (one known from only a single cranidium), from underlying trilobite zones; 3) to use this greatly expanded knowledge of the morphology of the type and closely related species to critically evaluate the various other species that have been assigned to *Pseudohystricurus*; and 4) to use new morphological information to explore potential relationship between *Pseudohystricurus* and the Middle-Late Ordovician *Dimeropyge* Öpik 1937.

LOCALITIES AND STRATIGRAPHY

This work is part of a general field-based revision of the Early and Middle Ordovician trilobite faunas of northern Laurentia (e.g., Adrain & Westrop 2006, 2007; Adrain & McAdams 2012; McAdams & Adrain 2009, 2011a, b, c). A history of study and overview of the sections, including full locality data and maps, was given by Adrain *et al*. (2009) and need

not be repeated here. Graphical section logs of the Stairsian portions of the sections were given by Adrain *et al*. (this volume). All of the horizons from which material is described herein are detailed in the latter work. Briefly, new material is from the Lower Ordovician (upper Tremadocian; Stairsian) portions of Section HC6 through the Garden City Formation in the Bear River Range, Franklin County, southeastern Idaho, and sections G and MME through the Fillmore Formation, Ibex area, Millard County, western Utah.

SYSTEMATIC PALAEONTOLOGY

Figured material is housed in the Paleontology Repository, Department of Earth and Environmental Sciences, University of Iowa, Iowa City, with specimen number prefix SUI, and the collections of the Geological Survey of Canada, Ottawa, with specimen number prefix GSC.

Family DIMEROPYGIDAE Hupé 1953

Pseudohystricurus Ross 1951

Type species. *Pseudohystricurus obesus* Ross 1951, Garden City Formation, Idaho, USA.

Other species. *Pseudohystricurus wigglesorum* sp. nov., Garden City Formation, Idaho, USA; *Pseudohystricurus* sp., Fillmore Formation, Utah, USA.

Diagnosis. Cranidium strongly vaulted, anterior region of glabella overhanging and obscuring anterior border of large specimens in dorsal view; glabella large and swollen, occupying most of cranidial area; palpebral lobes very narrow (tr.); most cephalic surfaces with dense sculpture of medium and small sized conical tubercles; anterior border narrow (tr.), short and transversely arched; librigena with fine row of small tubercles directly beneath eye; field narrow; small, slender, tuberculate, laterally curved genal spine, reduced in length with increasing size of librigena; pygidium of four segments, with prominent fulcral spine on posterior pleural band of each (merged into axis on posteriormost), smooth vertical region beneath spines, and prominent inflated border; pygidial doublure turned vertically.

Rejected species. Adrain *et al*. (2001, p. 953) considered that *Pseudohystricurus* included the type species plus the Tulean *P. orbus* Ross 1953, and the Stairsian *Pseudohystricurus* sp. of Ross (1951), and all three were included in a cladistic analysis of the dimeropygid genera *Ischyrotoma* Raymond 1925, and *Dimeropygiella* Ross 1951. Adrain *et al*. (2001, p. 950) questioned the relationship between *P. rotundus* Ross and the type species, and *P. rotundus* was not included in their analysis. *Pseudohystricurus rotundus* was described on the basis of three crackout cranidia from the Skullrockian Stage at Section HC5. Abundant silicified material from several sections confirms that it belongs to an as yet unnamed taxon represented by multiple new species in the sections, and is entirely unrelated to *Pseudohystricurus*. In addition, thorough resampling of all relevant sections and horizons has revealed that neither *P. orbus* nor *Pseudohystricurus* sp. of Ross (1951) are members of *Pseudohystricurus*. The former was revised as *Litzicurus orbus* by Adrain *et al*. (2009, p. 593). It was assigned in that work to Hystricuridae, but may possibly represent Bathyuridae.

"*Pseudohystricurus* sp." of Ross (1951, p. 75, pl. 16, figs 26, 27, 31) is known from a single cranidium from the *Bearriverops loganensis* Zone at HC5. This specimen definitely represents a dimeropygid, and as such it is broadly comparable in dimensions to cranidia of *P. obesus*. However, the specimen belongs to a species assigned by us in a forthcoming work to a new genus closely related to *Gonioteloides* Kobayashi 1955. Fortey & Owens (1975, p. 228) opined that "probable hystricurine pygidia with steeply sloping posterior margins not unlike those of *Ischyrotoma* species are present among unassigned pygidia (Ross 1951, pl. 19:13) from the same beds as *Pseudohystricurus*." This refers to the same beds as "*Pseudohystricurus* sp.", not *P. obesus*. Chatterton (1994, p. 542) commented that "if Fortey and Owens (1975) are correct in their association of the cranidium and pygidium mentioned above, *Pseudohystricurus* would probably be considered a junior subjective synonym of *Ischyrotoma*." In fact, the pygidium referred to (Ross 1951, pl. 19, figs 13, 14, 17), belongs to a species of *Hystricurus* s.s., illustrated by Adrain *et al*. (2003, fig. 4B, F, J) as "*Hystricurus* sp. nov. A". It does not closely resemble pygidia of species of *Ischyrotoma*, nor those of either species of *Pseudohystricurus* or species of the new genus to which "*Pseudohystricurus* sp." will be assigned.

Hintze (1951, p. 48; 1953, p. 32) listed "*Pseudohystricurus* sp." as a rare species at his locality G-3. This horizon is our G 26.6 m in the *Bearriverops alsacharovi* Zone. Here, a vaulted and tuberculate dimeropygid species occurs - it is a new species assigned to the new genus referenced in the preceding paragraph and will be described by us in a forthcoming work.

When he named the genus, Ross (1951, p. 74) suggested that *Hystricurus crassilimbatus* Poulsen 1937, from the Cape Weber Formation (Floian) of northwestern Greenland, and *Hystricurus abruptus* Cullison 1944, from the Jefferson City Formation (Floian) of Missouri, might belong to it. We are in the process of revising the type material of the former. While poorly preserved, it appears to belong to *Ischyrotoma*. "*Hystricurus*" *abruptus* is known from exceptionally tiny and poor photographs (Cullison 1944, pl. 34, figs 45–49) and until the specimens are adequately reillustrated it is very difficult to assess the affinity of the species. Derby (in Derby *et al*. 1991) assigned it to *Ischyrotoma* and assigned material from the Kindblade Formation of Oklahoma to it. Loch (2007, p. 74), however, considered that the Oklahoma material represents *Ischyrotoma*, and named *I. sila* for it, but that "*Hystricurus*" *abruptus* is not conspecific and does not represent *Ischyrotoma*. He suggested that it might be assigned to *Mesotaphraspis* Whittington & Evitt 1954. *Mesotaphraspis* comprises mostly Late Ordovician species, with the only exception being the Darriwilian *M. circumflexa* Tripp 1967. While "*H.*" *abruptus* does appear to have a long median preglabellar furrow, which is a characteristic of *Mesotaphraspis*, similar features occur widely in aulacopleuride trilobites.

"*Pseudohystricurus* sp." of Wilson (1954, p. 274, pl. 26, fig. 15), from an exotic Lower Ordovician boulder in the Woods Hollow Formation, Texas, is known from a single illustrated cranidium. Only the anterior region is preserved. The specimen is tuberculate and the short preglabellar field is crossed by a median furrow connecting the anterior border furrow and preglabellar furrow as in *Pseudohystricurus*. However, the specimen does not seem to be strongly dorsally convex and the frontal areas are broad and plainly visible in dorsal view. There are a number of hystricurid and dimeropygid taxa with broadly similar morphology, and it seems unlikely that the specimen

represents *Pseudohystricurus*. Much more information would be necessary to assess its affinities.

Fortey & Owens (1975, p. 228) suggested that *Hystricurus antiquus* Lisogor 1961, from the Agalatas Formation, upper Tremadocian, Kendyktas Mountains, North Tien Shan Terrane (see Alexyutin *et al*. 2005; Popov *et al*. 2009), southern Kazakhstan, might belong to *Pseudohystricurus*. The species is known from tiny dorsal photographs of three incomplete cranidia. The cranidia are vaulted and tuberculate and likely represent a "hystricurid" or dimeropygid. They bear little similarity to species of *Pseudohystricurus* described or revised herein. They have wide, long anterior borders clearly visible in dorsal view, broad frontal areas, wide interocular fixigenae, and large palpebral lobes. So little information is available that it is difficult to be certain whether the three illustrated cranidia represent the same species, and impossible to assess their affinities with any confidence. They might represent a species of *Parahystricurus* Ross 1951, but could as easily represent hintzecurines (see Adrain *et al*. 2003), or any number of other tuberculate aulacopleuride taxa.

"*Pseudohystricurus* sp." of Kindle & Whittington (1958, p. 323), from the Shallow Bay Formation, lower Tremadocian, Cow Head Peninsula, western Newfoundland, Canada, was not illustrated, but almost certainly refers to one of the species of *Tulepyge* Adrain & Westrop 2006, illustrated by Karim (2008).

"*Pseudohystricurus* sp." of Ross (1970, p. 72, pl. 10, figs 29–31), from the Goodwin Formation, Nevada, is a single cranidium with an inflated, tuberculate glabella. Its affinities are difficult to assess based on the available information, but its wide anterior border, anteriorly divergent anterior sections of the facial suture, and correspondingly large frontal areas are very different from the morphology seen in species of *Pseudohystricurus* and it is unlikely that the species represented belongs to the genus. "*Pseudohystricurus*? sp." of Ross (1970, p. 73, pl. 11, figs 1, 2), from the Pogonip Group, Nevada, also does not represent a member of the genus. Its affinities are difficult to assess on the basis of tiny photographs of a single specimen, but it may represent a species of *Bearriverops* Adrain & Westrop 2007.

"*Pseudohystricurus* sp. aff. *P. rotundus* Ross" of Fortey *et al*. (1982), from the Shallow Bay Formation, lower Tremadocian, western Newfoundland, was subsequently described as *Hystricurus paucituberculatus* Fortey 1983, and revised as *Tulepyge paucituberculata* by Adrain & Westrop (2006). *Tulepyge* is an earliest Ordovician (and possibly latest Cambrian) dimeropygid not closely related to *Pseudohystricurus*.

"*Pseudohystricurus* sp." of Dean (1989, p. 23 , pl. 14, figs 7, 8), from the Survey Peak Formation, Alberta, is difficult to evaluate because it consists of only the anterior portion of an exfoliated cranidium. Dean compared it with Ross's (1951) "*Pseudohystricurus* sp." from what is now the *Bearriverops loganensis* Zone. As noted above, work in progress indicates this cranidium belongs to a new dimeropygid genus. Dean's specimen might also belong to this genus, but it is so incomplete and poorly preserved that it could represent numerous taxa. It does not, however, belong to *Pseudohystricurus*, as it has large frontal areas, broad interocular fixigenae, and a wide and long anterior border plainly and entirely visible in dorsal view.

Remarks. As understood herein, *Pseudohystricurus* is known only from the upper portion of the Stairsian of northern Laurentia, with a separate species occurring in each of three of the uppermost four zones of the stage recognised by Adrain *et al*. (this volume).

The status and content of Dimeropygidae and the main outstanding phylogenetic problems were discussed by Adrain & Westrop (2007, pp. 338–343). Their main conclusions were: 1) that *Celmus* Angelin 1854, often considered a dimeropygid, is in fact a raymondinid related to such genera as *Glaphurus* Raymond 1905, and *Glaphurina* Ulrich 1930, but not related to dimeropygids; 2) Toernquistiidae Hupé 1953, rehabilitated by Chatterton *et al*. (1998), is a junior subjective synonym of Dimeropygidae; and 3) the most significant question in the phylogenetic structure of the family is how (or whether) a Middle and Late Ordovician group including *Dimeropyge*, *Chomatopyge* Whittington & Evitt 1954, *Mesotaphraspis*, and *Toernquistia* Reed 1896, is related to a mainly Early Ordovician group with different general morphology including *Dimeropygiella*, *Ischyrotoma*, *Parahystricurus*, *Bearriverops* and *Pseudohystricurus*.

