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Atlanticalymene, a new genus of Middle Ordovician (Darriwilian) calymenine trilobites, and revision of the calymenoidean genus *Protocalymene* Ross

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Table of contents

Abstract

Middle Ordovician (Darriwilian) species representing early Laurentian occurrences of the Subfamily Calymeninae Milne Edwards, 1840 (=Flexicalymeninae Siveter, 1977) are assigned to *Atlanticalymene* n. gen. (type species: *A. bardensis* **n. sp.** from the Table Cove Formation, western Newfoundland, Canada). They have routinely been confused with the older (Dapingian) calymenoidean taxon *Protocalymene* Ross, 1967. Revision of the type species of *Protocalymene*, *P. mcallisteri* Ross, 1967, from the Antelope Valley Formation, Funeral Mountains, California, indicates that it is not a calymenine, and that while it is clearly a calymenoidean its close affinity is otherwise difficult to determine. A single genuine calymenine species is known from the Laurentian Dapingian, and revised here as "Calymeninae **n. gen.**? **n. sp.** A" from the Antelope Valley Formation, Nevada, USA. A species from the Dapingian of Tarim, known from a single partial cranidium, appears to represent an older, extra-Laurentian species of *Atlanticalymene*.

Key words: Trilobita, silicified, Newfoundland, California, Laurentia, taxonomy

Introduction

The earliest occurrences of calymenoidean trilobites on the Laurentian paleocontinent have been poorly known

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and their taxonomy has been confused. Adrain (2013, pp. 309–310) reviewed the family-group classification of the Suborder Calymenina Swinnerton, 1915 (functionally equivalent to a Superfamily Calymenoidea Milne Edwards, 1840, as no other superfamilies are recognized). Three families were assigned with confidence (Calymenidae Milne Edwards, 1840, Homalonotidae Chapman, 1890, Pharostomatidae Hupé, 1953a [often regarded as ingroup Calymenidae]), and two (Bavarillidae Sdzuy, 1957; Bathycheilidae Přibyl, 1953) were regarded as of less certain affinity. The earliest known Laurentian calymenoideans are from the Middle Ordovician and are considered herein to represent three distinct genera. Two (*Atlanticalymene* n. gen. and an unnamed new genus) are assigned to the calymenid subfamily Calymeninae Milne Edwards, 1840 (=Flexicalymeninae Siveter, 1977; see below) and the third, *Protocalymene* Ross, 1967, is of uncertain family affinity.

Calymenines are well represented in Laurentian Upper Ordovician rocks, with species belonging to five genera recognized from the Sandbian Stage and over 30 named species occurring in the Katian. No Lower Ordovician calymenoidean species are known, and only two formally named Middle Ordovician species have been proposed: *Protocalymene mcallisteri* Ross, 1967, from the Dapingian Antelope Valley Formation in California (family affinity regarded as uncertain herein), and the calymenine *Platycalymene trapezoidalis* (Baldis and Pöthe de Baldis, 1995) (see Edgecombe *et al.*, 1998, p. 679, figs 2.1–2.31, 3.1–3.20, 4.1–4.6, 4.9–4.11, 4.13–4.17, 4.19–4.21; Waisfeld and Vaccari, 2003, p. 302, pl. 4, figs 13–21) from the Darriwilian Las Aguaditas Formation of the Laurentian-affinity Precordillera Terrane, San Juan Province, Argentina. This is in stark contrast with Gondwanaland, where members of all three calymenid subfamilies (Calymeninae, Colpocoryphinae Hupé, 1955, Reedocalymeninae Hupé, 1955) are present and collectively known from several dozen species in the Floian.

The purpose of the present work is to review most of the poorly known Middle Ordovician Laurentian taxa and to clarify their taxonomy with the aid of abundant new silicified collections of two of the species in question. In particular, the goals of this work are: 1) to revise *Protocalymene mcallisteri* Ross, 1967, on the basis of new collections of topotype material; 2) to describe a species from the Table Cove Formation, Newfoundland, previously reported in open nomenclature and often assigned to *Protocalymene*, as *Atlanticalymene bardensis* **n. gen. n. sp.**; 3) to clarify the affinity of other Laurentian species reported in open nomenclature and previously assigned to *Protocalymene*; and 4) to consider the affinities of *Protocalymene* and *Atlanticalymene*.

History of study

While only a handful of previously illustrated specimens are involved, the history of opinion on the species revised herein as *Atlanticalymene* and *Protocalymene* is complex. In essence, Middle Ordovician Laurentian species regarded herein as unambiguous calymenines and assigned to *Atlanticalymene* have been assigned in the past to *Calymenidius* Rasetti, 1944 (uppermost Cambrian of Laurentia; affinities uncertain but likely not calymenoidean), *Protocalymene* Ross, 1967 (Dapingian of Laurentia; certainly calymenoidean but otherwise of uncertain affinity), *Calymenia* Kolobova, 1978 (Sandbian or lower Katian, South Tien-Shan, Uzbekistan; also known from the lower Katian of Sardinia and assigned by recent consensus to Bathycheilidae Přibyl, 1953 [Hammann and Leone, 1997]), and the calymenine *Sthenarocalymene* Siveter, 1977 (see Adrain and Fortey, 1997, p. 105). With the description herein of one of the key species on the basis of abundant silicified material, the revision of most of the other questionable species, and the revision of the type species of *Protocalymene*, none of these assignments are any longer relevant, but they are reviewed below.

Upper Cambrian *Calymenidius* species. The earliest species from Laurentia that have been regarded as at least possible calymenids are latest Cambrian taxa from eastern Canada that have been assigned to the genus *Calymenidius*. Whittington (1966, p. 705, text-fig. 12) regarded *Calymenidius* as a "presumed ancestral form" of Calymenidae (Chatterton, 1971, p. 84). The type species, *C. tuberculatus* Rasetti, 1944 (p. 241, pl. 36, fig. 54), is known from one cranidium from the Lévis Conglomerate, southern Quebec (reillustrated by Ludvigsen and Westrop in Ludvigsen *et al*. [1989, pl. 50, fig. 27]). This specimen is strikingly calymenid-like and is at least superficially similar to *Atlanticalymene bardensis*, described herein, in its tuberculate sculpture, broad interocular fixigenae traversed by prominent eye ridges, and widely splayed posterior projections. However, like other specimens assigned to *Calymenidius*, it seems to have a conventional anterior border and glabellar furrows which, while deep, incise the glabella in standard fashion, without marked independent inflation of the glabellar lobes. Fortey (1983, p. 208, pl. 23, fig. 8) described *Calymenidius* sp. A from a single cranidium from the Stearing Island Member, Shallow

Bay Formation, Broom Point North, western Newfoundland. This specimen is perhaps even more like cranidia of *A. bardensis* in its nearly parallel sided glabella and relatively small, nearly isolated L1, but as Fortey pointed out the specimen is largely missing its anterior border and is mostly exfoliated, hampering comparison. Ludvigsen and Westrop (in Ludvigsen *et al*. [1989, p. 48, pl. 36, figs 22–24] illustrated two more cranidia from the Shallow Bay Formation which they interpreted as conspecific with Fortey's, and named the species *Heterocaryon forteyi*, assigning it to the "Family Entomaspidae Ulrich in Bridge, 1931". Adrain and Westrop (2006, pp. 1157–1158) considered that the species did not represent an entomaspidid and its affinities are unclear; species assigned to *Calymenidius* remain the closest morphological comparisons. Ludvigsen and Westrop's cranidia have intact anterior borders, and again these do not appear to show the sectoral calymenid morphology. Ludvigsen and Westrop (in Ludvigsen *et al*. [1989, p. 63, pl. 44, figs 19–22]) named *C. acutus* on the basis of three cranidia from various localities in the Shallow Bay Formation, western Newfoundland. Subsequently, Westrop (1995, p. 36, pl. 15, figs 23, 24) assigned two cranidia from the Rabbitkettle Formation of the Northwest Territories. This species is quite unlike others assigned to *Calymenidius*, as it has narrow interocular fixigenae, a very short preglabellar field, a prominent conventional anterior border, and equally prominent S1 and S2. Its affinities are presently indeterminate. Finally, Ludvigsen and Westrop (in Ludvigsen *et al*. [1989, p. 63, pl. 50, fig. 26]) described *Calymenidius* cf. *C. tuberculatus* based on a cranidium from the Shallow Bay Formation, Hickey Cove, western Newfoundland. It is more coarsely tuberculate, has a longer preglabellar field, and much narrower posterior projections than the unique holotype of *C. tuberculatus*, but is otherwise similar. It is extremely difficult to evaluate these species as they are known only from limited a number of cranidia, all of which are at least partially exfoliated. At this point there seems no compelling reason to consider them calymenoideans, as apart from some general dimensions they show no definite calymenoidean apomorphies. If they were calymenoideans, it would indicate an unsampled ghost lineage spanning the entire Early Ordovician in Laurentia, or multiple dispersal events.

Middle Ordovician taxa—period of assignment to *Calymenidius*. Whittington (1963, p. 50, pl. 6, figs 13–15) was first to illustrate a Laurentian Middle Ordovician calymenine, though he did not recognize it as such. He assigned the specimen, a cephalon with associated partial thorax from the Bed 14 megaconglomerate of the Shallow Bay Formation at Lower Head, western Newfoundland (revised below as *Atlanticalymene* **n. sp.** A) to "? *Ischyrophyma* sp. ind.". *Ischyrophyma* Whittington, 1963, is a junior subjective synonym of the raymondinid *Celmus* Angelin, 1854 (see Adrain and Fortey, 1997). Whittington (1965, p. 419, pl. 59, figs 10, 12, 13–15) then described two cranidia from the "Middle Table Head Formation" (now the Table Cove Formation) at Table Cove, western Newfoundland, as "aff. *Calymenidius* sp. ind." He also firmly assigned *Calymenidius* to Calymenidae. Several subsequent commentators followed the assignment of this species to *Calymenidius*, albeit sometimes with question (e.g., Fortey [1983, p. 208], Bruton *et al*. [2004, p. 129]). Adrain and Fortey (1997, p. 105) were first to point out that "? *Ischyrophyma* sp. ind." of Whittington (1963) and "aff. *Calymenidius* sp. ind." of Whittington (1965) were closely related and definitely calymenine, suggesting an assignment to *Sthenarocalymene* (an opinion revised herein; they are assigned to *Atlanticalymene* below).

Middle Ordovician taxa—period of assignment to *Protocalymene*. Ross (1967, p. D27) proposed *Protocalymene* with type species *P. mcallisteri* from the Antelope Valley Formation (likely Dapingian; see below) of eastern California. He assigned Whittington's (1965) "aff. *Calymenidius* sp. ind." from the Table Cove Formation to his new genus as the only other known species. Ross did not list higher taxonomic headings in his paper, but the main comparison he made of his new genus was with the reedocalymenine calymenid *Neseuretus* Hicks, 1873. Ross (1970, p. 92, pl. 18, figs 2–5) assigned specimens from Nevada to "*Protocalymene* sp." and considered that the species was "clearly congeneric" with Whittington's Table Cove specimens. Fortey (1990, p. 568) followed Ross in assigning Whittington's (1965) Table Cove Formation species to *Protocalymene*, which he unambiguously stated was a calymenid. Similarly, Fortey and Droser (1999, p. 199) suggested that Whittington's species was related to a species from Nevada they described as "*Protocalymene* new species A" (revised below as "Calymeninae **n. gen. n. sp.**").

Suggested relationships with *Calymenia*. Kolobova (1978) proposed *Calymenia* with type species *C. whittingtoni* from the Sandbian or lower Katian Obikalon Member, Šahriomon Formation, Zerafshan Range, South Tien Shan, Uzbekistan. The type material consists of distorted internal molds of three articulated individuals, a pygidium with an attached segment, and a cranidium. While clearly calymenoidean, the poor preservation makes interpretation difficult. Nevertheless, Kolobova assigned Whittington's "aff. *Calymenidius*" from the Table Cove Formation to her new species. Hammann and Leone (1997, p. 127, pl. 31, fig. 1) assigned a cranidium from the lower Katian

of the Portixeddu Formation, Sardinia, to *C. whittingtoni*. This is not implausible as there are several other closely similar taxa in the assemblages, but the state of preservation of Kolobova's type material makes confident species assignment impossible.

Hammann (1983) regarded *Calymenia* as a calymenoidean but considered its family affinity uncertain. Hammann and Leone (1997) assigned the taxon to Bathycheilidae Přibyl, 1953, and this was followed by Jell and Adrain (2003). While Shaw and Bolton (2011, p. 417) cited the classification of the Table Cove species as *Calymenia*, there is no basis for Kolobova's assignment in light of the description of *A. bardensis* herein.

Zhou and Zhou (2008, p. 218) considered *Ningnanaspis* Sheng, 1974, to be a junior subjective synonym of *Calymenia*. This is possible, but the available material of either taxon makes confident evaluation difficult. Sheng (1974, pl. 5, figs 11–13) described *Ningnanaspis* as an odontopleurid, and his type species, *N. ningnanensis* from the Darriwilian of southeastern Sichuan, China, was based on a tiny photograph of an apparently calymenoidean holotype cranidium, poorly preserved as an internal mold, and misassociated with two illustrated cheirurine pygidia. Subsequently Li (1978, p. 283, pl. 109, figs 6, 7) assigned a calymenoidean cephalon and a cheirurine pygidium to the type species, and proposed *N. subquadrata* on the basis of a single cranidium. The latter species may represent the pharostomatid *Thulincola* Tripp, 1962. Based on the published record, *Ningnanaspis* seems essentially uninterpretable.

Localities

Newfoundland. The Table Head Formation of western Newfoundland, Canada (Fig. 1) was formalized by Whittington and Kindle (1963) following original work by Schuchert and Dunbar (1934). These authors recognized three informal divisions, which Whittington and Kindle termed "lower", "middle", and "upper" Table Head. Klappa *et al*. (1980) elevated the unit to group rank, and named the three divisions as the Table Point Formation, Table Cove Formation, and Black Cove Formation, respectively. They also included within the group rocks overlying the Black Cove Formation, as their new Cape Cormorant Formation. Stenzel *et al*. (1990) revised the stratigraphy of the group, maintaining the Table Point Formation and Table Cove Formation, but excluding the Black Cove Formation from the group and restricting the Cape Cormorant Formation.

The Table Cove Formation consists of thin, nodular to ribbon bedded, dark, argillaceous, often bioclastic, lime mudstones interbedded with calcareous shales. It was deposited in a deep subtidal slope environment. The unit is precisely dated via conodonts (Stouge, 1984) as *Eoplacognathus suecicus* Zone and via graptolites as Maletz *et al*.'s (2011) *Holmograptus spinosus* Zone. Both are firmly indicative of a mid-Darriwilian age.

The Table Cove Formation contains rich trilobite faunas. Whittington (1965) described many taxa based on collections made at Table Point and Table Cove on the west coast of the Great Northern Peninsula. Here the trilobites are calcareous and were sampled using standard mechanical crackout methods. In the Hare Bay region on the northeast coast of the peninsula, silicified trilobites have been discovered at several localities. While the faunas share many species with those described by Whittington (1965), there are also many new taxa, and some species which were rare in Whittington's collections are common in the silicified samples. While there may be a biogeographic or environmental component to the differences between the collections, much of it is probably a reflection of mechanical sampling bias in the material studied by Whittington, as many of the new taxa are small, tuberculate, and/or spiny. Sclerites of this type are difficult to retrieve via mechanical sampling, as the rock tends not to break around them and their cuticle tends to adhere to the matrix.

Material described herein was obtained from a short section (Fig. 2) on the coast north of the town of Main Brook (Fig. 1.2). The section, termed TCM (Table Cove—Marechal), lies on a small spit of land opposite Marechal Island. The beds are steeply dipping, the erosional land surface is nearly flat, and strike is nearly parallel with the shoreline along the spit. The upper part of the section (above 6.5 m) is exposed only during low tide. Trilobites are very common in nodular lenses in the lower part of the section (around 2 m, not described herein), in ribbon limestones from 7.5 m upward (including sample TCM 14 herein), and especially in a thicker bioclastic bed, interpreted as a debris flow, at about 8.8 m (sample TCM 18). All are silicified, and preservation is good to excellent. The trilobite collections of all of the horizons from which material is described herein appear to share the same species, albeit in varying relative abundances.

California. Ross (1967) described trilobites from a silicified fauna collected from the Antelope Valley Forma-

tion on the west side of the Funeral Mountains, Inyo County, California. The locality, which now lies within Death Valley National Park, was relocated in 2012 and found to comprise a narrow (2–3 m) interval of recessive thin-bedded limestone that weathers to form a small saddle on an east-west trending spur on the west flank of the range. There are no age data available from other fossil groups for the Funeral Mountains fauna, so estimation of age must be based on the known genus ranges of the constituent taxa. A few of these (*Illaenus* Dalman, 1827, *Nileus* Dalman, 1827, *Raymondaspis* Přibyl in Prantl and Přibyl, 1949) are broadly conceived, morphologically conservative, species rich, and span much of the Ordovician. The closest comparison of *I. auriculatus* Ross, 1967, however, is *I.* cf. *auriculatus* of Fortey and Droser (1999, p. 192) from the Dapingian of the Antelope Valley Formation, Nevada. Fortey and Droser (1999, p. 193) also identified material of *Nileus* from the Dapingian of the Antelope Valley Formation as *N. hesperaffinis* Ross, 1967. This assignment is questionable and will be addressed when *N. hesperaffinis* is revised in a forthcoming work. However once again a very close morphological comparison is of unambiguous Dapingian age. Loch and Ethington (2017) described lower Dapingian trilobites from the Antelope Valley Formation at Whiterock Canyon Narrows, Monitor Range, Nye County, Nevada. While no species are definitely shared with the Funeral Mountains fauna, they again made multiple direct comparisons of their taxa with those described by Ross (e.g., *Raymondaspis* cf. *R. vespertina* Ross, 1967; *Protocalymene* sp.; *Illaenus* cf. *I. auriculatus* Ross, 1967 [which they mistakenly listed as 1972]; *Ampyx* cf. *A. compactus* Ross, 1967; *Nileus* cf. *N. hesperaffinis* Ross, 1967). Hence, while it must be confirmed with independent biostratigraphic data, a Dapingian age of the Funeral Mountains fauna seems very likely and is assumed herein.

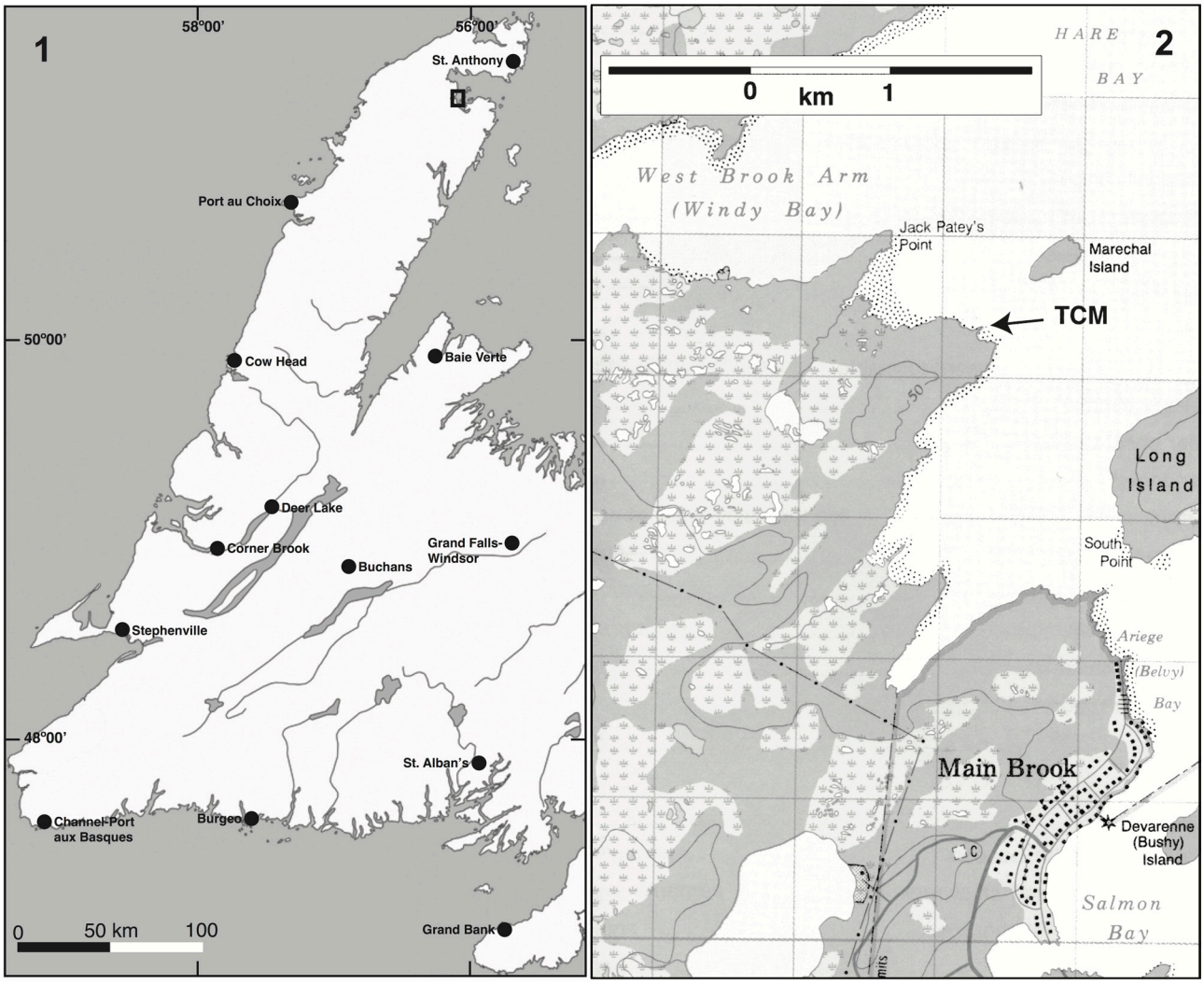

FIGURE 1. 1. Map of western Newfoundland, Canada. Position of detailed map of Fig. 1.2 is shown as small inset square. 2. Location of section TCM on coast north of town of Main Brook, Hare Bay, Great Northern Peninsula, western Newfoundland, Canada.

