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Revision of the Early Ordovician (late Tremadocian; Stairsian) cheirurid trilobite *Tesselacauda* Ross, with species from the Great Basin, western USA

JONATHAN M. ADRAIN[1] & TALIA S. KARIM[2]
[1]*Department of Earth and Environmental Sciences, 115 Trowbridge Hall, University of Iowa, Iowa City, Iowa 52242, USA*
E-mail: jonathan-adrain@uiowa.edu
[2]*University of Colorado Museum of Natural History, 265 UCB, University of Colorado, Boulder, CO 80309, USA*
E-mail: talia.karim@colorado.edu

Abstract

The Stairsian genus *Tesselacauda* Ross, 1951, has historically included two species, the poorly known type, *T. depressa* Ross, 1951 (*Bearriverops loganensis* Zone), and the even less well known *T. flabella* Kobayashi, 1955 (*Bearriverops alsacharovi* Zone), which may not belong to the genus. The family assignment of the genus has long been in question, with some workers assigning it to Cheiruridae and some to Pliomeridae. New field collections from western Utah and southeastern Idaho yield abundant material of *T. depressa*, which facilitates revision on the basis of multiple specimens of most exoskeletal parts. Two additional well known species are proposed, *T. morrisoni* (*Rossaspis leboni* Zone), and *T. kriegerae* (*Bearriverops alsacharovi* Zone). A third new species, very similar to *T. depressa*, is described in open nomenclature from the *Rossaspis leboni* Zone. Knowledge of hypostomes from silicified material helps to clarify the basal morphologies of cheirurid versus pliomerid trilobites. Pliomerids have anteroposteriorly elongate hypostomes with a basic pattern of three pairs of lateral hypostomal spines and a single posteromedian spine. Some or all of the spines are reduced or lost in various taxa. Cheirurids either lack paired spines or have only one or two pairs, and never have a posteromedian spine. Cheirurid hypostomes tend to be much shorter and more subquadrate than pliomerids. Other differences between the families are: a small, triangular or trapezoidal rostral plate in pliomerids versus a wide, short plate in cheirurids; a thoracic segment count commonly of 11–13 in Cheiruridae (fewer in one derived subfamily) versus commonly 15 or more in pliomerids (fewer in two derived subfamilies); thoracic pleurae with subequal bands and a prominent furrow in cheirurids versus a much more inflated and rib-like posterior band, reduced anterior band, and short, anteriorly placed furrow; and pygidia with four or fewer segments in cheirurids versus commonly five in pliomerids (again, fewer in two derived subfamilies). On these and other criteria, *Tesselacauda* is clearly a cheirurid, assigned for the present to the presumptively basal and possibly paraphyletic Subfamily Pilekiinae.

Key words: Utah, Nevada, Idaho, silicified, taxonomy, trilobites, Cheiruridae

Introduction

The Fillmore Formation of western Utah and the Garden City Formation of southeastern Idaho provide a rich record of early (late Tremadocian through early Dapingian) cheiruroidean trilobites. Elements of the Family Pliomeridae Raymond, 1913, have been described in an ongoing series of papers (McAdams and Adrain 2009, 2010, 2011a, 2011b, 2011c; McAdams *et al*. 2018). The present work begins description and revision of members of the Family Cheiruridae Hawle and Corda, 1847.

Tesselacauda was proposed by Ross (1951) as a monotypic late Tremadocian (Stairsian) genus (type: *T. depressa* Ross, 1951). The type species was based on two incomplete and poorly preserved cranidia, a hyposome, a mature pygidium, a transitory pygidium, and two thoracic segments. Together, the specimens reveal only a fraction of the morphology of the species, with cranidial morphology particularly difficult to interpret and the librigena entirely unknown. More material was assigned to the species and illustrated by Demeter (1973) and Terrell (1973). As documented below, Demeter's specimens belong to a different species of *Tesselacauda* (with the exception of one pygidium which belongs to a different cheirurid genus) and Terrell's specimens almost completely lack provenance and are impossible to assign at the species level. Hence, *Tesselacauda* has proven difficult to interpret, a fact made plain by ongoing disagreement about its family assignment, with some authors arguing for Cheiruridae and others

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Pliomeridae (see below). The only species other than the type that has been assigned to the genus is *T. flabella* Kobayashi, 1955, but this species remains known only from pygidia and its affinities are uncertain (see below).

New field collections permit a comprehensive revision of *T. depressa*, with abundant material from both Idaho and Utah. Well preserved material of three new species, two of which are well enough represented to formally name, has also been recovered. Together, the new collections transform *Tesselacauda depressa* from a single, definitely assigned but poorly known species to a small presumptive clade of four species with highly distinctive morphology.

Biostratigraphic zonation follows the scheme developed by Adrain *et al*. (2009; 2012; 2014). Full locality data and history of study is also given in those works.

Cheiruridae vs Pliomeridae

Due to uncertain stratigraphic occurrences it is difficult to determine the age of the earliest definite cheiruroidean trilobites. The genera *Eocheirurus* Rozova, 1960, and *Emsurina* Rozova, 1960, were proposed as cheirurids. Each contains obviously cheiruroidean species from the Tolstochi'kha Formation of Salair Ridge in the Altai-Sayan fold belt of southwestern Siberia. Rozova (1960) also proposed the genus *Emsurella* and considered it a cheirurid, but subsequent authors (Westrop, 1986, p. 68; Jell and Adrain, 2003, p. 371) have suggested it belongs to Cheilocephalidae Shaw, 1956. It is known from two species each represented only by cranidia. These are apparently proparian and with cheiruroidean dimensions, but seem to lack glabellar furrows. The similarly aged Siberian species *Parapliomera njuensis* (Maksimova, 1955), however, has an assigned cranidium (Maksimova, 1962, pl. 17, fig. 13; see also Timohin, 1989, pl. 9, figs 8, 10, 14) that also has effaced furrows and the pygidia of this species certainly resemble those of pliomerids. Lane (1971) assigned all three genera to Pilekiinae, though he queried the affinity of *Emsurella*. Rozova (1960) considered all of the species she described to be late Cambrian in age. This was accepted by Přibyl and Vaněk (in Přibyl *et al*., 1985), who considered *Eocheirurus* to be a pilekiine cheirurid, *Emsurina* a sphaerexochine cheirurid, and *Emsurella* a pliomerid. Lane (1971, p. 73) suggested the age of these genera might be Tremadocian and Edgecombe (1992, p. 168–169) considered a Late Cambrian age suspect. It is now clear from conodont work that the Tolstochi'kha Formation spans the Cambrian–Ordovician boundary (Sennikov *et al*., 2015, p. 606), with its upper part including assemblages assignable to the early Tremadocian *Iapetognathus fluctivagus* Zone and *Cordylodus angulatus* Zone (see also Petrunina *et al*., 2001). Rozova (1960) gave the provenance of all of the relevant species as the upper horizon of the formation. Hence the age remains equivocal and could be Late Cambrian, but is possible that they are all from the Ordovician (early Tremadocian).

"*Anacheirurus*? sp." of Apollonov and Čugaeva (in Apollonov *et al*., 1984, pl. 22, figs 5–7) was based on specimens derived from a horizon at 214 m in the Batyrbai Section, Malyi Karatau Range, southern Kazakhstan. This horizon lies within the *Cordylodus prion* assemblage of Apollonov *et al*. (1981, fig. 1), which correlates with the latest Cambrian *Cordylodus lindströmi* Zone. Hence, this species, known from only three incomplete cranidia, but clearly cheiruroidean, may represent the oldest known, apparently latest Cambrian, cheiruroidean taxon. Other cheirurid genera with putative early Tremadocian species include *Chashania* Lu and Sun in Zhou *et al*. (1977), *Parapilekia* Kobayashi, 1934, *Pseudopliomera* Lu and Qian in Yin and Li, 1978, *Seisonia* Kobayashi, 1934, and *Sinoparapilekia* Peng, 1990. It seems that cheiruroideans appeared in Siberia, North and South China, and other tropical terranes, around the time of the Cambrian–Ordovician transition.

No cheiruroideans are known from Laurentia prior to the beginning of the Stairsian Stage in the upper Tremadocian. *Rossaspis pliomeris* Demeter, 1973, is the oldest known Laurentian species, occurring only a few metres above the Skullrockian–Stairsian boundary. *Rossaspis* Harrington, 1957, will be revised with several new species in a forthcoming work. It appears to be a pliomerid. The northern Laurentian Stairsian contains both early pliomerids and considerable numbers of pilekiine cheirurids, including species belonging to *Pilekia* Barton, 1915, and several new genera, all currently under study.

Among all of these early cheiruroideans there has been considerable confusion over which taxa belong to Cheiruridae versus Pliomeridae, and what potential synapomorphies characterize each clade. *Tesselacauda* is emblematic of this, as it has been assigned to Pliomeridae by many authors (e.g., Ross, 1951 [Ross made no formal family assignments in his monograph, but he considered {Ross, 1951, fig. 2} *Tesselacauda* to be part of an evolutionary trend with the pliomerids *Rossaspis*, *Hintzeia* Harrington, 1957, and *Pseudocybele* Ross, 1951]; Kobayashi, 1955; Maksimova, 1962; Demeter, 1973; Jell and Adrain, 2003) and to Cheiruridae by others (e.g., Černyševa, 1960 [as

“Pilekiidae”]; Hupé, 1955; Lane, 1971; Dean, 1989; Lee and Chatterton, 1997; Edgecombe *et al*., 1999; Adrain, 2013; Adrain *et al*., 2014). Other early cheiruroidean genera have similar taxonomic histories.

Whittington (1961, p. 912–913) gave a diagnosis for Pliomeridae and contrasted pliomerids with pilekiine cheirurids. He considered that pilekiines differed from pliomerids in that they have “the glabella parallel-sided or narrowing forward, eye lobe situated far forward, eye ridge running inward to the axial furrow, and pleural furrow situated medially.” In the current state of knowledge none of these features seem at all diagnostic, as each is found in both early cheirurids and pliomerids. Other early diagnoses of Pliomeridae (e.g., Holliday, 1942, p. 473) were similarly composed of general features shared with cheirurids, and there have been no synthetic modern treatments of the group. In order to justify a familial assignment of *Tesselacauda*, and in an attempt to better characterize the early morphologies of pliomerids and cheirurids, we discuss below what seem to be the most salient differences between them.

In dorsal cephalic features, there are few differences between the groups. Floian pliomerids develop an adaxially curtailed fusion of the palpebral lobe and eye ridge which was termed a palpebro-ocular ridge by McAdams and Adrain (2009). In the genera *Hintzeia*, *Panisaspis* McAdams and Adrain, 2011b, *Pseudocybele*, and others, this feature, when not set in a crowded anterior position, is always separated from the axial furrow posteriorly by a pitted fixigenal field. However it is a feature that seems to have been developed at some point within the group, as it is absent from those Stairsian species we assign to Pliomeridae. The only other strong contrast between the groups is that some cheirurids develop median occipital spines or glabellar spines, and these features are completely unknown in pliomerids. Cheirurids have a tendency to possess more prominent tuberculate sculpture, but there is considerable overlap in this feature. There are few other dorsal cephalic differences.

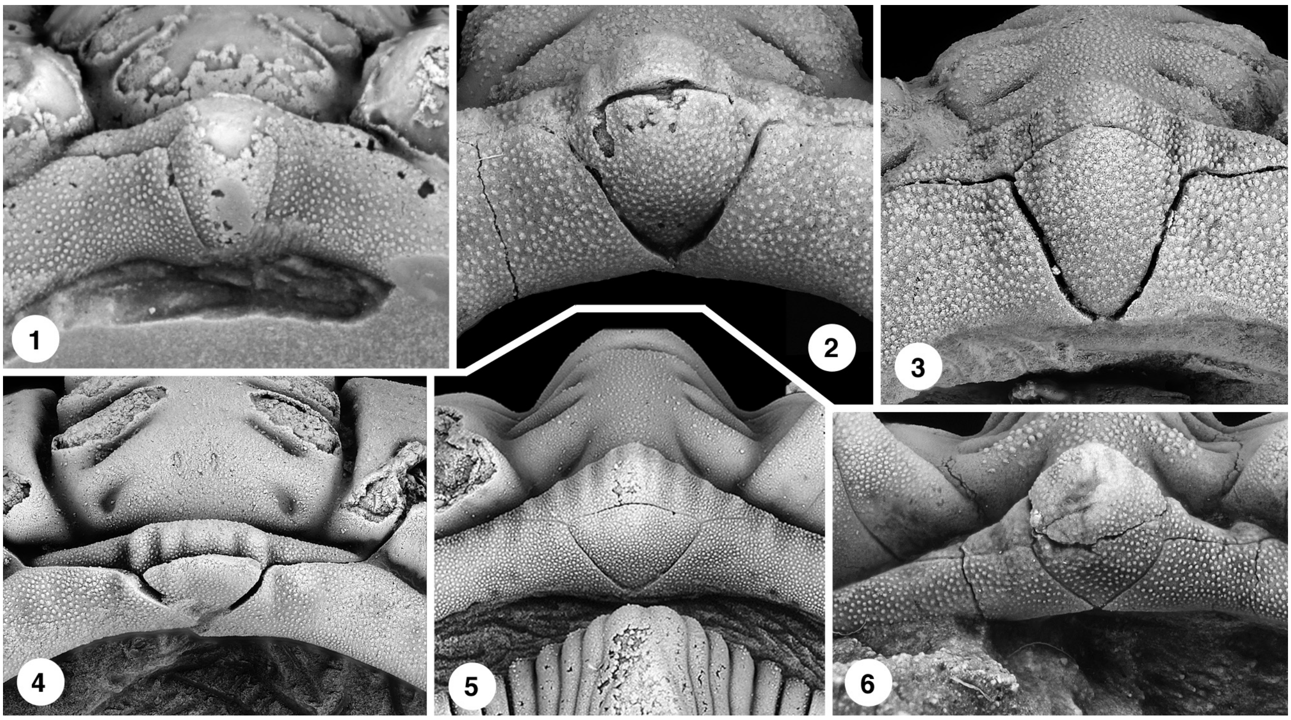

FIGURE 1. Rostral plates of species of *Pseudocybele* Ross, 1951, and *Lemureops* McAdams and Adrain, 2009. All specimens are currently under study and no species assignments have yet been made. All are from the Fillmore Formation, Tule Valley, Ibex area, Millard County, western Utah, USA. Figures 1, 3, and 4 are from talus on Hintze’s (1953) Section H. Figures 2 and 5 are from slopes on east side of Tule Valley. 1. *Pseudocybele* sp., KUMIP 204531, anterior view, x15. 2. *Pseudocybele* sp., KUMIP 314564, anterior view, x10. 3. *Pseudocybele* sp., KUMIP 319909, anterior view, x10. 4. *Pseudocybele* sp., KUMIP 319907, anterior view, x10. 5. *Lemureops* sp., KUMIP 204537, anterior view, x12. 6. *Lemureops willsonpiperi* McAdams and Adrain, 2009, KUMIP 2045333, anterior view, x15.

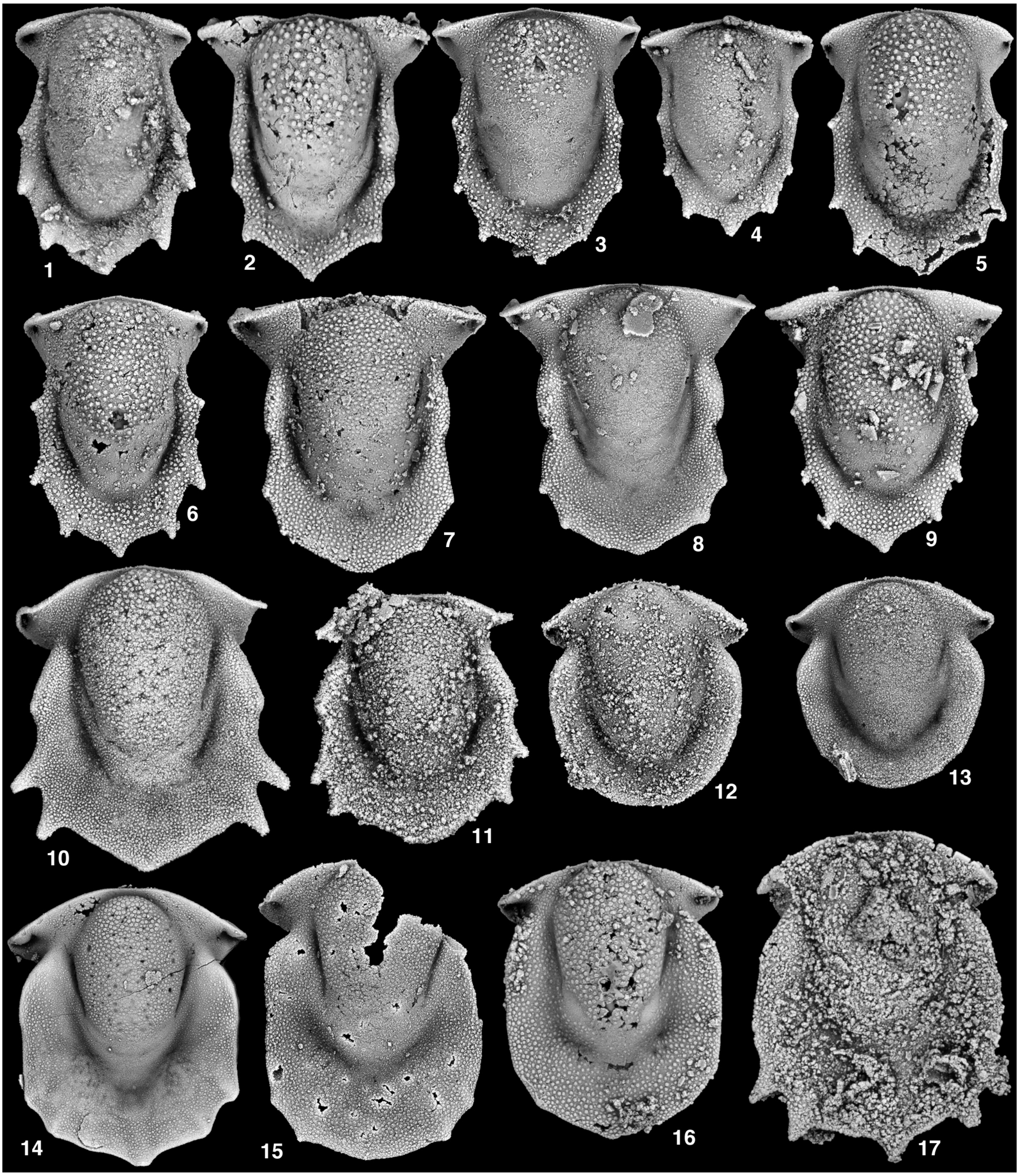

FIGURE 2.

FIGURE 2. Hypostomes of various species of Pliomeridae. 1. *Protopliomerella contracta* Ross, 1951, SUI 126034, Section G 210.2 m (Floian; Tulean; *Protopliomerella contracta* Zone), x15. 2. *Protopliomerella stegneri* McAdams and Adrain, 2011c, SUI 126071, Section G 142.0–144.5T m (Floian; Tulean; unzoned strata beneath *Psalikilopsis cuspidicauda* Zone), x12. 3. *Protopliomerella bowlesi* McAdams and Adrain, 2011c, SUI 126108, Section G 162.0T m (Floian; Tulean; low *Psalikilopsis cuspidicauda* Zone), x15. 4. *Protopliomerella okeefeae* McAdams and Adrain, 2011c, SUI 126330, Section G 258.2 m (Floian; Tulean; *Heckethornia hyndeae* Zone), x20. 5. *Protopliomerella kerouaci* McAdams and Adrain, 2011c, SUI 126173, Section HC6 203.0 m (Floian; Tulean; *Psalikilus typicum* Zone), x15. 6. *Protopliomerella seegeri* McAdams and Adrain, 2011c, SUI 126258, Section G 181.8 m (Floian; Tulean; low *Psalikilus hestoni* Zone), x12. 7. *Hintzeia parafirmimarginis* McAdams and Adrain, 2011a, Section HC6 165.2 m (Floian; Tulean; *Psalikilus spinosum* Zone), x10. 8. *Hintzeia firmimarginis* (Hintze, 1953), SUI 125507, Section G 99.0T-A (Floian; Tulean; *Psalikilus spinosum* Zone), x7.5. 9. *Hinteia celsaora* (Ross, 1951), SUI 125588, Section G 118.6 m (Floian; Tulean; *Hintzeia celsaora* Zone), x12. 10. *Panisaspis topscityensis* McAdams and Adrain, 2011b, SUI 125736, Section G 210.2 m (Floian; Tulean; *Protopliomerella contracta* Zone), x10. 11. *Panisaspis quattuor* (Hintze, 1953), SUI 125785, Section G 174.0 m (Floian; Tulean; *Psalikilus typicum* Zone), x12. 12. *Panisaspis sevierensis* McAdams and Adrain, 2011b, SUI 125663, Section H 173.2 m (Floian; Blackhillsian; *Psalikilus pikum* Zone), x10. 13. *Panisaspis millardensis* McAdams and Adrain, 2011b, SUI 125628, Section H 187.4 m (Floian; Blackhillsian; *Bathyurina plicolabeona* Zone), x12. 14. *Cybelopsis* sp. nov. 1 of Adrain *et al*. (2009, p. 575, fig. 21B, F), SUI 147645, Section H 290.4 m (Floian; Blackhillsian; "*Pseudocybele nasuta*" Zone"), x6. 15. *Cybelopsis depressa* (Young, 1973), SUI 147646, Section H 185.6 m (Floian; Blackhillsian; *Bathyurina plicolabeona* Zone), x10. 16. *Cybelopsis* n. sp. 2, SUI 147647, Section H 264.0–267.0T m (Floian; Blackhillsian; *Presbynileus ibexensis* Zone), x15. 17. *Cybelopsis* n. sp. 3, SUI 147648, Section J 35.3 m (Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), x10.

