

# Warm-water *Tcherskidium* fauna (Brachiopoda) in the Late Ordovician Northern Hemisphere of Laurentia and peri-Laurentia

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**Abstract.**—The Late Ordovician (late Katian) *Tcherskidium* fauna consisted of large- and thick-shelled virgianid pentamerid brachiopods characterized by large and ribbed shells of *Tcherskidium* and *Proconchidium* and usually associated with *Holorhynchus*, *Deloprosopus*, and *Eoconchidium*. This unique fauna was widely distributed across several tectonic plates, largely confined to the paleoequatorial and especially the northern paleotropical zones, such as northern Laurentia, accretionary terranes of Alaska, Kolyma, Baltica, Siberia, Kazakh and adjacent terranes, and South China. In Laurentia, the eponymous genus *Tcherskidium* was predominant in regions north of the paleoequator and, in sharp contrast, was absent south of the paleoequator. In this study, *Tcherskidium lonei* n. sp. and *Proconchidium schleyi* n. sp. are described from Alaska and North Greenland, respectively, adding new data on the *Tcherskidium* fauna of the Late Ordovician Northern Hemisphere. Shell gigantism, together with the sharp paleobiogeographic division, suggests that the Late Ordovician (late Katian) Northern Hemisphere had a prevailing warm-water mass, probably due to the lack of large landmass beyond the northern tropics. This was in sharp contrast to the Southern Hemisphere, which was frequently influenced by cold-water invasions from the ice-bearing Gondwana supercontinent centered on the South Pole.

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## Introduction

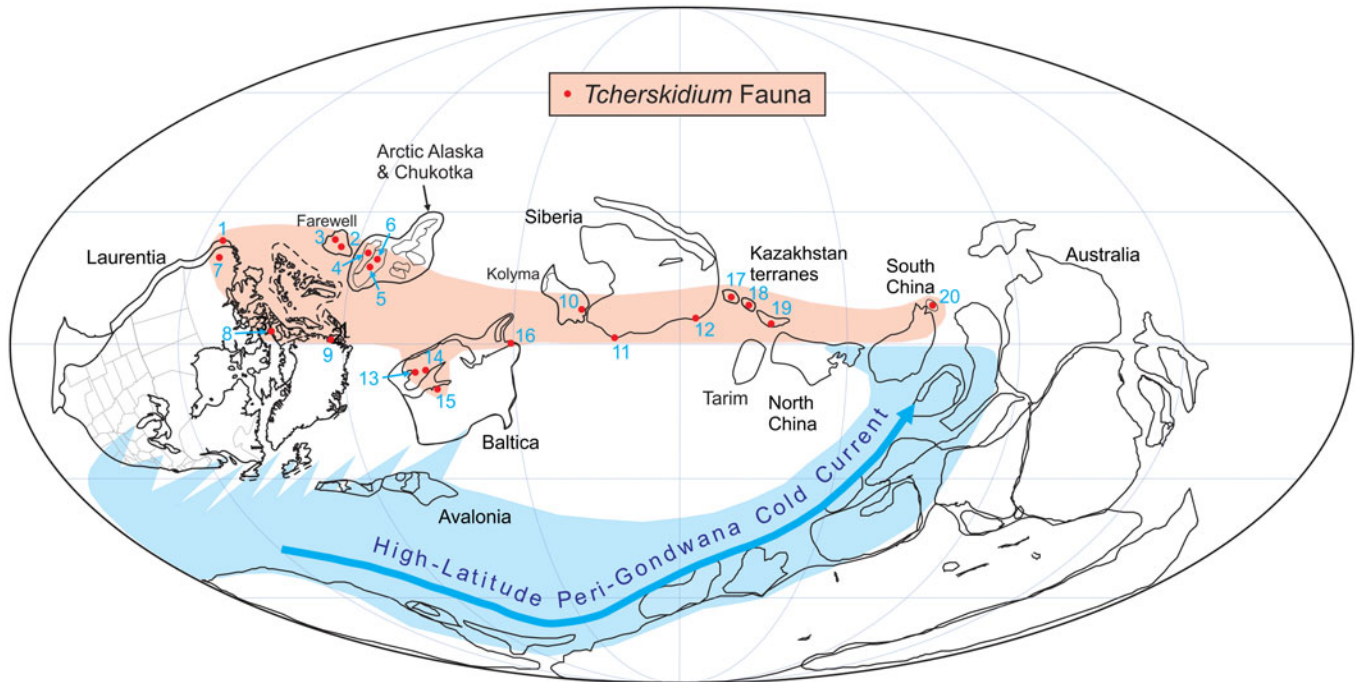
Large-shelled pentamerid brachiopods have been reported from Upper Ordovician (upper Katian) rocks of numerous regions since the description of *Holorhynchus* Kiær, 1902 from the Oslo Region. The predominance of large-shelled virgianid pentamerids in the Upper Ordovician, however, was not fully appreciated until they were widely reported by Russian paleontologists from Siberia and Kazakhstan (e.g., Nikolaev, 1968, 1974; Nikolaev and Sapelnikov, 1969; Sapelnikov and Rukavishnikova, 1975; Sapelnikov, 1985; Nikiforova, 1989; Modzalevskaya, 2018). In North America, the presence of *Tcherskidium* Nikolaev and Sapelnikov, 1969 and *Proconchidium* Nikolaev and Sapelnikov, 1969 was generally known, albeit poorly understood, because they appeared mostly in faunal lists and brief mentions in geological reports, without systematic descriptions (e.g., Blodgett et al., 1988, 2002; Blodgett, 2012). *Proconchidium* from the upper Katian of Brodeur Peninsula of Baffin Island (Rong et al., 1989) and the recently reported *Tcherskidium tenuicostatum* Jin and Blodgett, 2020 from east-central Alaska (marginal Laurentia) were the only systematically described Late

Ordovician virgianids from North America. Another factor bearing on the limited knowledge of Upper Ordovician virgianids in Laurentia and peri-Laurentia was their occurrences in invariably remote locations in Alaska, Arctic Canada, and North Greenland (Harper et al., 2007), exacerbated by their preservation predominantly in massive, well-cemented carbonate rocks, making it difficult to extract loose shells for taxonomic study.

Despite the limitation in fossil collections, the Late Ordovician large-shelled virgianids hold important clues for the evolution of marine shelly benthos, paleoenvironments, and paleogeography on a global scale. As noted by Rong et al. (1989), this group of virgianids occurs in several regions (e.g., Siberia, Kazakhstan, South China, Norway, Sweden, Estonia, northern Urals, North Greenland, Arctic Canada, and Alaska), which were located almost exclusively in the paleotropics of the Late Ordovician Northern Hemisphere in recent paleogeographic reconstructions (Fig. 1), with the exception of the Baltoscandian localities.

Material available recently demonstrated the diversity and wide paleogeographic distribution of characteristic genera of the Late Ordovician virgianid fauna, especially *Tcherskidium*, *Proconchidium*, and *Holorhynchus*. The main aim of this study is to describe a large suite of *Tcherskidium* collections from Alaska and some rarely available specimens of *Holorhynchus* from an accreted terrane of Alaska, as well as extremely abundant

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**Figure 1.** Paleogeographic map showing the distribution of the *Tcherskidium* fauna confined chiefly to the Late Ordovician Northern Hemisphere. *Holorhynchus* localities without *Tcherskidium*/*Proconchidium* are omitted. Base map modified from Torsvik and Cocks (2013), Popov and Cocks (2017), Cocks and Torsvik (2021), and Popov et al. (2021). Localities: 1, Black River quadrangle, NE Alaska (marginal Laurentia); 2, Lone Mountain area; 3, Taylor Mountain D-1; 4, White Mountains; 5, Shublik Mountain; 6, 66ATr82.6 (= USGS Locality 8164-SD; Hammond subterrane of the Arctic Alaska terrane); 7, NW Yukon (marginal Laurentia); 8, Brodeur Peninsula, northern Baffin Island (Laurentia); 9, Peary Land, North Greenland (Laurentia); 10, Mirny Creek, NE Siberia (Kolyma); 11, New Siberian Islands (marginal Siberia); 12, central Taimyr (marginal Siberia); 13–16, Oslo (Norway), Siljan (Sweden), Estonia, and Timan–northern Ural (Russia) regions (Baltica); 17–19, Chingiz, Selety, and Chu–Ili–Tienshan blocks (Kazakh terranes); 20, JYC area, lower Yangtze Platform (South China). For details, see Materials and methods section.

but poorly preserved (mostly ventral valves tightly cemented and embedded in carbonate rocks) *Proconchidium* from North Greenland, and to explore their paleoenvironmental implications.