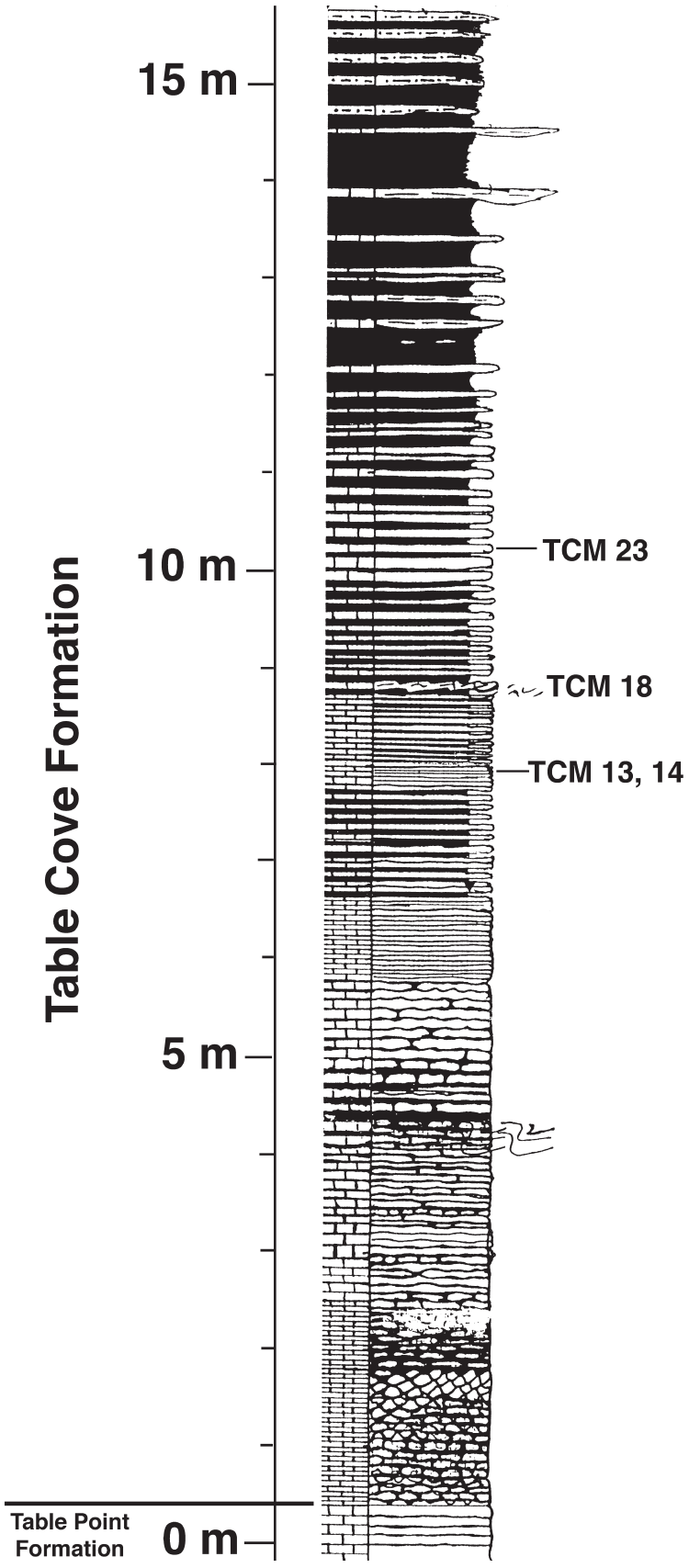

FIGURE 2. Stratigraphic column of Table Cove Formation at Section TCM, near Marechal Island, Hare Bay, Great Northern Peninsula, western Newfoundland (see Fig. 1 for exact geographic position). Horizons from which material is illustrated are shown. Light colored lithologies are limestones; dark interbeds are calcareous shales. Wavy symbols next to the column indicate beds that are debris flows.

Systematics

Repository. All material of *Atlanticalymene bardensis* **n. sp.** and *Atlanticalymene* **n. sp.** A is housed in the collections of the Geological Survey of Canada, Ottawa, with specimen number prefix GSC. Material of Calymeninae **n. gen. n. sp.** is housed in the Smithsonian Institution, Washington, DC, with specimen number prefix USNM. New material of *Protocalymene mcallisteri* is housed in the Paleontology Repository, Department of Earth and Environmental Sciences, University of Iowa, Iowa City, Iowa, with specimen number prefix SUI.

Superfamily Calymenoidea Milne Edwards, 1840

Family Calymenidae Milne Edwards, 1840

Subfamily Calymeninae Milne Edwards, 1840

=Flexicalymeninae Siveter, 1977

Discussion. Siveter (1977) restricted Calymeninae to those taxa with fixigenal buttresses to the glabellar lobes and assigned the remainder of taxa to his new Flexicalymeninae. While it appears likely that Calymeninae as thus restricted is monophyletic (though the concept has never been explored analytically), it is equally apparent that Flexicalymeninae is expressly paraphyletic, a grade left over by removal of Calymeninae. Hence we elect not to formally recognize it and follow Adrain (2013, pp. 309–310) in regarding all of the taxa in question as Calymeninae.

The early history of putative members of the subfamily Calymeninae Milne Edwards, 1840, is sparsely known. Three formally named species are known from the Floian, all from Gondwanan Armorica and assigned to *Platycalymene* Shirley, 1936, by Courtessole *et al*. (1983). No named calymenine species are known from the Dapingian, and nine occur globally in the Darriwilian. The subfamily became increasingly more common thereafter and at least 58 Katian species have been named. No potential Floian calymenines have been reported from Laurentia, but several Dapingian and lower Darriwilian occurrences have been described, though not always recognized as such. These are assigned herein to an unnamed, monotypic, new Dapingian genus and to the Darriwilian *Atlanticalymene* n. gen. (to which a Dapingian species from Tarim is also tentatively assigned).

Atlanticalymene n. gen.

Type species. *Atlanticalymene bardensis* **n. sp.**, from the Darriwilian Table Cove Formation of western Newfoundland, Canada.

Other species. *Atlanticalymene* **n. sp.** A ("? *Ischyrophyma* sp. ind." of Whittington [1963, p. 50, pl. 6, figs. 13-15]), Shallow Bay Formation (lower Darriwilian), Lower Head, western Newfoundland; *Sthenarocalymene* sp. indet. of Zhou *et al*. (2014, p. 114, fig. 56), Yijianfang Formation (Dapingian), Yijianfang, Bachu, northwestern Tarim, Xinjiang, China.

Etymology. From the Atlantic Ocean, on the western edge of which the type locality is situated, and the genus name *Calymene*; gender is feminine.

Diagnosis. Glabella long and parallel-sided anterior to L1; L1 well developed and nearly completely isolated; L2 and L3 scarcely developed, S2 faint and barely discernible, S3 not impressed; cranidial anterior border strongly bowed in anterior view; preglabellar area elongate (sag.; exsag.); eye ridge expressed dorsally; palpebral lobe small; sculpture of small to coarse fairly densely scattered tubercles over all skeletal parts except hypostome.

Discussion. As noted above, a consensus emerged in the recent literature (Fortey, 1990; Fortey and Droser, 1999; Turvey, 2002) that Middle Ordovician Laurentian calymenoidean species should all be assigned to *Protocalymene* and that they are unambiguous calymenids. Revision on the basis of new photographs herein demonstrates that a calymenid affinity is true of only a handful of the occurrences (those assigned by Adrain and Fortey [1997] to *Sthenarocalymene*), and not necessarily true of *Protocalymene mcallisteri*. The various reports break down into two morphological groups: taxa related to Darriwilian material described in open nomenclature by Whittington (1965) and taxa related to *P. mcallisteri*. The former collectively represent *Atlanticalymene* n.gen., whereas the latter, while certainly calymenoidean, are considered below to be of unclear family relationships.

The genus diagnosis is complicated by the fact that there is only one well known species, yet the genus is not monotypic. We have included morphological features of the cranidium that are shared between the known occurrences. Features that are known only from *A. bardensis* are listed in the species diagnosis of that taxon, with the understanding that both diagnoses should potentially be refined if other exoskeletal parts of other species are described.

Zhou *et al*. (2014) assigned a single partial cranidium to the genus *Sthenarocalymene*, following assignment of Whittington's (1965) Table Cove Formation specimens by Adrain and Fortey (1997, p. 105). With description of *A. bardensis* on the basis of abundant silicified material, it no longer appears that assignment to *Sthenarocalymene* is justified. The type species of *Sthenarocalymene*, *S. lirella* Siveter, 1977, is from the Vollen Formation (Sandbian), Oslo-Asker, Norway. The only other reliably assigned species is *S. aldonensis* (Reed, 1935), from the Superstes Formation (Sandbian) of the Laurentian-affinity Midland Valley Terrane, Scotland (see Tripp, 1976, p. 408, pl. 7, figs 8–12). Some workers (following Holloway [1980] and including, e.g., Edgecombe and Wright [2004], and Lin [2008]) have assigned a large number of Silurian and Devonian species, ranging from the Telychian to Emsian, considering *Apocalymene* Chatterton and Campbell, 1980, a junior subjective synonym. The basis for this is little more than that these species, some 27 formally named, are taxa which occur in Silurian and Devonian rocks yet lack glabellar buttresses and share a broadly conserved glabellar outline. Others (e.g., Siveter and Chatterton [1996, p. 57]; Edgecombe [2007, p. 60]) have regarded the question as open. Given the large stratigraphic gap between the earliest "*Apocalymene*" (Telychian species such as the Australian *Gravicalymene*? *vaccina* Holloway, 1994) and the species regarded here as *Sthenarocalymene* (Sandbian), together with the absence of any detailed phylogenetic work on the Siluro-Devonian group, it seems premature at best to assume they together represent a clade and *Sthenarocalymene* is restricted herein to the two species listed above.

Sthenarocalymene lirella is known from an internal mold of an articulated specimen lacking librigenae, an external mold of a cranidium, one well preserved cuticular cranidium, and two internal molds of cranidia. Its similarity to *A. bardensis* is scant. The younger Baltic species has much larger L1, strongly inflated L2 and L3, strongly incised S2 and clearly visible S3, a bell-shaped versus subparallel sided glabella, and narrower interocular fixigenae. While the pygidium is known only from the internal mold example on the articulated specimen (Siveter, 1977, fig. 12C), it is clearly narrower relative to its length, has axial furrows that are more strongly posteriorly convergent, and lacks the slightly bulbous paired swellings at the posterior of the axis characteristic of *A. bardensis*. Apart from both clearly being calymenines, there is little morphologically in common between the taxa and nothing that suggests *A. bardensis* should be assigned to *Sthenarocalymene*. *Sthenarocalymene aldonensis* is known only from poorly preserved molds. While difficult to interpret, the morphology of the available specimens seems to match closely that of the coeval *S. lirella*. One partial external mold of a librigena is known (Tripp, 1976, pl. 7, fig 10), but it is too incomplete to meaningfully compare.

Zhou *et al*.'s (2014, p. 114, fig. 56) "*Sthenarocalymene* sp.," from the Dapingian of Tarim, consists only of a single incomplete cranidium. Its morphology clearly indicates relationship with *A. bardensis*, as Zhou *et al*.'s discussion (2014, p. 115) indicates. In particular, it shares the development of L1 as the only prominent, inflated, glabellar lobe, together with an elongate, parallel-sided glabella. The anterior border is broken off so cannot be compared. The interocular fixigenae of the Tarim specimen are much narrower than those of *A. bardensis*. The specimen is relatively small, and retains expressed juvenile paired fixigenal spines.

Zhou *et al.* (2016, p. 322, fig. 20J, K) described a single partial cranidium from the lower Darriwilian Zhuozishan Formation of Wuhai, Inner Mongolia, as "*Sthenarocalymene* sp. indet." The affinity of this specimen, which consists of an external mold of a glabella, part of an occipital ring, and a small portion of posterior fixigena and posterior border, is difficult to determine. It has strongly inflated L1 and L2, but L1 seems smaller than L2 and laterally contiguous with the glabella, which is unusual for a calymenine. The glabella is also strongly vaulted with the anterior part steeply forwardly sloping. This species does not resemble *A. bardensis*. Because there is so little morphological information there are many possibilities for its affinity. It could conceivably represent a species similar to "Calymeninae **n. gen. n. sp.**" (below), but alternatively it might not represent a calymenine at all.

Atlanticalymene is compared with the Dapingian "Calymeninae **n. gen. n. sp.**" below. *Atlanticalymene bardensis* has little in common with the three Gondwanan Armorican Floian species from the Montagne Noire assigned by Courtessole *et al*. (1983) to *Platycalymene* (*P. (P.) pradesensis* from the La Maurerie Formation and *P. (P.) minervensis* and *P. (P.) villerembertensis* from the St.-Chinian Formation). All are known only from cranidia, which

feature non-isolated L1 and strongly impressed S2 and S3. The interocular fixigenae of *P. (P.) pradesensis* and *P. (P.) villerembertensis* are very narrow and the eye is in a more anterior position than in *A. bardensis*.

Atlanticalymene bardensis n. sp.

Plates 1–7

1965	*Ischyrophyma?* sp. ind.; Whittington, p. 340, pl. 19, figs 16, 19, 20.
1965	Komaspidid? pygidium; Whittington, p. 374, pl. 39, figs 8, 9.
1965	aff. *Calymenidius* sp. ind.; Whittington, p. 419, pl. 59, figs 10, 12–15.
1967	*Protocalymene* sp.; Ross, p. D27.
1970	*Protocalymene* sp.; Ross, p. 92.
1977	*Protocalymene* sp.; Siveter, p. 388.
1990	*Protocalymene* sp.; Fortey, p. 568.
1997	*Sthenarocalymene* sp.; Adrain and Fortey, p. 105.
1999	"aff. *Calymenidius* sp. ind." of Whittington; Fortey and Droser, p. 199.
2002	*Protocalymene* sp.; Turvey, p. 56.
2011	*Calymenia* sp.; Shaw and Bolton, p. 417.
2014	*Sthenarocalymene* sp.; Zhou *et al*., p. 115.
2016	*Sthenarocalymene* sp.; Zhou *et al*., p. 322.

Material. Holotype, cranidium, GSC 135298 (Pl. 2, figs 10, 13–15), and assigned specimens GSC 135289–135297, 135299–135358, from horizons TCM 13, TCM 14, and TCM 18, Table Cove Formation (Darriwilian), coast opposite Marechal Island, near Main Brook, Hare Bay, Great Northern Peninsula, western Newfoundland. Assigned specimens GSC 18345, 18346, 18369, 18569, Table Cove Formation (Darriwilian), Table Cove, west coast of Great Northern Peninsula, western Newfoundland, Canada.

Etymology. From Bard Island Tickle, a local name for the type locality.

Diagnosis. Interocular fixigena very broad; librigena subtriangular in outline, posterior facial suture hardly bowed compared with other calymenine taxa; eye small; rostal plate with gently ventrally curved ventral sector, longer exsagittally than sagittally in plan view, smooth and posteriorly concave doublural sector; hypostome with large anterior wings, lacking rhynchos, and with posteromedian spine in addition to the conventional paired posterolateral spines, posterior border long (sag.; exsag.); thoracic segments with anterior and posterior pleural bands subequal in length (exsag.), tuberculate sculpture on both but more prominent on posterior band; pygidium with four distinct axial rings, fourth not fully defined by ring furrow posteriorly in some specimens; pleural furrow of only the first segment well impressed distal to fulcrum; posterior of axis slightly inflated with a pair of subdued lateral swellings in large specimens; pleural region with faint interpleural furrows and dense fine tuberculate sculpture.

Description. Cranidial measurements are based on the large, intact specimens of Pl. 1, fig. 10, Pl. 2, figs 1, 2, 10, 12, 16, 18, and Pl. 3, figs 1–3, 12. Where part of the cranidial morphology was preserved on only one side, the distance to the sagittal line from this side was doubled. Cranidium strongly vaulted, covered with densely spaced tubercles that are sometimes flattened; maximum cranidial sagittal length 50.6% (47.5–55.3) maximum width across posterior border; width across anterior border furrow 42.1% (39.1–45.4) maximum width across posterior border; distance across γ 66.5% (61.8–70.9) maximum cranidial width; anterior border with length (sag.) 75.9% (62.7–95.5) LO sagittal length, slightly shorter (exsag.) abaxially, forming strongly bowed arch in anterior profile; anterior border flexed upward and back toward anterior tip of glabella, so that it partially obscures border furrow in anterior view, but it does not abut anterior margin of glabella in transverse profile; anterior border with sculpture of small and medium sized, densely spaced somewhat flattened tubercles, tubercles become smaller toward rostral suture; anterior border furrow confluent with preglabellar furrow, long (sag.), with length (sag.) nearly equal to that of anterior border in dorsal view on some specimens, dorsally concave, much deeper and shorter (exsag.) opposite frontal area; anterior sections of facial sutures gently laterally convex opposite anterior border, laterally concave opposite anterior border furrow, and strongly, but unevenly, laterally bowed opposite frontal areas with bow strongest opposite anterolateral corners of glabella; frontal areas strongly inflated, sloped strongly downward and mostly facing anteromedially with exsagittal portion facing slightly obliquely, anteriormost portion nearly vertical to slightly recurved under cranidium; palpebral lobe small, lobe strongly laterally bowed, comma shaped, with portion posterior to δ slightly longer than portion anterior to δ; distance across γ 131.5% (124.3–142.7) cranidial sagittal length;

distinct furrow clearly differentiating palpebral lobe from fixigena, furrow is shallow anteriorly, but deep along posterolateral corner of lobe; eye ridge faint, but discernible on dorsal surface of most specimens, clearly visible ventrally (Pl. 2, fig. 8), running obliquely from anterior portion of palpebral lobe to point just behind fossula; interocular fixigena very broad, with moderately strong dorsal inflation, sloping toward glabella; posterior fixigena with inflation similar to frontal area, strongly sloping downward from horizontal plane; fixigena covered with sculpture of medium and small sized scattered tubercles, tubercles become smaller and less dense toward genal angle; posterior section of facial suture nearly straight, slightly posterolaterally directed to nearly transverse; posterior border furrow relatively long (exsag.) and deep, nearly transverse, deeper and forming a sharp contact posteriorly with posterior border, shallower and forming a more gradational contact anteriorly with posterior fixigena, distal and proximal tips shallower; posterior border dorsally inflated, shortest (exsag.) proximally, lengthened distally from fulcrum, then slightly shortened distally from point opposite distal margin of posterior facial suture; border with fine background tubercles and a few larger tubercles arranged linearly along portion of border between fulcrum and axis; posterior margin of posterior border transversely straight to fulcrum, directed more posterolaterally from fulcrum to point opposite distal margin of posterior facial suture, directed anterolaterally from this point distally; ventral margin of posterior border between fulcrum and axis with narrow transverse articulating groove, additional thin subtriangular strip of doublure present beneath posterior border from fulcrum distally; genal angle developed into very short posterolaterally directed projection; glabella subtrapezoidal in dorsal view, with maximum width across L1 98.8% (87.9–104.1) sagittal length excluding LO, sagittal length (excluding LO) 64.8% (61.9–71.7) that of cranidium, strongly convex and dorsally inflated, with apex sitting above fixigena and situated opposite posterior fixigena in lateral view, anterior portion of glabella faces anteriorly and is nearly recurved under margin; axial furrows clearly impressed along majority of course, shallow and nearly effaced opposite LO, deeper and laterally bowed around L1, furrow broad in front of L1 forming a subtriangular depression along the lateral glabellar margin, tapers anteriorly, but broadens again at intersection with anterior border and preglabellar furrows, width across posterior contact of furrows with posterior margin 58.8% (53.6–63.7) cranidial sagittal length, laterally confluent with posterior border furrow; S1 deep, completely isolating L1 on some specimens (e.g., Pl. 2, fig. 2), but not quite on others (e.g., Pl. 2, fig. 10); S2 poorly developed, barely visible on some specimens; L1 bulbous, subtriangular, with strong dorsal inflation; L2 and L3 not prominent and without independent inflation; sculpture of mostly small densely spaced tubercles covers glabella, with a scattering of larger tubercles superimposed; LO long, sagittal length 36.9% (35.0–40.7) that of cranidium, longer sagittally than exsagittally, anterior and posterior margins nearly transverse medially, with distal tips directed anterolaterally, sculpture of small scattered tubercles, slightly less densely spaced than on glabella, prominent median node, situated slightly anterior to midline; SO deep and short (sag.) medially, with distal tips deeper and deflected around base of L1, nearly transverse medially, anterior and posterior edges with sharp contact with rear of main glabella and LO respectively, joining axial furrow in smooth curve without obvious disruption in course; doublure of broad, semicircular articulating surface underlying LO, anterior margin terminating just before ventral expression of SO, mostly smooth with very faint transverse lines; fossulae expressed dorsally on most specimens.

