

# An Edgewood-type Hirnantian fauna from the Mackenzie Mountains, northwestern margin of Laurentia

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**Non-technical Summary.**—A major glaciation can have fundamental effects on the diversity and global distribution of marine invertebrate organisms. This study documents brachiopods from a shelly benthic marine fauna in northwestern Canada during the first major glaciation of the Phanerozoic Era, in the latest Ordovician Period. The study area in the Mackenzie Mountains was located in the northern-hemisphere tropics during the Late Ordovician. The presence of a unique glaciation-age brachiopod fauna in both the southern-hemisphere tropics of ancient North America (in today's southeastern USA) and the Mackenzie Mountains indicates the far reach of the latest Ordovician glaciation centered in the southern Polar region.

**Abstract.**—Silicified brachiopods from Hirnantian strata in three sections of the lower Whittaker Formation, Mackenzie Mountains, northwestern Canada, yielded a moderately diverse, Edgewood-type Hirnantian fauna, consisting of 13 species: *Biparetis paucirugosus*, *Brevilamnulella laevis*, *Dalmanella edgewoodensis*, *Drabovia noixella*, *Eospirigerina putilla*, *Epitomyonia paucitropida*, *Epitomyonia sekwiensis*, *Glyptorthis papillosa* new species, *Gnamptorhynchos orbiculoidea*, *Katastrophomena mackenzii* new species, *K. parvicardinis*, *Parastrophina* cf. *P. minor*, and *Skenidioides* sp. Compared to the typical Edgewood fauna of the American Midcontinent, *Brevilamnulella laevis* has a notably smaller shell than *B. thebesensis*, and is interpreted as a deeper-water form. The strong faunal affinity of the Mackenzie Mountains fauna to the Edgewood-type Hirnantian fauna is indicated by the occurrence of *Biparetis*, *Brevilamnulella*, *Eospirigerina*, and *Gnamptorhynchos*. In addition to the Edgewood type area within Laurentia, *Biparetis*, *Eospirigerina*, and *Gnamptorhynchos* are characteristic taxa that also occur in the Ellis Bay Formation (Hirnantian) of Anticosti Island. Multivariate and network analyses strongly support the differentiation between an Edgewood-type Hirnantian fauna in Laurentia and peri-Laurentia and the typical *Hirnantia* fauna of the Kosov Province in Gondwana, peri-Gondwana, South China, Kazakhstan terranes, Avalonia, and Baltica.

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## Introduction

Compared to its widespread distribution, the classic *Hirnantia* fauna typical of the Kosov Province (see recent summary by Rong et al., 2020), characterized by the presence of *Hirnantia sagittifera* (M'Coy, 1851) and commonly associated species, is relatively rare in Laurentia; it is known so far only from two major areas along its eastern margin: Percé, Quebec (Lespérance and Sheehan, 1976) and Anticosti Island (Jin and Zhan, 2008; Copper et al., 2013; Zimmit and Jin, 2023). With increasing geochemical and palynological support for the entire Ellis Bay Formation being Hirnantian in age (Delabroye et al., 2011; Achab et al., 2013; Mauviel and Desrochers, 2016; Mauviel et al., 2020), it has become apparent that the Hirnantian fauna in eastern Laurentia had a surprisingly high overall diversity,

represented by nearly 60 species of brachiopods. In addition to the list of 55 species in Copper et al. (2013), several species belonging to *Cliftonia*, *Dalmanella*, *Gnamptorhynchos*, *Koigia*, and *Platytrichalos*, previously unknown from the Ellis Bay Formation, have been discovered from its top Laframboise Member, and await systematic description. The highly diverse brachiopod community is also reflected by the presence of two species of *Hirnantia*, with *H. notiskuani* Zimmit and Jin, 2023, in the basal part, and *H. sagittifera* in the top part of the formation.

Along the western margin of Laurentia, a Hirnantian-age brachiopod fauna has been generally known but has not been constrained either taxonomically or stratigraphically. In addition to the two samples of silicified brachiopods reported by Jin and Chatterton (1997) from the Avalanche Lake area (section AV1, 77.5–95.5 m, and section AV4B, 111.3–111.66 m), assigned by Rong et al. (2020) to the Edgewood-type fauna, another spot collection (S-2) from the central Mackenzie Mountains (made by Wigington in the 1970s as part of his MSc thesis project,

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but not described in the thesis) has yielded a silicified brachiopod assemblage that has a high level of similarity to the Avalanche Lake material, especially in the common occurrence of *Eospirigerina putilla* (Hall and Clarke, 1894), and *Gnamptorhynchos orbiculoidea* (Jin and Chatterton, 1997).

In terms of Late Ordovician paleogeography, the Mackenzie Mountains region straddled a transitional zone between the Mackenzie carbonate platform and the deep-water Selwyn Basin (Fig. 1; see also Cecile and Norford, 1993; Jin and Chatterton, 1997). Paleobiogeographically, this region was aligned along the same paleolatitudes as the late Katian warm-water *Tcherskidium* fauna that occurred abundantly in the paleoequatorial and lower paleotropics of the Late Ordovician northern hemisphere, such as northeastern Alaska (marginal Laurentia), Alaska accreted terranes, Kolyma, Siberia, northern Baltica, Kazakh terranes, and South China (Jin et al., 2022). In faunal composition, however, the Mackenzie Mountains region was characterized by a diverse Katian brachiopod fauna that resembled most closely the Red River brachiopod fauna in the southern paleotropics (Wigington, 1977; Mitchell, 1978; Jin and Lenzen, 1992). Within Laurentia, the Mackenzie Mountains brachiopod fauna appeared to show a high level of distinctness along the western margin of Laurentia, and a clear differentiation from the “epicontinental sea brachiopod fauna” from inland basins (Jin et al., 2014). Such a faunal differentiation appears to have persisted into the Hirnantian, as suggested by the Hirnantian fauna synthesized in this study, as will be discussed in more detail in subsequent sections. Nowlan et al. (1988) also recognized a similar conodont faunal distinctness of the southern Mackenzie Mountains because of the total lack of the *Amorphognathus* lineage, which was common in the American Midcontinent conodont fauna. The main objective of this study, therefore, is to examine the Hirnantian brachiopod fauna of the Mackenzie Mountains and explore its paleobiogeographic significance.

## Geological and stratigraphic settings

From Late Ordovician to early Silurian, the study area in southern and central Mackenzie Mountains was located on the southwestern margin of the extensive Mackenzie Platform in northwestern Laurentia (Fig. 1; Cecile and Norford, 1993). This part of the carbonate platform was bordered to the west by the deep-water Selwyn Basin, to the south by the Meilleur River Embayment, and to the southeast by the small Root Basin. The Avalanche Lake sections, in particular, were located in the transitional zone between platform carbonate and basinal facies of the Selwyn Basin (see Jin and Chatterton, 1997, textfig. 1). However, incursion of deep-water deposits in this area, represented by micritic and clay shales of the Road River Formation, occurred mostly in the Silurian, especially during the early and later Wenlock. During the Hirnantian sea-level lowstand, the study area received predominantly shallow-water deposits, represented by the fossiliferous carbonate of the lower Whittaker Formation.

In the Avalanche Lake sections, the Whittaker Formation was divided into three informal members by Over and Chatterton (1987), ranging from upper Katian or Richmondian (basal

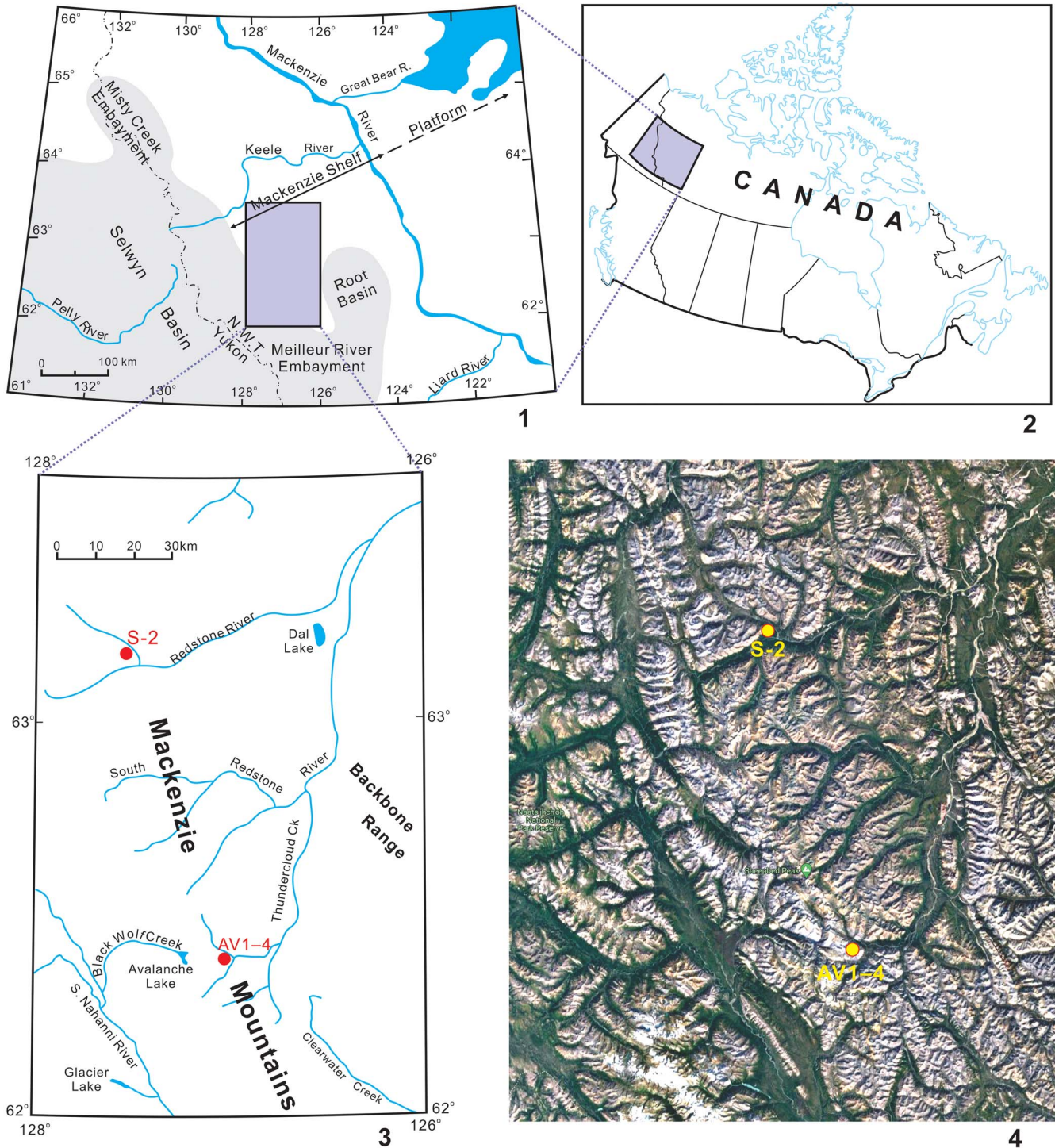
member 1; see Nowlan et al., 1988, p. 7) to basal Wenlock (uppermost member 3). The Hirnantian fauna described in this study occurs in the middle part of member 1, which consists of dark-gray, thin- to medium-bedded, argillaceous limestone, commonly with bands of silicified fossils, with brachiopods and trilobites (e.g., Chatterton and Perry, 1983) being most common.

Among the seven stratigraphic sections examined by Chatterton and his group (Chatterton and Perry, 1983, 1984), only two contained the Ordovician–Silurian boundary interval and yielded a Hirnantian fauna: section AV1 (77.5–97.5 m above base of section), and section AV4B (111.3–111.8 m above base of section). Conodonts from the Ordovician–Silurian boundary interval in either section AV1 and AV4B were considered undiagnostic (Over and Chatterton, 1987). Nowlan et al. (1988) identified the highest level of conodonts of Late Ordovician aspects at AV1 77.0 m and AV4 111.0 m, and the lowest level of conodonts of early Silurian aspects at AV1 84.5 m and AV4B 111.6 m, with conodonts from intervals AV1 77.0–84.5 m and AV4B 111.0–111.6 m being biostratigraphically undiagnostic. The graptolite data (provided by M.J. Melchin as an appended note in Wang et al., 1993), however, indicate that the upper Hirnantian *Normalograptus persculptus* Biozone occurs in AV4B 111.6–112.6 m, as indicated by the occurrence of *N. persculptus* (Elles and Wood, 1907) and other congeneric species. This strongly supports an overall Hirnantian age for the AV4B 111.3–111.8 m interval that yielded the brachiopod fauna described in this study. Section AV4B does not show any notable disconformity at the Ordovician–Silurian boundary interval except for a minor irregular (possibly erosional) bedding surface at 111.0 m. The lower Hirnantian *N. extraordinarius* Biozone, therefore, would easily encompass the AV4B 111.3–111.6 m interval (see Jin and Chatterton, 1997, for more detailed discussion).

The spot collection S-2 from the central Mackenzie Mountains was estimated by Wigington (1977) to be from a level about 15 ft from the top of the section exposing the lower Whittaker Formation. The sample label also indicates a stratigraphic level at 2150–2153 ft (655.3–656.2 m) above the base of the section. Collection S-2 shared three brachiopod species with the Avalanche Lake fauna, *Eospirigerina putilla*, *Gnamptorhynchos orbiculoidea*, and *Katastrophomena mackenzii* n. sp., which are the numerically dominant taxa in these faunas, and thus suggest their coeval relationships.

As discussed in the section on systematic paleontology, the Mackenzie Mountains fauna shared a number of key genera or species with the Edgewood fauna of Amsden (1974), such as *Biparetis paucirugosus* Amsden, 1974, *Brevilamnulella*, *Dra- bovia noixella* (Amsden, 1974), *Eospirigerina putilla*, *Epitomyonia*, and *Gnamptorhynchos orbiculoidea*. These seem to corroborate the Hirnantian age for the stratigraphic intervals examined in this study.

*Age of the Edgewood-type Hirnantian fauna in Laurentia.*—In North America and North Greenland, most of the Edgewood fauna intervals have not been dated precisely because of the lack of age-diagnostic graptolites and conodonts. Thus, the exact range of these strata within the Hirnantian remains to be determined.



**Figure 1.** Locality map showing occurrences of *Hirnantia* fauna in the Mackenzie Mountains (modified from Jin and Chatterton, 1997, and Chen et al., 2008). S-2, spot collection, central Mackenzie Mountains (see Wigington, 1977; Chen et al., 2008).

In the ongoing investigations regarding the early versus late Hirnantian age for the Edgewood fauna in Laurentia, three factors should be taken into consideration. (1) On Anticosti Island, the debate a decade ago was whether or not the lower part of the Ellis Bay Formation was upper Katian or Hirnantian. More recently, studies (see summaries in Achab et al., 2013; Copper

et al., 2013; Mauviel and Desrochers, 2016; Mauviel et al., 2020) have shown that not only is the entire Ellis Bay Formation Hirnantian, but a few meters of strata below and above the Ellis Bay Formation may also be Hirnantian. (2) In the Edgewood region of the American Midcontinent, the chemostratigraphic and paleontological data of Farnam et al. (2023) show that

some stratigraphic units overlying the classic Edgewood Group, previously thought to be lower Rhuddanian (e.g., the Wilhelmi Formation in northeastern Illinois, the Centerville Member of the Whippoorwill Formation in Ohio and Indiana) are Hirnantian in age. This would place the traditional Edgewood strata lower in the Hirnantian. (3) The diagnostic brachiopod taxa of the Edgewood fauna, at present, are not reliable for determining early versus late Hirnantian. In western Laurentia, for example, *Brevilamnulella* occurs as low as the uppermost Katian (Jin and Blodgett, 2020). Thus, its common occurrence in Laurentia in the Edgewood fauna cannot be constrained to the early or late Hirnantian. Similarly, other taxa of the Mackenzie Mountains examined in this study, such as *Eospirigerina*, *Epitomyonia*, *Glyptorthis*, *Gnamptorhynchos*, and *Parastrophinella*, can all be traced back to the late Katian or early Hirnantian elsewhere in Laurentia.

In light of the above, we have tentatively assigned a broad Hirnantian age to the Edgewood fauna in Laurentia in this study, although the Cathay fauna of South China, which may share some common taxa of the Edgewood fauna (e.g., *Brevilamnulella*, *Eospirigerina*, *Epitomyonia*, *Glyptorthis*), has been assigned a late Hirnantian age (Rong and Huang, 2023).