### Geological setting

*North Greenland occurrence of Proconchidium.*—The sub-equatorial platform–slope depositional environment of the Upper Ordovician–Lower Silurian carbonate succession in North Greenland (Peary Land) was discussed and summarized in a number of studies (Hurst, 1984; Smith et al., 1989; Higgins et al., 1991; Harper et al., 2007; Jin et al., 2013). At the G.B. Schley Fjord section (creek-level coordinates: UTM 0516847N, 9208172E), a relatively deep-water shelf carbonate succession is exposed containing thick, *Proconchidium*-dominated shell beds that are recurrent at many levels through the >350 m thick succession, with a general trend of increasing shelly size up-section. Thick shell beds of *Proconchidium* dominate the lower parts of the carbonate unit, with individual packstone-grade shell beds of 0.2–1.2 m thicknesses vertically stacked into shell-bed packages up to 3 m thick at several stratigraphic intervals. The shell beds and associated carbonate strata show a number of depositional features indicating a moderate water depth (within the photic zone) yet low-energy depositional environment: (1) predominantly in situ, concave-down orientation of extremely thickened ventral valves show no sorting, but the smaller and thinner dorsal valves are mostly absent; (2) absence of hummocky cross stratification; (3) association with

the large, globular receptaculitid alga and large aulacritid stromatoporoids. Most of the shell beds are separated by burrow-mottled, irregularly bedded, crumbly-weathering, dolomitic limestone. From elevation 170 m (creek level) to 355 m (UTM 0516757N, 9208143E), for example, the *Proconchidium* coquinas grade upward into favositid coral biostromes, with occurrences of macluritid gastropods and aulacritid stromatoporoids, which were typical of the shallow-water Red River fauna of Laurentia. At elevation 450 m (UTM 0516657N, 9207835E), a thick coquina unit (2–3 m thick) of large *Proconchidium* shells is succeeded again by burrow-mottled dolomitic limestone, grading upward into thin- and irregularly bedded lime mudstone and then a blocky stromatolitic unit (elevation 508 m, UTM 0516564N, 9207882E). The combination of these depositional features was the basis for an interpretation of a hurricane-free paleoequatorial shallow-water environment (Jin et al., 2013). The Schley Fjord *Proconchidium*-bearing section is considered an eastern equivalent to the Alegatsiaq Fjord Formation of western North Greenland and a somewhat deeper-water correlative to the Turesø Formation of central North Greenland (Higgins et al., 1991; Rasmussen, 2013). *Proconchidium*-bearing strata also occur in more proximal facies of the Baillarge Formation, Brodeur Peninsula, Baffin Island, Arctic Canada (Rong et al., 1989).

*Alaskan localities of Tcherskidium.*—In Alaska, *Tcherskidium* and *Holorhynchus* occur in areas that belong to either the early Paleozoic craton of Laurentia (Black River Quadrangle)

or accreted terranes of peri-Laurentia or peri-Siberian affinities (for a summary, see Blodgett et al., 2002; Blodgett, 2012). In both paleogeographic settings, these large-shelled virgianids occur exclusively in shallow-water, platform carbonate facies. This is further corroborated by the absence of large-shelled virgianids in the deep-water brachiopod fauna reported by Rasmussen et al. (2012) from western Alaska (Farewell terrane). The accreted terranes with occurrences of the *Tcherskidium* fauna include the Nixon Fork subterrane of the Farewell terrane, the White Mountains terrane, and the North Slope and Hammond subterrane of the Arctic Alaska terrane (Fig. 1). *Tcherskidium tenuicostatum* Jin and Blodgett, 2020 from an unnamed upper Katian stratigraphic unit in the Black River D-1 1:63,360 scale quadrangle of east-central Alaska belonged to the northeast margin of Laurentia. This finely ribbed form occurs also in the upper Katian strata (uppermost part of unit 8, Nanook Limestone) of Shublik Mountains, paleogeographically located in the North Slope subterrane of the Arctic Alaska terrane (Moore, 1992; Blodgett et al., 2002). The material of *Tcherskidium lonei* n. sp. described in this paper is from unnamed upper Katian carbonate rocks of Lone Mountain, McGrath C-4 1:63,360 scale quadrangle, an area that was part of the Farewell accreted terrane, known as the Nixon Fork subterrane (see Decker et al., 1994; Blodgett et al., 2002, for a summary).

### Paleobiogeographic significance of the *Tcherskidium* fauna

The term *Tcherskidium* fauna is used only in a qualitative sense in this study to refer to brachiopod faunas that contain the characteristically large, ribbed shells of virgianid brachiopods of late Katian age, *Tcherskidium* and *Proconchidium*, which are commonly associated with the smooth-shelled *Holorhynchus*, but some *Holorhynchus* localities do not contain *Tcherskidium* or *Proconchidium*. *Eoconchidium* and *Deloprosopus* are contemporaneous virgianid forms with notably smaller shells and more restricted paleogeographic distribution (Sapelnikov, 1985; Jin et al., 2006). So far, many of the available collections with any of these key taxa are either virtually mono-specific (e.g., localities reported in this study) or hampered by only partial systematic study (such as the Mirny Creek type locality of *Tcherskidium* in Siberia). Thus, it is premature to attempt any quantitative paleobiogeographic analysis because of the limitation of available faunal data of adequate quality. When describing *Proconchidium* from northern Baffin Island of Arctic Canada, Rong et al. (1989) documented the wide distribution of *Proconchidium* and *Holorhynchus* in paleogeographic regions that were in alignment with the “Uralian–Cordilleran” paleobiogeographic region, originally recognized primarily for Silurian biogeographic realms (Boucot and Hurst, 1979).

The systematic study of *Tcherskidium* from Alaska and adjacent Yukon Territories (this study, as well as Jin and Blodgett, 2020) has convincingly extended the paleogeographic range of the eponymous taxon of the *Tcherskidium* fauna in Laurentia and peri-Laurentia. More significantly, available data show that *Tcherskidium*, the largest ribbed shells among late Katian virgianids, occurred exclusively at or just north of the Late Ordovician equator (Fig. 1) when plotted on recent

paleogeographic maps (Torsvik and Cocks, 2013; Popov and Cocks, 2017; Cocks and Torsvik, 2021). The other two key taxa of the fauna, *Proconchidium* and *Holorhynchus*, have a similar paleogeographic distribution (see Fig. 1) but have also been found in northern Baltica (Timan–northern Ural region, see Beznosova, 2014), southern Norway (St. Joseph, 1938; Cocks, 1982), southern Sweden, Estonia, and Lithuania (for a summary, see Rong et al., 1989). *Holorhynchus*, for example, is found in the mud-mound facies of the Boda Limestone in the Siljan district of Sweden (Shiino et al., 2015), as well as in successions in northern Sweden assigned to the intra-Iapetus Virisen Terrane (Kulling, 1933; Dahlqvist and Rasmussen, 2013). In Baltica, however, *Tcherskidium* is generally absent.

At present, it is difficult to explain the Baltoscandian “outlier” of the *Tcherskidium* fauna, here represented by *Proconchidium* and *Holorhynchus*, located in tropical latitudes south of the Late Ordovician paleoequator according to most paleogeographic reconstructions. Given the extreme paucity of high-quality paleomagnetic data points for the Katian–Llandovery interval (Torsvik et al., 1996), the precise orientation of Baltica has been difficult to determine. For example, the position of Baltica around 450 Ma (Katian) reconstructed in Torsvik and Cocks (2013) was close to its modern orientation, but this was modified by Cocks and Torsvik (2021) with ~40° clockwise rotation, which actually agrees better with the distribution pattern of the *Tcherskidium* fauna. Here we argue that the Baltoscandian occurrences of *Proconchidium* and *Holorhynchus* would align with the predominantly late Katian Northern Hemisphere *Tcherskidium* fauna if Baltica were rotated about 80° clockwise, as reconstructed by Cocks and Torsvik (2005) for the 480–460 Ma interval, and positioned closer to the paleoequator. Aside from the uncertainties of the paleogeographic position of Baltica, the presence of *Holorhynchus* and associated pentamerides in the Boda limestone of Sweden has been interpreted by Shiino et al. (2015) to be sporadic opportunistic colonization of the mudmound habitat. It is conceivable that this outlier of the *Tcherskidium* fauna invaded the reef ecosystem only during episodes of oceanic warming (e.g., see Fortey and Cocks, 2005) or followed a warm-water stream from the paleoequatorial region. Similarly, the paleogeographic positions of the Kazakh terranes (e.g., Chingiz, Selety, and Chu-Ili) have been uncertain, interpreted in various studies to be in the northern tropics, along the equator, or in the southern tropics (e.g., Cocks and Torsvik, 2021) during the Late Ordovician. In this study, the northern tropical position of these terranes proposed by Popov and Cocks (2017) is adopted as these studies are based mainly on Katian faunal characteristics.