Librigenal measurements were made on the larger specimens of Pl. 4, figs 28–30, 34, 36, Pl. 5, figs 41, 44. Librigena subtriangular, with main body (excluding anterior projection) with maximum width 74.0% (66.7–76.9) exsagittal length; anterior section of facial suture with length 62.0% (55.1–68.3) exsagittal length of main body and posterior section of facial suture with length 53.5% (48.6–59.2) exsagittal length of main body; anterior section gently convex to nearly straight opposite field, with curve slightly more strong opposite abaxial half of field, curve strongly bent across lateral border; posterior section with gentle concave bow, curve continues smoothly across lateral border in some specimens, but in others curve is more strongly bent at lateral border; visual surface small, short, bulbous; eye separated from field by shallow furrow, deeper posteriorly, furrow covered by sculpture of small tubercles; field with background sculpture of very fine granules overlain by more prominent sculpture of densely spaced small and medium sized tubercles; lateral border furrow broad and relatively deep, distal tips slightly shallower on most specimens, background sculpture of fine granules covers furrow, but larger tubercles are mostly absent; lateral border with margin strongly but not evenly arcuate, curve strongest just anterior to midlength; border broad, strongly inflated with margin flattened forming a nearly vertical wall in ventrolateral profile (Pl. 5, figs 42, 43), with sculpture of very densely spaced small flattened tubercles, some slightly larger tubercles are present along the internal margin adjacent to lateral border furrow, ventrolateral margin with prominent raised line bounding margin; anterior projection moderately short, downturned from horizontal plane (Pl. 5, fig. 42), sculpture from border

continues without obvious disruption onto anterior projection; doublure broad and slightly narrower than lateral border and anterior projection, narrower posteriorly, strongly upturned toward ventral surface, largely smooth, lacking coarsely tuberculate sculpture present on dorsal surface; inner margin of doublure describes continuous arc, with sharp angular change posteriorly.

Rostral plate measurements were made on the four specimens of Plate 5. Rostral plate with width (tr.) at juncture of connective suture and inner arc 52.1% (44.5–60.8) width at rostral suture; length (sag.) of border sector 19.0% (16.7–22.6) maximum width at juncture of connective and rostral sutures, border sector lengthened (exsag.) abaxially; border sector strongly bowed, inner arc tighter than arc along rostral suture, with sculpture of densely spaced, flattened, medium and small sized tubercles; intersection of border and doublural sectors describing smooth arc; doublural sector smooth, lacking obvious tuberculate sculpture, posteriorly concave.

Hypostomal measurements were made on the six specimens of Plate 5. Hypostome with anterior border strongly ventrally flexed, forming a short wall along the anterior margin; anterior border furrow deep and incised medially along anterior margin of middle body, otherwise shallow; anterior margin of hypostome describing smooth arc, with medial portion more strongly arched than portion opposite anterior wing; lateral margin somewhat sinuous to nearly straight, but overall directed nearly parallel to sagittal axis; minimum hypostomal width (tr.) across middle body 57.5% (53.8–60.0) maximum hypostomal width across anterior wing; width across shoulder 69.6% (63.8–71.3) width across anterior wing; anterior wing large, extended far beyond lateral extent of shoulder, with subrectangular outline and small pit at posterolateral corner; lateral margin of shoulder directed gently posteromedially toward posterior margin; posterior wing developed into short dorsally directed process; lateral border furrow deep and incised, deeper opposite anterior portion of middle body; lateral border relatively wide (tr.), strongly inflated; posterior border furrow shallow, slightly deeper medially on some specimens, but clearly outlining posterior margin of middle body; posterior border long (sag., exsag.), flattened, extended into three relatively short posteriorly directed spines, held nearly parallel to horizontal plane; portion of posterior margin between spines strongly arched; middle body with moderate inflation, anterior lobe more strongly inflated than posterior lobe, lacking rhynchos; middle furrow generally shallow, but deeper anteriorly and nearly effaced medially, directed strongly posteromedially, forming a "V" or a "U" shape overall, separating middle body into ovate anterior lobe and roughly U-shaped posterior lobe; posterior lobe unevenly arcuate; posterior furrow variably impressed, describing more shallow U-shape than middle furrow (Pl. 5, figs 1, 5, 6, 12, 16); broad doublure present beneath posterior border, continues along hypostomal margin beneath posterior and lateral portion of shoulder; sculpture of fine granules covers entire ventral surface of hypostome; maculae indistinct.

Thorax known from three segments with the following morphology: axial ring with maximum width (tr.) 35.8% (34.4–38.3) maximum width of segment; axial ring with a band of medium and small sized tubercles, band located posteriorly on larger segments; narrow and deep ring furrow, with distal tips longer (exsag.); articulating half ring moderately large, lenticular to crescentic in outline, covered by small densely spaced granules; axial furrows very shallow to effaced; pleural furrow deep and long (exsag.) between axis and fulcrum, slightly shorter from fulcrum abaxially to facet, furrow continues a short distance onto facet, but does not reach margin; anterior and posterior pleural bands of nearly similar length (exsag.), with posterior band slightly longer (exsag.) on larger segment (Pl. 5, fig. 25); band of prominent tubercles present on axial ring continues across posterior pleural band as a single row of tubercles, tubercles continue around lateral margin of pleurae (Pl. 5, figs 27–29); anterior band with less prominent row of small tubercles along posterior margin; anterior and posterior bands with background sculpture of fine densely spaced granules; very narrow, transverse furrow set anterior to anterior band between axis and fulcrum, with the anterior edge of the articulating flange forming a very narrow transverse tongue which articulates with a narrow ventral transverse groove beneath the posterior edge of the pleurae of the next segment anteriorly (or the posterior border of the cranidium); anterolateral tip of posterior pleural band developed into broad facet, subtriangular in plan view with anterolateral corner developed into short point, rounded and lobate in lateral profile; very small axial process, that appears to be a continuation of the abaxial tip of the axial ring, set at the anterior end of the axial furrow articulates with a small pit in the posterior end of the next segment anteriorly (or the posterior of the cranidium); ventrally, doublure forms a broad articulating surface beneath the axial ring, small portion of doublure is also present along posterior margin of the posterior pleural band from the fulcrum distally; fulcrum set far distally, with portion of pleurae distal to fulcrum in transverse profile just slightly longer than portion between fulcrum and axis; portion of pleura distal to fulcrum turned down from horizontal plane between 55-65 degrees, portion of pleurae between fulcrum and axis nearly parallel to horizontal plane to just slightly inclined toward axis.

Pygidial measurements were made on the largest and most complete specimens of Pl. 6, figs 1–3, 13, 15, 16, 26. Distance to sagittal line was doubled where one side of the pygidium was broken. Pygidium with maximum width across anterior margin of fourth segment 178.5% (163.4–194.2) sagittal length; axis of four segments and terminal piece, with width across first segment 32.9% (28.1–36.4) maximum pygidial width, width across fourth segment 77.9% (70.0–93.9) width across first segment, length of axis excluding articulating half ring 78.7% (74.3–82.0) total sagittal length of pygidium; articulating half ring semilunate, slightly smaller than first axial segment, sagittal length 11.5% (10.7–12.4) total pygidial length, anterior margin subsemicircular, ring held almost horizontal to sagittal profile of axis, weakly dorsally convex in sagittal profile, strongly bowed in transverse profile (along with rest of axis), with sculpture of very small tubercles; articulating furrow deep, short, and moderately strongly anteriorly bowed; first ring furrow as deep as first, very slightly more transverse; second ring furrow very shallow medially but with distal tips deep, nearly transverse to describing gently anteriorly concave arc; third ring furrow shallow, mostly effaced medially, describing more strongly anteriorly concave arc; first axial ring longer sagittally than exsagittally, with sculpture of about five to six tubercles oriented linearly (tr.) just anterior to mid-length of segment, background sculpture of fine closely spaced granules; posterior rings progressively smaller, but with essentially the same morphology; axis terminated by broad, lightly inflated terminal piece, poorly developed into two lateral swellings in larger specimens (Pl. 6, figs 1–3), densely tuberculate; axis distinctly terminated by change in slope and shallow furrow; axial furrow shallow opposite first axial segment, deepest opposite second and third segments, remaining deep opposite anterior portion of fourth segment, but shallower opposite posterior portion of fourth segment and terminal piece; first segment with maximum exsagittal pleural length 23.6% (21.6–24.7) sagittal axial length, anterior margin almost exactly transversely straight to fulcrum, which is set extremely close to axis, margin directed sharply posterolaterally distal to fulcrum; anterior pleural band set off from margin by very faint transverse accessory furrow (Pl. 6, fig. 10), well inflated, with sculpture of small tubercles arranged linearly along posterior margin of band, background sculpture of fine granules, band of similar length (exsag.) along entire course; posterior pleural band of similar length (exsag.) as anterior band, but slightly longer distally, with mixture of medium and smaller sized tubercles scattered across entire band, slightly more densely spaced distally, finer background tubercles less prominent; pleural furrow deep from axis, past fulcrum, to point just before lateral margin, short (exsag.), terminated before pygidial margin; interpleural furrow much shallower than pleural furrow, deepest between axis and fulcrum, shallower from fulcrum abaxially, extending to pygidial margin; subsequent pleural and interpleural furrows progressively shallower, but remaining deep and discernible adjacent to axial furrow; subsequent pleural segments progressively less clearly defined, overall shorter (exsag.) adjacent to axis, with anterior bands much shorter than posterior bands and nearly pinched out adjacent to axis; pleural region covered by sculpture of prominent medium and a few small sized tubercles, which are distinct and closely spaced adaxially, but become more densely spaced and somewhat flattened abaxially, faint row of single isolated tubercles present on first four segments at fulcrum, background sculpture of fine granules present; border covered by very densely spaced, flattened medium sized tubercles, which merge without disruption from pleural region onto border; ventral aspect of border covered by sculpture of fine granules, that are slightly larger than those composing background sculpture on dorsal surface of pygidium; pygidial margin bowed upward medially in posterior profile; doublure strongly upturned against ventral surface of pygidium in ventral profile (Pl. 6, figs 9, 14), in anterior profile (Pl. 6, fig. 20) doublure clearly visible, apparently smooth and lacking tuberculate sculpture present elsewhere on pygidium.

Ontogeny. Ontogenetic stages of calymenids are relatively poorly known, with descriptions by Chatterton *et al*. (1990) the main exception. Small specimens of *A. bardensis* compare closely with those of Silurian species of "*Calymene* sensu lato" illustrated by Chatterton *et al.* (1990, fig. 9).

The cranidium undergoes several changes in morphology during ontogeny in addition to changes in size. Smaller cranidia (Pl. 4, fig. 17) are covered in densely spaced small spines, especially on the anterior portion of the cranidium and along the facial suture, which become greatly reduced throughout ontogeny into prominent tubercles (Pl. 1, fig. 20). The glabella features sets of paired spines. L1 becomes more clearly outlined and bulbous throughout ontogeny and the glabella become slightly wider with respect to length.

The overall shape of smallest librigenae is similar to that of larger librigenae, but again there is an obvious change in the morphology of the sculpture throughout ontogeny from longer spines/tall tubercles into densely spaced and more flattened tubercles. This is most apparent on the lateral border and field. The smaller librigenae possess a very faint background sculpture of fine granules with clearly isolated, tall tubercles/spines on the field. This sculpture changes throughout ontogeny into the overall more prominent background sculpture of fine granules

with more subdued isolated tubercles on the larger cheeks. The same change is seen on the lateral border. The field also become larger with respect to the lateral border throughout ontogeny.

The smallest pygidium (Pl. 6, fig. 37) possesses prominent tall tubercle/spine pairs on each axial segment, whereas the next smallest pygidium (Pl. 6, fig. 34) has the tall tubercles/spines reduced into a band of prominent tubercles along each axial segment. These tubercles continue to become more reduced and subdued throughout ontogeny. A similar patten of reduction is seen in the line of tubercles present on the pleural region adjacent to the axis. The smallest pygidium displays a prominent row of spines that runs along the fulcrum of pleural region, with the largest sitting anteriorly, and that become progressively smaller and shorter posteriorly. The spines are reduced, but still clearly visible and distinct on the next smallest pygidium, and throughout ontogeny the row of spines is further reduced to a band of small tubercles that are progressively harder to distinguish on larger specimens. The posterior margin of the smallest pygidia is broadly rounded and lacking a point medially. This curve becomes more strong throughout ontogeny and with larger pygidia having more of a broadly rounded point medially. The pygidium also becomes more strongly vaulted with the portion distal to the fulcrum lengthened throughout ontogeny (cf. Pl. 6, fig. 33, Pl. 6, figs 27, 38).

Discussion. Two cranidia assigned by Whittington (1965, p. 419, pl. 59, figs 10, 12-15) to "aff. *Calymenidius* sp. ind." have been cited repeatedly in the literature (figured herein as Pl. 7, figs 5, 8, 10–12). With description of *A. bardensis* on the basis of abundant material, it becomes evident that these specimens belong to the species and that Whittington also illustrated other material of the species in his monograph, misassigned to other taxa. Another cranidium (Whittington, 1965, p. 340, pl. 19, figs 16, 19, 20; reillustrated as Pl. 7, figs 1–3, 7 herein) was assigned to "*Ischyrophyma*? sp. ind." This reflects his earlier assignment of a cephalon and thoracic segments from the older Shallow Bay Formation (Whittington, 1963, p. 50, pl. 6, figs 13–15) to the same taxon (see *Atlanticalymene* **n. sp.** A below). Finally, an exfoliated pygidium (Whittington, 1965, p. 374, pl. 39, figs 8, 9; Pl. 7, figs 4, 6, 9, herein) was illustrated as "Komaspidid? pygidium."

Atlanticalymene n. sp. A

Fig. 3

1963 ? *Ischyrophyma* sp. ind.; Whittington, p. 50, pl. 6, figs 13–15.

Material. Cephalon and associated partial thorax, GSC 16161 (Fig. 3), from the Shallow Bay Formation, Bed 14 (lower Darriwilian), Lower Head, near Cow Head, Great Northern Peninsula, western Newfoundland, Canada.

Discussion. A single specimen from the lower Darriwilian Shallow Bay Formation clearly represents a species of *Atlanticalymene*, but comparison with *A. bardensis* is hampered by the fact that it is mostly exfoliated. The species shares *Atlanticalymene* apomorphies of a well inflated and nearly isolated L1, a lack of inflated L2 or L3, lack of incised S2 or S3, and an elongate, subparallel-sided glabella. It differs from *A. bardensis* most obviously in the possession of much narrower interocular fixigenae and a more anterior eye position. The course of the posterior section of the facial suture also appears to be more obviously anteriorly bowed (Fig. 3.3).

Calymeninae n. gen. n. sp.

Fig. 4

1999 *Protocalymene* new species A; Fortey and Droser, p. 197, fig. 8.11–8.14.
2013 "unnamed species described as '*Protocalymene* n. sp. A' by Fortey & Droser (1999)"; Adrain, p. 310.

Material. Figured specimens USNM 495698, 495699, and 511808 from the Antelope Valley Formation (Dapingian), "olenid bed" at Little Rawhide Mountain, Nye County, central Nevada, USA. Note that USNM 511808 was listed by Fortey and Droser (1999, p. 197) as "USNM 495700". However they had earlier in their paper assigned the latter number to a librigena of a species of *Dimeropygiella* (Fortey and Droser, 1999, p. 192, explanation of fig. 5.5); the calymenid specimen reillustrated herein has subsequently been assigned the number USNM 511808.

Discussion. Fortey and Droser (1999) illustrated specimens from a deep water olenid-dominated assemblage in the Dapingian part of the Antelope Valley Formation. They assigned the material to *Protocalymene*. In its cranidial

dimensions the species appears to be a calymenine. Its most unusual feature is the presence of a very long preglabellar field (e.g., Fig. 4.4) with fine tuberculate sculpture similar to that on the rest of the cranidium. Some younger calymenines have a long area between the glabella and anterior border, but it is typically a deep well that resembles an expanded anterior border furrow (e.g., *Calymene* (s.l.) *frontosa* Lindström, 1885—see Clarkson and Howells [1981, pl. 79, figs 6, 7, 11]; species of *Arcticalymene* Adrain and Edgecombe, 1997). None show what appears to be a standard, sculptured preglabellar field as most have the front of the glabella separated from the anterior border only by a relatively deep and short anterior border furrow. The morphology in Fortey and Droser's species could represent a transitional form. The anterior parts of the fixigenae are inflated and typically calymenine. They are separated from the sculptured preglabellar area by abrupt changes in slope running forward from the axial furrows. The anterior border appears to be calymenine in aspect, though it is not well known. Alternatively, the inferred environment of deposition is deep water and dysaerobic. The cranidia are very broad and have much more prominent caecal sculpture (including, especially, the bicomposite eye ridge) underlying the fine tubercles than is typical for a calymenine. It is conceivable that the unusual preglabellar morphology is part of a suite of adaptations to an oxygen-stressed environment.

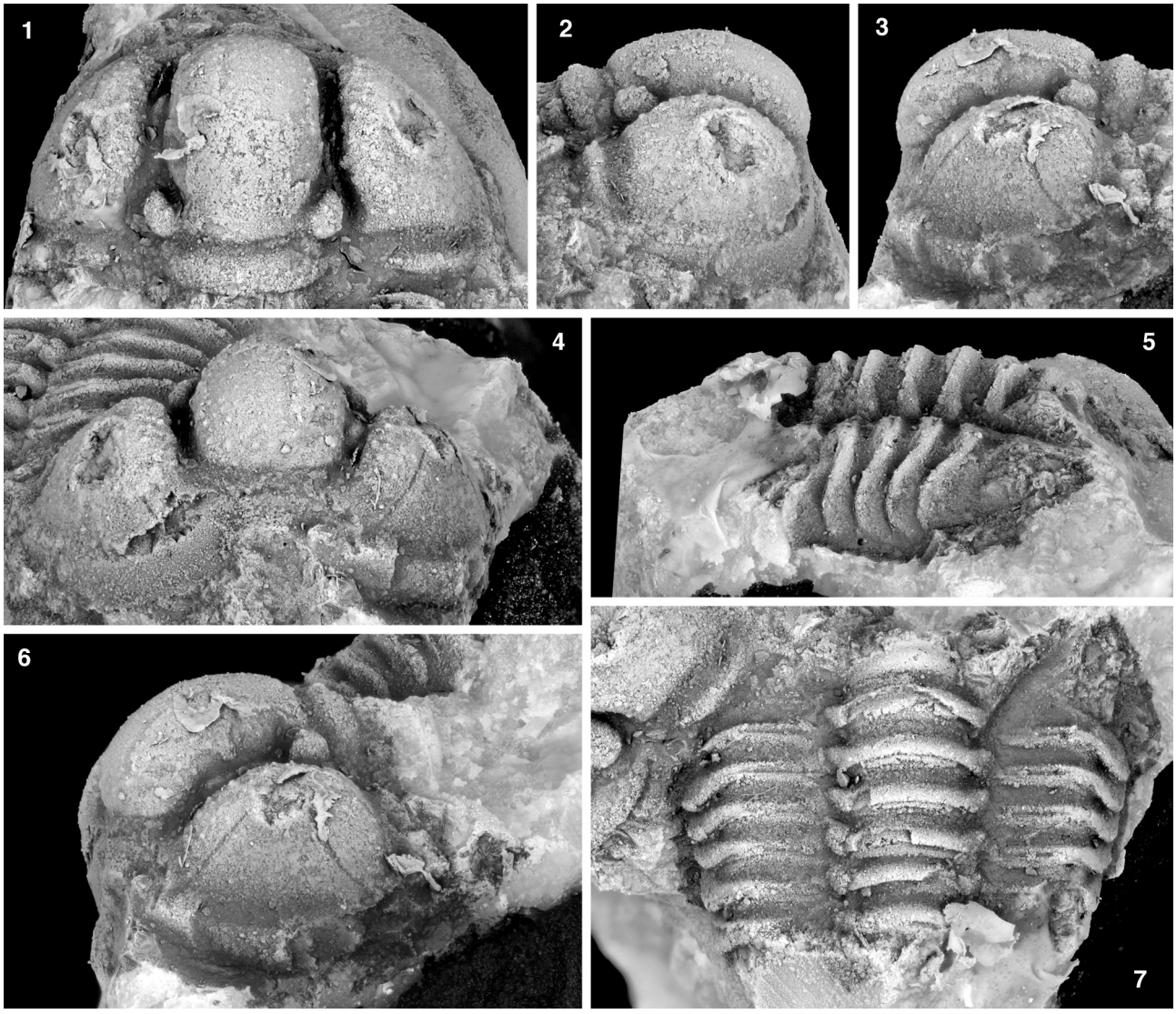

FIGURE 3. *Atlanticalymene* **n. sp.** A, from the Shallow Bay Formation, Bed 14 (lower Darriwilian), alpha boulder at Lower Head, near Cow Head, western Newfoundland, Canada. 1–7. Cephalon and associated partial thorax, GSC 16161 ("? *Ischyrophyma* sp. ind." of Whittington, 1963, p. 50, pl. 6, figs. 13–15), dorsal cephalic, right lateral cephalic, left lateral cephalic, anterior cephalic, right lateral thoracic, oblique cephalic, and dorsal thoracic views, x15.