### Paleobiogeography of the Mackenzie Mountains Hirnantian fauna

Since its recognition in the mid-1960s, the Hirnantian brachiopod fauna has been a key focus of research because of its biostratigraphic association with the Ordovician–Silurian boundary, as well as its paleoecological and paleobiogeographic importance for understanding the latest Ordovician glaciation and mass extinction. In particular, the *Hirnantia* fauna (Bancroft, 1933; Temple, 1965), which dominated early–middle Hirnantian assemblages, was distributed across the globe, from the South Pole to the tropics. This was probably the most cosmopolitan of any Phanerozoic marine fauna. An initial global assessment of Hirnantian brachiopod faunas (Rong and Harper, 1988) recognized a subpolar Bani Province, the mid-latitude Kosov Province, and the low-latitude Edgewood Province. In the intervening 35 years, chronostratigraphy, paleogeography, and the taxonomy of these faunas have improved massively and many new faunas have been described, especially from the Kosov Province in South China (Rong et al., 2020). In contrast, the Hirnantian affinity of several faunas from the paleotropics, such as those within the Edgewood Province, has received considerably less attention. This is due, at least partly, to the lack of biostratigraphically diagnostic graptolites to constrain the ages of these faunas, especially in Laurentia. Recent paleontological and chemostratigraphical studies, however, have helped constrain ages for various Hirnantian faunas in Laurentia, such as those from the entire Ellis Bay Formation and the basal Becscie Formation of Anticosti Island (Jin and Zhan, 2008; Delabroye et al., 2011; Achab et al., 2013; Mauviel and Desrochers, 2016; Mauviel et al., 2020; Zimmt and Jin, 2023) and Manitoulin Island (Stott and Jin, 2007; Bergström et al., 2011). Moreover, recent work indicates that there may be a link between the late Hirnantian faunas of the South China–Sibumasu region and the Edgewood faunas, combining to form an Edgewood–Cathay Fauna (Rong et al., 2020).

The paleobiogeographic analysis of this study does not intend to duplicate the detailed, in-depth, global analysis of Hirnantian faunas of Rong et al., 2020, but to provide updates and updated discussions, as outlined below.

(1) This study provides a revised taxonomic update of the Hirnantian assemblage of the Mackenzie Mountains, based on three clusters of localities: two sections in the Avalanche Lake area, southern Mackenzie Mountains, and two localities in the central Mackenzie Mountains (see Material and methods section for details): section S-2 and the Mount Sekwi locality 4 (Lenz, 1977). The Mount Sekwi assemblage, originally assigned an early Llandovery age, contains four species that bear strong affinity to the Hirnantian fauna from Avalanche Lake and locality S-2: *Eospirigerina* cf. *E. putilla*, *Epitomyonia sekwiensis* Lenz, 1977, *Katastrophomena* sp., and *Skenidioides* cf. *S. scoliodus* Temple, 1968. Mount Sekwi (63°27'60"N, 128°39'13"W) is about 50 km to the northwest of locality S-2 (63°06'N, 127°24'W) in the central Mackenzie Mountains, and the two localities likely expose coeval strata. It is notable that *Skenidioides* cf. *S. scoliodus*, which is morphologically similar to *Skenidioides* sp. from the Avalanche Lake area, has been reported recently from the Wanyaoshu Formation (Hirnantian) of Yunnan, southwestern China (Sibumasu microplate; Huang et al., 2020b).

(2) This study also provides a revised faunal list of Hirnantian fauna from Anticosti Island, including brachiopods from the entire Ellis Bay Formation and the basal Becscie Formation (see discussion above). In addition to the faunal list of Copper et al. (2013) for the Ellis Bay Formation, this study also incorporated new faunal information from Zimmt and Jin (2023), and unpublished data on an assemblage from a reefal facies of the Laframboise Member of the Ellis Bay Formation, with the following taxa previously not assigned to the Hirnantian fauna of Anticosti Island (the new collection from the Laframboise Member will be described in a separate study): *Becscia* (basal Fox Point Member, Becscie Formation), *Biparetis* (basal Fox Point Member), *Brevilamnulella* (basal Fox Point Member), *Cliftonia* (Laframboise Member, Ellis Bay Formation), *Hypsitycha* (basal Ellis Bay Formation), *Katastrophomena* (basal Fox Point Member), *Koigia* (Laframboise Member–basal Fox Point Member).

(3) Finally, this study provides a taxonomic update of the Edgewood fauna of the American Midcontinent. Recent biostratigraphic and chemostratigraphic data (Farnam et al., 2023) indicate a late Hirnantian Age for several formations in the American Midcontinent, including the Centerville Member of the Whippoorwill Formation in Ohio and Indiana, and its largely coeval strata of the basal Bowling Green Dolomite, the Keel and basal Cochrane formations in south-central Oklahoma, the Leemon Formation in southern Illinois and southeastern Missouri, the Cyrene and Bryant Knob formations in northeastern Missouri, the Wilhelmi Formation in northeastern Illinois, and lower Mosalem Formation in northwestern Illinois and eastern Iowa. As a result, the following taxonomic updates (see also Systematic Paleontology section) have been made to the fauna reported by Amsden (1974):

*Dicoelosia* sp. Amsden, 1974 = *Epitomyonia* sp.  
*Hirnantia noixella* Amsden, 1974 = *Drabovia noixella* (Amsden, 1974).

*Platystrophia* sp. Amsden, 1974 = *Gnamptorhynchos orbiculoidea* (Jin and Chatterton, 1997).

*Rafinesquina* sp.? (Amsden, 1974). This taxon of doubtful assignment is ignored in the paleobiogeographic analysis of this study.

*Glyptorthis* sp. (Farnam et al., 2023), Centerville Member, Whipoorwill Formation, Indiana.

For the numerical paleobiogeographic analyses of this study, 107 Hirnantian genera across 42 localities were compiled, with most of the locality and faunal data from Rong et al. (2020), but with the updates listed above (see Supplemental data). As shown in Figure 3, the presence/absence data matrix of 42 localities was subjected to the interrogation of non-metric multidimensional scaling (NMDS) using the software package PAST (Hammer et al., 2001), based on the Raup–Crick similarity coefficient. In the analysis, the cohesion of the classic Kosov-type *Hirnantia* brachiopod faunas is brought out clearly by the first two eigenvector scores. In contrast, the Edgewood–Cathay faunas are positioned outside the main cluster of Kosov-type faunas, scattered to the left and bottom of the figure. The stress value for the analysis is less than 2 and considered acceptable (see Shepard plot, bottom right inset of Fig. 3).

Network analysis, first used to analyze human social interactions, explores the relationships between localities and taxa (Fig. 4). The *Hirnantia* brachiopod fauna (Kosov Province, light blue circles) occupies much of the central part of Figure 4 and forms a relatively tight cluster, corroborating the result of NMDS analysis. To the right on Figure 4 are the high-latitude Gondwana faunas of the Bani Province (circles in green) and to the lower left are the low-latitude (predominantly tropical) Edgewood–Cathay faunas. The exceptionally diverse Hirnantian fauna of Anticosti Island shows links with both the cool-water *Hirnantia* fauna of the Kosov Province and the warm-water *Brevilamnulella* fauna of the Edgewood Province but is marked by a large number of “endemic” genera (for the Hirnantian Age) that represent holdover taxa of the Richmondian fauna of Laurentia. On the extreme left of Figure 4 are the two Cathay faunas of South China.

On the basis of the NMDS and network analyses, the following are relevant to the Hirnantian faunas of Laurentia and peri-Laurentia. (1) The Mackenzie Mountains fauna has a strong affinity with coeval faunas from other areas of Laurentia and peri-Laurentia, notably the Edgewood region in Midcontinent USA, Anticosti Island, Girvan (Scotland), and Kolyma (northeastern Siberia). Despite that, the Edgewood-type Hirnantian faunas do not appear to form as tight a cluster as the Kosov-type faunas, they are linked by the common occurrences of *Brevilamnulella* (and its closely related early forms of *Viridita*), *Eospirigerina*, *Biparetis*, and *Gnamptorhynchos* (in particular, the small-shelled, rhynchonellide-like *G. orbiculoidea*), with *Hindella* (note its large circle in Figure 4) being shared also with many Kosov-type faunas. The relatively loose paleobiogeographic affinities among them also can be attributed to the large number of taxa confined (or endemic) to each region during the Hirnantian, especially those in the diverse faunas of Anticosti Island, the American Midcontinent, and Kolyma (see Hirnantian fauna list in Supplementary Data).

(2) The relatively tight cluster of classic *Hirnantia* faunas comprises localities in the predominantly cool-water Kosov Province in peri-Gondwana, with internal Raup–Crick similarity values > 0.9 for many of them. This cluster, however, also includes paleotropical or paleo-equatorial plates and terranes, such as Baltica, Kazakh blocks, and South China. During the Late Ordovician, South China is interpreted to have been within an equatorial cold-water tongue, analogous to the modern Eastern Pacific Equatorial Cold-water Tongue (Jin et al., 2018). The Kosov Province also includes a fauna from Percé, in the Gaspé Peninsula of eastern Canada. During the Late Ordovician, the Percé locality was part of the “Gaspé belt”, which comprised mainly deep-water siliciclastic sedimentary basins associated with island arcs and affected by the Taconic Orogeny, estimated to have been ~200 km farther offshore from its present position (Bourque et al., 2000), which is in close proximity to Anticosti Island in the Gulf of St. Lawrence. In terms of sedimentary facies and paleogeography, this area would have been far offshore from the southern margin of Laurentia at that time and more closely linked to Avalonia in terms of faunal affinities. The uniqueness of the Percé *Hirnantia* fauna is reflected by both lithofacies and faunal composition. The fauna occurs in unit 5 of the White Head Formation, comprising a predominantly siliciclastic facies of quartz sandstone and mudstone, with minor limestone interbeds at the base (Lespérance et al., 1981). In contrast, the coeval Ellis Bay Formation of Anticosti Island is characterized by a carbonate succession, with coral-stromatoporoid–microbial reefs at the top. The Percé brachiopod fauna has a much lower diversity than the Ellis Bay fauna and is composed of characteristic species of the Kosov-type *Hirnantia* fauna, such as those of *Hirnantia*, *Kinnella*, *Dalmanella*, *Eostropheodonta*, and *Plectothyrella* (Lespérance and Sheehan, 1976).

(3) Despite its close geographic proximity to the Gaspé Peninsula today, Anticosti Island was beyond the Taconic and subsequent Appalachian orogenic fronts (with its Upper Ordovician–lower Silurian strata unaffected tectonically) and has remained in the same position on the southeastern margin of Laurentia throughout the Phanerozoic. As a result, the Hirnantian fauna of Anticosti Island shows a much lower degree of paleobiogeographic affinity to the Kosov-type *Hirnantia* fauna, with only *Hirnantia sagittifera* and *Cliftonia* sp. from the Laframboise Member of the uppermost Ellis Bay Formation being the Kosov-type taxa, in addition to the eurytopic and widespread *Eospirigerina* and *Hindella*. The rich and diverse fauna of the lower Ellis Bay Formation (lower Hirnantian) contains a large number of holdover taxa that are typical of the Richmondian fauna of Laurentia, such as *Plaesiomys*, *Hebertella*, *Nasutimena*, *Megamyonia*, and *Hypsipytycha* (e.g., Dewing, 1999; Jin and Zhan, 2008; Copper et al., 2013), although it also includes a new species of *Hirnantia* (Zimmit and Jin, 2023). This refugium effect makes Anticosti Island appear as a striking outlier among the other Hirnantian faunas analyzed in this study.

(4) Compared to the Kosov-type *Hirnantia* fauna, the Edgewood-type Hirnantian fauna is considered to have occupied relatively warm-water, predominantly carbonate environments. Compared to the late Katian Red River brachiopod fauna in intracratonic basins (Jin et al., 2014; Stigall, 2023) and especially the paleo-equatorial–northern paleotropical *Tcherskidium*

fauna, which has been regarded as truly warm-water shelly benthos (Jin et al., 2022), the Edgewood fauna would be best characterized as a warm-water type under frequent cool-water influence. Several intervals of cool-water sedimentary facies have been recognized in areas adjacent to the southeastern margin of Laurentia during the Late Ordovician, associated with cool-water upwelling from the Appalachian foreland basin or the Sebree trough (e.g., Holland and Patzkowsky, 1996; Ettensohn, 2010). It is conceivable that, during the Hirnantian glaciation, such cool-water upwelling would have intensified in the depositional basins along the southern margin of Laurentia that faced Gondwana. This interpretation finds support in the presence of numerous small-shelled brachiopods in the Edgewood fauna, and the occurrence of iron-oolite facies in the Edgewood Group of the American Midcontinent (Amsden, 1974). Ferruginous oolite is commonly interpreted as upwelling related, especially those in the Middle–Late Ordovician, which was a period especially rich in iron-oolite deposits (for a recent summary see Dunn et al., 2021). A puzzling aspect of the Mackenzie Mountains fauna reported in this study is that, despite its paleogeographic position well within the “true warm-water” belt of the *Tcherskidium* fauna in northern-hemisphere Laurentia, diagnostic taxa of the *Tcherskidium* fauna (typically large and extravagantly calcified virgianid pentamerides; see Jin et al., 2022) do not occur in the otherwise diverse Richmondian brachiopod fauna of the Mackenzie Mountains. Farther north, in east-central Alaska along the northwestern margin of Laurentia, a small-shelled species of *Brevilamnuella* co-occurs with *Tcherskidium* in the uppermost Katian carbonate strata, but only *Brevilamnuella* survived into the Hirnantian in the Mackenzie Mountains. This may be an indication that the Gondwana cool-water invaded the western margins of northern-hemisphere Laurentia during the Hirnantian, establishing a faunal link between the Edgewood region and Mackenzie Mountains, located then at the opposite ends of the paleocontinent.

## Material and methods

This study is based mainly on silicified brachiopod fossils derived from acid-digested samples of carbonate rocks of the lower Whittaker Formation, collected in the 1970s by various geologists (mainly B.D.E. Chatterton, A.C. Lenz, and R.J.S. Wigington) from three localities in the Mackenzie Mountains, northwestern Canada (Figs. 1, 2): two in the Avalanche Lake area (see detailed sample and locality information in Jin and Chatterton, 1997), and one in the uppermost stream of the Redstone River (see also Wigington, 1977; Chen et al., 2008, fig. 5).

*Avalanche Lake sections AV1 (77.5–95.5 m above base of section) and AV4B (111.3–111.8 m above base of section).*—AV1 and AV4B are among a cluster of closely spaced sections (AV1–6) located in the Avalanche Lake area (approximate coordinates: 62°24'12"N, 127°04'07"W). Brachiopods from these samples were described in detail by Jin and Chatterton (1997) and are summarized or updated as necessary in this study (Table 1).