Features of the ventral cephalic sutures are profoundly different between the groups, however. All known cheirurid rostral plates are wide, anteroposteriorly short strips that match or nearly match the width of the hypostomal suture. Examples include the cheirurine *Hadromeros edgecombei* Chatterton and Ludvigsen, 2004 (pl. 57, fig. 2), the acanthoparyphines *Kawina arnoldi* Whittington, 1963 (pl. 27, fig. 1), *Cydonocephalus torulus* Whittington, 1963 (pl. 27, fig. 19), and *Hyrokybe julli* Chatterton and Perry, 1984 (pl. 13, fig. 12), the sphaerexochine *Sphaerexochus dimorphus* Perry and Chatterton, 1977 (Chatterton and Perry, 1984, pl. 29, fig. 4), and the deiphonine *Deiphon barrandei* Whittard, 1934 (Lane, 1971, pl. 12, figs 6, 9; Holloway, 1980, pl. 11, figs 15, 18). Those of pliomerids are very different as they are much narrower and in many species either triangular or trapezoidal (see Whittington, 1961, text-figs 1–5 for reconstructions of the shape in *Pliomera* Angelin, 1854, *Pliomerops* Raymond, 1905, *Pseudomera* Holliday, 1942, *Ectenonotus* Raymond, 1920, and *Colobinion* Whittington, 1961. The small, triangular, rostral plate of *Hintzeia parafirmimarginis* was illustrated by McAdams and Adrain (2011a, pl. 8, fig. 4). Rostral plates of species of *Pseudocybele* and *Lemureops* McAdams and Adrain, 2009, have not been well known, but examples are illustrated herein from work in progress (Fig. 1); all are small and triangular or trapezoidal. Pliomerid rostral plates closely resemble those of encrinurids (e.g., Evitt and Tripp, 1977, pl. 17, fig. 1b, pl. 18, fig. 7; Edgecombe and Chatterton, 1993, pl. 10, figs 3, 15, 19; Adrain and Edgecombe, 1997, pl. 9, fig. 4, pl. 19, fig. 2) and it is likely that the latter family falls within the phylogenetic structure of Pliomeridae.

The rostral plate of *T. depressa* is visible on the articulated specimen of Plate 1, figure 2. The plate is sitting just behind the anterior margin of the cranidium, slightly overlapped by a stray thoracic segment, and has flipped over so that its dorsal (i.e., internal) surface is showing. It is transversely wide and anteroposteriorly short, and clearly similar to known cheirurid rostral plates.

Pliomerid hypostomes are also very distinctive (Figs 2, 3), and very clearly distinct from those of unambiguous cheirurids (Fig. 4.5–4.14). Pliomerid hypostomes tend to be much longer than they are wide and they broadly share a pattern of three pairs of lateral spines and a posteromedian spine, though some or all are lost in derived taxa (e.g., Fig. 3.10–3.13). Even when the posteromedian spine is not expressed, pliomerid hypostomes tend to come to a distinct posteromedian point (e.g., Fig. 3.10–3.12). Cheirurid hypostomes almost always have a sagittal length smaller than their maximum width, giving them a subquadrate or transversely widened appearance. Only rarely are paired lateral spines expressed, and normally only one posterior pair (e.g., Fig. 3.10). A posteromedian spine is never developed and the posteromedian area is invariably either a smooth posterior arc (Fig. 3.9, 3.10, 3.13) or a median embayment (Fig. 3.5–3.8, 3.11, 3.12, 3.14). As with the rostral plate, pliomerid hypostomes are much more like those of Encrinuridae Angelin, 1854, than those of Cheiruridae.

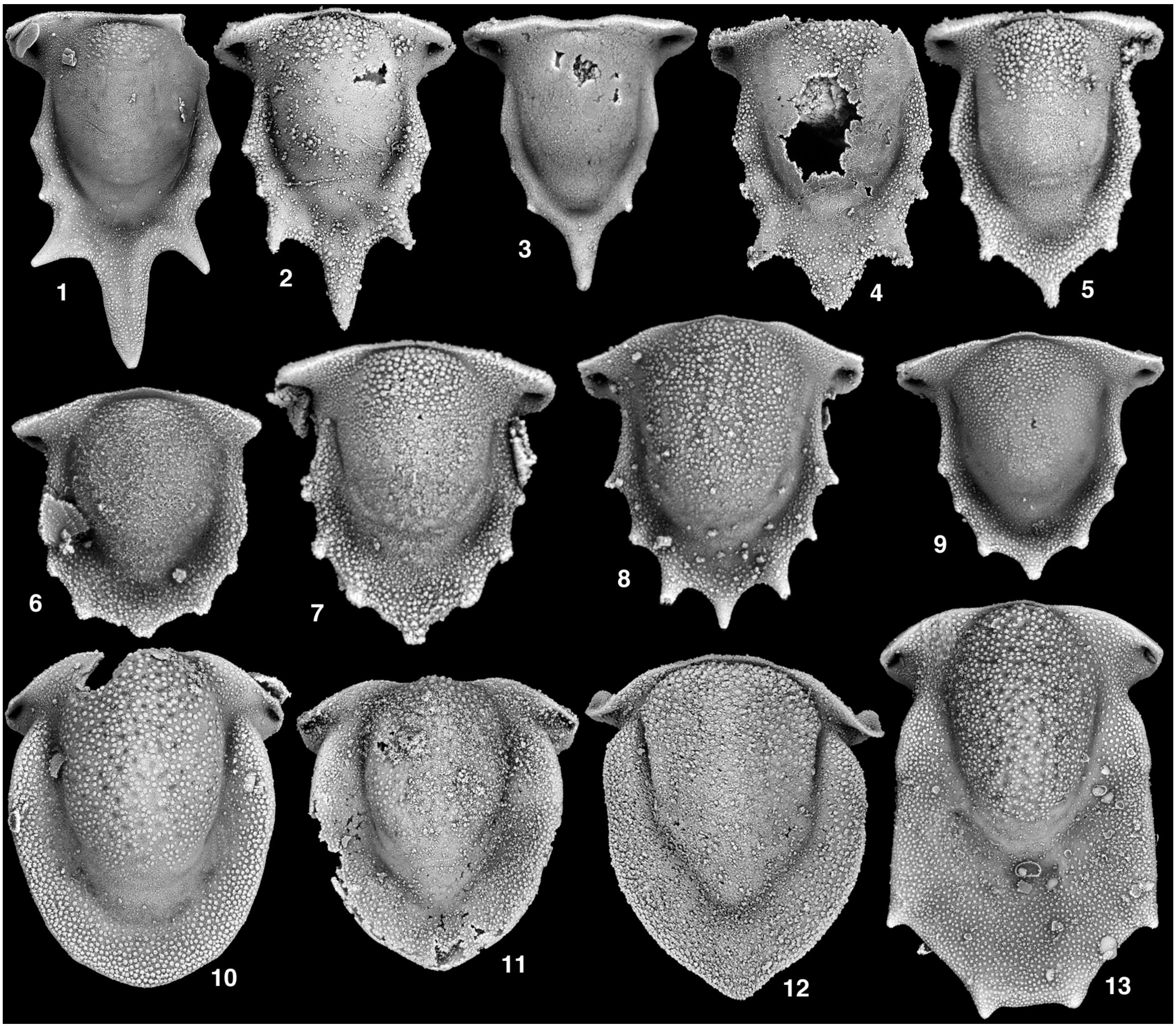

FIGURE 3. Hypostomes of various species of Pliomeridae. 1. *Pseudocybele* n. sp. 1, SUI 147649, Section H 301.1 m (Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), x7.5. 2. *Pseudocybele nasuta* Ross, 1951, SUI 147650, Section ROH 70.1T m (Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), x12. 3. *Pseudocybele* n. sp. 2, SUI 147651, Section J 16.1 m (Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), x10. 4. *Pseudocybele* n. sp. 3, SUI 147652, Section J 40.0 m (Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), x10. 5. *Pseudocybele paranasuta* McAdams and Adrain, 2010, SUI 122323, Section H 285.0T m (Floian; Blackhillsian; *Pseudocybele paranasuta* Zone), x12. 6. *Lemureops kilbeyi* McAdams and Adrain, 2009, SUI 110183, Section H 191.7 m (Floian; Blackhillsian; *Bathyina plicolabeona* Zone), x10. 7. *Lemureops koppesi* McAdams and Adrain, 2009, SUI 110298, Section H 172.5T m (Floian; Blackhillsian; *Psalikilus pikum* Zone), x12. 8. *Lemureops willsonpiperi* McAdams and Adrain, 2009, SUI 110259, Section H 264.0–267.0T m (Floian; Blackhillsian; *Presbynileus ibexensis* Zone), x10. 9. *Lemureops lemurei* (Hintze, 1953), SUI 110336, Section H 251.4 m (Floian; Blackhillsian; *Presbynileus ibexensis* Zone), x7.5. 10. *Pseudomera* n. sp. 2, SUI 147653, Section K 1.5T m (Dapingian; *Pseudoolenoides dilectus* Zone), x12. 11. *Pseudomera* n. sp. 3, SUI 147654, Section J 28.1 m (Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), x6.5. 12. *Ectenonotus* n. sp., SUI 147655, Antelope Valley Formation (probably Dapingian), Funeral Mountains, Death Valley National Park, California, x6.5. 13. *Kanoshia kanoshensis* (Hintze, 1953), SUI 147656, Section K 1.5T m (Dapingian; *Pseudoolenoides dilectus* Zone), x7.5.

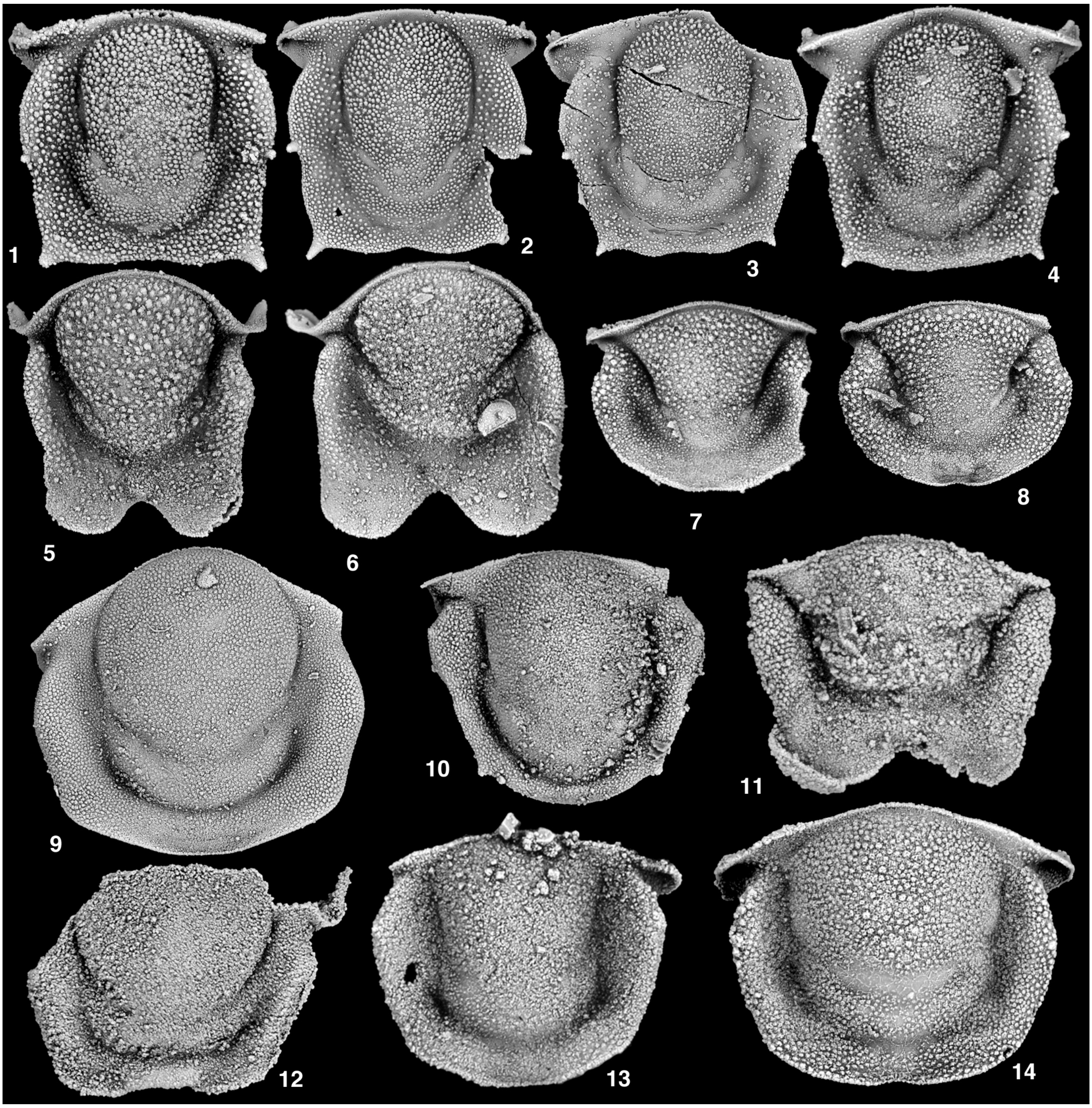

FIGURE 4. Hypostomes of various species of Cheiruridae. 1, 2. *Tesselacauda kriegerae* **n. sp.** (upper Tremadocian; Stairsian; *Bearriverops alsacharovi* Zone). 1. SUI 147614 (see also Pl. 15, figs 1, 5, 9, 13, 17), Section G 26.6 m , x12. 2. SUI 147639 (see also Pl. 18, figs 11, 12, 14, 16), Section HC6 124.0 m, x12. 3, 4. *Tesselacauda depressa* Ross, 1951 (upper Tremadocian; Stairsian; *Bearriverops loganensis* Zone). 3. SUI 147516 (see also Pl. 2, figs 13–16), Section HC5 106.7 m, x9. 4. SUI 147539 (see also Pl. 5, figs 3, 7, 11, 15, 19), Section MME 75.5 m, x10. 5. *Cydonocephalus* n. sp. 1, SUI 147657, Antelope Valley Formation (probably Dapingian), Funeral Mountains, Death Valley National Park, California, x12. 6. *Cydonocephalus* n. sp. 2, GSC 135352, Table Cove Formation (Darriwilian), near Main Brook, northwestern Newfoundland, Canada, x12. 7. Heliomerinae n. gen. n. sp. 1, SUI 147658, Section H 127.1 m (Floian; Tulean; *Heckethornia bowiei* Zone), x15. 8. Heliomerinae n. gen. n. sp. 2, SUI 147659, Section H 191.7 m (Floian; Blackhillsian; *Bathyurina plicolabeona* Zone), x15. 9. *Kawina* n. sp. 1, SUI 147660, Section K 1.5T m (Dapingian; *Pseudoolenoides dilectus* Zone), x10. 10. *Sycophantia polydora* (Billings, 1865), GSC 135353, Table Cove Formation (Darriwilian), near Main Brook, northwestern Newfoundland, Canada, x15. 11. *Sphaerexochus* n. sp. 1, GSC 135354, Table Cove Formation (Darriwilian), near Main Brook, northwestern Newfoundland, Canada, x20. 12. *Kawina* n. sp. 2, GSC 135355, Table Cove Formation (Darriwilian), near Main Brook, northwestern Newfoundland, Canada, x12. 13. *Forteyops* n. sp. 1, SUI 147661, Section H 222.1 m (Floian; Blackhillsian; *Carolinites nevadensis* Zone), x25. 14. Acanthoparyphinae n. gen. n. sp. 1, SUI 147662, Section J 40.0 m (Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), x20.

Tesselacauda hypostomes (Fig. 4.1–4.4) are slightly longer than is typical for cheirurids, but their sagittal length is slightly less than their maximum width as in Cheiruridae. They have two pairs of lateral spines. They have no sign of a posteromedian spine and most specimens have a slight posteromedian embayment. In all of these respects they clearly resemble Cheiruridae, and do not resemble Pliomeridae.

Pliomerids and cheirurids have significant differences in thoracic morphology and segment counts. A common cheirurid body plan involves 15 thoracopygidial body segments. All Cheirurinae Hawle and Corda, 1847, show this pattern, with an 11 segment thorax and a four segment pygidium (generally, only the first three pygidial segments have associated pleural spines, but in almost all species a tiny transverse fourth ring is expressed). Derived Acanthoparyphinae Whittington and Evitt, 1954, have only two pygidial segments. The articulated holotype specimen of *Pandaspinapyga salsa* Esker, 1964 (Esker, 1964, pl. 2, fig. 6; Shaw, 1974, pl. 8, figs 3–5), which has two pygidial segments, and 13 thoracic segments, the highest known for a cheirurid, but in keeping with a total of 15 segments. Older Laurentian species assigned to *Kawina* Barton, 1915, and *Cydonocephalus* Whittington, 1963, are very like those conventionally assigned to Acanthoparyphinae except that they have pygidia with three segments. There is considerable diversity of similar species in the Ibex-Garden City collections and we regard them as basal acanthoparyphines. One would expect such taxa to have a 12 segment thorax, and indeed that is what *Kawina arnoldi* Whittington, 1963 (pl. 26, figs 7–9, 11, 12, 14) displays. Species assigned by Lane (1971) to his Eccoptochilinae have 11 or 12 thoracic segments. Two subfamilies have fewer: species of Sphaerexochinae have 10 and those of Deiphoninae have nine. It is possible that these clades had paedomorphic origins.

The most common early pliomerid body plan is very different, and seems to involve 20 thoracopygidial segments, with 15 in the thorax and five in the pygidium. This arrangement is present in *Hintzeia* (*H. parafirmimarginis* McAdams and Adrain, 2011a, pl. 8, fig. 1). Current work in progress features well preserved articulated specimens which demonstrate the same segment count in species of *Pseudocybele*, *Lemureops*, and *Kanoshia* Harrington, 1957 (*Kanoshia* is likely a junior synonym of *Pseudomera*). Whittington (1961) described *Colobinion* as having "at least 15" thoracic segments, and illustrated a specimen of *Pseudomera* cf. *barrandei* (Billings, 1865) with 15 (Whittington, 1961, pl. 100, fig. 17). Some later pliomerids display reduced thoraces and there seem to have been several independent trends toward fewer segments. The pliomerine *Pliomerina austrina* Webby, 1971, for example, has 10 segments (Webby, 1971, pl. 114, fig. 1). Some derived groups, such as the Placopariinae Hupé, 1953 with 11 or 12 segments, and the possibly related Hammatocneminae Kielan, 1960, with 10, are also known to have fewer than 15 and overlap the range of Cheiruridae. Once more, it seems possible these groups may have had paedomorphic origins.

Tesselacauda has a thorax of 12 segments (known only in one species, *T. depressa*). It is not identical to the more general cheirurid body plan in that it has a four segment pygidium for a total of 16 body segments, rather than the more common 15, but it is clearly more like cheirurids in this respect than pliomerids.

The morphology of thoracic and pygidial segments is also quite different between cheirurids and pliomerids. Cheirurids tend to feature pleural areas with the anterior and posterior bands subequal in size, bisected by a deep and prominent pleural furrow. Even in derived taxa such as younger acanthoparyphines and deiphonines in which the pleural region becomes more or less a single inflated and tuberculate rib, this rib is derived by merging the anterior and posterior bands, and there is usually evidence retained proximally on the segment of independent, similarly sized bands. Pliomerids almost universally have the posterior band much larger than the anterior band, and often developed into an inflated rib. The anterior band is typically a very short (exsag.) strip (e.g., McAdams and Adrain, 2011a, pl. 8, fig. 1 [*Hintzeia*]; McAdams and Adrain, 2011b, fig. 9.1, 9.4, 9.11, 9.14 [*Panisaspis*]; McAdams and Adrain, 2011c, pl. 7, figs 1, 4, 9, 11, 19, 31, 32, 34 [*Protopliomerella*]). On pliomerid pygidia, the anterior band is only visible on the first and sometimes the second segment; the pleural furrow and anterior band is not expressed in posterior pygidial segments.

Thoracic segments of species of *Tesselacauda* have equally sized anterior and posterior pleural bands, bisected by a deep pleural furrow. This is clearly the cheirurid condition, and not the pliomerid condition. Pygidia of species of *Tesselacauda* only show the anterior band on the first two segments, but where expressed here it is prominent.

Most pliomerids have pygidia with five segments. The count is reduced to four or fewer in the derived subfamilies Placopariinae and Hammatocneminae. As discussed above, these are also the only pliomerids with a markedly reduced thoracic segment count and they likely had paedomorphic origins. It seems very likely that both the reduced thoracic and pygidial segment counts represent a derived condition within Pliomeridae. Cheirurids universally have four or fewer pygidial segments. In this respect again, *Tesselacauda*, with four segments, is within the range of cheirurids, but not the general and apparently basal condition of five seen in pliomerids.

In sum, all relevant comparisons of rostral plate, hypostomal, thoracic, and pygidial morphology indicate that

Tesselacauda is a cheirurid, and not a pliomerid. It differs from other cheirurids in the presence of two pairs of hypostomal spines and 16 total thoracopygidial segments, but does not resemble the common pliomerid condition for either feature.

Systematics

Repository. Illustrated specimens are housed in the Paleontology Repository, Department of Earth and Environmental Sciences, University of Iowa, Iowa City, Iowa, USA, with specimen number prefix SUI; the University of Kansas Museum of Invertebrate Paleontology, Lawrence, Kansas, USA, with specimen number prefix KUMIP, and the Geological Survey of Canada, Natural Resources Canada, Ottawa, Ontario, Canada, with specimen number prefix GSC.