While this Dapingian species broadly resembles *A. bardensis* in cranidial dimensions, especially the wide interocular fixigenae, it lacks the glabellar morphology considered apomorphic for *Atlanticalymene*. It has well de-

veloped L2 and L3 and a deep S2. The glabella is relatively short compared to that of *A. bardensis*, but it is nearly parallel-sided versus the bell shape typical of calymenines. We agree with Fortey and Droser (1999) that the species, while very distinctive, is not well enough known to formally name. It is important as the oldest known Laurentian calymenine and the only known Dapingian species. It appears to represent a genus distinct from *Atlanticalymene*, formal naming of which must await the recovery of more material or related species from elsewhere.

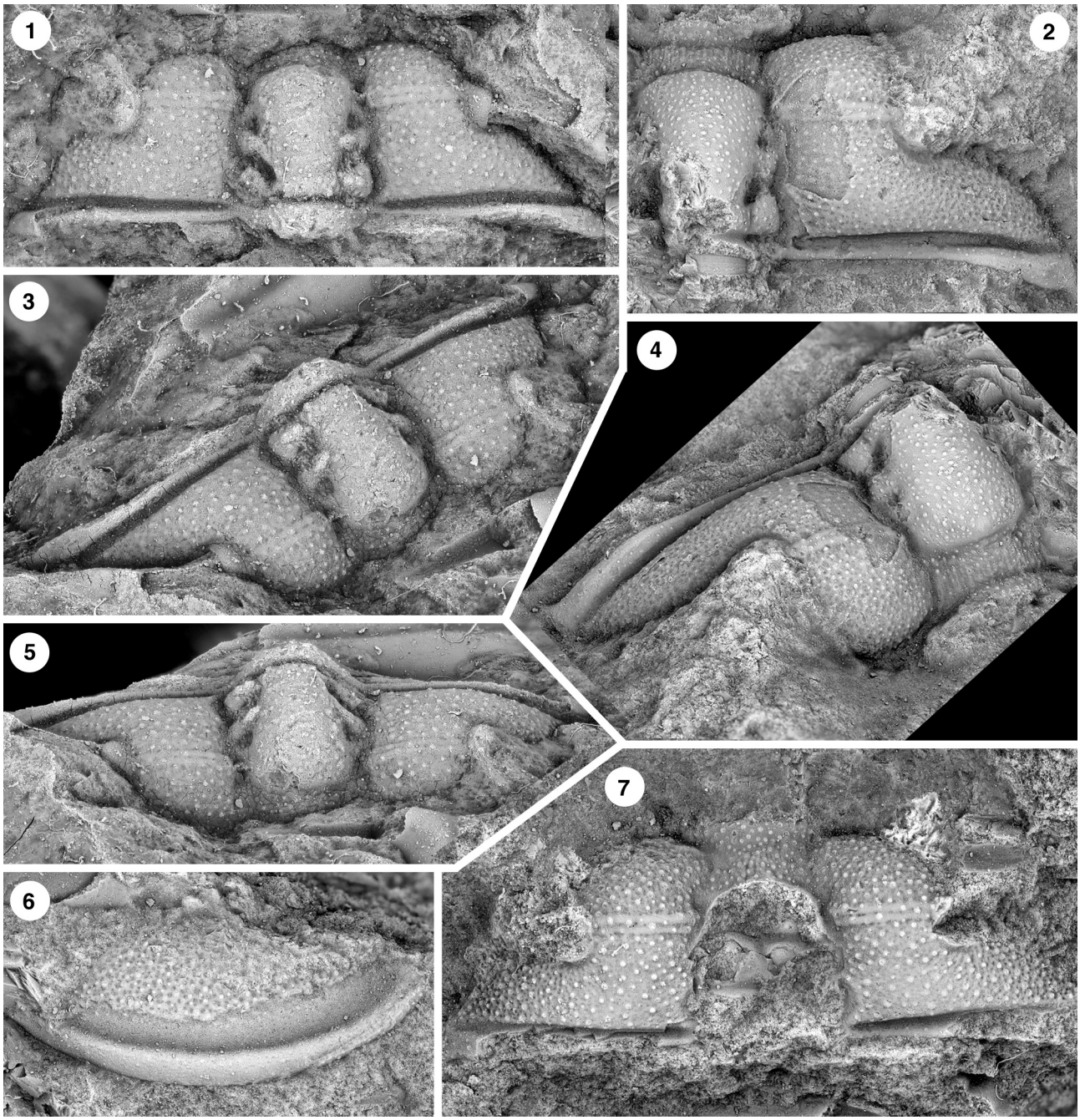

FIGURE 4. Calymeninae **n. gen. n. sp.**, from the Antelope Valley Formation (Dapingian), "olenid bed" at Little Rawhide Mountain, Nye County, central Nevada ("*Protocalymene* new species A" of Fortey and Droser, 1999, p. 197, fig. 8.11–8.14). 1, 3, 5, 7. Cranidium, USNM 495699 (original of Fortey and Droser, 1999, fig. 8.13, 8.14), dorsal, oblique, and anterodorsal views of latex from external mold, and dorsal view of testate counterpart, x10. 2, 4. Cranidium, USNM 495698 (original of Fortey and Droser, 1999, fig. 8.11, 8.12), dorsal and oblique views, x7.5. 6. Left librigena, USNM 511808, external view, x10 (not illustrated by Fortey and Droser, 1999, but listed by them as USNM 495700, see text for explanation).

Family Uncertain

***Protocalymene* Ross, 1967**

Type species. *Protocalymene mcallisteri* Ross, 1967, from the Antelope Valley Formation (Dapingian) of California, USA.

Other species. *Protocalymene* sp. of Ross (1970, p. 92, pl. 18, figs 2–5), Antelope Valley Formation, Ike's Canyon, Monitor Range, Nye County, Nevada; *Protocalymene* sp. of Loch and Ethington (2017, p. 310, fig. 13.6), uppermost Ninemile Formation, Whiterock Canyon Narrows, Monitor Range, Nye County, Nevada.

Diagnosis. Frontal and preglabellar area long and uninflated; anterior border furrow shallow; anterior border not strongly dorsally inflated; L1 prominent, displaced laterally so glabella bell-shaped in outline; L2 well inflated; glabella with lateral indentation in front of L2 where faint oblique eye ridge runs into axial furrow from anterior part of palpebral lobe; median occipital node prominent; cranidial sculpture of medium sized tubercles; posterior projections prominent, bearing robust and long, posteriorly-directed genal spines; hypostome with ventrally smooth middle body and large, triangular posterior spines; librigena with nearly straight anterior and posterior sections of the facial suture, visual surface set atop independently inflated band of socle; pygidium with four axial rings discernible in most specimens, often with larger pair of tubercles on each ring; pygidium relatively narrow, each posterior pleural band with prominent tubercle at fulcrum.

Discussion. Whittington (1971, p. 456) excluded *Protocalymene* from his discussion of calymenid taxonomy "because of the difficulty in determining the systematic position of the small specimens on which it is based." Similarly, Fortey and Droser (1999, p. 197) noted that Ross's (1967) illustrated material was all "rather small". This is true, but in light of our new collections it appears that this is because the species reached a diminutive maximum size. Our new silicified collections contain thousands of trilobite sclerites and *P. mcallisteri* is one of the most common species. The largest cranidia we have recovered are only about 3.3 mm in sagittal length (e.g., Pl. 8, figs 1, 3). There is no reason to suspect the silicified sample is inherently biased toward lack of preservation of larger specimens. Specimens belonging to a species of the pliomerid *Ectenonotus* Raymond, 1920, for example, are common. Many cranidia of this species have been recovered that are as large or larger than the single calcareous cranidium assigned by Fortey and Droser (1996, fig. 16.3, 16.6, 16.7) to their new *E. progenitor*. These specimens are more than double the size of the largest *P. mcallisteri* cranidia. Given that the species are of broadly similar general morphology, it is likely also that hydrodynamic sorting can be ruled out as an explanation for the small maximum size of *P. mcallisteri* material. Very large illaenid specimens are also common in the collections. *Protocalymene mcallisteri* appears simply to have been a small trilobite. In addition to the species noted above, Ross (1972, p. 14) listed "*Protocalymene* sp." from the Antelope Valley Formation above the massive bioherm at Meiklejohn Peak, Nye County, Nevada. This occurrence has not been illustrated.

Almost all previous commentators have treated *Protocalymene* as Calymenidae, and often as Calymeninae (=Flexicalymeninae; see above) (Fortey, 1975, p. 346; Hammann, 1983, p. 46; Fortey, 1990, p. 568; Fortey and Droser, 1999, p. 197; Jell and Adrain, 2003, pp. 431, 468; Loch and Ethington, 2017, p. 310), and as detailed above there has been repeated confusion of Ross's taxon with the material described by Whittington (1965) in various open nomenclature assignments and formalized here as *Atlanticalymene bardensis*. The latter, as argued above, is an unambiguous calymenine calymenid. The affinity of *Protocalymene* is much less clear. A few authors have regarded *Protocalymene* as of less certain affinity. Kobayashi and Hamada (1977, pp. 124–125), for example, questionably assigned it to a calymenid Subfamily Ptychometopinae Balašova in Černyševa, 1960, along with *Ptychometopus* Schmidt, 1894, and *Endocrania* Kobayashi, 1956. *Ptychometopus* is variably considered either a pharostomatid (e.g., Jell and Adrain, 2003, pp. 436, 476) or a calymenid (e.g., Fortey and Cocks, 2003, p. 267). *Endocrania* is a junior subjective synonym of the leiostegiid *Leiostegium* Raymond, 1913 (Zhou and Fortey, 1986, p. 172).

Although it has been regarded as a calymenine, few aspects of the morphology of *P. mcallisteri* resemble members of this subfamily. In particular, the species has a "normal" preglabellar area and anterior border. In most calymenids, the frontal regions are inflated and the preglabellar field is lost, with a more or less inflated anterior border abutting the front of the glabella. This morphology is reminiscent of that of some species of pharostomatids, such as *Pharostoma narinosum* Siveter, 1977 (fig. 3A–H). *Protocalymene mcallisteri* does not appear to be a pharostomatid, however, as species of that group have a posterior facial suture which cuts the anterior border

adaxial to the genal spine, with the genal spine positioned on the librigena. In all other calymenoideans the genal spine is on the cranidium, and the posterior facial suture cuts the lateral border, not the posterior border. This is emphatically the case in *P. mcallisteri*, which has huge genal spines developed on the cranidium. These spines themselves are unusual features in a calymenoidean. Some bathycheilids have large and long genal spines (e.g., *Bathycheilus gallicus* Dean, 1965) but, again, these are librigenal, not cranidial features.

Protocalymene mcallisteri does not resemble species of Reedocalymeninae or Colpocoryphinae, all of which have prominent adaptations for coaptation which *P. mcallisteri* entirely lacks.

Despite its unusual morphology, *P. mcallisteri* has unmistakably calymenoidean features. The rostral plate (Pl. 13, figs 15, 16, 18, 19) is typically calymenoidean, with a border sector and a doublural sector. The hypostome (Pl. 13, figs 1–3) is of typical calymenoidean aspect, with a pair of large posterior spines. The librigena is slightly odd looking due to its nearly straight facial sutures, but it is once again of standard calymenoidean form. In the absence of any obvious close comparisons, but equally obvious calymenoidean affinity, for the time being we elect not to make a family assignment of the genus.

Protocalymene mcallisteri Ross, 1967

Plates 8–15

	1967	*Protocalymene mcallisteri* Ross, p. D27, pl. 9, figs 1–28.
	1970	*Protocalymene mcallisteri* Ross; Ross, p. 92.
	1977	*Protocalymene macallisteri* [*sic*] Ross; Kobayashi and Hamada, p. 125.
non	1983	*Protocalymene mcallisteri* Ross; Andrawis *et al*. p. 66, fig. 1.
	1990	*Protocalymene mcallisteri* Ross; Geyer, p. 111.
	1999	*Protocalymene mcallisteri* Ross; Fortey and Droser, p. 197.
	2002	*Protocalymene mcallisteri* Ross; Turvey, p. 56.
	2003	*Protocalymene mcallisteri* Ross; Jell and Adrain, p. 431.
	2005	*Protocalymene mcallisteri* Ross; Turvey, text-fig. 1.
non	2012	*Protocalymene mcallisteri* Ross; Basse, p. 35.

Material. Holotype, cranidium, USNM 145848 (Ross, 1967, pl. 9, figs 5–7), and assigned specimens SUI 137444–137520, Antelope Valley Formation (Dapingian), north of Pyramid Peak, west flank of Funeral Mountains, Death Valley National Park, California, USA.

Diagnosis. See genus diagnosis.

Description. Cranidial measurements were made on specimens from Pl. 8, figs 1–3, 10, 15, 21, Pl. 9, figs 1-3, 11, 13, 19, 21, Pl. 10, figs 1–3, 10–12, 19, 20. Cranidium with strong dorsoventral relief, anterior and posterior fixigena strongly flexed downward from occipital lobe in lateral view, and anterior fixigena flexed upward toward glabella in anterior view; sagittal length 50.9% (46.5–55.2) width across posterior border; sagittal length 84.1% (79.2–89.1) width across δ; sagittal length 125.4% (115.2–140.9) width across anterior border furrow; sagittal length 106.1% (97.5–113.8) width (tr.) across γ; width across posterior border 247% (229.2–270.7) width across anterior border furrow; glabella subtrapezoidal in outline, sagittal length 83.4% (71.8–96.4) maximum width (tr.) across L1, moderately strong dorsal inflation, with apex sitting just below that of palpebral lobes in anterior view (e.g., Pl. 8, fig. 7), sculpture of prominent larger tubercles present, especially on median portion of glabella, with background sculpture of coarse granules; L1 clearly developed, bulbous, displaced laterally giving glabella overall bell shape, inner margin not isolated from glabella, deep "C"-shaped furrow composed of S1, axial furrow, and distal portion of LO define external margin of L1; S1 deep, short, directed posteromedially; L2 less well developed than L1, but still prominent, set off anteriorly by extremely short, deep S2; axial furrow narrow and shallow from intersection with posterior cranidial margin to base of L1, deep and laterally deflected around L1, shallower and broad opposite L2 (on most specimens), faint continuation of axial furrow from fossulae anteriorly to intersection with anterior border furrow clearly separates preglabellar field from anterior fixigena, furrows are anteriorly divergent; distance between intersection of axial furrows with posterior cranidial margin 96.9% (91.3–104.0) maximum glabellar width; fossulae deep and pit-like on dorsal surface, ventrally expressed as small raised region; eye ridge poorly developed, oriented obliquely with proximal termination creating an indentation in lateral margin of glabella, defined anteriorly by shallow furrow running from fossulae to γ; preglabellar furrow incised along entire course, medial portion slightly deeper on some specimens (e.g., Pl. 8, fig. 3), anteriorly

arched; preglabellar field relatively long, with sagittal length 12.7% (8.2–16.7) cranidial length, lengthens (exsag.) slightly abaxially, sculpture of densely spaced granules; anterior border furrow moderately short, shallow, lateral portions opposite anterior fixigenae deeper than medial portion opposite anterior glabellar margin, gently anteriorly arched; anterior border in dorsal view longest medially, with sagittal length 14.1% (10.7–17.6) cranidial length (sag.), shorter abaxially with distal portion tapered to a point at intersection with anterior facial suture, anterior margin more strongly anteriorly arched than posterior margin; dorsal inflation weak; anterior border in anterior view strongly dorsally arched (e.g., Pl. 8, fig. 7), thickens nearly equal along entire course, covered with densely spaced granules of medium and small size; lateral profile of preglabellar area forms moderate ventrally sloping surface, slight break in slope at anterior border furrow, with anterior border slightly independently inflated; articulating furrow for rostral plate present ventrally beneath anterior border, broad, forming distinct groove, with posterior and anterior margins defined by distinct inflated rims, anteriorly arched as anterior border; fixigena covered by small to medium densely spaced granules, with few isolated small tubercles (especially on interocular fixigena); interocular fixigena relatively broad; palpebral lobe with length between γ and ε 51.8% (45.0–58.5) glabellar length (sag.), gentle independent inflation, δ situated opposite L2, γ situated opposite point between S2 and fossulae, and ε opposite anterior portion of L1; lobe set off from fixigena by narrow shallow furrow; posterior projection extends far beyond lateral extent of palpebral lobe in dorsal view, strongly downturned from horizontal plane (e.g., Pl. 8, figs 14, 17); narrow inflated ridge continuing from posterior portion of palpebral lobe around anterior margin of posterior fixigena, progressively narrower and weaker toward intersection with posterior border furrow, deep narrow furrow bounds inner margin of ridge opposite point just behind ε; posterior fixigena tapering (exsag.) to a point abaxially, portion distal to fulcrum directed posterolaterally; posterior border furrow distinct, shallow adjacent to axial furrow, lengthening (exsag.) toward fulcrum, deepest at fulcrum, abruptly shallow just before intersection with posterior facial suture so that furrow terminates before reaching intersection; posterior border short (exsag.) adjacent to LO, directed subparallel to transverse axis, gently lengthening abaxially to fulcrum, then significantly longer (exsag.) from fulcrum abaxially, portion distal to fulcrum directed posterolaterally, confluent with genal spine; doublure beneath posterior border subtriangular in outline; genal spine long and stout, directed subparallel to sagittal axis; SO relatively short (sag., exsag.), clearly incised, slightly shallower medially, deepest opposite posterior margin of L1, gently anteriorly arched, merging smoothly around L1 into axial furrow; LO generally lenticular in outline, sagittal length 18.6% (16.7–22.0) cranidial length (sag.), anterior margin anteriorly arched, posterior margin posteriorly arched, with median portion nearly subparallel to transverse axis in some specimens (e.g., Pl. 8, figs 2, 15), median tubercle prominent and elongated, in lateral view tubercle merges smoothly with anterior margin of LO so that an uninterrupted slope is formed, tubercle angled upwards and back in lateral view, in some specimens tubercle appears to be hooked backwards (e.g., Pl. 8, fig. 22); a few small isolated tubercles present along posterior margin of median portion of LO, some specimens exhibit two distinct tubercles flanking larger median tubercle (e.g., Pl. 8, figs 15, 21, Pl. 9, fig. 2), others possess three or four small tubercles situated in an arc along posterior margin (e.g., Pl. 8, fig. 2); LO and median tubercle visible in anterior view sitting just above glabellar apex; doublure present beneath LO broad, terminates before reaching ventral expression of SO, surface largely smooth, with a few scattered very fine granules mostly situated near posterior margin.

Librigena (Pl. 12, figs 10, 11, 13, 14, 16–18, 20–28) with maximum width 57.1% (52.6–63.3) exsagittal length (excluding anterior projection); length of anterior portion of facial suture 36.5% (30.6–42.3) exsagittal length of main body, length of posterior facial suture 44.8% (42.3–50.6) exsagittal length of main body;
visual surface of eye large; eye socle clearly developed, short, with width less than half that of visual surface, clearly set off from visual surface by narrow distinct furrow;furrow separating eye socle from field broader with width almost equal to that of eye socle, marks distinct change in slope between eye socle and field; field large, subtrapezoidal in outline, moderately inflated sitting above border in lateral view, with sculpture of densely spaced small granules, overlain by small less densely spaced tubercles, sculpture subdued in band adjacent to border furrow; lateral border furrow shallow and nearly effaced at intersection with posterior facial suture, becoming deeper anteriorly, abruptly shallow at intersection with anterior facial suture; lateral border broad in external view, narrowest anteriorly, progressively broader posteriorly from about midlength to posterior facial suture, in lateral view border tall, (e.g., Pl. 13, fig. 26) and gently flexed upward medially, sculpture similar to that on field, with fewer prominent isolated small tubercles, sculpture present on entire external surface; anterior projection short, hook-like; anterior facial suture nearly straight to very gently arcuate across field, strong change

in course at intersection with lateral border; posterior projection longer than anterior; posterior facial suture nearly straight to very gently convex across proximal portion of field, becoming concave across distal portion of field and posterior projection, with maximum point of curvature across from field just adjacent to lateral border furrow; broad doublure present beneath lateral border and anterior and posterior projections, portion beneath posterior projection forming small flange that is visible in external view as small subtriangular point (e.g., Pl. 12, fig. 14); doublure with sculpture of very fine granules present along external margin, becoming progressively effaced toward inner margin, narrow inflated ridge-like rim developed along external margin (e.g., Pl. 12, fig. 17, Pl. 13, fig. 24).