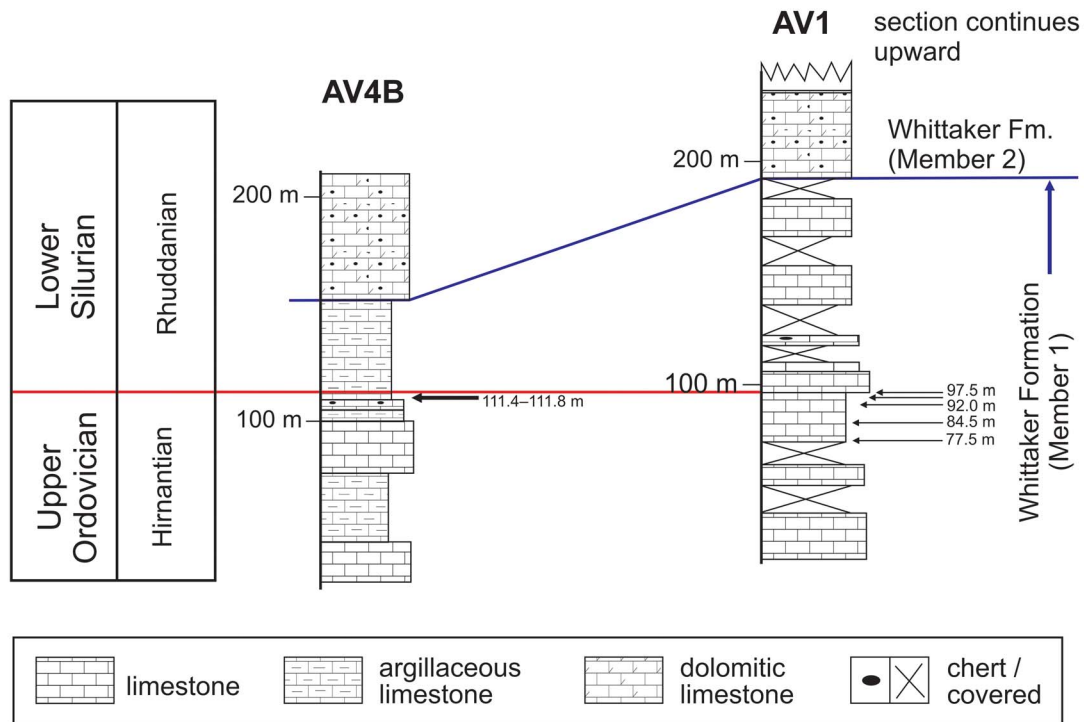
*Uppermost stream of Redstone River (sample S-2).*—This is a single spot sample from section S-2 (63°06'N, 127°24'W), on a north branch in the uppermost stream area of the Redstone

River, 45 km west of Dal Lake, central Mackenzie Mountains, about 15 ft (4.57 m) from the top of the section, lower Whittaker Formation (Wigington, 1977, p. 141). Brachiopods etched out of the sample are summarized in Table 1.

The finely silicified, delicate shells were strengthened using a 99% alcohol solution of Butvar B-98, as commonly used for fossil conservation in museums because the solution helps hold crumbly skeletal materials together without obscuring their microstructural details. The shells were coated with ammonium chloride sublimate and then photographed on a copy stand with a Nikon DSLR camera, or under a Nikon SMZ1500 stereomicroscope equipped with a Nikon Ri-2 microscope camera. Extended depth of focus (EDF) in the photographs was achieved using Nikon NIS-Elements software.

*NMDS and network analyses.*—In this study, the presence (1) and absence (0) of 107 brachiopod genera of Hirnantian age in 42 localities worldwide are compiled into a dataset (see Supplementary Data). The faunal list for each “locality” includes all the brachiopod taxa present within the total range of Hirnantian Age at that locality without any further differentiation. A non-metric multidimensional scaling (NMDS) analysis was performed using PAST (a widely adopted software package for analyzing paleontological data; see Hammer et al., 2001), with the aim to detect paleobiogeographic affinities of the Mackenzie Mountains faunal assemblage in relation to those from other regions. By treating faunal localities as cases and brachiopod genera as variables, the Raup–Crick similarity coefficient was used to map the faunal affinities among Hirnantian fossil assemblages from major paleogeographic regions. This coefficient has the advantage of generating more clearly differentiated clusters by enforcing the significance of shared rare taxa (genera in this study), based on the concept that the probability for two regions to share a rare taxon is lower than the probability for two regions to share a common (cosmopolitan and/or long ranging) taxon. In other words, a shared rare taxon is a stronger proxy than a shared common taxon for indicating a close biogeographic affinity between two regions. In this sense, the Raup–Crick coefficient shares a certain degree of similarity with paleobiogeographic analysis using a cladistic (parsimony) approach, such as that used for studying Devonian faunal biogeography (e.g., Lieberman, 2003; Stigall Rode and Lieberman, 2005). Similar to the mapping of synapomorphic characters shared between two taxa, cladistic biostratigraphic analysis would emphasize “unique taxa” shared between two geographic areas and hence their significance for paleobiogeographic affinity.

Network Analysis is an ordination method that generates a network diagram indicating the relationships between localities and taxa together with their relative generic richness (indicated by the diameter of the circle for each locality), as well as the number of localities where each genus occurs (the number of occurrences per genus is also indicated by the circle size). The analysis utilized the Gephi software package (Bastian et al., 2009) and the bipartite network, showing both localities and genera accordingly. A locality node is connected to a genus node if the genus is found in that locality. In this plot, nodes are repelled from each other but attracted by edges using the ForceAtlas2 algorithm.



**Figure 2.** Stratigraphy of the Ordovician–Silurian boundary interval of the lower Whittaker Formation. AV, Avalanche Lake sections, southern Mackenzie Mountains (see Jin and Chatterton, 1997).

**Table 1.** *Brevilamulella*–*Eospirigerina* fauna of the Mackenzie Mountains (dv = dorsal valve; sh = conjoined shell; vv = ventral valve).

Brachiopod species	Section AV1 (77.5–95.5 m)	Section AV4B (111.3–111.66 m)	S-2 (spot collection)
<i>Biparetis paucirugosus</i>			2 sh
<i>Brevilamulella laevis</i>	1 sh, 2 vv, 1 dv	2 sh, 18 vv, 4 dv	
<i>Cyclospira</i> sp. of Jin and Chatterton, 1997 (= juveniles of <i>Eospirigerina putilla</i> )	3 sh		
<i>Dalmanella edgewoodensis</i>	16 vv, 11 dv	2 vv, 1 dv	
<i>Drabovia noixella</i>			6 sh, 3 vv, 2 dv
<i>Eospirigerina putilla</i>	9 sh	33 sh, 9 vv, 9 dv	97 sh, 4 vv, 3 dv
<i>Epitomyonia paucitropida</i>			51 sh, 2 vv, 3 dv
<i>Epitomyonia sekwiensis</i>	4 sh, 10 vv	11 sh, 2 vv, 4 dv	
<i>Glyptorthis papillosa</i> n. sp.			4 vv, 3 dv
<i>Gnamptorhynchos orbiculoidea</i>	5 sh, 27 vv/dv		6 sh, 6 vv, 8 dv
<i>Katastrophomena mackenzii</i> n. sp.	31 vv, 41 dv	1 vv, 1 dv	1 sh, 1 vv, 3 dv
<i>Parastrophina</i> sp.			1 dv
<i>Skenidioides</i> sp.	2 vv		

*Repositories and institutional abbreviations.*—GSC, Geological Survey of Canada, Ottawa, Canada. OU, University of Oklahoma (Sam Noble Museum), Norman, Oklahoma, USA. UA, University of Alberta, Edmonton, Canada. UI, University of Illinois, Champaign-Urbana, USA.

**Systematic paleontology**

- Order Orthida Schuchert and Cooper, 1932
- Superfamily Orthoidea Woodward, 1852
- Family Glyptorthisidae Schuchert and Cooper, 1931
- Genus *Glyptorthis* Foerste, 1914

*Type species.*—*Orthis insculpta* Hall, 1847, upper Katian (Richmondian) strata, Ohio, USA.

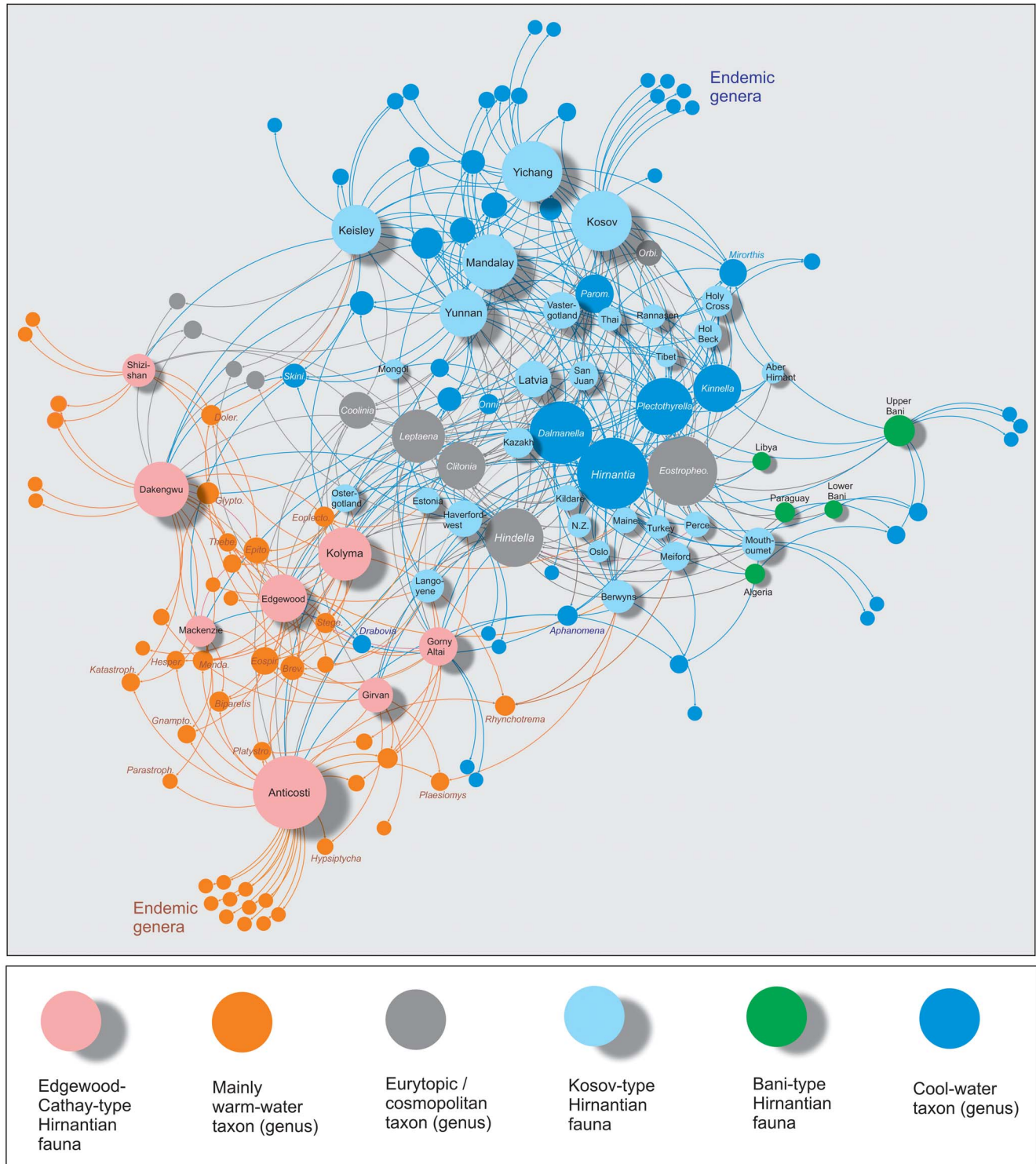
*Glyptorthis papillosa* new species  
Figure 5.1–5.11

*Types.*—Holotype. GSC 131852 (Fig. 5.1–5.3), locality S-2, Hirnantian strata of the lower Whittaker Formation, central Mackenzie Mountains, NWT, Canada. Figured paratypes, GSC 131853–131855 (Fig. 5.4–5.11), same locality.

*Diagnosis.*—Small shells of *Glyptorthis* with fine, closely spaced growth lamellae bearing tubercular papillae.







**Figure 4.** Network analysis of Hirnantian faunas using Gephi software package (Bastian et al., 2009) and the bipartite network. The size of a locality circle (shadow-bearing) is positively related to the number of genera it contains and, similarly, the size of a taxon (genus) circle (shadowless) is positively related to the number of localities where it occurs (connected by a line). Note the relatively clear spatial differentiation of warm-water Edgewood-type from the cool-water Kosov-type Hirnantian faunas. The Bani-type represents cold-water Hirnantian faunas in Gondwana.

ridged cardinal process. Posterior pair of adductor scars slightly larger and wider than anterior pair, but overall weakly impressed. Brachiophores short, blunt.

*Etymology.*—From the Latin adjective, *papillosus* (feminine, *papillosa*), having nipples or pimples, denoting the tubercles on the growth lamellae in the new species.

*Materials.*—Locality S-2 (4 ventral valves, 3 dorsal valves).

*Measurements.*—The two valves are variously damaged, with approximate measurements in millimeters.

Specimen	length	width	remarks
GSC 131852 (holotype)	7.0 (estimate)	10.2	ventral valve
GSC 131853 (paratype)	5.1	6.0 (estimate)	ventral valve

*Remarks.*—*Glyptorthis* has been shown to be a relatively common taxon of the Hirnantian fauna in several regions, such as in South China and the UK (Rong et al., 2013, 2020). *Glyptorthis papillosa* n. sp. can be distinguished easily from other congeneric species by its generally small shell, very fine and closely spaced growth lamellae that bear well-developed, rounded, tubercular papillae.

Family Skenidioidae Kozłowski, 1929  
Genus *Skenidioides* Schuchert and Cooper, 1931

*Type species.*—*Skenidioides billingsi* Schuchert and Cooper, 1931, Rockland Formation (lower Katian), Ottawa River, Quebec.

*Skenidioides* sp.  
Figure 5.12–5.15

*Materials.*—AV1 75.5 m (1 ventral valve); AV1 77.5 m (1 ventral valve).

*Remarks.*—Two ventral valves from the lower Whittaker Formation of Avalanche Lake section AV1 (75.5–77.5 m above base) were listed, but not illustrated, by Jin and Chatterton (1997) under *Skenidioides operosa* Johnson, Boucot, and Murphy, 1976, which has a long stratigraphic range (Llandovery to Ludlow) in the Mackenzie Mountains and other regions of Arctic Canada (Lenz, 1977; Zhang, 1989). The two ventral valves, however, differ from those of typical *S. operosa* from higher stratigraphic levels in being transversely elliptical, more uniformly convex, with a moderately inclined apsacline interarea, and rounded, less-numerous costae (Fig. 5.12–5.14), although the short median septum (Fig. 5.15) is typical of the genus. Typical *S. operosa*, predominantly of Wenlock–Ludlow age in North America, commonly have a strophic shell, more-numerous and frequently bifurcating costae, and a catacline to strongly inclined apsacline ventral interarea to give the ventral valve a pyramidal appearance (see Zhang, 1989; Jin and Chatterton, 1997). In these respects, the two ventral valves illustrated here resemble more closely “*Skenidioides* cf. *S. scoliodus*” reported by Lenz (1977) from lower Llandovery (likely Hirnantian in modern stratigraphy) strata of the Road River Formation in his locality 4, Mount Sekwi area, central Mackenzie Mountains. The Mount Sekwi shells also have a moderately inclined apsacline ventral interarea, a hinge line that is slightly shorter than maximum shell width, rounded costae showing only weak bifurcation, unlike *S. scoliodus* from the UK, which tends to have a strophic shell with prominent ears (e.g., Temple, 1968, pl. 5, figs. 7, 8, 22, 23).

Unfortunately, no dorsal valves have been found in samples from AV1 75.5–77.5 m. This precludes a specific identification of *Skenidioides*.

Family Plectorthidae Schuchert and LeVene, 1929  
Subfamily Platystrophiinae Schuchert and LeVene, 1929  
Genus *Gnamptorhynchos* Jin, 1989

*Type species.*—*Gnamptorhynchos regularis* var. *globata* Twenhofel, 1928 (= *Gnamptorhynchos inversum* Jin, 1989), Ellis Bay Formation (Hirnantian), Anticosti Island, eastern Canada (see Jin and Zhan, 2000, for detailed discussion).

*Gnamptorhynchos orbiculoidea* (Jin and Chatterton, 1997)  
Figure 6

1974 *Platystrophia* sp. Amsden, p. 32, p. 6, figs. 5a–e.

