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The Early Ordovician bathyurid trilobites *Licnocephala* and *Ibexocephala*

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Non-technical Summary.—Bathyurid trilobites are one of the most common shallow-marine groups of the Early Ordovician of Laurentia. During the Ordovician, Laurentian North America straddled the Equator, and the current western region formed the northern continental margin. Sampling of secondarily silicified trilobite faunas along this margin in the Great Basin has yielded a wealth of new information, including many dozens of new species of bathyurids. This new knowledge permits an assessment of currently understood natural evolutionary groups within the family. The genus *Licnocephala*, which in the past has been widely applied, has quite different morphology than has been attributed to it in previous literature. The type species is revised on the basis of new specimens and four new species (two well enough known to formally name) are illustrated. A related new genus, *Ibexocephala*, includes two new species with highly unusual cranidial morphology involving a sharp posterior change in angle in sagittal (midline) profile. All of the new and revised taxa are Tulean (late Tremadocian, Early Ordovician) in age. They were collected from the Fillmore Formation in western Utah and the Garden City Formation of southeastern Idaho.

Abstract.—Revision of the type species of the Early Ordovician (Tulean, late Tremadocian) bathyurid trilobite *Licnocephala* Ross, 1951 demonstrates that it has significantly different morphology than that ascribed to it in the earlier literature, which was based largely on species now assigned to a different genus. In addition to the type species, *L. bicornuta* Ross, 1951, which is fully revised on the basis of new material, four species, all apparently new, have been recovered, two of which, *L. ngi* n. sp. and *L. bradleyi* n. sp., are well enough known to formally name. The overall phylogenetic structure of bathyurids is yet to be determined, but several apparent clades can now be recognized and are discussed. Among these is what is termed the "*Chapmanopyge* group," including *Chapmanopyge* Fortey and Bruton, 2013, *Punka* Fortey, 1979, *Uromystrum* Whittington, 1953, and *Licnocephala*. These genera are united in the occurrence of much of the anterior cephalic border on the librigenal anterior projection, with most of the anterior margin of the cranidium representing the suture, the possession of very short (exsag.) strap-like posterior cranidial projections, and extremely narrow visual surfaces. A fifth genus of the group, *Ibexocephala* n. gen., is represented by two new species, *I. lossoae* (type species) and *I. dekosterae*. The taxon features a remarkable cranidial morphology involving a strong deflection of the posteriormost part of the cranidium from the anterior part in sagittal profile.

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Introduction

Part of a comprehensive revision of the Early and Middle Ordovician faunas from the then-northern Laurentian margin originally treated by Ross (1951) and Hintze (1953) has involved an episodic revision of one of the most common and diverse groups, Bathyuridae Walcott, 1886. Previous works have dealt with the genera *Gladiatoria* Hupé, 1955 (Adrain et al., 2011a), *Psalikilopsis* Ross, 1953 (Adrain et al., 2011b), *Aponileus* Hu, 1963, and *Psephosthenaspis* Whittington, 1953 (Adrain and McAdams, 2012), *Pseudoolenoides* Hintze, 1953 (Adrain et al., 2012), and *Bathyurina* Poulsen, 1937 (Adrain et al., 2014). Treatment of Bathyuridae is continued with revision herein of *Licnocephala* Ross, 1951, a genus known originally from a total of three sclerites assigned to the type species, *L. bicornuta* Ross, 1951 (one of which was assigned with question), but which nevertheless became widely applied to Laurentian bathyurid species. A second taxon, *Ibexocephala* n. gen., has previously been entirely overlooked in the classic Lower Ordovician sections. All of the species revised or described herein are quite rare, but collecting during the course of an extended field-based revision of the faunas has yielded more material of *Licnocephala bicornuta*, confirming the sclerite associations, in addition to five new species assigned to the genus (two of which are well enough known to formally name), transforming it from a historically misunderstood monotypic enigma to a reasonably well-known group of six species. *Ibexocephala* includes two new species with highly unusual cranidial morphology. The goals of the present work are to describe

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the new species, to assess the relationships of the two genera in light of the abundant new data, and to provide an interim assessment of potential phylogenetically related groups within Bathyuridae.

Localities and stratigraphy

Comprehensive details of the geological setting, history of study, and localities involved were given by Adrain et al. (2009). Descriptions of all sections and sampling horizons listed herein may also be found in that work. Adrain et al. (2009, fig. 3) introduced a new, species-level, trilobite zonation for the northern Laurentian Tulean and Blackhillsian stages (upper Tremadocian to end-Floian). Continuing work has amplified and supplemented this scheme, and the current state of knowledge, featuring the internal subdivision of several of the original zones and the identification of multiple additional, unnamed, zones, was summarized by McAdams et al. (2018, p. 4–5, fig. 1). Citation of trilobite zones herein follows the latter work.

Classification of Bathyuridae

Bathyurids are among the most common faunal elements of the Laurentian Tulean and Blackhillsian stages (global upper Tremadocian to end-Floian), and the group has a Laurentian record extending to the lower Katian. To this point, 40 valid genera are generally accepted in the literature, and 239 formally named and distinct species are recognized. The group is overwhelmingly Laurentian, with only a few generally poorly known taxa assigned from other low-latitude paleocontinents. For several decades, the family was divided into the nominate subfamily and Bathyurellinae Hupé, 1953. The modern basis for this was outlined by Fortey and Owens (1975, p. 228–229), and species assigned to either subfamily were described and revised in the influential work of Fortey (1979). The classification was widely adopted in the subsequent literature (Ingham et al., 1986; Boyce, 1989; Tremblay and Westrop, 1991; Brett and Westrop, 1996; Landing and Westrop, 2006; Loch, 2007; McCobb et al., 2014).

In the original assessment (Fortey and Owens, 1975, p. 228), bathyurines included genera such as *Goniotelina* Whittington and Ross in Whittington, 1953, and *Acidiphorus* Raymond, 1925, featuring species that are often tuberculate, with thick cuticle, nasute anterior borders, often long, curved genal spines that are not confluent with the librigenal field and lateral border, and pygidia with strongly downturned margins and commonly with posteromedian spines. Bathyurellines were characterized as having "a flat, wide pygidium, broad anterior border to the cranidium and blade-like genal spines" (Fortey and Owens, 1975, p. 228–229). Fortey and Owens (1975) compared the bathyurines with “hystricurids” such as *Pseudohystricurus orbus* Ross, 1953, and the bathyurellines with the “hystricurid” *Psalikilopsis* Ross, 1953, concluding that “It seems possible that the *Acidiphorus*/*Goniotelina* type of bathyurid may have had an origin in the Hystricurinae independent of that of the *Licnocephala*/*Bathyurellus* type” and that “if this view is substantiated the separation of the *Goniotelina*-type bathyurids from *Licnocephala*/*Bathyurellus*-type bathyurids into two subfamilies (Bathyurinae and Bathyurellinae respectively) as proposed by Hupé (1958, p. 198) will be justified.” If these ideas were correct, then the resulting “family” would in fact have been polyphyletic. Both of the “hystricurid” comparisons, however, now seem to be ingroup Bathyuridae. *Psalikilopsis* was revised with new species by Adrain et al. (2011b). *Pseudohystricurus orbus* is the type species of *Litzicurus* Adrain, McAdams, and Westrop, 2009. This genus was described as Hystricuridae, but as pointed out by Adrain et al. (2011b, p. 370), it likely represents a bathyurid.

Fortey and Bruton (2013, p. 28) considered that Bathyurellinae as they circumscribed it was monophyletic, but that Bathyurinae “is a paraphyletic assemblage of genera, comprising all remaining bathyurids with the clade Bathyurellinae removed.” Their diagnosis of Bathyurellinae (Fortey and Bruton, 2013, p. 55) listed “relatively large, frequently flattened pygidia with wide borders and with equally wide doublure with inner edge usually reflexed close to dorsal surface” as well as falcate librigenae in which the genal spines are essentially an extension of the field, parallel-sided glabellae, and dorsal sculpture that is either smooth or terrace ridges, not tuberculate. They assigned *Bathyurellus* Billings, 1865, *Punka* Fortey, 1979, *Uromystrum* Whittington, 1953, *Licnocephala*, *Grinnellaspis* Poulsen, 1948, and *Chapmanopyge* Fortey and Bruton, 2013 (a replacement name for the preoccupied *Chapmania* Loch, 2007) as belonging. While several of these genera seem certainly to be closely related, it is not obvious that *Bathyurellus* itself is part of this group (see discussion that follows), and hence that Bathyurellinae with this composition is a clade.

Current field-based revision of the shallow-water faunas of the (Ordovician geography) northern Laurentian margin, based mainly on secondarily silicified material, is resulting in better knowledge of many bathyurid taxa (some of which was discussed by Fortey and Bruton, 2013, p. 19–21) and has yielded dozens of new species and genera, many of which have yet to be described. These will certainly inform any analysis of the overall phylogenetic structure of the family, and such an endeavor is best deferred until most of these data are published. Nevertheless, several phylogenetically related bathyurid subgroups now seem apparent, and they are discussed here.

The Chapmanopyge *group.*—A set of genera that often (but not always) feature species with broad, fan-shaped pygidia with very broad borders composes much of Fortey and Bruton’s (2013) Bathyurellinae. The taxa thus grouped seem certain to be closely related. Both of the genera treated in the systematics section belong to this group. There are many new and revised species of the group awaiting detailed treatment in the silicified faunas, and the phylogenetic structure and composition of the genera *Punka*, *Chapmanopyge*, and *Uromystrum* will be addressed when they are described. These three genera together with *Licnocephala* and *Ibexocephala* n. gen. seem to form a clade, which is here termed the *Chapmanopyge* group. Although pygidial features have in the past been emphasized and most of the genera feature species with fan-shaped pygidia, *Ibexocephala lossoae* n. gen. n. sp. has an apparently derived, effaced pygidium. All of the taxa, however, share three cephalic features. First, the anterior section of the facial suture does not cut more or less directly anteriorly across the anterior border. In most bathyurids it does, and then runs in a marginal or ventral position around the front of the cranidium. Hence, in most bathyurids, the

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anterior margin of the anterior border is developed mostly on the cranidium and occupies a broad median portion. In species of the *Chapmanopyge* group, the suture cuts obliquely across the anterior border for most of its width, apparently including all of the distance to the lateral edge of the rostral plate below, where it cuts the margin and runs into the ventral connective suture. Hence, the anterior margin of the cranidium in these species is almost entirely the facial suture. The anterior dorsal portion of the cephalic border and the anterior margin of the anterior border are part of the librigenal anterior projection. Second, in all species of the group, the cranidial posterior border furrow is completely or nearly completely effaced, and at least proximally, the posterior fixigenal projection is very short (exsag.). Where complete, the projection resembles a narrow strap, and it is often turned posteriorly and somewhat lengthened (exsag.) distally. Third, all species belonging to this group have exceptionally narrow eyes. Those of *Licnocephala bicornuta* Ross, 1951 are typical (Figs. 1.1, 1.2, 2.2, 2.9, 2.11). The palpebral lobe is large and flat, forming a subsemicircular platform with a margin describing slightly more than one semicircle (Fig. 1.1). The visual surface (Fig. 2.2, 2.9, 2.11) is composed of a narrow, convex strip that wraps around the subsemicircular margin of the palpebral lobe along the suture. Bathyurid eyes have a range of morphology. Many are relatively narrow (e.g., *Gladiatoria,* Adrain et al., 2011a, fig. 3P, V; *Bathyurellus,* Fortey, 1979, pl. 32, figs. 10, 11; *Psalikilopsis,* Adrain et al., 2011b, fig. 2A, H), and they range from broader but still elongate forms (e.g., *Bathyurina,* Adrain et al., 2014, fig. 7A, C, K) to species with bulbous eyes that are as wide as or wider than the librigenal field (e.g., *Pseudoolenoides*, Adrain et al., 2012, pl. 18, figs. 7, 15). The narrowest of these of other taxa, however, are at least twice as wide as those of any species of the *Chapmanopyge* group. All three of these features are unique within the family and are likely synapomorphies of this putative clade.

The Gladiatoria *group.*—*Bathyurellus* has none of the preceding cephalic features. The anterior section of the facial suture cuts more or less directly anteriorly across the anterior border, and the anterior margin of the cranidium is formed mostly from the anterior margin of the border (Fortey, 1979, pl. 31, figs. 1, 3, pl. 32, fig. 1). The posterior fixigenal projection has an obvious posterior border furrow (Fortey, 1979, pl. 32, fig. 1), although it tends to be obscured by either shadow or matrix in the Catoche Formation specimens. It is plainly visible, however, in the Svalbard *B. diclementsae* Fortey and Bruton, 2013 (Fortey and Bruton, 2013, fig. 19C, F, I). As outlined by Adrain et al. (2011a, p. 323), *Bathyurellus* is obviously related to *Gladiatoria* Ross, 1951, with the only real question being whether the genera are sister taxa or whether the latter possibly creates paraphyly in the former. Species of either genus agree in almost all aspects of their morphology, with the only substantial differences being the large, extended pygidial posterior spine developed in *Gladiatoria* and a tendency for its species to become more dorsally effaced. The genera are here termed the *Gladiatoria* group. The poorly known *Grinnellaspis* may prove to be related to this group.

The Benthamaspis *group.*—A third set of taxa, termed here the *Benthamaspis* group, includes bathyurids that become broadly illaeniform in their more derived species, with *Benthamaspis* Poulsen, 1946 the most obvious example. *Harlandaspis* Fortey and Bruton, 2013 appears to belong, as Fortey and Bruton (2013, p. 69–71) discussed close pygidial and librigenal similarities with species of *Benthamaspis*. Northern Laurentian silicified collections contain multiple new, apparently related, genera as well as new species of both *Benthamaspis* (see illustrations in Adrain et al., 2009) and *Harlandaspis*. *Benthamaspis* was for a period assigned to the Cambrian family Lecanopygidae Lochman, 1953 (e.g., Fortey, 1979, 1986; Dean, 1989), but since the work of Ludvigsen et al. (1989) and Boyce (1989), it has generally been accepted as Bathyuridae (Fortey and Bruton, 2013, p. 60). The *Benthamaspis* group seems to be monophyletic, but because much of it remains undescribed, discussion is deferred to forthcoming works in progress.

The Bolbocephalus *group.*—Species of *Bolbocephalus* Whitfield, 1890 feature inflated, strongly forwardly expanded glabellae and distinctive pygidia in which there is typically a mismatch between the relative widths and courses of the pleural and interpleural furrows, with adjacent furrows typically not running parallel to one another. Included in the group are *Hadrohybus* Raymond, 1925 (see Fortey, 1988) and *Rananasus* Cullison, 1944. Adrain and Westrop (2005, p. 1538) considered the latter a junior subjective synonym of *Bolbocephalus*, but Loch (2007) treated it as a valid taxon, albeit clearly related to *Bolbocephalus*. *Petigurus* Raymond, 1913 differs from the preceding taxa in featuring species with less forwardly expanding glabellae and coarse tuberculate sculpture but may belong. In addition, there are multiple species from western Utah with a variety of glabellar morphologies, ranging from the inflated but evenly convex form typical of *Bolbocephalus* (e.g., Adrain et al., 2009, fig. 17Y, EE), to species with conical glabellar dorsal protrusions similar to that of *Hadrohybus dunbari* Raymond, 1925 (e.g., "*Goniotelus* (?)" *unicornis* Young, 1973), to species with elaborate paired glabellar spines (e.g., "*Amblycranium* (?)" *linearus* Young, 1973). The genus-level classification of this group is the subject of ongoing work, but by every indication it forms a clade within Bathyuridae. Fortey and Bruton (2013, p. 20) thought that the type species of *Gelasinocephalus* Loch, 2007 "seems clearly related to *Bolbocephalus*…" but it lacks a strongly forwardly expanding glabella and has an extended preglabellar field and a transversely arcuate anterior border. Its pygidium (Loch, 2007, pl. 9, figs. 6–11) has narrow pleural regions with only the first pleural furrow well impressed. It does not appear to have any of the features that unite the preceding set of genera and probably does not belong to the group.

The Acidiphorus *group.*—A diverse clade ranging from the upper Tremadocian to Darriwilian includes the Darriwilian type species of *Acidiphorus* Raymond, 1925 (*A. spinifer* Raymond, 1925; see Whittington, 1965, p. 383, pl. 44, figs. 3–16) and is here termed the *Acidiphorus* group. Belonging are species that are generally vaulted, with thick, tuberculate

Figure 1. *Licnocephala bicornuta* Ross, 1951, from Section HC5 195.7 m, east side of Hillyard Canyon, and Section HC6 189.3 m, west crest of Hillyard Canyon, Garden City Formation (upper Tremadocian, Tulean, low *Psalikilopsis cuspidicauda* Zone), Bear River Range, Franklin County, southeastern Idaho, USA. (**1, 4, 7, 10**) Cranidium, SUI 115185, dorsal, right lateral, anterior, and ventral views (HC5 195.7 m). (**2, 5, 8**) Cranidium, SUI 148484, dorsal, left lateral, and anterior views (HC6 189.3 m);. (**3, 6, 9, 14**) Cranidium, SUI 148485, dorsal, right lateral, anterior, and ventral views (HC5 195.7 m). (**11–13**) Cranidium, SUI 148486, left lateral, dorsal, and anterior views (HC5 195.7 m). Scale bars = 0.5 mm.

exoskeletons; a forwardly expanding glabella that extends anteriorly to just behind, or immediately in contact with, the rear of the anterior border furrow and does not overhang the border; a convex, subcylindrical anterior border with prominent raised line sculpture and usually an anteromedian, subtriangular extension; very large eyes and palpebral lobes; librigenal lateral borders and genal spines with robust raised line sculpture; and pygidia with a broad, flattened border lacking a dorsally convex margin and with a usually robust posteromedian spine. Some species have a nearly entirely reduced posteromedian spine in large specimens or a small, thorn-like spine, but in these, a longer spine is present in earlier ontogeny and becomes progressively reduced with larger size. Not all of these features are unique to the group. A robust posteromedian spine, for example, is seen in species of *Litzicurus* Adrain, McAdams, and Westrop, 2009 and *Aponileus* Hu, 1963 (see Adrain and McAdams, 2012), both of which lack most of the other features of the *Acidiphorus* group.