Family Cheiruridae Hawle and Corda, 1847

Subfamily Pilekiinae Sdzuy, 1955

Discussion. Pilekiinae has generally been conceived of as consisting of early, plesiomorphic species of Cheiruridae which lack the synapomorphies of other subfamilies. Lane, for example (1971, text-figs 10, 12, 13) depicted the taxon on his evolutionary tree diagrams as a basal Tremadocian bar from which other lineages were multiply derived. As such it has been considered a paraphyletic group. There is as yet little insight into its phylogenetic structure, nor that of the family in general. Pilekiinae is used here for convenience, with the understanding that as more Tremadocian (and possibly late Cambrian) taxa are revised and described its phylogeny can be formally explored.

Tesselacauda Ross, 1951

Type species. *Tesselacauda depressa* Ross, 1951, from the Garden City Formation (late Tremadocian; Stairsian; *Bearriverops logani* Zone), southeastern Idaho, USA.

Other species. *Tesselacauda kriegerae* n. sp., Fillmore Formation, western Utah; *T. morrisoni* n. sp., Fillmore Formation, western Utah; *Tesselacauda* n. sp. A, Fillmore Formation, western Utah.

Diagnosis. Dorsal exoskeleton relatively flat, only slightly vaulted; anterior border forming a prominent rim; glabella large and broadly subrectangular; hypostome slightly wider than sagittally long, with small lateral spine at shoulder and slightly larger spine at posterolateral corner, entire ventral surface covered with fine, dense tubercles; twelve thoracic segments, anterior and posterior bands equally prominent, with proximal tip of anterior band extended further adaxially than posterior band, pleural furrow deep; pygidium of four segments, pleural tips bluntly terminated, anterior pleural band developed only on first two segments, sculpture of dense granules arranged into distinct rim around pygidial margin.

Discussion. Jell (1985, p. 79, pl. 32, fig. 1) assigned a partial cranidium from the Digger Island Formation (Tremadocian) of Victoria, Australia, to *Tesselacauda*. Peng (1990, p. 114) reassigned it with question to his new *Sinoparapilekia*. Boyce and Stouge (1997, p. 188) reported "*Tesselacauda* sp. cf. *T. depressa*" from the Boat Harbour Formation (Stairsian) of western Newfoundland, Canada, but this occurrence has never been illustrated. It is the only report of the genus from southern Laurentia (in Ordovician geography). Aitken and Norford (1967, p. 194) listed but did not describe "*Tesselacauda* sp." from the middle member of the Survey Peak Formation at Mount Wilson, Banff National Park, Alberta, Canada. The stepped nature of the proximal tips of the anterior and posterior pleural bands on the thorax is included in the diagnosis for *Tesselacauda* herein and is likely synapomorphic for the group. A more comprehensive examination of other "pilekiine" thoracic segments is planned and will shed light on the extent of this morphology.

Tesselacauda depressa Ross, 1951
(Plates 1–8)

	1951	*Tesselacauda depressa* Ross, p. 130, pl. 31, figs 27–31, pl. 34, figs 1–4, 18.
	1955	*Tesselacauda depressa* Ross; Hupé, fig. 231.11.
	1962	*Tesselacauda depressa* Ross; Maksimova, p. 143.
non	1973	*Tesselacauda depressa* Ross; Terrell (*partim*), p. 48, pl. 1, figs 5, 6, 10, 14, 15 (only; pl. 1, figs 5, 6, 10, 15 = *T. kriegerae* n. sp.; pl. 1, fig. 14 = Pilekiinae gen. nov. 3 sp. nov. B of Adrain *et al*. [2014, p. 179, fig. 12EE]).
?	1973	*Tesselacauda depressa* Ross; Demeter, p. 89, pl. 2, figs 6, 9, 13.
	1985	*Tessalacauda* [*sic*] *depressa* Ross; Jell, p. 79.
	1989	*Tesselacauda depressa* Ross; Dean, p. 17.
?	1997	*Tesselacauda depressa* Ross; Lee and Chatterton, p. 685, figs 3.1–3.6, 4.1–4.13, 5.1, 8.2, 8.5, 8.8, 8.12, 8.16.
	1997	*Tesselacauda depressa* Ross; Ross *et al.*, p. 45.
	1999	*Tesselacauda depressa* Ross; Edgecombe *et al*., p. 1171.
	2003	*Tesselacauda depressa* Ross; Jell and Adrain, p. 452.
	2012	*Tesselacauda depressa*; Dai and Zhang, p. 650.
	2014	*Tesselacauda depressa* Ross; Adrain *et al.*, p. 178, fig. 10Q, U.

Material. Assigned specimens SUI 147509–147511, 147514–147520, from Section HC5 106.7 m, east side of Hillyard Canyon, SUI 147513 from Section HC6 88.3, west side of Hillyard Canyon, and SUI 147507, 147508, and 147512, from Section FB7 102.1 m, Franklin Basin, all Garden City Formation (upper Tremadocian; Stairsian; *Bearriverops loganensis* Zone), Bear River Range, Franklin County, southeastern Idaho. Assigned specimens SUI 134129, 134130, 147511–147523, 147524–147546, 147547–147551, from Section MME 75.5 m, Fillmore Formation (upper Tremadocian; Stairsian; *Bearriverops loganensis* Zone) and SUI 147552, 147554, 147555, 147557, 147560, 147561, from Section MME 84.0 m (upper Tremadocian; Stairsian; *Bearriverops deltaensis* Zone), both Middle Mountain, and SUI 147556, 147558, 147562, and 147563, from Section AAA 79.5 m (upper Tremadocian; Stairsian; *Bearriverops deltaensis* Zone), northern House Range, all Ibex area, Millard County, western Utah. Assigned specimens SUI 147553, 147559, from Section HC6 107.5 m, Garden City Formation (upper Tremadocian; Stairsian; *Bearriverops deltaensis* Zone), west side of Hillyard Canyon, Bear River Range, Franklin County, Idaho, USA.

Diagnosis. Glabella with moderately dense sculpture of fine tubercles; anterior border medially transverse and only slightly forwardly arched, longer sagittally in dorsal view than in other species; posterior projections less downturned than in other species, cephalon less vaulted; exsagittal length of fixigena behind palpebral lobe relatively short; librigenal lateral border with prominent band largely free of tuberculate sculpture; pygidial axial rings with moderately dense tuberculate sculpture, terminal piece wider than long.

Description. Measurements for the cranidium were made on the largest and best preserved specimens of Plates 1, 3 and were doubled from the mid-line where preservation was incomplete. Cranidium very broad and generally flattened in appearance with gentle dorsal inflation, sagittal length 45.4% (39.8–48.2%) maximum width (excluding genal spine); length 110.3% (104.1–121.6%) width across ε, 75.2% (72.3–78.6%) across γ; anterior border moderately short (sag.), sagittal length 5.7% (4.8–6.8%) cranidial length, generally describing broad anteriorly directed arc, with medial portion slightly more transverse, in anterior view border very gently dorsally arched medially, independently inflated sitting below anterior margin of glabella (Pl. 3, fig. 9), sculpture of densely spaced granules present on anterior rim (in dorsal view) and anterior face so that in anterior view border appears covered in granules (e.g., Pl. 3, fig. 6); anterior border furrow deeply incised, gently bowed anteriorly as anterior border; glabella with length (sag.) 96.8% (86.6–104.3%) maximum width (tr.), with lateral margins slightly bowed outward, maximum width achieved between anterior portion of L1 and L2, gently tapered (tr.) anteriorly, anterolateral corners more evenly rounded than posterolateral corners, which are more squared off, anterior margin broadly rounded, posterior margin with medial portion gently anteriorly bowed, weak dorsal inflation, anterior portion sloped downward from horizontal, sculpture of fine tubercles covers glabella, tubercles generally evenly spaced, but more concentrated medially along sagittal axis on some specimens; S1–3 deeply incised, narrow, extending about a third across glabella; S1–2 subparallel, directed gently posteromedially, with proximal tip of S1 extending a little more inward and gently posteriorly curved (Pl. 3, Fig. 13); S3 directed more strongly posteromedially than S1–2; SO similar in depth and length (sag., exsag.) to other glabellar furrows; LO moderately long, with sagittal length 14.0% (12.3–15.6%) cranidial length, tapered abaxially with distal ends gently swollen and rounded, posterior margin transverse, inflation similar to that of glabella, sculpture of small scattered tubercles concentrated on median portion of LO with distal ends more smooth; L1 wedge shaped, posterior margin swollen, but otherwise lacking independent inflation; fixigenal field with maximum length (exsag.) 109.6% (101.7–114.5%) width; proximal posterior corner of field is extended around L1 forming small rounded extension of field that is situated obliquely opposite the anterolateral corner of LO, field ends just behind S3 anteriorly, posterior margin of field gently anterolaterally directed, inter-ocular portion of field small, subtriangular; post-ocular field relatively short (exsag.); field with sculpture of deep pits overlain by scattered small tubercles, except for narrow smooth bands opposite posterior border and glabella; posterior projections gently flexed anteroventrally distal to fulcrum; fulcrum set relatively close to glabella (e.g., Pl. 3, figs 4, 21); posterior border furrow narrowest adaxially where fixigenal field is pinched toward LO, lengthens abaxially so that is longest opposite medial portion of field, pinches down again towards genal angle; lateral border furrow similar to narrower portion of posterior border furrow, ends abruptly before reaching intersection with facial suture (Pl. 3, fig. 8); posterior border shortest (exsag.) opposite LO, gradually lengthens abaxially, reaches maximum length at point where border abruptly changes course from transverse to anterolaterally directed; genal spine forming small nubbin (Pl. 1, figs 7, 8; Pl. 3, figs 12, 14); lateral border widest at genal angle, pinches out anteriorly; palpebral lobe small, set anteriorly opposite anterior portion of L3, bound anteriorly by very shallow furrow expressed more as change in slope, external margin strongly sinuous with nearly 90 bend before posterior termination, posterior portion of lobe extending into short laterally directed "tail" abaxially from this bend; palpebral furrow deep, narrow, sinuous, running from intersection with axial furrow just opposite anterolateral corner of L3 posteriorly toward facial suture, but ending abruptly just before reaching suture; axial furrows similar in depth to glabellar furrows; fossula forming deep pit just anterior to intersection of S3 with axial furrow, clearly visible ventrally as laterally directed projection (e.g. Pl. 3, fig. 17); all dorsal furrows are fringed by row of fine granules or microtubercles (especially visible on specimens from MME); doublure beneath LO short, only extending about half way across LO, with small articulating flange at posterolateral corner; short strip of doublure present beneath transverse portion of posterior border, with narrow articulating groove present along posterior margin; small triangular piece of doublure situated obliquely beneath genal angle.

Rostral plate identified ventrally on one partially articulated specimen (Pl. 1, fig. 2), with plate flipped so that the dorsal (interior) surface is visible; forming moderately wide (tr.) strip, with length (sag., exsag.) much shorter than width; narrow ridge developed along hypostomal suture; sculpture of coarse granules present adjacent to hypostomal suture, becoming progressively effaced across plate.

Hypostome with sagittal length 85.1% (76.4–90.7%) maximum width (tr. across anterior wings); with lateral margins rounded and gently expanded laterally across shoulders, posteriorly lateral margin gently constricted (tr.); anterior margin gently anteriorly arched; anterior border short (sag., exsag.), merging smoothly with anterior wings, differentiated from middle body by shallow, but distinct anterior border furrow; anterior wings prominent, subtriangular, extending laterally just beyond lateral margins of hypostome, with elongate (tr.) pit developed near anterior margin of wing, pit expressed dorsally as large strongly dorsally deflected wing process (e.g., Pl. 2, fig. 15); lateral notch prominent and moderately deep in lateral profile (e.g., Pl. 2, fig. 15), smooth; posterior wings small, strongly deflected dorsally; middle body long, subovoid, with anterior lobe much longer (sag.) than posterior lobe; anterior lobe oval shaped with posterior margin more pointed medially and anterior margin more evenly rounded, inflation moderate; posterior lobe of middle body short (sag.), U-shaped, inflation distinct, but slightly less than that of anterior lobe; anterior and posterior lobes separated by very shallow middle furrow, that is most distinct laterally and nearly effaced medially; maculae small, oval shaped with long axis directed anterolaterally, smooth; lateral border furrow deep, narrow, clearly setting off anterior portion of middle body from lateral border; border furrow disrupted at anterior margin of posterior lobe of middle body; furrow deep posterolaterally, clearly setting off posterior lobe of middle body from border; lateral and posterior borders moderately broad, expanded laterally at shoulder and posterolateral corner of hypostome, posterior border shortest (sag.) medially, lengthening (exsag.) abaxially, somewhat flattened in lateral and posterior views; border deflected dorsally in lateral profile at posterior shoulder; in posterior view border nearly transverse; two sets of lateral spines developed; smaller spine pair present at posterior edge of shoulder, directed laterally to slightly posterolaterally; larger spine pair present at posterolateral corner of hypostome, directed more strongly posterolaterally; posterior margin of hypostome broadly W-shaped with slight median embayment (more well developed on some specimens than others; cf. Pl. 2, fig. 3 and Pl. 5, fig. 1); anterior lobe with most densely spaced and coarsest sculpture, granules larger anteriorly, progressively finer posteriorly; posterior lobe with finer granular sculpture that is nearly effaced in some specimens; lateral and posterior borders with granular sculpture that is less densely spaced than that on anterior lobe; ventrally, doublure broad and smooth beneath lateral and posterior borders.

Librigena elongate, slender; eye small, bulbous, set far forward on librigena, differentiated from field by greater inflation and very shallow furrow developed around base of eye, furrow slightly deeper along posterior margin; field expressed as long thin triangular extension posteriorly from base of eye, posterior extension of field generally longer than anterior portion with anterior portion minute in some specimens, field is somewhat variable in length with some specimens possessing a rather longer pinched out tail posteriorly, while others terminate more rapidly (cf. Pl. 4, figs 9 and 10); deep furrow separates field from border, sinuous, on most specimens furrow is slightly wider opposite posterior margin of eye and field, furrow significantly tapered toward posterior facial suture, furrow terminated abruptly before reaching anterior facial suture, row of very fine granules lines margins of furrow; border elongate, medial portion broadest, shorter anteriorly and posteriorly, in ventrolateral view anterior portion of border flexed upwards before anterior projection strongly flexed downward; inner portion of border generally smooth, lacking tubercles, outer margin and external surface with band of densely spaced fine tubercles, sculpture stops abruptly and does not continue ventrally onto doublure (Pl. 4, fig. 11); anterior projection subtriangular, much shorter than posterior projection, strongly flexed downward in ventrolateral view; posterior projection extended into long sweeping projection, in external view tip of posterior projection almost level with top of eye and portion of doublure visible distally, held roughly in line with main portion of border in ventrolateral view; anterior facial suture outwardly convex opposite eye, distinct change in course opposite border furrow, nearly straight across anterior projection; posterior facial suture long, sinuous with slight outwardly convex bump across field just behind eye, suture describing gently concave arc across posterior projection, with arc more strongly curved distally along tip of posterior projection; doublure smooth, extending inward to dorsal expression of border furrow anteriorly and posteriorly, but medial portion only extending about halfway across border to furrow.

Thorax composed of 12 segments (Pl. 4, fig. 1); articulating half-ring short (sag., exsag.), with anterior margin gently anteriorly arched, posterior margin nearly transverse, set off from axial ring by short, deep articulating furrow, with line of small tubercles across posterior margin of half-ring (Pl. 1, fig. 3; Pl. 8, fig. 6); axis broad (tr.), gently tapered posteriorly, with moderately weak dorsal inflation, sitting above pleurae in lateral profile; pleurae broad (tr.) anteriorly, progressively narrower posteriorly; axial ring very gently anteriorly bowed, more so on posterior segments, with distal tips rounded and slightly inflated, sculpture of scattered tubercles; axial furrow deep, broad; short (exsag.) articulating flange present along anterior margin of pleurae, set off from anterior pleural band by moderately shallow and short articulating furrow (Pl. 1, fig. 3); pleurae divided into clear anterior and posterior bands by deep pleural furrow, furrow shallower distal to fulcrum, then abruptly terminated before reaching end of pleural tip; anterior and posterior pleural bands of roughly equal length between axis and fulcrum, proximal termination of bands forming rounded tips with that of anterior band extending slightly further towards axis than posterior band; anterior segments with anterior and posterior bands less clearly differentiated toward termination of pleurae, which are lengthened into short, pointed, anteriorly flexed pleural spines (Pl. 4, figs 1, 2); on more posteriorly located segments, anterior pleural band occupies progressively less space distal to fulcrum becoming pinched out with the posterior band becoming more dominant (lengthened exsagittally) and clearly extended into a more tab-like and less pointed pleural tip; clear raised rim visible ventrally marking termination of segment, with pleural spine extended beyond; first six segments with pleural spines flexed anteriorly, posterior segments with spines directed progressively posteriorly so that they appear to wrap around thorax and pygidium.

Pygidial measurements were made on the largest and most complete specimens of Plates 2, 5, and 6. Pygidium with overall low dorsal inflation, broad with sagittal length (excluding articulating half-ring) 47.7% (43.3–52.6%) maximum width; fulcrum set relatively close to axis, with pleurae strongly downturned from fulcrum outward; articulating half-ring shorter (sag.) than first axial ring, anterior margin anteriorly bowed, posterior margin transverse, generally smooth except for row of scattered tubercles present along posterior margin, some tubercles very slightly elongated; axis broad, composed of four segments and terminal piece, length 104% (95–110.1%) maximum width across first segment, maximum width across first segment 41.5% (39.8–45.7%) pygidial width, axis remains relatively broad posteriorly, but sharply pinched (tr.) at terminal piece; first two axial segments of similar shape with the second being only slightly shorter (sag.), distal tips rounded or bulbous; third segment shorter (sag., exsag.) than first two with distal tips less bulbous; fourth segment with anterior margin broadly W-shaped so that medial portion is bowed slightly anteriorly and lateral portions posteriorly, terminating with distal tips swept anteriorly (e.g., Pl. 6, fig. 1), this curve is very flattened on some specimens so that the anterior margin appears nearly transverse; terminal piece triangular, with width (tr.) greater than length (sag.), clearly isolated by axial furrows, circumscribed by fourth posterior pleural band; inter-ring furrows with middle third shallowest, lateral thirds more deeply incised, articulating furrow similarly incised; axial furrows similarly broad as inter-ring and pleural furrows, forming wider areas at intersection with ring and pleural furrows; very narrow articulating flange present along anterior pleural margin of first segment, set off by narrow articulating furrow; first pleural segment with anterior and posterior bands clearly defined by deep pleural furrow cutting obliquely across segment, furrow abruptly shallows before reaching pygidial margin, posterior band terminates in large tab that continues on past pygidial border as semi-fused pleural spine; second pleural segment similar to first in that segment is cut obliquely by clearly incised pleural furrow that divides segment into anterior and posterior bands, furrow is confluent with first interpleural furrow so that the anterior band is totally isolated; third and fourth pleural segments lacking anterior pleural band; fourth segment is subtriangular in dorsal view; all four pleurae extended into short semi-fused tab-like pleural spines; on one specimen from HC5 (Pl. 2, fig. 24) the tabs are more fused (cf. others specimens from both HC5 and MME where tabs are clearly separated (e.g., Pl. 6, fig. 8)); pygidial border expressed ventrally as pronounced short and narrow rim, extends anteriorly only to just cover posterior tip of terminal piece, in dorsal view the anterolateral tips of the rim are just visible as a small spike at the distal termination of the anterior band of the first pleural segment; doublure short, upturned so that it is best seen in anterior profile (e.g., Pl. 6, fig. 12), smooth; scattered small tubercles concentrated on medial portion of axis, few scattered tubercles on pleural region on most specimens, tubercles concentrated in a distinct rim around external margin of pygidium along with band of dense granules ringing posterior pygidial margin (e.g., Pl. 6, fig. 11), granular sculpture is continued ventrally to pygidial border (Pl. 2, figs 23, 24), pygidia from HC5 seem to possess fewer overall tubercles on dorsal surface compared to pygidia from MME; very fine row of tubercles also line the margins of most of the pygidial furrows.

Ontogeny. Glabella slightly longer (sag.) than wide, becoming more subquadrate to slightly wider than long throughout ontogeny. Smaller cranidia are much more densely tuberculate, especially on the palpebral lobes and anterior border (Pl. 3, fig. 18). The fringe of small tubercles outlining the dorsal furrows is not obvious on smallest specimens, but develops and becomes more prominent throughout ontogeny. The hypostome becomes more elongate, with both sets of spine pairs becoming smaller, and the maculae becoming larger throughout ontogeny. Similar to the crandium, the fringe of fine tubercles outlining dorsal furrows on the pygidium is not as well developed on smaller specimens (cf. Pl. 2, fig. 29, Pl. 6, fig. 1) as it is on larger specimens. The dorsal furrows on the pygidium broaden, but their depth remains relatively constant.

Discussion. *Tesselacauda depressa* is compared with *T. morrisoni* and *T. kriegerae* in the differential description of those species. Terrell (1973, p. 89, pl. 2, figs 6, 9, 13) assigned three specimens to *T. depressa*. Unfortunately, he did not give the provenance for any of the specimens illustrated in his paper beyond listing the zone to which he assigned them. The illustrated specimens comprise a small cranidium, a pygidium, and a hypostome. The cranidium is juvenile, and is densely tuberculate. Similar small, highly tuberculate specimens are illustrated herein for *T. depressa* (e.g., Pl. 3, fig. 27), *T. morrisoni* (e.g., Pl. 10, figs 3, 7, 9), and *T. kriegerae* (e.g., Pl. 17, figs 3, 11). Given the small photographs, that the only illustrated cranidium is a juvenile, and the lack of horizon or section information, it is impossible to assign Terrell's specimens with any confidence.