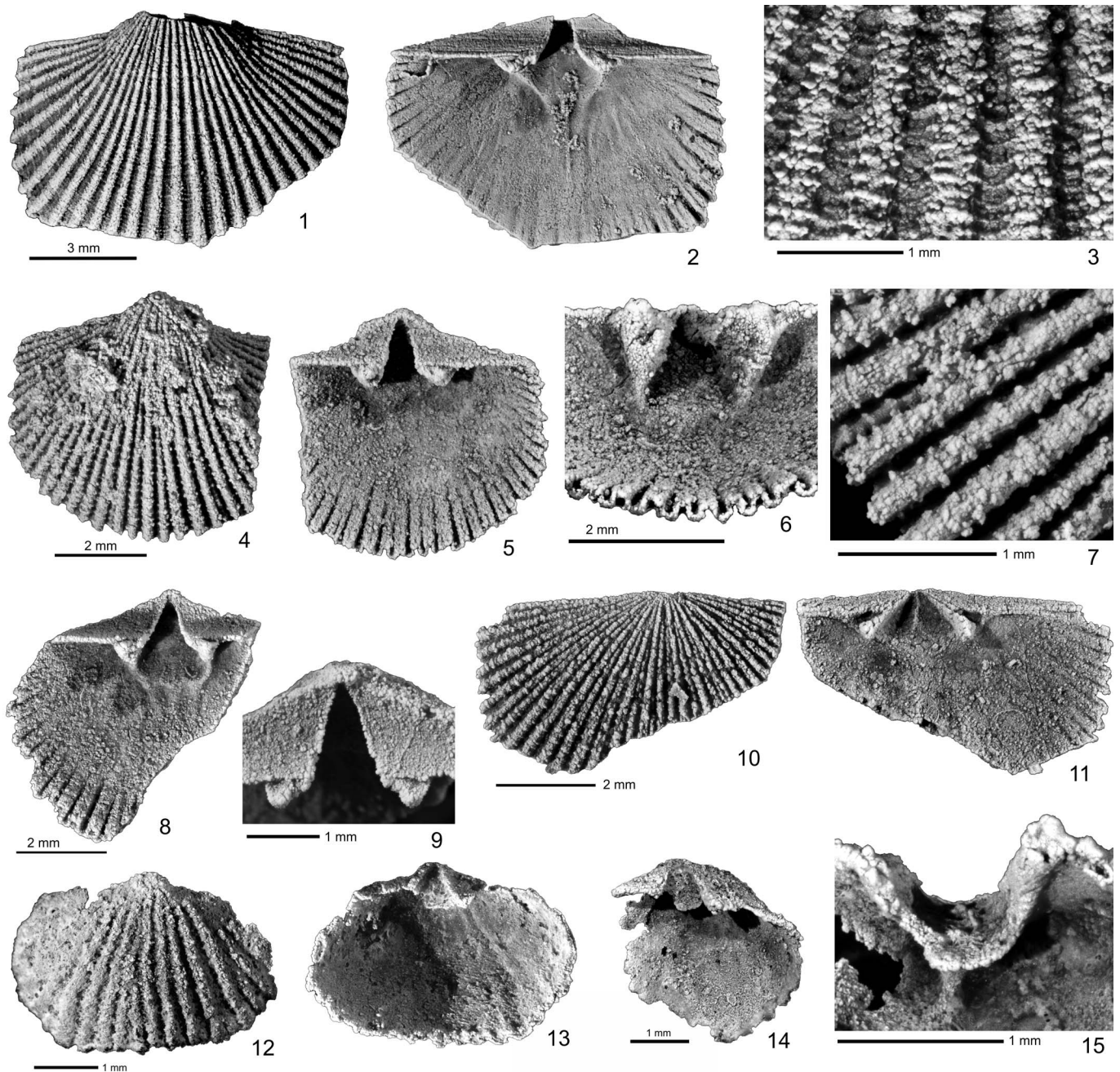
1997 *Platystrophia orbiculoidea* Jin and Chatterton, p. 21, pl. 3, figs. 6–24.

2007 *Platystrophia* cf. *P. daytonensis*; Stott and Jin, p. 453, figs. 6–10.

*Holotype.*—UA 10499, by original designation (re-illustrated herein, Fig. 6.1–6.4); section AV4B, 111.3–111.6 m above base of section, lower Whittaker Formation, Hirnantian, Avalanche Lake, southern Mackenzie Mountains, northwestern Canada.

*Materials.*—Total 43 specimens. AV4B 111.3–111.4 m (2 conjoined shells, 8 disarticulated valves); AV4B 111.4–111.6 m (8 disarticulated valves and fragments); AV4B 111.5 m (1 conjoined shell, 3 disarticulated valves); AV4B 111.6 m (1 shell, 8 disarticulated valves); AV4B 111.8 m (1 conjoined shell, 1 ventral valve); S2 (6 conjoined shells, 1 ventral valve, 3 dorsal valves).

*Remarks.*—A detailed description of the Avalanche Lake material was provided by Jin and Chatterton (1997). The newly discovered shells from northern Mackenzie Mountains (locality S-2) resemble the types from Avalanche Lake in their small, weakly transverse, subelliptical, nearly equibiconvex shell. S-2 specimens reach a maximum size of 7.8 mm in length and 9.8 mm in width, comparable to the maximum length (8.8 mm) and width (9.8 mm) for the Avalanche Lake material, although the S-2 shells seem slightly more extended transversely. Both the Avalanche Lake and S-2 shells have a relatively low (barely attaining 1 mm in height), narrow (about one-third shell width), apsacline, ventral interarea (Fig. 6.3, 6.11, 6.16); moderately convex ventral umbo with a small, suberect beak; and a well-delimited dorsal fold and ventral sulcus leading to an uniplicate anterior commissure. The strong, subrounded to subangular costae are typical of shells from both regions, usually simple, two in the sulcus, three on the fold, six to eight on each flank, with only rare intercalation in the sulcus (Fig. 6.15). Microscopic tubercles or spines are present on shells from both regions (Fig. 6.4, 6.8), as is typical of *Gnamptorhynchos* (Jin and Zhan, 2000), *Platystrophia*, and other closely related platystrophiids (Zuykov and Harper, 2007; Jin and Zhan, 2008).

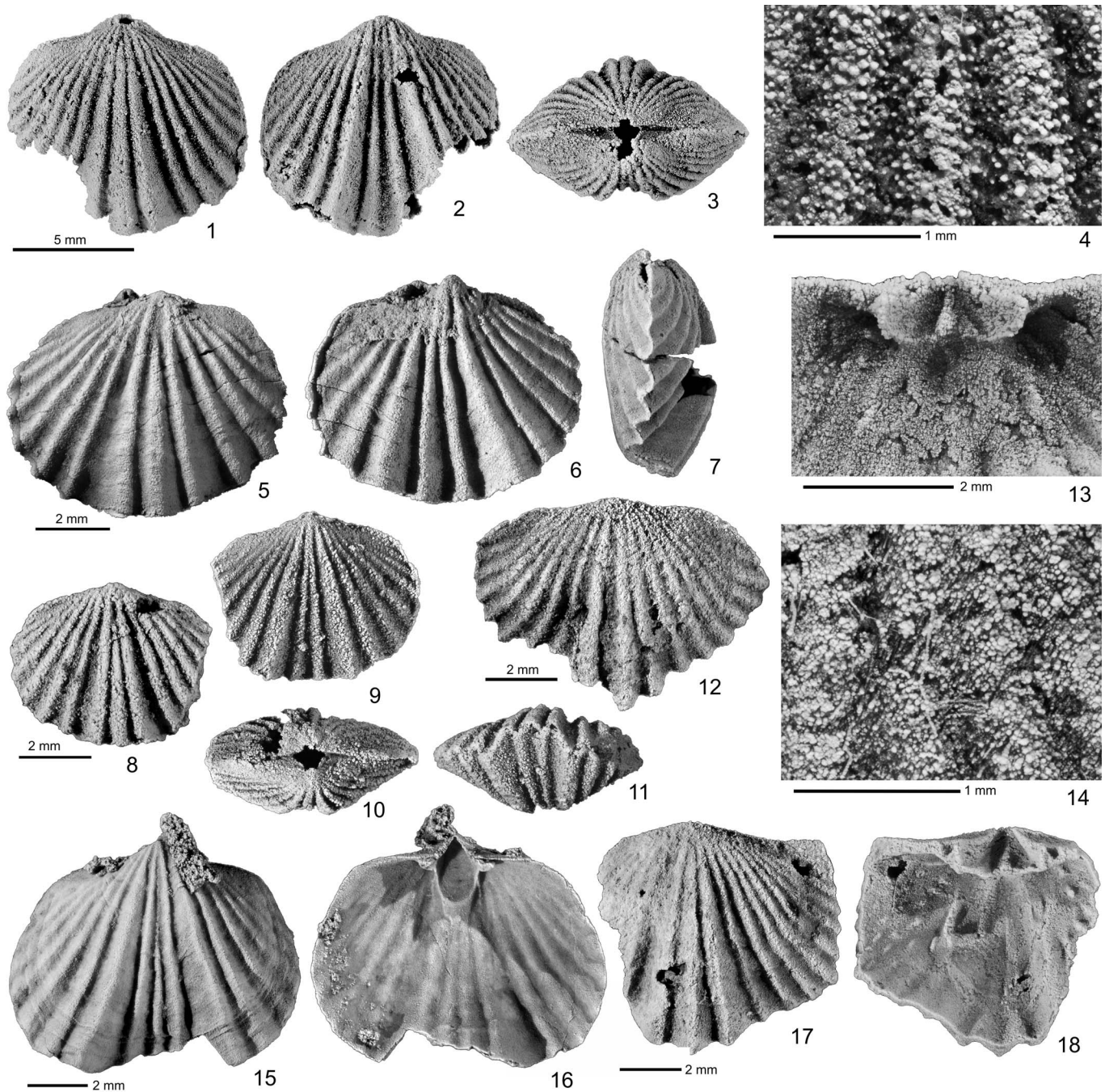


**Figure 5.** (1–11) *Glyptorthis papillosa* new species, locality S-2, Hirnantian strata of the lower Whittaker Formation, central Mackenzie Mountains. (1–3) GSC 131852, holotype, exterior, interior, and details of papillae-bearing growth lamellae of anteriorly damaged ventral valve (largest specimen available for the new species). (4–7) GSC 131853, paratype, exterior, interior, enlarged image of dental plates, and papillae-bearing growth lamellae of small, incomplete ventral valve. (8, 9) GSC 131854, paratype, interior and detailed view of delthyrium and teeth of small, laterally damaged ventral valve. (10, 11) GSC 131855, paratype, exterior and interior of dorsal valve, showing weak, blade-like cardinal process. (12–15) *Skenidioides* sp. from Hirnantian strata of Whittaker Formation, Avalanche Lake area, southern Mackenzie Mountains: (12, 13) GSC 131856, exterior and interior view of ventral valve, section AV1, 77.5 m above base of section; (14, 15) GSC 131857, interior and tilted apical views of incomplete ventral valve, showing spondylium supported by short median septum (15).

Internally, the ventral valves from both regions possess strong teeth, supported by prominent dental plates, which extend anteriorly beyond the hinge line as low ridges to bound an elongate-oval, antero-medially raised muscle field (Fig. 6.16); the muscle field floor is smooth, without clearly defined adductor or diductor muscle scars. The notothyrial platform in the dorsal valve is raised at its anterior margin, laterally bounded by brachiophore plates to form a pseudocruralium-like structure

that bears a low median ridge resembling a cardinal process (Fig. 6.14, 6.18). As is typical of this genus, the dorsal adductor scars are poorly impressed.

In their revision of *Gnamptorhynchos*, Jin and Zhan (2000) proposed to assign this small-shelled platystrophiid species to the genus. Since then, more specimens similar to *G. orbiculoides* have been discovered from coeval strata of other areas, such as the S-2 collection from northern Mackenzie Mountains,



**Figure 6.** *Gnamptorhynchos orbiculoidea* (Jin and Chatterton, 1997). (1–4) UA 10499, holotype, dorsal, ventral, posterior views, and enlarged view of tubercular shell surface (4) of incomplete, conjoined shell, section AV4B, 111.3–111.6 m above base of section, lower Whittaker Formation, Hirnantian, Avalanche Lake, southern Mackenzie Mountains. (5–18) Four specimens from locality S-2, Hirnantian strata of the lower Whittaker Formation, central Mackenzie Mountains; (5–7) GSC 131858, dorsal, ventral, and lateral views of conjoined shell (slightly offset between two valves posteriorly); (8–11) dorsal, GSC 131859, dorsal, ventral, posterior, and anterior views of small shell; (12–14) GSC 131860, exterior, posterior interior showing anteriorly raised notothyrium and ridge-like cardinal process, and shell surface tubercles (some preserved as long filaments) of dorsal valve; (15, 16) GSC 131861, exterior and interior of ventral valve, showing typical platystrophiid muscle field; (17, 18) GSC 131862, exterior and interior of dorsal valve.

and the Laframboise Member of uppermost Ellis Bay Formation, Anticosti Island (the latter will be reported in a separate study). On Anticosti Island, the type species, *Gnamptorhynchos globatum* (Twenhofel, 1928), is confined to the aulaceridid biostrome unit of the Prinsta Member, now considered the basal Ellis Bay Formation (see Copper et al., 2013), where it occurs together

with *Hirnantia notiskuani* Zimmt and Jin, 2023. *Gnamptorhynchos orbiculoidea* has a much smaller shell size than the type species (average width ~16 mm, and maximum width 20 mm), although the shells of both species attain a similarly strong, globular biconvexity, commonly an indication of an adult growth stage.

Amsden (1974) reported *Platystrophia* sp. from the Edgewood fauna, noting its rhynchonellide-like (or *Plectothyrella*-like) shell morphology with a narrow hinge line and interarea. Its overall morphology is similar to *Gnamptorhynchos orbiculoidea*, especially in its simple costae, with two in the ventral sulcus and three on the fold. *Plectothyrella*, which is a true rhynchonellide and a common taxon of the *Hirnantia* fauna in the Kosov faunal province, is characterized by strong, angular, and commonly bifurcating costae. The presence of *Gnamptorhynchos* in the type area of the Edgewood fauna emphasizes the significance of this genus in the Hirnantian fauna of Laurentia.

The three specimens illustrated by Stott and Jin (2007) from the non-reefal facies of the lower Manitoulin Dolomite of Manitoulin Island, Ontario, are virtually identical to the Mackenzie Mountains shells, especially in their “rhynchonellide-like” posterior. This fauna has been considered to be Hirnantian in age, which is supported by chemostratigraphic dating of the lower Manitoulin Dolomite (Bergström et al., 2011).

Superfamily Dalmanelloidea Schuchert and Cooper, 1932

Family Dicoelosiidae Cloud, 1948

Genus *Epitomyonia* Wright, 1968

*Type species.*—*Epitomyonia glypha* Wright, 1968, Boda Limestone (uppermost Katian), Sweden.

*Epitomyonia paucitropida* Chen, Jin, and Lenz, 2008  
Figure 7

2008 *Epitomyonia paucitropida* Chen, Jin, and Lenz, p. 95, figs. 9A–S.

*Types.*—Holotype, GSC 131794, Hirnantian beds, lower Whittaker Formation, section S-2 (63°06'N, 127°24'W), 45 km west of Dal Lake, Mackenzie Mountains, northwestern Canada.

*Materials.*—S-2 (51 articulated shells, 2 ventral valves, 3 dorsal valves).

*Remarks.*—This species has been described in detail by Chen et al. (2008). *Epitomyonia paucitropida* resembles most closely *E. sekwiensis* Lenz, 1977, from lower Llandovery strata of Mount Sekwi (~50 km northwest of locality S-2) in its shell size (average length 4.7 mm compared to 4.4 mm for the holotype of *E. sekwiensis*), rather strong costae for the genus, and weak transverse ridges in the dorsal valve. As noted by Chen et al. (2008), *E. paucitropida* can be distinguished easily from *E. sekwiensis* in having a pair of wavy transverse ridges located at about mid-length of the dorsal valve (Fig. 7.7), whereas in *E. sekwiensis* the transverse ridges are located near the anterior margin of the dorsal valve.

The dicoelosiid specimens from the Bowling Green Dolomite (Edgewood Group) of Missouri, reported by Amsden (1974) as *Dicoelosia* sp., were poorly preserved as molds in coarse-grained dolomite, yielding little information on internal structures. Amsden (1974, p. 42) commented on the possibility that these specimens were *Epitomyonia* because of their wide

hinge line, very shallow anterior emargination, and overall similarity to *Epitomyonia glypha* in external morphology. The affinity of these specimens to *Epitomyonia* also was suggested by Lenz (1977). In its general shell shape and relatively even costae (due to weak bifurcation), the Missouri *Dicoelosia* sp. is most similar to *Epitomyonia paucitropida*, and is thus assigned to *Epitomyonia* rather than *Dicoelosia* in this study.

*Epitomyonia paucitropida* is similar also to *E. glypha* from the Boda Limestone (uppermost Katian) in shell size (usually < 5 mm in length), with the dorsal transverse ridges located close to mid-length of the valve. The Boda species, however, differs in having notably sharper costae (and an especially strong medial costa in the ventral valve) that bifurcate more intensely, and much stronger, anteriorly tilting transverse ridges in the dorsal valve (Wright, 1968, pl. 1, figs. 5, 14, 15). In this respect, the specimens reported as *E. glypha* by Rubel (2011, pl. 33, figs. 1, 2) from Rhuddanian strata of Estonia are more closely allied with *E. paucitropida*. Another Hirnantian species of *Epitomyonia*, *E. americana* Sheehan and Lespérance, 1979, from Percé, Quebec, differs from *E. paucitropida* in having a distinctly wider, planoconvex shell, with a notably shorter dorsal median septum.