Other taxa belonging to the group include *Goniotelus* Ulrich, 1927 and *Goniotelina* Whittington and Ross in Whittington, 1953. Whittington (1965, p. 383) considered *Goniotelus* a junior subjective synonym of *Acidiphorus*, and Brett and Westrop (1996, p. 421) subsequently suggested synonymy of *Goniotelina*. While these opinions may bear out, the *Acidiphorus* group is large and morphologically diverse. There

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exist at least 25 formally named species that seem to belong, and new collections from Utah and Idaho suggest that more than a dozen well-preserved and undescribed species remain to be added. Work is in progress, but it seems evident that multiple groups of related species that might represent distinct genera are involved.

The Bathyurus *group.*—This group includes two genera, *Bathyurus* Billings, 1859 and *Raymondites* Sinclair, 1944 (see Swisher et al., 2015). The earliest species is Dapingian in age, and the group includes the youngest known bathyurid species, from the early Katian. The morphology of the group features a glabella on which, in many species, the glabellar furrows are unusually well impressed; an inflated and rounded anterior glabellar region; a relatively flat anterior border with a nearly even curvature of the anterior margin, which tends to match the anterior curvature of the anterior glabellar region; markedly posteriorly placed palpebral lobes; librigenae with flattened lateral borders; lateral border furrows that run posteriorly along a relatively elongate genal spine, and narrow fields, and pygidia with well-impressed pleural furrows that continue across the flattened border; and particularly an axis with many more axial rings than the four typically seen in bathyurids. Ludvigsen (1979) has demonstrated the presence in multiple species of a distinctive hypostome with a laterally deep middle furrow and an arcuate anterior margin that docked with the rear of the rostral plate (Ludvigsen, 1979, pl. 5, figs. 31–35), indicating that species of this group had a secondarily conterminant hypostome condition (sensu Fortey, 1990).

Other bathyurids.—While the groups discussed here all seem to represent potential clades, their relationships to one another and the overall phylogenetic structure of the family remain uncertain. Genera not contained in any of these groups but that feature well-known species include *Aponileus*, *Bathyurina* (see Adrain et al., 2014), *Catochia* Fortey, 1979, *Madaraspis* Fortey and Droser, 1996, *Psephosthenaspis* Whittington, 1953 (see Fortey and Droser, 1996; Adrain et al., 2012), *Pseudoolenoides* Hintze, 1953 (see Adrain et al., 2012), and others.

Materials

Repositories and institutional abbreviations.—The type specimens of *Licnocephala bicornuta* Ross, 1951 are housed in the collections of the Yale Peabody Museum, New Haven, Connecticut, with specimen number prefix YPM. New type and figured material is housed in the Paleontology Repository, Department of Earth and Environmental Sciences, University of Iowa, Iowa City, with specimen number prefix SUI.

Systematic paleontology

Family Bathyuridae Walcott, 1886

Remarks.—As discussed, no subfamilies are recognized pending a better understanding of the phylogenetic structure of the family.

Genus *Licnocephala* Ross, 1951

Type species.—*Licnocephala bicornuta* Ross, 1951 from the Garden City Formation (upper Tremadocian, Tulean, *Psalikilopsis cuspidicauda* Zone), southeastern Idaho, USA.

Other species.—*Licnocephala bradleyi* n. sp., Garden City Formation (upper Tremadocian, Tulean, *Psalikilus hestoni* Zone to *Protopliomerella contracta* Zone), southeastern Idaho, USA; *Licnocephala ngi* n. sp., Garden City Formation (upper Tremadocian, Tulean, *Psalikilopsis cuspidicauda* Zone), southeastern Idaho USA; *Licnocephala* sp. 1, Fillmore Formation (upper Tremadocian, Tulean, *Psalikilopsis cuspidicauda* Zone) western Utah, USA; *Licnocephala* sp. 2, Garden City Formation (upper Tremadocian, Tulean, *Psalikilus typicum* Zone) southeastern Idaho, USA.

Diagnosis.—Glabella relatively short (sag.), parallel-sided, and narrow, only modestly dorsally inflated and lacking dorsal sculpture; preglabellar field and frontal areas very long, anterior sections of facial suture laterally bowed; anterior border and anterior border furrow nearly evenly anteriorly arcuate; anterior border furrow with sharp posterior change in slope abutting preglabellar field and frontal area; anterior border flat and lacking sculpture; preglabellar field, frontal areas, and librigenal field all with sculpture of inflated, in some cases anastomosing, cecal trunks, subdued in some specimens and species; eyes long, arcuate, but very narrow; librigenal lateral border broad and flat with raised line sculpture set subparallel to lateral margin; robust genal spine with broad furrow running down abaxial part, adaxial part inflated with prominent raised line sculpture; librigenal field narrow (tr.); cephalic doublure broad; pygidia with narrow axis that tapers posteriorly, very broad border, and well-impressed pleural and interpleural furrows; interpleural furrows or anterior segments significantly deeper distally.

Remarks.—*Licnocephala* has had a varied taxonomic history. Initially, the genus was known only from three assigned specimens of the type species (Ross, 1951, pl. 28, figs. 12–14, pl. 30, fig. 25), of which the pygidium was tentatively assigned. Hence, *Licnocephala bicornuta* presented a limited basis for comparison with other species. Hintze (1953) supplemented apparent knowledge of the genus with his description of *L. cavigladius* Hintze, 1953. This species (Hintze, 1953, pl. 10, figs. 1–5) was based on two cranidia, two librigena (note that Hintze, 1953, pl. 10, figs. 5a, b, listed them as dorsal and ventral views of the same specimen, but the dorsal view is of a right librigena and the ventral view is of a left librigena of different size), a hypostome, and a pygidium, all nearly complete. This better-known species was influential in subsequent workers' interpretations of the genus. Discussions (e.g., Fortey, 1979, p. 94; Fortey and Peel, 1990, p. 15–17) generally referred to the morphology of *L. cavigladius*. Adrain and Westrop (2005, p. 1529) considered that *L. bicornuta*, *L. cavigladius*, and *L. ovata* Ross, 1953 resembled each other but that relationship with other previously assigned species was less clear, a view echoed by Loch (2007, p. 60). Adrain et al. (2009, p. 553) considered that the concept of *Licnocephala* would be subject to revision once relevant species were described (i.e., the present work). Fortey and Bruton (2013, p. 21, 74) noted that much depended on better knowledge of the type species but advocated a concept of the genus based on species "with thin cuticle that have very low convexity (sag.) on both cephalon and pygidium, often combined with a wide, flat anterior cephalic border." They also discussed pygidial features.

With revision of the type species and description of several obviously related new species, it is now clear that *L. cavigladius* and *L. ovata* should likely be assigned to *Chapmanopyge*, as should the species assigned to *Licnocephala* by Fortey and Bruton (2013). *Chapmanopyge* itself currently includes species with a substantial range of morphologies. There are many species present in the Great Basin sections, and its status and potential phylogenetic structure will be addressed in a future work. *Licnocephala* is certainly a member of the *Chapmanopyge* group, as discussed earlier, but the type species and the new taxa described here share numerous features not seen in any other species of the group and seem certain to represent a distinct clade.

One aspect of pygidial morphology is unusual in both *L. bicornuta* and *L. ngi*. Four pygidia have been found that are obviously associated with *L. bicornuta*. Their morphology is variable. The largest nearly intact specimen (Fig. 3.3) has four axial rings. The pleural bands of the first segment run slightly posterolaterally, and only the first interpleural furrow is deeply impressed on the broad border. A large fragmentary specimen (Fig. 3.2) seems to have the same morphology. The two most intact pygidia (Fig. 3.1, 3.9) are smaller, although not very much so. Each has five axial rings. Unlike the specimen with four rings, each has a clear pseudo-articulating half ring in front of the second segment. Distally (Fig. 3.1), the pleural tips of the first segment appear free and only partially contiguous with the second segment. This is confirmed ventrally (Fig. 3.6) where there is a notch in the doublural margin separating the first segment from the second on both the outer and inner edge of the doublure on both sides of the specimen. There are two possibilities: (1) the pygidia that have five axial rings are last meraspid degree transitory pygidia that retain an unreleased thoracic segment; (2) these pygidia represent variation in a species that was in pedomorphic transition to incorporation of what was the posterior thoracic segment into the adult pygidium. The second of these seems most likely to be correct. Although relatively small, the specimens with five axial rings are far larger than any documented bathyurid transitory pygidia. Further, as noted, they seem to reflect an intermediate state of partial release, with some portions unfused and free and some clearly still merged with the anterior edge of the pygidium.

Other aspects of morphology lend support to a hypothesis of pedomorphosis. Ross's original specimens of *L. bicornuta* have been described, accurately, as "small" (Fortey and Bruton, 2013, p. 21). Ross's holotype cranidium has a sagittal length of about 5.3 mm. However, the reason for this is almost certainly that species of this genus were small animals. Most of the cranidia of species of *Licnocephala* illustrated in the present work are about the same size as Ross's specimen or a little smaller. The largest fragmentary specimen we have found has an extrapolated sagittal length of approximately 9.9 mm. This is much smaller than most of the specimens of the broad *Licnocephala*–*Chapmanopyge*–*Punka* group illustrated by Fortey and Bruton (2013). However, multiple species of both *Chapmanopyge* and *Punka* also occur in the Fillmore Formation and Garden City Formation, and their sclerites are large, with a size range almost identical to that of the mechanically prepared "crackout" specimens with calcareous preservation treated by Fortey and Bruton (2013). All species of *Licnocephala* are fairly rare at the horizons at which they occur, and it is possible that small sample sizes could bias adult size estimates toward smaller specimens. But all the positive information available suggests that species of *Licnocephala* were simply small as compared with those of related genera, which is consistent with a pedomorphic origin.

Among other species previously assigned to *Licnocephala*, "*Licnocephala* ? sp." of Hintze (1953, pl. 8, fig. 7a, b) represents a new Stairsian genus of uncertain affinity. It will be described in a forthcoming work. *Licnocephala sanddoelaensis* Adrain and Westrop, 2005 and *Licnocephala* n. sp. A of Adrain and Westrop (2005) should be assigned to *Chapmanopyge*. Citing personal communication of Fortey, Jell and Adrain (2003, p. 368) considered *Domina* Gorovceva in Gorovceva and Semenova, 1977 a junior subjective synonym of *Licnocephala*. It does not belong to the genus as understood herein but appears to be a member of the *Chapmanopyge* group.

Licnocephala bicornuta Ross, 1951
Figures 1, 2, 3.1–3.10, 3.13, 3.14

1951 *Licnocephala bicornuta* Ross, p. 110, pl. 28, figs. 12–14, pl. 30, fig. 25.
1951 *Licnocephala bicornuta*; Hintze, p. 41.
1953 *Licnocephala bicornuta*; Ross, p. 642.
1953 *Licnocephala bicornuta*; Hintze, p. 192.
1955 *Licnocephala bicornis* [sic]; Kobayashi, p. 448.
1966 *Licnocephala bicornuta*; Lochman, p. 541.
1979 *Licnocephala bicornuta*; Fortey, p. 94.
1988 *Licnocephala bicornuta*; Dean, p. 2.
1989 *Licnocephala bicornuta*; Dean, p. 13.
1990 *Licnocephala bicornuta*; Fortey and Peel, p. 15.
1997 *Licnocephala bicornuta*; Ross et al., p. 44.
1997 *Licnocephala bicornuta*; Lee and Chatterton, p. 439.
1998 *Licnocephala bicornuta*; White and Lieberman, p. 81.
2003 *Licnocephala bicornuta*; Jell and Adrain, p. 398.
2005 *Licnocephala bicornuta*; Adrain and Westrop, p. 1532.
2007 *Licnocephala bicornuta*; Loch, p. 60.
2009 *Licnocephala bicornuta*; Adrain et al., p. 559, fig. 10L, Q.
2013 *Licnocephala bicornuta*; Fortey and Bruton, p. 21, 74.

Holotype.—Cranidium, YPM 18180 (Ross, 1951, pl. 28, figs. 13, 14), from the Garden City Formation (upper Tremadocian, Tulean), "Zone G(2)a," locality 6, west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA.

Diagnosis.—Cranidium with very subdued cecal trunk sculpture, barely visible in some specimens; glabella relatively broad relative to length; palpebral lobe describing only slightly more than semicircle in dorsal outline, versus a greater portion of a circle in all other species; cecal trunk sculpture on librigenal field variable from well expressed to nearly indiscernible; pygidial axis broader relative to pygidial width than in any other species; pygidial sagittal length shorter relative to pygidial width than in any other species.

Occurrence.—Sections HC5 195.7–204.2T m, east side of Hillyard Canyon, and HC6 189.3 m, west crest of Hillyard Canyon, Garden City Formation (upper Tremadocian, Tulean, low *Psalikilopsis cuspidicauda* Zone) Bear River Range, Franklin County, Idaho, USA.

Description.—Where features (frontal area and palpebral lobes) are preserved on only one side of a specimen, ratios were calculated by doubling the distance to the sagittal midline. Ratios throughout the paper are reported as means and ranges. Cranidium with width across maximum divergence of anterior facial sutures (β) 100% (93–103%) sagittal length and 110% (107–114%) width across palpebral lobes; anterior facial sutures strongly anteriorly divergent, not evenly arcuate but forming one slight angle not far in front of palpebral lobe, opposite anterior part of glabella, then running with only a slight lateral bow to reach maximum point of divergence just posterior to point where anterior border furrow is cut, then turning to become anteriorly convergent, cutting anterior border obliquely for much of its width and reaching anterior cephalic margin (α) only near sagittal mid-length (so that a significant portion of the anterior part of the cephalic anterior border is located on the anterior projection of the librigena, e.g., Fig. 2.5, 2.11); anterior border forming anterior margin of cephalon only in narrow median portion, the width of which can be seen ventrally (Fig. 1.10) where it is matched by a tiny strip of doublure between where the connective sutures meet the anterior margin; over most of width, the anterior margin of the cranidium is the anterior section of the facial suture obliquely cutting the anterior border; cranidial portion of anterior border longest sagittally, where it is slightly longer than the sagittal length of LO, of similar length sagittally and exsagittally in median region where it forms anterior cephalic margin, progressively shorter (exsag.) across broad region where it is cut obliquely by anterior facial suture; slight anterior rim developed on anteriorly facing aspect of anterior border in median region (best seen in Fig. 1.7, but also Fig. 1.9); dorsal surface of cranidial anterior border essentially flat and lacking sculpture; anterior border furrow shallow but distinct, longer sagittally, slightly shorter and distinctly shallower exsagittally near where it is cut by the anterior facial suture; preglabellar field and frontal area above anterior border furrow slightly swollen and very slightly overhanging rear of furrow (Fig. 1.5, 1.6); preglabellar field and frontal area long and broad, sagittal length between anterior and preglabellar furrows 35% (31–39%) cranidial sagittal length and 35% (33–38%) width of maximum divergence of anterior facial sutures; preglabellar field and frontal area covered with large, thick, subtly inflated cecal trunks radiating forward and laterally from region around anterior glabellar lobe; some trunks bifurcate anteriorly (see especially Fig. 1.1, both left and right sides); trunks range from subdued but clearly distinct (Fig. 1.1) to nearly effaced (Fig. 1.3); very faint eye ridge running from just behind anterior edge of palpebral lobe to region of L3, set obliquely and running slightly anteromedially, dorsally effaced in one specimen (Fig. 1.3) but barely visible ventrally (Fig. 1.14, beside right palpebral lobe, or left side of ventral specimen); palpebral lobes large, flat, margin describing very slightly more than a semicircle, less arcuate in most anterior region near γ, lacking dorsal sculpture; no palpebral furrow developed, interocular fixigena flat, confluent with dorsal surface of palpebral lobe with no change in slope, lacking dorsal sculpture; posterior fixigena sloped posteriorly from interocular fixigena; posterior fixigenal projection with only proximal portion preserved in two specimens (Fig. 1.1, 1.12), anterior edge with marked posterior arc behind palpebral lobe, posterior fixigena extended onto projection and forming most of length (exsag.), faint, shallow, and quite elongate (exsag.) developed in front of posterior margin, but posterior border and posterior border furrow not obviously developed, posterior margin with small ridge along its width; glabella relatively small, sagittal length excluding LO 133% (122–145%) maximum width and 45% (44–46%) sagittal length of cranidium; preglabellar furrow and axial furrows confluent, distinguished only by an increase in curvature around the point of contact with the adaxial end of the eye ridge, narrow, shallow but well incised, course prominently expressed on ventral surface by rounded ridge (Fig. 1.10); axial furrows subparallel for most of course, deflected laterally around LO and more subtly around L1 and L2; preglabellar furrow strongly anteriorly arcuate, more curved medially than laterally; as a result glabella is more or less straight sided for about four-fifths of its length, with the anterior lobe describing an inverted “U” to slightly “V” shape; glabella with moderate dorsal inflation above surrounding interocular fixigena, slightly more dorsally arcuate posteriorly than anterior in transverse view (Fig. 1.5), lacking dorsal sculpture; glabellar lobes and furrows best expressed on Figure 1.2, L1 and L2 subtly differentiated, with slight independent inflation; L1 elongate (exsag.), extended a small distance laterally; S1 a shallow lateral notch; L2 about half length of L1, slightly laterally protruded, S2 slightly smaller than S1, also a shallow notch; L3 small, with weak independent inflation across from and anterior to adaxial termination of eye ridge; SO slightly deeper than axial furrow sagittally, shorter (exsag.) and shallower exsagittally near contact with axial furrow, with moderate posterior arc; LO shorter sagittally than exsagittally, lengthened near axial furrow, posterior margin posteriorly arcuate but not as strongly so as SO, lacking dorsal sculpture of any kind; doublure of small, lensoid articulating surface beneath LO, with no obvious ventral sculpture, very thin strip along posterior margin on proximal part of posterior fixigenal projection, and very short (sag.; exsag.) strip on anterior margin between α, connective sutures obliquely set, posterior margin with slight posterior curvature, sculpture of a single raised line subparallel with anterior margin.