Species from the *Bearriverops deltaensis* Zone tend to be very similar to congeneric species from the underlying *B. loganensis* Zone. In most cases, however, they are clearly differentiated, as in the example of the zonal name bearers (see Adrain and Westrop [2007]). Whereas the sample of *Tesselacauda* sclerites from the *B. deltaensis* Zone (Plates 7, 8) is not as large as that from the *B. loganensis* Zone (Plates 1–6), especially for cranidia, there are no apparent differences between them and *T. depressa* seems to be a rare example of a species ranging through both zones.

***Tesselacauda morrisoni* n. sp.**
(Plates 9–11, Plate 12, figs 1–12, 17)

2014 *Tesselacauda* sp. nov. 1; Adrain *et al*., p. 174, fig. 8A, E.

Material. Holotype, cranidium, SUI 134075 (Pl., 9, figs 3, 5, 6, 9, 12), and assigned specimens SUI 147564, 147565–147586, from Section MME 49.8 m, Fillmore Formation (upper Tremadocian; Stairsian; *Rossaspis leboni* Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

Etymology. After Scott Morrison.

Diagnosis. Dorsal surface of cranidium almost entirely lacking tuberculate sculpture in larger specimens, with only a scattering of very fine tubercles developed on the anterior border and anterior aspect of the glabella in some specimens; posterior projections narrow, exsagittally long behind palpebral lobe, and strongly downturned; pygidium with tuberculate sculpture restricted to distal pleura on most large specimens; pygidial axial terminal piece large, significantly longer than wide.

Description. *Tesselacauda morrisoni* is similar to *T. depressa* and a detailed comparison of their differences is provided rather than a separate description. Cranidia of *T. morrisoni* possess narrower, longer (exsag.) posterior projections (especially abaxially) that are more strongly ventrally flexed; fixigenal field possesses a less obviously pitted sculpture; the palpebral lobes are thinner and the external margins less sinuous, with the strong (almost 90) bend present posteriorly on *T. depressa* being much more obtuse on *T. morrisoni*, so that the posterior extensions of the palpebral lobes are much smaller and more posterolaterally directed; the lobes are also slightly more flattened and narrower (tr.) in anterior view, with the furrows bounding anteromedial margins more clearly defined especially adjacent to the fossulae, which are more prominent; palpebral furrow intersects axial furrow about two thirds of the way along L3 instead of closer to the anterolateral corner of L3; the glabella is slightly narrower, more tapered and rounded anteriorly, with stronger dorsal inflation; larger specimens lacking tubercles on the glabella, except for a few scattered on the anterior portion of the frontal lobe (e.g., Pl. 9, fig. 9); the axial furrows are more outwardly bowed; the anterior border is shorter (sag., exsag.); LO is slightly longer (sag.) and effaced.

The hypostome and rostral plate of *T. morrisoni* have not been identified so a comparison cannot be made.

Librigena of *T. morrisoni* are much more densely tuberculate with tubercles extending across entire border to furrow rather than restricted to a dense strip along the external margin of the border; the border furrow is generally more even in width along the entire course rather than being expanded medially; row of fine tubercles along margins of border furrow is much less prominently developed.

Three isolated thoracic segments have been identified for *T. morrisoni* (see Pl. 12). Thoracic segments strongly dorsally arched, with distal tips flexed gently outward from main arc; articulating half-ring with sagittal length 83.4% (82.6–84.1%) that of axial ring, width 80.0% (79.6–80.5%) that of axial ring, anterior margin anteriorly arched, with posterior margin more transverse to gently anteriorly arched medially and lined with row of small tubercles; articulating furrow deep; axial ring with distal portion rounded and slightly bulbous, in posterior view distal portion of ring extended into short lateral projections (e.g., Pl. 12, fig. 9); axial furrows deep with small articulating surface present anteriorly abaxial to articulating half-ring; pleurae with short (exsag.) articulating flange developed along anterior margin, distal portion of flange longer (exsag.); pleurae clearly divided into subequal anterior and posterior bands by deep pleural furrow; both bands with proximal terminations rounded and anterior band extended further adaxially than posterior band; anterior band pinched out abaxially, with posterior band extending past termination of anterior band into short anterolaterally directed blunt spine bearing scattering of granules (e.g., Pl. 12, fig. 1), pleurae otherwise generally smooth.

Pygidia of *T. morrisoni* appear taller in posterior view, with ventral margin of tips of pleurae forming a gentle concave arc, whereas on *T. depressa* they form a more transverse margin; in ventral view, the pleural spines are longer and less merged, forming more isolated tab-like spines; axis is more tapered, with a longer (sag.) terminal piece with length (sag.) much greater than width (tr.); the anterior band of the second pleural segment is generally smaller than that of *T. depressa*; fewer tubercles are present and are generally limited to the portion of pygidium distal to the fulcrum, with the axis almost totally lacking tubercles, except on the terminal piece; pygidia of *T. morrisoni* also lack the rows of fine tubercles along margins of furrows, except for along the posterior margin of the articulating half-ring.

Ontogeny. Smaller cranidia are densely tuberculate with a small genal spine. Throughout ontogeny the tubercles become nearly effaced, except on the anterior border and frontal lobe of the glabella; glabella becomes broader; distinct genal spine on smaller specimens (e.g., Pl. 10, figs 7, 8, 10, 12) becomes reduced to a small nubbin.

Discussion. As noted previously, *T. morrisoni*, the oldest species, is much more similar to *T. kriegerae*, the youngest, than either is to the intermediate species, *T. depressa*. *Tesselacauda morrisoni* and *T. kriegerae* both have anterior borders which are short sagittally and distinctly anteriorly bowed medially, versus the longer, medially transverse border of *T. depressa*. They share posterior projections which are exsagittally longer than in *T. depressa* as well as more steeply inclined. They differ in that the projections of *T. morrisoni* are longer and more inclined than those of *T. kriegerae*. *Tesselacauda morrisoni* also differs from *T. kriegerae* in its nearly completely effacement of dorsal cranidial tuberculation, versus variable development with fine, sparse tubercles retained on most specimens of *T. kriegerae*. Pygidia of *T. morrisoni* differ from those of *T. kriegerae* in: the absence of tubercles other than on the distal pleurae in most specimens, versus their common presence on the axis, and particularly in the possession of a much larger axial terminal piece which is much longer than wide.

***Tesselacauda kriegerae* n. sp.**
(Plate 13, Plate 14, figs 1–16, 19, Plates 15–18)

	1953	*Tesselacauda* sp.; Hintze, p. 32.
?	1953	*Tesselacauda* aff. *T. depressa* Ross; Hintze, p. 237, pl. 21, figs 2, 3.
	1973	*Tesselacauda depressa* Ross; Demeter (*partim*), p. 48, pl. 1, figs 5, 6, 10, 15 (only; pl. 1, fig. 14 = Pilekiinae gen. nov. 3 sp. nov. B of Adrain *et al*. [2014, p. 179, fig. 12EE]).
	2014	*Tesselacauda* sp. nov. 2; Adrain *et al.*, p. 179, fig. 12Y, DD.

Material. Holotype, cranidium, SUI 147597 (Pl. 13, figs 10, 12, 13, 18), and assigned specimens SUI 147599, 147601, 147606, 147617, 147618, 147620, and 147622, from Section C 111.6 m, southern House Range, assigned specimens SUI 147595–134173, 147598, 147600, 147603–147605, 147607–147611, 147614–147616, 147623–147625, 147627, from Section G 26.6 m, and assigned specimens SUI 147602, 147619, 147621, 147626, from Section G 27.0 m, southern Confusion Range, all Fillmore Formation (upper Tremadocian; Stairsian; *Bearriverops alsacharovi* Zone), Ibex area, Millard County, western Utah. Assigned specimens SUI 147628, 147633, 147642, 147643, from Section HC6 122.5 m, and SUI 147629–147632, 147634–147641, from Section HC6 124.0 m, Garden City Formation (upper Tremadocian; Stairsian; *Bearriverops alsacharovi* Zone), west side of Hillyard Canyon, Franklin Basin, Bear River Range, Franklin County, southeastern Idaho.

Etymology. After Elinor Krieger Coble.

Diagnosis. Dorsal cranidial surfaces with very fine tuberculate sculpture, effaced on glabella in some specimens; posterior projections of intermediate size between *T. depressa* and *T. morrisoni*, and of intermediate slope; pygidium with most of dorsal pleural regions effaced, tubercles expressed on at least medial and posterior parts of pygidial axis of large specimens, over entire axis of some specimens; terminal piece small, with length and width subequal.

Description. As with *T. morrisoni*, a comparison of *T. kriegerae* and *T. depressa* is provided. The cranidium of *T. kriegerae* has the fulcrum set slightly closer to glabella and the posterior projections more strongly downturned giving the appearance that it is overall narrower than *T. depressa*; the glabella is broader (tr.) posteriorly and gently tapered anteriorly, with the anterior margin gently anteriorly arched so that overall the glabella appears much less subquadrate, in lateral profile the glabella is held more parallel to horizontal plane with only the front portion (from anterior portion of L3 forward) sloping downward, and LF more strongly inflated; anterior border is shorter (sag.) and more evenly anteriorly arched; the fossulae are deeper; the palpebral lobes are slightly smaller and less steeply angled, with the posterior extension of the palpebral lobe thinner and more posterolaterally directed; the palpebral furrow intersects the axial furrow a little further back along L3; sculpture smooth or with finer tubercles.

Hypostomes of *T. kriegerae* and *T. depressa* are very similar, but those of the former are slightly more subquadrate with sagittal length 92.9% (90.8–95.7%) maximum width; the posterior margin of *T. kriegerae* is more sinuous with a more clearly developed median embayment; middle body less inflated; posterior lobe of middle body more clearly covered with fine granules; anterior wings not as laterally extensive, terminating about level with lateral extent of shoulders, and they are more strongly dorsally flexed; posterior spine pair more robust.

Librigenae of *T. kriegerae* possess coarse granules on the adaxial portion of border, whereas that portion is smooth and lacks sculpture in those of *T. depressa*; sculpture along abaxial portion of the border is coarser; border furrow is broader; overall librigenae are less elongate.

Thoracic segments with much more prominent tubercles on axial ring and distinct row of prominent tubercles on anterior and posterior pleural bands.

Pygidia are narrower (tr.) and dorsoventrally taller, so that pleurae appear longer in posterior view; first pleural segment is directed more posteriorly than in *T. depressa*, giving anterolateral corner an angular rather than gently rounded appearance; row of tubercles along posterior margin of articulating half-ring more prominent along entire margin (cf. Pl. 16, fig. 2; Pl. 6, fig. 2); first axial segment is slightly longer (sag., exsag.) than *T. depressa*; terminal piece is narrower, with width (tr.) and length (sag.) subequal, and on one specimen it is absent (Pl. 16, figs 7, 10; the fourth pair of pleural spines on this specimen are also noticeably smaller than the previous three pairs [see Pl. 16, fig. 13], which is unlike the other recovered *T. kriegerae* pygidia); sculpture of larger tubercles, which are primarily located on the axis and tips of pleurae, with the occasional tubercle present on the pleurae just adjacent to the axis; doublure taller, especially medially, in anterior view.

Ontogeny. Several juvenile sclerites were recovered from the Garden City Formation at the HC6 section and allow for a more detailed description of the ontogeny of *T. kriegerae* as follows. The glabella broadens (tr.) posteriorly and gently expands laterally so that it becomes less subrectangular throughout ontogeny; LO–L3 become broader (cf. Pl. 17, fig. 11; Pl. 13, fig. 1); the posterior projections broaden distal to fulcrum and become less strongly downturned from horizontal plane; and a very small nubbin-like genal spine is present on smaller specimens (e.g., Pl. 17, figs 3, 9), it becomes greatly reduced throughout ontogeny. One of the most noticeable ontogenetic changes is the reduction in the prominent tuberculate sculpture present on smaller specimens. The tubercles are coarse, densely spaced, and sometimes elongated (see Pl. 17, figs 11, 12), but they become less dense, much smaller, and less prominent, and totally effaced on some parts of the cranidium of the larger specimens. The pattern of reduction of these prominent tubercles appears to proceed from the posterior portion of the cranidium anteriorly. For example, tubercles cover the fixigenal field on the smallest specimens, but start to become effaced on the posteromedial portion of field (Pl. 17, fig. 2), and eventually the field is nearly free of any larger tubercles (see e.g., Pl. 13, fig. 13); this change also allows for the background sculpture of deep pits on the fixigena to become the dominant sculpture on larger specimens. A similar pattern also appears to be present on the glabella, with a progressive forward reduction in tubercles (cf. Pl. 17, 11; Pl. 14, fig. 1, and Pl. 13, fig. 13). A similar pattern of progressively forward reduction can be seen on the posterior and lateral borders, palpebral lobe, and anterior border; the latter retains a sculpture of much finer granules on the largest specimens.

The smallest hypostome (Pl. 18, fig. 18) has sagittal length 87.0% the maximum width (tr. across the anterior wings) and is relatively slightly wider compared to larger specimens; a sculpture of coarser tubercles (especially on anterior portion of middle body) is present, which becomes finer and more densely spaced; the shoulders become more laterally expanded and rounder; the anterior portion of middle body lengthens; the posterior margin is more transverse, with the median embayment developing later in ontogeny; the anterior spine pair are more posteriorly directed on smallest specimen, and become more laterally directed throughout ontogeny; and the posterior border furrow becomes more effaced, with smallest specimen possessing clear definition between posterior lobe of middle body and posterior border.

The librigena becomes more elongate, with the posterior projection becoming much longer and also thinner; the smallest librigenae possess a region of larger tubercles on the inner portion of the librigenal border, which become reduced throughout ontogeny, with the region covered by much smaller tubercles in larger specimens; the coarse granular sculpture present along the external and ventral margins of the border also become finer throughout ontogeny.

Throughout ontogeny, the pygidium becomes dorsoventrally taller and more inflated, partly due to a lengthening of the pleural region distal to the fulcrum; the axial segments and ring furrows become more transverse and less anteriorly arched; the width of the terminal piece (across its anterior margin) becomes more noticeably smaller than that of the fourth segment; the anterior band of the third pleural segment is just visible on the smallest pygidium (Pl. 18, fig. 28), but is lost during ontogeny and not present on larger specimens.

Discussion. *Tesselacauda kriegerae* was compared with *T. morrisoni* in discussion of the latter species. Hintze (1953, p. 237, pl. 21, figs 2, 3) assigned a partial cranidium and a hypostome to "*Tesselacauda* aff. *T. depressa*". The given provenance was his locality C-6, which was at 390' (118.9 m) in his Section C. We have not resampled this horizon, but a collection we made from 380' (115.8 m), following Hintze's painted numbers, is from the *Pseudoclelandia weymouthae* Zone. In all of our sampling, we have not encountered any material of *Tesselacauda* from this zone or any younger rocks. *Tesselacauda kriegerae* n. sp. occurs at C 111.6 m and Hintze's specimens most likely represent this species.

***Tesselacauda* n. sp. A**
(Plate 12, figs 13–16, 18–29)

Material. Assigned specimens SUI 147587–147594, from Section MME 36.4 m, Fillmore Formation (upper Tremadocian; Stairsian; *Rossaspis leboni* Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

Discussion. Specimens retrieved from Section MME 36.4 m are from lower in the same zone as those of *T. morrisoni*. The sample from MME 36.4 m is in general fragmentary and sparse, but most species seem to occur also in the assemblage at MME 49.8 m. The *Tesselacauda* specimens, however, definitely do not belong to *T. morrisoni*. The dorsal pygidial surfaces of most specimens are almost completely effaced, and lack the clusters of tubercles on the distal parts of the pleurae which characterize *T. morrisoni*. The terminal piece, while relatively large, is about as wide as it is long, whereas those of pygidia of *T. morrisoni* are much longer than wide. The MME 36.4 m material seems to represent a poorly known but distinct species, the oldest member of the genus thus far recovered.

Tesselacauda? flabella Kobayashi, 1955

(Plate 14, figs 17, 18, 20)

1955 *Tesselacauda flabella* Kobayashi, p. 417, pl. 2, figs 8a, b.
1989 *Tesselacauda flabella* Kobayashi; Dean, p. 17, pl. 2, fig. 12 (*non* pl. 2, figs 2, 4, 7, 8, 10, 11).

Material. Assigned specimens SUI 147612 and 147613, from Section G 26.6 m, Fillmore Formation (upper Tremadocian; Stairsian; *Bearriverops alsacharovi* Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

Discussion. Kobayashi (1955, p. 417, pl. 2, figs 8a, b) established this species on the basis of a single illustrated pygidium from the McKay Group of southeastern British Columbia, Canada. Dean (1989, pl. 2, figs 2, 4, 7, 8, 10–12) reillustrated this holotype and assigned three pygidia (two fragmentary) and a fragmentary cranidium from the middle member of the Survey Peak Formation, Wilcox Pass, Jasper National Park, Alberta. While possibly representing a related species, Dean's specimens are obviously much less effaced than Kobayashi's holotype and are unlikely to be conspecific. In fact, the Survey Peak specimens are not effaced at all, and the effacement of both the posterior axial and ring furrows and most of the pleural and interpleural furrows is the most striking feature of the holotype. The affinity of the cranidial fragment associated by Dean is impossible to assess; it appears to represent a cheirurid, but consists only of part of a glabella and part of an occipital ring.

Two pygidia from the *Bearriverops alsacharovi* Zone appear much closer in morphology to Kobayashi's (1955) holotype. A smaller specimen preserving the anterior part of the axis and left pleural region (Pl. 14, fig. 20) is nearly identical to the holotype. A specimen more than twice the size preserving most of the left pleural region (Pl. 14, figs 17, 18) seems conspecific, and, if so, shows that the pygidium became increasingly effaced with size. Unfortunately the species is extremely rare, as these are the only specimens found and no prospective cranidia were recovered. They are of some potential importance, however, in that they may anchor some of Kobayashi's (1955) species to the trilobite zonal scheme presented by Adrain *et al.* (2014).

So little is known of the species that its affinities are impossible to determine with any confidence. The pygidia are broadly comparable to those of species of *Tesselacauda*, but the smaller silicified example (Pl. 14, fig. 20) appears to show the pleural region of the third segment with an expressed pleural furrow. This is absent from all large pygidia assigned to *Tesselacauda* herein. It is expressed on a single specimen, a very small pygidium assigned to *T. kriegerae* (Pl. 18, fig. 28). Much more information would be required to meaningfully evaluate the taxon, but it is documented here because of its possible biostratigraphic significance.

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PLATE 1

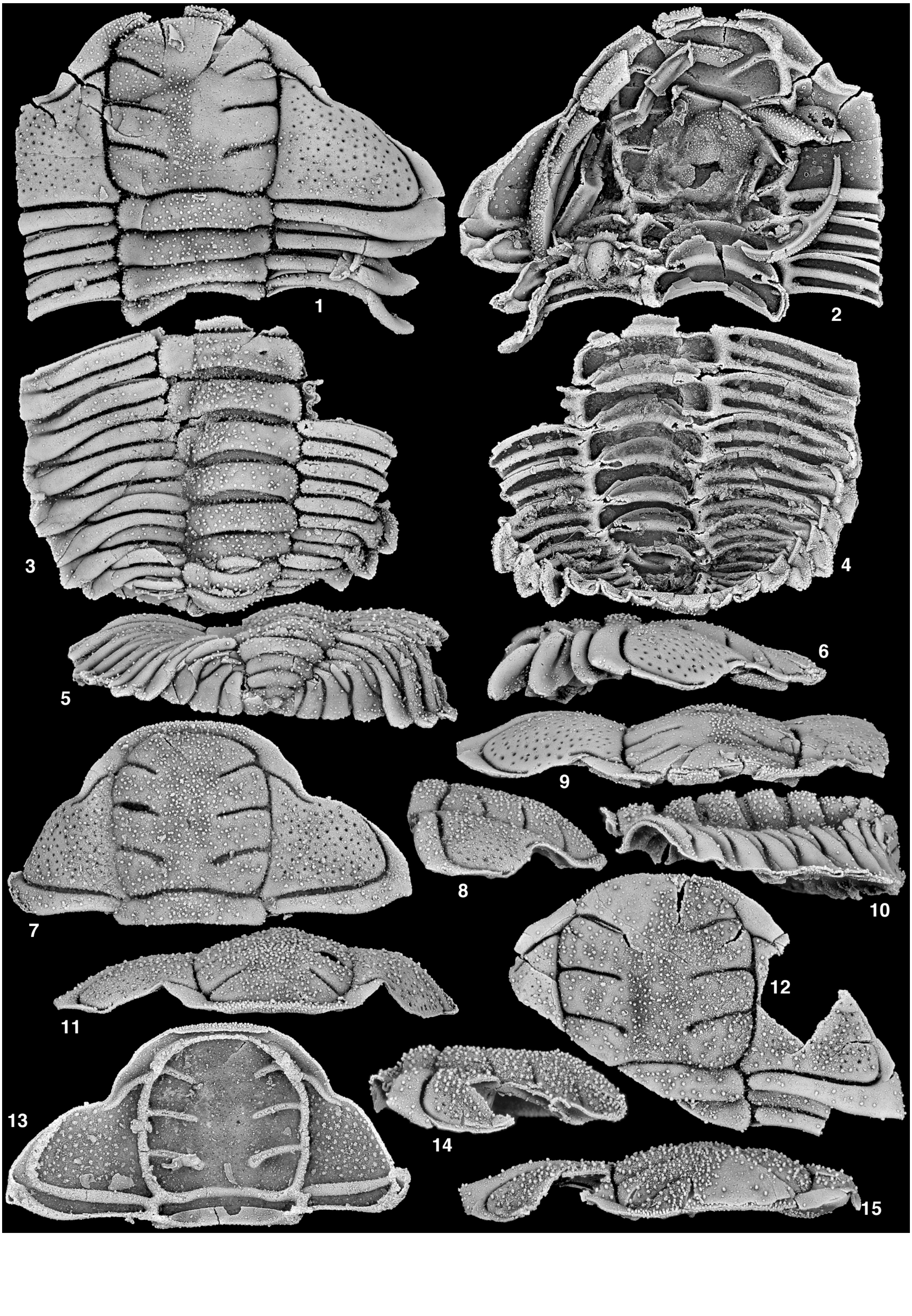

PLATE 1. *Tesselacauda depressa* Ross, 1951, from Section HC5 106.7 m, east side of Hillyard Canyon, and Section FB7 102.1 m, Franklin Basin, both Garden City Formation (upper Tremadocian; Stairsian; *Bearriverops loganensis* Zone), Bear River Range, Franklin County, southeastern Idaho, USA.