With the material described herein, along with silicified material of some early species of *Dimeropyge* from the Darriwilian Table Cove Formation of western Newfoundland, Canada, it is now possible to suggest phylogenetic links between these two groups. Cranidia of *Dimeropyge* sp. nov. 1 from the Table Cove Formation (Fig. 1B, F, I) differ only in minor proportion from small cranidia of *Pseudohystricurus obesus* (Fig. 1A, E, H), with the exception of the unusual pair of long spines on the anterior border of the former (which is an autapomorphy of this species). Anterior and lateral profiles are all but identical, though the *Dimeropyge* species has a short preglabellar field. The species also share very small, narrow palpebral lobes of nearly the same relative size. Small pygidia of *P. obesus* (Fig. 1C) and *Dimeropyge* sp. nov. 2 (Fig. 1D) are also extraordinarily similar, with fine transverse lines of tiny tubercles on the pleurae, paired pleural spines of unequal length on each segment, two tiny spines at the rear of the axis, and a smooth vertical region underlying the pleural region and spines. Librigenae are less strikingly alike, but that of *Dimeropyge* sp. nov. 1 (Fig. 1G) is much more like Early Ordovician dimeropygids that those of later species of *Dimeropyge*, which have strongly inflated genal spines (e.g., *D. spinifera* Whittington & Evitt 1954, pl. 22, figs 31–33). In overall dimensions and genal spine length, the librigenae are reasonably close to those of *P. obesus* (Fig. 1J). Most strikingly, an articulated specimen of *P. obesus* from western Utah illustrated by Demeter (1973, pl. 6, figs 13a-c) appears to show a seven segment thorax, the same unusually low number displayed where known by all species in the derived Middle-Late Ordovician group including *Dimeropyge*. Demeter (1973) described the specimen as a "juvenile" but it is not particularly small for the species and its cranidial and pygidial morphology indicate it is a holaspid. Taken together, this is potentially strong evidence that *Dimeropyge* and the derived Middle-Late Ordovician clade are closely related to *Pseudohystricurus*, and that Dimeropygidae is monophyletic.

Yuan *et al*. (2006) illustrated silicified material of *Pseudopetigurus deprati* Turvey, Zhou & Yuan 2006, from the Dawan Formation (Dapingian) of Hunan, South China. *Pseudopetigurus* is known from species from South China, Bohemia, Kazakhstan and the Urals, ranging in age from Dapingian to early Katian. It has generally been assigned to either Bathyuridae Walcott 1866, Bathyuroidea (e.g., Přibyl & Vaněk 1968; Dean 1973; Mergl 1991) or Isocolidae Angelin 1854 (e.g., Ancygin 1977; Jell & Adrain 2003; Turvey

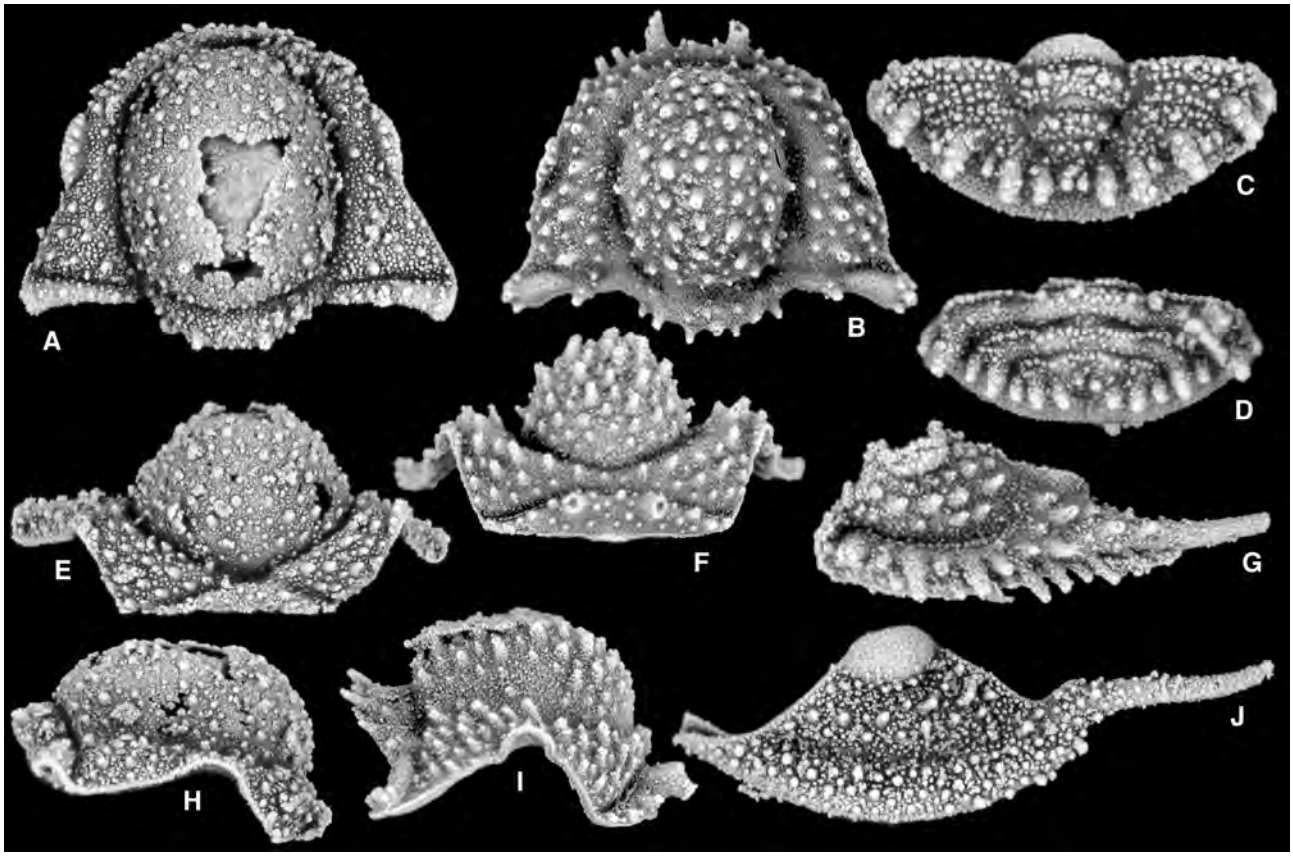
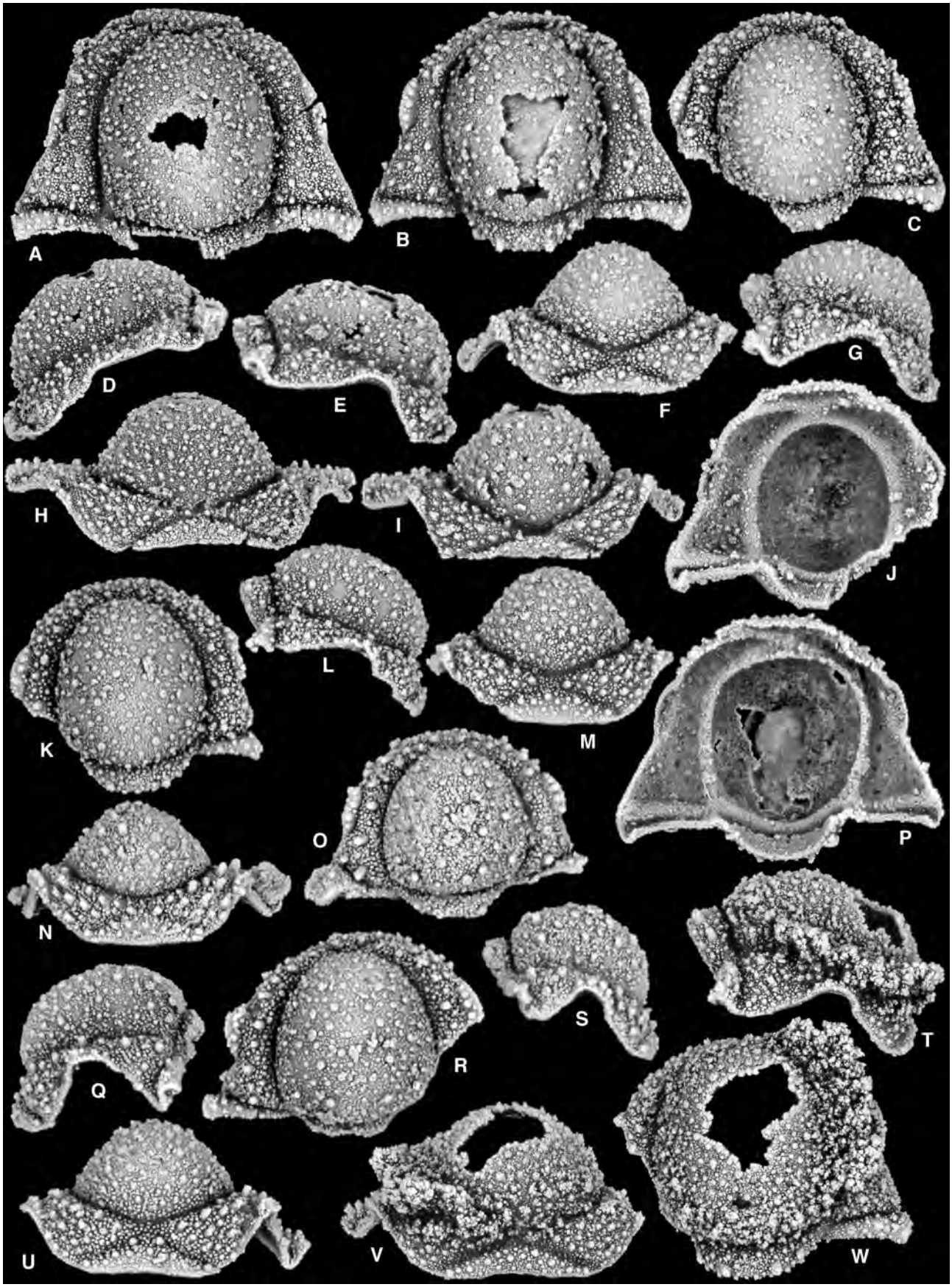


Figure 1. Comparison of morphology of species of *Pseudohystricurus* with that of early species of *Dimeropyge*. **A**, **C**, **E**, **H**, **J**, ***Pseudohystricurus obesus*** Ross 1951, from Section HC6 134.0T m, Garden City Formation (upper Tremadocian; Stairsian; *Pseudohystricurus obesus* Zone), west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA. **A**, **E**, **H**, cranidium, SUI 134788 (see also Fig. 2B, E, I, P), dorsal, anterior, and right lateral views, x25. **C**, pygidium, SUI 134809 (see also Fig. 4J, O, R), dorsal view, x40. **J**, left librigena, SUI 134798 (see also Fig. 3G, I), external view, x30. **B**, **F**, **G**, **I**, ***Dimeropyge* sp. nov. 1**, from the Table Cove Formation (Darriwilian), near Main Brook, Hare Bay, western Newfoundland, Canada. **B**, **F**, **I**, cranidium, GSC 135356, dorsal, anterior, and right lateral views, x20. **G**, left librigena, GSC 135357, external view, x20. **D**, ***Dimeropyge* sp. nov. 2**, locality as for *Dimeropyge* sp. nov. 1, pygidium, GSC 135358, dorsal view, x40.

et al. 2006). However, Yuan *et al*. (2006) demonstrated, convincingly, that *Pseudopetigurus* is a dimeropygid at least superficially similar to *Pseudohystricurus*. In particular, species of the genera share a cranidium with a strongly inflated glabella which overhangs a narrow anterior border. Librigenae are unknown for any species of *Pseudopetigurus*. Pygidia are also unknown for most species, but Yuan *et al*. (2006, text-fig. 4C, D, I, L, P, R) illustrated several examples assigned to *Pseudopetigurus deprati*. These are not closely similar to those of species of *Pseudohystricurus*, as they lack free pleural spines. Nevertheless, the pygidium of *Pseudohystricurus wigglesorum* (Fig. 8R–T, V, X) would be reasonably close to that of *Pseudopetigurus deprati* if the pleural spines were not expressed. Yuan *et al*. (2006, table 1, text-fig. 1) presented a cladistic analysis including species assigned to *Dimeropygiella*, *Ischyrotoma*, *Dimeropyge* and *Pseudopetigurus*, and based largely on an analysis of *Dimeropygiella* and *Ischyrotoma* carried out by Adrain *et al*. (2001). Unfortunately, the analysis of Yuan *et al*. (2006) analysis also included species assigned to *Celmus* and *Glaphurella* Dean 1971. This is understandable, as these taxa were assigned to Dimeropygidae by Adrain (in Jell & Adrain 2003). However, as noted above, we now regard them as Raymondinidae Clark 1924 (see also Adrain 2011). Hence, Yuan *et al*. (2006) likely analysed a polyphyletic ingroup. In addition, the selected outgroups belong to a mixture of hystricurines and hintzecurines, and the nature of any relationship between the outgroups and between the outgroups and the ingroup, remains at best obscure. Nevertheless, Yuan *et al*. (2006) retrieved a monophyletic Dimeropygidae. Based on discussion of a potential close relationship between *Pseudohystricurus* and *Dimeropyge* above, we suggest that this portion of their cladogram is likely generally accurate, but suffers from an incorrect root provided by the unrelated raymondinids and dubiously related outgroup taxa. Also problematical is their retrieval of *Pseudohystricurus obesus* as sister to a *Dimeropygiella*/*Ischyrotoma* clade, rather than to *Dimeropyge*, but this was informed by the incorrect pygidial assignment of Adrain *et al*. (2001), which Yuan *et al*. (2006) used in their codings.