Hypostome elongate with maximum width achieved across anterior wings; width (tr.) across shoulder 82.7% (80.5–83.9) that across anterior wings; anterior margin forming gently anteriorly bowed curve, cut strongly posterolaterally at anterolateral corner forming obtuse angle; anterior border flattened, broad, strongly flexed ventrally (e.g. Pl. 13, figs 6, 7, 12, 13), with narrow rim developed along anterior margin; anterior border furrow forming, broad depression medially, lateral portions shallower; anterior wing large, posterolateral corner forming nearly right angle in ventral view, flexed dorsally (e.g., Pl. 13, fig. 9); pit of wing process deep ventrally, clearly visible dorsally (Pl. 13, figs 4, 14); hypostome strongly constricted (tr.) just below anterior wing and opposite anterior portion of middle body before shoulder, with lateral margin strongly expanded (tr.) outward around shoulder, then turning sharply posteromedially toward posterior margin; middle body elongate, with length 138.5% (135.4–142.3) maximum width, anterior margin sloping gently toward anterior border furrow, with only moderate dorsoventral convexity; anterior lobe of middle body with length (sag.) approximately just over twice that of posterior lobe; middle furrow moderately incised, directed posteromedially, deepest abaxially, shallowing medially eventually becoming effaced so that anterior portion of middle body is very faintly isolated; lateral border clearly set off from middle body by distinct lateral border furrow; lateral border furrow with portion anterior to middle furrow deepest, slit-like, directed almost parallel to sagittal axis; lateral border furrow shallower just posterior to intersection with middle furrow, slightly deeper again opposite shoulder; posterolateral corners developed into two distinct posteriorly directed pointed projections (Pl. 13, fig. 3); posterior margin strongly arched medially, forming deep "V" with apex directed anteriorly; posterior border furrow shallow, clearly setting off posterior margin of middle body from posterior border; broad doublure present beneath lateral and posterior borders (Pl. 13, fig. 4), narrow inflated rim developed along inner margin, which forms a broadly rounded "U".

Rostral plate wide (tr.) (Pl. 13, figs 15, 16, 18, 19), relatively short in lateral profile (Pl. 13, fig. 17); border sector wider (tr.) than doublural sector, anterior and posterior margins moderately arched so that border sector forms curved band (Pl. 13, fig. 19), of similar length (sag., exsag.) along majority of band with distal portions opposite connective sutures pinched out; distinct and abrupt change in slope between border and doublural sectors; doublural sector forms curved band similar to border sector, but shorter (sag., exsag.) and slightly concave, similarly shorter opposite connective sutures, but with distal tips more rounded; connective sutures cut strongly obliquely across border and doublural sectors, forming deep "V" with apex pointing medially; scattered coarse granules cover external surface of border sector, especially on distal portion opposite connective suture; external surface of doublural sector more smooth.

Thoracic segment (Pl. 13, figs 21–23, 25, 28) with overall strong dorsal convexity (Pl. 13, figs 25, 28), axis strongly convex, pleural region between axis and fulcrum nearly parallel to horizontal plane, and portion distal to fulcrum strongly downturned from horizontal; fulcrum set relatively close to axis; distinct articulating half-ring, with sagittal length 72.2% that of axial ring, anterior margin gently anterior arched, posterior margin almost exactly transverse, distal tips forming distinct points; ring furrow incised along entire course with medial portion shallow, distal portion deep and slit-like, medial portion transverse with distal tips directed more anterolaterally; axial ring of similar length (sag. and exsag.) along entire course, with lateral portions directed more anterolaterally and medial portion very gently anteriorly arched; axial furrow shallow; width (tr.) of pleurae in dorsal view 71.5% (68.8–75.0) that of axis (tr.); pleural furrow deeply incised from axial furrow abaxially, abruptly terminated before reaching margin (Pl. 13, fig. 23); anterior and posterior pleural bands of similar length (exsag.), both shortest adjacent to axis, lengthening slightly abaxially; posterior pleural band extended distally into short articulating facet, with distal tip forming distinct, small posterolaterally directed spike, anterior corner of facet developed into short articulating process; semilunate strip of doublure present beneath articulating half-ring (Pl. 13, fig. 22); doublure also present below pleural facet (Pl. 13, fig. 28), continuing along anterior margin of pleurae and terminating at fulcrum (Pl. 13, fig. 22); sculpture of closely spaced granules covers external surface of segment, with additional larger granules present along posterior portion of posterior pleural band.

Pygidial measurements made on the most complete specimens of Plates 14 and 15. Pygidium with strong dorso-ventral convexity, sagittal length (excluding articulating half-ring) 55.3% (49.0–63.3) maximum width (tr.); axis with strong independent inflation, composed of articulating half-ring, four clearly defined axial rings, terminated by broadly rounded and inflated terminal piece; maximum axial width (tr.) 37.0% (33.5–40.8) maximum pygidial width; axis gently tapered (tr) posteriorly; posterior margin of axis faintly discernible in dorsal view, more clearly defined in lateral and posterior view by change in slope between terminal piece and pleural region; dorsal surface of axis gently sloping downward toward posterior margin in lateral profile, with articulating half-ring and first axial ring situated highest, axial rings distinct with clear independent inflation; articulating half-ring with sagittal length similar to that of first axial ring, anterior margin gently anteriorly arched, posterior margin nearly transverse (e.g., Pl. 14, fig. 13) to gently anteriorly arched (e.g., Pl. 14, fig. 28), lateral margins pinch out to form distinct points before reaching lateral extent of first axial ring, sculpture of fine granules, prominent paired tubercles absent; first axial ring with sagittal length 14.4% (9.8–17.4) that of pygidium (excluding articulating half-ring), length generally similar across ring, except for slightly shorter distal tips, which appear to merge abaxially into pleural band across a shallow axial furrow on some specimens (e.g., Pl. 14, fig. 13), sculpture of densely spaced granules, overlain by scattered distinct small tubercles (on some specimens, e.g., Pl. 14, fig. 1), with distinct pair of prominent tubercles adjacent to sagittal line (e.g., Pl. 14, fig. 11); second axial ring similar to first, but shorter (sag., exsag.), width (tr.) nearly equal to that of first axial ring, sculpture also similar; third and fourth rings generally similar to first two, progressively smaller; articulating furrow distinct along entire course, nearly transverse to gently anteriorly arched, clearly setting off articulating half-ring from first axial ring; second and third ring furrows deepest and longest (exsag.) abaxially, shallower and shorter (sag.) medially, directed almost exactly transverse medially; subsequent ring furrows similar to previous, but progressively shallower and more effaced; anterior pygidial margin gently sloping posterolaterally from axial furrow to fulcrum, with slight change in course at fulcrum so remainder of margin directed slightly more posteriorly; first pleural furrow clearly incised, portion between axis and fulcrum deep, straight, directed posterolaterally, portion abaxial to fulcrum progressively shallower towards pygidial margin, generally directed posterolaterally with gentle anterolateral arch, terminated before reaching pygidial margin; first interpleural furrow weakly incised (e.g. Pl. 15, fig. 1), difficult to discern on many specimens; subsequent pleural and interpleural furrows progressively effaced; prominent isolated tubercle present on posterior pleural bands at fulcrum (e.g., Pl. 14, figs 11, 12, 15); fulcrum set very close to axis, becoming progressively closer to axis posteriorly; pleural region distal to fulcrum strongly downturned from horizontal plane; sculpture of densely spaced granules covers pleural region, overlain by larger isolated tubercles around and adjacent to pygidial margin; lateral and posterior pygidial margin broadly rounded in dorsal view, in posterior view margin moderately arched upward medially; border not clearly differentiated, in posterior view appears to possess very slight independent inflation, sculpture more dense and finer compared to that of pleural region; doublure short (e.g., Pl. 15, fig. 13), strongly turned upward to ventral surface, covered with sculpture of densely spaced granules, in ventral view inner margin describes broadly rounded and slightly "V" shaped curve.

Ontogeny. The glabella on the smallest recovered specimens is elongate and rectangular (e.g., Pl. 12, figs 2, 3) and strongly dorsally inflated. It becomes shorter, broader, and more trapezoidal in outline throughout ontogeny and also less strongly inflated. The genal spine becomes longer relative to the length (sag.) of the cranidium. In the smallest specimens it is about 25–30% as long as the cranidium, whereas in larger specimens (e.g., Pl. 8, fig. 21) it is more than 50% as long. The median tubercle on LO occupies almost entire length (sag.) of LO and is slightly posteriorly situated. It becomes reduced in size and more anteromedially situated. The tubercle also exhibits extreme dorsal relief (see lateral and anterior views) in smaller specimens and becomes less tall in larger specimens. L1 is small and poorly developed, becoming larger and more clearly defined by more prominent S1. L2 and S2 are not clearly expressed on smallest cranidia, but are progressively more well developed and clearly visible on larger specimens. The preglabellar field lengthens throughout ontogeny. The anterior margin of the anterior border in dorsal view is subparallel to the transverse axis, but becomes more anteriorly arched so that on the largest specimen the anterior margin is strongly arched. A similar change occurs in the course of the anterior border furrow. The anterior facial suture between γ and the intersection with the anterior border furrow is nearly straight and directed anteromedially. Throughout ontogeny the posterior portion of the suture becomes oriented more subparallel to sagittal axis with a strong anteromedial bend just before intersecting the anterior border furrow. There is also a change in the sculpture from being more coarsely tuberculate to more subdued, densely

spaced granules with scattered tubercles. The pygidium becomes more elongate relative to width, with a more posteriorly tapered margin. The sculpture overall is reduced in coarsness, and the prominent tubercles on the axial rings reduce to mainly the paired axial tubercles. The axis becomes more strongly vaulted (sag., tr.) and each ring becomes slightly more independently inflated and set off by longer inter-ring furrows. Anterior bands of second and sometimes third pleurae develop stronger independent inflation. The lateral and posterior borders become slightly more independently inflated.

Discussion. Andrawis *et al*. (1983, p. 66) assigned a single cranidium from a well core in western Egypt to *P. mcallisteri*. As pointed out by Geyer (1990, p. 111), the specimen appears to represent a species of the Cambrian Series 2 ellipsocephalid *Kingaspidoides* Hupé, 1953b.

Although *Protocalymene* is not monotypic, we have not attempted to separate the genus diagnosis from that of the only well known species, *P. mcallisteri*. This is because the other two occurrences are extremely poorly known (a total of four specimens).

Protocalymene sp. of Ross (1970, p. 92, pl. 18, figs 2–5) is known from a cranidium, a librigena, and a pygidium. The quality of the material and illustrations hampers comparison, but it could conceivably be related to *P. mcallisteri*. However, it has a strongly inflated anterior border which directly abuts the front of the glabella, versus a long preglabellar field in *P. mcallisteri*. The librigenal lateral border appears deeper than that of *P. mcallisteri*. The pygidium has six well defined axial rings, whereas those of *P. mcallisteri* have only four. The Ikes Canyon species is obviously calymenoidean, but more material would be required to confirm its genus assignment.

Loch and Ethington (2017, fig. 13.6) illustrated a single partial pygidium as "*Protocalymene* sp." Their specimen has fine tuberculate sculpture on its pleural areas, which matches the morphology in *P. mcallisteri*, but obviously much more material would be necessary to meaningfully evaluate the occurrence.

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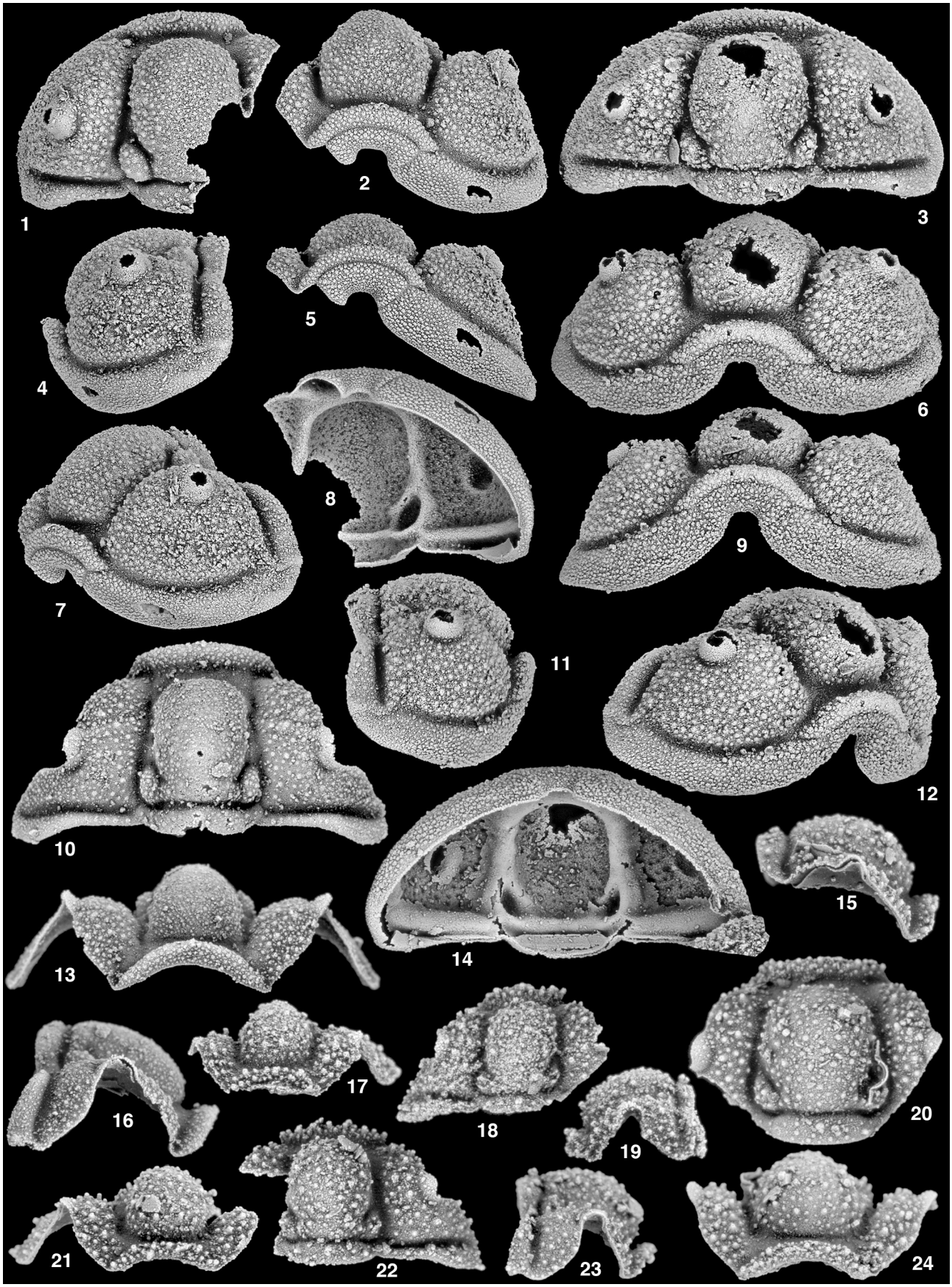

PLATE 1

PLATE 1. *Atlanticalymene bardensis* **n. gen. n. sp.**, from horizon TCM 18 (except where noted), Table Cove Formation (Darriwilian), near Marechal Island, Hare Bay, western Newfoundland, Canada.

1, 2, 4, 5, 7, 8. Cephalon, GSC 135289, dorsal, anterior, left lateral, anteroventral, oblique, and ventral views, x9.
3, 6, 9, 11, 12, 14. Cephalon, GSC 135290, dorsal, anterior, anteroventral, right lateral, oblique, and ventral views, x10.
10, 13, 16. Cranidium, GSC 135291, dorsal, anterior, and right lateral views, x7.5.
15, 20, 24. Cranidium, GSC 135292, right lateral, dorsal, and anterior views, x12 (TCM 14).
17–19. Cranidium, GSC 135293, anterior, dorsal, and left lateral views, x12 (TCM 14).
21–23. Cranidium, GSC 135294, anterior, dorsal, and right lateral views, x12 (TCM 13).

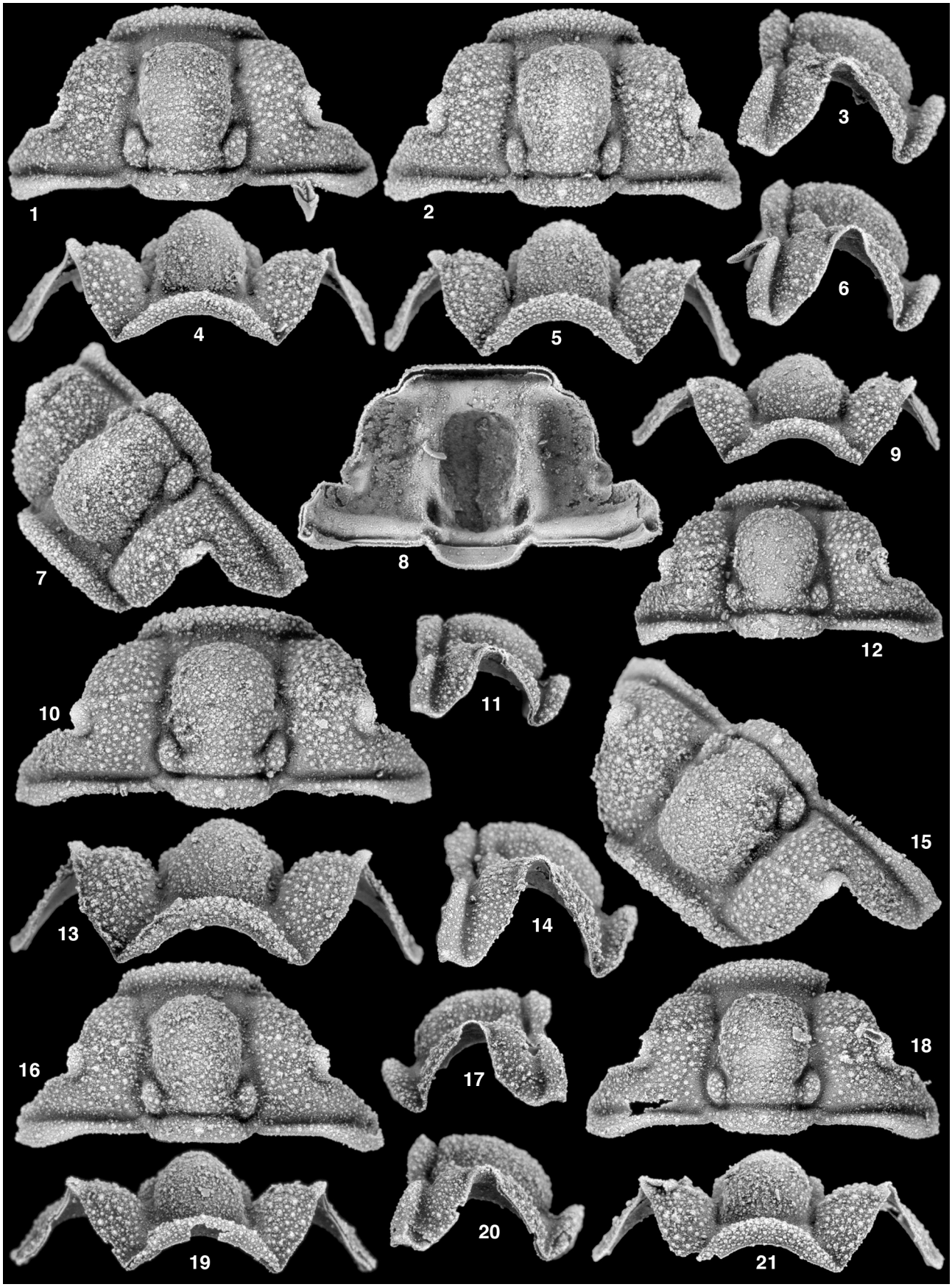

PLATE 2

PLATE 2. *Atlanticalymene bardensis* **n. gen. n. sp.**, large cranidia from horizon TCM 18, Table Cove Formation (Darriwilian), near Marechal Island, Hare Bay, western Newfoundland, Canada. All magnifications are x7.5.