1, 2, 6, 9. Cephalon and thoracic segments, SUI 147507, dorsal, ventral, right lateral, and anterior views, x7.5 (FB7 102.1 m).
3–5, 10. Thoracic segments and pygidium, SUI 147508, dorsal, dorsal, ventral, posterior, and left lateral views, x7.5 (FB7 102.1 m).
7, 8, 11, 13. Cranidium, SUI 147509, dorsal, dorsal, right lateral, anterior, and ventral views, x10 (HC5 106.7 m).
12, 14, 15. Cranidium and thoracic segment, SUI 147510, dorsal, dorsal, right lateral, and anterior views, x10 (HC5 106.7 m).

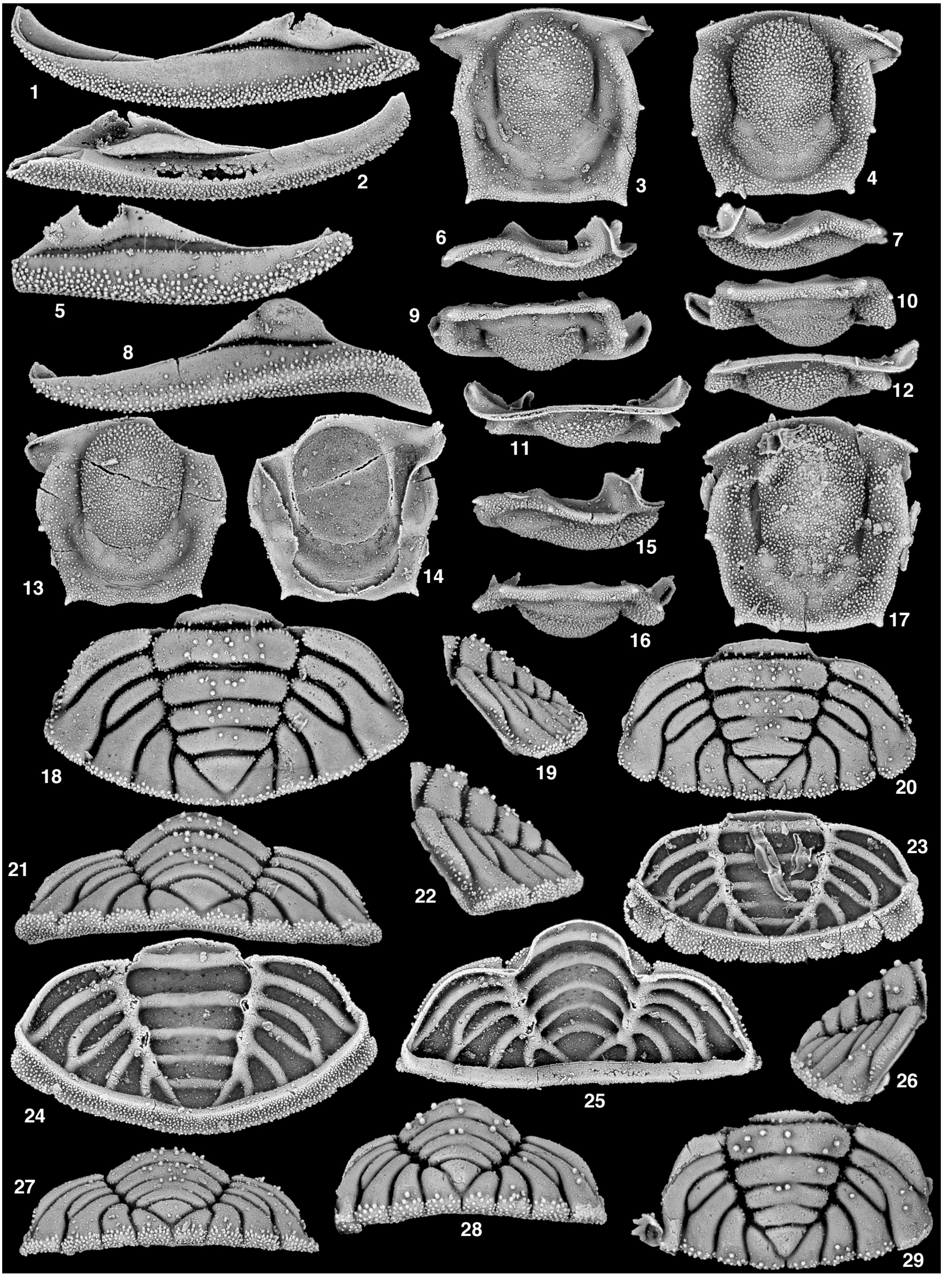

PLATE 2

PLATE 2. *Tesselacauda depressa* Ross, 1951, from Section HC5 106.7 m, east side of Hillyard Canyon, HC6 88.3 m, west side of Hillyard Canyon, and Section FB7 102.1 m, Franklin Basin, both Garden City Formation (upper Tremadocian; Stairsian; *Bearriverops loganensis* Zone), Bear River Range, Franklin County, southeastern Idaho, USA.

1, 2. Right librigena, SUI 147511, external and internal views, x10 (HC5 106.7 m).
3, 6, 9, 11. Hypostome, SUI 147512, ventral, right lateral, posterior, and anterior views, x8 (FB7 102.1 m).
4, 7, 10, 12. Hypostome, SUI 147513, ventral, left lateral, posterior, and anterior views, x10 (HC6 88.3 m).
5. Left librigena, SUI 147514, external view, x12 (HC5 106.7 m).
8. Right librigena, SUI 147515, external view, x15 (HC5 106.7 m).
13–16. Hypostome, SUI 147516, ventral, dorsal, right lateral, and posterior views, x8 (HC5 106.7 m).
17. Hypostome, SUI 147517, ventral view, x10 (HC5 106.7 m).
18, 21, 22, 24, 25. Pygidium, SUI 147518, dorsal, posterior, left lateral, ventral, and anterior views, x10 (HC5 106.7 m).
19, 20, 23, 27. Pygidium, SUI 147519, left lateral, dorsal, ventral, and posterior views, x10 (HC5 106.7 m).
26, 28, 29. Pygidium, SUI 147520, right lateral, posterior, and dorsal views, x14 (HC5 106.7 m).

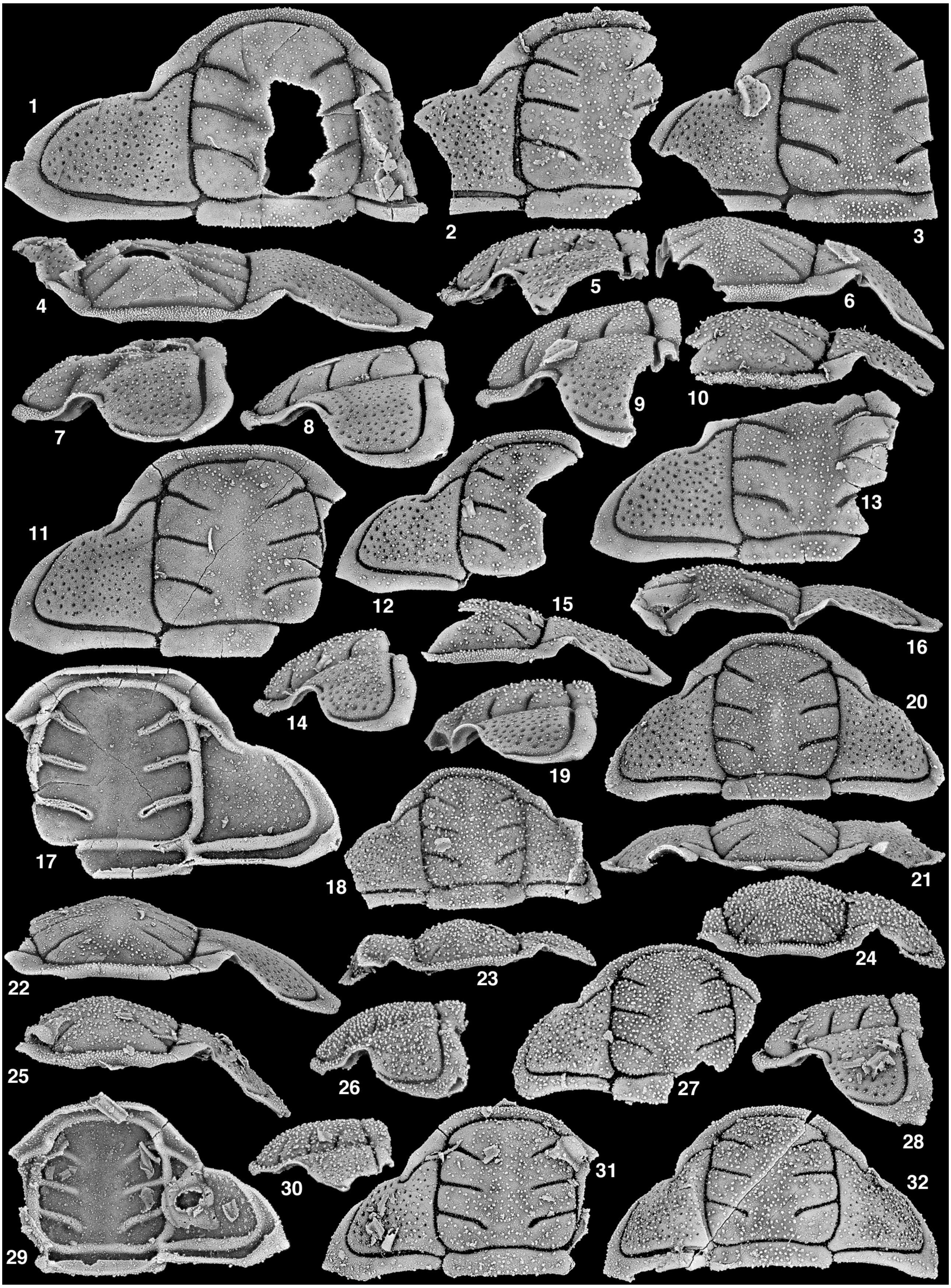
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PLATE 3

PLATE 3. *Tesselacauda depressa* Ross, 1951, from Section MME 75.5 m, Fillmore Formation (upper Tremadocian; Stairsian; *Bearriverops loganensis* Zone), Middle Mountain, Ibex area, Millard County, western Utah, USA.

1, 4, 7. Cranidium, SUI 147521, dorsal, anterior, and left lateral views, x5.
2, 5, 10. Cranidium, SUI 147522, dorsal, left lateral, and anterior views, x6.
3, 6, 9. Cranidium, SUI 147523, dorsal, anterior, and left lateral views, x6.
8, 11, 17, 22. Cranidium, SUI 134129, left lateral, dorsal, ventral, and anterior views, x6.
12, 14, 15. Cranidium, SUI 147524, dorsal, left lateral, and anterior views, x6.
13, 16, 19. Cranidium, SUI 147525, dorsal, anterior, and left lateral views, x5.
18, 23, 30. Cranidium, SUI 147526, dorsal, anterior, and left lateral views, x9.
20, 21. Cranidium, SUI 147527, dorsal and anterior views, x6.
24, 26, 27. Cranidium, SUI 147528, anterior, left lateral, and dorsal views, x9.
25, 28, 29, 31. Cranidium, SUI 147529, anterior, left lateral, ventral, and dorsal views, x6.
32. Cranidium, SUI 147530, dorsal view, x6.

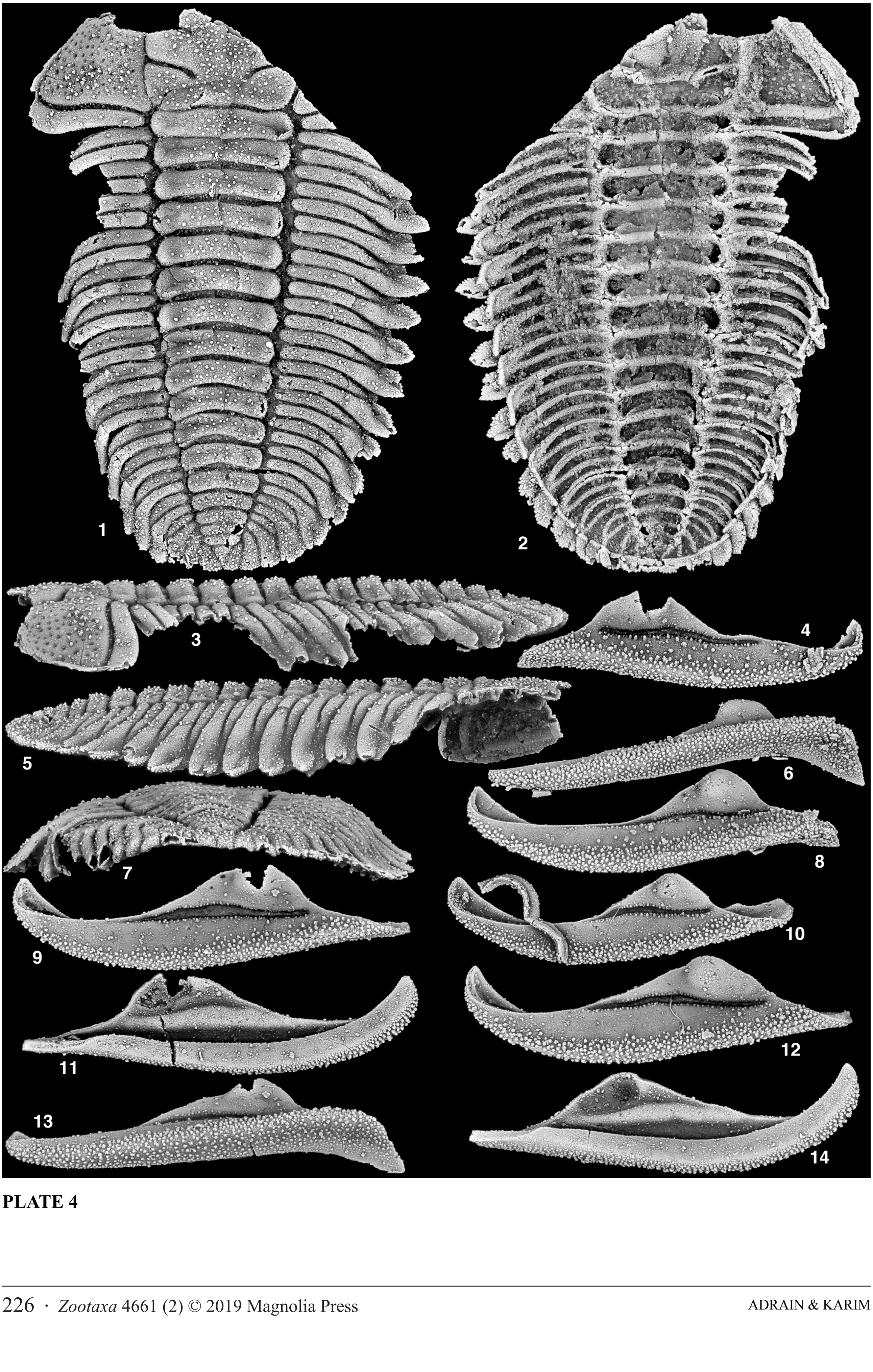

PLATE 4

PLATE 4. *Tesselacauda depressa* Ross, 1951, from Section MME 75.5 m, Fillmore Formation (upper Tremadocian; Stairsian; *Bearriverops loganensis* Zone), Middle Mountain, Ibex area, Millard County, western Utah, USA.

1–3, 5, 7. Dorsal exoskeleton, SUI 147531, dorsal, ventral, left lateral, right lateral, and posterior views, x12.
4. Left librigena, SUI 147532, external view, x12.
6, 8. Right librigena, SUI 147533, ventrolateral and external views, x10.
9, 11, 13. Right librigena, SUI 147534, external, internal, and ventrolateral views, x12.
10. Right librigena, SUI 147535, external view, x10.
12, 14. Right librigena, SUI 147536, external and internal views, x12.

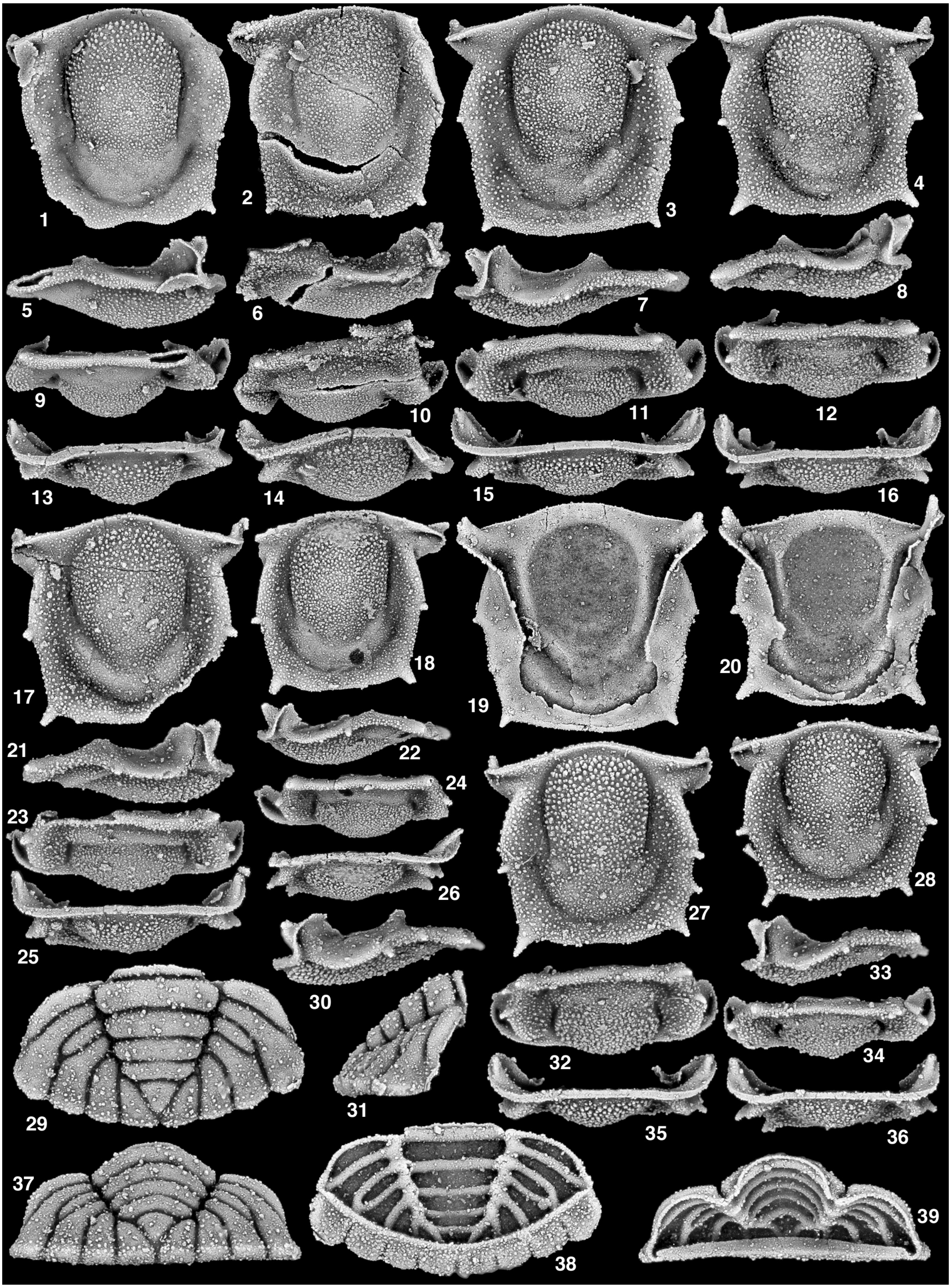
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PLATE 5

PLATE 5. *Tesselacauda depressa* Ross, 1951, from Section MME 75.5 m, Fillmore Formation (upper Tremadocian; Stairsian; *Bearriverops loganensis* Zone), Middle Mountain, Ibex area, Millard County, western Utah, USA.

1, 5, 9, 13. Hypostome, SUI 147537, ventral, right lateral, posterior, and anterior views, x10.
2, 6, 10, 14. Hypostome, SUI 147538, ventral, right lateral, posterior, and anterior views, x10.
3, 7, 11, 15, 19. Hypostome, SUI 147539, ventral, left lateral, posterior, anterior, and dorsal views, x10.
4, 8, 12, 16, 20. Hypostome, SUI 147540, ventral, right lateral, posterior, anterior, and dorsal views, x12.
17, 21, 23, 25. Hypostome, SUI 147541, ventral, right lateral, posterior, and anterior views, x12.
18, 22, 24, 26. Hypostome, SUI 147542, ventral, left lateral, posterior, and anterior views, x12.
27, 30, 32, 35. Hypostome, SUI 147543, ventral, left lateral, posterior, and anterior views, x15.
28, 33, 34, 36. Hypostome, SUI 147544, ventral, left lateral, posterior, and anterior views, x15.
29, 31, 37–39. Pygidium, SUI 147545, dorsal, right lateral, posterior, ventral, and anterior views, x15.