*Epitomyonia sekwiensis* Lenz, 1977

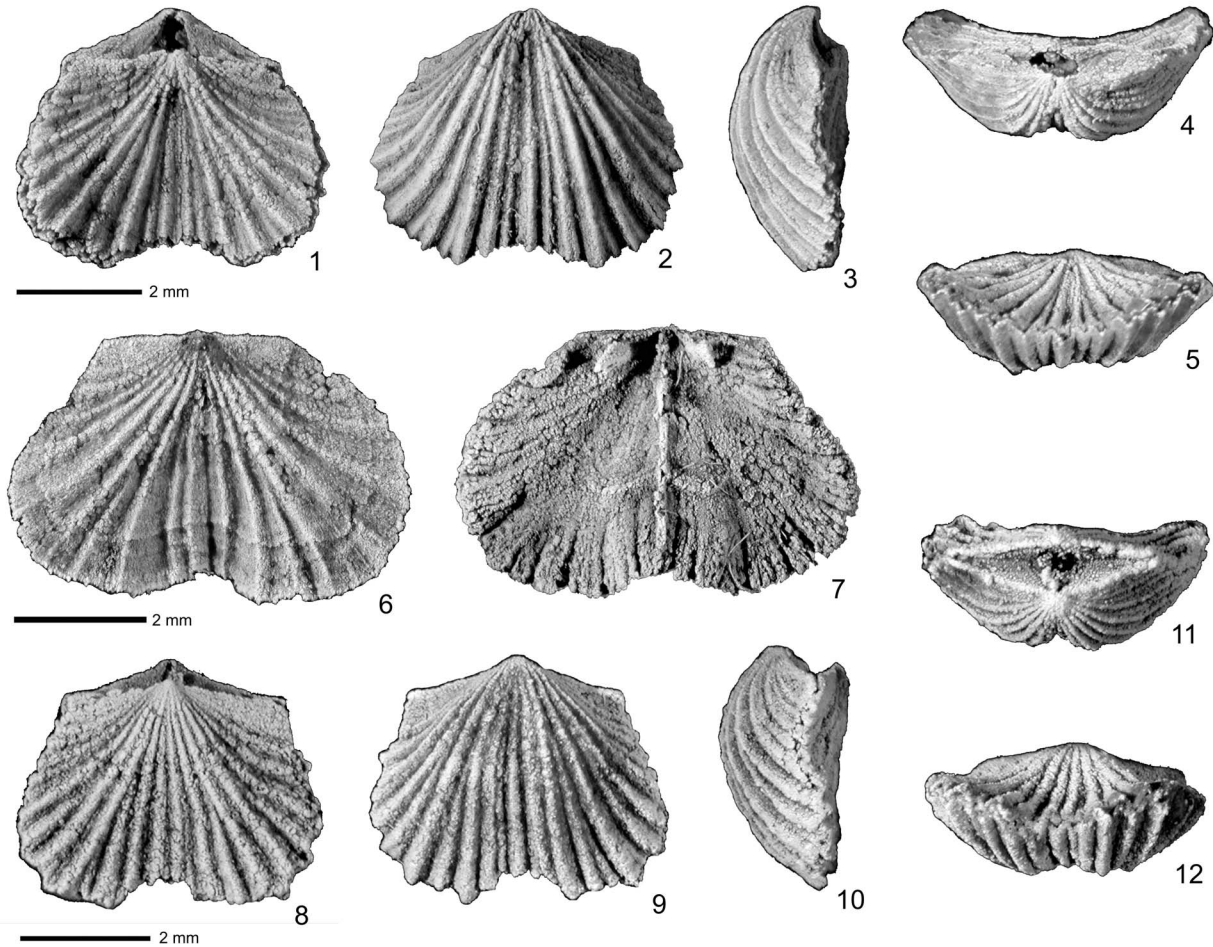
1977 *Epitomyonia sekwiensis* Lenz, p. 1532, pl. 4, figs. 8, 9, 11–23, 26, 27.

1997 *Epitomyonia sekwiensis*; Jin and Chatterton, p. 19, pl. 7, figs. 11–23.

*Holotype.*—GSC48019, lower Llandovery beds, Road River Formation, Mount Sekwi (locality 4 of Lenz, 1977, p. 1523, 1530) Mackenzie Mountains, Northwest Territories.

*Materials.*—Total 30 specimens. Hirnantian to Aeronian. AV1 77.5 (4 conjoined shells); AV1 84.5 (7 ventral valves); AV1 95.5 (3 ventral valves); AV4B 111.3–111.4 (1 conjoined shell, 1 ventral valve, 1 dorsal valve); AV4B 111.4–111.6 (2 conjoined shells, 1 dorsal valve); AV4B 111.5 (2 broken shells); AV4B 111.6 (1 shell); AV4B 111.64–111.66 (4 shells, 1 ventral valve, 2 dorsal valves).

*Remarks.*—Detailed description and illustration of this species were provided by Jin and Chatterton (1997). Specimens from Avalanche Lake are assigned to *E. sekwiensis* based on their similarity to those described by Lenz (1977) in the development of subtriangular ventral valves in some shells, coarse costae, and a relatively deep anteromedial emargination for the genus. As noted by Lenz (1977), some triangular forms with prominent lobes are externally homeomorphic with the Late Ordovician *Dicoelosia lata* Wright, 1968. *Epitomyonia glypha* from lower Llandovery rocks Estonia (Rubel, 1971, pl. 8, fig. 6; Rubel, 2011, p. 51, pl. 33, figs. 1, 2) also has a strongly bilobate shell with anteromedial emargination and, importantly, a pair of simple transverse septa in the antero-middle to anterior part of the dorsal valve. Lenz (1977) distinguished *E. sekwiensis* from the approximately coeval *E. glypha* by a more strongly convex ventral valve in the Sekwi species.



**Figure 7.** *Epitomyonia paucitropida* Chen, Jin, and Lenz, 2008, locality S-2, Hirnantian strata of the lower Whittaker Formation, central Mackenzie Mountains. (1–5) GSC 131796, paratype, dorsal, ventral, lateral, posterior, and anterior views. (6, 7) GSC 131794, holotype, exterior and interior; note transverse ridges located close to mid-length of valve. (8–12) GSC 131798, dorsal, ventral, lateral, posterior, and anterior views.

Family Dalmanellidae Schuchert, 1913

Subfamily Dalmanellinae Schuchert, 1913

Genus *Dalmanella* Hall and Clarke, 1893

*Type species.*—*Orthis testudinaria* Dalman, 1828. Dalmanitina Beds (Hirnantian), Västergötland, Sweden (for taxonomic update see Jin and Bergström, 2010).

*Dalmanella edgewoodensis* Savage, 1913

1913 *Dalmanella edgewoodensis* Savage, p. 123, pl. 6, figs. 11–13.

1974 *Dalmanella edgewoodensis*; Amsden, p. 35, pl. 6, figs. 6a–c, pl. 7, figs. 1a–z, pl. 8, figs. 1a–b, 2a–c, 3a–j.

1997 *Dalmanella edgewoodensis*; Jin and Chatterton, p. 21, pl. 10, figs. 1–23.

*Lectotype.*—UI X-865, selected by Amsden (1974, pl. 8, figs. 2a–c), Hirnantian–Rhuddanian boundary interval, Edgewood Group, near Edgewood, Missouri.

*Materials.*—AV1 95.5 m (16 ventral valves, 11 dorsal valves); AV4B 111.3–111.66 m (2 ventral valves, 1 dorsal valve).

*Remarks.*—In the Mackenzie Mountains, this species has been found only in the Avalanche Lake locality, as described by Jin and Chatterton (1997). The Avalanche Lake specimens resemble those from the Edgewood Group of Missouri and Illinois (Amsden, 1974) in their subrounded, ventribiconvex shell with rounded multicostellae or weakly developed fascicostellae. The affinity of these specimens to typical *Dalmanella* (as assessed by Jin and Bergström, 2010, based on type specimens from the Hirnantian strata of Sweden) is supported by the presence of an interspace (instead of a rib) along the medial line in the dorsal umbonal area, a relatively small ventral muscle field (relative to valve size), and a relatively delicate cardinal process with a bilobed and crenulated myophore. Relatively large Edgewood shells may reach 15 mm long and develop a fairly deep dorsal valve. In comparison, the Mackenzie shells rarely exceed 10 mm in length and are typically ventribiconvex, as are the smaller Edgewood forms. The maximum shell size may be related to another minor difference—the Edgewood shells have a slightly wider ventral muscle field with prominently arched laterally bounding ridges, compared to the slightly narrower ventral muscle field with subparallel to weakly arched lateral

bounding ridges (compare Amsden, 1974, pl. 7, figs. 1v, 1zz and pl. 8, figs. 1a, 3f, with Jin and Chatterton, 1997, pl. 10, figs. 1, 3, 19, 21, 23). However, the ventral muscle field in specimens from both regions shows notable variations in its outline in terms of its relative size (especially width) relative to the valve, as well as the curvature and strength of bounding ridges.

Superfamily Enteletoidea Waagen, 1884  
 Family Draboviidae Havlíček, 1950  
*Drabovia* Havlíček, 1950

*Type species.*—*Orthis redux* Barrande, 1848, Letná Formation (Sandbian), Czech Republic.

*Drabovia noixella* (Amsden, 1974)  
 Figure 8

1974 *Hirnantia noixella* Amsden, p. 45, pl. 10, figs. 1a–y.

*Holotype.*—By original designation, OU 6780, Noix Limestone, Edgewood Group, Hirnantian, Missouri.

*Materials.*—Locality S-2 (8 conjoined shells, with some being incomplete, 3 ventral valves, 2 dorsal valves).

*Remarks.*—Amsden (1974) originally assigned the species to *Hirnantia* based mainly on dorsal internal structure. This Edgewood draboviid, however, has a considerably smaller shell (generally < 6 mm in length or 7 mm in width) but strong biconvexity and very coarse ribs for shell size. Amsden (1974, p. 46) incorrectly compared the ventribiconvex shell of *D. noixella* to a “ventribiconvex” *Hirnantia sagittifera* because the latter is characterized by a distinctly dorsibiconvex shell; he also incorrectly contrasted the Edgewood species with “*Drabovia* and *Pionodema* with dorsibiconvex shells” since the latter two are typically ventribiconvex. The type species of *Hirnantia* has fine, fairly even-sized multicostellae, which clearly differ from the coarse, unevenly bifurcating ribs (fascicostellae) of *D. noixella*. In its small, ventribiconvex shell and such coarse ribs (with wide interspaces), the Edgewood species is regarded here to have a much stronger affinity to *Drabovia* than to *Hirnantia*.

The Mackenzie specimens are assigned to *D. noixella* on account of their similarly small ventribiconvex shells, relatively coarse ribbing, and strong growth lamellae near the anterior margin. An average-sized complete shell measures 6.5 mm in length, 6.9 mm in width, and 4.1 mm in thickness (Fig. 8.1–8.5), matching those reported by Amsden (1974). In shell ribbing, the Mackenzie Mountains specimens resemble Amsden’s (1974) illustrations from the Noix Limestone in several aspects: (1) the ribs are strong and coarse relative to shell size; (2) the medial line is occupied by an interspace in the dorsal valve, and a strong costa in the ventral valve (compare Fig. 8.2 with Amsden, 1974, pl. 19, fig. 1k; and Fig. 8.7 with Amsden’s, 1974, pl. 10, fig. 1b); and (3) the bifurcating ribs range from multicostellate (compare Fig. 8.1 with Amsden’s, 1974, pl. 10, fig. 1s) to weakly fascicostellate (compare Fig. 8.7 and 8.11 with Amsden’s, 1974, pl. 10, fig. 1k). Dorsal valves from

both Missouri and the Mackenzie Mountains show the diagnostic internal characters of *Drabovia*, especially the antero-laterally divergent brachiophore plates along the valve floor, and the slender cardinal process, with a bilaterally crenulated myophore, sitting directly on the valve floor because of the lack of a notothyrial platform (Fig. 8.8–8.10, 8.12–8.14). Despite their generally small size, the shells show a relatively strong biconvexity for *Drabovia*, a truncated anterior margin with densely spaced growth lamellae, and robust and high hinge plates (Fig. 8.10, 8.14, 8.18), suggesting that these are mature individuals. The anterior and posterior pairs of adductor scars are small and narrow relative to valve size, bearing a gently developed myophragm (medial ridge; see Fig. 8.8, 8.12).

*Drabovia? minuta* Hints, 2012, from Porkuni strata (Hirnantian) of Estonia is similar to *D. noixella* in its small shell with a fairly strong biconvexity for this genus, relatively short hinge line, relatively coarse fascicostellae, and strong growth lamellae in the anterior part of the shell. The Estonian shells seem to have a proportionally small cardinalia (relative to shell size) in comparison to the North American specimens.

Order Strophomenida Öpik, 1934  
 Superfamily Strophomenoidea King, 1846  
 Family Strophomenidae King, 1846  
 Genus *Katastrophomena* Cocks, 1968

*Type species.*—*Strophomena antiquata* var. *woodlandensis* Reed, 1917, Woodland Formation (Rhuddanian), Girvan, Scotland.

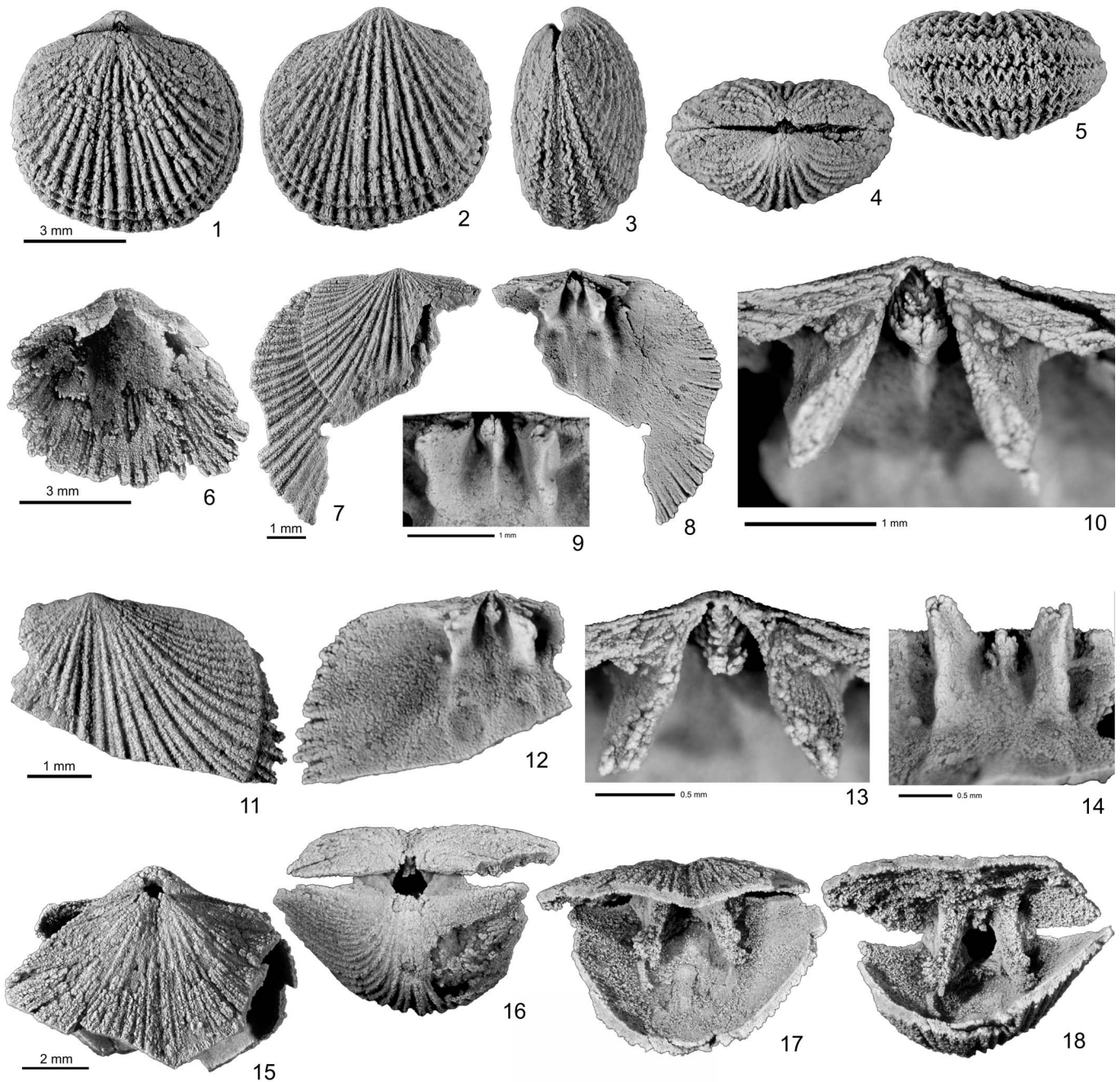
*Remarks.*—Typical species of *Katastrophomena* are usually considered common in the Ordovician–Silurian boundary interval. A review of the genus by Cocks (2008) demonstrated its fairly long stratigraphic range, from upper Katian (Cautleyan) to Ludlow.