1, 6, 4. Cranidium, GSC 135295, dorsal, anterior, and right lateral views.
2, 3, 5, 7, 8. Cranidium, GSC 135296, dorsal, right lateral, anterior, oblique, and ventral views.
9, 11, 12. Cranidium, GSC 135297, anterior, right lateral, and dorsal views.
10, 13–15. Cranidium, **holotype**, GSC 135298, dorsal, anterior, right lateral, and oblique views.
16, 19, 20. Cranidium, GSC 135299, dorsal, anterior, and right lateral views.
17, 18, 21. Cranidium, GSC 135300, left lateral, dorsal, and anterior views.

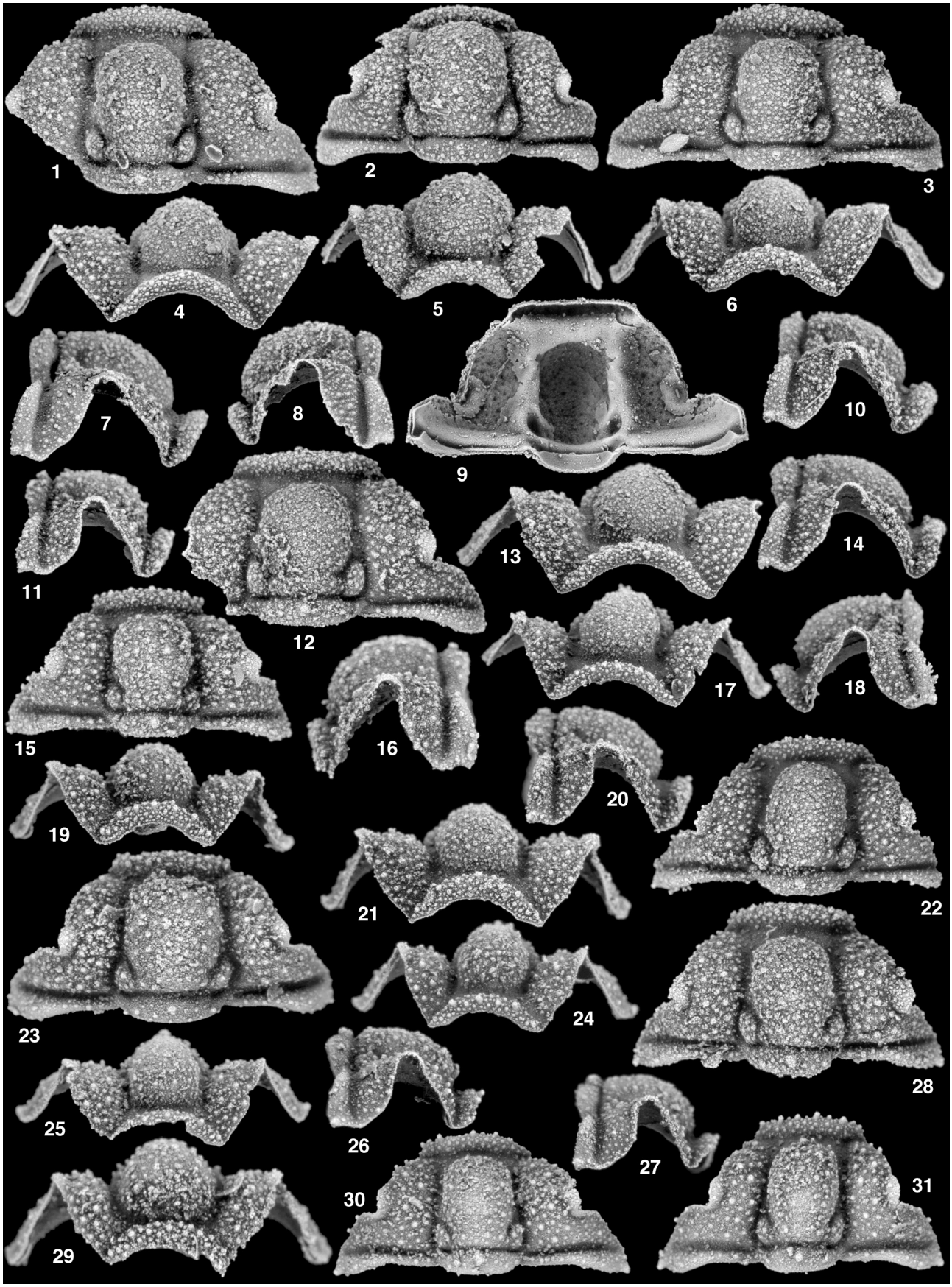
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PLATE 3

PLATE 3. *Atlanticalymene bardensis* **n. gen. n. sp.**, moderate sized and small cranidia from horizon TCM 18, Table Cove Formation (Darriwilian), near Marechal Island, Hare Bay, western Newfoundland, Canada.

1, 4, 7. Cranidium, GSC 135301, dorsal, anterior, and right lateral views, x7.5.
2, 5, 8. Cranidium, GSC 135302, dorsal, anterior, and left lateral views, x7.5.
3, 6, 9, 10. Cranidium, GSC 135303, dorsal, anterior, ventral, and right lateral views, x7.5.
11, 15, 19. Cranidium, GSC 135304, right lateral, dorsal, and anterior views, x10.
12–14. Cranidium, GSC 135305, dorsal, anterior, and right lateral views, x7.5.
16, 23, 29. Cranidium, GSC 135306, left lateral, anterior, and dorsal views, x12.
17, 18, 22. Cranidium, GSC 135307, anterior, left lateral, and dorsal views, x10.
20, 21, 28. Cranidium, GSC 135308, right lateral, anterior, and dorsal views, x10.
24, 26, 31. Cranidium, GSC 135309, anterior, right lateral, and dorsal views, x12.
25, 27, 30. Cranidium, GSC 135310, anterior, right lateral, and dorsal views, x12.

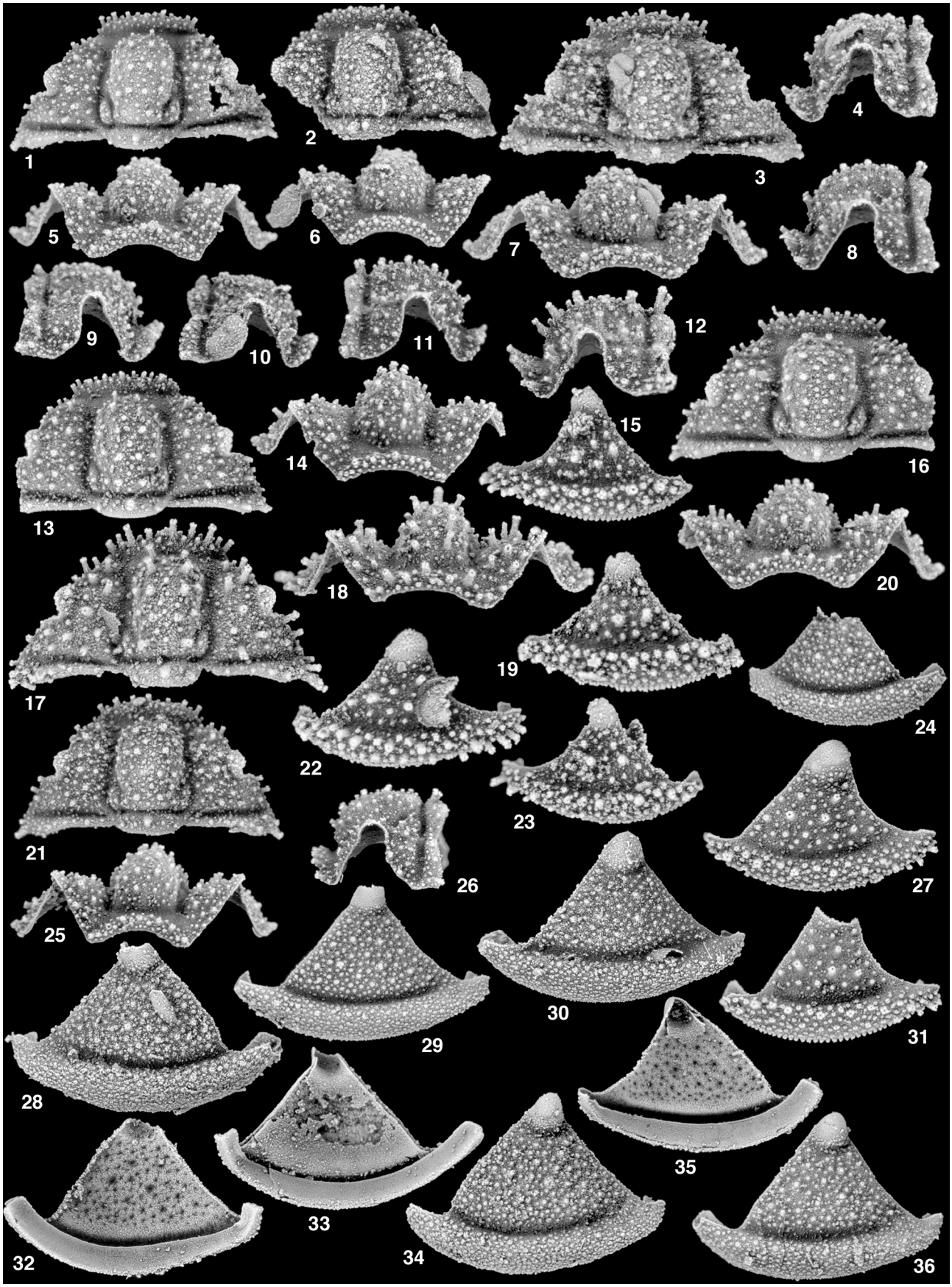
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PLATE 4

PLATE 4. *Atlanticalymene bardensis* **n. gen. n. sp.**, small cranidia and librigenae from horizon TCM 18, Table Cove Formation (Darriwilian), near Marechal Island, Hare Bay, western Newfoundland, Canada.

1, 5, 9. Cranidium, GSC 135311, dorsal, anterior, and right lateral views, x12.
2, 6, 10. Cranidium, GSC 135312, dorsal, anterior, and right lateral views, x12.
3, 4, 7. Cranidium, GSC 135313, dorsal, left lateral, and anterior views, x15.
8, 16, 20. Cranidium, GSC 135314, left lateral, dorsal, and anterior views, x15.
11, 13, 14. Cranidium, GSC 135315, right lateral, dorsal, and anterior views, x15.
12, 17, 18. Cranidium, GSC 135316, left lateral, dorsal, and anterior views, x20.
15. Right librigena, GSC 135317, external view, x25.
19. Right librigena, GSC 135318, external view, x25.
21, 25, 26. Cranidium, GSC 135320, dorsal, anterior, and left lateral views, x12.
22. Left librigena, GSC 135321, external view, x25.
23. Right librigena, GSC 135322, external view, x25.
24. Right librigena, GSC 135319, external view, x12.
27. Left librigena, GSC 135323, external view, x20.
28, 32. Right librigena, GSC 135324, external and internal views, x10.
29, 33. Left librigena, GSC 135325, external and internal views, x10.
30. Left librigena, GSC 135326, external view, x10.
31. Left librigena, GSC 135327, external view, x20.
34. Left librigena, GSC 135328, external view, x10.
35, 36. Left librigena, GSC 135329, internal and external views, x10.

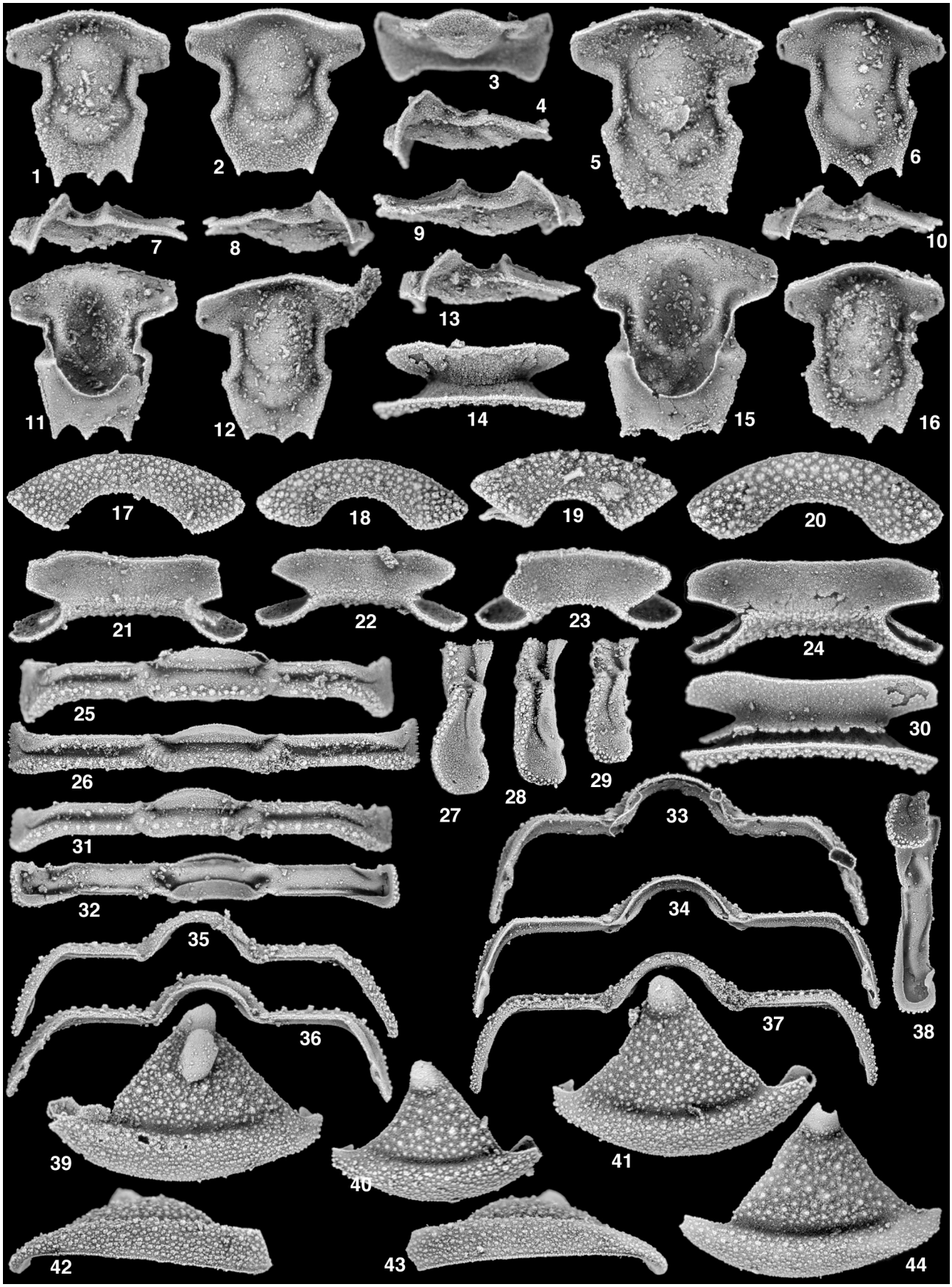
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PLATE 5

PLATE 5. *Atlanticalymene bardensis* **n. gen. n. sp.**, hypostomes, rostral plates, thoracic segments, and librigenae from horizon TCM 18, Table Cove Formation (Darriwilian), near Marechal Island, Hare Bay, western Newfoundland, Canada.

1, 7, 11. Hypostome, GSC 135330, ventral, left lateral, and dorsal views, x12.
2–4. Hypostome, GSC 135331, ventral, posterior, and left lateral views, x12.
5, 9, 15. Hypostome, GSC 135332, ventral, right lateral, and dorsal views, x12.
6, 10. Hypostome, GSC 135333, ventral and left lateral views, x15.
8, 12. Hypostome, GSC 135334, right lateral and ventral views, x12.
13, 16. Hypostome, GSC 135335, left lateral and ventral views, x12.
14, 18, 22. Rostal plate, GSC 135336, internal, ventral, and posterior views, x15.
17, 21. Rostral plate, GSC 135337, ventral and posterior views, x15.
19, 23. Rostral plate, GSC 135338, ventral and posterior views, x20.
20, 24, 30. Rostral plate, GSC 135339, ventral, posterior, and internal views, x20.
25, 27, 33. Thoracic segment, GSC 135340, doral, right lateral, and anterior views, x10.
26, 28, 34, 37. Thoracic segment, GSC 135341, dorsal, right lateral, anterior, and posterior views, x10.
29, 31, 32, 35, 36, 38. Thoracic segment, GSC 135342, right lateral, dorsal, ventral, posterior, anterior, and distal doublural views, x10.
39. Left librigena, GSC 135343, external view, x10.
40. Right librigena, GSC 135344, external view, x12.
41, 42. Right librigena, GSC 135345, external and ventrolateral views, x10.
43, 44. Left librigena, GSC 135346, ventrolateral and external views, x10.

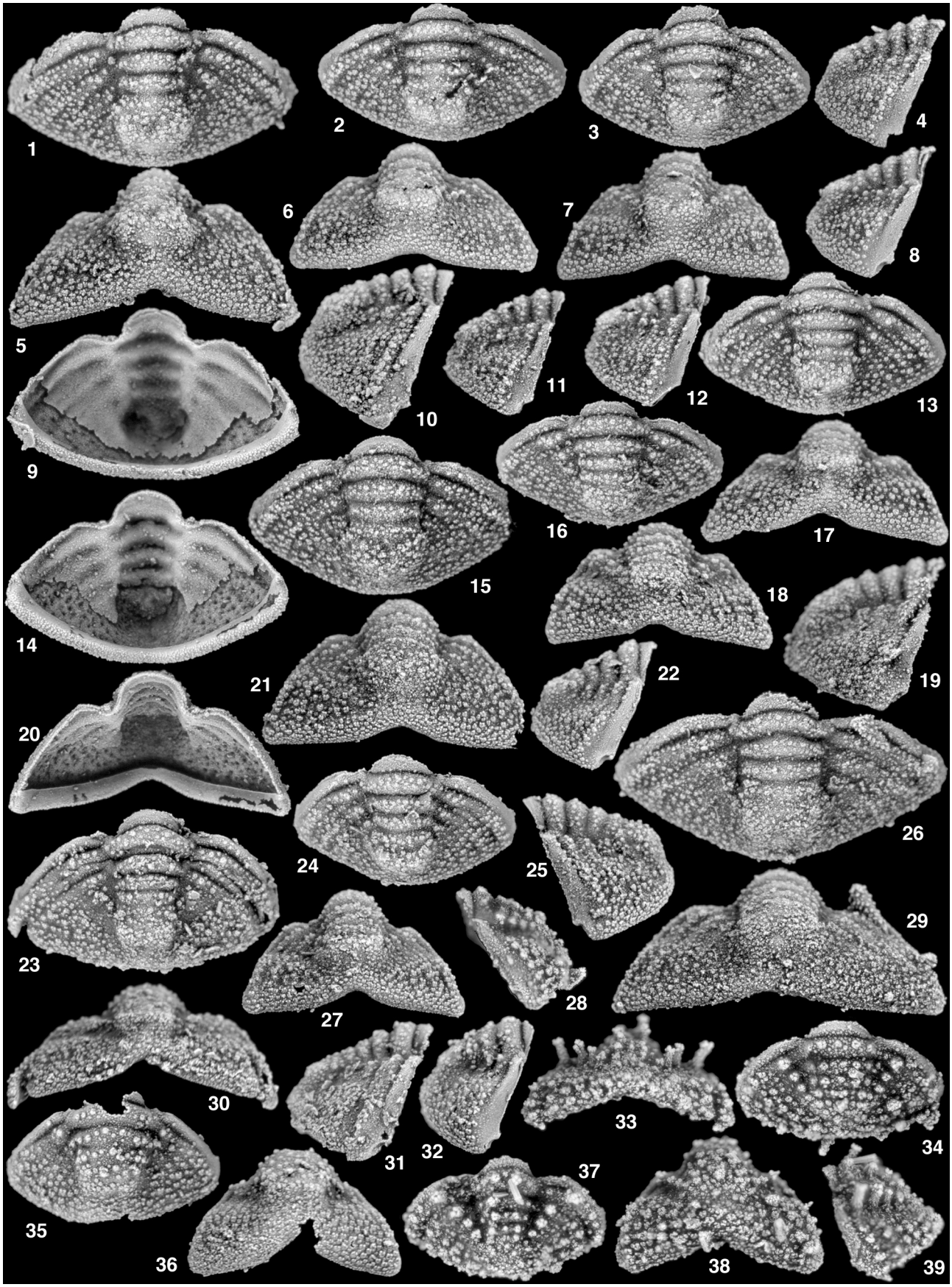
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PLATE 6

PLATE 6. *Atlanticalymene bardensis* **n. gen. n. sp.**, pygidia from horizon TCM 18, Table Cove Formation (Darriwilian), near Marechal Island, Hare Bay, western Newfoundland, Canada.