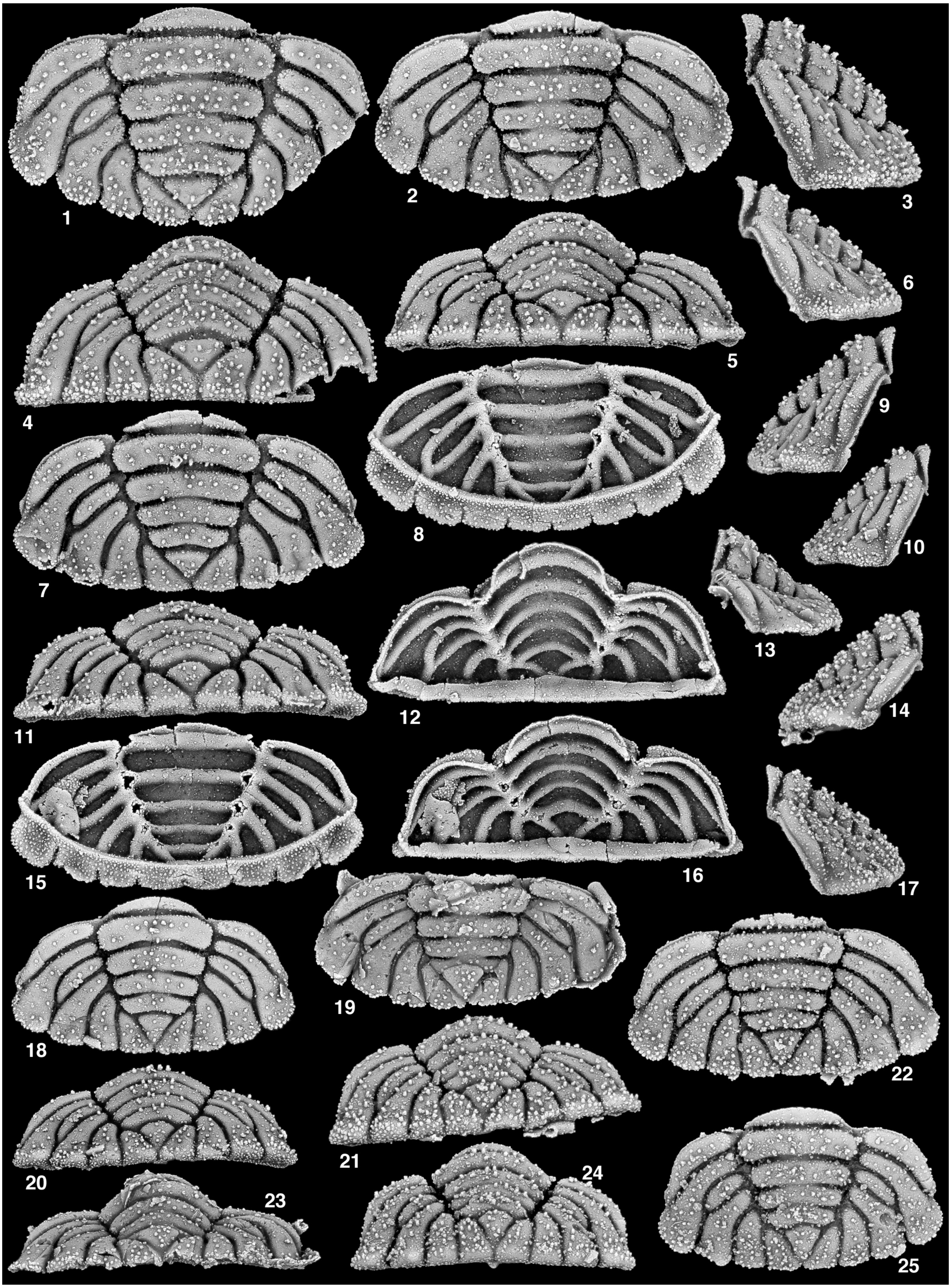

PLATE 6

PLATE 6. *Tesselacauda depressa* Ross, 1951, from Section MME 75.5 m, Fillmore Formation (upper Tremadocian; Stairsian; *Bearriverops loganensis* Zone), Middle Mountain, Ibex area, Millard County, western Utah, USA.

1, 3, 4. Pygidium, SUI 147546, dorsal, left lateral, and posterior views, x10.
2, 5, 6, 8, 12. Pygidium, SUI 134130, dorsal, left lateral, posterior, ventral, and anterior views, x10.
7, 9, 11, 15, 16. Pygidium, SUI 147547, dorsal, right lateral, posterior, ventral, and anterior views, x10.
10, 18, 20. Pygidium, SUI 147548, right lateral, dorsal, and posterior views, x10.
13, 19, 23. Pygidium, SUI 147549, left lateral, dorsal, and posterior views, x10.
14, 21, 22. Pygidium, SUI 147550, right lateral, posterior, and dorsal views, x12.
17, 24, 25. Pygidium, SUI 147551, left lateral, posterior, and dorsal views, x12.

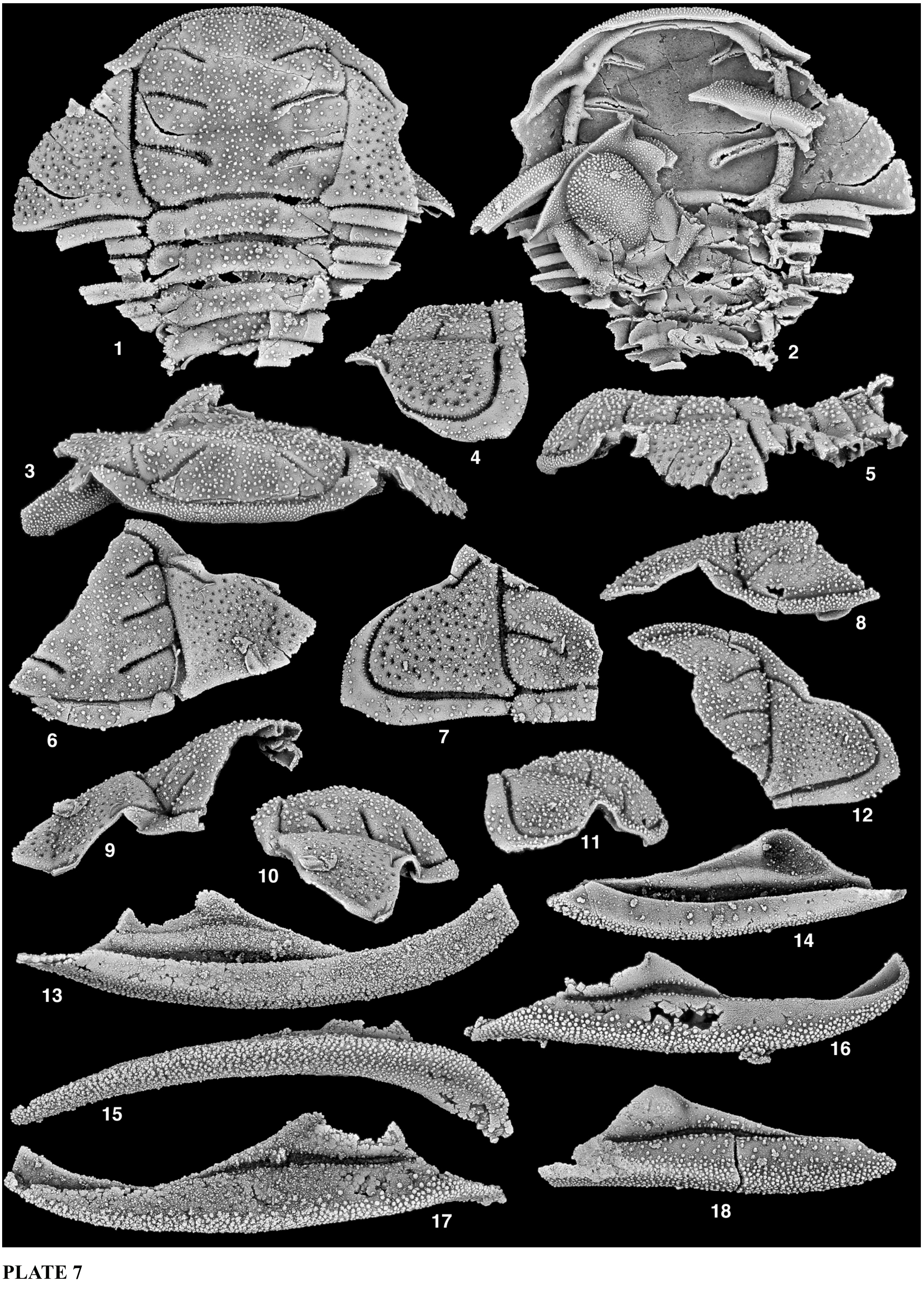

PLATE 7

PLATE 7. *Tesselacauda depressa* Ross, 1951, from Section MME 84.0 m, Middle Mountain, AAA 79.5 m, northern House Range, both Fillmore Formation, Ibex area, Millard County, western Utah, USA, and HC6 107.5 m, Garden City Formation, west side of Hillyard Canyon, Bear River Range, Franklin County, Idaho, USA (all upper Tremadocian; Stairsian; *Bearriverops deltaensis* Zone).

1, 2, 3, 5. Cephalon and thoracic segments, SUI 147552, dorsal, ventral, anterior, and left lateral views, x9 (MME 84.0 m).
4, 7. Cranidium, SUI 147553, left lateral and dorsal views, x7.5 (HC6 107.5 m).
6, 9, 10. Cranidium, SUI 147554, dorsal, anterior, and right lateral views, x10 (MME 84.0 m).
8, 11, 12. Cranidium, SUI 147555, anterior, right lateral, and dorsal views, x12 (MME 84.0 m).
13, 15, 17. Right librigena, SUI 147556, internal, ventrolateral, and external views, x10 (AAA 79.5 m).
14, 18. Left librigena, SUI 147557, internal and external views, x12 (MME 84.0 m).
16. Left librigena, SUI 147558, external view, x12 (AAA 79.5 m).

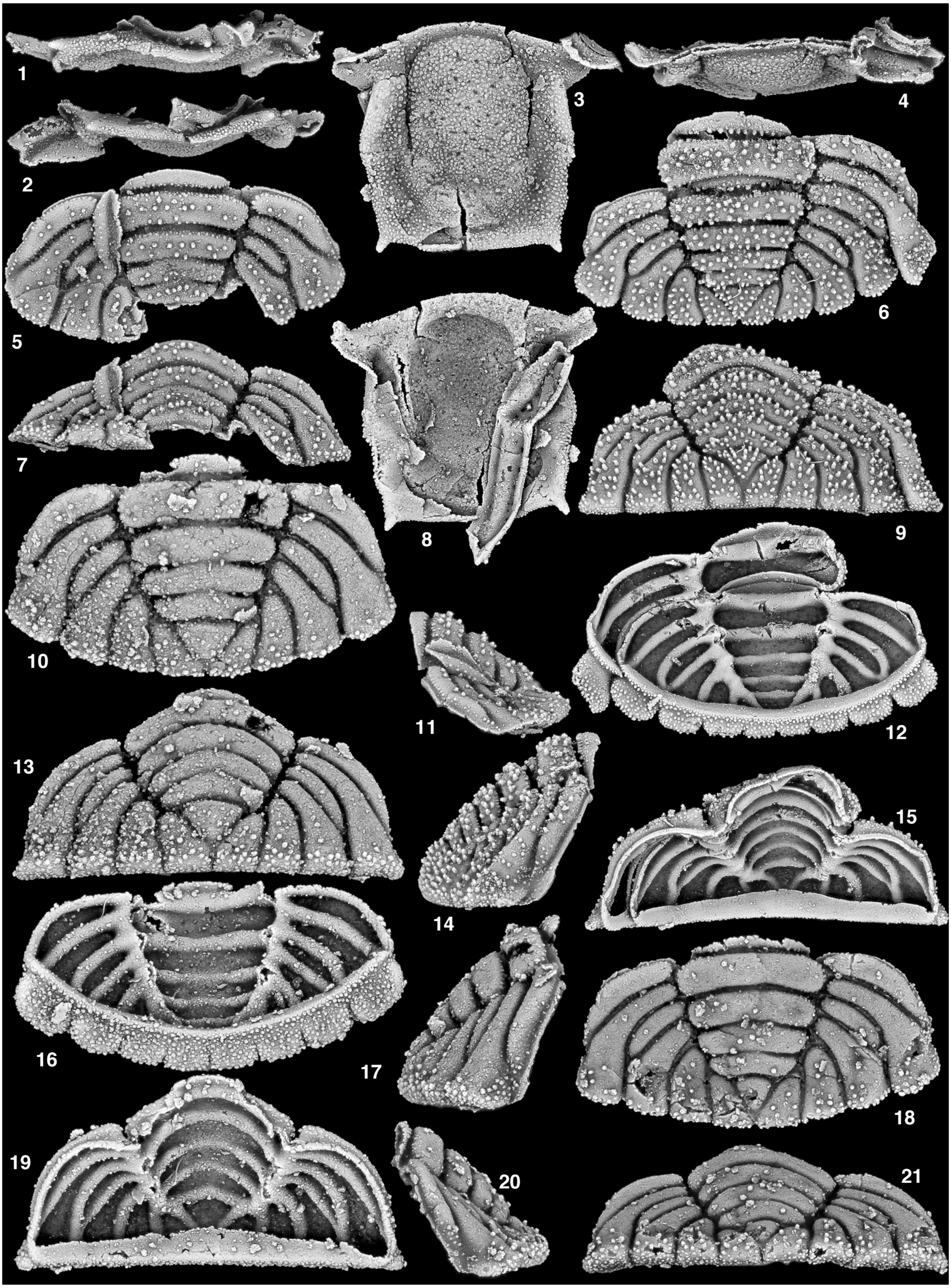

PLATE 8

PLATE 8. *Tesselacauda depressa* Ross, 1951, from Section MME 84.0 m, Middle Mountain, AAA 79.5 m, northern House Range, both Fillmore Formation, Ibex area, Millard County, western Utah, USA, and HC6 107.5 m, Garden City Formation, west side of Hillyard Canyon, Bear River Range, Franklin County, Idaho, USA (all upper Tremadocian; Stairsian; *Bearriverops deltaensis* Zone).

1–4, 8. Hypostome, SUI 147559, right lateral, posterior, ventral, anterior, and dorsal views, x12 (HC6 107.5 m).
5, 7, 11. Pygidium, SUI 147560, dorsal, posterior, and left lateral views, x12 (MME 84.0 m).
6, 9, 12, 14, 15. Pygidium and thoracic segment, SUI 147561, dorsal, posterior, ventral, right lateral, and anterior views, x12 (MME 84.0 m).
10, 13, 16, 17, 19. Pygidium, SUI 147562, dorsal, posterior, ventral, right lateral, and anterior views, x15 (AAA 79.5 m).
18, 20, 21. Pygidium, SUI 147563, dorsal, left lateral, and posterior views, x15 (AAA 79.5 m).

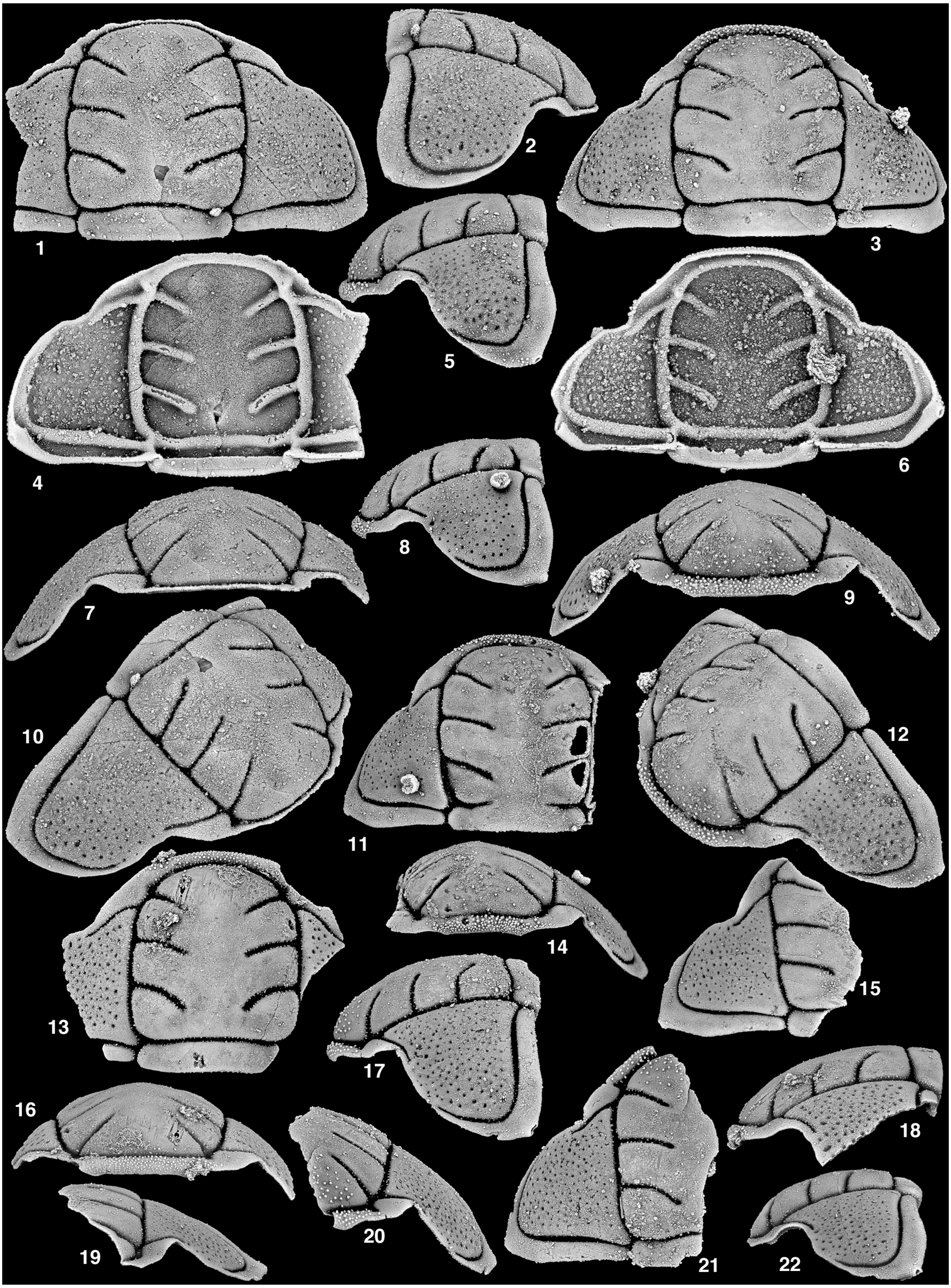

PLATE 9

PLATE 9. *Tesselacauda morrisoni* **n. sp.**, from Section MME 49.8 m, Fillmore Formation (upper Tremadocian; Stairsian; *Rossaspis leboni* Zone), Middle Mountain, Ibex area, Millard County, western Utah, USA.

1, 2, 4, 7, 10. Cranidium, SUI 147564, dorsal, right lateral, ventral, anterior, and oblique views, x7.5.
3, 5, 6, 9, 12. Cranidium, **holotype**, SUI 134075, dorsal, left lateral, ventral, anterior, and oblique views, x10.
8, 11, 14. Cranidium, SUI 147565, left lateral, dorsal, and anterior views, x7.5.
13, 16, 18. Cranidium, SUI 147566, dorsal, anterior, and left lateral views, x6.
15, 19, 22. Cranidium, SUI 147567, dorsal, anterior, and left lateral views, x7.5.
17, 20, 21. Cranidium, SUI 147568, left lateral, anterior, and dorsal views, x7.5.

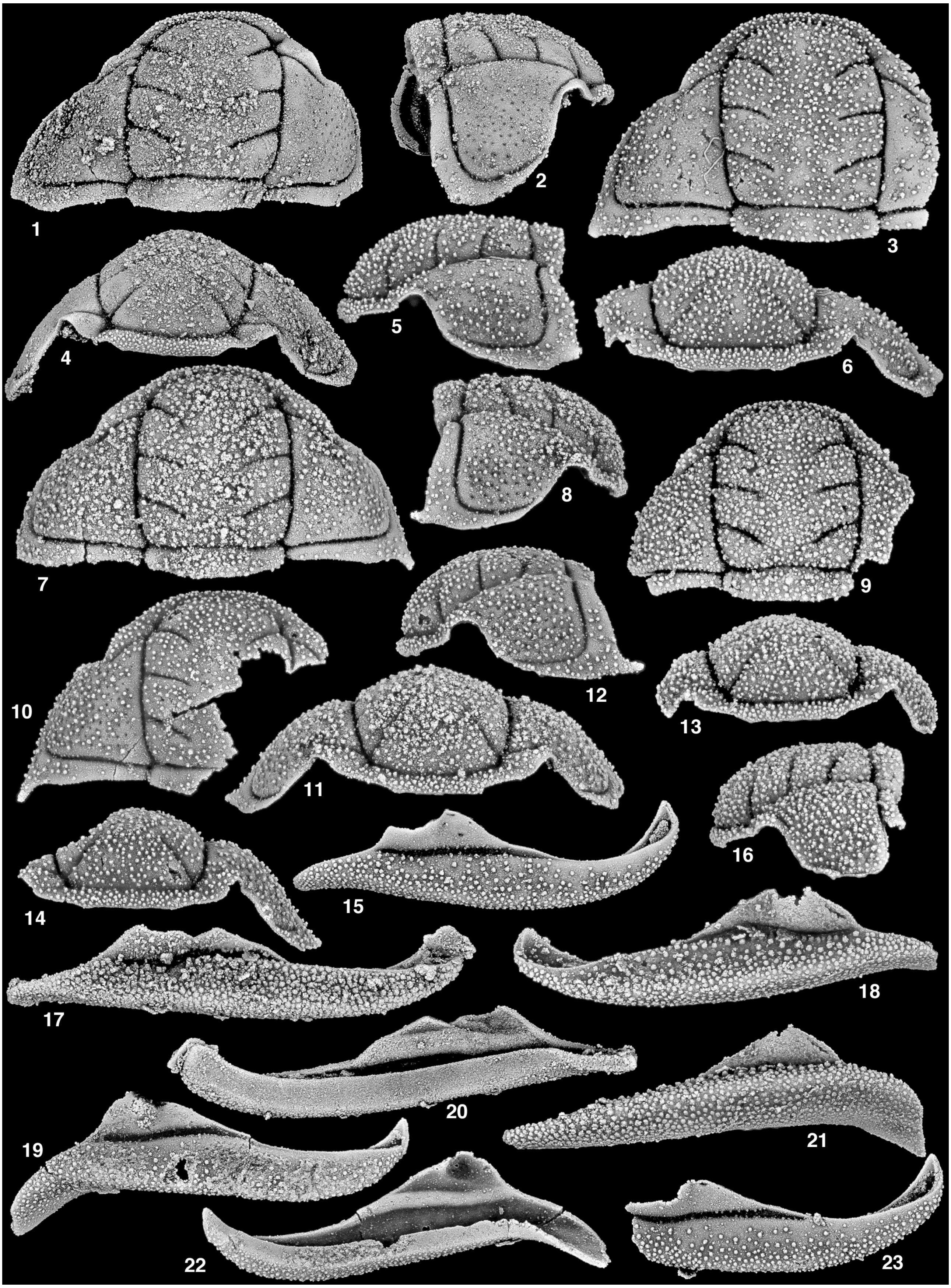

PLATE 10

PLATE 10. *Tesselacauda morrisoni* **n. sp.**, from Section MME 49.8 m, Fillmore Formation (upper Tremadocian; Stairsian; *Rossaspis leboni* Zone), Middle Mountain, Ibex area, Millard County, western Utah, USA.