In their global paleobiogeographic analysis, Harper et al. (2013, p. 138, fig. 11.12) recognized a “low-latitude province” of late Katian brachiopod faunas, which straddled the equator and extended to the tropics of both hemispheres. The *Tcherskidium* fauna, qualitatively refined in this study, was a part of the low-latitude faunal province, but this fauna appeared to be much more sensitive to paleogeographically controlled environmental factors because of its confinement, largely to the Northern Hemisphere. During the Late Ordovician, subtropical southern Laurentia and even the equator-straddling South China plate were susceptible to episodic cool-water invasions (Holland and Patzkowsky, 1996; Etensohn, 2010; Pohl et al., 2016; Jin

et al., 2018). In Laurentia, this led to a differentiation of a cool-water brachiopod fauna in subtropical regions (e.g., Appalachian foreland basin and adjacent areas east of the Cincinnati Arch) and a warm-water brachiopod fauna in inland seas along the paleoequator (e.g., the Hudson Bay basin, Williston basin), as summarized by Sproat and Jin (2017). In most previous paleobiogeographic analyses of Late Ordovician brachiopod faunas of Laurentia, however, the *Tcherskidium* fauna was hardly considered because of the lack of adequate faunal data.

The updated data presented in this study suggest that the *Tcherskidium* fauna represented the “true warm-water brachiopod fauna” confined largely to the Late Ordovician northern hemisphere. The lack of any significant landmass in the northern temperate and polar latitudes (Torsvik and Cocks, 2013) would have contributed to the lack of a cold-water psychrosphere and upwelling, in sharp contrast to the Southern Hemisphere. Stable carbon and oxygen isotope data have been used extensively as proxies to track environmental changes in the Late Ordovician leading to the Hirnantian glaciation. A general cooling trend has been demonstrated for the Ordovician (Trotter et al., 2008). However, highly resolved  $\delta^{18}\text{O}$  values during the Katian show that at least the lower-middle part of that stage experienced considerable warming (Goldberg et al., 2021). This corresponds well to the so-called Boda Event, where faunal and sedimentological evidence from more southerly warm-water carbonates near the margins of Gondwana was interpreted as a global-warming event (Fortey and Cocks, 2005; Rasmussen et al., 2010; Colmenar and Rasmussen, 2018; Colmenar et al., 2018). The same set of data was used to argue for an opposite scenario—a late Katian cooling phase (Cherns and Wheeley, 2007). The stable isotope record corroborates a gradual onset of the Hirnantian glaciations, as inferred from a positive drift of  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values in the Katian and a pronounced positive kick in the uppermost Hirnantian (i.e., the Hirnantian Isotopic Carbon Excursion [HICE]). So far, such Late Ordovician chemostratigraphic curves based on stable C and O isotopes are known predominantly from localities from the Late Ordovician Southern Hemisphere. In a small number of localities near or north of the paleoequator, it has been difficult to recognize a similar cooling trend in the Katian or the HICE. For example, Kaljo et al. (2012) noted the unique shape of their  $\delta^{13}\text{C}$  curve from the Mirny Creek section of NE Siberia (Kolyma plate), showing notably more consistent values from the late Katian to Hirnantian when compared with drastic excursions in  $\delta^{13}\text{C}$  profiles from localities of the Southern Hemisphere.

The “true warm-water fauna” hypothesis is corroborated by the brachiopod shell morphology. The unusually large shells of *Tcherskidium*, *Proconchidium*, and *Holorhynchus* for Late Ordovician brachiopods show characteristics of an extreme degree of extravagant calcification. *Tcherskidium* and *Proconchidium*, for example, typically have extremely thickened shell walls in the ventral-valve posterior, with the large and strongly arched umbonal area filled completely by secondarily precipitated shell substance, which attains a thickness up to 10 mm and lacks the typical layered microstructure of the shell proper. These genera also have a long and thick (up to 5 mm thick posteriorly) median septum extending almost to the anterior shell margin, a morphological feature rarely seen in Katian–Telychian pentameride shells from south of the paleoequator

(for example, see Jin and Copper, 2000). Such gigantism and extravagant calcification are typical of shells living in warm waters that are supersaturated with respect to  $\text{CaCO}_3$  precipitation. For example, extravagantly thickened shells of *Proconchidium* occur abundantly in relatively deep-water shelf facies of the G.B. Schley Fjord region in North Greenland. Such excessive calcification at relatively deep shelf settings implies that the warm-water conditions in paleoequatorial seas during the late Katian probably penetrated deep into the water column on the carbonate shelves, promoting regional warm-water incursions into the southern tropics.

## Materials and methods

*Materials from the Nixon Fork subterranean of the Farewell terrane (Alaska).*—These include the collections from Lone Mountain and Taylor Mountains.

Collection from the Lone Mountain area—Six small blocks with embedded ventral valves and a total of 563 silicified specimens of *Tcherskidium lonei* n. sp. etched out from dark gray to black limestone, including 429 ventral valves (incomplete to various degrees) and 134 dorsal valves (mostly fragmentary), from unnamed upper Katian strata. The collection locality is a silicified megafossil-bearing limestone bed about 1 m thick, exposed along the ridge crest west of Lone Mountain, Alaska (154°50'33" W, 62°31'59" N), center of SW1/4, NE1/4 of sec. 9, T28N, R30W, McGrath C-4 1:63,360 scale quadrangle, west-central Alaska. Gastropods from this locality (USNM locality 32023) were described by Rohr and Blodgett (1985).

Collection 84RB134 from Taylor Mountains D-1 1:63,360 scale quadrangle—A total of 44 calcareous specimens (43 ventral valves and one dorsal valve), including some variants with coarse costae. The *Tcherskidium* sample locality is situated in sec. 3, T10N, R39W, Taylor Mountains D-1 1:63,360 scale quadrangle (156.1726° W, 60.0941° N). The shells occur as a coquina bed in the Olss unit of Blodgett and Wilson (2001, fig. 2, fossil locality 6). This unit consists of brown, medium- to thick-bedded packstone to wackestone with abundant *Tcherskidium*. The same locality was shown as locality 90 on the map of Karl et al. (2011). Sedimentological and paleontological evidence suggests a shallow-water, carbonate platform environment for the *Tcherskidium*-bearing limestone, although limited field observations also suggest the possibility of locally developed mass-flow deposits (Blodgett and Wilson, 2001). These authors reported preliminary identification of *Tcherskidium* n. sp., a smooth new genus aff. *Tcherskidium*, and either *Proconchidium* or *Eoconchidium* sp. Closer examination of the “smooth pentameroids” in this study, however, revealed that the shells were exfoliated, with costae still visible under low-angle lighting. A well-preserved ventral valve shows a well-delimited interarea, indicating an affinity to *Tcherskidium lonei* n. sp.

*Materials from the North Slope subterranean of the Arctic Alaska terrane.*—Only one collection from the Shublik Mountain belonging to this tectonic unit is included in this study: 66 calcareous specimens of *Tcherskidium tenuicostatum* Jin and Blodgett, 2020, exclusively ventral valves, mostly embedded in medium-gray, massive, well-cemented limestone, from upper Katian strata of Member 8 of the Nanook Limestone as

refined by Blodgett et al. (1992). *Tcherskidium* was recognized from two measured sections (87NA-1 and 87NA-2 of Blodgett et al., 1988). Most of the *Tcherskidium* specimens were recovered from the 87NA-1 section at U.S. Geological Survey (USGS) locality 10632-CO (SW1/4, SE1/4, SW1/4 of sec. 13, T2N, R26E, Mount Michelson C-3 1:63,360 scale quadrangle, 69°31'17"W, 145°38'26"N). Earlier study by Blodgett et al. (1988, figs. 4A–D) included a figured ventral valve of *Tcherskidium* from this locality.

*Materials from the Hammond subterrane of the Arctic Alaska terrane.*—One block of limestone sampled from locality 66ATr82.6, Baird Mountains C-1 1:63,360 scale quadrangle (159°27.5'N, 67°44.15'N) of the northwestern Brooks Range. These samples were part of the collection made by I. Tailleux (USGS) in 1966 from three closely spaced localities, with his field numbers 66ATr82.3, 82.5, and 82.6 (subsequently assigned USGS locality numbers USGS 8161-SD, 8163-SD, and 8164-SD), situated ~60.8 m above the base of an unnamed carbonate unit. The material was reported earlier as *Conchidium* (of Silurian age) in an unpublished internal USGS Report on Referred Fossils (also known as USGS E&R Fossil Report) by J.T. Dutro (29 May 1968), later reported as possible *Tcherskidium unicum* (Nikolaev, 1968) by Blodgett et al. (2002, p. 282).

*White Mountains terrane of east-central Alaska.*—This essentially includes a collection from White Mountains, locality 86ABd5 (= 86ABd60A), 14 ventral valves and one dorsal valve, calcareous specimens of *Holorhynchus giganteus* Kiær, 1902, uppermost beds of the Fossil Creek Volcanics, upper Katian, Livengood C-1 1:63,360 scale quadrangle, locality 86ABd60A (65°37'16"N, 147°21'11"W), east-central Alaska, White Mountains terrane (for details, see Blodgett et al., 1987, p. 54, fig. 1). In total, three localities have been noted bearing *Holorhynchus*: localities 86ABd5 and 86ABd60A (two samples from the locality; =USGS locality 10429-CO) and nearby locality 86ABd4 (=USGS locality 10428-CO). These are shown as fossil localities 7 and 8, respectively, on the map of Weber et al. (1994).