Figure 2. A–**S**, **U**, ***Pseudohystricurus obesus*** Ross 1951, from Section HC6 134.0T m, Garden City Formation (upper Tremadocian; Stairsian; *Pseudohystricurus obesus* Zone), west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA. **A**, **D**, **H**, cranidium, SUI 134787, dorsal, left lateral and anterior views, x20. **B**, **E**, **I**, **P**, cranidium, SUI 134788, dorsal, right lateral, anterior and ventral views, x25. **C**, **F**, **G**, **J**, cranidium, SUI 134789, dorsal, anterior, right lateral, and ventral views, x25. **K**–**M**, cranidium, SUI 134790, dorsal, right lateral and anterior views, x25. **N**, **O**, **S**, cranidium, SUI 134791, anterior, dorsal (*continued opposite*)



and right lateral views, x30. **Q**, **R**, **U**, cranidium, SUI 134792, left lateral, dorsal and anterior views, x30. **T**, **V**, **W**, ***Pseudohystricurus* sp.**, from Section MME 121.6 m, Fillmore Formation (upper Tremadocian; Stairsian; *Pseudoclelandia cornupsittaca* Zone), Middle Mountain, Ibex area, Millard County, western Utah, USA, cranidium, SUI 134793, right lateral, anterior, and dorsal views, x20.

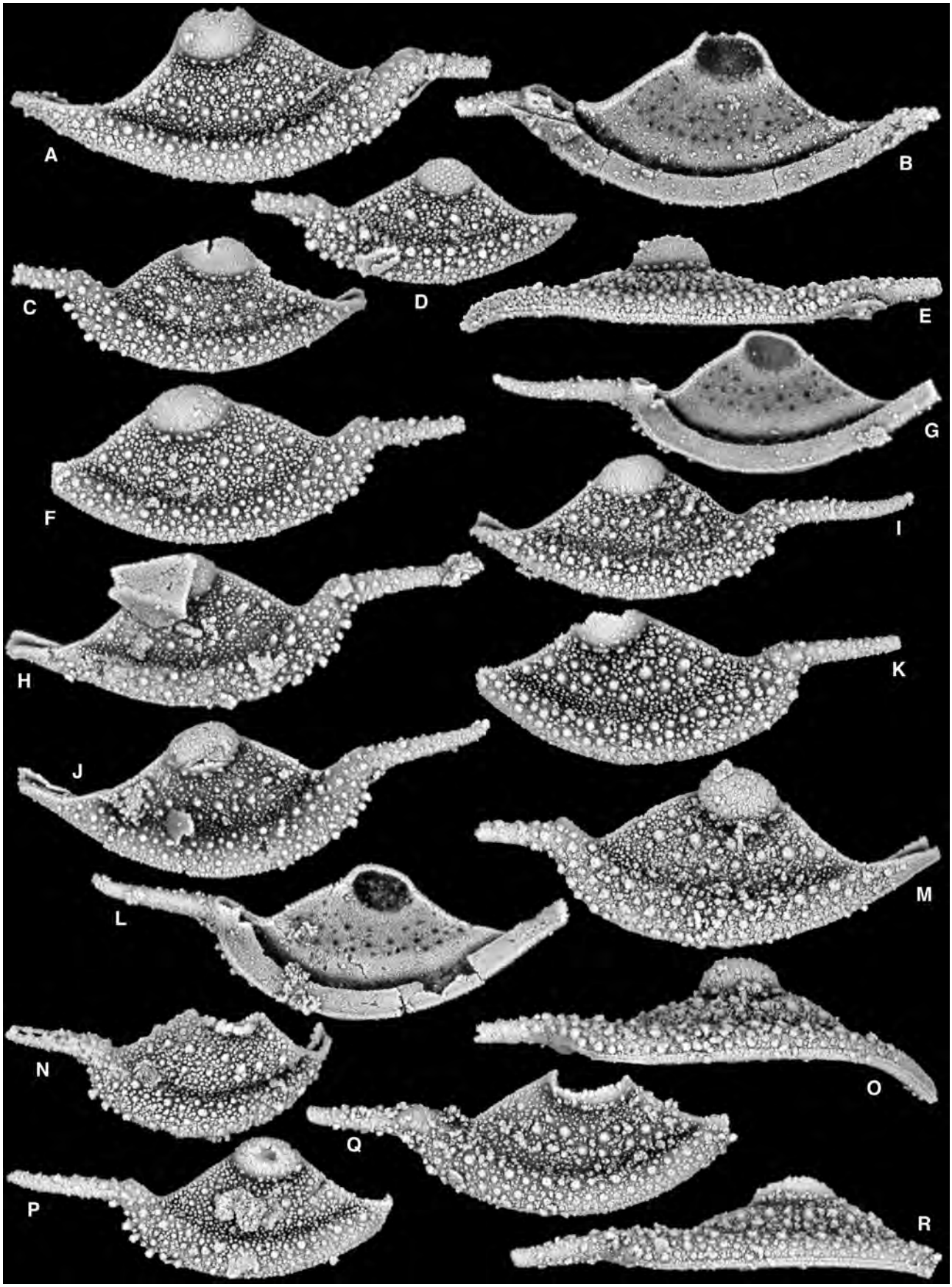


Figure 3. ***Pseudohystricurus obesus*** Ross 1951, from Section HC6 134.0T m, Garden City Formation (upper Tremadocian; Stairsian; *Pseudohystricurus obesus* Zone), west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA. All magnifications are x30. **A**, **B**, **E**, left librigena, SUI 134794, external, internal, and ventrolateral views. (*continued opposite*)

Despite this, it is clear that *Pseudopetigurus* is a dimeropygid, possibly sister to a clade of *Pseudohystricurus*+*Dimeropyge* +derived Middle-Late Ordovician taxa. These ideas will be tested via broader phylogenetic analysis once many more relevant Early Ordovician taxa are described and revised.

Pseudohystricurus obesus Ross 1951 (Figs 1A, C, E, H–J, 2A–S, U, 3–6)

1951 *Pseudohystricurus obesus*; Ross, p. 74, pl. 16, figs 25, 30, 34.
1970 *Pseudohystricurus obesus* Ross; Ross, p. 73.
1973 *Pseudohystricurus obesus* Ross; Terrell p. 88, pl. 5, fig. 1.
1973 Unmentioned specimen (pygidium); Terrell pl. 6, unnumbered figure near centre.
1973 *Pseudohystricurus obesus* Ross; Demeter, p. 64, pl. 6, figs 13, 14.
1997 *Pseudohystricurus obesus* Ross; Ross *et al*., p. 18, 45.
1998 *Pseudohystricurus obesus* Ross; White & Lieberman, p. 113.
2001 *Pseudohystricurus obesus* Ross; Adrain *et al*., p. 953.
2003 *Pseudohystricurus obesus* Ross; Jell & Adrain, p. 434.
2009 *Pseudohystricurus obesus* Ross; Adrain *et al*., p. 593.

Material. The holotype is a cranidium, YPM 18049 (Ross 1951, pl. 16, figs 25, 30, 34), from "Zone F" at HC6, but almost certainly from HC6 134.0T m. Assigned specimens SUI 134787–134792, 134794–134810, from Section HC6 134.0T m, Garden City Formation (upper Tremadocian; Stairsian; *Pseudohystricurus obesus* Zone), west side of Hillyard Canyon, Franklin County, southeastern Idaho, USA; assigned specimens SUI 134236, 134237, 134811–134822, from Section G 48.5 m, Fillmore Formation (upper Tremadocian; Stairsian; *Pseudohystricurus obesus* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Diagnosis. Cephalic sculpture of fine medium and small sized tubercles against a background of dense granules; cranidial posterior projections extended laterally well past lateral edge of palpebral lobes; frontal area relatively small; librigena with narrow lateral border furrow; eye socle lacking inflated raised band; pygidium with relatively long pleural spines.

Description. Cranidial measurements were made on the largest and most complete specimens of Figures 2, 4–6. Cranidium subtrapezoidal in outline, with sagittal length 72.6% (68.0–80.5) maximum width across posterior border, sagittal length 87.6% (83.1–95.8) width across midpoint of palpebral lobes; majority of cranidium covered by prominent sculpture of distinct medium and small sized tubercles, background sculpture of fine granules also present; anterior border subtriangular in outline (in anterior view), with anterior margin strongly arched medially and posterior margin very gently arched medially, border inflated, jutting out a short distance anteriorly, but not beyond the anterior extent of the glabella, sculpture of small densely spaced tubercles present on majority of border, except thin strip along anteroventral margin, which is covered only by fine, densely spaced granules; anterior border furrow deep, moderately broad, strongly arched medially, not visible dorsally on large undeformed specimens, sculpture of fine granules present in furrow on some specimens (Fig. 2M); preglabellar and anterior border furrows medially confluent (see anterior view) forming a broad "X"; preglabellar furrow deep, describing a generally smooth arc in anterior view; frontal areas broadly subtriangular in anterior view, strongly downturned from horizontal, sculpture of fine granules and mixed small and medium sized tubercles, with many tubercles extended into short spines; anterior portion of facial suture forming rounded margin, directed strongly anteromedially from γ forward; glabella with sagittal length 110.0% (103.2–118.5) maximum width, very strongly dorsally inflated and bulbous, with apex sitting very high above fixigenae, anterior margin overhanging anterior margin of cranidium, with sculpture of fine granules overlain by small and medium sized scattered tubercles, size distribution of tubercles varies with some possessing nearly uniform small or medium sized tubercles (e.g., Figs 2K, 5B) and other possessing a mixture of the two sizes (e.g., Fig. 5L); palpebral lobe very small, sliver-like, length from γ to ε 28.2% (24.0–31.9) total cranidial sagittal length, situated far forward on cranidium, with ε situated opposite about widest point of glabella, abaxial margin gently laterally arched, row of prominent tubercles aligned linearly subparallel to length of lobe, smaller tubercles also interspersed on some specimens; lobe set off from fixigena by deep and narrow furrow, anterior and posterior tips narrower; interocular fixigena forming relatively narrow strip; overall figixena narrowest opposite palpebral lobe, becoming wider posteriorly behind palpebral lobe; posterior fixigena widest opposite posterior border, dorsal inflation weak, sloping gently away from glabella with posterolateral corners most strongly downturned from horizontal; fixigena sculpture consists of densely spaced fine granules and larger scattered tubercles, latter sometimes aligned loosely into row subparallel to the lateral margin of the glabella (e.g., Fig. 5C), tubercles also sometimes elongated into short spines; posterior portion of facial suture almost straight, directed posterolaterally from ε posteriorly, course slightly deflected at intersection with posterior border furrow; posterior border furrow deep, narrow along majority of course, although in some specimens furrow lengthens slightly distally (Fig. 5L), almost exactly transverse to slightly anteriorly arched, with portion between axis and fulcrum directed slightly anterolaterally, portion distal to fulcrum directed slightly posterolaterally; fine densely spaced granules present in distal portion of furrow on some specimens (e.g., Fig. 5C); posterior border shortest (exsag.) adjacent to axial furrow, lengthens slightly abaxially toward fulcrum; from fulcrum distally border is progressively lengthened terminating in a subquadrate tip with posterolateral corner rounded and forming a short posteriorly directed projection; anterior margin with course similar to that of posterior border furrow; course of posterior margin also similar, but with portion distal to fulcrum more strongly directed posterolaterally;

C, right librigena, SUI 134795, external view. **D**, right librigena, SUI 134796, external view. **F**, left librigena, SUI 134797, external view. **G**, **I**, left librigena, SUI 134798, internal and external views. **H**, left librigena, SUI 134799, external view. **J**, **L**, left librigena, SUI 134800, external and internal views. **K**, left librigena, SUI 134801, external view. **M**, **O**, right librigena, SUI 134802, external and ventrolateral views. **N**, right librigena, SUI 134803, external view. **P**, right librigena, SUI 134804, external view. **Q**, **R**, right librigena, SUI 134805, external and ventrolateral views.