*Katastrophomena mackenzii* new species  
 Figures 9, 10.12–10.15

1977 *Katastrophomena* sp Lenz p. 1538, pl. 7, figs. 1–6.  
 1997 *Katastrophomena* cf. *K. woodlandensis*; Jin and Chatterton, p. 28, pl. 18, figs. 7–13.

*Types.*—Holotype, GSC 131868 (Fig. 9.7, 9.8), dorsal valve, from locality S-2, lower Whittaker Formation, central Mackenzie Mountains. Figured paratypes, GSC 131869–131873, 2 conjoined shells (Figs. 9.4–9.6, 10.12–10.15), 2 ventral valves, (Fig. 9.1–9.3, 9.17, 9.18), and 3 dorsal valves, also from Hirnantian strata in the lower Whittaker Formation, including two from locality S-2 (Fig. 9.9–9.13) and one from the Avalanche Lake section AV4B (Fig. 9.14–9.16). All type specimens have various degrees of damage.

*Diagnosis.*—Shell relatively small for genus, weakly biconvex, with rectimarginate anterior commissure; costae coarse, uneven, commonly sinuous, and crooked, strongly fascicostellate. Internal structures same as in type species.

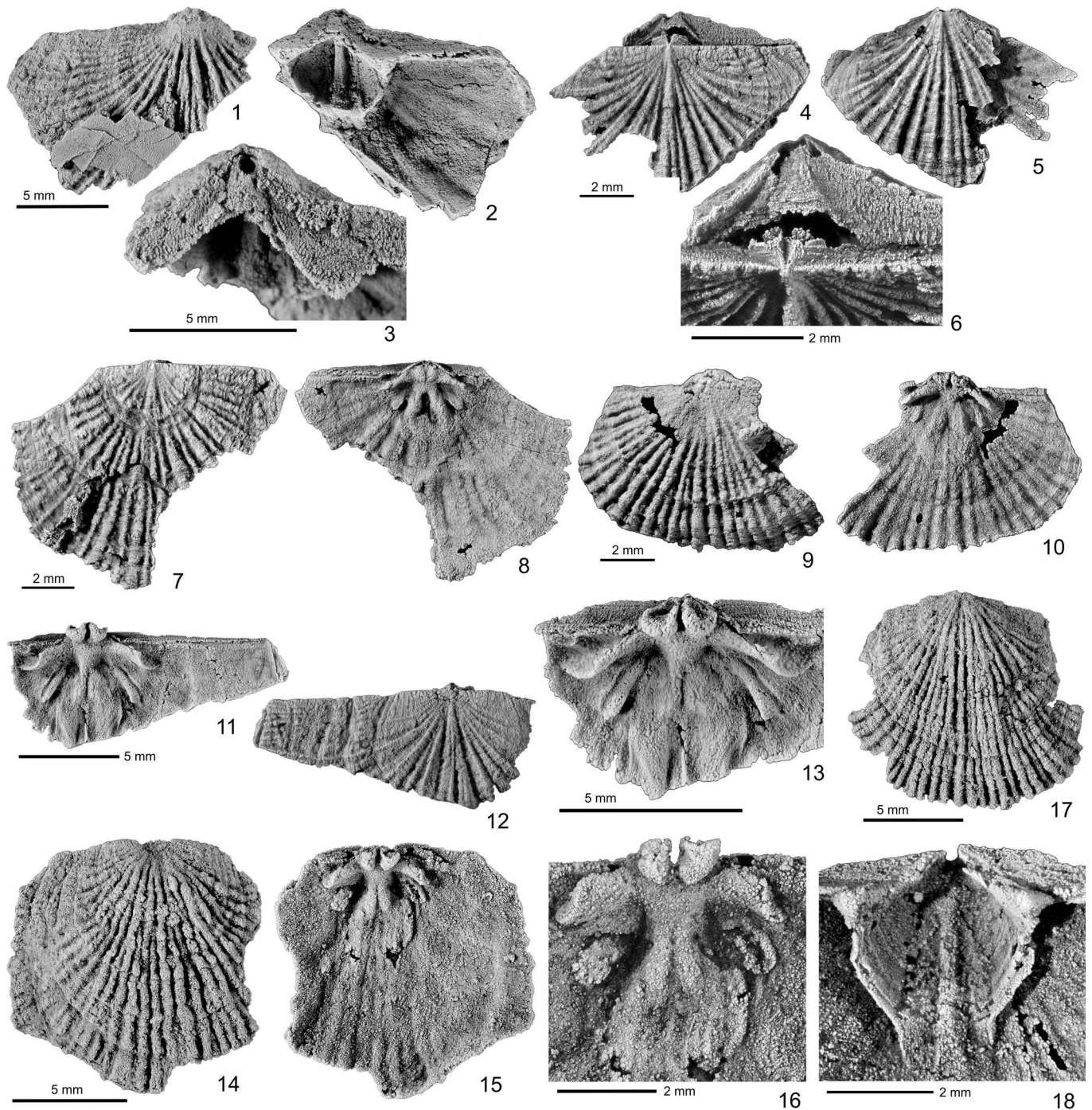


**Figure 8.** *Drabovia noixella* (Amsden, 1974), locality S-2, Himantian strata of the lower Whittaker Formation, central Mackenzie Mountains. (1–5) GSC 131863, dorsal, ventral, lateral, posterior, and anterior views of small, ventribiconvex shell, with strong growth lamellae near anterior margin; (6) GSC 131864, interior of incomplete ventral valve, showing muscle field; (7–10) GSC 131865, exterior view of incomplete dorsal valve showing interspace along medial line of valve (7), interior showing cardinalia and small adductor scars (8), and detailed views of cardinalia from anterior (9) and posterior (10), showing thin shaft of cardinal process sitting directly on valve floor (9) and bilobed, crenulated myophore (10); (11–14) GSC 131866, exterior, interior of dorsal valve, and two views of cardinalia from posterior (13) and anterior (14); (15–18) GSC 131867, dorsal, posterior, anterior, and tilted anterior views of incomplete, strongly biconvex, conjoined shell.

*Description.*—Shell small to medium-sized for genus, with estimated average width of ~15 mm, and maximum width of ~20 mm (Fig. 9.1–9.3, 9.11–9.13); wider than long, but variable in length/width ratios (e.g., Fig. 9.7, 9.9, 9.14, 9.17); plano-convex to weakly biconvex (Fig. 10.12–10.15), attaining ~5 mm thickness in an incomplete shell estimated at ~20 mm wide. Hinge line wide, straight, but usually shorter than maximum shell width, forming rounded

cardinal extremities (Fig. 9.1, 9.4, 9.11). Anterior commissure largely rectimarginate. Costae coarse for strophomenids, averaging 3 per 2 mm in anterior parts of relatively large shells, commonly sinuous, crooked with knotted or otherwise irregular crests (e.g., Fig. 9.7, 9.9, 9.14), increasing anteriorly by frequent, asymmetrical bifurcation to form clearly defined fascicostellae (Fig. 9.1, 9.4, 9.7, 9.12).





**Figure 9.** *Katastrophomena mackenzii* new species. (1–13) Five specimens from locality S-2, Hirnantian strata of the lower Whittaker Formation, central Mackenzie Mountains; (1–3) GSC 131870, paratype, exterior, interior, and posterior views of incomplete ventral valve; note fascicostellae and semi-tubular pseudodeltidium (3); (4–6) GSC 131869, paratype, dorsal, ventral, and posterior views of incomplete, conjoined shell; note strongly developed fascicostellae; (7, 8) GSC 131868, holotype, exterior and interior views of dorsal valve; note short central pair of trans-muscle septa, and knobby lateral septa (8); (9, 10) GSC 131871, paratype, exterior and interior of relatively small dorsal valve; (11–13) GSC 131872, paratype, interior and exterior views of posterior fragment of relatively large dorsal valve, and detailed view of cardinalia (13), note well-developed fascicostellae and oval-shaped adductor scars; (14–18) two specimens from section AV4B, 111.3–111.6 m above base of section, lower Whittaker Formation, Hirnantian, Avalanche Lake, southern Mackenzie Mountains; (14–16) UA 10636, paratype, exterior, interior of dorsal valve, and detailed view of cardinalia (16); (17, 18) UA 10635, paratype, exterior and detailed view of ventral muscle field.

Ventral valve moderately convex in umbonal area, becoming weakly convex to flat laterally and anteriorly, without fold or sulcus; beak low but clearly defined, erect to suberect. Ventral interarea moderately high in apical area (up to 2 mm in height),

becoming lower gradually towards cardinal extremities, with predominantly planar surface (Fig. 9.2, 9.4). Delthyrium covered by arched to semi-tubular pseudodeltidium, bearing rounded apical foramen (Fig. 9.3).

Dorsal valve flat to weakly convex; umbonal area flattened, marked by strong costae in umbonal area along medial line (Fig. 9.4, 9.7, 9.12). Dorsal interarea notably lower than ventral, close to being orthocline. Notothyrium covered apically by arched chilidium, anteriorly occupied by bilobed crests of cardinal process.

Ventral interior: dental plates well developed, extending anteriorly into high, laterally arched, and tiled bounding ridges of muscle field (Fig. 9.2, 9.18). Muscle field small, occupying about one-quarter of shell length or width, sub-rounded in outline, antero-medially open, bearing strong medial ridge, but without sharply differentiated adductor and diductor scars.

Dorsal interior: hinge sockets elongated along hinge line, bounded anteriorly by “semi-tubularly” curved and suspended hinge plates (Fig. 9.11, 9.13). Cardinal process bilobed, sitting on raised notothyrial platform; each lobe with posterior-facing myophore and spoon-like crest (Fig. 9.11, 9.13, 9.15, 9.16). Adductor muscle field oval in outline, raised slightly above valve floor, bounded postero-laterally by stubby, rod-like lateral trans-muscle septa, laterally by pair of weak, slender central-lateral septa, and postero-medially by pair of rounded septa that converge and merge onto notothyrial platform. Brachio-phores poorly preserved.

*Etymology.*—After the Mackenzie Mountains, where the new species occurs.

*Materials.*—AV4B 111.3–111.4 m (1 ventral valve, 1 dorsal valve). S-2 (1 conjoined shell; 1 ventral valve, 3 dorsal valves).

*Remarks.*—The new species is most similar to *Katastrophomena woodlandensis* (Reed, 1917) from Rhuddanian rocks of Scotland and Wales in its coarse, sinuous, and crooked costae and in overall internal structure, but differs in having a predominantly biconvex shell with strongly developed fascicostellae. Temple (1970, 1987) observed that ribbing density is the only consistent character for distinguishing *Katastrophomena woodlandensis* from *K. scotica* (Bancroft, 1949). In the Scottish material, *K. woodlandensis* has coarser, more crooked, and uneven costae than *K. scotica*. Cocks (2008) agreed with Temple (1987) that *K. scotica* should be treated as a subspecies of *K. woodlandensis*. The crooked and knotted ribbing in the two specimens (ventral and dorsal valves, both convex) from section AB4B is nearly identical to that of *K. woodlandensis* (e.g., Cocks, 1968, pl. 2, figs. 1, 3) in addition to their similarly small ventral muscle field with prominent bounding ridges and a rounded median ridge, a dorsal median septum that abuts against the notothyrial platform and bifurcates immediately to form the central trans-muscle seta, and a pair of rod-like lateral trans-muscle septa. The fascicostellae in AV4B specimens are less strongly developed than in those from locality S-2 but are more like the less-distinct fascicostellae in the paratype of *K. woodlandensis scotica* illustrated by Cocks (1968, pl. 3, fig. 5) and Temple (1987, pl. 7, fig. 6). The British specimens reach a large size of over 20 mm long and 30 mm wide and are variably resupinate at adult stage (from flat to nearly geniculate). The dorsal valve

resembles that illustrated in Cocks (1968, pl. 2, fig. 6) in its relatively strong convexity.

In his description of *Katastrophomena woodlandensis* from the Rhuddanian of Estonia, Rubel (2011) commented that they are identical to conspecific material from Wales and Norway (Temple, 1968, 1987; Baarli, 1995), but observed two significant variations in the Estonian specimens: (1) the shell curvature changes from convexo-planar to weakly resupinate; and (2) the ribbing ranges from fairly regular (non-crooked) and somewhat unequally parvicostellate to strongly crooked (Rubel, 2011, pl. 1, fig. 5). The Mackenzie shells most closely resemble the variants with relatively coarse and crooked ribs, or a convexo-planar lateral profile. The internal structures in shells from Estonia and the Mackenzie Mountains are nearly identical, especially in its small ventral muscle field with prominent, semicircular, lateral bounding ridges and a medial ridge (compare Fig. 9.2, 9.18 with Rubel, 2011, pl. 1, figs. 8), and in the blunt, rod-like lateral trans-muscle septa (compare Fig. 9.8, 9.10, 9.11, 9.15, 9.16 with Rubel, 2011, pl. 1, figs. 10–14). The Mackenzie Mountains species differs from the Estonian *K. woodlandensis* in having a weak biconvex shell and distinct fascicostellae.

Lenz (1977) reported a doubtful and unidentified species *Katastrophomena* from lower Llandovery strata of the Road River Formation, Mount Sekwi (Mackenzie Mountains); it is similar to the Avalanche Lake and S-2 specimens in having a biconvex shell and strong and irregular costae, as well as similar internal structures and, therefore, it is considered conspecific with the new species described here.

*Katastrophomena parvicardinis* Jin and Chatterton, 1997

1997 *Katastrophomena parvicardinis* Jin and Chatterton, p. 28, pl. 23, figs. 1–20.

*Holotype.*—UA 10673 (Jin and Chatterton, 1997, pl. 23, figs. 13, 14), section AV1, 95.5 m above base, upper Hirnantian beds of the lower Whittaker Formation.

*Materials.*—AV1 95.5 m (31 ventral valves, 41 dorsal valves).

*Remarks.*—In the Avalanche Lake area of southern Mackenzie Mountains, *Katastrophomena parvicardinis* occurs in section AV1 and is stratigraphically coeval with *K. cf. K. woodlandensis* from section AV4. This is another species of *Katastrophomena* with a biconvex shell, although shells are generally very small and only weakly convex, with a thickness < 1 mm, average length of 4 mm (max. 5.5 mm) and average width of 5 mm (max. 7.5 mm). Despite the small shell size, *K. parvicardinis* shares some similarities with *K. cf. K. woodlandensis*, such as the well-developed apsacline ventral interarea, relatively large pseudodeltidium, and relatively strong rounded ribs that tend to become fascicostellate (see Jin and Chatterton, 1997, pl. 23, figs. 6, 18), although not as distinctly fascicostellate as in *K. cf. K. woodlandensis*. *Katastrophomena parvicardinis* has a rounded ventral muscle field with curved lateral bounding ridges and a low median ridge, which are typical of the early forms of *Katastrophomena* described by Cocks (1968) from the UK,

but the Avalanche Lake species differs from those British species in its notably smaller and thinner-walled shell, finer costellae, poorly developed growth lamellae and lack of lateral trans-muscle septa in the dorsal valve. *K. woodlandensis* from the British type area, for example, commonly reach sizes of more than 20 mm in length and 30 mm in width, with well-defined lateral trans-muscle septa in the dorsal valve.