*Materials from North Greenland.*—For *Proconchidium schleyi* n. sp., there are two conjoined shells and 21 small blocks with embedded ventral valves collected during the 2006 expedition from upper Katian strata, stratigraphically equivalent to the lower Turesø and Alegatsiaq Fjord formations, Schley Fjord section, UTM 0516770N, 9207758E, elevation 381 m, in Peary Land, North Greenland, Laurentia (see also Harper et al., 2007). Additional material (~70 ventral valves) of *P. schleyi* collected by J.R. Ineson from the same area (UTM coordinates 27YVN 370 082) during the 1978 field expedition of the Geological Survey of Greenland (now GEUS) is housed in the Natural History Museum of Denmark (Copenhagen), bearing GGU sample numbers 197505, 197506, 197510, 197521, 197527, and 197533.

*Tcherskidium tenuicostatum* collection.—GGU Loc. 254729, about 445 specimens (predominantly ventral valves), collected by J. M. Hurst during the 1978 field expedition from the

section at his “Camp 6” (82°58'31"N, 33°33'28.1"W), south side of Frederick E. Hyde Fjord, central Peary Land. The shells are from limestone boulders encased in lower Rhuddanian black shales, probably assignable to the Citronens Fjord Member of the Merqujoq Formation. The limestone boulders were originally suggested by Hurst and Surlyk (1982) as olistoliths slumped into the basin from upper Ordovician strata higher up on the carbonate platform. In this study, the recognition of *Tcherskidium* in the limestone boulders supports the early interpretation.

*Materials from Siberia.*—Topotypes of *Tcherskidium unicum* from Ina River, Omulevsk Mountains, NE Siberia (Kolyma terrane): two incomplete conjoined shells and five incomplete ventral valves.

*Repositories and institutional abbreviations.*—All figured specimens from Alaska and Siberia in this study are deposited in the Type Collection of the Geological Survey of Canada (GSC), Ottawa, Canada; those from North Greenland are in the Natural History Museum of Denmark (MGUH), Copenhagen, Denmark.

## Systematic paleontology

Order Pentamerida Schuchert and Cooper, 1931  
 Suborder Pentameridina Schuchert and Cooper, 1931  
 Superfamily Pentameroidea M'Coy, 1844  
 Family Virginianidae Boucot and Amsden, 1963  
 Genus *Tcherskidium* Nikolaev and Sapelnikov, 1969

*Type species.*—*Conchidium* (?) *unicum* Nikolaev, 1968. Iryuda Formation (upper part), Iryuda Horizon, upper Katian, Ina River, 3 km above junction with Mirny Creek, Kolyma River basin, Omulevsk Mountains, northeast Siberia (Kolyma paleoplate).

*Diagnosis (emended).*—Shell large, elongate oval, ventribiconvex with strongly convex ventral valve and high, arched ventral umbo and beak. Costae coarse to fine. Fold and sulcus absent. Ventral interarea present in some species. Spondylium long, deep, usually extending beyond mid-length of shell; median septum high, longer than spondylium, extending almost to anterior margin of shell, attaining about half of valve depth. Outer hinge plates relatively wide, extending slightly beyond hinge line; inner hinge plates notably lower and shorter than outer hinge plates. Crura rod-like, prominently free-hanging distally.

*Occurrence.*—Late Ordovician (late Katian); Siberia (Kolyma and Siberian Platform), Kazakhstan, North America (northeastern margin of Laurentia and accreted terranes of Alaska).

*Remarks.*—Nikolaev and Sapelnikov (1969, p. 14) originally stated that “true interarea is absent” when establishing *Tcherskidium*. The finely silicified shells of *Tcherskidium lonei* n. sp. from Alaska (see the following) has a clearly defined ventral interarea, and it resembles the type species in all other diagnostic characters. *Deloprosopus* Jin, Zhan, and

Rong, 2006 from the upper Katian of South China is the only other Late Ordovician virgianid genus known to have a well-developed ventral interarea, but the Chinese genus differs from *Tcherskidium* in having a much shorter ventral median septum (extending to about mid-length of the shell) than *Tcherskidium*. Nikolaev and Sapelnikov (1969) also established *Tcherskidium* on the basis of its *Conchidium*-like external shell morphology but *Virgiana*-like internal structures. The similarity in internal structures between *Tcherskidium* and *Virgiana*, however, is limited to the dorsal valve since in the ventral valve of *Virgiana* the median septum is very short, confined to the umbonal area, supporting a shorter spondylium than in *Tcherskidium* (for example, see Jin and Copper, 2000).

In overall diagnostic characters, *Tcherskidium* resembles most closely the coeval *Proconchidium* Sapelnikov in Nikolaev and Sapelnikov, 1969, with the only difference that *Proconchidium* has better developed inner hinge plates that are higher and longer than the outer hinge plates (see Sapelnikov, 1985, p. 37–39, figs. 17, 18).

Among the known species of *Tcherskidium*, the type species from the type locality has the largest shells, with a very strongly arched, tumid, ventral umbo, and a beak incurved over the dorsal umbo, and coarsest costae at about 8–10 per 10 mm in the anterior part of the shell (Fig. 2.1–2.4). The largest complete shell reported by Nikolayev (1974, p. 68) is 81 mm long, 53 mm wide, and 53.7 mm thick, close to the topotype (length = 78.3 mm) illustrated herein (Fig. 2.1–2.4).

Judging from available material, the type species *Tcherskidium unicum* does not occur in Laurentia or on the accreted terranes of Alaska. Blodgett et al. (2002, p. 282) reported possible *T. unicum* on the basis of sample 66ATr82.6 from the Baird Mountains C-1 1:63,360 scale quadrangle (see Materials from the Hammond subterrane of the Arctic Alaska terrane). The shells are poorly preserved and, through reexamination of sample 66ATr 82.6 in this study, it can be confirmed that the material from Baird Mountains has ventral internal structures that are identical to those of *T. tenuicostatum*, but the ribbing is too poorly preserved for comparison with other species.

Several reasonably well-preserved shells from Taylor Mountains (84RB134) show coarse costae (seven to eight ribs per 10 mm) that are comparable to the most coarsely ribbed forms of *T. unicum* (Fig. 2.5–2.12). These specimens, however, are generally much smaller, and more important, they have a well-delimited ventral interarea, similar to that in *T. lonei* n. sp. described in the following. According to Nikolaev and Sapelnikov (1969), the type species lacks a ventral interarea (see also Sapelnikov, 1985).

*Tcherskidium tenuicostatum* Jin and Blodgett, 2020

Figure 3

2002 *Tcherskidium* n. sp.; Blodgett, Rohr, and Boucot, p. 267, fig. 3.1–3.5.

2020 *Tcherskidium tenuicostatum* Jin and Blodgett, p. 637.

2020 *Tcherskidium tenuicostatus* Jin and Blodgett, p. 647, fig. 7.1–7.8.

*Types*.—Holotype, GSC 131829, by original designation, upper Katian, east-central Alaska (marginal Laurentia).

*Materials*.—Alaska: 66 ventral valves, uppermost part of member 8, Nanook Limestone, upper Katian, Shublik Mountain, Alaska. North Greenland: GGU locality 254729, about 433 ventral valves, 12 dorsal valves, mostly with matrix attached (see Materials and methods section).

*Remarks*.—In the original description, Jin and Blodgett (2020) used “*tenuicostatum*” in the Abstract but “*tenuicostatus*” in the text by mistake; as the generic name is neuter in case, “*tenuicostatum*” should be the correct spelling.

The Shublik Mountain shells (Fig. 3.1–3.3) resemble the finely costate shells of *T. tenuicostatum* and *T. lonei* n. sp. (see the following) in their ribbing pattern and extremely long median septum (Fig. 3.1–3.3). The lack of a ventral interarea confirms the affinity of the Shublik Mountain shells as *T. tenuicostatum*. In the Shublik Mountain collection, most specimens with reasonably well-preserved surface ornaments show about 13 costae per 10 mm (e.g., Fig. 3.2), whereas a few specimens have notably finer, and usually faint (partly due to shell exfoliation or corrosion), costae, up to 16 costae per 10 mm in the anterior part of the shell (Fig. 3.1), which are somewhat finer than those in *T. tenuicostatum* from east-central Alaska (usually 14 costae per 10 mm; see Jin and Blodgett, 2020). At the other end of the spectrum, the type species, *T. unicum*, may have coarsely ribbed variants with eight costae per 10 mm, but more commonly 10–12 costae per 10 mm (see Fig. 2.1–2.4).

The North Greenland specimens are similar to those from Alaska in their high, strongly arched ventral umbo, fine, neatly parallel, and non-branching costae, and prominent ventral median septum reaching the anterior margin (Fig. 3.4–3.11). The only noticeable difference is that, in general, they are somewhat smaller than the Alaskan shells.