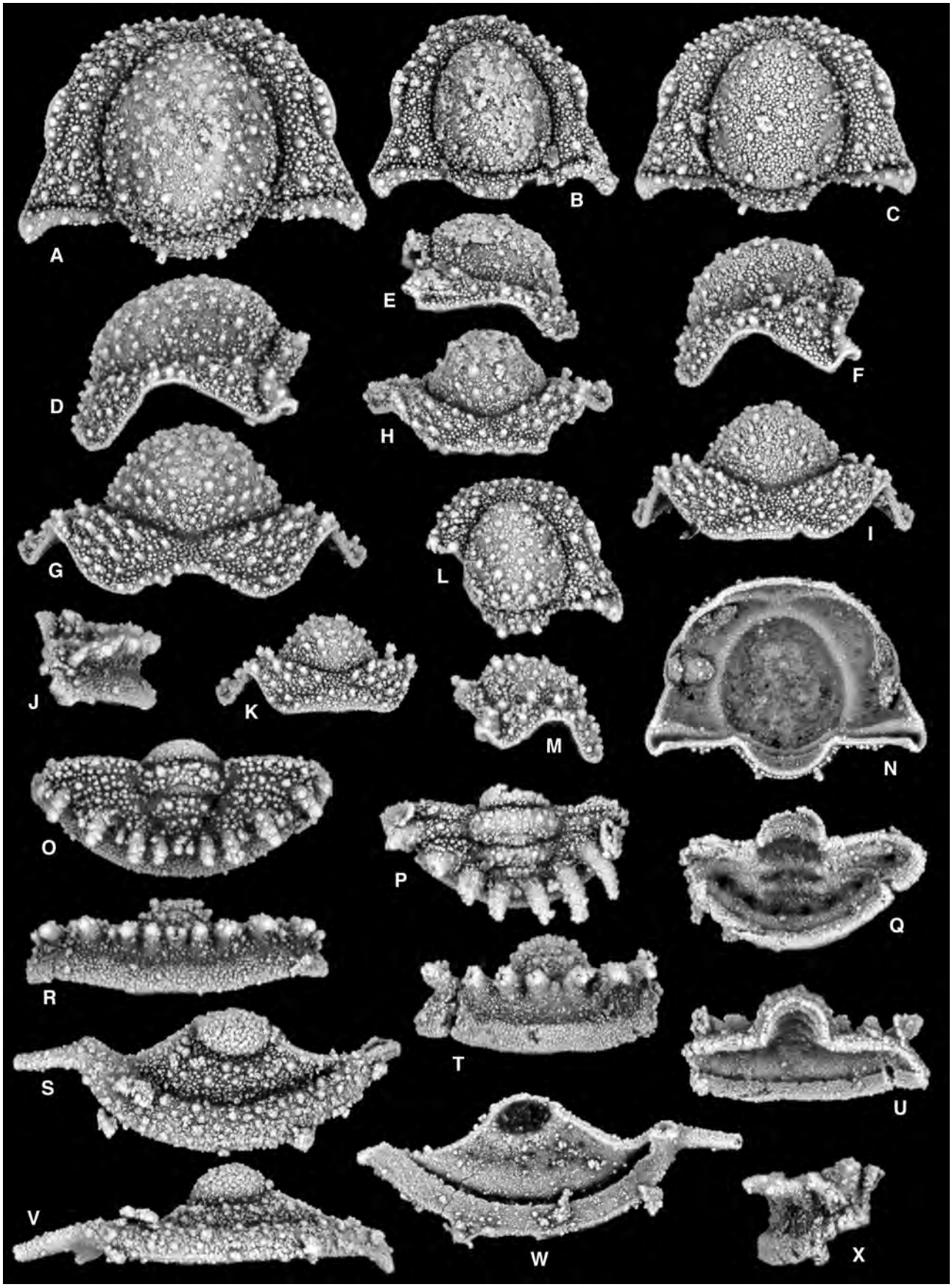


Figure 4. ***Pseudohystricurus obesus*** Ross 1951. **A**–**O**, **R**, specimens from Section HC6 134.0T m, Garden City Formation (upper Tremadocian; Stairsian; *Pseudohystricurus obesus* Zone), west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA. **A**, **D**, **G**, cranidium, SUI 134806, dorsal, left lateral, and anterior views, x30. **B**, **E**, **H**, cranidium, (*continued opposite*)

main face of border is flexed so that it faces anteriorly when observed in lateral profile (Fig. 5E), SO similar to posterior border furrow in depth and breadth, gently curved posteriorly around rounded posterior margin of glabella, slightly shallower at intersection with axial furrow; LO long medially with sagittal length 12.9% (10.9–16.5) total cranidial length, progressively shorter (exsag.) abaxially, with distal tips nearly pinching out, anterior and posterior margins posteriorly arched, with curve of posterior margin stronger, in lateral profile LO slopes posteriorly away from main portion of glabella, entire LO covered by densely spaced fine granules, larger tubercles also present and mostly arranged along posterior margin of LO as seen in dorsal view, with distinct median tubercle situated about equidistant from anterior and posterior margins of LO, additional pair of prominent tubercles present on either side of median tubercle, but closer to posterior margin of LO, this tubercle pair is often elongated into a pair of very short spines, even on larger specimens (e.g., Fig. 2B); axial furrows smoothly confluent with preglabellar furrow and SO so that glabella appears circumscribed by a continuous furrow, axial furrow deep, slightly wider opposite medial portion of glabella, slightly shallower at intersection with posterior border furrow, and still shallower behind this contact, width between intersection of axial furrows with posterior cranidial margin 41.3% (36.8–46.7) maximum cranidial width; doublure beneath LO broad, with anterior margin nearly reaching ventral expression of SO, strongly flexed upward against ventral surface of LO, posterior margin appears slightly thickened forming a rim; narrow ventral groove present along ventral margin of posterior border (Fig. 5F).

Librigena elongate; field forming broad long band, with width opposite anterior facial suture 35.6% (32.3–38.4) maximum field length, width of field opposite posterior facial suture 38.5% (35.8–43.2) maximum field length, moderately inflated, sitting a short distance above lateral border in ventrolateral view, sculpture of densely spaced fine granules overlain by small and medium sized isolated tubercles, some elongated into short spines, tubercles aligned in band across middle portion of field, sometimes tubercles appear loosely arranged into rows (e.g., Fig. 3K); anterior facial suture gently concave across field, with slight change in course across lateral border furrow; posterior facial suture just slightly convex across proximal portion of field, strongly bent (almost 90°) at intersection with border furrow, nearly straight across posterior border; lateral border furrow moderately deep and broad, slightly shallower at genal angle, covered by sculpture of fine granules that continue without disruption from field across furrow and onto lateral border; lateral border broad, with portion anterior to genal spine slightly wider, dorsal inflation strong giving border rolled appearance in external view, lateral margin from tip of anterior projection to base of genal spine describing broadly curved arc, curve slightly tighter just before genal spine, sculpture of small densely spaced tubercles covers dorsal aspect, with finer granules interspersed, some tubercles elongated, granules also present on lateral aspect of border, ventral margin outlined by series of a few thread like raised lines (Fig. 3E), also just visible along ventral portion of lateral margin in internal view (Fig. 3G), lines terminate at base of genal spine and do not continue onto spine; anterior projection long, with length about 32% maximum length of field, anterior tip slightly downturned from horizontal (Fig. 3E), sculpture from lateral border continues without obvious change; ventrally, broad doublure present beneath lateral border and anterior projection, flexed gently upwards toward ventral surface. Panderian notch small and situated just adjacent to base of genal spine, doublure surface smooth; posterior border and associated ventral doublure greatly reduced; genal spine relatively long, with length about 63% that of genal field, slender, cylindrical in cross section, distally tapering to a point with tip slightly hooked (Fig. 3I, J), tuberculate sculpture continues from border onto dorsal aspect of spine, but becomes progressively subdued toward spine tip, ventral aspect with very faint sculpture of fine granules, angle between spine and lateral border obtuse; visual surface relatively small, bulbous, sitting high above main portion of field in ventrolateral view, distance between intersection of visual surface with anterior and posterior facial sutures 34.8% (29.6–41.8) width of field; eye socle very narrow, expressed primarily as band of small tubercles bounding base of visual surface; socle set off from field by narrow furrow, largely covered by granulate sculpture.

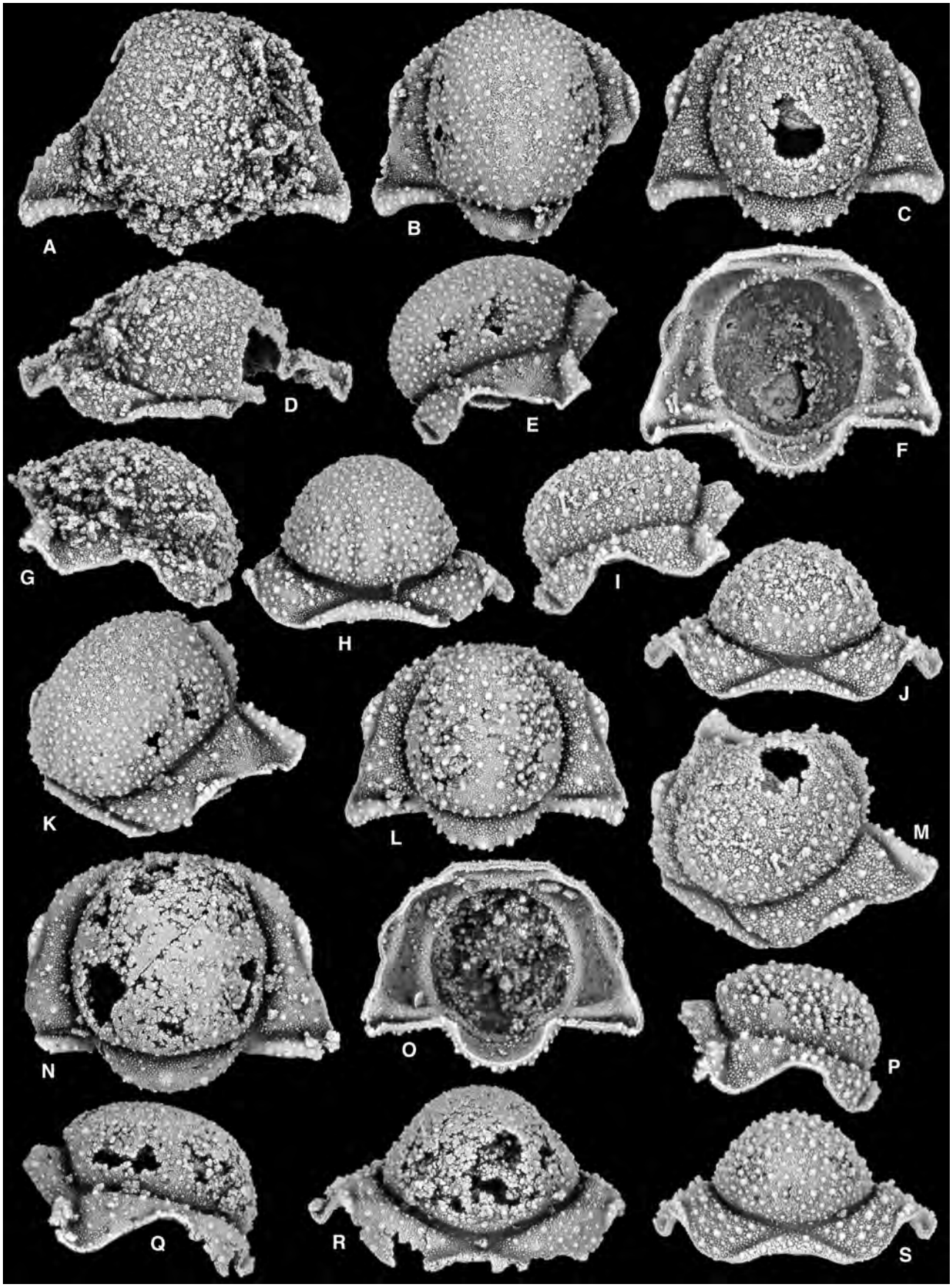
Hypostome and rostral plate unknown.