In the Avalanche Lake locality (section AV1), resupinate shells of *Katastrophomena* sp. (see Jin and Chatterton, 1997, p. 29, pl. 23, figs. 21–23) occur 30 m above the level of *K. parvicardinis*, in strata of Rhuddanian age.

Family Rafinesquinidae Schuchert, 1893  
Subfamily Leptaeninae Hall and Clarke, 1894  
Genus *Biparetis* Amsden, 1974

*Type species.*—*Biparetis paucirugosus* Amsden, 1974; basal Leeman Formation (Hirnantian), Missouri, USA.

*Remarks.*—Cocks and Rong (2000) assigned *Biparetis* to Family Strophomenidae (Subfamily Furcitellinae). However, the sharp dorsal geniculation, concentric rugae, and convergent lobes of the cardinal process at their crest of *Biparetis* suggest a closer affinity to Family Rafinesquinidae (Subfamily Leptaeninae), as originally proposed by Amsden (1974), which was adopted by Dewing (1999), and is followed in this study. At present, *Biparetis* is a monospecific taxon.

*Biparetis paucirugosus* Amsden, 1974  
Figure 10.1–10.11

1974 *Biparetis paucirugosus* Amsden, p. 55, pl. 21, figs. 1A–R; pl. 22, figs. 1A–K.

1999 *Biparetis paucirugosus*; Dewing, p. 49, pl. 19, figs. 7, 8.

*Holotype.*—OU 6707, basal Leeman Formation (Hirnantian), Girardeau County, Missouri, USA.

*Materials.*—Locality S-2 (2 conjoined shells).

*Remarks.*—Only two specimens are available for study, one conjoined mature shell with a damaged posterior, and the other immature. These are assigned to *Biparetis paucirugosus* based mainly on the strong dorsal geniculation of the shell with weak, concentric rugae (Fig. 10.6, 10.7). The two lobes of the cardinal process have a tendency to converge at their apices in the type material (e.g., Amsden, 1974, pl. 21, figs. 1e, m, n), as is visible also in the immature shell from locality S-2 (Fig. 10.4). Amsden (1974, pl. 21, figs. 1i–k) showed a relatively narrow shell with a prominent trail, giving the shell an apparent equidimensional (as long as wide) appearance; but the majority of the type specimens have a transversely extended shell outline typical of leptaenids. The Mackenzie Mountains form is mostly similar to paratypes with a transverse outline and faint rugae (e.g., Amsden, pl. 21, fig. 1o, r). The prominent pair of trans-muscle septa in the dorsal valve, as is diagnostic of the genus, can be partly observed

when viewed from the damaged posterior inward. Some specimens reported as *Lepaena rugosa* Dalman, 1828 (see Bergström, 1968) from Hirnantian strata also have weaker concentric rugae similar to *Biparetis paucirugosus*, such as those from the Porkuni (Hirnantian) strata of Estonia (Hints and Harper, 2015) and the Kuanyinqiao (Hirnantian) and Weiba (upper Hirnantian) formations of South China (Huang et al., 2020a, b; Rong and Huang, 2023); but these leptaenids do not seem to have the prominent pair of trans-muscle septa in the dorsal valve.

The strongly concave dorsal valve of *B. paucirugosus* seems to have been susceptible to epibiont encrustation, as seen in specimens from Missouri (Amsden, 1974, pl. 21, fig. 1f) and the Mackenzie Mountains (Fig. 10.5, 10.10, 10.11).

Outside of the Edgewood type area in the USA, *Biparetis* have been found so far only as a rare taxon in the Mackenzie Mountains and on Anticosti Island, eastern Canada. Dewing (1999) reported only two specimens of *B. paucirugosus* from the basal Fox Point Member of the Becscie Formation, a level regarded by some as uppermost Hirnantian based on chemostratigraphic and biostratigraphic data (Mauviel et al., 2020; Zimmit and Jin, 2023).

Order Pentamerida Schuchert and Cooper, 1931  
Family Parastrophinidae Ulrich and Cooper, 1938  
Genus *Parastrophina* Schuchert and LeVene, 1929

*Type species.*—*Atrypa hemiplicata* Hall, 1847, “Trenton Limestone” (lower Katian), northwestern New York State.

*Parastrophina* cf. *P. minor* (Roy, 1941)  
Figure 11.1–11.3

1941 *Parastrophinella hemiplicata minor* Roy, p. 94, fig. 57.

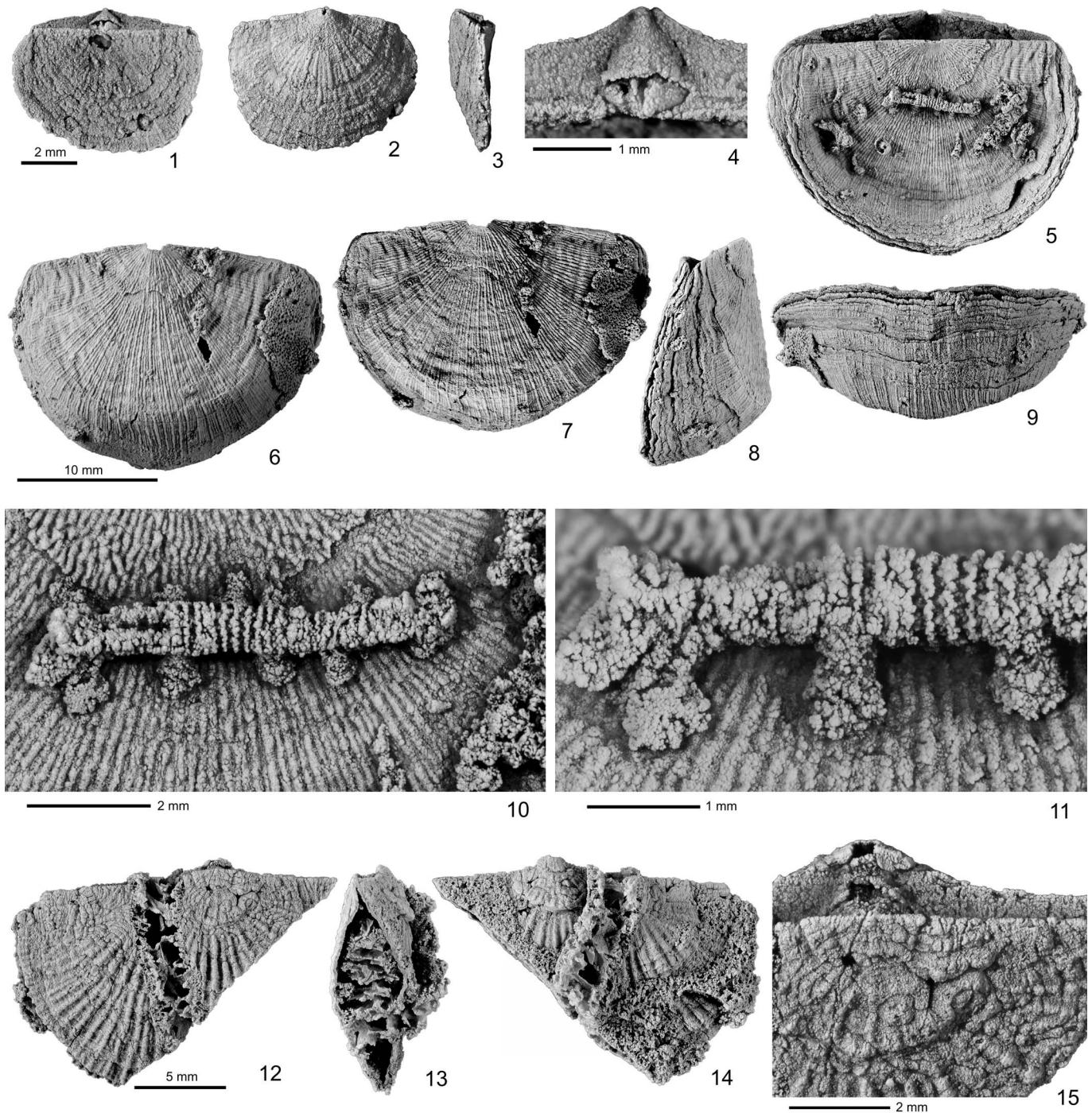
2000 *Parastrophina minor*; Bolton, pl. 20, figs. 3–6, 8, 18.

2015 *Parastrophina minor*; Sproat et al., p. 172, fig. 14A–T.

*Types.*—Holotype, USNM 28156, by original designation of Roy (1941), Amadjuack Formation (middle Katian, Edenian), Silliman’s Fossils Mount, Baffin Island, Canada.

*Material.*—Locality S-2 (1 incomplete dorsal valve).

*Remarks.*—The only specimen available for study, an incomplete dorsal valve, is assigned to *Parastrophina* on account of its well-developed cruralium, which consists of a pair of crural plates merging onto the low median septum, which protrudes above the cruralium floor as a blade-like medial ridge, especially in the anterior part of the structure (Fig. 11.2, 11.3); this morphological feature is typical of the type and other species and *Parastrophina*, as demonstrated by Sproat et al. (2015, p. 168, fig. 8). The alate plates are small but well defined (Fig. 11.3). The S-2 specimen is compared to *P. minor* in its relatively small but moderately convex dorsal valve with strong concentric growth lamellae, but the S-2 specimen differs from other species of *Parastrophina* in having a strongly pointed umbo and beak. Several species



**Figure 10.** (1–11) *Biparetis paucirugosus* Amsden, 1974, two specimens from locality S-2, Hirnantian strata of the lower Whittaker Formation, central Mackenzie Mountains. (1–4) GSC 131874, dorsal, ventral, lateral, and posterior apical views of immature, concavo-convex shell, showing presence of concentric rugae; (5–11) GSC 131875, dorsal, ventral (slightly tilted to show trail), ventral (low-angle lighting to show weak concentric rugae), lateral, and anterior views of concavo-convex shell with sharp geniculation and prominent trail (8), and details of epibionts on dorsal valve (10, 11). (12–15) *Katastrophomena mackenzii* new species, GSC 131873, paratype, dorsal, lateral, ventral, and apical views of incomplete shell showing biconvexity, locality S-2, Hirnantian strata of the lower Whittaker Formation, central Mackenzie Mountains.

from Dulankara and Anderken strata (upper Sandbian–lower Katian) of Kazakhstan, such as *Parastrophina plena* Sapelnikov and Rukavishnikova, 1975, *P. portentosa* (Nikitin and Popov in Nikitin et al., 1996), and *P. iliiana* Popov, Cocks, and Nikitin, 2002, have a posteriorly tapering dorsal

valve, but these older forms have a much better-developed dorsal median septum that begins at the valve apex (see Popov et al., 2002; Jin and Popov, 2008). In the S-2 specimen, the dorsal median septum is so low posteriorly as to make the cruralium nearly sessile.

Family Virgianidae Boucot and Amsden, 1963  
Genus *Brevilammulella* Amsden, 1974

*Type species.*—*Clorinda? thebesensis* Savage, 1913, Leemon Formation (Hirnantian), Illinois, USA.

*Brevilammulella laevis* (Sapelnikov and Rukavishnikova, 1975)  
Figure 11.4–11.14

1975 *Antigaleatella laevis* Sapelnikov and Rukavishnikova, p. 74, pl. 17, figs. 8–16.

1985 *Brevilammulella laevis*; Sapelnikov, p. 25, pl. 4, figs. 9–13.

1997 *Brevilammulella laevis*; Jin and Chatterton, p. 35, pl. 31, figs. 12–25.

*Types.*—The specimens figured by Sapelnikov and Rukavishnikova (1975) are from the *Holorhynchus giganteus* Zone, Tolen Beds (highest Katian), eastern Kazakhstan.

*Materials.*—AV1 77.5 m (1 conjoined shell, 2 ventral valves, 1 dorsal valve); AV4B 111.3–111.4 m (1 conjoined shell, 4 ventral valves); AV4B 111.4–111.6 m (4 ventral valves); AV4B 111.64–111.66 m (10 ventral valves, 4 dorsal valves).

*Remarks.*—Sapelnikov (1985) assigned this species to *Brevilammulella* because he treated *Antigaleatella* as a junior synonym of *Brevilammulella*. It is more difficult, however, to distinguish *Brevilammulella* from early forms of *Clorinda*, such as *Clorinda undata* (J. de C. Sowerby, 1839) of earliest Silurian (early Llandovery) age by external morphology alone because both genera have a small, moderate to strongly biconvex shell bearing a ventral sulcus and dorsal fold, as observed by Amsden (1974), Sapelnikov and Rukavishnikova (1975), and Sapelnikov (1985). Such a ventral sulcus and dorsal fold are well developed in relatively large specimens of *B. laevis* from the Avalanche Lake area (Fig. 11.4–11.7, 11.12–11.14). This problem was also encountered by Temple (1968, 1970, 1987) in his study of the Hirnantian–Rhuddanian pentamerides from Wales. Internally, *Brevilammulella* can be distinguished from *Clorinda* in having smaller hinge plates, confined largely to the apical area (e.g., Fig. 11.14) and, in transverse cross section, the inner hinge plates range from subparallel to basio-medially inclined to each other in *Brevilammulella*, whereas they are basio-laterally divergent from each other in *Clorinda* (e.g., see Jin et al., 1993). Along their junctions with the valve floor, however, the inner hinge plates become wider apart from each other anteriorly (Fig. 11.10, 11.14). In addition, the crus forms a prominent flange at its junctions with the inner and outer hinge plates in *Clorinda*, but merges smoothly with the hinge plates in *Brevilammulella*.

In the Mackenzie Mountains, *Brevilammulella* has been found only from the Avalanche Lake area, not in the S-2 material. These are assigned to *B. laevis*, originally reported from eastern Kazakhstan (Sapelnikov and Rukavishnikova, 1975; Sapelnikov, 1985) based on their predominantly smooth, subequally biconvex shell with a low and pointed ventral umbo, and

a faint plica in the anteriorly developed ventral sulcus in some relatively large specimens (Fig. 11.4). Nearly all the shells from the Avalanche Lake collection are incomplete due to various degrees of damage, and a relatively large dorsal valve with minor damage in the collection is estimated to be 10 mm in length or width (Fig. 11.12–11.14). The type species, *B. thebesensis*, attains a maximum width of 15 mm (Amsden, 1974), although the Avalanche Lake shells fall within the average shell width (~10 mm) of the type species. The two species differ in that the Avalanche Lake forms have a prominently pointed posterior in both the ventral and dorsal valves.

Farther north along the western margin of Laurentia, a latest Katian species of *Brevilammulella*, *B. minuta* Jin and Blodgett, 2020, occurs in east-central Alaska, which belonged to the stable margin of Laurentia. This relatively old species differs from the Mackenzie Mountains form in having a very small shell (< 6 mm in length or width) and a posteriorly tapering shell.

Compared to the miniscule internal structures (hinge plates) of the dorsal valve, the internal structures of the ventral valves are rather prominent relative to shell size, especially in its broadly V-shaped spondylium supported by a high, blade-like median septum that extends for about one-third of the valve length.

Order Atrypida Rzhonsnitskaya, 1960

Superfamily Atrypoidea Gill, 1871

Family Atrypidae Gill, 1871

Genus *Eospirigerina* Boucot and Johnson, 1967

*Type species.*—*Zygospira putilla* Hall and Clarke, 1894. Edgewood Group (probably Bryant Knob Formation), Hirnantian–Rhuddanian boundary interval, Missouri.

*Eospirigerina putilla* (Hall and Clarke, 1894)

Figure 12

1894 *Zygospira putilla* Hall and Clarke, p. 356, pl. 54, figs. 35–37.

1913 *Atrypa praemarginalis* Savage, p. 129, pl. 6, figs. 14–16. [page range and plate number shown according to reprint dated 1917]

1967 *Spirigerina (Eospirigerina) praemarginalis*; Boucot and Johnson, p. 91, pl. 1, figs. 1–16.

1974 *Eospirigerina putilla*; Amsden, p. 72, pl. 17, figs. 7a–e, pl. 18, figs. 1–19, pl. 19, figs. 1–8.

1974 *Atrypa praemarginalis*; Amsden, p. 128, pl. 18, figs. 9a–d.