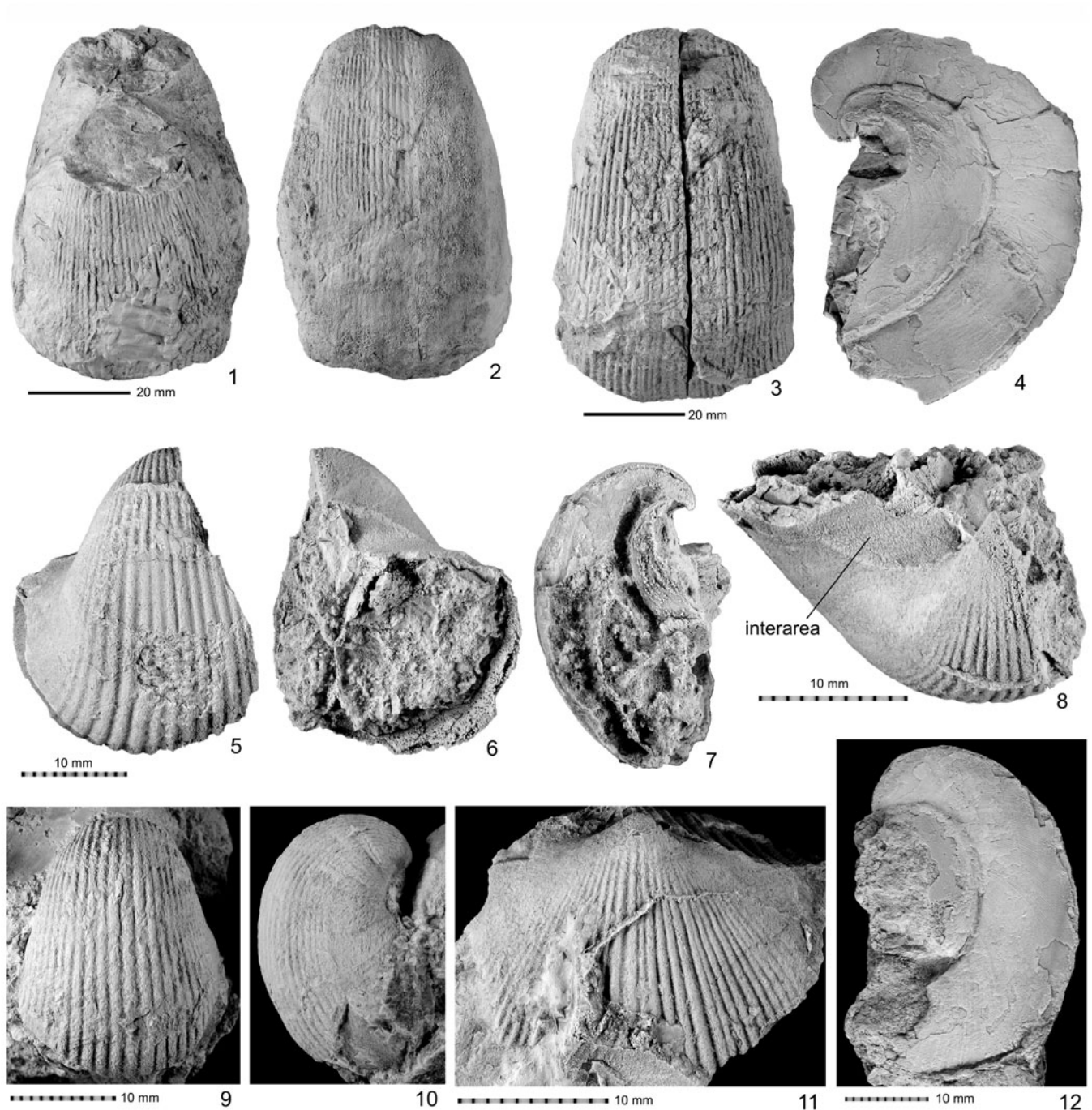
*Tcherskidium lonei* new species

Figures 2.5–2.12, 4–6

*Types*.—Holotype, GSC 131837 (Fig. 4.1–4.4), ventral valve; figured paratypes, GSC 131838–131844, four ventral valves and three dorsal valves (Figs. 4.5–4.8, 5, 6), upper Katian strata of an unnamed formation, McGrath C-4 1:63,360 scale quadrangle, west-central Alaska; GSC 131845–131847, three ventral valves and one dorsal valve, Taylor Mountains collection (84AB134), upper Katian strata (Olss unit).

*Diagnosis*.—Large, strongly ventribiconvex shells of *Tcherskidium*. Costae relatively fine to rarely coarse. Ventral interarea well developed. Large, strong outer hinge plates and slightly shorter but much lower inner hinge plates extending just anterior of hinge line. Crura slender, projecting anteroventrally as prominent, free, rod-like processes.

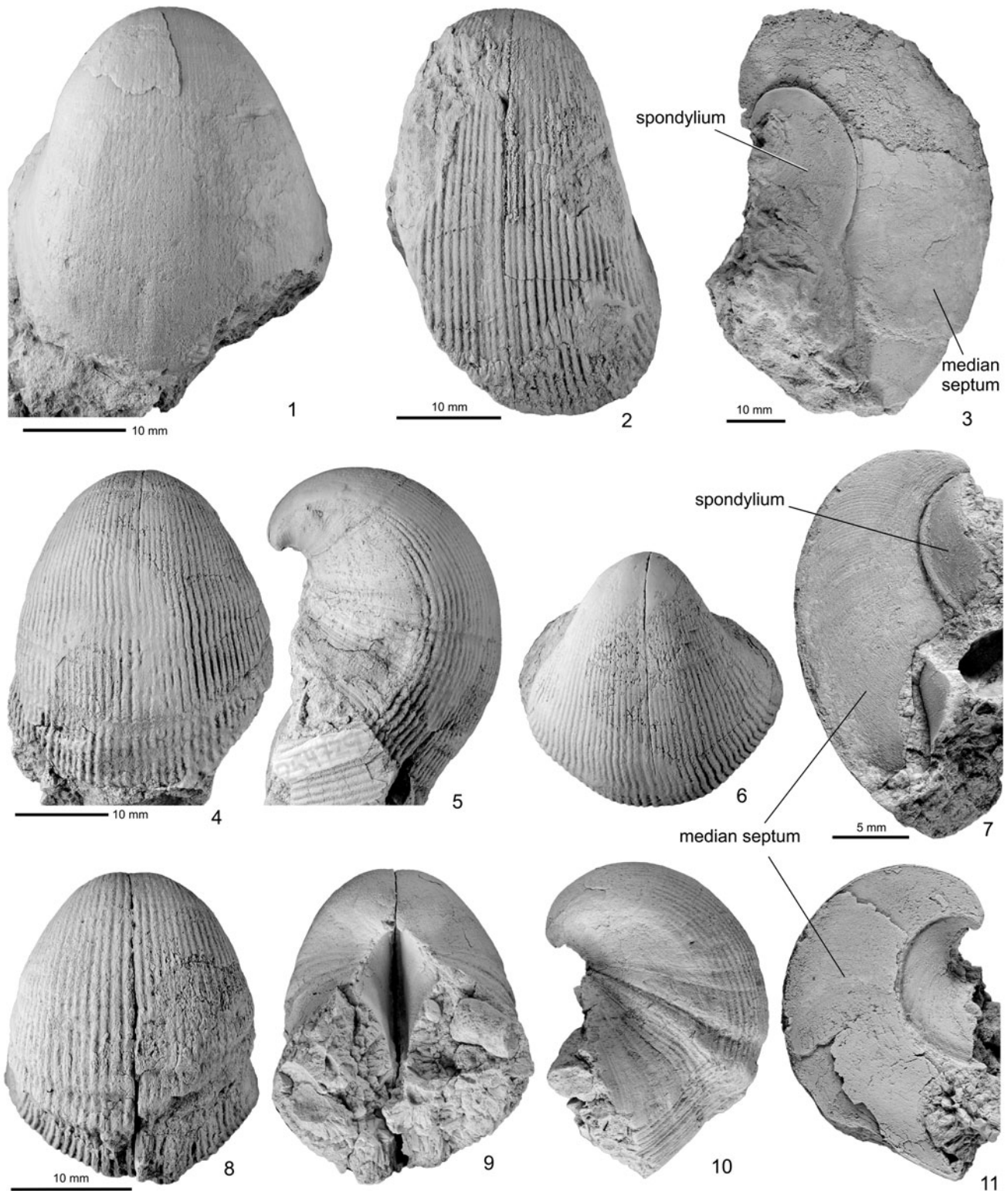
*Description*.—Shell moderate-sized for genus, from longitudinally elliptical to elongate suboval, prominently



**Figure 2.** (1–4) *Tcherskidium unicum* (Nikolaev, 1968), two topotypes from Ina River, Omulevsk Mountains, NE Siberia: (1, 2) GSC 131832, dorsal and ventral views of posteriorly damaged, conjoined shell; (3, 4) GSC 131833, ventral and medial-interior (split along median septum and one side of spondylium) views of strongly convex ventral valve with highly arched umbo. (5–8) *Tcherskidium lonei* n. sp., four specimens from the Taylor Mountains collection (84AB134): (5–8) GSC 131845, partial ventral valve showing well-defined interarea, coarse costae (7 per 10 mm), and long median septum; (9, 10) GSC 131846, ventral valve with strong costae (8 per 10 mm); (11) GSC 131847, incomplete dorsal valve; (12) medially split ventral valve showing long median septum extending near anterior margin and partly preserved spondylium.