Librigena widest (tr.) at rear of eye; visual surface describing slightly more than a semicircle to mirror morphology of palpebral lobe, very narrow, slightly narrower posteriorly, separated from field by moderately deep, narrow furrow; field extended adaxially around visual surface both posteriorly and anteriorly,

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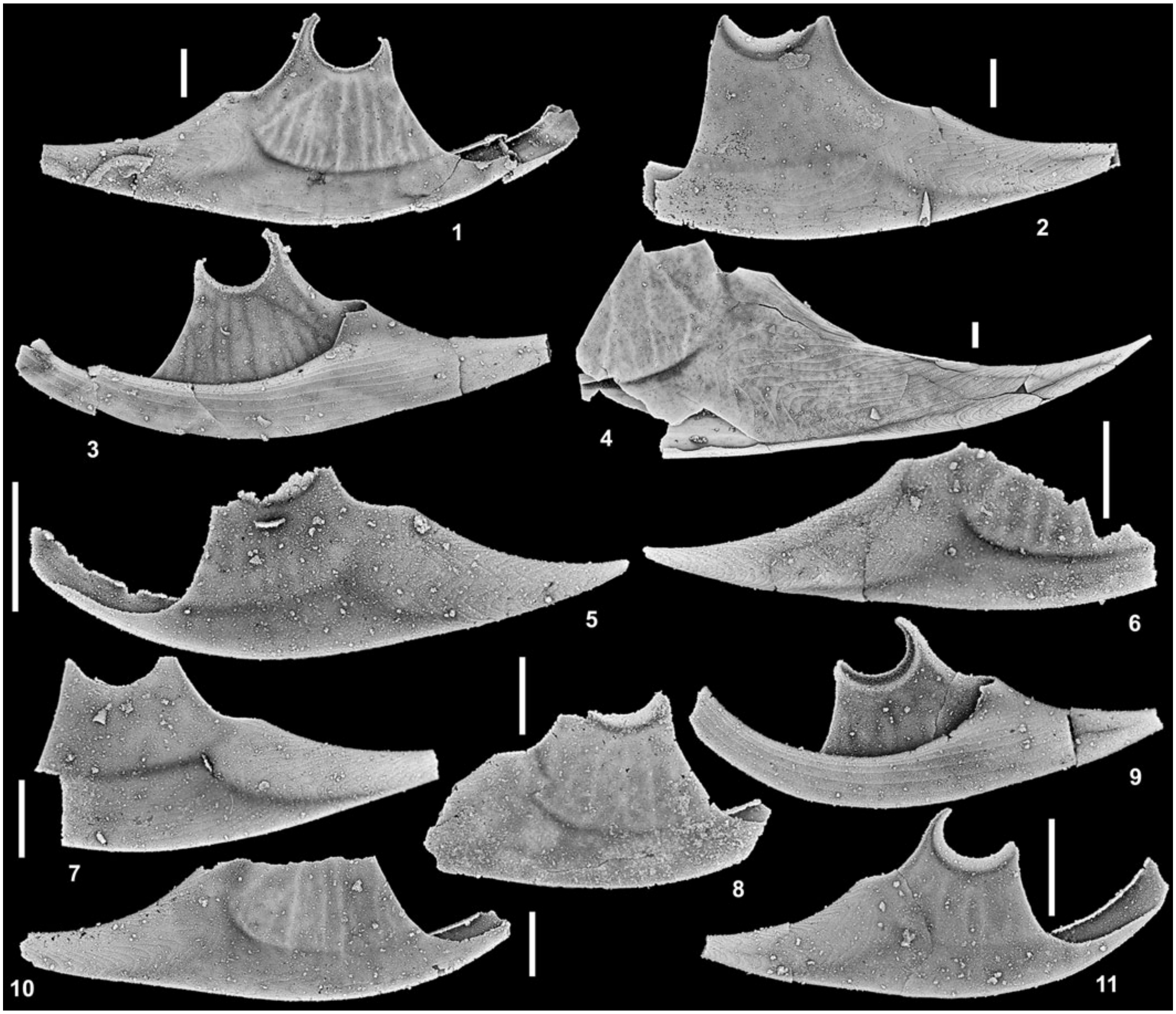

Figure 2. *Licnocephala bicornuta* Ross, 1951, from Section HC5 195.7 m, 203.7–204.2T m, east side of Hillyard Canyon, and Section HC6 189.3 m, west crest of Hillyard Canyon, Garden City Formation (upper Tremadocian, Tulean, low *Psalikilopsis cuspidicauda* Zone), Bear River Range, Franklin County, southeastern Idaho, USA. (**1, 3**) Right librigena, SUI 148487, external and internal views (HC6 189.3). (**2**) Left librigena, SUI 148488, external view (HC5 195.7 m). (**4**) Left librigena, SUI 148489, external view (HC6 189.3 m). (**5**) Left librigena, SUI 148490, external view (HC5 195.7 m). (**6**) Right librigena, SUI 148491, external view (HC6 189.3 m). (**7**) Left librigena, SUI 148492, external view (HC5 195.7 m). (**8**) Right librigena, SUI 148493, external view (HC5 203.7–204.2T m). (**9, 11**) Right librigena, SUI 148494, internal and external views (HC5 195.7 m). (**10**) Right librigena, SUI 148495, external view (HC5 195.7 m). Scale bars = 1 mm.

further so posteriorly, in narrow, curved strips; adaxial part of field bounded posteriorly by sharp and prominent sutural ridge along posterior section of facial suture, ridge separated from field by narrow furrows ranging from quite deep (Fig. 2.1) to shallow and nearly effaced (Fig. 2.2, 2.5); abaxial part of rear of field separated from base of genal spine by posteriorly curved furrow, deepest at abaxial contact with lateral border furrow, much shallower on adaxial half, with slight posterior curvature, in some specimens (Fig. 2.2, 2.5, 2.11) nearly effaced; anterior edge of field defined by curved anterior section of facial suture, curvature as described for cranidium, with no sign of a sutural ridge; five to eight inflated cecal trunks developed on field, some of which bifurcate on some specimens, most oriented with transverse course, radiating slightly abaxially; one prominent trunk set obliquely, running from just behind mid-length of eye to adaxial region of base of genal spine (best seen in Fig. 2.1 but faintly visible even on the most effaced specimens, e.g., Fig. 2.2.); apart from inflated trunks, field with mottled raised cecal sculpture but no pits or other external sculpture; lateral border furrow more laterally arcuate than lateral librigenal margin, deepest posterior at angular junction with border defining rear of field, slightly shallower immediately anterior to this junction, of similar depth and very narrow anteriorly along most of its length, then significantly shallowed immediately behind the point where it is cut by the anterior section of the facial suture; lateral border broad and dorsally flattened, becoming steadily wider posteriorly, terminating posteriorly in a shallow, adaxially arcuate, furrow that pinches it out as a very narrow strip along lateral edge of anterior portion of genal spine; this furrow is shallowed adaxially and barely contacts the junction of the lateral border furrow and furrow defining the rear of the field in most specimens, although a tripartite junction is clear in some specimens (e.g., Fig. 2.5, 2.7); genal spine broad at base, composed mostly of gently independently inflated adaxial portion defined anteriorly by furrow marking rear of field and anterolaterally by furrow separating it from lateral border; genal spine tapering in width posteriorly, elongate, forming long, sharp tip (best preserved in Fig. 2.4); sculpture on main, adaxial, inflated part of spine of chevron-like subparallel fine raised lines, with bottom of "V" shape directed anteriorly toward base; lateral border with sculpture of similar fine raised lines running subparallel to margin; apart from raised lines, no other dorsal sculpture on genal spine or lateral border; anterior projection, with long, tapering dorsal surface running contiguous with anterior part of lateral border and forming part of cephalic anterior border; doublure broad, exactly underlying lateral border and all of genal spine, inner edge beneath lateral border furrow with slight, rounded, ventral ridge along margin, turned up and in to form raised "wall" of doublure in dorsal view (Fig. 2.1, 2.10, 2.11); anterior projection long and curved; shape of connective sutures described below under rostral plate; beneath lateral border ventrally flat; that beneath genal spine with some ventral inflation; doublure with sculpture of raised lines, more robust than those on the dorsal part of genal spine and lateral border, set subparallel to inner and outer margins, more broadly spaced over most of abaxial area, finer and tightly crowded along and near inner margin, and more closely spaced on anterior projection than under lateral border.

Rostral plate, hypostome, and thorax not recovered. Shape of rostral plate revealed by anterior cranidial doublure (Fig. 1.10) and intact anterior projections on some specimens (Fig. 2.5, 2.9, 2.11); plate was small and subtriangular, and librigenal projections appear to have abutted behind it to form a median suture on the posterior part of their doublure (see Discussion).

(Following the preceding genus discussion, the anteriormost segment seen on Fig. 3.1, 3.9 is regarded as an unreleased posteriormost thoracic segment and described as such. Description of the pygidium focuses on the posterior four segments of the pygidium proper, as in Fig. 3.3). Posteriormost thoracic segment, recovered fused to the adult pygidium in two specimens, short (sag.; exsag.); axis occupying 19% total segment width; fulcrum set two-thirds distance adaxially on pleural lobe; axial ring low, of same length sagittally and exsagittally, lacking dorsal sculpture; ring furrow transversely straight and narrowly incised; articulating half ring very short; pleural lobes lacking any dorsal sculpture; anterior pleural band about half the length of posterior band; pleural furrow shallow, nearly obsolete, near axial furrow, much deeper abaxially, shallowed completely just abaxial to fulcrum, above adaxial portion of articulating facet; portion of pleura abaxial to fulcrum turned posterolaterally; articulating facet describing short (exsag.) shallow triangle; doublure underlying most of pleural region abaxial to fulcrum, with sculpture of 7–9 raised lines running at nearly right angle to anterior and posterior margin.

(See note in preceding paragraph.) Pygidium with dorsal surface lacking granular or tuberculate sculpture, nearly smooth; pygidium wide and relatively short, sagittal length 43% (40–46%) maximum width across first segment; fulcrum set 62% (61–64%) distance distally of width of pleural lobe at anterior margin of first segment; axis with maximum width across anterior part of first ring 18% pygidial maximum width and 68% (65–72%) sagittal length of axis; sagittal length of axis 55% (49–60%) sagittal length of pygidium; anterior margin and pleural portion of first segment transversely straight proximal to fulcrum, turned posteriorly distal to fulcrum; pleural lobes turned down at fulcrum at about a 30° angle anteriorly (Fig. 3.4); first segment with pleural furrow visible but very shallow proximally at contact with axial furrow, much deeper distally starting at about half distance to fulcrum and continuing just distal to fulcrum, then completely shallowed; anterior pleural band shorter (exsag.) than posterior band but relatively longer than anterior band of posteriormost thoracic segment; first interpleural furrow discernible between axial furrow and fulcrum, deepest near fulcrum, shallower but extended laterally across flattened border region nearly to lateral margin; expression of second pleural and interpleural furrows similar to that of first, although the furrows are narrower (tr.) and turned more posterolaterally; third pleural furrow strongly expressed but third interpleural furrow very weakly impressed; furrows associated with fourth pygidial segment barely expressed; axial rings short, very slightly shorter sagittally than exsagittally, successive posterior rings very slightly shorter than the next anterior; terminal piece long, subtrapezoidal, with a pair of small, faint swellings at rear (Fig. 3.3, 3.9); axial furrows nearly straight, slightly laterally deflected around each axial ring, posteriorly convergent, not meeting posteromedially, interrupted by rear of axis and short, subdued axial keel extended posteriorly from rear of axis; flattened border region very broad, separated from adaxial pleural regions by narrow, shallow border furrow, deeper posteriorly; border furrow interrupted by axial keel; pygidial margin broadly arcuate, in some specimens with very shallow anteromedian embayment (Fig. 3.1, 3.9); doublure broad, over most of area ventrally slightly concave, inner portion developed into shallow ventrally inflated ridge with doublure upturned anterodorsally along posteromedian region of ridge; broad, slightly concave abaxial region with sculpture of prominent but relatively sparsely spaced raised lines running subparallel to pygidial margin and inner margin of doublure, approximately 6–8 set in parallel at any point; adaxial swollen ridge with much more closely spaced, finer raised lines; anteromedian edge of doublure with small posterior embayment underlying rear of axis.

Materials.—SUI 115185, 115186, 148484–148498.

Remarks.—One of the things to emerge from a large-scale, field-based revision of the Lower and Middle Ordovician trilobite faunas of the (Ordovician) northern Laurentian margin is a realistic assessment of trilobite intraspecific variation. A full discussion of the subject is beyond the scope of this work, but when examining well-preserved silicified specimens with excellent stratigraphic control and relatively large illustrated samples, it has become clear (demonstrated in more than 20 systematic publications) that true intraspecific variation is very limited. Some bathyurids form modest exceptions, and *Licnocephala* is one. While there is little

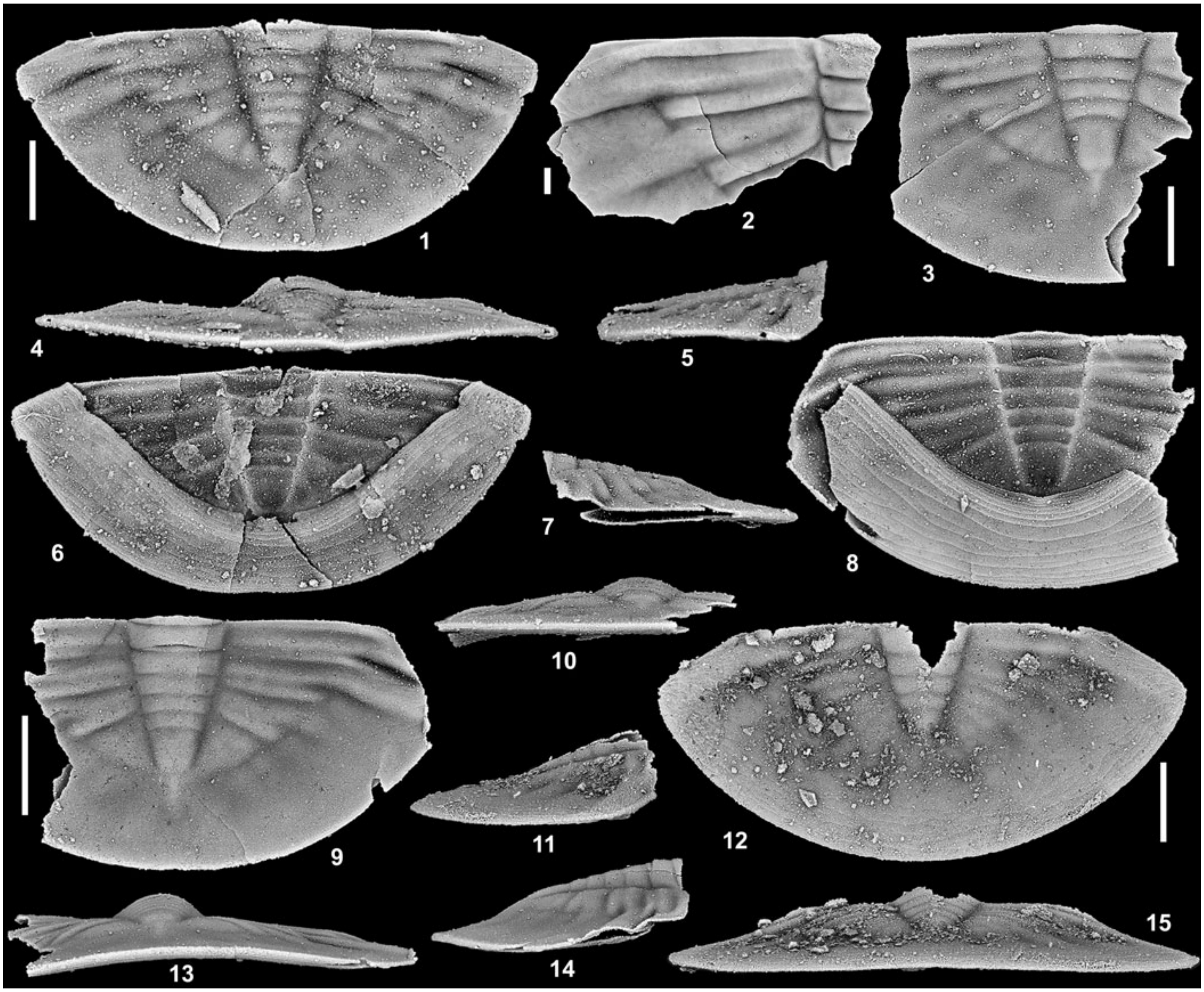

Figure 3. (**1–10, 13, 14**) *Licnocephala bicornuta* Ross, 1951, from Section HC6 189.3 m, Garden City Formation (upper Tremadocian, Tulean, low *Psalikilopsis cuspidicauda* Zone), west crest of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA: (**1, 4–6**) pygidium, SUI 148496, dorsal, posterior, right lateral, and ventral views; (**2**) pygidium, SUI 148497, dorsal view; (**3, 7, 10**) pygidium, SUI 148498, dorsal, left lateral, and posterior views; (**8, 9, 13, 14**) pygidium, SUI 115186, ventral, dorsal, posterior, and right lateral views. (**11, 12, 15**) *Licnocephala* species 1, from Section G 162.0T m, Fillmore Formation (upper Tremadocian; Tulean; low *Psalikilopsis cuspidicauda* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA, pygidium, SUI 148499, right lateral, dorsal, and posterior views. Scale bars = 1 mm.