1, 5, 9, 10. Pygidium, GSC 135347, dorsal, posterior, ventral, and right lateral views, x12.
2, 6, 8. Pygidium, GSC 135348, dorsal, right lateral, and posterior views, x12.
3, 4, 7. Pygidium, GSC 135349, dorsal, posterior, and right lateral views, x12.
11, 16, 18. Pygidium, GSC 135350, right lateral, dorsal, and posterior views, x12.
12, 13, 17. Pygidium, GSC 135351, right lateral, dorsal, and posterior views, x12.
14, 15, 20, 21, 25. Pygidium, GSC 135352, ventral, dorsal, anterior, posterior, and left lateral views, x12.
19, 26, 29. Pygidium, GSC 135353, right lateral, dorsal, and posterior views, x12.
22, 24, 27. Pygidium, GSC 135354, right lateral, dorsal, and posterior views, x12.
23, 30, 31. Pygidium with attached thoracic segment, GSC 135355, dorsal, posterior, and right lateral views, x12.
28, 34, 38. Pygidium, GSC 135356, left lateral, dorsal, and posterior views, x25.
32, 35, 36. Pygidium, GSC 135357, right lateral, dorsal, and posterior views, x15.
33, 37, 39. Pygidium, GSC 135358, posterior, dorsal, and left lateral views, x30.

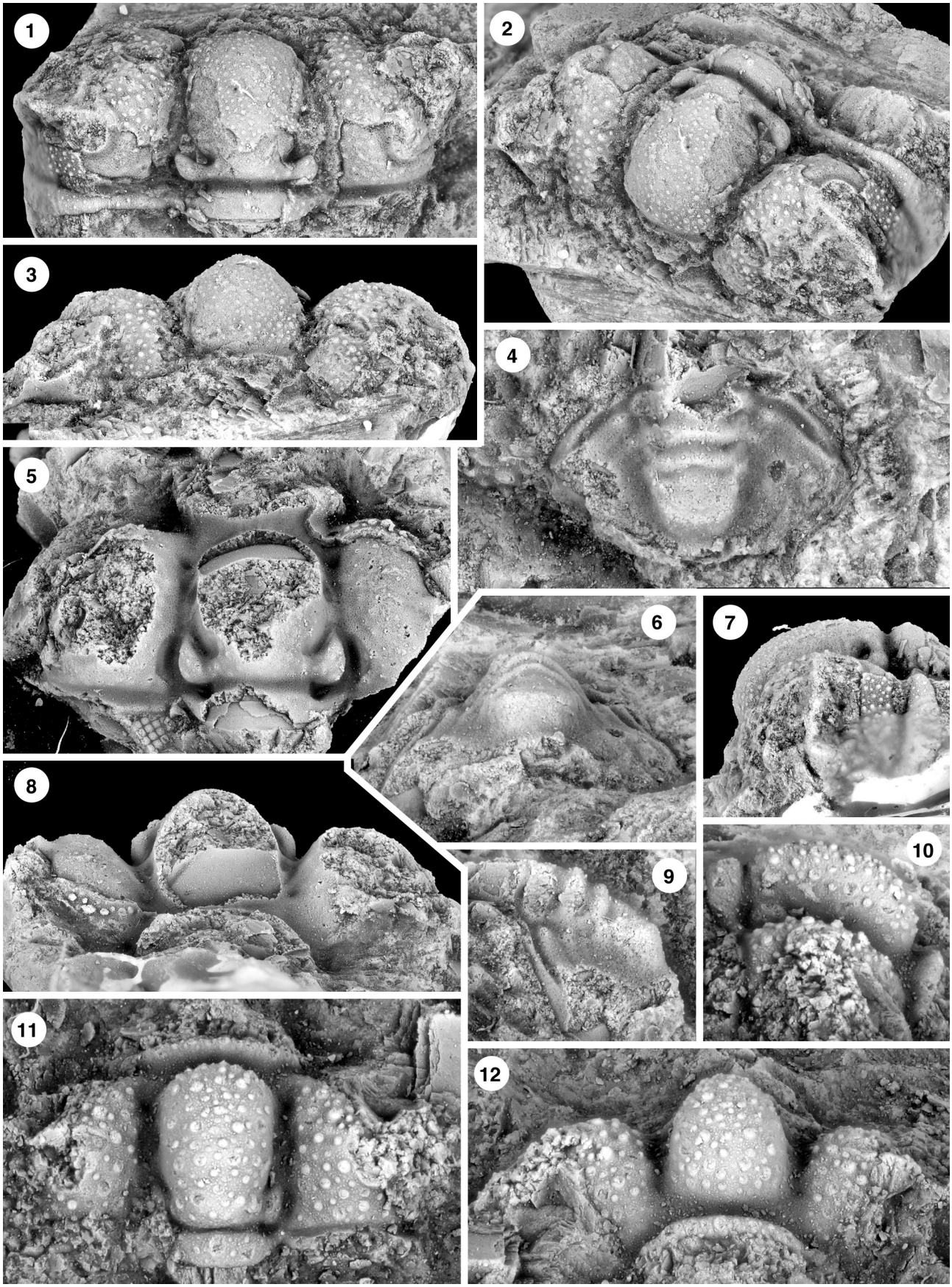

PLATE 7

PLATE 7. *Atlanticalymene bardensis* **n. gen. n. sp.**, calcareous "crackout" specimens from the Table Cove Formation (Darriwilian), Table Cove, west coast of the Great Northern Peninsula, western Newfoundland, Canada.

1–3, 7. Cranidium, GSC 18469 ("*Ischyrophyma*? sp. ind." of Whittington, 1965, p. 340, pl. 19, figs. 16, 19, 20), dorsal, oblique, anterior, and left lateral views, x12.
4, 6, 9. Pygidium, GSC 18569 ("Komaspidid? pygidium" of Whittington, 1965, p. 374, pl. 39, figs. 8, 9), dorsal, posterior, and left lateral views, x20.
5, 8. Cranidium, GSC 18345 ("aff. *Calymenidius* sp. ind." of Whittington, 1965, p. 419, pl. 59, figs. 14, 15), dorsal and anterior views, x10.
10–12. Cranidium, GSC 18346 ("aff. *Calymenidius* sp. ind." of Whittington, 1965, p. 419, pl. 59, figs. 10, 12, 13), right lateral, dorsal, and anterior views, x25.

PLATE 8

PLATE 8. *Protocalymene mcallisteri* Ross, 1967, from the Antelope Valley Formation (Dapingian), west flank of Funeral Mountains, Death Valley National Park, Inyo County, eastern California, USA.

1, 4, 7. Cranidium, SUI 137444, dorsal, right lateral, and anterior views, x10.
2, 5, 8, 11, 12. Cranidium, SUI 137445, dorsal, ventral, anterior, oblique, and left lateral views, x10.
3, 6, 9. Cranidium, SUI 137446, dorsal, anterior, and right lateral views, x12.
10, 13, 14, 16, 17. Cranidium, SUI 137447, dorsal, ventral, left lateral, oblique, and anterior views, x12.
15, 18, 19. Cranidium, SUI 137448, dorsal, left lateral, and anterior views, x12.
20–22. Cranidium, SUI 137449, anterior, dorsal, and left lateral views, x12.

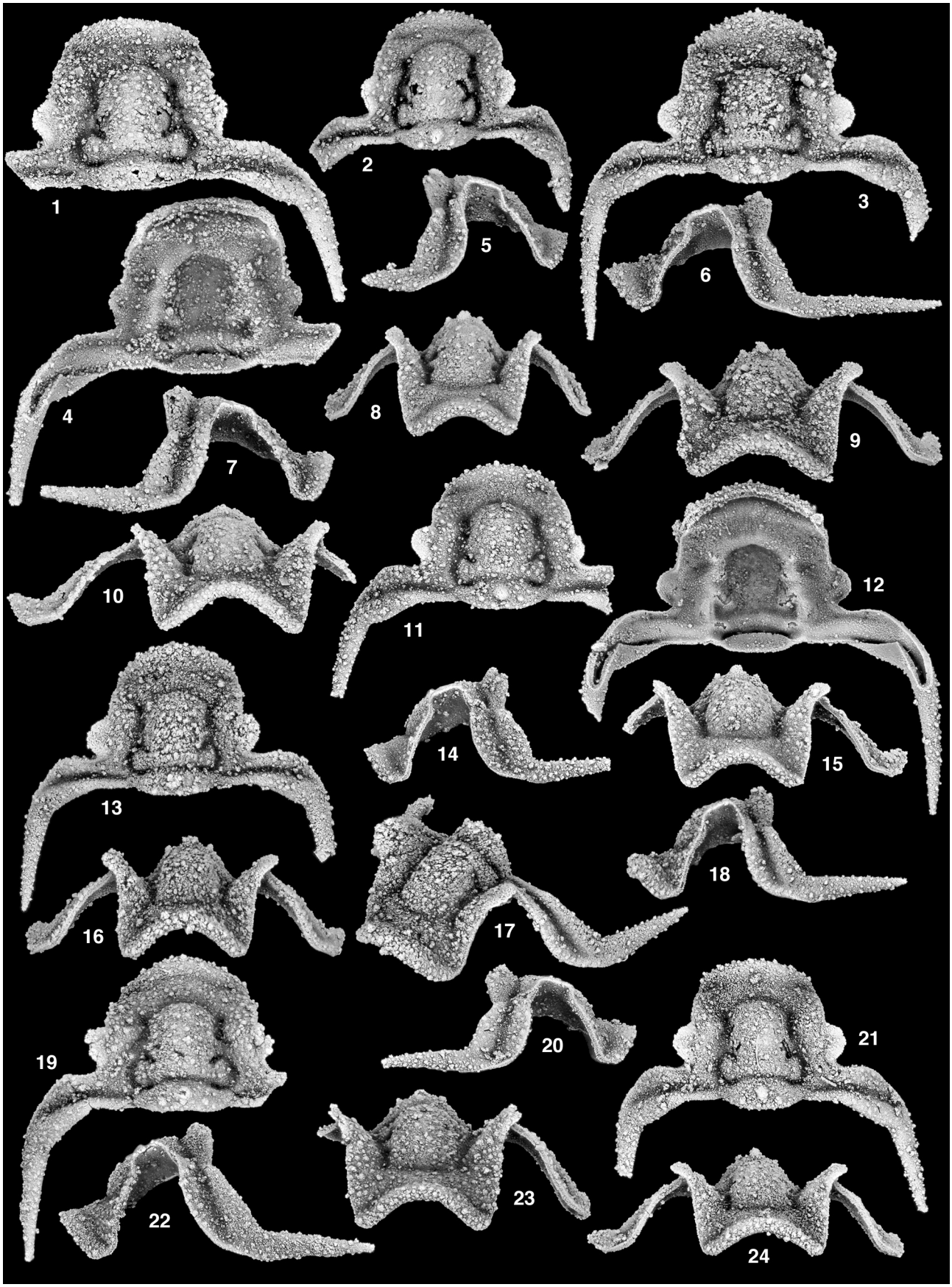

PLATE 9

PLATE 9. *Protocalymene mcallisteri* Ross, 1967, from the Antelope Valley Formation (Dapingian), west flank of Funeral Mountains, Death Valley National Park, Inyo County, eastern California, USA. All magnifications are x12.

1, 4, 7, 10. Cranidium, SUI 137450, dorsal, ventral, right lateral, and anterior views.
2, 5, 8. Cranidium, SUI 137451, dorsal, right lateral, and anterior views.
3, 6, 9, 12. Cranidium, SUI 137452, dorsal, left lateral, anterior, and ventral views.
11, 14, 15. Cranidium, SUI 137453, dorsal, left lateral, and anterior views.
13, 16–18. Cranidium, SUI 137454, dorsal, anterior, oblique, and left lateral views.
19, 22, 23. Cranidium, SUI 137455, dorsal, left lateral, and anterior views.
20, 21, 24. Cranidium, SUI 137456, right lateral, dorsal, and anterior views.

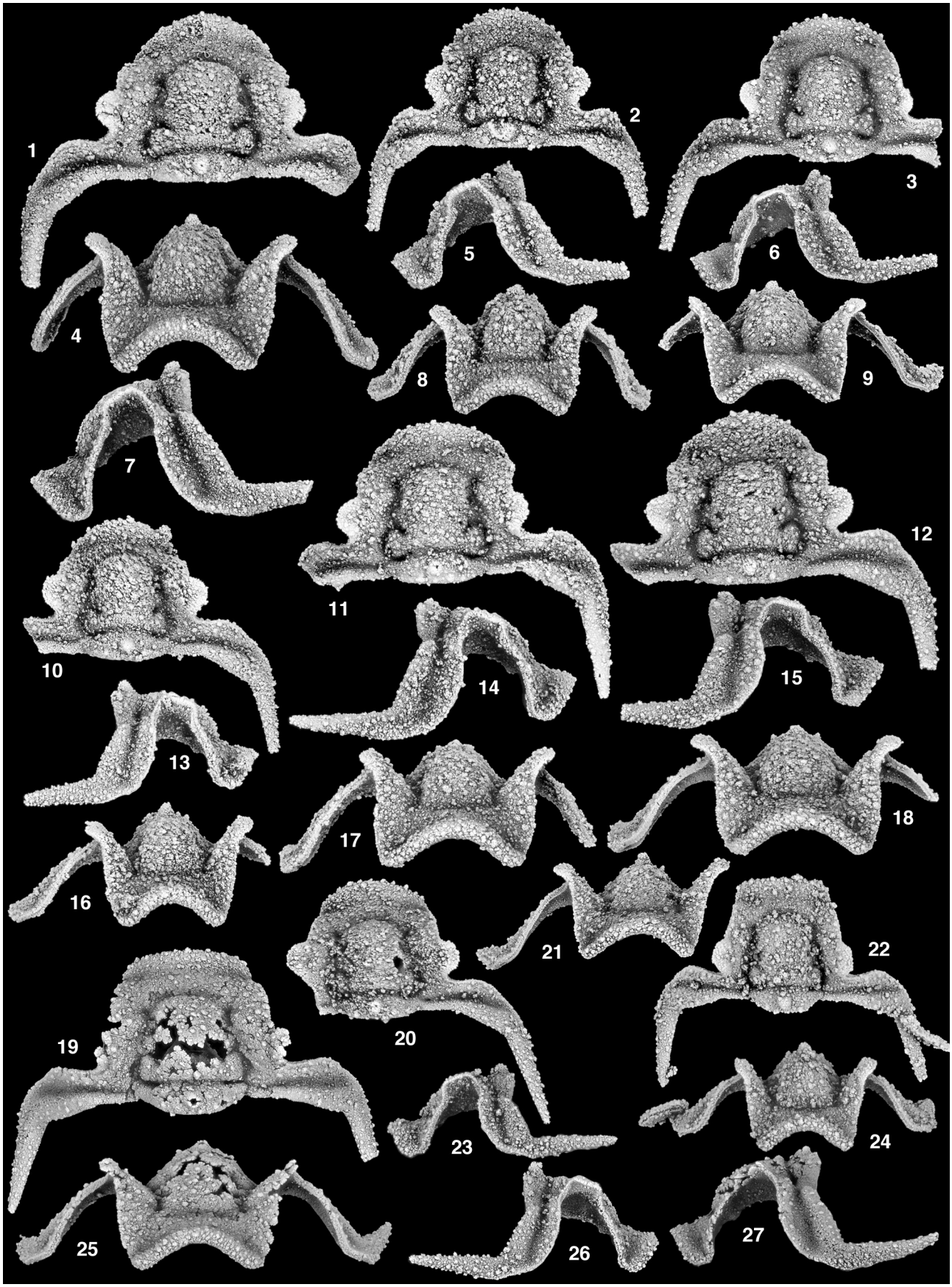

PLATE 10

PLATE 10. *Protocalymene mcallisteri* Ross, 1967, from the Antelope Valley Formation (Dapingian), west flank of Funeral Mountains, Death Valley National Park, Inyo County, eastern California, USA. All magnifications are x12.

1, 4, 7. Cranidium, SUI 137457, dorsal, anterior, and left lateral views.
2, 5, 8. Cranidium, SUI 137458, dorsal, left lateral, and anterior views.
3, 6, 9. Cranidium, SUI 137459, dorsal, left lateral, and anterior views.
10, 13, 16. Cranidium, SUI 137460, dorsal, right lateral, and anterior views.
11, 14, 17. Cranidium, SUI 137461, dorsal, right lateral, and anterior views.
12, 15, 18. Cranidium, SUI 137462, dorsal, right lateral, and anterior views.
19, 25, 27. Cranidium, SUI 137463, dorsal, anterior, and left lateral views.
20, 21, 26. Cranidium, SUI 137464, dorsal, anterior, and right lateral views.
22–24. Cranidium, SUI 137465, dorsal, left lateral, and anterior views.

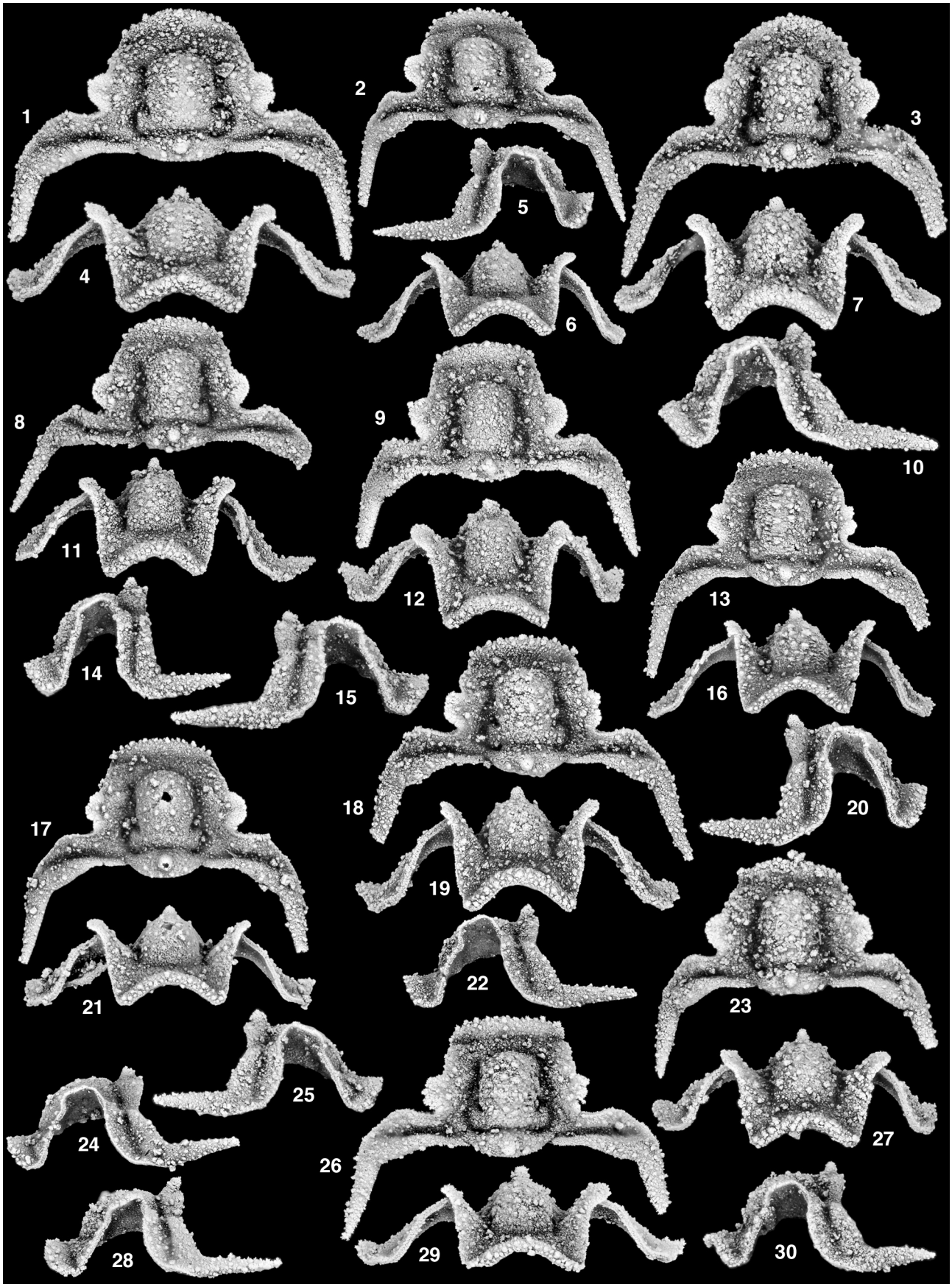
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PLATE 11

PLATE 11. *Protocalymene mcallisteri* Ross, 1967, from the Antelope Valley Formation (Dapingian), west flank of Funeral Mountains, Death Valley National Park, Inyo County, eastern California, USA.