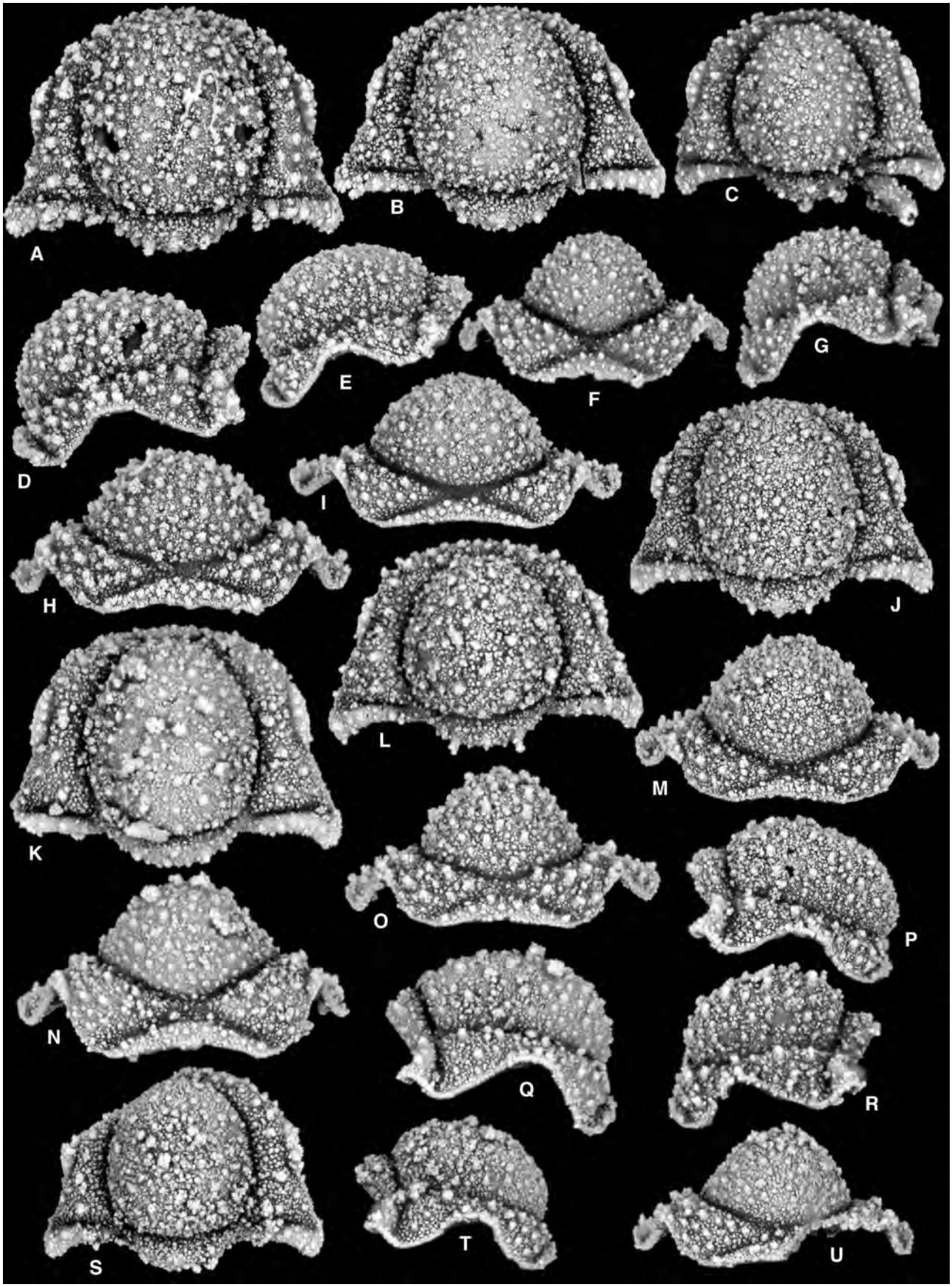
Demeter (1973, pl. 6, fig. 13) figured an articulated specimen of *P. obesus*, which is the only source of information for thoracic morphology for the species. Unfortunately, the images are small and rather unclear, making details of the thorax difficult to ascertain. The specimen appears to have seven thoracic segments, with the fourth and fifth segments

(*continued from opposite*) SUI 134807, dorsal, right lateral, and anterior views, x30. **C**, **F**, **I**, **N**, cranidium, SUI 134808, dorsal, left lateral, anterior, and ventral views, x30. **J**, **O**, **R**, transitory pygidium, SUI 134809, left lateral, dorsal, and posterior views, x40. **K**–**M**, cranidium, SUI 134810, anterior, dorsal, and right lateral views x30. **P**, **Q**, **S**–**X.** specimens from Section G 48.5 m, Fillmore Formation (upper Tremadocian; Stairsian; *Pseudohystricurus obesus* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. All magnifications are x30. **P**, **Q**, **T**, **U**, **X**, pygidium, SUI 134237, dorsal, ventral, posterior, anterior, and right lateral views. **S**, **V**, **W**, right librigena, SUI 134811, external, ventrolateral, and internal views.

Figure 5 (*overleaf*)**.** ***Pseudohystricurus obesus*** Ross 1951, from Section G 48.5 m, Fillmore Formation (upper Tremadocian; Stairsian; *Pseudohystricurus obesus* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. **A**, **D**, **G**, cranidium, SUI 134812, dorsal, anterior, and right lateral views, x17. **B**, **E**, **H**, **K**, cranidium, SUI 134813, dorsal, left lateral, anterior, and oblique views, x17. **C**, **F**, **I**, **J**, **M**, cranidium, SUI 134814, dorsal, ventral, left lateral, anterior, and oblique views, x20. **L**, **O**, **P**, **S**, cranidium, SUI 134236, dorsal, ventral, right lateral, and anterior views, x20. **N**, **Q**, **R**, cranidium, SUI 134815, dorsal, right lateral, and anterior views, x20.

Figure 6 (*page 225*)**.** ***Pseudohystricurus obesus*** Ross 1951, from Section G 48.5 m, Fillmore Formation (upper Tremadocian; Stairsian; *Pseudohystricurus obesus* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. **A**, **D**, **H**, cranidium, SUI 134816, dorsal, left lateral, and anterior views, x25. **B**, **E**, **I**, cranidium, SUI 134817, dorsal, left lateral, and anterior views, x25. **C**, **F**, **G**, cranidium, SUI 134818, dorsal, anterior, and left lateral views, x30. **J**, **M**, **P**, cranidium, SUI 134819, dorsal, anterior, and right lateral views, x25. **K**, **N**, **Q**, cranidium, SUI 134820, dorsal, anterior, and right lateral views, x30. **L**, **O**, **R**, cranidium, SUI 134821, dorsal, anterior, and left lateral views, x30. **S**–**U**, cranidium, SUI 134822, dorsal, right lateral, and anterior views, x30.


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U

each possessing an axial spine (Demeter 1973, pl. 6, fig. 13C). Each segment is covered by tubercles similar to those on the cranidium and pygidium. The larger tubercles appear to be arranged linearly along each segment.

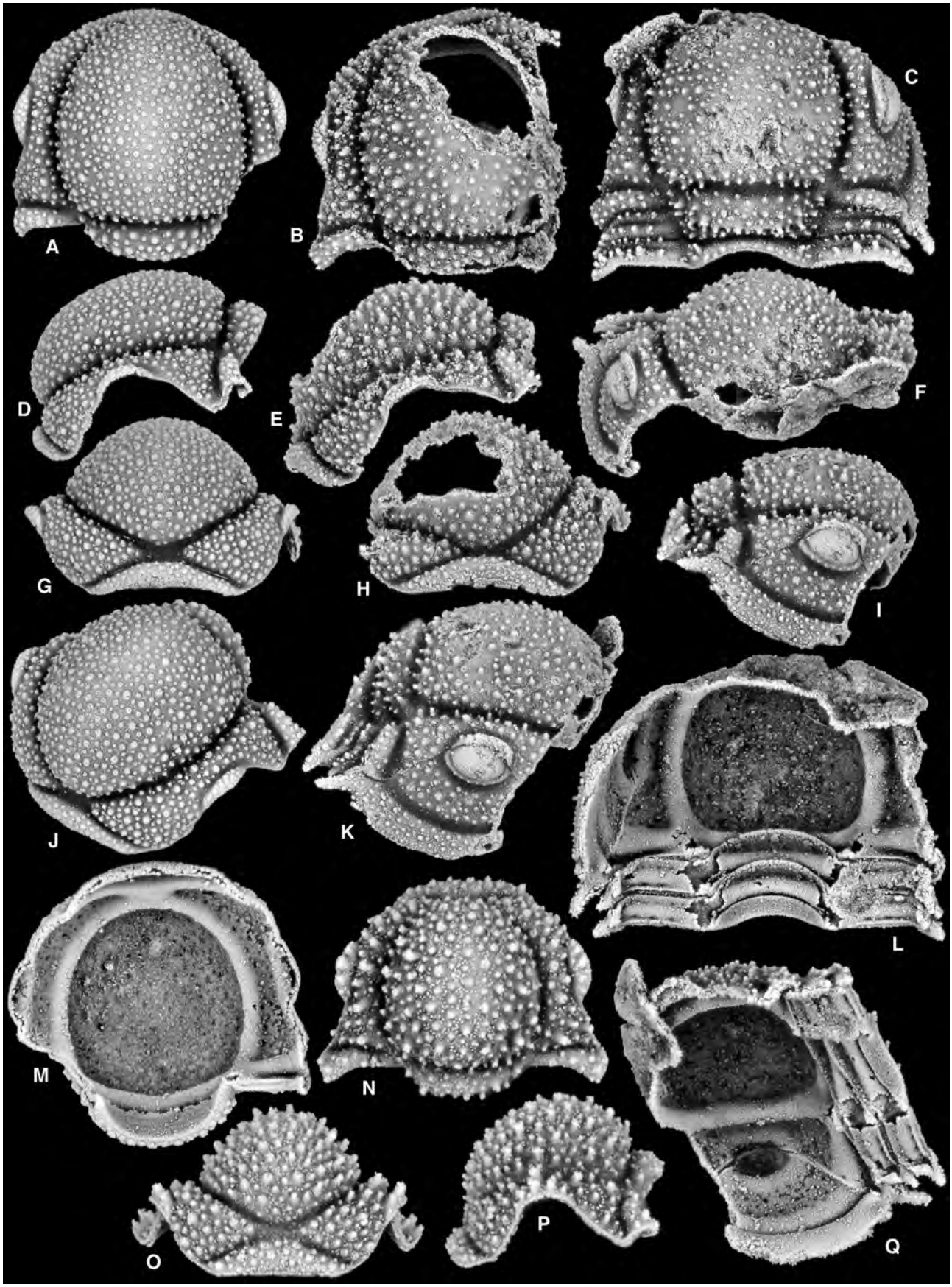
Pygidium with width about two times length; axis strongly dorsally convex, composed of three clearly defined segments and minute fourth segment, widest across midline of first axial segment, strongly tapering posteriorly with width across anterior margin of third segment 64.2% maximum axial width; first axial segment long (sag.; exsag.) with length (including pseudo-articulating half-ring of second segment) 37.3% pygidial length (excluding articulating half-ring), maximum width about one third maximum pygidial width, anterior margin gently anteriorly arched, posterior margin slightly more strongly posteriorly arched, strongly dorsally inflated so that segment sits above main profile of axis in lateral view; second axial segment shorter (sag.; exsag.) and narrower than first, slightly shorter sagittally than exsagittally, posterior margin nearly transverse, dorsal inflation poor compared to first segment; third axial segment much smaller (sag.; exsag; tr.) than previous two; fourth segment expressed as small isolated inflated region between fourth pleural spine pair; pseudo-articulating half-ring of second segment clearly developed, small, lenticular, with length 29.0% that of first axial segment (including pseudo-articulating half-ring); pseudo-articulating half-ring of third segment largely merged with second segment, barely visible; sculpture of coarse granules/small tubercles covers axial segments, except for pseudo-articulating half-ring of second segment (subdued fine granules); articulating half-ring large, crescent-shaped, with anterior margin apparently strongly anteriorly bowed and posterior margin less so, sagittal length apparently less than that of first segment, sculpture of subdued fine granules; axial ring furrows deep, narrow, with posterior furrows slightly shallower; axial furrow deepest opposite axial ring furrows, otherwise shallow, narrow, strongly laterally bowed around lateral margins of first axial segment; pleural region with first pleural and interpleural furrow narrow, but clearly defined; first pleural furrow deepest at fulcrum, shallower adaxially; first interpleural furrow incised along entire course; anterior band of first pleural segment short, distal tip slightly longer; posterior band similarly short near axis, but progressively longer abaxially, with distal tip apparently ending in free spine, but broken on either side of largest specimen; second pleural segment much smaller, with short anterior band terminating at border furrow, posterior band developed into moderately long spine, in dorsal view spine curved with proximal portion directed posterolaterally and distal portion directed more strongly posteriorly, in lateral and posterior views spine directed upward and back with distal tip slightly curved downward (Fig. 4T, X), distal spine tip extended past pygidial margin in dorsal view; third pleural segment composed of spine developed from posterior band, with anterior band greatly reduced, spine orientation similar to that of second segment, but directed slightly more posteriorly, and distal tip extended beyond that of second spine; fourth pleural segment expressed primarily as spine pair, with anterior pleural band not clearly developed, spines apparently shorter than those of third pair; pleural region between axis and border furrow with sculpture of coarse granules, spines with sculpture of subdued fine granules; border furrow relatively shallow, very broad, oriented almost vertically (Fig. 4X) so that border is barely visible in dorsal view, distinctly separating pleural spines from border, sculpture of scattered granules; pygidial border of similar breadth as furrow and oriented vertically, sculpture of densely spaced fine granules; border and border furrow together form short vertical wall beneath pleural region and axis; pygidial margin broadly rounded in dorsal view, with ventral margin nearly transverse in posterior view; doublure beneath border relatively narrow, flexed upward and situated flush against vertically oriented border.