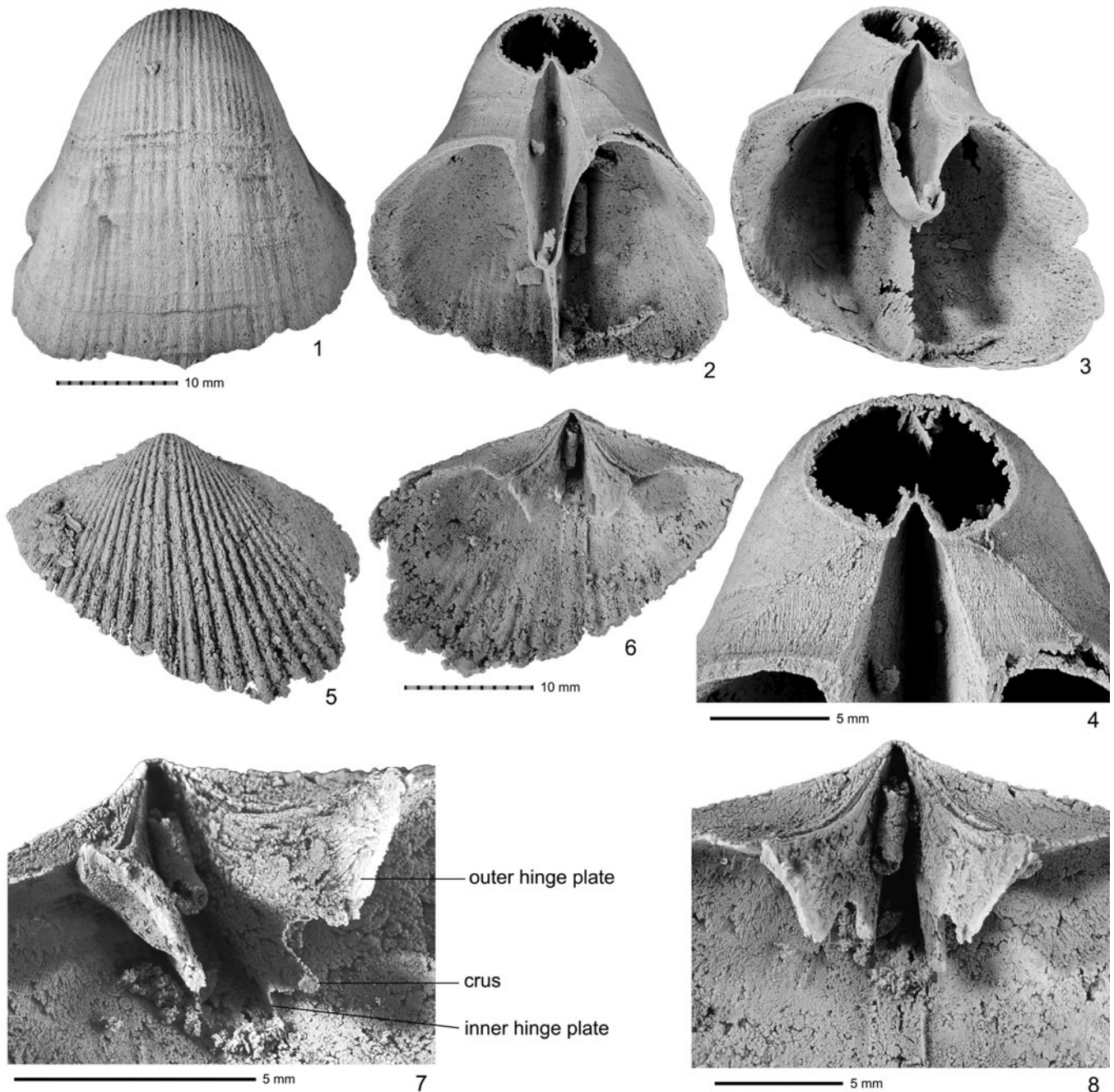
ventribiconvex, with ventral valve two to three times as deep as the dorsal valve; maximum length estimated at 56 mm, width 40 mm, and depth 25 mm based on imperfectly preserved ventral valves; shell widest in anterior half or close to anterior margin. Hinge line attaining approximately one-third to one-half of maximum width of shell. Fold and sulcus absent. Ventral valve considerably larger and more convex than

dorsal, with obtuse and uniformly convex ventral umbo arching up to 15 mm above hinge line and its apex up to 5 mm above recurved beak in large shells; delthyrium entirely open; interarea well delimited in well-preserved shells, attaining height up to 6 mm and width of 4–5 mm on each side of delthyrium (Figs. 4.2–4.4, 5.2–5.4). Umbonal portion of ventral valve prominently thickened, with umbonal cavity



**Figure 3.** *Tcherskidium tenuicostatum* Jin and Blodgett, 2020. (1–3) Three specimens from Shublik Mountain, Member 8 of the Nanook Limestone (upper Katian): (1) GSC 131834, exterior of exfoliated ventral valve with traces of very fine ribbing (~16 costae per 10 mm); (2) GSC 131835, exterior of ventral valve with well-preserved costae (~13 per 10 mm); (3) GSC 131836, medially split ventral valve showing deep spondylium and long median septum extending near anterior margin of valve. (4–11) Three specimens from slumped limestone boulders (upper Katian) within the lower Rhuddanian black shale of the Citronens Fjord Member, Merqujoq Formation: (4–6) MGUH 34053, ventral, lateral, and posterior views of nearly complete ventral valve; (7) MGUH 34054, ventrally split ventral valve exposing prominent median septum and one side of spondylium; (8–11) MGUH 34055, exterior, interior, lateral, and medial-interior views of ventral valve; note two major growth interruptions and changes in direction of shell growth.



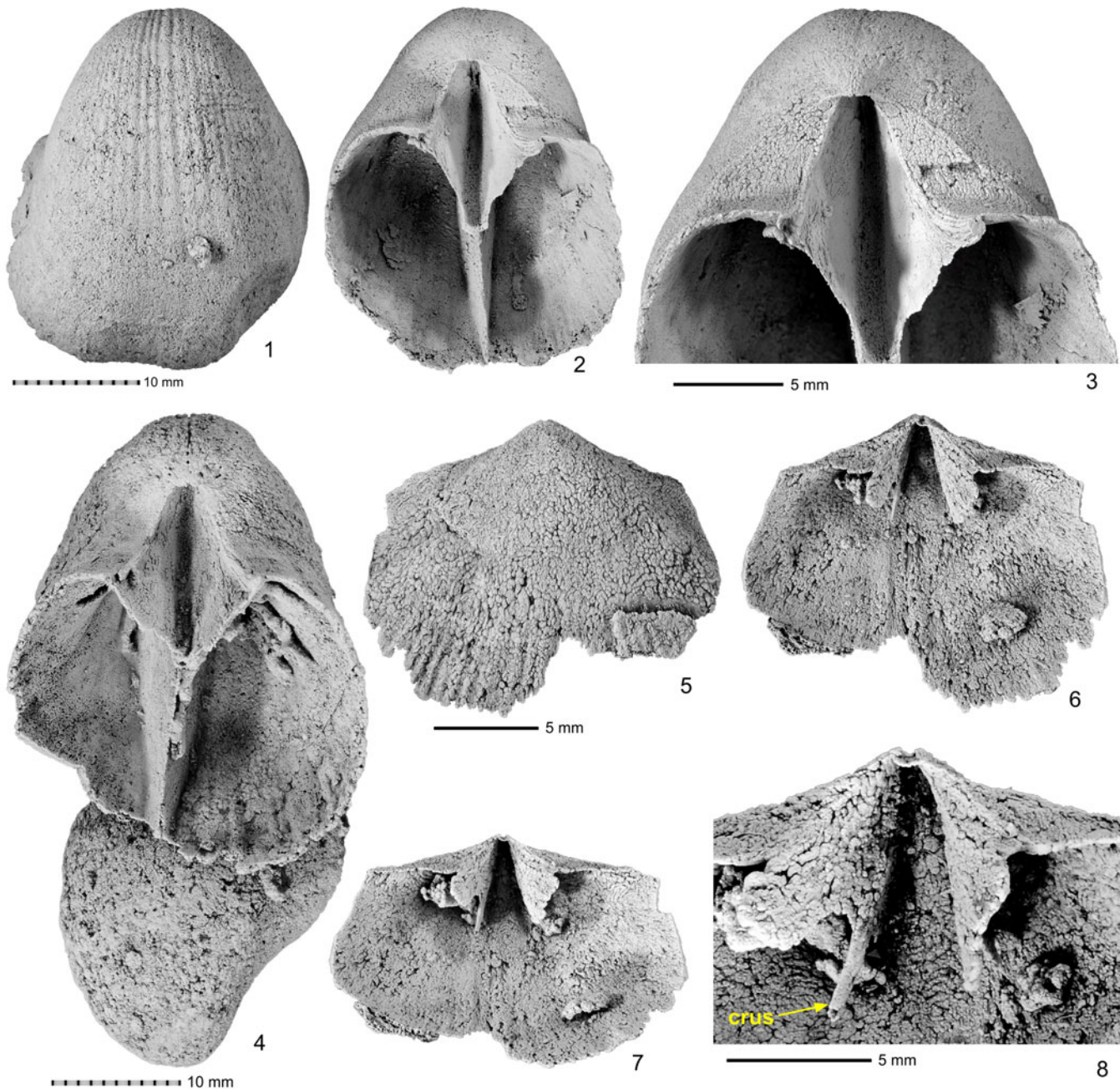


**Figure 4.** *Tcherskidium lonei* n. sp. Silicified specimens from upper Katian strata of an unnamed stratigraphic unit, McGrath C-4 1:63,360 scale quadrangle, west-central Alaska. (1–4) GSC 131837, holotype, exterior, interior, tilted interior views showing median septum and base of spondylium and enlarged posterior views showing well-delimited interarea of incomplete ventral valve. (5–8) GSC 131838, paratype, exterior, interior, posterolaterally tilted interior (to show configuration of inner hinge plate, crus, and outer hinge plate), and enlarged cardinalia of incomplete dorsal valve; note large outer hinge plates and much reduced inner hinge plates.