variation in shape and dimensions (controlling for ontogeny and preservational deformation), there is substantial and genuine variation in degree of expression of the cephalic cecal sculpture. In cranidia of *L. bicornuta*, this varies from relatively well expressed (Fig. 1.1, 1.2) to nearly effaced (Fig. 1.3). Variation is more pronounced on librigenae as there are specimens with strongly inflated cecal trunks (Fig. 2.1), ones that are nearly effaced (Fig. 2.2), and others that are somewhere in between (Fig. 2.5, 2.11). The possibility that this variation reflects the presence of multiple species instead of intraspecific variation must be considered. It seems unlikely for three reasons. First, as noted, there is no prominent variation in any other aspects of cephalic morphology. Second, there are no disjunct sets of obviously distinct morphs. Instead, while sample size is not high, there is a range of variation in expression that seems essentially continuous, and specimens with differently expressed cecal sculpture occur together at the same horizons (e.g., Fig. 2.2 and 2.10 are both from Section HC5 195.7 m). Third, the new species *Licnocephala bradleyi* also shows a similar range of variation in the same feature and a similar lack of variation in other aspects of morphology.

Licnocephala bicornuta occurs together with *L. ngi* n. sp., but both frequency of occurrence and strong morphological correspondence of sclerite types make sclerite associations uncomplicated. *Licnocephala bicornuta* is distinguished from *L. ngi* in the following ways. The cranidial anterior border is much longer. The anterior sections of the facial sutures are strongly laterally bowed over their entire course versus nearly straight between β and γ. The preglabellar field is considerably shorter (sag.) relative to the overall cranidial dimensions. The preglabellar field and frontal areas have much less extent and

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have a sculpture of very weakly expressed cecal trunks, in some specimens almost effaced, versus strongly expressed, closely spaced trunks adorned with large, low tubercles. The glabella occupies a much larger area of the cranidium in plan view and is relatively wider. The margins of the palpebral lobe describe only slightly more than a single semicircle while those of *L. ngi* describe about 65% of a full circle. The anterior cranidial doublure is a tiny strip in both species, but that of *L. bicornuta* is narrower (tr.) and longer (sag.). The librigenal field of *L. bicornuta* has variably expressed swollen cecal trunks, ranging from robust to almost completely effaced. However, they are more widely spaced than those of *L. ngi* and show no evidence of tubercles atop them. The librigenal posterior facial suture is much less sinuous in *L. bicornuta*. The librigenal lateral border is wider posteriorly than that of *L. ngi*. The genal spine appears to be longer and to taper more rapidly posteriorly in *L. bicornuta*, but caution must be exercised as the tip is incomplete in the only known example of *L. ngi*. The pygidial axis occupies a much larger area of the pygidium in *L. bicornuta* and extends about two-thirds distance posteriorly versus less than half. The pygidial fulcrum is set somewhat nearer to the axis in *L. bicornuta*. The pygidial posterior pleural bands of *L. bicornuta* have no tubercle rows. The pygidial border of *L. bicornuta*, together with the doublure underlying it, is narrower, particularly posteriorly.

Licnocephala bicornuta differs from *L. bradleyi* in the following ways. The anterior border is relatively shorter sagittally, and the difference in length sagittally versus exsagittally/abaxially is much less pronounced. The anterior sections of the facial sutures are much more laterally bowed, and β is set much less laterally, only slightly abaxial to the abaxial edge of the palpebral lobe versus far abaxial to the edge of the lobe in *L. bradleyi*. The point of maximum divergence of the anterior sections of the facial sutures occurs opposite the preglabellar field, behind the point where the sutures cut the anterior border furrow, as opposed to anterior to that point in *L. bradleyi*. Whereas the preglabellar field and frontal area can have clearly expressed cecal trunks in specimens of *L. bicornuta*, even in those specimens where the trunks are expressed most prominently (Fig. 1.2) they are less inflated and less prominent than in any specimen of *L. bradleyi*. The glabella is shorter (sag.) and wider (tr.) in *L. bicornuta*, and there is no sign of the anteroposterior furrows seen on either side of the glabella in *L. bradleyi*. The lateral margins of the palpebral lobe describe only slightly more than a semicircle in *L. bicornuta*, versus much more in *L. bradleyi*. The occipital ring is narrow posteriorly in *L. bicornuta*, and the axial furrows opposite the ring are less posteriorly divergent. The librigenal field in specimens of *L. bicornuta* is markedly longer (exsag.), so that when cecal trunks are well expressed, there is a greater number of subparallel trunks. The librigenal lateral border is markedly narrower in *L. bicornuta*. The portion of the genal spine adaxial to the oblique furrow that separates it from the lateral border is much broader in *L. bicornuta*. The pygidial fulcrum is set more distally in *L. bicornuta* and the border is much narrower both anteriorly and posteriorly. The pygidium is considerably shorter relative to its width. The pygidial axis is much longer relative to the sagittal length of the pygidium. The pygidial border of *L. bicornuta* lacks the complex, swollen series of paired ridges characteristic of *L. bradleyi*.

Licnocephala ngi new species
Figure 4

Holotype.—Cranidium, SUI 148500 (Fig. 4.1, 4.3, 4.5, 4.7), from Section HC6 189.3 m, Garden City Formation (upper Tremadocian, Tulean, low *Psalikilopsis cuspidicauda* Zone) west crest of Hillyard Canyon, Bear River Range, Franklin County, Idaho, USA.

Diagnosis.—Anterior border very short (sag., exsag.); preglabellar field very long; preglabellar field, frontal areas, and librigenal field with sculpture of very prominent cecal trunks, with each trunk topped by a linear series of tubercles for part or all of its length; palpebral lobe with margin describing considerably more than a semicircle in plan view; librigenal lateral border narrow; pygidium with transverse row of small–medium tubercles on posterior pleural bands proximal to the fulcrum.

Occurrence.—Section HC5 195.7 m, east side of Hillyard Canyon, and HC6 189.3 m, west crest of Hillyard Canyon, Garden City Formation (upper Tremadocian, Tulean, low *Psalikilopsis cuspidicauda* Zone) west crest of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA.

Description.—Cranidial ratios cannot be calculated due to the incomplete nature of the specimens. Preglabellar field very long (sag.), longer than cranidial length from the front of the glabella to the rear of LO; anterior sections of facial sutures strongly anteriorly divergent, running nearly straight from γ, curved anteriorly just posterior to β, which is set just behind where suture cuts anterior border furrow; anterior border longest sagittally, of similar length along medial region where it forms anterior margin of the cranidium (marked by the extent of doublure ventrally; see Fig. 4.7), shorter abaxially where it is cut over most of its width by the facial suture; anterior border dorsally flat and lacking sculpture; anterior border furrow with relatively shallow anterior slope onto border and relatively steep and abrupt posterior break in slope to preglabellar field and frontal area, short (sag., exsag.), relatively deep, describing nearly even anterior arc; interocular fixigena, frontal area (anterior fixigena) and preglabellar field all with prominent sculpture of robust raised cecal trunks, radiating from around glabella, running subparallel to one another, relatively wide, tapering in width only in distal regions near anterior border furrow, bifurcating and in some cases trifurcating distally; trunks with moderate dorsal inflation, but not sharply separated laterally from background dorsal surface, rather forming subtly swollen raised regions; large but subdued tubercles developed in evenly spaced lines along tops of trunks (best seen ventrally; Fig. 4.7); palpebral lobe nearly flat, lacking dorsal sculpture, circular, with margin describing about 65% of a full circle between γ and ε; very faint, shallow, and broad palpebral furrow developed on lobe, set subparallel to margin and describing similar circle (Fig. 4.4, both sides); interocular fixigena wide, slightly wider than palpebral lobe, with a few cecal trunks running laterally from the axial furrow toward the lobe, inflated mainly proximally; glabella small and egg shaped, broadest just anterior to position of ε, tapered strongly anteriorly; axial furrows laterally bowed, anteriorly convergent, running into preglabellar furrow of identical depth and width with no obvious inflection point, preglabellar furrow describing strong anterior arc to define tapered anterior tip of glabella; glabella with moderate dorsal inflation, lacking dorsal sculpture; glabellar lobes not independently defined, glabellar furrows largely effaced; SO short (sag., exsag), deeply incised, with strong posterior arc in dorsal palpebral view (Fig. 4.4); LO relatively long, longer exsagittally than sagittally, posterior margin with posterior curvature less strong than that of SO, lacking dorsal sculpture; posterior fixigenal projection short (exsag.) behind mid-width of palpebral lobe (Fig. 4.4), running laterally in proximal part, turned sharply posteriorly distally, slightly lengthened distally; posterior border furrow and posterior border not obviously developed; there is a very short (exsag.) raised ridge along the posterior margin, negligible proximally but increasingly long and sharply defined distally and set off from a slightly swollen mid-length inflation of the fixigena by a shallow furrow; doublure known only anteriorly, where a very short (sag., exsag.) strip is defined medially by the anterior facial and connective sutures.

Librigena known from a single specimen missing the anterior region (Fig. 4.8, 4.9). Eye very narrow (tr.), strongly inflated, describing more than half a circle to match margin of palpebral lobe; eye set off from field by relatively broad, deep furrow, subcircular in cross section (cross-sectional shape best seen ventrally; Fig. 4.9); posteriorly, a very short strip of field separates the entire posterior edge of the eye from the posterior facial suture; an even shorter strip appears to do the same anteriorly, but the region is not fully preserved; field very broad, covered by closely spaced wide and prominent cecal trunks similar to those of frontal area but more closely spaced, trunks with linear rows of large but subdued tubercles, similar to those on frontal area and preglabellar field but more strongly expressed; some of the trunks bifurcate distally near the lateral border furrow; the eye is surrounded by an arc of subdued tubercles not clearly associated with the cecal trunks, which begin just abaxial to the tubercle arc; posterior facial suture strongly sinuous in course, bending posteriorly around eye and anteriorly opposite proximal part of field, distal portion running nearly posteriorly along proximal part of adaxial region of base of genal spine; lateral border with only posterior portion preserved, relatively narrow, flat, blade-like, with slight rim along lateral margin, widening posteriorly, terminated posteriorly against oblique furrow running posteriorly on abaxial region of genal spine; lateral border furrow narrow, relatively deep, edge abutting field steeper than abutting border, running with slight inflection into transverse posterior border furrow of similar shape and depth, posterior border furrow effaced about two-thirds distance adaxially of base of genal spine; genal spine with base merged with posterior border and set off from lateral border by oblique posteriorly directed furrow, broader and shallower anteriorly, narrower and deeper posteriorly, terminated anterior to tip of spine; genal spine broad, with slight rim on abaxial margin and broader, less-defined rim on adaxial margin, external surface with only slight inflation, distal region and tip not preserved; genal spine with sculpture of fine raised lines, forming anteriorly directed chevron shape, with points of chevrons set about three-quarters distance toward abaxial margin; lateral border with sculpture of subparallel fine raised lines contiguous with those of genal spine; doublure incompletely preserved (Fig. 4.9), convex, with sculpture of fine raised lines, forming posteriorly directed chevron pattern beneath genal spine, with contiguous lines running subparallel to the lateral margin beneath lateral border; doublure raised line sculpture more robust and widely spaced than that on external surfaces of genal spine and lateral border.

Rostral plate and hypostome not recovered.

As for *Licnocephala bicornuta*, the anterior segment attached to the pygidium (Fig. 4.11) is interpreted as a partially released posteriormost thoracic segment and described here as such. It has clearly released at the axis, where the pygidium's articulating half ring is fully exposed, and on the pleurae proximal to the fulcrum, where on the right side it has broken off, revealing the free anterior margin of the pygidium, and on the left side, it has clearly separated (best seen ventrally; Fig. 4.13). However, the portions distal to the fulcrum and above the doublure seem to be fused and unreleased. This is certainly true of the left side, where the doublure of the distal segment is merged with that of the pygidium (Fig. 4.13), and the fact that the right distal region is retained and attached to the pygidium when the wide proximal pleural and axial region broke off strongly suggests that it is the case there as well.

Posterior thoracic segment with very narrow axis, occupying approximately 15% of total width; pleural region proximal to fulcrum wide, accounting for 60% total pleural width; axis not preserved; pleural parts of segment very short (exsag.); pleural furrow set slightly obliquely, running in a slight posterolateral direction distally, effaced abaxial to axial furrow, moderately long (exsag.) and deep, somewhat better impressed distally than proximally, terminated distally at fulcrum; anterior margin of pleura transversely straight between axis and fulcrum, turned slightly posteriorly distal to fulcrum; posterior margin with course essentially matching anterior margin; anterior pleural band short (exsag.), about half the length of the posterior band proximally, lengthening distally due to the obliquely set pleural furrow, slightly inflated; posterior band more strongly inflated than anterior band, longer (exsag.) proximally but still well expressed distally near fulcrum, with a transverse row of moderately large but subdued tubercles similar in size, shape, and spacing to those developed on the cecal trunks of the librigenal field; portion of pleura distal to fulcrum longer (exsag.) than proximal pleura, entire distance between fulcrum and tip along anterior margin occupied by short (exsag.), slightly crescentic articulating facet; posterior dorsal region of distal area with sculpture of fine raised lines set obliquely to anterior and posterior margins, running mainly posteromedially; posterior tip nearly square, with straight lateral margin; fulcrum and entire distal region underlain by doublure, with sculpture of closely set raised lines set subparallel to straight distal margin but course slightly scalloped.