Ontogeny. In addition to an overall increase in size, ontogenetic changes include: elongated tubercles on cranidium become shorter and less spine like, with tubercle pair on LO retaining the most elongation; librigenal field broadens; distal tips of anterior pleural bands developed into very short and think spines on transitory pygidium but in holaspis become reduced and eventually absent; spines of posterior pleural bands develop into longer more robust spines; axis becomes broader; length increases relative to width so that pygidium is narrower.

Remarks. Material of *Pseudohystricurus obesus* from the type locality in southeastern Idaho is on average smaller and more juvenile than the sample recovered from the Fillmore Formation in western Utah. As is generally true of the faunas, specimens from the Garden City Formation have finer preservation of surface detail but are frequently partially compacted. Those from the Fillmore Formation are relatively undistorted but feature slightly coarser silicification. Accounting for these preservational factors, when similarly sized, relatively undistorted specimens from either region are compared (e.g., Fig. 2B, E, I, P vs. Fig. 5L, O, P, S), no consistent differences can be observed and there is no question the occurrences represent the same species.

Pseudohystricurus obesus differs from *P. wigglesorum* in the following ways. The cephalic tuberculate sculpture of *P. wigglesorum* is relatively larger, and lacks the fine background granulation seen in *P. obesus*. The posterior cranidial projections of *P. wigglesorum* extend laterally only a short distance past the palpebral lobes; they are much more laterally extended in *P. obesus*. LO is covered with medium sized tubercles across its entire dorsal surface in *P. wigglesorum*; it is mostly free of tubercles except along the posterior edge and the median node, and displays only fine granulation in *P. obesus*. Similarly, the interocular fixigena and posterior fixigena are much more tuberculate in *P. wigglesorum*. In anterior cranidial view, the frontal areas of *P. wigglesorum* have significantly larger dimensions. The librigena of *P. wigglesorum* has an eye socle of an inflated narrow band with a row of tiny tubercles on it; that of *P. obesus* retains the tubercle row, but the band is all but effaced. The librigenal lateral border furrow is broad and deep in *P. wigglesorum*; it is barely more than a change in slope between the field and the lateral border in *P. obesus*. The genal spine of *P. wigglesorum* is shorter. The pygidium of *P. wigglesorum* has stronger dorsal tuberculate sculpture, much shorter pleural spines, and a vertical region beneath the spines which is distinctly taller medially, versus about the same height everywhere in *P. obesus*.

Figure 7. ***Pseudohystricurus wigglesorum*** sp. nov., from Section HC6 124.0 m, Garden City Formation (upper Tremadocian; Stairsian; *Bearriverops alsacharovi* Zone), west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA. **A**, **D**, **G**, **J**, **M**, cranidium, holotype, SUI 134823, dorsal, left lateral, anterior, oblique, and ventral views, x20. (*continued opposite*)



B, **E**, **H**, cranidium, SUI 134824, dorsal, left lateral, and anterior views, x20. **C**, **F**, **I**, **K**, **L**, **Q**, cephalon and anterior thoracic segments, SUI 134825, dorsal, anterior, right lateral, external librigenal, ventral, and internal librigenal views, x20. **N**–**P**, cranidium, SUI 134826, dorsal, anterior, and left lateral views, x30.

Pseudohystricurus wigglesorum sp. nov. (Figs 7, 8)

Material. Holotype, cranidium, SUI 134823 (Fig. 7A, D, G, J, M), and assigned specimens SUI 134824–134832, from Section HC6 124.0 m, Garden City Formation (upper Tremadocian; Stairsian; *Bearriverops alsacharovi* Zone), west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA.

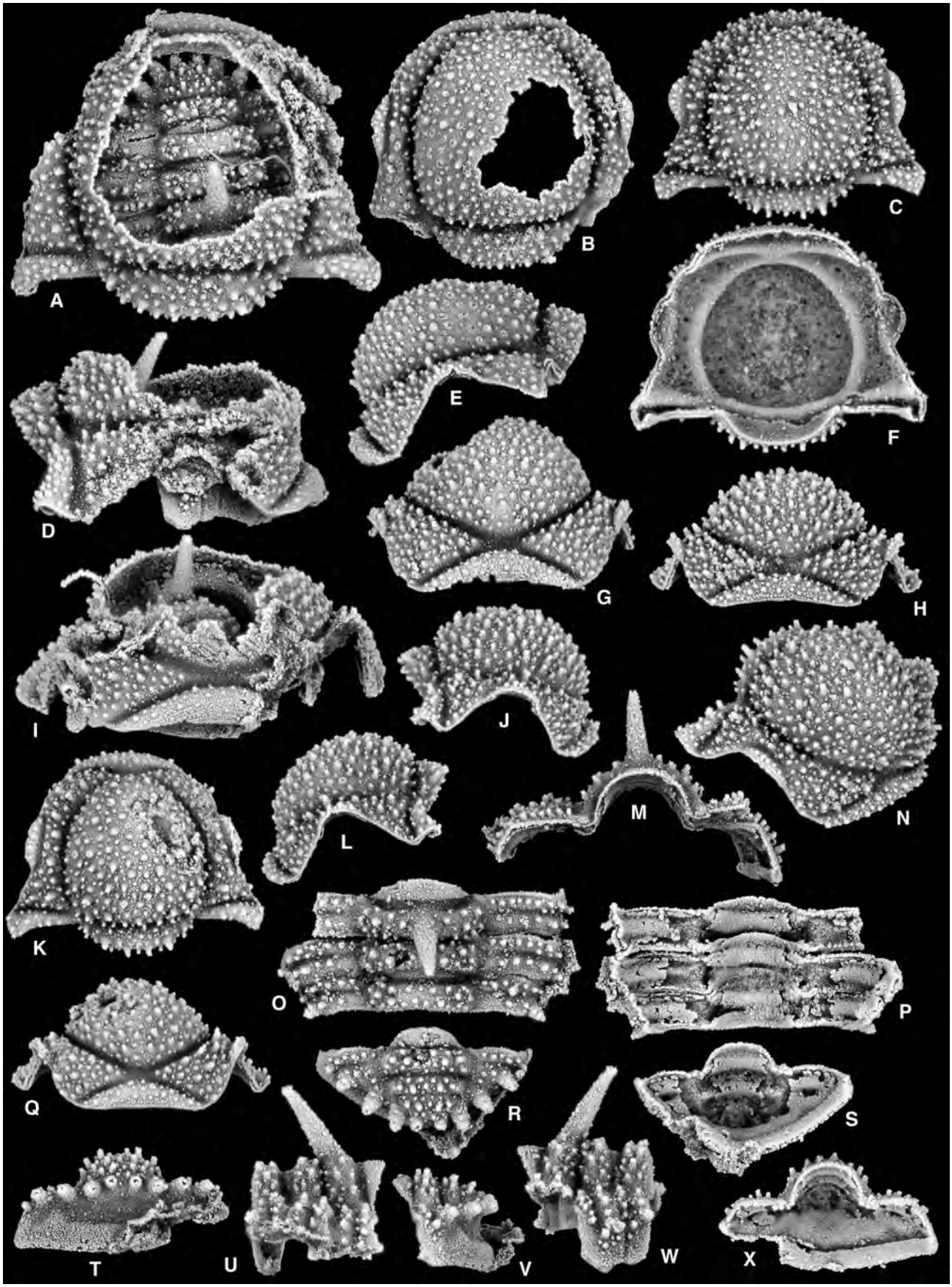
Etymology. After The Wiggles.

Diagnosis. Cephalic sculpture relative coarse and lacking background tuberculation; LO, interocular and posterior fixigenae with prominent tuberculate sculpture on all dorsal surfaces; posterior projections not extended laterally far past palpebral lobes; frontal areas relatively large; eye socle of inflated narrow band; librigenal lateral border broad and deep and genal spine short; pygidial pleural spines short.

Description. Cranidium with sagittal length 80.5% (74.0–89.0) width across posterior border, 92.0% (84.5–96.2) width across midpoint of palpebral lobes, very densely tuberculate, with some tubercles elongate; glabella with sagittal length 104.6% (97.3–110.3) maximum width, bulbous, strongly dorsally inflated, in lateral profile apex just opposite rear of palpebral lobe, portion posterior to apex gently sloping posteroventrally, portion anterior to apex more strongly sloping anteroventrally with anteriormost portion of glabella strongly downturned from horizontal so that it is subvertical, sculpture of densely spaced small and medium sized tubercles covers glabella, sculpture of fine granules also present between tubercles most obviously along sagittal axis and adjacent areas, lateral areas with granules more subdued to absent; preglabellar furrow deeply incised, forming broad and deep "V" in anterior view, intersects anterior border furrow medially with the two forming a broad "X" shape in anterior view; medial region where furrows merge, forms wide and long depressed rectangular region (e.g., Fig. 8Q), width of region about 21% maximum width of anterior border in anterior view; anterior border furrow of similar depth to preglabellar furrow, but slightly narrower, strongly upwardly bowed in anterior view, partially visible in dorsal view; anterior border with medial portion just visible in dorsal view, best observed in anterior view with posterodorsal margin much more strongly bowed than anteroventral margin, which is nearly transverse, width just slightly narrower than glabella in anterior view, longest sagittally, progressively shorter abaxially, sculpture of prominent tubercles covers anterior border with fine granules interspersed, thin strip situated medially along anteroventral margin with sculpture only of fine granules; frontal areas broad, best observed in anterior view as strongly downturned from horizontal plane, sculpture nearly identical to that of glabella; anterior facial sutures directed slightly anteromedially from γ forward, then more strongly directed anteromedially; palpebral lobes minute, with length from γ to ε 27.1% (24.2–28.9) total cranidial length, maximum width 67.8% (60–73.3) that of interocular fixigena (opposite midpoint of palpebral lobe), lobes with moderate independent inflation, appearing ridge like in anterior view, majority of lobe sloping anteroventrally in lateral profile with only small posterior portion sloping posteroventrally; lobe completely set off from interocular fixigena by distinctly incised furrow, furrow oriented just slightly anteromedially; interocular fixigena narrow, widening posteriorly into posterior fixigena, with minimum width of interocular fixigena 40.4% (35.1–44.4) maximum width of posterior fixigena, slope similar to that of palpebral lobe; posterior fixigena narrowest just behind ε, widening posteriorly with maximum width achieved opposite posterior border furrow, posterolateral corners strongly downturned from horizontal plane; interocular and posterior fixigena with sculpture similar to that of frontal areas and glabella; posterior border furrow long, deep, slightly shallower and longer (Fig. 7A) adjacent to contact with axial furrow, distal portion adjacent to posterior facial suture also slightly longer, smooth; posterior border shortest adjacent to axial furrow, lengthens abaxially, dorsal inflation strong (Fig. 7D), posterior margin between axis and fulcrum nearly transverse to slightly posterolaterally directed, portion distal to fulcrum more strongly directed posterolaterally, sculpture of densely spaced small and medium sized tubercles with subdued fine granules present between tubercles; short strip of doublure present ventrally beneath posterior border, with deep articulating groove developed along transverse axis (Fig. 7M); posterior facial suture nearly straight, directed posterolaterally, with course slightly disrupted at intersection with posterior border furrow; SO deep, with length similar to that of posterior border furrow, gently posteriorly bowed to nearly transverse; LO long, with sagittal length 13.3% (11.5–14.3) that of cranidium, progressively shorter abaxially, with distal tips pinched to a distinct point, course of anterior margin similar to that of SO, posterior margin more strongly posteriorly bowed, in lateral profile LO strongly sloped posteriorly (Fig. 8E), sculpture of densely spaced medium and small sized tubercles with tubercles along posterior margin sometimes more strongly elongated (e.g., Fig. 8A), posteriormost tubercles visible in ventral view (Fig. 7M); doublure beneath LO forming broad largely smooth surface (Figs 7M, 8F), few very faint lines run across doublure subparallel to transverse margin.