filled by secondary deposits of shell substance extending from apex to 5–10 mm anteriorly. Dorsal valve considerably smaller, less convex, and with a much thinner shell wall than ventral valve. Costae fine and of fairly gentle relief, simple, with subrounded crest and narrow interspace, averaging 14 per 10 mm in posterior part of shell; each costa increasing in size gradually toward anterior margin to reach average of 10 costae

per 10 mm; intercalation or bifurcation extremely rare, observed only in medial part of some shells (e.g., Fig. 4.5). Growth lines poorly preserved in silicified shells, but irregularly spaced coarser growth lamellae present in some specimens.

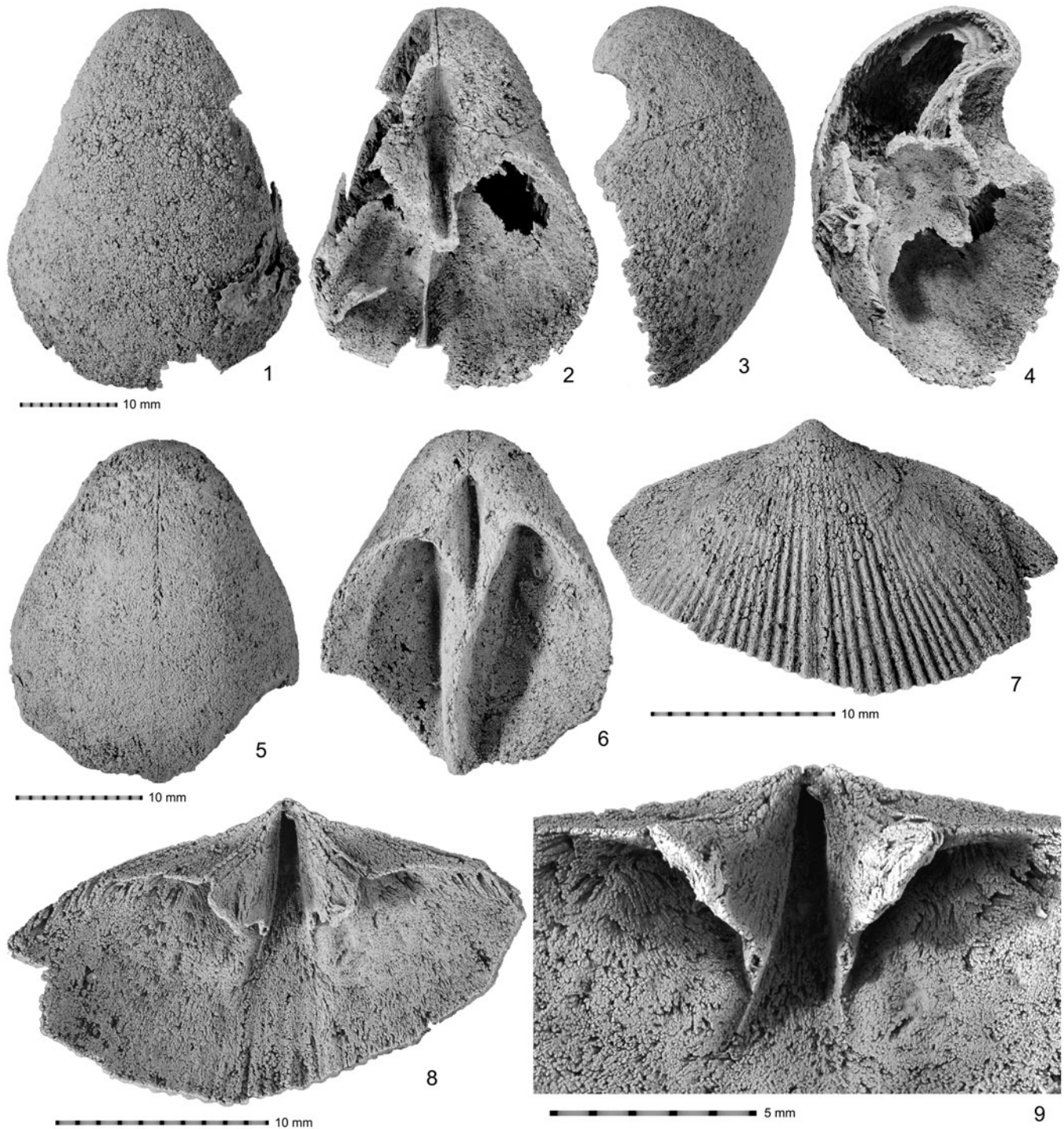
Spondylium long, deep, attaining approximately one-half depth and slightly over one-half length of ventral valve, with



**Figure 5.** *Tcherskidium lonei* n. sp. Silicified specimens from upper Katian strata of an unnamed stratigraphic unit, McGrath C-4 1:63,360 scale quadrangle, west-central Alaska. (1–3) GSC 131839, paratype, exterior, interior, enlarged spondylium of nearly complete ventral valve, with anterior costae abraded; note long and posteriorly thickened median septum. (4) GSC 131840, paratype, two incomplete and abraded ventral valves showing strongly thickened median septum and umbonal cavity filled completely by secondary shell substance posterior of hinge line. (5–8) GSC 131841, paratype, exterior, interior, tilted interior, and enlarged cardinalia showing long, rod-like crura of anteriorly damaged dorsal valve.

relatively narrow U-shaped basal portion, but overall V-shaped cross section due to accelerated widening of spondylial opening in dorsal direction (Figs. 4.2, 4.3, 5.2, 5.4, 6.2, 6.6). Median septum thick toward junction with valve floor, thickened most prominently in umbonal area (Figs. 5.2, 5.4, 6.6), thinning anterodorsally, with its ventral edge extending along valve floor and reaching nearly anterior margin of valve, but dorsal edge receding toward distal end of spondylium and leaving distal end of spondylium free-hanging. Hinge teeth weak to poorly

developed; hinge sockets in dorsal valve represented by narrow groove on each side of notothyrium (e.g., Fig. 4.8). Cardinalia notably delicate compared with spondylium and median septum of ventral valve. Inner hinge plates discrete, extending slightly anterior of hinge-line level, diverging anterolaterally from each other overall (Fig. 6.8, 6.9), but may be slightly inclined basomedially just at junctions with valve floor in some specimens (Fig. 4.7); outer hinge plates considerably larger, dorsoventally higher, but longitudinally shorter, than



**Figure 6.** *Tcherskidium lonei* n. sp. Silicified specimens from upper Katian strata of an unnamed stratigraphic unit, McGrath C-4 scale 1:63,360 quadrangle, west-central Alaska. (1–4) GSC 131842, paratype, exterior, interior, lateral, and other lateral view of incomplete ventral valve; note large umbonal cavity filled by secondary thickening (anterior side silicified and preserved but fillings inside cavity only incompletely silicified and preserved); ribbing poorly preserved. (5, 6) GSC 131843, paratype, anterior and interior of incomplete ventral valve with strongly thickened median septum and infilled umbonal cavity but poorly preserved ribbing. (7–9) GSC 131844, paratype, exterior, interior, and enlarged cardinalia, with crura broken off, showing circular cross sections of crural bases (hollow centers as result of incomplete silicification).

inner hinge plates, extending slightly anterior of hinge line to become laterally deflected, ear-like structures. Crural bases rod-like, circular in cross section, forming smooth junctions with inner and outer hinge plates, without any abrupt flanges, extending distally into relatively long, free-hanging, round-

rod crura, curving weakly in ventrolateral direction (Figs. 4.7, 4.8, 5.6–5.8, 6.8, 6.9). Weakly impressed adductor scars slender, located anterior of inner hinge plates, visible in some specimens but usually poorly preserved in silicified material.

*Etymology.*—Named after the type locality of the new species, Lone Mountain, Alaska.