Pygidium with sagittal length approximately 47% maximum width; axis very narrow, anteriorly occupying approximately 15% pygidial width; axis with anterior width 65% sagittal axial length; axis confined to about anterior half of pygidium, with axial sagittal length 49% total pygidial sagittal

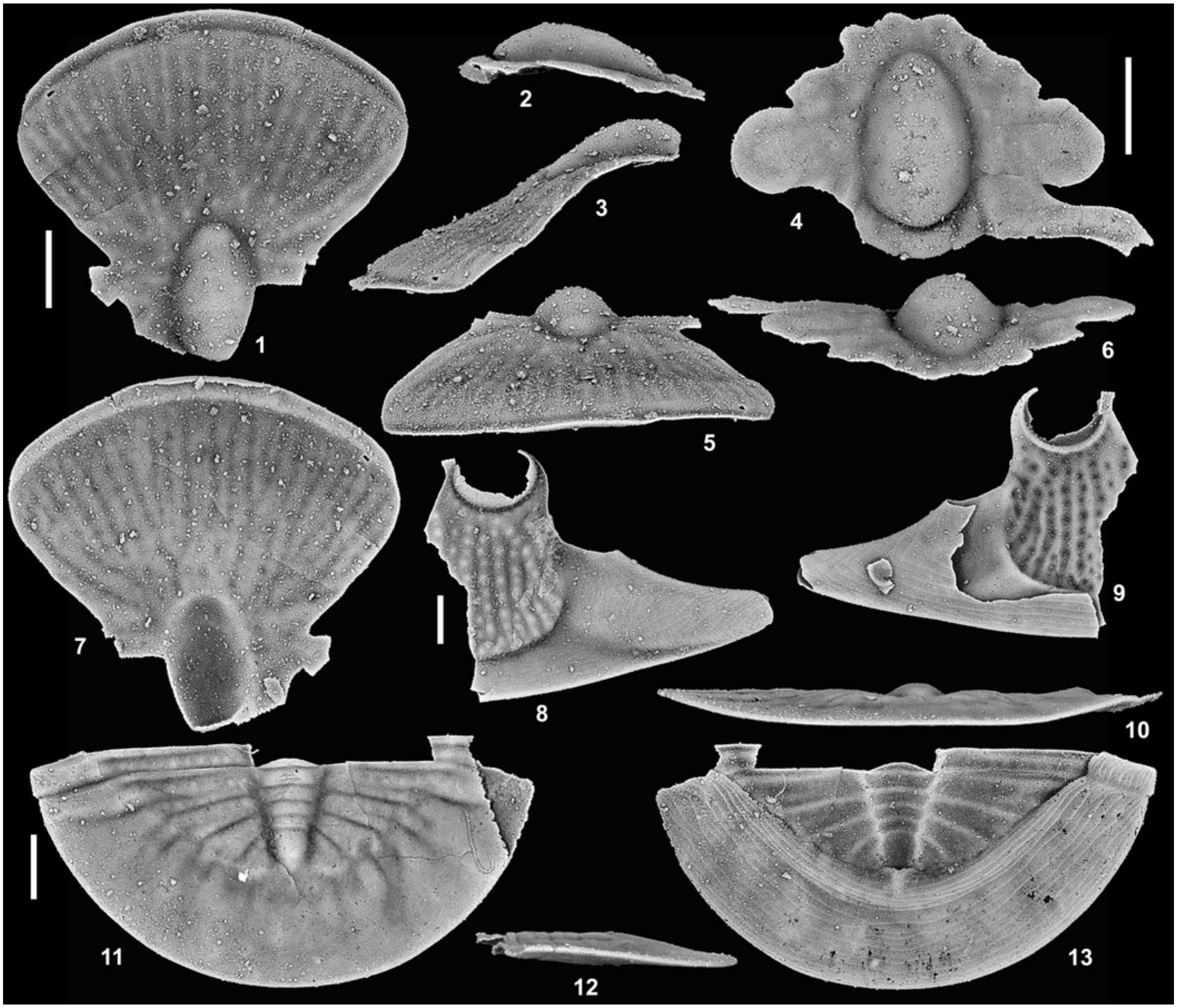

Figure 4. *Licnocephala ngi* n. sp., from Section HC5 195.7 m, east side of Hillyard Canyon, and Section HC6 189.3 m, west crest of Hillyard Canyon, Garden City Formation (upper Tremadocian, Tulean, low *Psalikilopsis cuspidicauda* Zone), Bear River Range, Franklin County, southeastern Idaho, USA. (**1, 3, 5, 7**) Cranidium, holotype, SUI 148500, dorsal, left lateral, anterior, and ventral views (HC6 189.3 m). (**2, 4, 6**) Cranidium, SUI 148501, right lateral, dorsal, and anterior views (HC6 189.3 m). (**8, 9**) Left librigena, SUI 148502, external and internal views (HC5195.7 m). (**10–13**) Pygidium, SUI 148503, posterior, dorsal, left lateral, and ventral views (HC6 189.3 m). Scale bars = 1 mm.

length; axis with four rings and long terminal piece, each posterior ring narrower than that anterior to it; first segment with short (sag., exsag.), slightly crescentic articulating half ring, length strongly tapered distally; ring furrow short (sag., exsag.), moderately deep, nearly transverse; axis with slight dorsal inflation (Fig. 4.10); first ring short (sag., exsag.), shorter than pleural region of segment, posterior rings successively slightly shorter; posterior ring furrows similar in depth to first but with course showing slight anterior arc; first and second rings with very faintly expressed pseudo-articulating half rings; axial furrows broad (tr.), relatively shallow, posteriorly convergent, almost completely shallowed posteriorly, not meeting at rear of axis; rear of axis defined only by break in slope between swollen terminal piece and flat border region; pleural region of first segment with fulcrum set about 55% distance distally from axial furrow; anterior edge of proximal part of pleurae transversely straight; first pleural furrow turned slightly posterolaterally, and posterior interpleural and pleural furrows turned progressively more posterolaterally; anterior and posterior pleural bands both very short (exsag.), anterior band about half the length of posterior band; anterior band of first segment dorsally lacking sculpture; anterior band of second and third segments with very subdued transverse row of small tubercles; posterior band of first three segments with similar transverse tubercle rows, most prominent on first segment; pleural furrow quite deep and well expressed proximal to fulcrum, similarly well expressed on all four segments but progressively narrower posteriorly; distal to fulcrum, pleurae effaced to form broad border, but both pleural and interpleural furrows continue onto border past fulcrum but become completely effaced distally well before half the distance to the margin; there is a definite change in slope from nearly horizontal to ventrally sloping at the fulcral transition from the proximal pleurae to the border, but its extent is difficult to judge as the only available specimen is mostly flattened (Fig. 4.10); doublure with 9–10 raised lines on flattened main part, set subparallel with margin and more or less evenly spaced; flattened area with subtle inflations and depressions reflecting dorsal expression of pleural bands and furrows; inner edge of doublure marked by relatively broad, inflated ridge with ventral sculpture of finer, more crowded raised lines than on main part of doublure.

Etymology.—After Reuben Ng.

Materials.—In addition to the holotype, SUI 148501–148503.

Remarks.—*Licnocephala ngi* was compared with the type species, *L. bicornuta*, in the preceding. It differs from *L. bradleyi* n. sp. in the following ways. The anterior border is much shorter and of more similar length sagittally versus exsagittally as compared with much longer sagittally. The preglabellar field and frontal areas are much longer compared with the glabella and have a sculpture of a much greater number of more crowded raised cecal trunks. The trunks have tubercle rows atop them whereas those of *L. bradleyi* lack dorsal sculpture. The anterior sections of the facial sutures are more laterally bowed and reach their point of maximum divergence well posterior to the intersection with the anterior border furrow versus anterior to this intersection. The glabella is relatively smaller compared with the overall cranidial dimensions, the axial furrows are more laterally bowed, and the glabellar furrows are nearly effaced versus generally well expressed. The eye ridge is faint and more transversely set. The librigenal field features a much greater number of prominent cecal trunks, all with prominent tubercle rows versus lacking sculpture. The librigenal lateral border is much narrower, less than half the relative length. The single pygidium available has the posterior thoracic segment partially merged, while all three pygidia of *L. bradleyi* lack this. The pygidium has a relatively larger proximal pleural region and a relatively smaller border. The pygidial pleural bands on the proximal region have transverse tubercle rows while those of *L. bradleyi* lack dorsal sculpture. The pleural bands and furrows are weakly expressed and not inflated only proximally on the border and not inflated into elaborate radiating structures as in *L. bradleyi*. The ridge bounding the inner edge of the pygidial doublure is broad and has closely spaced raised lines, whereas in *L. bradleyi* is very narrow and rim-like and lacks any space for raised lines.

Licnocephala bradleyi new species
Figures 5–8

Holotype.—Pygidium, SUI 148520 (Fig. 8.1–8.4), from Section HC5 213.4T m, Garden City Formation (upper Tremadocian, Tulean, low *Psalikilus hestoni* Zone), east side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA.

Diagnosis.—Anterior border relatively longer sagittally than in any other species; anterior sections of facial suture with point of maximum divergence just in front of where suture cuts anterior border furrow; anterior sections of the facial sutures more widely divergent from γ and nearly straight, much less laterally bowed than in other species; cecal trunks on preglabellar field and front area large and prominent, lacking tubercles, major trunks 9–10 in number; eye ridges better expressed in many specimens and more posterolaterally directed than in other species; glabellar furrows relatively well impressed; librigenal lateral border much broader than in other species; pygidium not found with posterior thoracic segment merged or partially merged; pleural region abaxial to fulcrum separated from very wide border by sharply incised arcuate furrow crossing medially behind rear of axis; pleural region with four distinctive pairs of raised and inflated ridges radiating across border, apparently reflecting the segmental pleural bands bounding the pleural furrows, but spatially disassociated from the matching features abaxial to the fulcrum.

Occurrence.—Section HC5 213.4T m–225.6 m, east side of Hillyard Canyon, and HC6 205.5–224.5 m, west crest of Hillyard Canyon, Garden City Formation (upper Tremadocian, Tulean, low *Psalikilus hestoni* Zone to high *Protopliomerella contracta* Zone), Bear River Range, Franklin County, southeastern Idaho, USA.

Description.—Despite a relatively high number of specimens, ratios of cranidial dimensions are difficult to calculate due to incomplete preservation; they are compared qualitatively with those of other species in discussions. Anterior margin describing shallow anterior arc in median portion (representing the region of the anterior margin of the border occurring on the cranidium) and elongate very shallow posterior arc in lateral portion (representing the region in which the anterior facial suture cuts obliquely across the border); anterior border very long sagittally where entire length is preserved on cranidium, progressively shorter exsagittally, pinching out laterally in crescent-shaped strip just in front of β; anterior border furrow short (sag., exsag.), describing continuous shallow anteriorly bowed arc, less curved and more transverse in median region; preglabellar field with sagittal length 78% that of glabella excluding LO; preglabellar field and frontal area with prominent, robust, raised cecal trunks set subparallel to one another and radiating from near anterior of glabella and interocular fixigenae; most specimens with 9–10 trunks; some trunks bifurcate distally; pair of trunks set near facial sutures with much more markedly transverse course than others; trunks and regions between lacking sculpture; glabella narrow and elongate, relatively weakly dorsally inflated, lacking dorsal sculpture; S1 expressed in most specimens as a strongly posteromedially directed shallow but quite broad furrow, nearly isolating a small, narrow L1 that otherwise lacks independent inflation; S2 expressed in most specimens as a shallow notch; S3 expressed in some specimens as a faint notch not obvious in others; preglabellar furrow describing strong anterior arc, running without interruption into axial furrows, narrow and sharply incised but relatively shallow; axial furrows weakly laterally bowed, slightly anteriorly convergent, somewhat shallower than preglabellar furrow; eye ridges with expression ranging from strong (Figs. 5.1, 6.2) to

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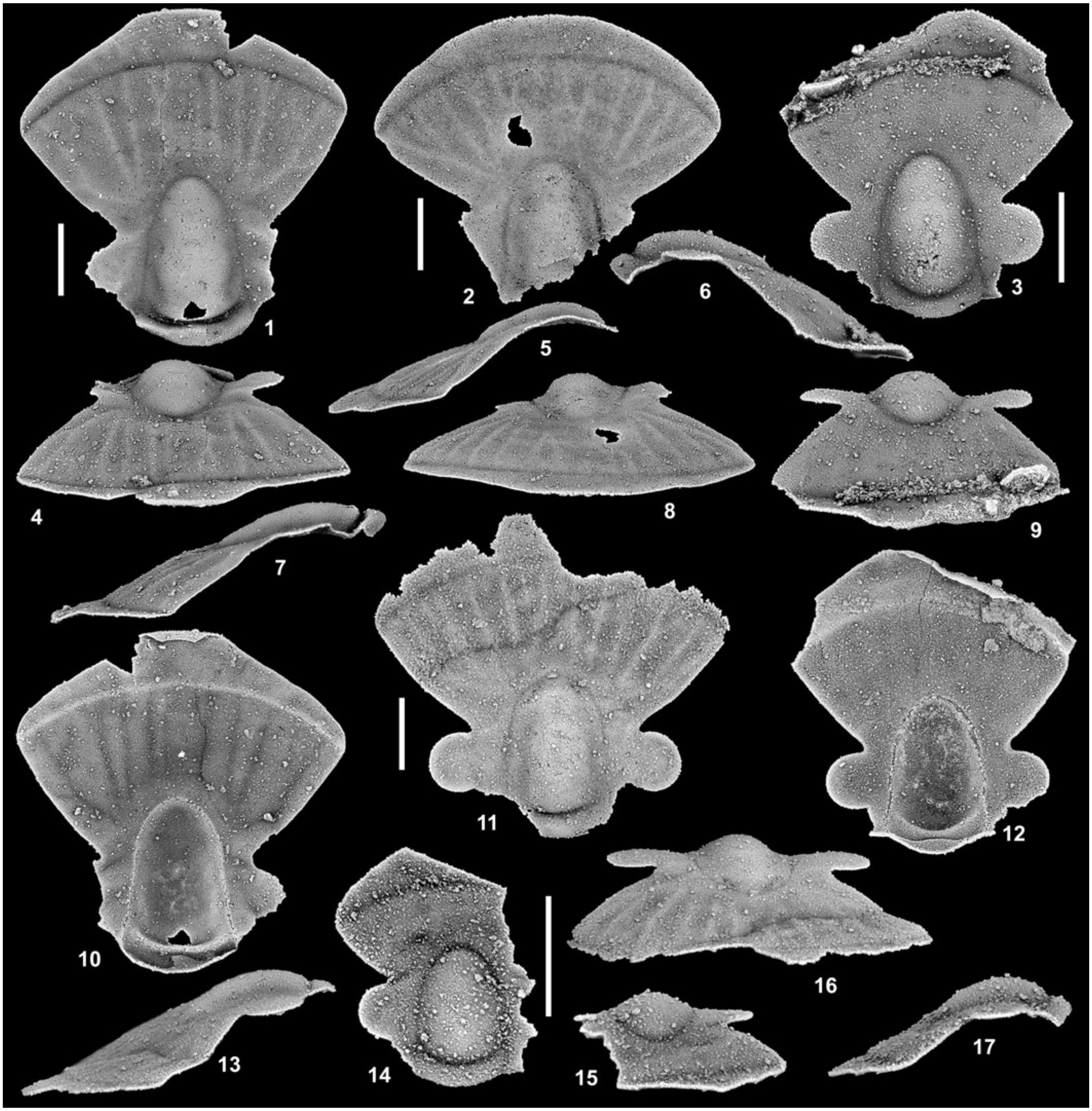

Figure 5. *Licnocephala bradleyi* n. sp., from Section HC6 205.5–221.5 m, Garden City Formation (upper Tremadocian, Tulean, *Psalikilus hestoni* Zone to *Protopliomerella contracta* Zone), west crest of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA. (**1, 4, 7, 10**) Cranidium, SUI 148504, dorsal, anterior, left lateral, and ventral views (HC6 221.5 m). (**2, 5, 8**) Cranidium, SUI 148505, dorsal, left lateral, and anterior views (HC6 205.5 m). (**3, 6, 9, 12**) Cranidium, SUI 148506, dorsal, right lateral, anterior, and ventral views (HC6 218.0 m). (**11, 13, 16**) Cranidium, SUI 148507, dorsal, left lateral, and anterior views (HC6 207.0 m). (**14, 15, 17**) Cranidium, SUI 148508, dorsal, anterior, and left lateral views, (HC6 218.0 m). Scale bars = 1 mm.

barely visible (Fig. 6.11), low ridge dorsally but plainly bifurcate ventrally in some specimens (e.g., Fig. 5.10), running strongly posterolaterally from opposite S3 to anterior edge of palpebral lobe; interocular fixigena narrow, with no independent dorsal inflation, lacking sculpture, confluent with dorsal surface of palpebral lobe; palpebral furrow not developed; palpebral lobe flat in anterior profile, with slight break in slope from more steeply inclined interocular fixigena; palpebral lobe relatively large, margin changing through ontogeny from described approximately a semicircle in smaller specimens (Fig. 5.14) to much more than a semicircle in the largest (Fig. 6.3), with a faint raised rim around margin, dorsal surface of lobe lacking sculpture; LO short, in most specimens of similar length sagittally versus exsagittally, with adaxial parts very slightly longer in some (e.g., Fig. 5.3), both anterior and posterior margins describing posteriorly bowed arc,