Librigena with visual surface bulbous, separated from socle by narrow, relatively shallow furrow; eye socle relatively broad, strongly inflated, sculpture of very small, faint tubercles aligned in row along socle; socle separated from field by broad, incised furrow, width similar to that of lateral border furrow, smooth; field slightly broader posteriorly than anteriorly, sculpture of medium and small tubercles with very subdued background sculpture of fine granules; anterior margin of librigena not preserved on recovered specimen; posterior facial suture sinuous across field, sharp change in course at intersection with posterior border; posterior border and furrow greatly reduced; lateral border furrow very broad, without obvious sculpture, describing gently curved arc mirroring lateral margin of librigena; lateral border broad, sculpture of small tubercles sitting above densely spaced finer granules present on main external portion of field, lateral margin with granules only, few coarse lines present along ventrolateral margin (Fig.

Figure 8. ***Pseudohystricurus wigglesorum*** sp. nov., from Section HC6 124.0 m, Garden City Formation (upper Tremadocian; Stairsian; *Bearriverops alsacharovi* Zone), west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA. **A**, **D**, **I**, cranidium (attached thorax and pygidium illustrated separately, with separate specimen numbers), SUI 134827, dorsal, right lateral, and anterior views, x20. **B**, **E**, **G**, cranidium, SUI 134828, dorsal, left lateral, and anterior views, x22. **C**, **F**, **H**, **J**, **N**, cranidium, SUI 134829, dorsal, ventral, anterior, right lateral, and oblique views, x22. **K**, **L**, **Q**, cranidium, SUI 134830, (*continued opposite*)



dorsal, left lateral, and anterior views, x20. **M**, **O**, **P**, **U**, **W**, thoracic segments (from same individual as pygidium of Fig. 8R), SUI 134831, anterior, dorsal, ventral, right lateral, and left lateral views, x20. **R**–**T**, **V**, **X**, pygidium (from same individual as thoracic segments of Fig. 8O), SUI 134832, dorsal, ventral, posterior, left lateral, and anterior views, x20.

7L); genal spine short, thorn-like; broad doublure present beneath lateral border, inner margin mirroring arc of lateral border furrow, small depression present along outer portion of doublure adjacent to genal angle. Panderian notch small, adjacent to genal angle almost in line with genal spine (Fig. 7Q).

Hypostome and rostral plate unknown.

Thorax known from two articulated anterior segments (Fig. 7C, F, I, K, L, Q) and three articulated posterior segments (Fig. 8M, O, P, U, W). Posterior segments were articulated with pygidium (see Fig. 8A) at time of collection and represent the three posteriormost segments of *P. wigglesorum*. Recovered segments possess the following general morphology: axis strongly convex (Fig. 8M); articulating half ring large, lenticular, with anterior margin more strongly bowed than posterior margin, sculpture of subdued fine granules; ring furrow best seen on anterior segment of posterior three segments (Fig. 8O), deep, very long, medial portion almost exactly transverse, with distal tips slightly pinched and directed anterolaterally; axial lobe covered with sculpture of prominent isolated small tubercles that are sometimes arranged loosely into two rows; large axial spine present on third segment from posterior, spine tapers to a point distally, directed upward and back from main profile of axis, in dorsal view spine appears to originate from posterior half of axial ring, in lateral view spine appears to originate from entire length of axial ring; axial furrow shallow, gently bowed laterally around abaxial margin of each axial ring; pleural region with anterior band slightly shorter (exsag.) than posterior band, portion of pleurae between axial furrow and fulcrum held nearly parallel to horizontal plane, portion of pleurae distal to fulcrum strongly downturned from horizontal; anterior and posterior bands covered with tubercles, some tubercles elongated into short spines, some segments with tubercles arranged in rows (Fig. 8O), tubercle rows also visible ventrally (Fig. 7L), sculpture of fine granules interspersed between tubercles, with distal tips of at least posterior two segments with sculpture of subdued fine granules only (Fig. 8W); pleural furrow shallow adjacent to axis, becoming deep and relatively long toward fulcrum and abaxially adjacent to fulcrum, furrow terminates a short distance away from pleural tip so that anterior and posterior bands are merged distally forming a short pointed tip on posterior segments and more of a short spine similar to librigenal spine on anterior segments; small triangular doublure developed beneath distal tip of pleurae, with small secondary protrusion developed along anterior margin (Fig. 7L); anterior margin of anterior pleural band bounded short inflated rim, rim shortest adjacent to axis and slightly lengthening abaxially, set off from band by very narrow and shallow furrow, rim articulates with narrow groove present ventrally on next segment (Fig. 7L); doublure beneath axis broad, smooth (Fig. 7L), mirroring articulating half ring of next segment anteriorly.

Pygidium with maximum width 205.2% sagittal length, dorsoventrally tall; anterior margin (excluding articulating half-ring) almost parallel to transverse axis, with very minute thorn-like spine developed on anterolateral corner (Fig. 8V); lateral and posterior margins broadly rounded; articulating half-ring large with sagittal length 81.3% that of first axial segment, 23.6% of axial length (excluding articulating half-ring, and 16.9% total pygidial length, anterior margin strongly arched, posterior margin nearly transverse and sitting just level with first axial segment in lateral profile, sloping gently anteriorly toward thorax so that anterior portion sits just below first axial segment, sculpture of subdued fine granules; axis of four segments, strongly dorsally convex (Fig. 8X), gently tapering posteriorly with width of first segment 145.5% that of third segment (across anterior margin); first axial segment large, with width 40.5% maximum pygidial width, sagittal length 29.1% sagittal axial length (excluding articulating half-ring); second and third axial segments progressively smaller than first, clearly defined; fourth segment minute, less clearly defined, best observed in lateral view by independent row of small tubercles behind third segment; first axial segment with strongest dorsal inflation and sitting the highest in lateral profile, posterior segments progressively less inflated and sitting closer to pleural region; pseudo-articulating half-ring of second segment expressed, but very short sagittally; pseudo-articulating half-rings of subsequent segments not clearly expressed; axis covered with sculpture of prominent small and medium sized tubercles, larger tubercles sometimes elongated into short spines, a few fine granules are interspersed between tubercles, tubercles on second axial segment are loosely arranged into two rows, with an anterior row of smaller tubercles and a posterior row of slightly larger and elongated tubercles, third axial segment appears to have the same tubercle arrangement; tubercles on first and second axial segments directed almost vertically in lateral profile, those of third and fourth segments directed more posterolaterally; first axial ring furrow deep, moderately narrow, nearly transverse; second axial ring furrow similar to first; third axial ring furrow much shallower overall with only distal tips more deeply incised, slightly shorter than first and second ring furrows; fourth axial ring furrow very faint, just barely setting off fourth segment from third; axial furrows very shallow, forming slightly depressed region between axis and pleural region; pleural region with first pleural segment the most clearly developed into distinct anterior and posterior bands; anterior band of first segment short, with distal tip developed into very small and short tubercle-like pleural spine, with sculpture of small and medium sized tubercles (smaller than spine) loosely arranged linearly along band; posterior band of first segment slightly longer (exsag.), with distal tip developed into short, rounded spine; first pleural furrow deep adjacent to fulcrum, pinches out adaxially toward axis and nearly effaced adjacent to axis; interpleural furrow faint, but clearly separates first pleural segment from second; subsequent pleural segments with only posterior band clearly developed and primarily visible due to distal tip being developed into prominent spine; spine pair of second and third segments largest and directed posterolaterally, that of fourth segment much smaller (in both diameter and length) and directed almost exactly posteriorly; border furrow and border oriented almost vertically and largely obscured in dorsal view by pleural spines, border furrow longest medially (Fig. 8T), much narrower with course disrupted between first and second pleural spines where small triangular protrusion from border intrudes into border furrow region (Fig. 8T, V), furrow continues to narrow toward point opposite distal tip of anterior band of first pleural segment, does not reach anterior pygidial margin, in lateral profile border furrow gently concave, subvertical behind axis; border broad, with length behind axis slightly shorter than that of furrow, border longer between first and second pleural bands, covered with sculpture of very densely spaced fine granules; relatively narrow doublure present beneath border, flexed upward against vertical border, sculpture of fine granules, much less densely spaced on dorsal surface of border, additional

sculpture of fine raised line present along outer margin.

Remarks. *Pseudohystricurus wigglesorum* was compared with *P. obesus* above.

Pseudohystricurus sp. (Fig. 2T, V, W)

Material. Assigned specimen SUI 134793, from Section MME 121.6 m, Fillmore Formation (upper Tremadocian; Stairsian, *Pseudoclelandia cornupsittaca* Zone), Middle Mountain, Ibex area, Millard County, western Utah, USA.

Remarks. *Pseudohystricurus* is known from a single cranidium from the *Pseudoclelandia cornupsittaca* Zone in the Fillmore Formation at Middle Mountain, Ibex area. Of the two named species, it is much more similar to *P. obesus* than to *P. wigglesorum*. It shares lateral protruded posterior projections, background granular sculpture, and relatively small frontal areas with cranidia of *P. obesus*. However, its LO is densely tuberculate everywhere as is its posterior fixigena. Specimens of *P. obesus* from both the Garden City Formation and the Fillmore Formation are consistent in their paucity of tuberculate sculpture in these areas, strongly suggesting that the *P. cornupsittaca* Zone species is distinct.

ACKNOWLEDGEMENTS

Fieldwork was supported by National Science Foundation grants EAR 9973065, EAR 0308685 and DEB 0716065. We are grateful to Tiffany Adrain for assistance with curation and SUI numbers. Comments from two anonymous reviewers improved the manuscript.

REFERENCES

Adrain, J.M., 2011. Class Trilobita Walch, 1771. 104–109 in Zhang, Z.-Q. (Ed.), Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. *Zootaxa 3148*.

Adrain, J.M., Lee, D.-C., Westrop, S.R., Chatterton, B.D.E. & Landing, E., 2003. Classification of the trilobite subfamilies Hystricurinae and Hintzecurinae subfam. nov., with new genera from the Lower Ordovician (Ibexian) of Idaho and Utah. *Memoirs of the Queensland Museum 48*, 553–586.

Adrain, J.M. & McAdams, N.E.B., 2012. The Lower Ordovician (upper Floian) bathyurid trilobite *Aponileus* Hu, with species from Utah, Texas, and Greenland. *Zootaxa 3293*, 1–67.

Adrain, J.M., McAdams, N.E.B. & Westrop, S.R., 2009. Trilobite biostratigraphy and revised bases of the Tulean and Blackhillsian Stages of the Ibexian Series, Lower Ordovician, western United States. *Memoirs of the Association of Australasian Palaeontologists 37*, 541–610.