1, 2, 4. Cranidium, SUI 147569, dorsal, right lateral, and anterior views, x10.
3, 5, 6. Cranidium, SUI 147570, dorsal, left lateral, and anterior views, x15.
7, 8, 11. Cranidium, SUI 147571, dorsal, right lateral, and anterior views, x15.
9, 13, 16. Cranidium, SUI 147572, dorsal, anterior, and left lateral views, x17.
10, 12, 14. Cranidium, SUI 147573, dorsal, left lateral, and anterior views, x15.
15. Left librigena, SUI 147574, external view, x12.
17, 20. Left librigena, SUI 147575, external and internal views, x12.
18, 21. Right librigena, SUI 147576, external and ventrolateral views, x12.
19, 22. Left librigena, SUI 147577, external and internal views, x12.
23. Left librigena, SUI 147578, external view, x12.

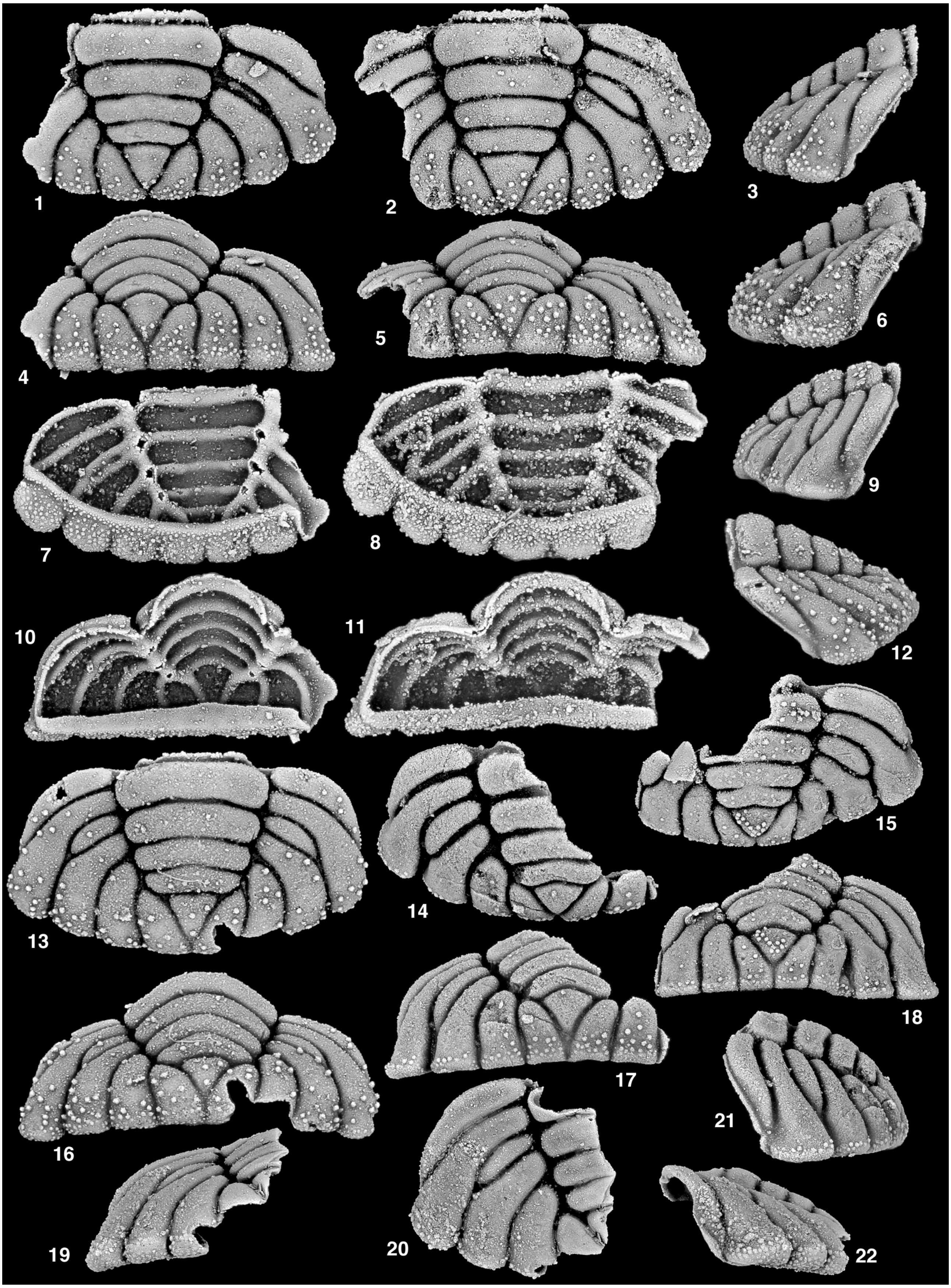

PLATE 11

PLATE 11. *Tesselacauda morrisoni* **n. sp.**, from Section MME 49.8 m, Fillmore Formation (upper Tremadocian; Stairsian; *Rossaspis leboni* Zone), Middle Mountain, Ibex area, Millard County, western Utah, USA.

1, 3, 4, 7, 10. Pygidium, SUI 147579, dorsal, right lateral, posterior, ventral, and anterior views, x12.
2, 5, 6, 8, 11. Pygidium, SUI 147580, dorsal, posterior, right lateral, ventral, and anterior views, x15.
9, 15, 18. Pygidium, SUI 147581, right lateral, dorsal, and posterior views, x12.
12, 13, 16. Pygidium, SUI 134076, left lateral, dorsal, and posterior views, x15.
14, 17, 21. Pygidium, SUI 147582 dorsal, posterior, and left lateral views, x12.
19, 20, 22. Pygidium, SUI 147583, posterior, dorsal, and left lateral views, x12.

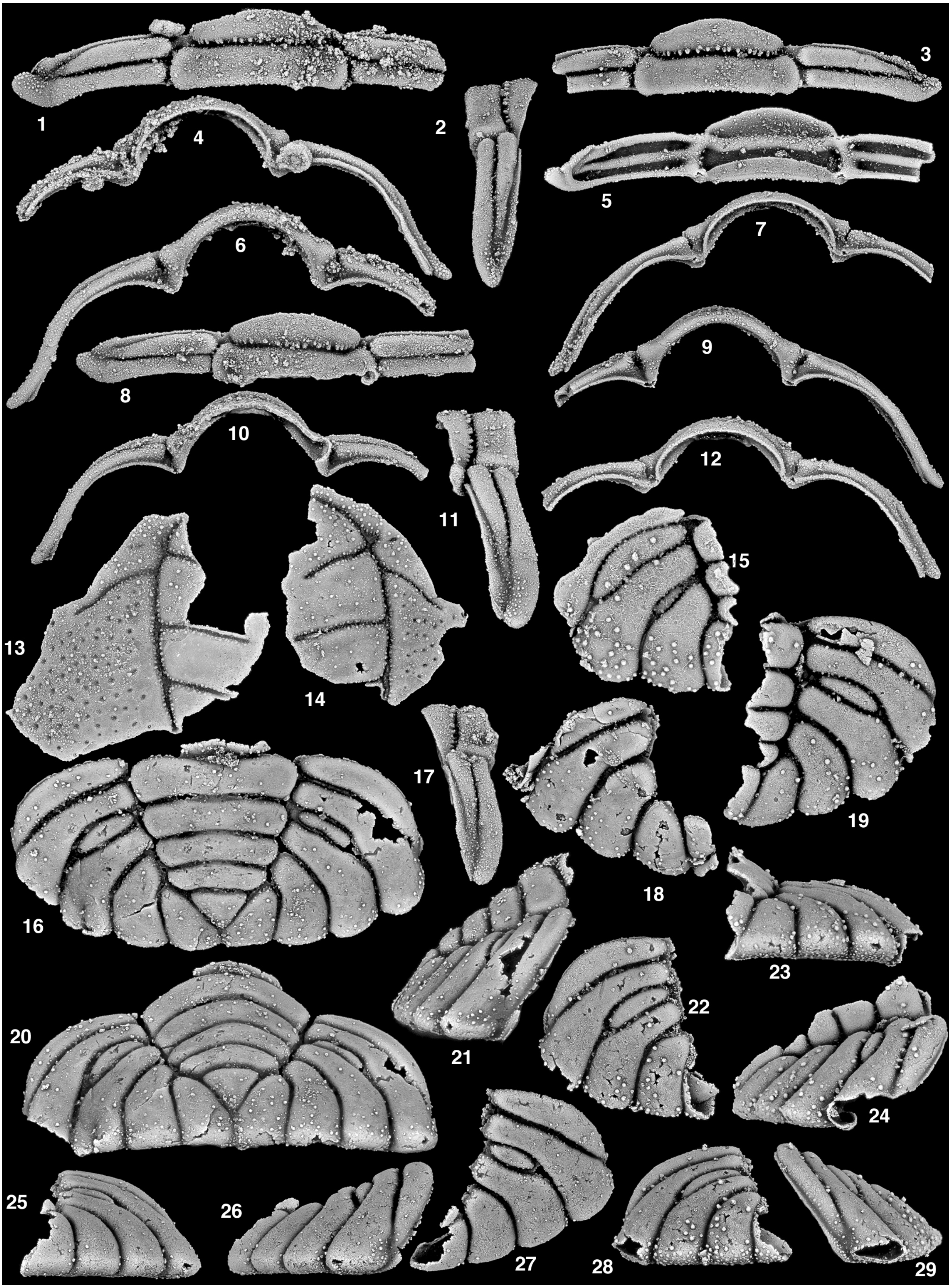

PLATE 12

PLATE 12.
1–12, 17. *Tesselacauda morrisoni* **n. sp.**, from Section MME 49.8 m, Fillmore Formation (upper Tremadocian; Stairsian; *Rossaspis leboni* Zone), Middle Mountain, Ibex area, Millard County, western Utah, USA.

1, 4, 6, 11. Thoracic segment, SUI 147584, dorsal, anterior, posterior, and left lateral views, x10.
2, 3, 5, 7, 9. Thoracic segment, SUI 147585, right lateral, dorsal, ventral, anterior, and posterior views, x8.
8, 10, 12, 17. Thoracic segment, SUI 147586, dorsal, posterior, anterior, and left lateral views, x10.

13–16, 18–29. *Tesselacauda* n. sp. A, from Section MME 36.4 m, Fillmore Formation (upper Tremadocian; Stairsian; *Rossaspis leboni* Zone), Middle Mountain, Ibex area, Millard County, western Utah, USA.

13. Cranidial fragment (probably from same individual as fig. 14), SUI 147587, dorsal view, x7.5.
14. Cranidial fragment (probably from same individual as fig. 13), SUI 147588, dorsal view, x7.5.
15. Pygidium, SUI 147589, dorsal view, x15.
16, 20, 21. Pygidium, SUI 147590, dorsal, right lateral, and posterior views, x12.
18. Pygidium, SUI 147591, dorsal view, x12.
19, 23, 24. Pygidium, SUI 147592, dorsal, posterior, and right lateral views, x15.
22, 28, 29. Pygidium, SUI 147593, dorsal, posterior, and left lateral views, x12.
25–27. Pygidium, SUI 147594, posterior, right lateral, and dorsal views, x12.

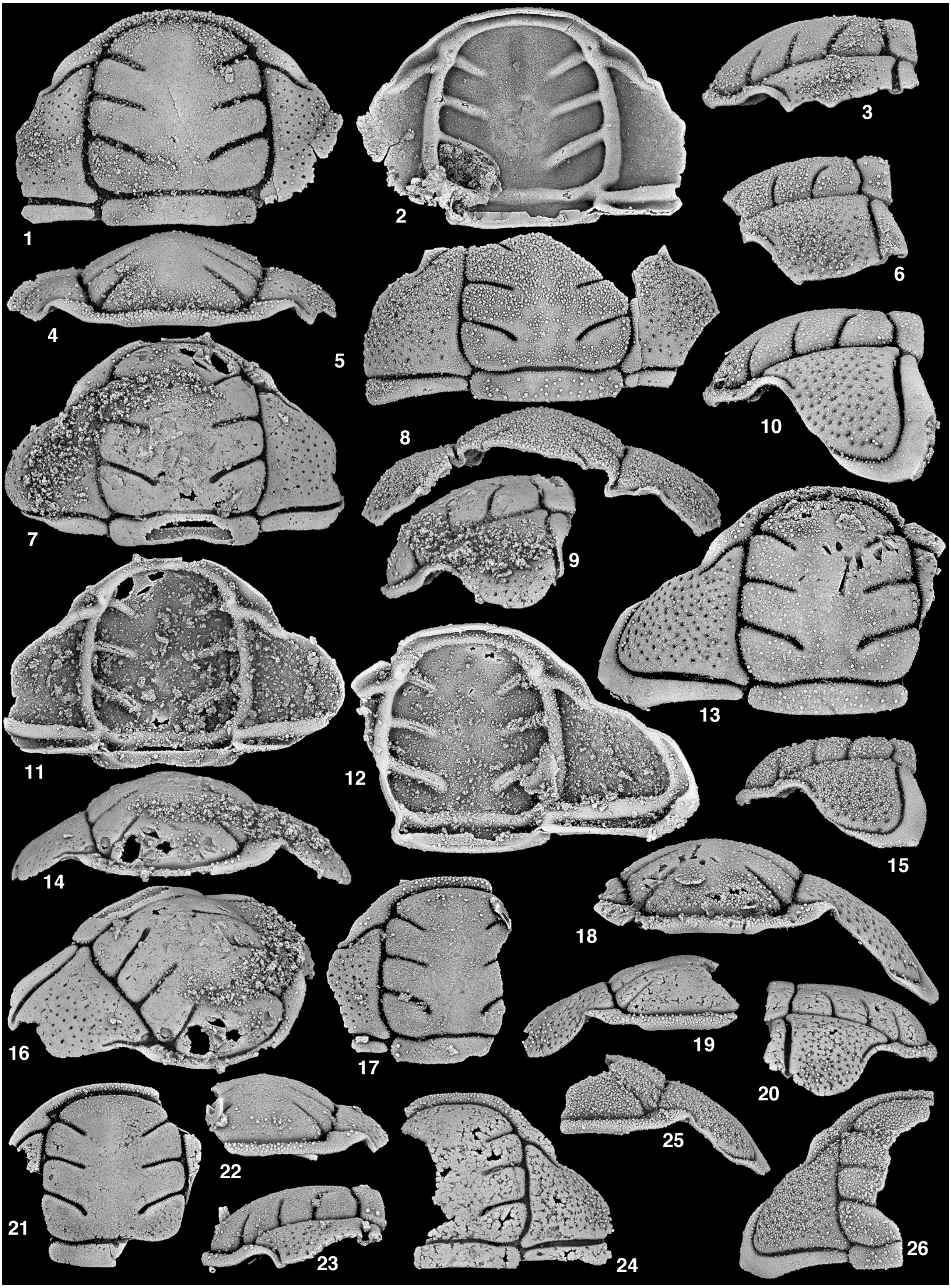

PLATE 13

PLATE 13. *Tesselacauda kriegerae* **n. sp.**, from Section G 26.6 m and Section C 111.6 m, both Fillmore Formation (upper Tremadocian; Stairsian; *Bearriverops alsacharovi* Zone), Ibex area, Millard County, western Utah, USA.

1–4. Cranidium, SUI 147595, dorsal, ventral, left lateral, and anterior views, x6 (G 26.6 m).
5, 6, 8. Cranidium, SUI 147596, dorsal, left lateral, and anterior views, x6 (G 26.6 m).
7, 9, 11, 14, 16. Cranidium, SUI 134173, dorsal, left lateral, ventral, anterior, and oblique views, x7.5 (G 26.6 m).
10, 12, 13, 18. Cranidium, **holotype**, SUI 147597, left lateral, ventral, dorsal, and anterior views, x6 (C 111.6 m).
15, 25, 26. Cranidium, SUI 147598, left lateral, anterior, and dorsal views, x6 (G 26.6 m).
17, 22, 23. Cranidium, SUI 147599, dorsal, anterior, and left lateral views, x8 (C 111.6 m).
19, 20, 24. Cranidium, SUI 147600, anterior, right lateral, and dorsal views, x6 (G 26.6 m).
21. Cranidium, SUI 147601, dorsal view, x6 (C 111.6 m).

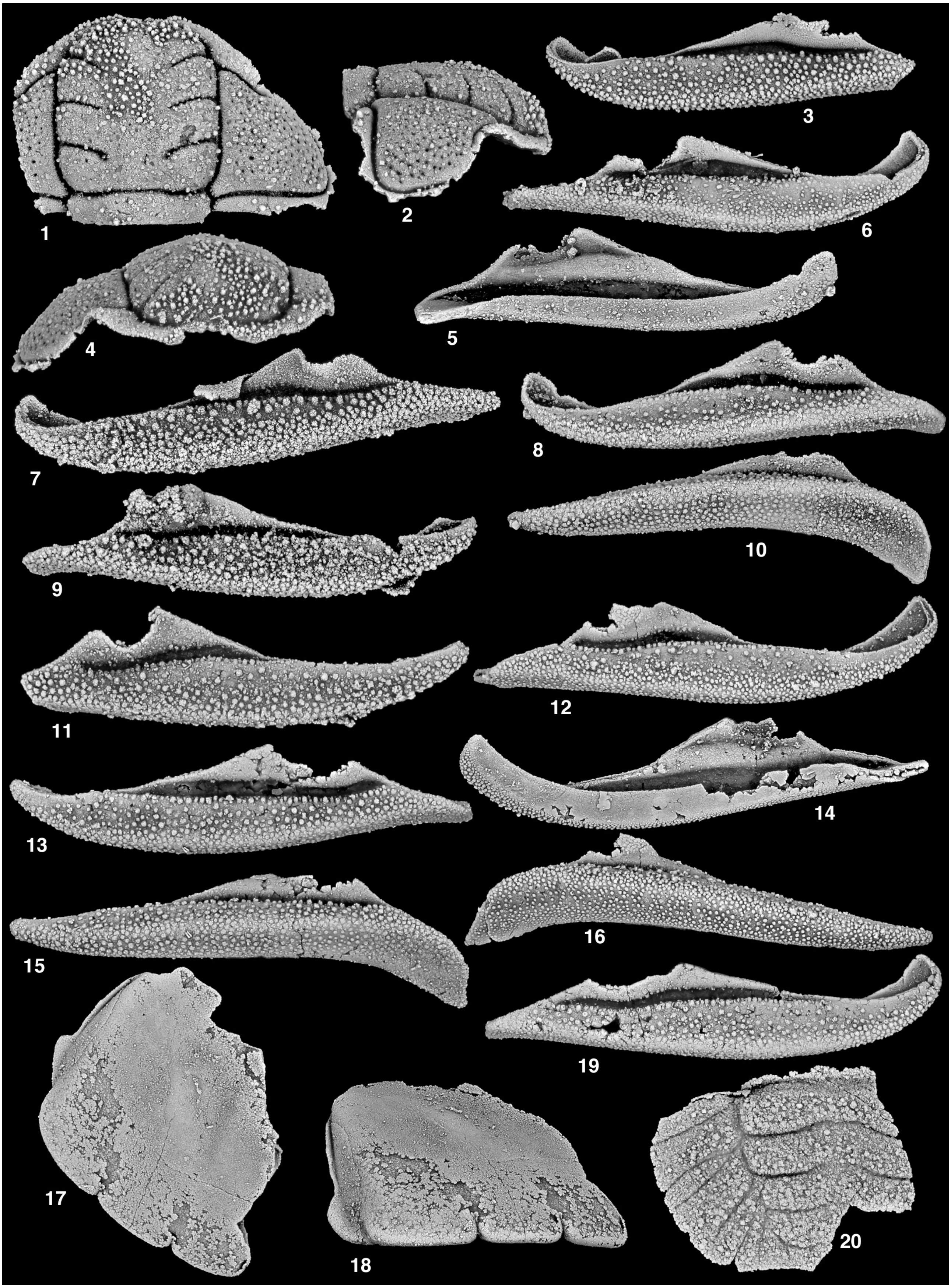

PLATE 14

PLATE 14.
1–16, 19. *Tesselacauda kriegerae* **n. sp.**, from Section G 26.6–27.0 m and Section C 111.6 m, both Fillmore Formation (upper Tremadocian; Stairsian; *Bearriverops alsacharovi* Zone), Ibex area, Millard County, western Utah, USA.