1, 4, 15. Cranidium, SUI 137466, dorsal, anterior, and right lateral views, x15.
2, 5, 6. Cranidium, SUI 137467, dorsal, right lateral, and anterior views, x15.
3, 7, 10. Cranidium, SUI 137468, dorsal, anterior, and left lateral views, x15.
8, 11, 14. Cranidium, SUI 137469, dorsal, anterior, and left lateral views, x15.
9, 12, 25. Cranidium, SUI 137470, dorsal, anterior, and right lateral views, x15.
13, 16, 22. Cranidium, SUI 137471, dorsal, anterior, and left lateral views, x15.
17, 21, 24. Cranidium, SUI 137472, dorsal, anterior, and left lateral views, x17.
18–20. Cranidium, SUI 137473, dorsal, anterior, and right lateral views, x17.
23, 27, 30. Cranidium, SUI 137474, dorsal, anterior, and left lateral views, x20.
26, 28, 29. Cranidium, SUI 137475, dorsal, left lateral, and anterior views. x17.

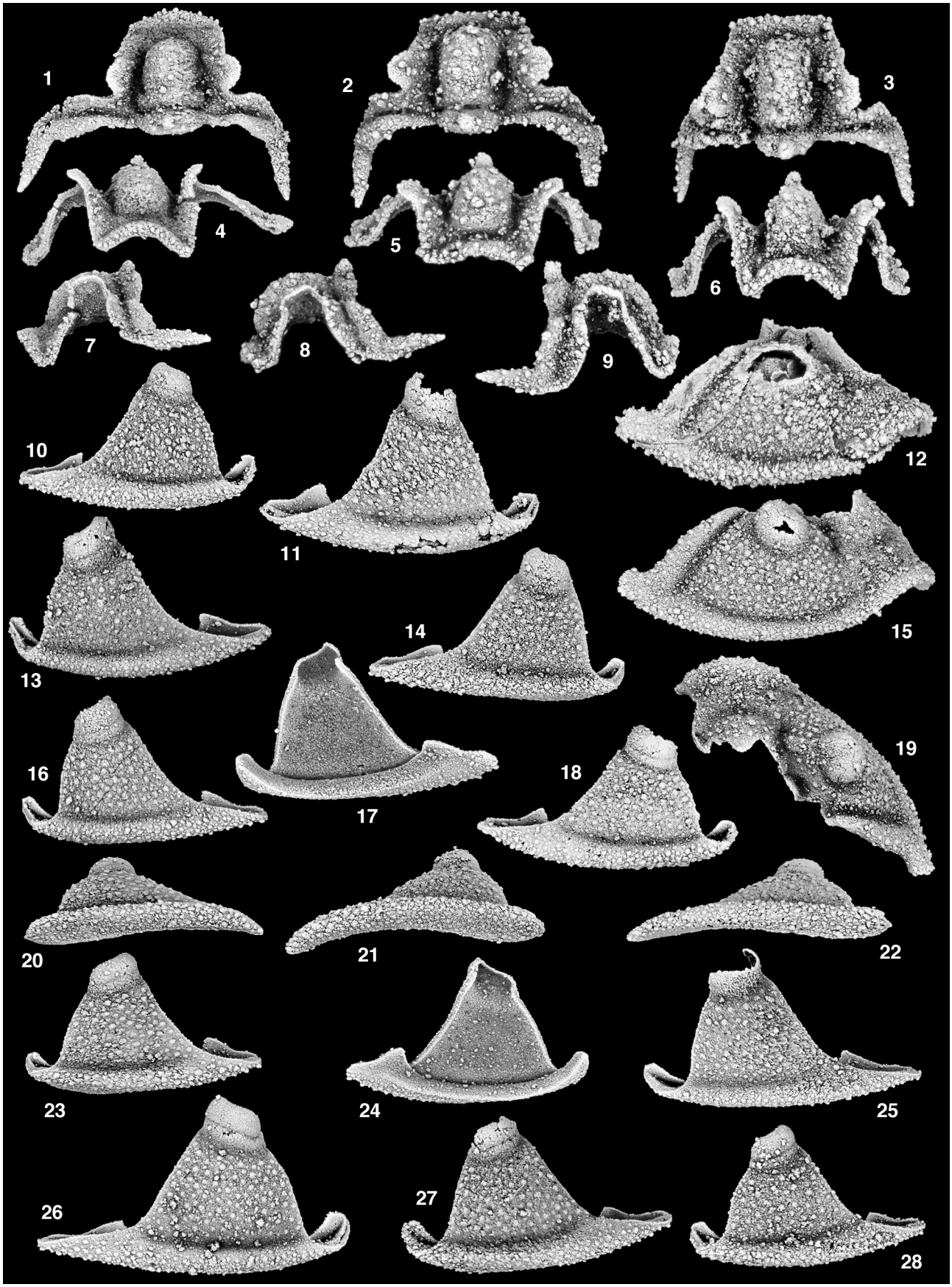

PLATE 12

PLATE 12. *Protocalymene mcallisteri* Ross, 1967, from the Antelope Valley Formation (Dapingian), west flank of Funeral Mountains, Death Valley National Park, Inyo County, eastern California, USA.

1, 4, 7. Cranidium, SUI 137476, dorsal, anterior, and left lateral views, x15.
2, 5, 8. Cranidium, SUI 137477, dorsal, anterior, and left lateral views, x25.
3, 6, 9. Cranidium, SUI 137478, dorsal, anterior, and right lateral views, x25.
10. Right librigena, SUI 137479, external view, x12.
11. Right librigena, SUI 137480, external view, x12.
12. Fragment of cranidium and right librigena, SUI 137481, external view, x15.
13. Left librigena, SUI 137482, external view, x12.
14, 17, 21. Right librigena, SUI 137483, external, internal, and ventrolateral views, x12.
15, 19. Fragment of cranidium and right librigena, SUI 137484, external and dorsal views, x12.
16. Left librigena, SUI 137485, external view, x12.
18, 22. Right librigena, SUI 137486, external and ventrolateral views, x12.
20, 23, 24. Left librigena, SUI 137487, ventrolateral, external, and internal views, x12.
25. Left librigena, SUI 137488, external view, x12.
26. Right librigena, SUI 137489, external view, x12.
27. Left librigena, SUI 137490, external view, x12.
28. Left librigena, SUI 137491, external view, x12.

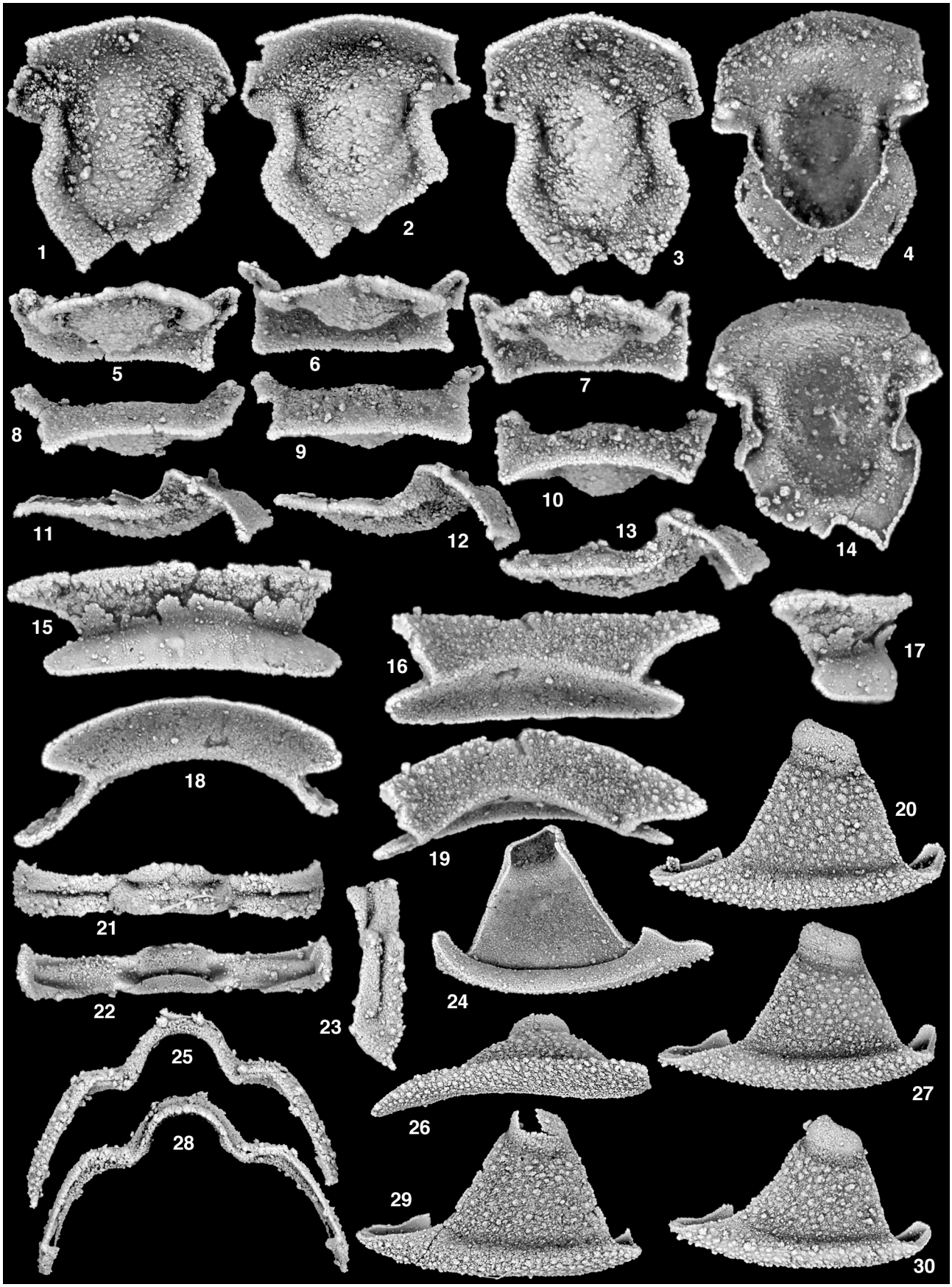
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PLATE 13

PLATE 13. *Protocalymene mcallisteri* Ross, 1967, from the Antelope Valley Formation (Dapingian), west flank of Funeral Mountains, Death Valley National Park, Inyo County, eastern California, USA.

1, 5, 8, 11, 14. Hypostome, SUI 137492, ventral, posterior, anterior, right lateral, and dorsal views, x30.
2, 6, 9, 12. Hypostome, SUI 137493, ventral, posterior, anterior, and right lateral views, x30.
3, 4, 7, 10, 13. Hypostome, SUI 137494, ventral, dorsal, posterior, anterior, and right lateral views, x30.
15–19. Rostral plate, SUI 137495, internal, external, left lateral, doublural, and border sector views, x30.
20. Right librigena, SUI 137496, external view, x15.
21–23, 25, 28. Thoracic segment, SUI 137497, dorsal, ventral, left lateral, posterior, and anterior views, x20.
24, 26, 27. Right librigena, SUI 137498, internal, ventrolateral, and external views, x15.
29. Right librigena, SUI 137499, external view, x15.
30. Right librigena, SUI 137500, external view, x15.

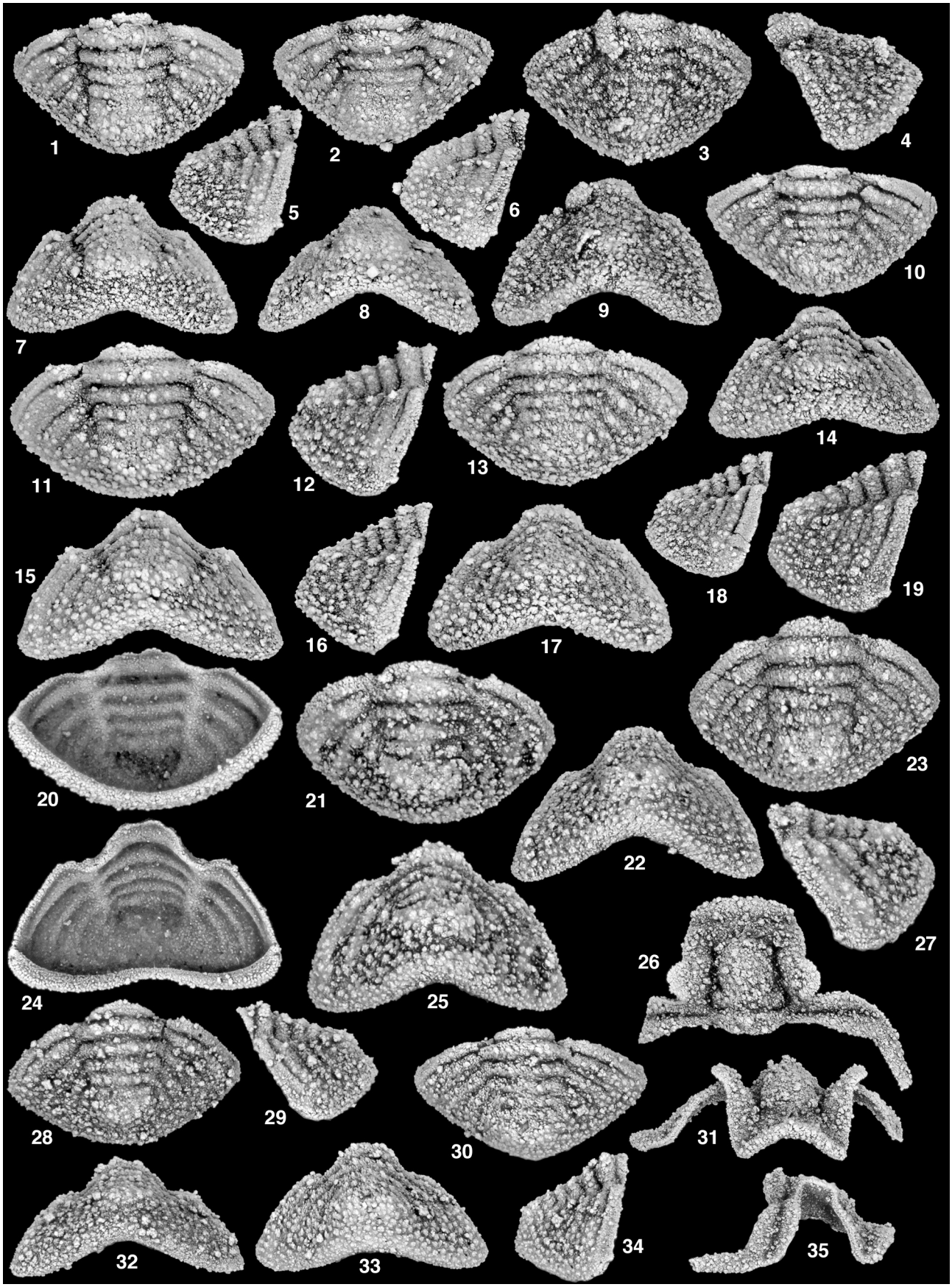
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PLATE 14

PLATE 14. *Protocalymene mcallisteri* Ross, 1967, from the Antelope Valley Formation (Dapingian), west flank of Funeral Mountains, Death Valley National Park, Inyo County, eastern California, USA.

1, 5, 7. Pygidium, SUI 137501, dorsal, right lateral, and posterior views, x20.
2, 6, 8. Pygidium, SUI 137502, dorsal, right lateral, and posterior views, x20.
3, 4, 9. Pygidium, SUI 137503, dorsal, left lateral, and posterior views, x20.
10, 14, 18. Pygidium, SUI 137504, dorsal, posterior, and right lateral views, x20.
11, 12, 15, 20, 24. Pygidium, SUI 137505, dorsal, right lateral, posterior, ventral, and anterior views, x25.
13, 16, 17. Pygidium, SUI 137506, dorsal, right lateral, and posterior views, x25.
19, 22, 23. Pygidium, SUI 137507, right lateral, posterior, and dorsal views, x25.
21, 25, 27. Pygidium, SUI 137508, dorsal, posterior, and left lateral views, x25.
26, 31, 35. Cranidium, SUI 137509, dorsal, anterior, and right lateral views, x12.
28, 29, 32. Pygidium, SUI 137510, dorsal, left lateral, and posterior views, x20.
30, 33, 34. Pygidium, SUI 137511, dorsal, posterior, and right lateral views, x20.

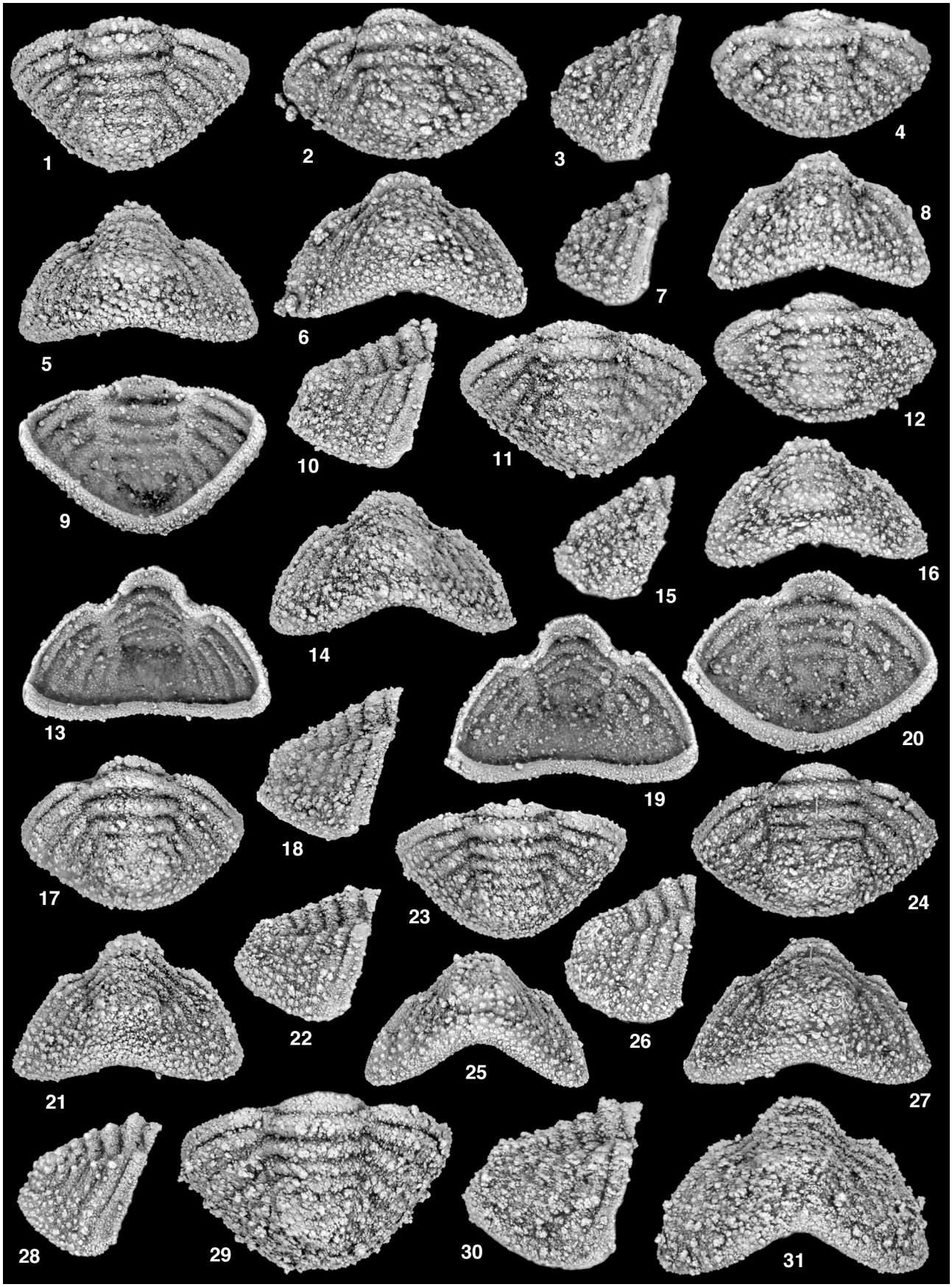
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PLATE 15

PLATE 15. *Protocalymene mcallisteri* Ross, 1967, from the Antelope Valley Formation (Dapingian), west flank of Funeral Mountains, Death Valley National Park, Inyo County, eastern California, USA.

1, 5, 9, 10, 13. Pygidium, SUI 137512, dorsal, posterior, ventral, right lateral, and anterior views, x20.
2, 3, 6. Pygidium, SUI 137513, dorsal, right lateral, and posterior views, x25.
4, 7, 8. Pygidium, SUI 137514, dorsal, right lateral, and posterior views, x30.
11, 14, 18–20. Pygidium, SUI 137515, dorsal, posterior, anteiror, and ventral views, x20.
12, 15, 16. Pygidium, SUI 137516, dorsal, right lateral, and posterior views, x25.
17, 21, 28. Pygidium, SUI 137517, dorsal, posterior, and right lateral views, x20.
22, 23, 25. Pygidium, SUI 137518, right lateral, dorsal, and posterior views, x20.
24, 26, 27. Pygidium, , SUI 137519, dorsal, right lateral, and posterior views, x20.
29–31. Pygidium, SUI 137520, dorsal, right lateral, and posterior views, x20.