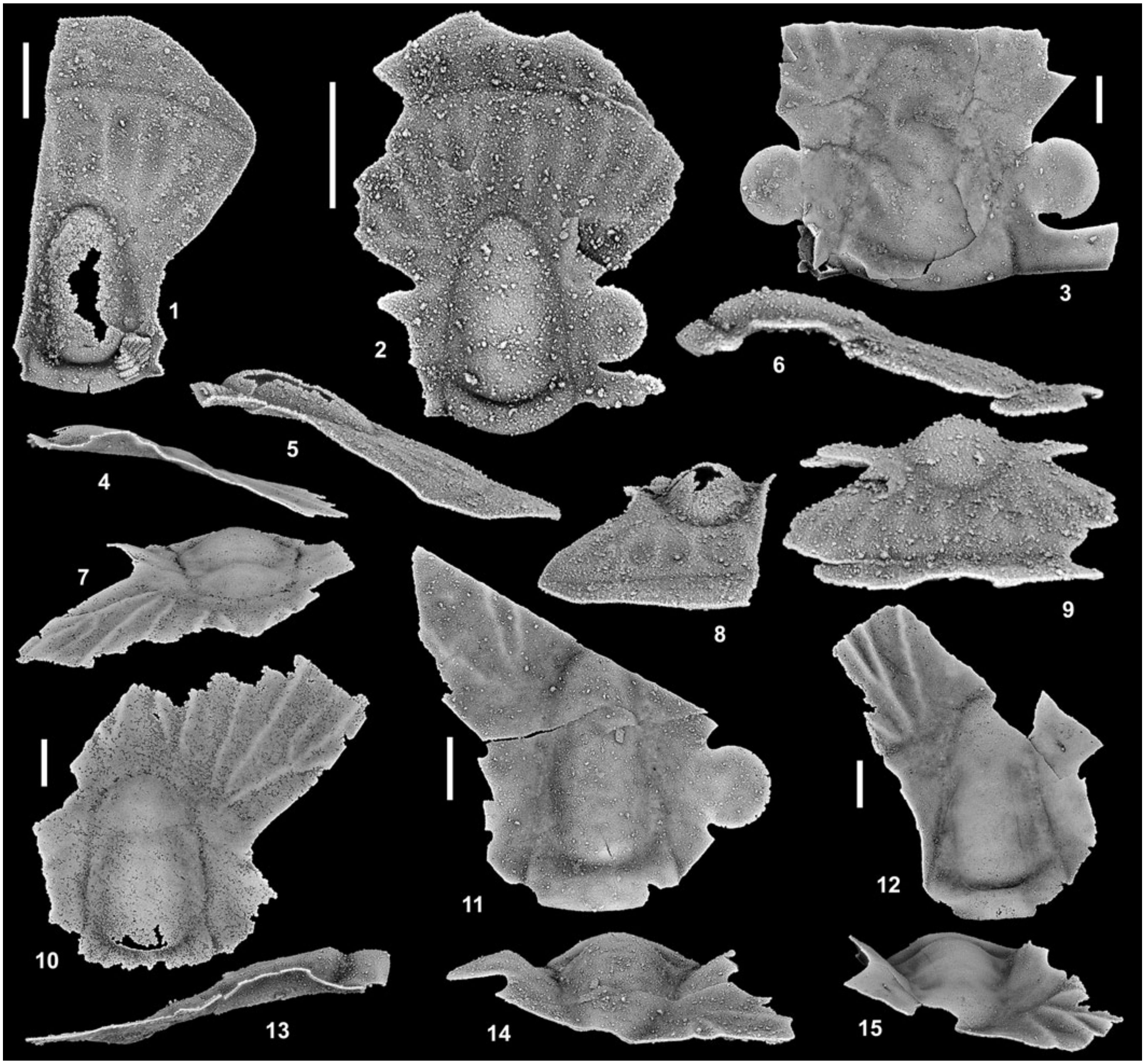

Figure 6. *Licnocephala bradleyi* n. sp., from Section HC5 225.6 m, east side of Hillyard Canyon, and Section HC6 205.5–224.5 m, west crest of Hillyard Canyon, Garden City Formation (upper Tremadocian, Tulean, *Psalikilus hestoni* Zone to *Protopliomerella contracta* Zone), Bear River Range, Franklin County, southeastern Idaho, USA. (**1, 5, 8**) Cranidium, SUI 148509, dorsal, right lateral, and anterior views (HC6 218.0 m). (**2, 6, 9**) Cranidium, SUI 148510, dorsal, right lateral, and anterior views (HC6 224.5 m). (**3**) Cranidium, SUI 148511, dorsal view (HC6 221.5 m). (**4, 7, 10**) Cranidium, SUI 148512, right lateral, anterior, and dorsal views (HC6 205.5 m). (**11, 13, 14**) Cranidium, SUI 148513, dorsal, left lateral, and anterior views (HC5 225.6 m). (**12, 15**) cranidium, SUI 148514, dorsal and anterior views (HC6 224.5 m). Scale bars = 1 mm.

lacking any dorsal sculpture, wider than glabella; SO deep, short (sag., exsag.); posterior extension not fully preserved in any specimen, very short (exsag.), with faint posterior border furrow at least proximally (Fig. 6.3) and very short furrow running directly along posterior margin (Fig. 6.3); doublure consisting of a small anteromedian region (Fig. 5.10) with oblique lateral connective sutures and posterior margin describing shallow anterior arc; doublure beneath LO (Fig. 5.12) with anterior margin describing a very shallow "W" shape, otherwise ellipsoid, longest sagittally, with slight ventral concavity; doublure of posterior projection not preserved in any specimen.

Librigena with very narrow visual surface set off from field by furrow ranging from shallow (Fig. 7.1) to deep (Fig. 7.5); anterior section of facial suture nearly straight, with only slight posterior deflection about one-third distance from eye to lateral border, long; posterior facial suture describing shallow posterior arc, about half the length of anterior suture; field long and broad, with five or six prominent cecal trunks similar to those on frontal area of cranidium, most set subparallel and transecting field; one trunk set at an angle to the others, running from behind the midpoint of the eye toward the posterior section of the facial suture (see expression ventrally on Fig. 7.2 and dorsally on Fig. 7.5);

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Figure 7. *Licnocephala bradleyi* n. sp., from Section HC5 213.4T–217.0T, east side of Hillyard Canyon, and Section HC6 218.0 m, west crest of Hillyard Canyon, Garden City Formation (upper Tremadocian, Tulean, *Psalikilus hestoni* Zone to *Protopliomerella contracta* Zone), Bear River Range, Franklin County, southeastern Idaho, USA. (**1, 2**) Left librigena, SUI 148515, external and internal views (HC6 218.0 m). (**3, 4**) Left librigena, SUI 148516, external and internal views (HC5 217.0T m). (**5**) Right librigena, SUI 148517, external view (HC5 213.4T m). (**6**) Left librigena, SUI 148518, external view (HC5 215.8T m). (**7**) Left librigena, SUI 148519, external view (HC5 217.0T m). Scale bars = 1 mm.

trunks and intervening surfaces of field lacking sculpture; lateral border furrow narrow but sharply incised, running more or less parallel to lateral margin; posterior border furrow very shallow, marked mainly by a break in slope between the posterior aspect of the field and the inflated adaxial base of the genal spine; lateral and posterior border furrows unite at base of genal spine and run posterolaterally as a single furrow set obliquely to the main length of the genal spine, with gentle posterior curvature, terminating at lateral margin more than half the length posteriorly of the spine; spine long, longer than field, main part developed adaxial to joined posterior and lateral border furrows, inflated, lacking sculpture; spine broad at base, tapered strongly posteriorly, curved posteriorly along length, tip tapered to sharp, curved point; lateral border very broad, flat, lacking dorsal sculpture, broader posteriorly than anteriorly, with slight dorsal concavity; lateral margin with gentle lateral bow, running without interruption into margin of genal spine, with subtle adaxial deflection at about half length of spine; anterior projection slightly longer than field, slightly less than half of area composed dorsally of part of the cephalic lateral border, bounded adaxially by dorsal facial suture; connective suture not definitively preserved on any specimen; lateral margin confluent with that of main librigenal margin and of similar curvature; inner margin with sharp dorsal rim; doublure underlying lateral and posterior borders broad, confluent with ventral aspect of genal spine; all with sculpture of subparallel raised lines, seven in number beneath lateral border, widely spaced near lateral margin and more tightly spaced toward inner edge of doublure, continued posteriorly long ventral aspect of genal spine; entire doublure with slight ventral concavity.

Rostral plate, hypostome, and thorax not recovered.

Pygidial measurements based on nearly intact but transversely distorted specimen of Figure 8.1. Pygidium with sagittal length 48% maximum width; axis anteriorly with maximum width 14% that of pygidium and 64% sagittal length of axis; fulcrum anteriorly set at 56% distance laterally from sagittal plane; pleural region distal to fulcrum separated from very broad border by continuous incised furrow, arc subparallel to pygidial margin, running uninterrupted around posterior aspect of axis, of similar depth everywhere along course; axis with tiny, short (sag., exsag.) articulating half ring on first segment, four axial rings and elongate terminal piece; axial furrows deep, straight, posteriorly convergent so axial rings narrow steadily from anterior to posterior, terminating at arcuate furrow bounding adaxial pleurae; axial rings short, slightly longer exsagittally, lacking sculpture; ring furrows very short (sag., exsag.), transverse; terminal piece about two-thirds as long as wide, narrower posteriorly; proximal pleural regions

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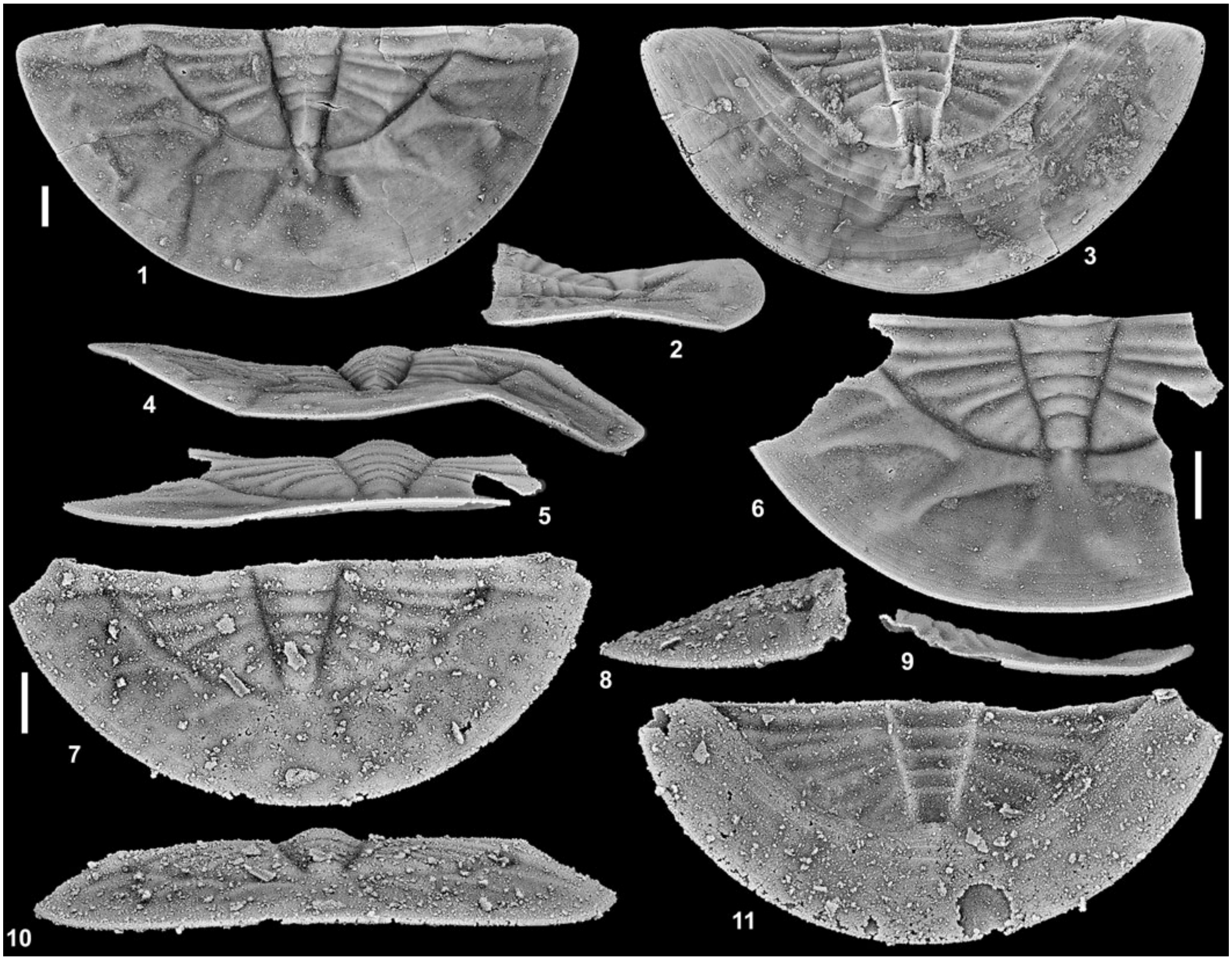

Figure 8. *Licnocephala bradleyi* n. sp., from Section HC5 213.4T, east side of Hillyard Canyon, and Section HC6 224.5 m, west crest of Hillyard Canyon, Garden City Formation (upper Tremadocian, Tulean, *Psalikilus hestoni* Zone to *Protopliomerella contracta* Zone), Bear River Range, Franklin County, southeastern Idaho, USA, and Section G 258.2 m, Fillmore Formation (upper Tremadocian, Tulean, *Heckethornia hyndeae* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. (**1–4**) Pygidium, holotype, SUI 148520, dorsal, left lateral, ventral, and posterior views (HC5 213.4T m). (**5, 6, 9**) Pygidium, SUI 148521, posterior, dorsal, and left lateral views (HC6 224.5 m). (**7, 8, 10, 11**) Pygidium, SUI 148522, dorsal, right lateral, posterior, and ventral views (G 258.2 m). Scale bars = 1 mm.

with both anterior and posterior pleural bands short (exsag.) but inflated, posterior band slightly longer than anterior band, lacking sculpture; pleural furrow long (exsag.) and shallow; first segment transverse, posterior segments with steadily increasing posterior deflection; fourth segment with pleural bands nearly effaced; border extremely broad, with unique, splayed, inflated structures, broad proximally and tapering rapidly distally, apparently reflecting expression of pleural bands; first pygidial segment continued across anterior aspect of border with only slight lengthening (exsag.), bounded posteriorly by first interpleural furrow, which extends nearly to pygidial margin; all three posterior segments with inflated "Y"-shaped structures arranged in radial fashion around remainder of border; border otherwise flat and lacking sculpture; doublure with 10–12 subparallel raised lines running more or less with the same arc as the pygidial margin, approximately equally spaced over most of doublure, more crowded adaxially in anterior region; inner edge of doublure bounded by narrow ventral ridge.

Etymology.—After Alex Bradley.

Materials.—In addition to the holotype, SUI 148504–148519, 148521, 148522.

Remarks.—*Licnocephala bradleyi* was compared with *L. bicornuta* and *L. ngi* under discussion of those species.

Licnocephala species 1
Figure 3.11, 3.12, 3.15

Occurrence.—Section G 162.0T m, Fillmore Formation (upper Tremadocian, Tulean, low *Psalikilopsis cuspidicauda* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Materials.—SUI 148499.

Remarks.—A single pygidium from the *Psalikilopsis cuspidicauda* Zone of the Fillmore Formation differs from those of species of the genus from the same zone in the Garden City Formation in the presence of a much shorter axis, a more substantial posterior deflection of the first segment distal to the fulcrum, substantially more effaced proximal pleural regions, and lack of an incised furrow separating the proximal pleural regions from the border. In other respects, it is more like pygidia of species of *Licnocephala* than any other known taxon and likely represents a rare new species of the genus.

Licnocephala species 2
Figure 9

2009 *Licnocephala* sp. nov. A; Adrain et al., p. 561, fig. 11N.

Occurrence.—Section HC5 210.3T m, east side of Hillyard Canyon, and HC6 203.5 m, west crest of Hillyard Canyon, Garden City Formation (upper Tremadocian, Tulean, *Psalikilus typicum* Zone), Bear River Range, Franklin County, southeastern Idaho, USA.

Materials.—SUI 115222, 148523.

Remarks.—Two cranidia from the Garden City Formation are stratigraphically intermediate between the older *L. bicornuta* and *L. ngi* and the younger *L. bradleyi*. Of these species, they most closely resemble *L. bradleyi*, particularly in the relatively long anterior border and the possession of a similar number of similarly prominent cecal trunks on the preglabellar field and frontal areas. The glabella is also of similar dimensions and has at least S1 expressed with similar course. They differ from those of *L. bradleyi* in the possession of an anterior border that is of nearly the same length sagittally versus exsagittally as opposed to much longer sagittally, less anteriorly divergent anterior facial sutures that are more laterally bowed, and largely effaced versus generally prominent eye ridges. Once again, a rare but distinct species is likely represented.

Genus *Ibexocephala* new genus

Type species.—*Ibexocephala lossoae* n. sp., from the Garden City Formation (upper Tremadocian, Tulean, *Psalikilopsis cuspidicauda* Zone), southeastern Idaho, USA.

Other species.—*Ibexocephala dekosterae* n. sp., from the Fillmore Formation (upper Tremadocian, Tulean, *Psalikilopsis cuspidicauda* Zone), western Utah, USA.

Diagnosis.—Cranidium with most dorsal elements nearly entirely effaced and a very strong posterior "kink" in lateral profile, with the entire rear region set at a very slightly obtuse to acute angle to the main anterior region; librigena also nearly effaced, lacking lateral or posterior border furrows, with elongate, curved genal spine with sculpture of a few prominent raised lines along adaxial margin; pygidium (known only for type species) very short (sag.) relative to width, dorsally nearly entirely effaced (axial features visible

Figure 9. *Licnocephala* species 2, from Section HC5 210.3T, east side of Hillyard Canyon, and Section HC6 203.5 m, west crest of Hillyard Canyon, Garden City Formation (upper Tremadocian, Tulean, *Psalikilus hestoni* Zone), Bear River Range, Franklin County, southeastern Idaho, USA. (**1, 2, 4, 6**) Cranidium, SUI 115222, dorsal, ventral, right lateral, and anterior views (HC6 203.5 m). (**3, 5, 7, 8**) Cranidium, SUI 148523, dorsal, left lateral, anterior, and ventral views (HC5 210.3T m). Scale bar = 1 mm.

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ventrally), dorsal surface lacking sculpture and slightly dorsally concave, bounded along margin by narrow dorsal rim, abaxial part of pleural turned vertical to form short vertical "wall" beneath marginal rim and above inflated border; pygidial border with raised line sculpture; pygidial doublure narrow, matching narrow inflated border and turned nearly vertically.

Etymology.—From the Ibex region.

Remarks.—Cranidia of species of *Ibexocephala* have such an unusual morphology that if one were encountered in isolation it might be assumed that it was distorted. However, multiple examples belonging to two species have been recovered, and they confirm that the taxon featured heads with the posterior region turned back at a very strong angle to most of the main anterior part, creating a distinct, down-turned "kink" in lateral profile. This strong folding of the rear of the cranidium seems unique to the genus among trilobites in general and is certainly not shared with any other bathyurids. Despite this unusual morphology and the high degree of effacement, however, *Ibexocephala* displays the three cardinal features of the *Chapmanopyge* group delineated earlier. It has the facial suture cutting dorsally across the anterior border, such that most of the anterior cranidial margin is the suture (Fig. 10.1), tiny strap-like posterior projections, and an extremely narrow visual surface (Figs. 11.14, 14.7).