Adrain, J.M. & Westrop, S.R., 2006. New genus of dimeropygid trilobites from the earliest Ordovician of Laurentia. *Acta Palaeontologica Polonica 51*, 541–550.

Adrain, J.M. & Westrop, S.R., 2007. *Bearriverops*, a new Lower Ordovician trilobite genus from the Great Basin, western USA, and classification of the family Dimeropygidae. *Canadian Journal of Earth Sciences 44*, 337–366.

Adrain, J.M., Westrop, S.R., Karim, T.S. & Landing, E., this volume. Trilobite biostratigraphy of the Stairsian Stage (upper Tremadocian) of the Ibexian Series, Lower Ordovician, western United States. *Memoirs of the Association of Australasian Palaeontologists 45*, 167–214.

Adrain, J.M., Westrop, S.R., Landing, E. & Fortey, R.A., 2001. Systematics of the Ordovician trilobites *Ischyrotoma* and *Dimeropygiella*, with species from the type Ibexian area, western U.S.A. *Journal of Paleontology 75*, 947–971.

Alexyutin, M.V., Bachtadse, V., Alexeiev, D.V. & Nikitina, O.I., 2005. Palaeomagnetism of Ordovician and Silurian rocks from the Chu-Yili and Kendyktas mountains, south Kazakhstan. *Geophysical Journal International 162*, 321–331.

Ancygin, N., 1977. Trilobity Karakol-Mikhailovskogo Gorizonta Rannego Ordovika yuzhnego Urala. *Trudy Instituta Geologii i Geokhimii 126,* 68-95.

Angelin, N.P., 1854. *Palaeontologica Scandinavica. II. Crustacea formationis transitionis*. Samson & Wallin, Lund, pp. 22–92.

Chatterton, B.D.E., 1994. Ordovician proetide trilobite *Dimeropyge*, with a new species from northwestern Canada. *Journal of Paleontology 68*, 541–556.

Chatterton, B.D.E., Edgecombe, G.D., Waisfeld, B.G. & Vaccari, N.E., 1998. Ontogeny and systematics of Toernquistiidae (Trilobita, Proetida) from the Ordovician of the Argentine Precordillera. *Journal of Paleontology 72*, 273–303.

Clark, T.H., 1924. The paleontology of the Beekmantown Series at Lévis, Quebec. *Bulletins of American Paleontology 10(41)*, 1–134.

Cullison, J.S., 1944. The stratigraphy of some Lower Ordovician formations of the Ozark uplift. *Bulletin of the School of Mines and Metallurgy, University of Missouri, Technical Series 15(2)*, 1–112.

Dean, W.T., 1971. The trilobites of the Chair of Kildare Limestone (upper Ordovician) of eastern Ireland. Part 1. *Monographs of the Palaeontographical Society 531*, 1–60.

Dean, W.T., 1973. The Lower Palaeozoic stratigraphy and faunas of the Taurus Mountains near Beysehir, Turkey. III. The trilobites of the Sobova Formation (Lower Ordovician). *Bulletin of the British Museum (Natural History), Geology Series 24*, 279–348.

Dean, W.T., 1989. Trilobites from the Survey Peak, Outram and Skoki formations (Upper Cambrian–Lower Ordovician) at Wilcox Pass, Jasper National Park, Alberta. *Geological Survey of Canada Bulletin 389*, 1–141.

Demeter, E.J., 1973. Lower Ordovician pliomerid trilobites from western Utah. *Brigham Young University Geology Studies 20*, 37–65.

Derby, J.R., Bauer, J.A., Miller, M.A., Creath, W.B., Repetski, J.E., Dresbach, R.I., Ethington, R.L., Loch, J.D., Stitt, J.H., Sweet, W.C., McHargue, T.R., Taylor, J.F., Miller, J.F. & Williams, M., 1991. Biostratigraphy of the Timbered Hills, Arbuckle, and Simpson Groups, Cambrian and Ordovician, Oklahoma: A review of correlation tools and techniques available to the explorationist. *Oklahoma Geological Survey Circular 92*, 15–40.

Fortey, R.A., 1983. Cambrian–Ordovician trilobites from the boundary beds in western Newfoundland and their phylogenetic significance. 179–211 in Briggs, D.E.G. & Lane, P.D. (eds), *Trilobites and other early arthropods. Papers in honour of Professor H. B. Whittington, F.R.S.* Special Papers in Palaeontology 30.

Fortey, R.A., Landing, E. & Skevington, D., 1982. Cambrian–Ordovician boundary sections in the Cow Head Group western Newfoundland. 95–129 in Bassett, M.G. & Dean, W.T. (eds), *The Cambrian–Ordovician boundary: sections, fossil distributions, and correlations*. National Museum of Wales, Geological Series No. 3.

Fortey, R.A. & Owens, R.M., 1975. Proetida - a new order of trilobites. *Fossils and Strata 4*, 227–239.

Hintze, L.F., 1951. Lower Ordovician detailed stratigraphic sections for western Utah. *Utah Geological and Mineralogical Survey Bulletin 39*, 1–99.

Hintze, L.F., 1953. Lower Ordovician trilobites from western Utah and eastern Nevada. *Utah Geological and Mineralogical Survey Bulletin 48*, 1–249. [for 1952]

Hupé, P., 1953. Classe des Trilobites. 44–246 in Piveteau, J. (ed.), *Traité de Paléontologie. Tome 3. Les Formes Ultimes d'Invertébrés. Morphologie et Évolution. Onycophores. Arthropodes. Échinoderms. Stomocordés*. Masson et Cie, Paris.

Jell, P.A. & Adrain, J.M., 2003. Available generic names for trilobites. *Memoirs of the Queensland Museum 48*, 331–553.

Karim, T.S., 2008. Olenid-dominated trilobite fauna from the Shallow Bay Formation (Cow Head Group), Cambrian-Ordovician boundary interval, western Newfoundland. *Canadian Journal of Earth Sciences 45*, 407–425.

Kindle, C.H. & Whittington, H.B., 1958. Stratigraphy of the Cow Head region, western Newfoundland. *Geological Society of America Bulletin 69*, 315–342.

Kobayashi, T., 1955. The Ordovician fossils of the McKay Group in British Columbia, western Canada, with a note on the early Ordovician palaeogeography. *Journal of the Faculty of Science, Tokyo University, Section 2 9*, 355–493.

Lisogor, K.A., 1961. Trilobity Tremadokskikh i smezhnykh s nimi otlozheniy Kendyktasa. *Trudy Geologicheskogo Instituta 18*, 52–92.

Loch, J.D., 2007. Trilobite biostratigraphy and correlation of the Kindblade Formation (Lower Ordovician) of Carter and Kiowa Counties, Oklahoma. *Oklahoma Geological Survey Bulletin*, *149*, 1–157.

McAdams, N.E.B. & Adrain, J.M., 2009. *Heckethornia*, a new genus of dimeropygid trilobites from the Lower Ordovician (Ibexian; Tulean and Blackhillsian) of the Great Basin, western USA. *Canadian Journal of Earth Sciences 46*, 875–914.

McAdams, N.E.B. & Adrain, J.M., 2011a. *Panisaspis*, a new genus of pliomerid trilobites from the Lower Ordovician (Ibexian; Tulean and Blackhillsian) of the Great Basin, western USA. *Zootaxa 2969*, 1–68.

McAdams, N.E.B. & Adrain, J.M., 2011b. Revision of the Lower Ordovician (lower Floian; Tulean) pliomerid trilobite *Protopliomerella*, with new species from the Great Basin, western USA. *Zootaxa 3144*, 1–113.

McAdams, N.E.B. & Adrain, J.M., 2011c. Systematics of the Lower Ordovician pliomerid trilobite *Hintzeia*, with species from the Great Basin, western USA. *Zootaxa 2910*, 1–45.

Mergl, M., 1991. New Lower Ordovician (Arenig) trilobite assemblages in Bohemia. *Časopis pro Mineralogii a Geologii 36*, 193–203.

Öpik, A.A., 1937. Trilobiten aus Estland. *Tartu Ülikooli Geoloogia-Intituudi Toimetused 52*, 1–163.

Popov, L.E., Bassett, M.G., Zhemchuzhnikov, V.G., Holmer, L.E. & Klishevich, I.A., 2009. Gondwanan faunal signatures from Early Palaeozoic terranes of Kazakhstan and Central Asia: evidence and tectonic implications. 23–64 in Bassett, M.G. (ed.), *Early Palaeozoic Peri-Gondwana Terranes: New Insights from Tectonics and Biogeography.* Geological Society, London, Special Publications 325.

Poulsen, C., 1937. On the Lower Ordovician faunas of East Greenland. *Meddelelser om Grønland 119(3)*, 1–72.

Přibyl, A. & Vaněk, J., 1968. Einige Trilobiten aus dem böhmischen Ordovizium. *Vestník Ústředního Ústavu Geologického 43*, 191–197.

Raymond, P.E., 1905. The trilobites of the Chazy Limestone. *Annals of the Carnegie Museum 3*, 328–386.

Raymond, P.E., 1925. Some trilobites of the lower Middle Ordovician of eastern North America. *Bulletin of the Museum of Comparative Zoology, Harvard University 67*, 1–180.

Reed, F.R.C., 1896. The fauna of the Keisley Limestone, Part. I. *Quarterly Journal of the Geological Society of London 52*, 407–437.

Ross, R.J., Jr, 1949. Stratigraphy and trilobite faunal zones of the Garden City Formation, northeastern Utah. *American Journal of Science 247*, 472–491.

Ross, R.J., Jr, 1951. Stratigraphy of the Garden City Formation in northeastern Utah, and its trilobite faunas. *Peabody Museum of Natural History, Yale University, Bulletin 6*, 1–161.

Ross, R.J., Jr, 1953. Additional Garden City (Early Ordovician) trilobites. *Journal of Paleontology 27*, 633–646.

Ross, R.J., Jr, 1970. Ordovician brachiopods, trilobites, and stratigraphy in eastern and central Nevada. *United States Geological Survey Professional Paper 639*, 1–103.

Ross, R.J., Jr, Hintze, L.F., Ethington, R.L., Miller, J.F., Taylor, M.E. & Repetski, J.E., 1997. The Ibexian, lowermost series in the North American Ordovician. *United States Geological Survey Professional Paper 1579*, 1–50.

Taylor, J.F., Repetski, J.E., Loch, J.D. & Leslie, S.A., 2012. Biostratigraphy and chronostratigraphy of the Cambrian-Ordovician great American carbonate bank. 15–35 in Derby, J.R., Fritz, R.D., Longacre, S.A., Morgan, W.A. & Sternbach, C.A. (eds), *The great American carbonate bank: The geology and economic resources of the Cambrian-Ordovician Sauk megasequence of Laurentia*. American Association of Petroleum Geologists Memoir 98.

Terrell, F.M., 1973. Silicified trilobite zonation in the Lower Fillmore Formation in western Utah. *Brigham Young University Geology Studies 20*, 67–90.

Tripp, R.P., 1967. Trilobites from the upper Stinchar Limestone (Ordovician) of the Girvan District, Ayrshire. *Transactions of the Royal Society of Edinburgh 67*, 43–94.

Turvey, S.T., Zhou Z.-Y. & Yuan W.-W., 2006. Two new species of *Pseudopetigurus* (Trilobita) from the Arenig-Llanvirn of South China. *Paläontologische Zeitschrift 80*, 52–59.

Ulrich, E.O., 1930. Ordovician trilobites of the family Telephidae and concerned stratigraphic correlations. *Proceedings of the United States National Museum 76*, 1–101.

Walcott, C.D., 1886. Second contribution to the studies on the Cambrian faunas of North America. *United States Geological Survey Bulletin 30*, 1–369.

White, R.D. & Lieberman, B.S., 1998. A type catalog of fossil invertebrates (Arthropoda: Trilobita) in the Yale Peabody Museum. *Postilla, Peabody Museum of Natural History 214*, 1–151.

Whittington, H.B. & Evitt, W.R., 1954. Silicified Middle Ordovician trilobites. *Geological Society of America Memoir 59*, 1–137.

Wilson, J.L., 1954. Late Cambrian and early Ordovician trilobites from the Marathon Uplift, Texas. *Journal of Paleontology 28*, 249–285.

Yuan W.-W., Fortey, R.A. & Turvey, S.T., 2006. Ontogeny and relationships of the trilobite *Pseudopetigurus* Prantl and Přibyl. *Palaeontology 49*, 537–546.