1, 2, 4. Cranidium, SUI 147602, dorsal, right lateral, and anterior views, x17 (G 27.0 m).
3. Right librigena, SUI 147603, external view, x15 (G 26.6 m).
5, 8, 10. Right librigena, SUI 147604, internal, external, and ventrolateral views, x12 (G 26.6 m).
6. Left librigena, SUI 147605, external view, x12 (G 26.6 m).
7. Right librigena, SUI 147606, external view, x15 (C 111.6 m).
9. Left librigena, SUI 147607, external view, x15 (G 26.6 m).
11. Left librigena, SUI 147608, external view, x15 (G 26.6 m).
12, 14, 16. Left librigena, SUI 147609, external, internal, and ventrolateral views, x12 (G 26.6 m).
13, 15. Right librigena, SUI 147610, external and ventrolateral views, x15 (G 26.6 m).
19. Left librigena, SUI 147611, external view, x12 (G 26.6 m).

17, 18, 20. *Tesselacauda*? *flabella* Kobayashi, 1955, from Section G 26.6 m, Fillmore Formation (upper Tremadocian; Stairsian; *Bearriverops alsacharovi* Zone), Ibex area, Millard County, western Utah, USA.

17, 18. Pygidium, SUI 147612, dorsal and left lateral views, x6.
20. Pygidium, SUI 147613, dorsal view, x12.

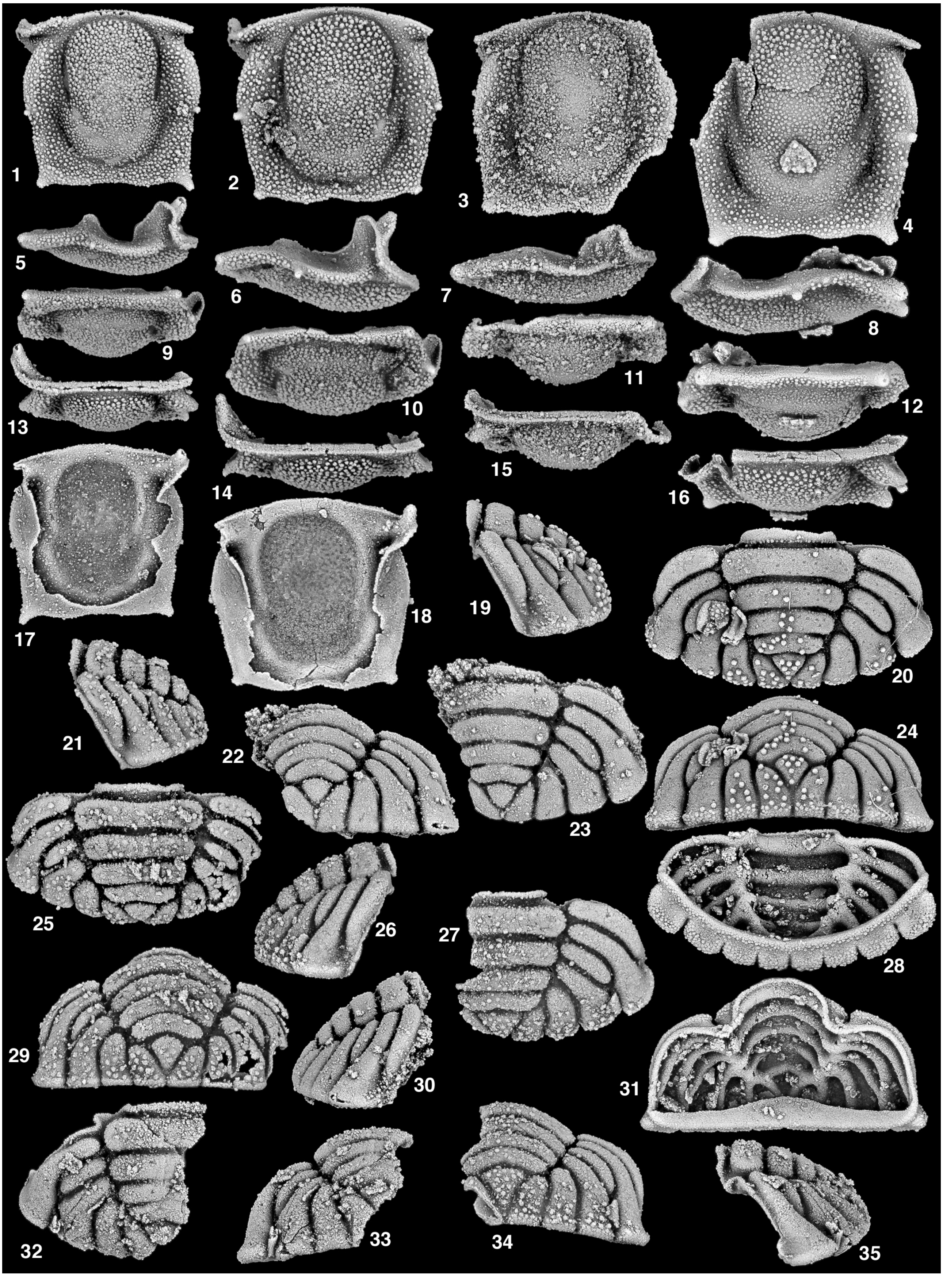
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PLATE 15

PLATE 15. *Tesselacauda kriegerae* **n. sp.**, from Section G 26.6–27.0 m and Section C 111.6 m, both Fillmore Formation (upper Tremadocian; Stairsian; *Bearriverops alsacharovi* Zone), Ibex area, Millard County, western Utah, USA.

1, 5, 9, 13, 17. Hypostome, SUI 147614, ventral, right lateral, posterior, anterior, and dorsal views, x12 (G 26.6 m).
2, 6, 10, 14, 18. Hypostome, SUI 147615, ventral, right lateral, posterior, anterior, and dorsal views, x15 (G 26.6 m).
3, 7, 11, 15. Hypostome, SUI 147616, ventral, right lateral, posterior, and anterior views, x10 (G 26.6 m).
4, 8, 12, 16. Hypostome, SUI 147617, ventral, left lateral, posterior, and anterior views, x15 (C 111.6 m).
19, 20, 24, 28, 31. Pygidium, SUI 147618, left lateral, dorsal, posterior, ventral, and anterior views, x10 (C 111.6 m).
21, 25, 29. Pygidium, SUI 147619, left lateral, dorsal, and posterior views, x10 (G 27.0 m).
22, 23, 30. Pygidium, SUI 147620, posterior, dorsal, and right lateral views, x12 (C 111.6 m).
26, 27, 34. Pygidium, SUI 147621, right lateral, dorsal, and posterior views, x10 (G 27.0 m).
32, 33, 35. Pygidium, SUI 147622, dorsal, posterior, and left lateral views, x10 (C 111.6 m).

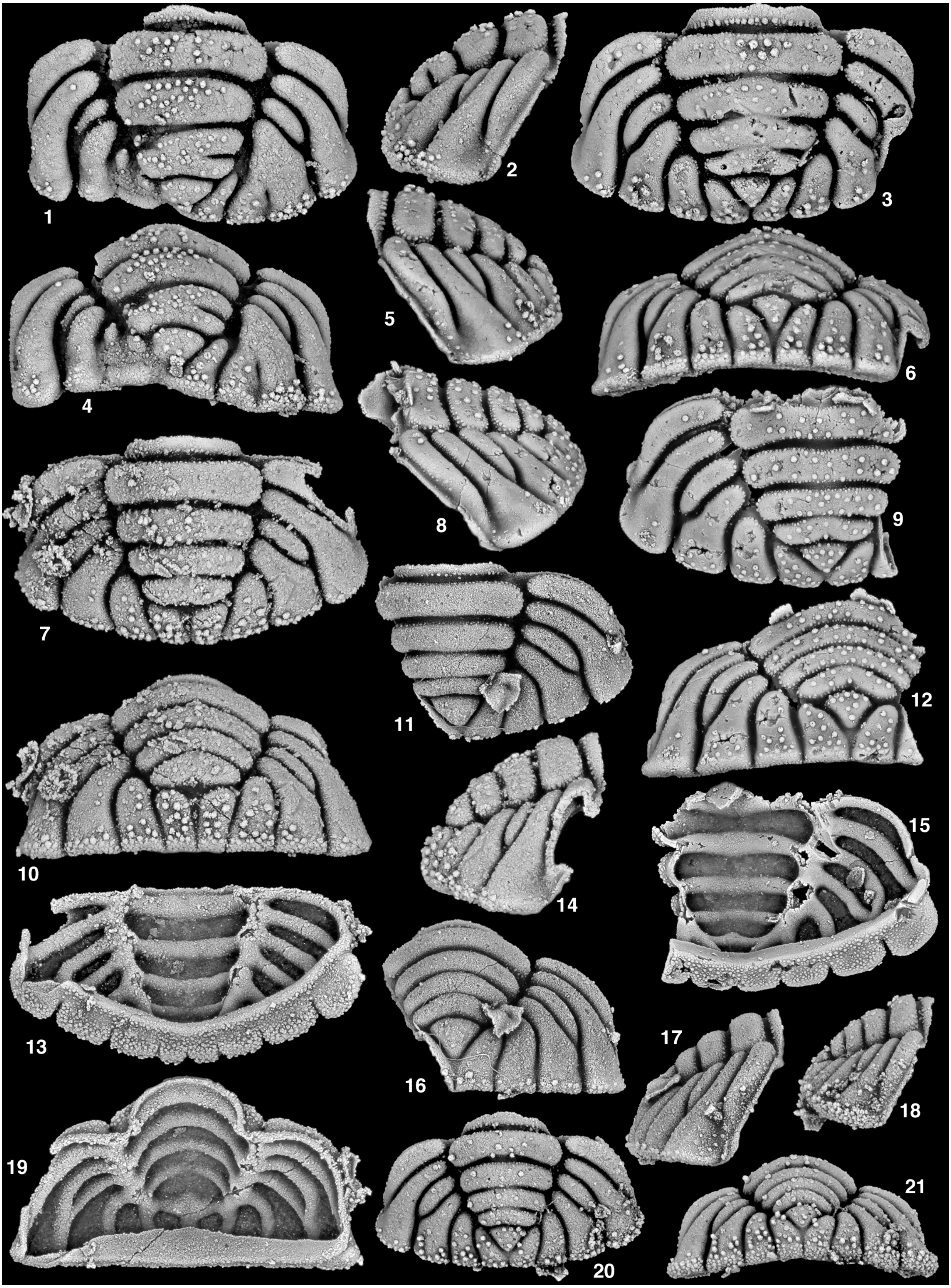

PLATE 16

PLATE 16. *Tesselacauda kriegerae* **n. sp.**, from Section G 26.6–27.0 m, Fillmore Formation (upper Tremadocian; Stairsian; *Bearriverops alsacharovi* Zone), Ibex area, Millard County, western Utah, USA.

1, 2, 4. Pygidium, SUI 147623, dorsal, right lateral, and posterior views, x15 (G 26.6 m).
3, 5, 6. Pygidium, SUI 134174, dorsal, left lateral, and posterior views, x14 (G 26.6 m).
7, 10, 13, 14, 19. Pygidium, SUI 147624, dorsal, posterior, right lateral, ventral, and anterior views, x14 (G 26.6 m).
8, 9, 12, 15. Pygidium, SUI 147625, left lateral, dorsal, posterior, and ventral views, x12 (G 26.6 m).
11, 16, 17. Pygidium, SUI 147626, dorsal, posterior, and right lateral views, x15 (G 27.0 m).
18, 20, 21. Pygidium, SUI 147627, right lateral dorsal, and posterior views, x15 (G 26.6 m).

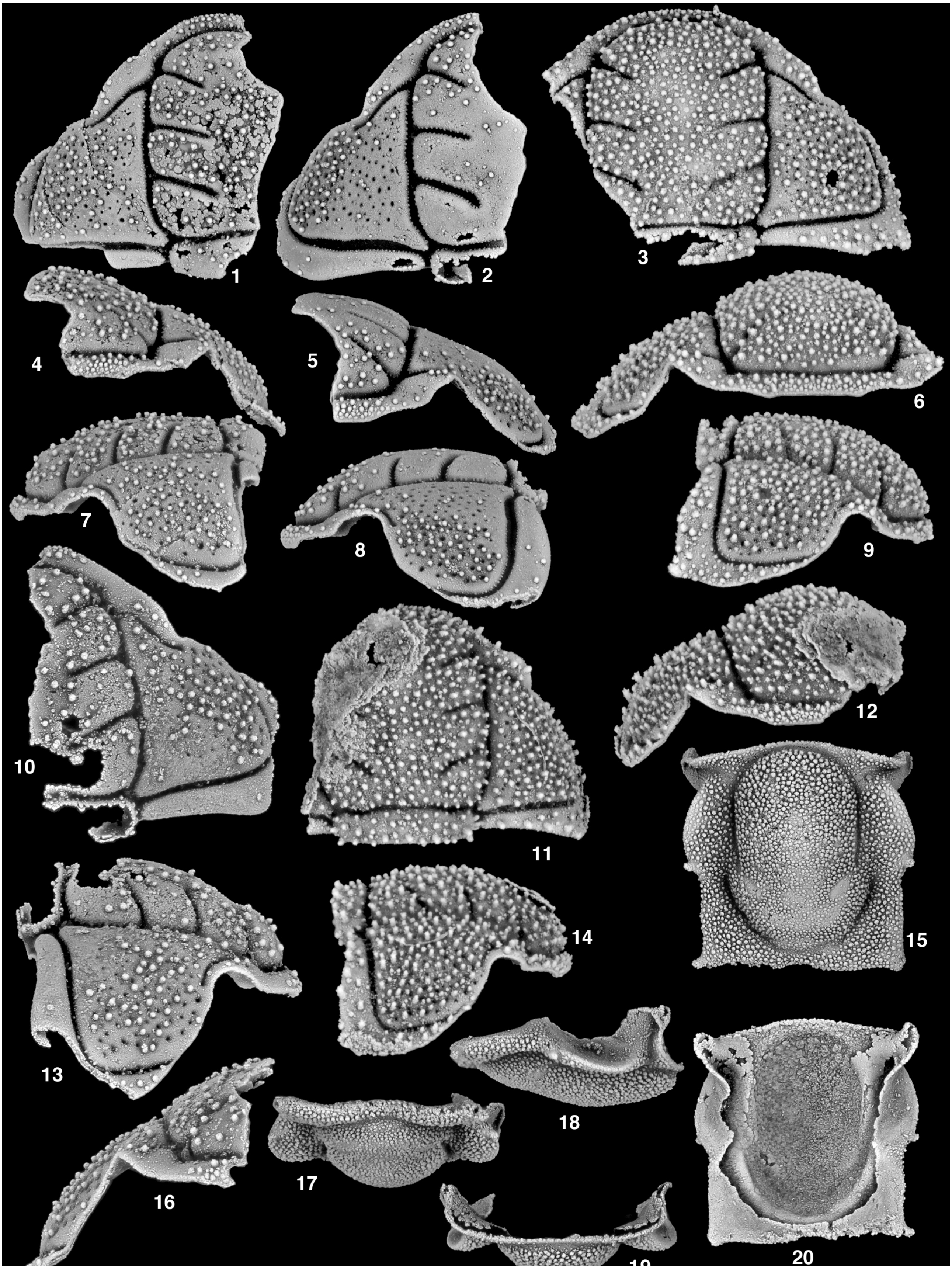

PLATE 17

PLATE 17. *Tesselacauda kriegerae* **n. sp.**, from Section HC6 122.5–124.0 m, Garden City Formation (upper Tremadocian; Stairsian; *Bearriverops alsacharovi* Zone), west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA.

1, 4, 7. Cranidium, SUI 147628, dorsal, anterior, and left lateral views, x15 (HC6 122.5 m).
2, 5, 8. Cranidium, SUI 147629, dorsal, anterior, and left lateral views, x15 (HC6 124.0 m).
3, 6, 9. Cranidium, SUI 147630, dorsal, anterior, and right lateral views, x20 (HC6 124.0 m).
10, 13, 16. Cranidium, SUI 147631, dorsal, right lateral, and anterior views, x20 (HC6 124.0 m).
11, 12, 14. Cranidium, SUI 147632, dorsal, anterior, and right lateral views, x20 (HC6 124.0 m).
15, 17–20. Hypostome, SUI 147633, ventral, posterior, right lateral, anterior, and dorsal views, x15 (HC6 122.5 m).

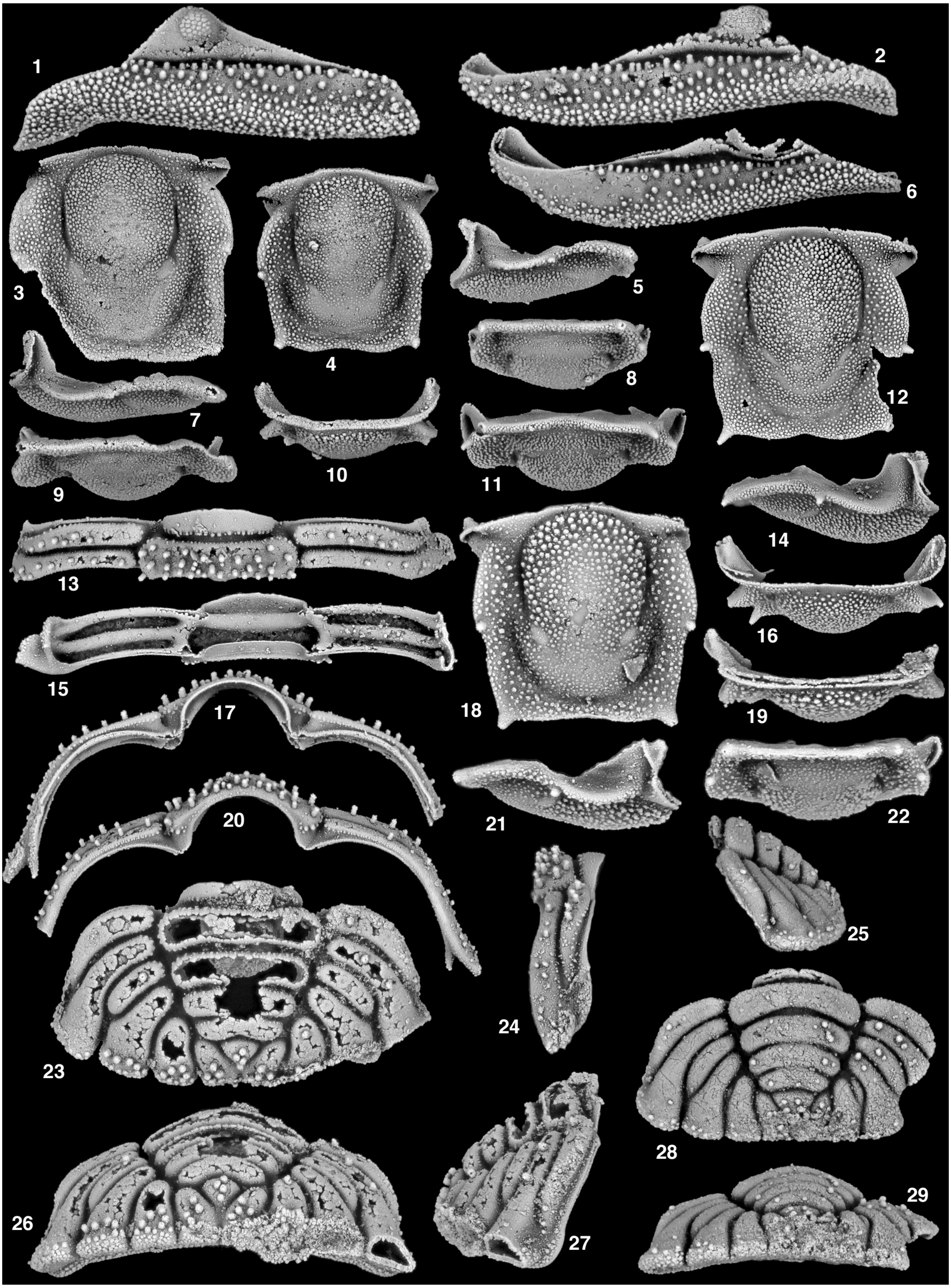

PLATE 18

PLATE 18. *Tesselacauda kriegerae* **n. sp.**, from Section HC6 122.5–124.0 m, Garden City Formation (upper Tremadocian; Stairsian; *Bearriverops alsacharovi* Zone), west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA.

1. Left librigena, SUI 147634, external view, x20 (HC6 124.0 m).
2. Right librigena, SUI 147635, external view, x20 (HC6 124.0 m).
3, 7, 9. Hypostome, SUI 147636, ventral, left lateral, and posterior views, x12 (HC6 124.0 m).
4, 5, 8, 10. Hypostome, SUI 147637, ventral, left lateral, posterior, and anterior views, x15 (HC6 124.0 m).
6. Right librigena, SUI 147638, external view, x15 (HC6 124.0 m).
11, 12, 14, 16. Hypostome, SUI 147639, posterior, ventral, right lateral, and anterior views, x12 (HC6 124.0 m).
13, 15, 17, 20, 24. Thoracic segment, SUI 147640, dorsal, ventral, anterior, posterior, and right lateral views, x15 (HC6 124.0 m).
18, 19, 21, 22. Hypostome, SUI 147641, ventral, anterior, right lateral, and posterior views, x25 (HC6 124.0 m).
23, 26, 27. Pygidium, SUI 147642, dorsal, posterior, and right lateral views, x15 (HC6 122.5 m).
25, 28, 29. Pygidium, SUI 147643, left lateral, dorsal, and posterior views, x20 (HC6 122.5 m).