Ibexocephala lossoae new species
Figures 10–12

2009 Bathyuridae gen. nov. 1 sp. nov. 1; Adrain et al., p. 559, fig. 10J, O.

Holotype.—Cranidium, SUI 148524 (Fig. 10.1–10.3, 10.5, 10.6, 10.12), from Section HC6 189.3 m, Garden City Formation (upper Tremadocian, Tulean, low *Psalikilopsis cuspidicauda* Zone) west crest of Hillyard Canyon, Bear River Range, Franklin County, Idaho, USA.

Diagnosis.—Anterior border furrow well defined as a sharp break in slope between anterior border and preglabellar field; cranidium relatively narrow compared with sagittal length; "kink" in cranidial sagittal profile describing slightly obtuse angle; genal spine relatively short.

Occurrence.—Section HC5 195.7–204.2T m, east side of Hillyard Canyon, and HC6 189.3 m, west crest of Hillyard Canyon, Garden City Formation (upper Tremadocian, Tulean, low *Psalikilopsis cuspidicauda* Zone) west crest of Hillyard Canyon, Bear River Range, Franklin County, Idaho, USA. Section D 88.9 m, southern House Range, and G 162.0T m, southern Confusion Range, Fillmore Formation (upper Tremadocian, Tulean, low *Psalikilopsis cuspidicauda* Zone), Ibex area, Millard County, western Utah, USA.

Description.—Cranidium with sagittal length 66% maximum width across posterior fixigenal projections (calculated from Fig. 10.1 by doubling the distance from the tip of the left projection to the sagittal midline); width across palpebral lobes 92% width across maximum point of divergence of anterior facial sutures and 94% sagittal length; width across maximum point of divergence of anterior facial sutures 103% sagittal length; entire dorsal cranidial surface smooth and lacking sculpture; anterior border long sagittally, progressively shorter (exsag.) abaxially, almost entire anterior margin formed by anterior section of facial suture cutting obliquely across border; anterior margin describing very shallow "S" shape on either side, anteriorly convex distally, anteriorly concave proximally, sides meeting medially to form anterior prow; anterior border dorsally concave in section (Fig. 10.5), anterior border furrow short (sag., exsag.), appears well incised in dorsal view of large individual (Fig. 10.1), but this is due mainly to a break in slope between the dorsally convex anterior part of the preglabellar field and the dorsally concave furrow (Fig. 10.5)—the furrow itself is shallow (Fig. 10.5) and shallower in smaller specimens (Fig. 10.7, 10.9, 10.13), describing gentle anterior arc, interrupted by slight posterior flexure in medial region; anterior sections of facial suture strongly anteriorly divergent, β set just behind point where suture cuts anterior border furrow, suture with strongest divergence in front of palpebral lobe, flexed slightly behind front of glabella to run more anteriorly behind β, anterior to β turned strongly adaxially to cut across most of width of anterior border; preglabellar field and front area dorsally convex, swollen slightly anteriorly in sagittal profile (Fig. 10.5), featureless; preglabellar furrow entirely (Fig. 10.7, 10.9, 10.13) or nearly (Fig. 10.1) dorsally effaced but clearly visible ventrally (Fig. 10.2, 10.12); axial furrows not visible dorsally or ventrally; preglabellar furrow with strong anterior arc, shape of glabella behind this region unknown; cranidium in transverse profile (Fig. 10.3) with anterior surface describing more or less even, moderate, dorsal arc from one edge of the palpebral lobes to the other, axial furrows and glabella not defined; palpebral lobes long (exsag.), relatively narrow, γ set slightly more adaxially than ϵ; palpebral furrow not defined, top of palpebral lobe dorsally convex, confluent with interocular fixigena; cranidium with sharp posteroventral bend in sagittal profile, initiated opposite rear third of palpebral lobe (Fig. 10.5); posterior part of glabella, posterior fixigena, and occipital ring with sagittal profile describing a slope that forms an acute angle with the sagittal profile of the anterior section of the facial suture; SO and LO not well defined—between the sharp change in slope and the rear margin of LO there is only a shallow, wide, dorsally concave depression (Fig. 10.1, 10.5, 10.6); posterior margin of LO describing shallow posterior arc, slightly stronger medially; posterior fixigenal projection oriented nearly vertically in dorsal palpebral view (Fig. 10.1) but relatively wide (Fig. 10.3), similar length (exsag.) proximally and distally, turned slightly posterolaterally in dorsal view, posterior margin gently anteriorly arcuate; posterior border furrow and posterior border not discernible; posterior section of facial suture with very shallow "S"-shaped course in dorsal view (Fig. 10.1), cut sharply posteriorly and slightly laterally at distal tip of projection; cranidial doublure limited to very short (exsag.) strip beneath rear of posterior fixigenal projection, slightly longer abaxial to outer edge of palpebral lobe, and lensoid articulating surface beneath occipital region, ventrally

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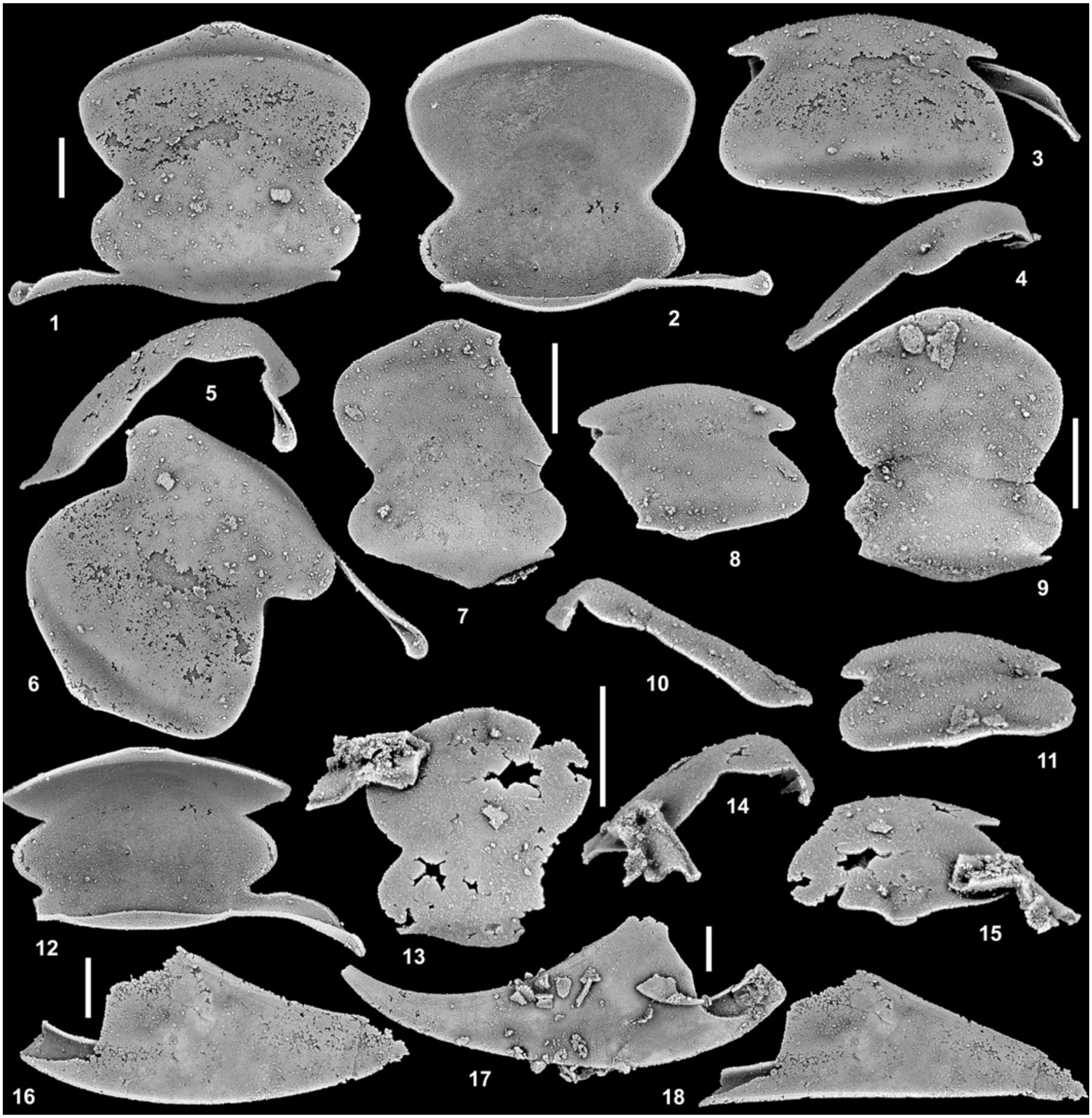

Figure 10. *Ibexocephala lossoae* n. gen. n. sp., from Section HC5 195.7–204.2T m, east side of Hillyard Canyon, and Section HC6 189.3 m, west crest of Hillyard Canyon, Garden City Formation (upper Tremadocian, Tulean, low *Psalikilopsis cuspidicauda* Zone), Bear River Range, Franklin County, southeastern Idaho, USA), and Section D 88.9 m, Fillmore Formation (upper Tremadocian, Tulean, low *Psalikilopsis cuspidicauda* Zone), southern House Range, Ibex area, Millard County, western Utah, USA. (**1–3, 5, 6, 12**) Cranidium, holotype, SUI 148524, dorsal, ventral, anterior, left lateral, oblique, and ventral occipital ring views (HC6 189.3 m). (**4, 7, 8**) Cranidium, SUI 148525, left lateral, dorsal, and anterior views (HC6 189.3 m). (**9–11**) Cranidium, SUI 115181, dorsal, right lateral, and anterior views (HC5 195.7 m). (**13–15**) Cranidium, SUI 148526, dorsal, left lateral, and anterior views (D 88.9 m). (**16, 18**) Left librigena, SUI 148527, external and ventrolateral views (HC5 203.7–204.2T m). (**17**) Right librigena, SUI 148528, external view (D 88.9 m). Scale bars = 1 mm.

slightly concave, with one or two very faint raised lines on anterior part.

Librigena with posterior margin of posterior border and adaxial margin of genal spine intergrading, with no obvious transition point; lateral border and abaxial margin of genal spine intergrading, with no transition point; visual surface very narrow (tr.) but relatively long, angled anteriorly relative to main body of librigena; visual surface moderately inflated, set off from field by narrow, shallow furrow (best expressed ventrally; e.g., Fig. 11.7); posterior margin only slightly arcuate, nearly straight behind eye for about two-thirds of distance to tip of genal spine, posterior third more strongly curved, reflected

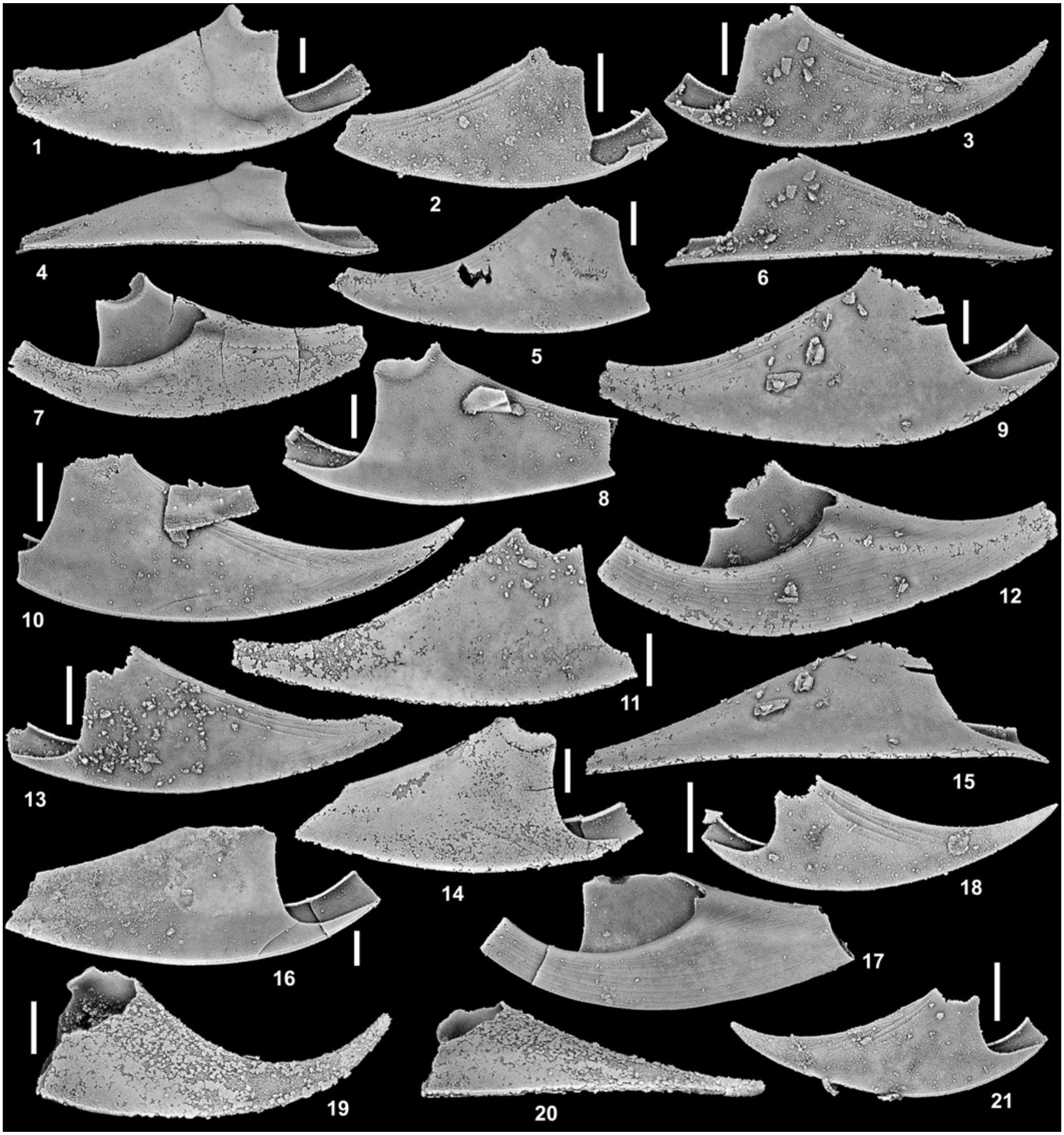

Figure 11. *Ibexocephala lossoae* n. gen. n. sp., from Section HC5 195.7–204.2T m, east side of Hillyard Canyon, and Section HC6 189.3 m, west crest of Hillyard Canyon, Garden City Formation ((upper Tremadocian, Tulean, low *Psalikilopsis cuspidicauda* Zone), Bear River Range, Franklin County, southeastern Idaho, USA), and Section D 88.9 m, southern House Range, and Section G 155.6–162.0T m, southern Confusion Range, Fillmore Formation (upper Tremadocian, Tulean, low *Psalikilopsis cuspidicauda* Zone), Ibex area, Millard County, western Utah, USA. (**1, 4, 7**) Right librigena, SUI 148529, external, ventrolateral, and internal views, (HC5 203.7–204.2T m). (**2**) Right librigena, SUI 148530, external view (HC6 189.3 m). (**3, 6**) Left librigena, SUI 148531, external and ventrolateral views (G 162.0T m). (**5**) Right librigena, SUI 148532, external view (D 88.9 m). (**8**) Left librigena, SUI 148533, external view (HC6 189.3 m). (**9, 12, 15**) Right librigena, SUI 148534, external, internal, and ventrolateral views (D 88.9 m). (**10**) Left librigena, SUI 148535, external view (HC6 189.3 m). (**11**) Right librigena, SUI 148536, external view (G 162.0T m). (**13**) Left librigena, SUI 148537, external view (G 162.0T m). (**14**) Right librigena, SUI 148538, external view (HC5 203.7–204.2T m). (**16, 17**) Right librigena, SUI 148539, external and internal views (HC6 189.3 m). (**18**) Left librigena, SUI 148540, external view (HC5 195.7 m). (**19, 20**) Left librigena, SUI 148541, external and ventrolateral views (G 155.6 m). (**21**) Right librigena, SUI 148542, external view (D 88.9 m). Scale bars = 1 mm.

posterior curvature of genal spine; lateral margin more evenly curved over entire length than posterior margin, with slightly stronger curvature opposite rear of eye and posteriorly where genal spine is more strongly curved; posterior section of facial suture restricted to narrow region behind eye; anterior section of facial suture with moderate posterior arc opposite field,

Figure 12. *Ibexocephala lossoae* n. gen. n. sp., from Section HC5 195.7 m, east side of Hillyard Canyon, and Section HC6 189.3 m, west crest of Hillyard Canyon, Garden City Formation ((upper Tremadocian, Tulean, low *Psalikilopsis cuspidicauda* Zone), Bear River Range, Franklin County, southeastern Idaho, USA), and Section D 88.9 m, southern House Range, and Section G 162.0T m, southern Confusion Range, Fillmore Formation (upper Tremadocian, Tulean, low *Psalikilopsis cuspidicauda* Zone), Ibex area, Millard County, western Utah, USA. (**1–4, 6**) Pygidium, SUI 148543, dorsal, ventral, posterior, anterior, and left lateral views (D 88.9 m). (**5, 7, 8**) Pygidium, SUI 148544, posterior, right lateral, and dorsal views (D 88.9 m). (**9, 13, 14, 16**) Pygidium, SUI 115182, right lateral, dorsal, posterior, and ventral views (HC5 195.7 m). (**10–12**) Pygidium, SUI 148545, left lateral, dorsal, and posterior views (G 162.0T m). (**15, 17, 20**) Pygidium, SUI 148546, left lateral, dorsal, and posterior views (HC5 195.7 m). (**18, 19, 21**) Pygidium, SUI 148547, right lateral, dorsal, and posterior views (HC6 189.3 m). Scale bars = 1 mm.