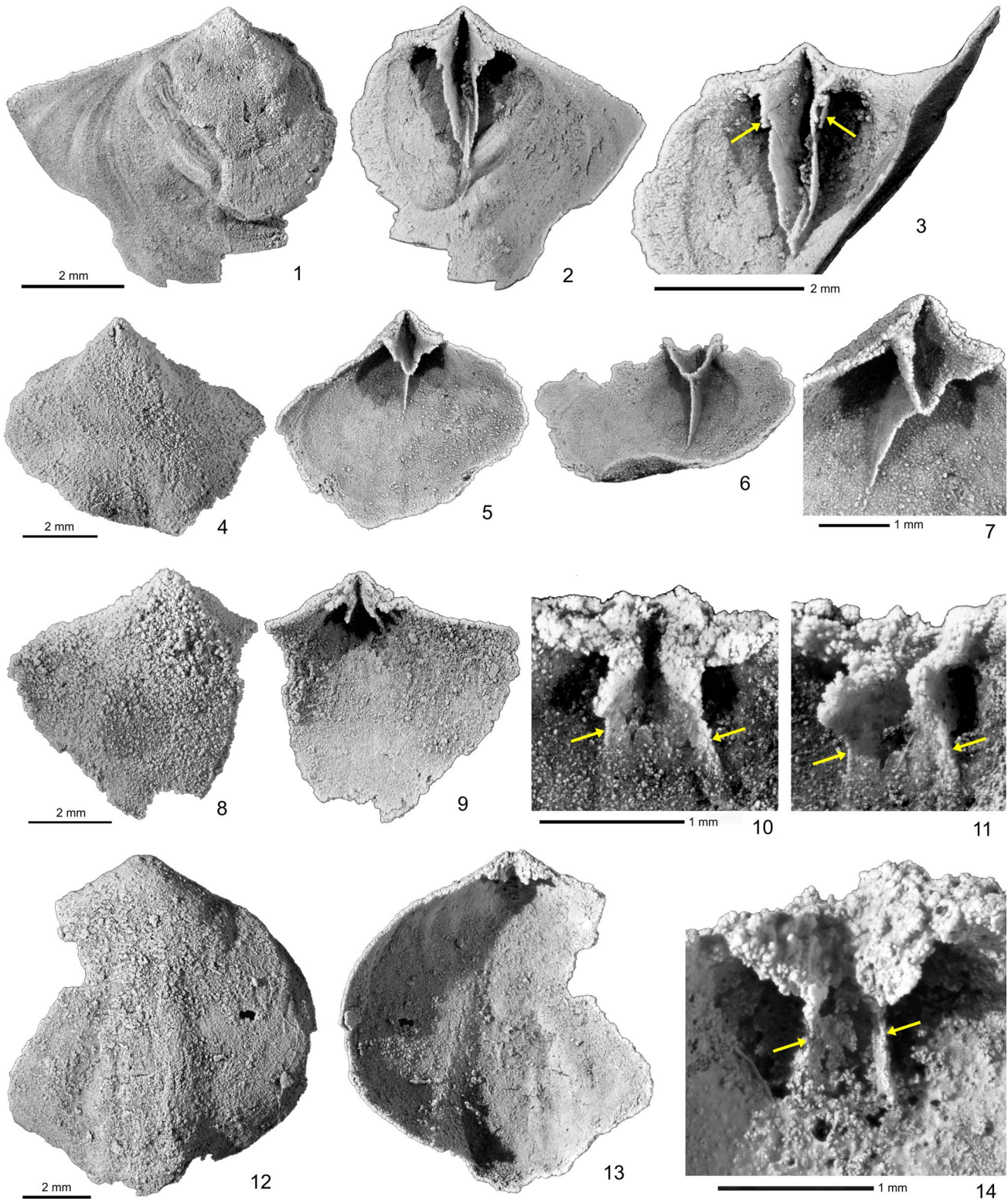
1977 *Eospirigerina cf. putilla*; Lenz, p. 1542, pl. 10, figs. 13, 17–28.

1985 *Eospirigerina praemarginalis*; Kulkov et al., p. 149, pl. 20, figs. 3a–d.

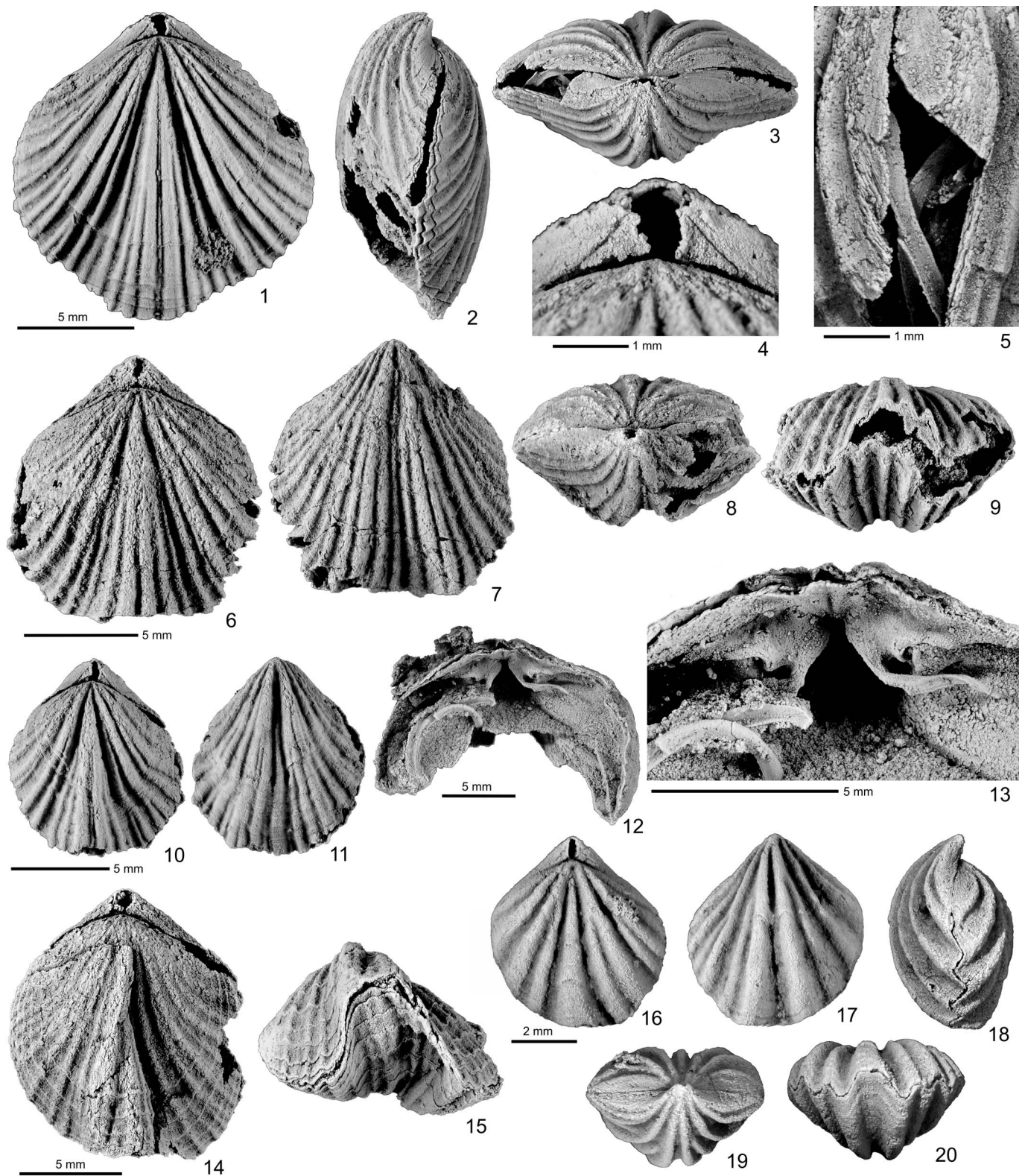
1997 *Eospirigerina putilla*; Jin and Chatterton, p. 41, pl. 36, figs. 7–23.

2022 *Eospirigerina putilla*; Wang and Huang, p. 9, figs. 9A–H.

*Types.*—Neotype of *Zygospira putilla*, UI-RX519, selected by Amsden (1974, p. 73, pl. 18, figs. 8b–f); lectotype of *Atrypa praemarginalis* (regarded as a subjective junior synonym of *Z.*



**Figure 11.** (1–3) *Parastrophina* cf. *P. minor* (Roy, 1941), GSC 131876, incomplete dorsal valve from locality S-2, Hirnantian strata of the lower Whittaker Formation, central Mackenzie Mountains; exterior, interior, and tilted anterior view showing alate plates (arrows in 3) and long cruralium raised anteriorly above valve floor by median septum. (4–7) *Brevilammulella laevis* (Sapelnikov and Rukavishnikova, 1975); (4–7) UA 107307, ventral valve from section AV4B, 111.3–111.4 m above base of section, lower Whittaker Formation, Hirnantian, Avalanche Lake, southern Mackenzie Mountains; exterior, interior, tilted anterior, and tilted lateral views, showing high median septum supporting broad V-shaped spondylium; (8–11) UA10736, dorsal valve from section AV1, 77.5 m above base of section, lower Whittaker Formation, Hirnantian, Avalanche Lake, southern Mackenzie Mountains; exterior, interior, tilted anterior, tilted lateral views showing short and low inner hinge plates (arrows in 10, 11); (12–14) GSC 131877, exterior, interior, and tilted apical views of dorsal valve with minor damage, also from section AV1, 77.5 m (arrows indicate inner hinge plates).



**Figure 12.** *Eospirigerina putilla* (Hall and Clarke, 1894), six specimens from locality S-2, Hirnantian strata of the lower Whittaker Formation, central Mackenzie Mountains. (1–5) GSC 131878, dorsal, lateral, posterior, apical, and additional, enlarged lateral views; note well-preserved deltidial plates (4), and spirialium visible through damaged part ventral valve (5). (6–9) GSC 131879, dorsal, ventral, posterior, and anterior views; note well-developed fascicostellae in medial part of both valves. (10, 11) GSC 131880, dorsal and ventral views of small shell. (12, 13) GSC 131881, interior and detail view of apical part of dorsal valve showing crura and spirial lamella. (14, 15) GSC 131882, dorsal and anterior views of distorted shell, with strong growth lamellae. (16–20) GSC 131883, dorsal, ventral, lateral, posterior, and anterior views of immature shell.

*putilla* by Amsden, 1974), UI X-4757, selected by Amsden (1974, p. 73, pl. 18, figs. 9a–e (misstated as “figs. 9a–d ... IU X-4757” on p. 73). All from the same locality and horizon in Pike County, Missouri, Bryant Knob Formation, Edgewood Group, Hirnantian.

**Materials.**—Total 164 specimens. AV1 77.5 m (9 conjoined shells); AV4B 111.3–111.4 m (3 conjoined shells, 3 ventral valves, 3 dorsal valves); AV4B 111.4–111.6 m (2 conjoined shells, 1 ventral valve, 2 dorsal valves); AV4B 111.5 m (3 conjoined shells); AV4B 111.6 m (10 conjoined shells, 2 ventral valves, 3 dorsal valves); AV4B 111.64–111.66 m (15 conjoined shells, 3 ventral valves, 1 dorsal valve); S-2 (97 conjoined shells, 4 ventral valves, 3 dorsal valves).

**Remarks.**—The Mackenzie Mountains specimens are assigned to *Eospirigerina putilla* based on their similarity to both the immature and adult shells figured by Amsden (1974) from the Edgewood type area. Specimens smaller than 6 mm in length are generally elongate, teardrop-shaped, ventribiconvex, with a dorsal median furrow, ventral carina, and an erect ventral beak; deltidial plates appear to be lacking in the small shells from Avalanche Lake (Jin and Chatterton, 1997, pl. 36, figs. 15–19), but are clearly present in well-preserved S-2 specimens (Fig. 12.10, 12.11, 12.15–12.19). With ontogeny, larger shells become less elongate or equidimensional, equibiconvex, with some relatively large shells even becoming dorsibiconvex, such as the shell illustrated by Jin and Chatterton (pl. 36, figs. 7, 8), which is similar to the strongly dorsibiconvex shell of *E. putilla* illustrated by Amsden (1974, pl. 19, fig. 2a) from the Leemon Formation of Illinois, and by Rong and Huang (2023, figs. 4.20, 4.24–4.27) from Hirnantian strata of Yunnan, South China. Most of the Mackenzie Mountains specimens have well-preserved, medially conjoined deltidial plates and an apical foramen (Fig. 12.1, 12.3, 12.6, 12.8, 12.10, 12.13). A similar ontogenetic morphological transformation from elongate younger forms to nearly equidimensional adult ones, with concomitant reduction in size and height of the ventral beak relative to shell size, also has been observed in a large population of silicified specimens of *E. putilla* from the Hirnantian Wulipo Formation in Yunnan, southwestern China (Wang and Huang, 2022; Rong and Huang, 2023).

The ribs in specimens from both the Avalanche Lake and S-2 localities are strong but uneven due to asymmetrical bifurcations, which are somewhat more frequent in large specimens from S-2 than those from Avalanche Lake. A single strong costa in the dorsal apical area increases anteriorly through bifurcation, reaching up to eight (from left to right furrow that delimits the fold) near the anterior margin of some relatively large shells (e.g., Fig. 12.1). Correspondingly, in the ventral valve, two prominent costae form a carina in the ventral umbonal area, increasingly anteriorly to become a bundle of up to four fascicostellae, which mark the rounded margin on each side of the sulcus (Fig. 12.7, 12.11, 12.16). The tendency to develop fascicostellae also was observed by Amsden (1974) in *E. putilla* from the Edgewood type area. Also, as in Edgewood material, a delicate medial capilla in the ventral umbonal may develop anteriorly into a normal medial costa (compare Fig. 12.7 and 12.11 with Amsden, 1974, pl. 18, fig. 8f), but the corresponding medial capilla in the dorsal valve, if present, remains delicate with shell growth

(compare Fig. 12.1, 12.10 with Amsden, 1974, pl. 18, fig. 8b). The overall number of costae on each valve may increase to as many as 34 mainly through bifurcation (uncommonly by interaction) at anterior margin of mature shells. In well-preserved shells, very fine growth lines (~15 per mm) can be observed, superimposed by coarser, irregularly spaced (1–2 per mm) growth lamellae (Fig. 12.1, 12.7, 12.10, 12.11, 12.13, 12.14).

Regarding *E. putilla* based on the Edgewood types, the internal structures of its dorsal valve deserve more attention because some immature specimens shown by Amsden (1974) have a horizontal plate (“cardinal plate”) arching between the pair of hinge plates. In this respect, these young *E. putilla* shells resemble adult shells of *Alispira gracilis* Nikiforova (in Nikiforova and Andreeva, 1961) from the lower–middle Llandovery of Siberia. Such a ventrally convex “cardinal plate” is present also in *A. gracilis* from coeval strata of western Canada (Jin and Norford, 1992). Moreover, young forms of *E. putilla* are similar to *A. gracilis* in their elongate shell with a pair of strong costae defining the ventral sulcus. This led Kulkov and Rybkina (1982) to regard *E. putilla* as a species of *Alispira*. For this study, no such a “cardinal plate” has been observed in either immature or adult specimens of *E. putilla*, but this may have been due to the poor preservation of the silicified material.

Dimensions (mm):	length	width	thickness/depth
AV4B 111.3–111.4	12.7	12.0	9.8 (conjoined shell)
AV4B 111.3–111.4	11.0	11.8	4.8 (dorsal valve)
AV4B 111.3–111.4	5.0	4.0	3.0 (conjoined shell, immature)
AV1 77.5	5.0	4.5	2.4 (conjoined shell, immature)
AV1 77.5	5.2	4.2	2.4 (conjoined shell, immature)

Specimens of *Eospirigerina putilla* from the Mackenzie Mountains have a certain degree of similarity to *E. gaspeensis* (Cooper, 1930) from Rhuddanian strata of the Oslo region (Baarli, 2021, p. fig. 12–19) in their slightly elongate outline, pointedly tapering ventral posterior, and a tendency to develop fascicostellae on both sides of the sulcus, but differ in having a much stronger, wider dorsal fold that bears more numerous costae (up to eight fascicostellae) anteriorly, resulting from bifurcations (Fig. 12.1, 12.6, 12.10).

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## Declaration of competing interests

The authors declare none.



## Data availability statement

### Hirnantian Faunal List [Dataset].

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.98sf7m0qd>

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