running up anterior projection adaxial to margin, so that the anterior portion of the cephalic anterior border is held on the dorsal part of the projection; external surface of librigena nearly featureless, posterior border, posterior border furrow, lateral border, and lateral border furrow not expressed; external surface slightly externally convex in region around eye and upper part of field, forming a broad, shallow, externally concave trough in abaxial half up to lateral margin (Fig. 11.15); posterior margin with two or three fine and closely spaced raised lines subparallel with and near margin (Fig. 11.3, 11.18), and three or four more robust and more widely spaced lines, also subparallel with margin but with straighter course and not as long, set further from

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the margin; where rear of librigena narrows and curves into genal spine, some specimens have fine chevron-shaped raised lines, with the points of the chevrons directed posteriorly, and the lateral limbs faint and petering out near lateral margin (Fig. 11.9, 11.10); lateral margin with a single fine raised line running subparallel to and very close to margin along entire length; lateral margin flattened and ventrolaterally blade-like; genal spine with strong posterior curvature, tapered rapidly to sharp distal tip (Fig. 11.3); anterior projection long and broad, anterior region containing strip of anterior cephalic border, inner edge in dorsal view marked by low raised wall; doublure extensive, underlying all of librigena except relatively small region of field around eye (Fig. 11.7); most of doublure forming nearly flat ventral area inside lateral margin, slightly ventrally concave, covered with subparallel raised lines, more crowded anteriorly on anterior projection, more widely spaced posteriorly; inner edge of anterior projection and inner edge of doublure beneath field forming curved, low, quite broad ventral ridge, innermost edge of doublure turned dorsally to form small wall (Fig. 11.2, 11.4, 11.15, 11.16); posteriorly the ridge along the inner margin deflects sharply posteriorly to form a second ridge, with about the same dimensions and inflation, running along ventral aspect of genal spine (Fig. 11.12, 11.17); adaxial to this ridge is a ventrally concave trough between the ridge and the posterior margin; both the ridge and the trough are crossed by the raised lines running posteriorly from the anterior projection; prominent "U"-shaped panderian notch where doublure contacts posterior margin (Fig. 11.7, 11.12, 11.17).

Rostral plate, hypostome, thorax, not recovered.

Pygidium with sagittal length 35% maximum width; anterior pleural margin almost exactly transversely straight, slight posterior deflection at very distally placed fulcrum discernible only on some specimens (Fig. 12.13, 12.19); posterior margin of upper region of pygidium describing shallow, nearly even posterior arc, with slight increase in curvature in posteromedian region; margin of upper region inflated into sharp, slightly upturned (Fig. 12.6, 12.15) ridge with sculpture of around six fine, closely set, raised lines; ridge set off from dorsal aspect of pygidium by shallow trough; dorsal aspect of pygidium with most structures nearly or completely dorsally effaced; axial furrows not evident dorsally on some specimens (Fig. 12.1, 12.11, 12.19), very weakly expressed on others (Fig. 12.17), slightly posteriorly convergent; axis with anterior width 27% total pygidial width and 93% axial length; articulating half ring very short (sag., exsag.), slightly longer sagittally, with slight independent inflation (best seen ventrally; e.g., Fig. 12.16), set off from first ring by very faint and short (exsag.) furrow (Fig. 12.17); axial rings and ring furrows dorsally nearly (Fig. 21.17) to completely (Fig. 12.11) obscure, best seen ventrally but only reasonably clearly expressed in some specimens (e.g., Fig. 12.2); four rings present plus a fairly large terminal piece that on some specimens appears to feature a pair of lateral slightly inflated regions (Fig. 12.1); rear of axis separated from posterior margin of upper pygidial region by a small strip of pleura; pleural and interpleural furrows not discernible, pleural region featureless; below posterior rim of dorsal region, a nearly vertical wall runs ventrally to an inflated ridge-like ventral border; the wall is more (Fig. 12.7) or less (Fig. 12.6, 12.15) posteriorly extended, so the ventral border is visible in dorsal view in some specimens (Fig. 12.11) and not in others (Fig. 12.1, 12.13); the wall is outwardly concave, and its external surface is featureless; the ventral margin is more inflated than the ridge surrounding the dorsal region, about twice the width, and has a sculpture of much more robust and more widely spaced raised lines, set subparallel to the margin; in posterior (Fig. 12.3) and ventral (Fig. 12.2) view, the border has a gentle posteromedian embayment; doublure is limited to a narrow strip held nearly vertically above the ventral margin of the border, best seen in anterior view (Fig. 12.4), with sculpture of closely spaced fine raised lines much less robust than those on the border; the ventral margin of the border in posterior (Fig. 12.3) and anterior (Fig. 12.4) view not flat, but describing gentle ventral arc on either side of pygidium, flexed upward at posteromedian embayment.

Etymology.—After Sarah Losso.

Materials.—In addition to the holotype, SUI 115181, 115182, 148525–148547.

Remarks.—*Ibexocephala lossoae* is compared with the only other species, *I. dekosterae*, in the following differential description of the latter.

Ibexocephala dekosterae new species
Figures 13, 14

Holotype.—Cranidium, SUI 148548 (Fig. 13.1, 13.2, 13.4, 13.7), from Section D 106.4 m, Fillmore Formation (upper Tremadocian, Tulean, high *Psalikilopsis cuspidicauda* Zone), southern House Range, Ibex area, Millard County, western Utah, USA.

Diagnosis.—Anterior border furrow largely effaced; cranidium broad relative to its length; posterior "kink" in cranidial lateral profile describing a slightly acute angle; genal spine elongate, distally tapering, and strongly curved.

Occurrence.—Section D 106.4 m, Fillmore Formation (upper Tremadocian, Tulean, high *Psalikilopsis cuspidicauda* Zone), southern House Range, Ibex area, Millard County, western Utah, USA.

Description.—*Ibexocephala dekosterae* is similar enough to *I. lossoae* that description lists only all of the discernible morphological differences. Cranidium with anterior sections of the facial sutures more straight posteriorly, less anteriorly divergent; anterior border slightly longer abaxially (exsag.); anterior border furrow considerably more effaced; width across γ 75% versus 70% cranidial sagittal length; palpebral lobe shorter (exsag.); posterior "kink" in cranidial sagittal profile describing slightly acute versus slightly obtuse angle; genal spine much longer, with distal regions comparatively narrower and much more strongly posteriorly curved.

Etymology.—After Rebecca DeKoster.

Materials.—In addition to the holotype, SUI 148549–148562.

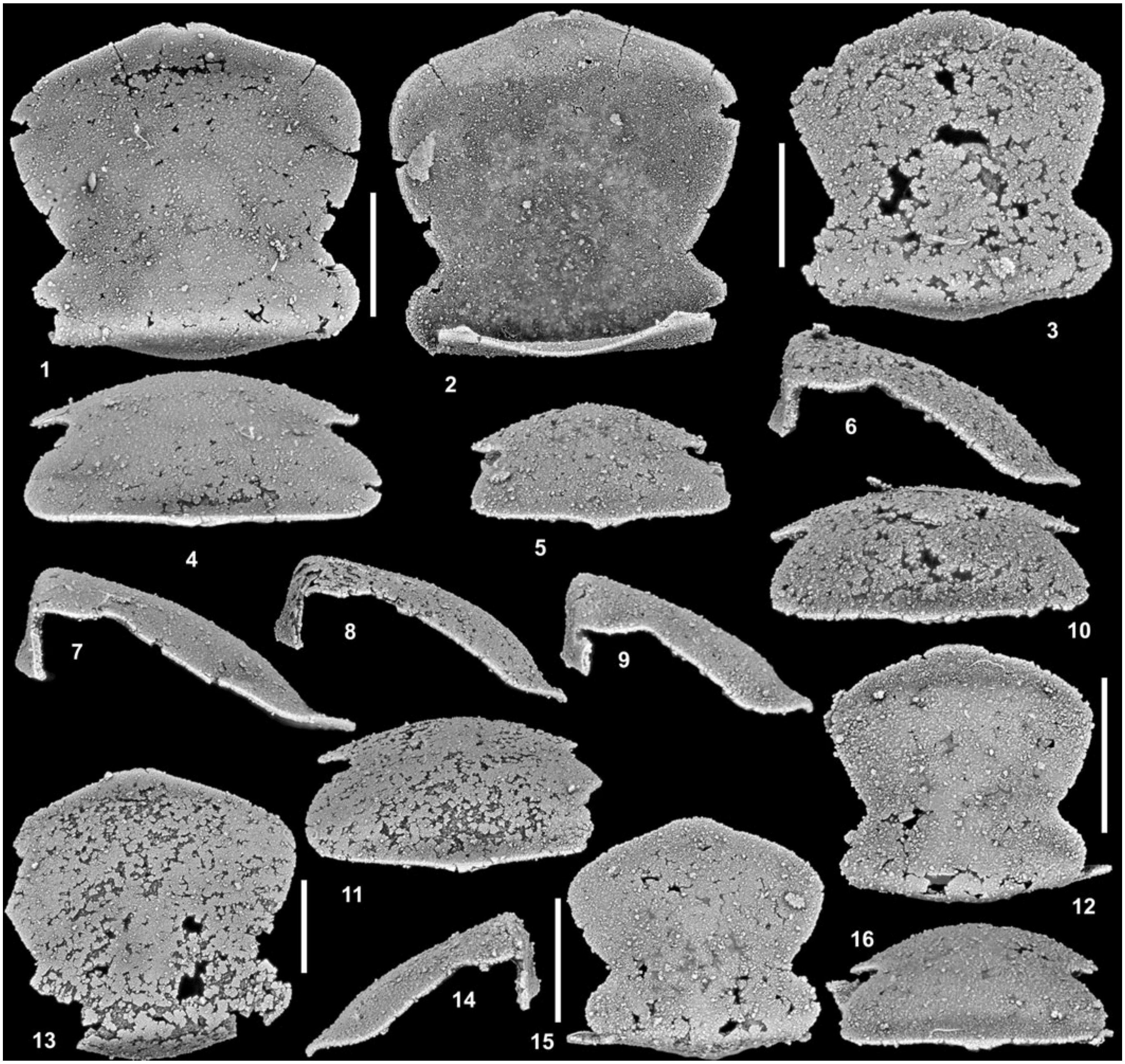

Figure 13. *Ibexocephala dekosterae* n. gen. n. sp., from Section D 106.4 m, Fillmore Formation (upper Tremadocian, Tulean, high *Psalikilopsis cuspidicauda* Zone), southern House Range, Ibex area, Millard County, western Utah, USA. (**1, 2, 4, 7**) Cranidium, holotype, SUI 148548, dorsal, ventral, anterior, and right lateral views. (**3, 6, 10**) Cranidium, SUI 148549, dorsal, right lateral, and anterior views. (**5, 14, 15**) Cranidium, SUI 148550, anterior, left lateral, and dorsal views. (**8, 11, 13**) Cranidium, SUI 148551, right lateral, anterior, and dorsal views. (**9, 12, 16**) Cranidium, SUI 148552, right lateral, dorsal, and anterior views. Scale bars = 1 mm.

Remarks.—Congeneric bathyurid species from the upper versus lower part of the *Psalikilopsis cuspidicauda* Zone have previously been found to be closely similar yet pervasively differentiated in a small number of morphological features. Examples are *Gladiatoria harrisi* Adrain, McAdams, and Westrop, 2011 (Adrain et al., 2011a) versus *G. gladiator* (Ross, 1951) (see Adrain et al., 2011a) and *Psalikilopsis paracuspidicauda* Adrain et al., 2011 (Adrain et al., 2011b) versus *P. cuspidicauda* (Ross, 1951) (see Adrain et al., 2011b). Species of *Ibexocephala* continue this trend, differing in the features listed in the differential description. Pygidia are generally very rare at horizon D 106.4 m, most likely owing to local taphonomic sorting, and the sclerite has not been found for *I. dekosterae*. However, given that the species is represented by fairly abundant cranidia and librigenae and that both sclerite types indicate obvious differences from the older type species, it seems preferable to formally name it rather than consigning it to open nomenclature.

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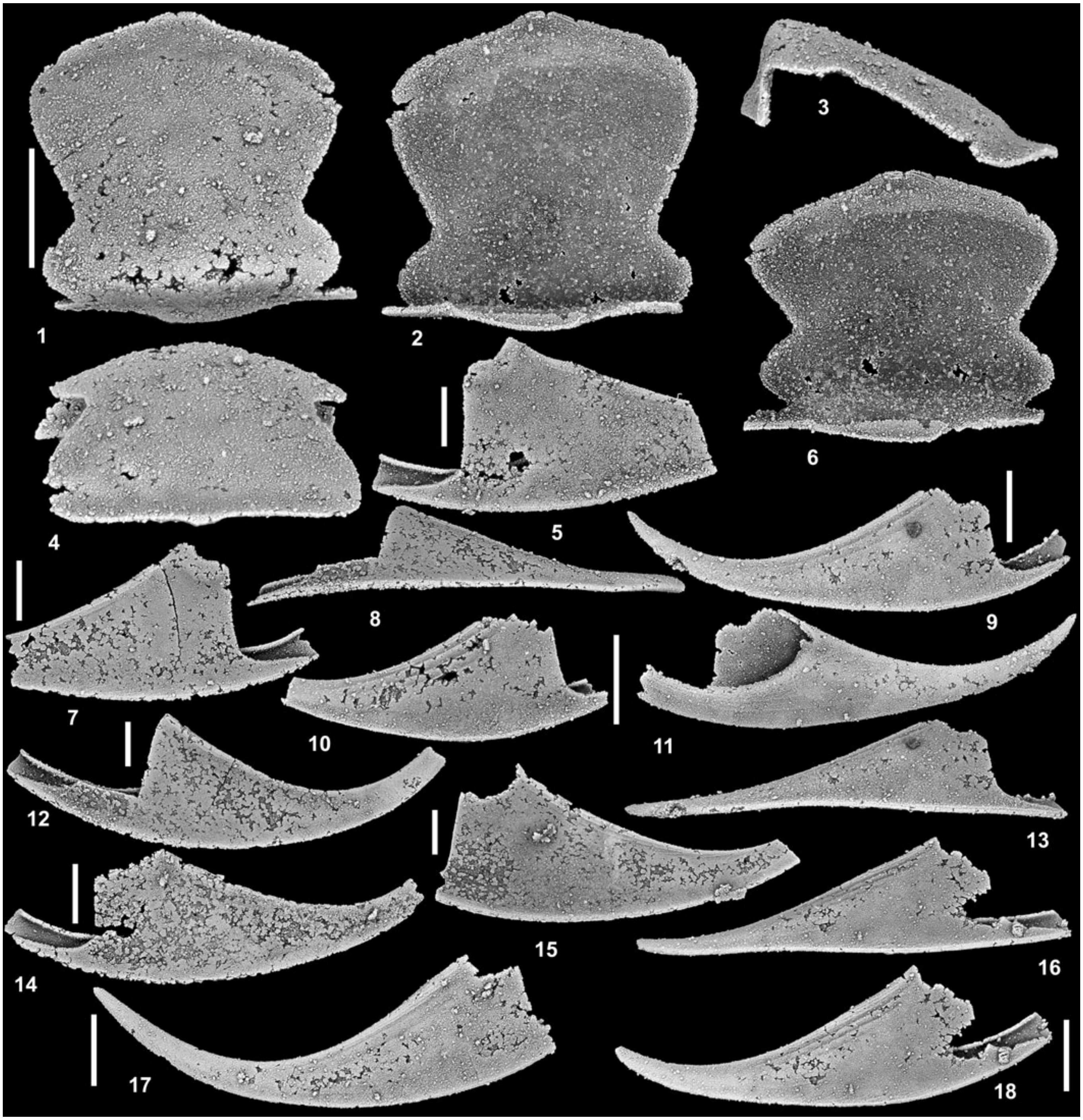

Figure 14. *Ibexocephala dekosterae* n. gen. n. sp., from Section D 106.4 m, Fillmore Formation (upper Tremadocian, Tulean, high *Psalikilopsis cuspidicauda* Zone), southern House Range, Ibex area, Millard County, western Utah, USA. (**1–4, 6**) Cranidium, SUI 148553, dorsal, ventral, right lateral, anterior, and ventral occipital views. (**5**) Left librigena, SUI 148554, external view. (**7**) Right librigena, SUI 148555, external view. (**8, 12**) Left librigena, SUI 148556, ventrolateral and external views. (**9, 11, 13**) Right librigena, SUI 148557, external, internal, and ventrolateral views. (**10**) Right librigena, SUI 148558, external view. (**14**) Left librigena, SUI 148559, external view. (**15**) Left librigena, SUI 148560, external view. (**16, 18**) Right librigena, SUI 148561, ventrolateral and external views. (**17**) Right librigena, SUI 148562, external view. Scale bars = 1 mm.

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Declaration of competing interests

The author declares none.

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