*Materials.*—Lone Mountain collection: 429 ventral valves, 134 dorsal valves, plus several small blocks with embedded specimens, all silicified. Taylor Mountains collection 84RB134, 43 ventral valves, one dorsal valve.

*Remarks.*—Among species of *Tcherskidium*, the new species is unique in having a well-defined ventral interarea, whereas its predominantly simple costae, extremely long median septum, and reduced size of inner hinge plates are characteristic of the type species, *T. unicum*. According to the descriptions of Nikolaev (1974, p. 67, fig. 1) and Sapelnikov (1985, p. 40, fig. 19), *T. unicum* has a more notable reduction in its inner hinge plates that are extremely low and recede before reaching the hinge line. By comparison, the inner hinge plates of *T. lonei* n. sp. extend a short distance anterior of the level of the hinge line (Figs. 4.7, 6.8, 6.9).

The late Katian virgianid from South China, *Deloprosopus jiangshanensis* (Liang in Liu et al., 1983) is also known to have a well-developed ventral interarea and was originally described as a species of *Tcherskidium*. As noted by Jin et al. (2006), however, this Chinese form has a much shorter median septum, extending approximately for only one-half of the shell length, thus atypical of *Tcherskidium*.

Compared with the new species, the type species, *T. unicum*, attains a much larger maximum shell size, up to 80 mm long and 48 mm wide, with an extremely obtuse ventral apex (only slightly narrower than maximum shell width, giving the shell a subrectangular ventral view; see Fig. 2.1–2.3), prominently arched ventral umbo and incurved beak over the dorsal umbo (Fig. 2.4), and the coarsest costae of all congeneric species, in the range of 8–10 per 10 mm in anterior part of shell (see also Nikiforova, 1989; Modzalevskaya, 2018), compared with 14 per 10 mm in the new species. A few ventral valves in the Taylor Mountains collection (84RB134), however, exhibit rather strong and coarse costae (seven to eight per 10 mm; see Fig. 2.5, 2.9), despite their small size, although most other specimens have costae similar to those of the Lone Mountain material. This emphasizes the strong intra-population variation in the coarseness of costae as noted by Oradovskaya (1983) and the importance of statistical evaluation of this character when large populations are available for study.

In Alaska, including both accretionary terranes and the northwestern margin of Laurentia (Black River D-1 1:63,360 scale quadrangle), various forms of *Tcherskidium* are common in upper Katian strata. *Tcherskidium tenuicostatum* Jin and Blodgett, 2020, from the Black River quadrangle of east-central Alaska, is most similar to the new species in having rather fine costae for the genus but differs in lacking a ventral interarea. *Tcherskidium lonei* n. sp. was initially reported as an undescribed species of *Tcherskidium* from the Lone Mountain (Farewell accretionary terrane) by Blodgett et al. (2002). At present, the paleoecological significance of predominantly finer ribbing in the Alaskan species compared with the type species from northeastern Siberia (Kolyma) is poorly understood. The Alaskan species occurs predominantly in shallow-water carbonate platform facies that also contain common gastropods. This

morphological feature may be analogous to the earliest Silurian (Rhuddanian) *Virgiana* from Anticosti Island of eastern Canada, which has been found to have coarser and stronger costae in species from deeper-water facies (e.g., *V. mayvillensis* Savage, 1916) than in species from shallow-water facies (*V. barrandei* Billings, 1857; see Jin and Copper, 2000; Jin, 2008).

Oradovskaya (1983) examined large collections of *Tcherskidium* from the Omulevsk and Chukotsk mountains and considered *T. kovechovi* Nikolaev, 1974 and *T. tchukoticum* Nikolaev, 1974 junior synonyms of the type species. This assessment, however, appears to have been based primarily on external morphology. In terms of detailed internal structures, *T. kovechovi* lacks inner hinge plates and has a notably shorter median septum supporting only the posterior part of the spondylium; *T. tchukoticum* has better developed inner and outer hinge plates than *T. unicum* and *T. kovechovi*. Subsequently, Sapelnikov (1985) treated these three forms as subspecies of *T. unicum*. Given that the external morphology is not a distinguishing character even at the generic level to separate *Tcherskidium* from *Proconchidium*, the differences in internal morphology are considered adequate in this study for treating the three Siberian species of *Tcherskidium*—*T. unicum*, *T. kovechovi*, and *T. tchukoticum*—as separate species.

*Tcherskidium?* sp. reported by Nikolaev (1974) from the Selenyakh Range, northeast Siberia, of questionable Late Ordovician age, is similar to *T. lonei* n. sp. and *T. tenuicostatum* in having well-developed inner and outer hinge plates but differs in having a median septum that is shorter than the spondylium, as in *T. kovechovi*.

*Tcherskidium? ulkuntasensis* Rukavishnikova and Sapelnikov, 1973 has a notably smaller shell than other species of the genus and has a ventral interarea. It is more similar to *Deloprosopus* than to *Tcherskidium*.

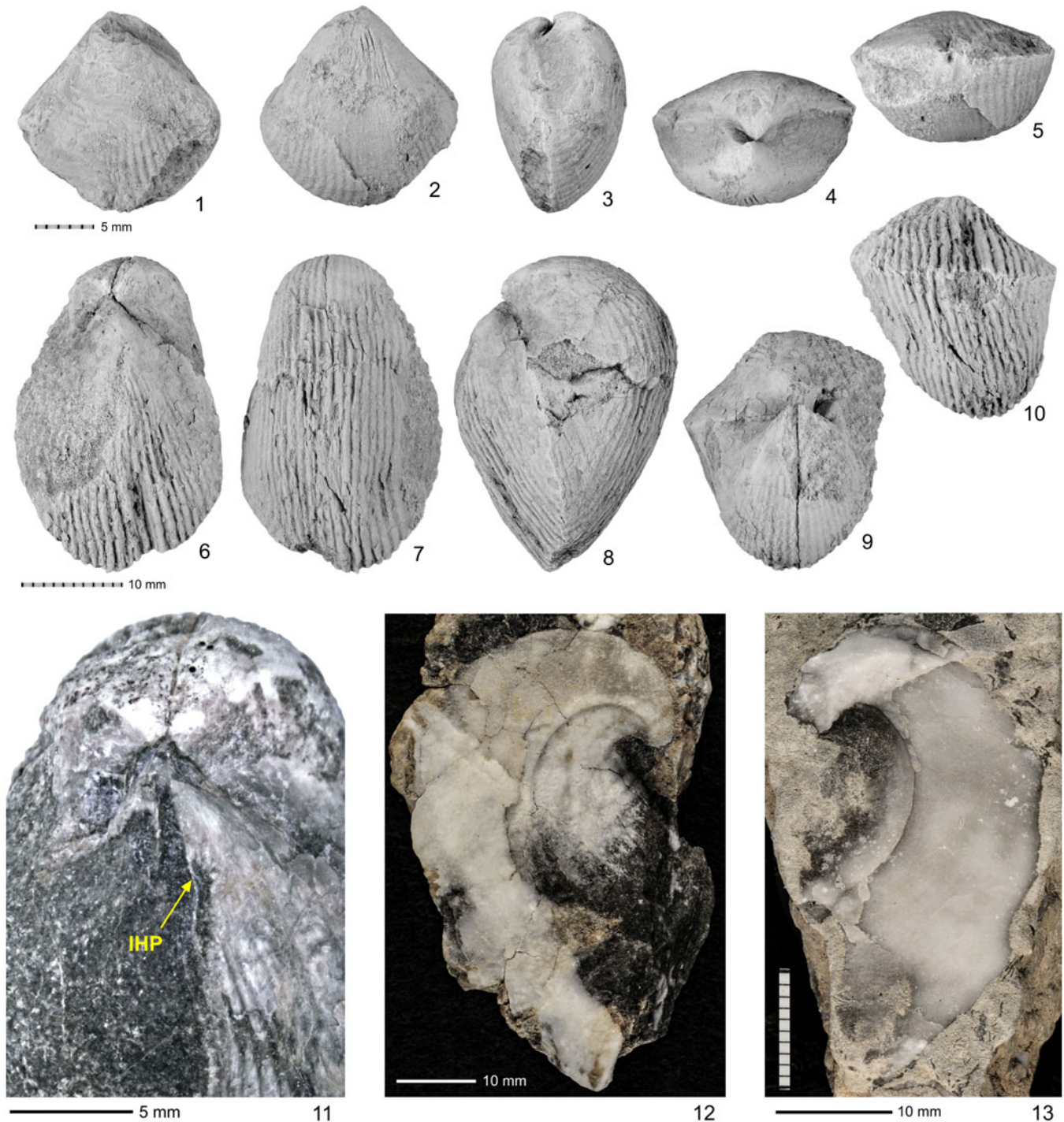
*Proconchidium* Sapelnikov in Nikolaev and Sapelnikov, 1969

*Type species.*—*Conchidium muensteri* St. Joseph, 1938. Upper Katian, southern Norway. The type species was identified also from coeval strata (Archalyk beds), Zeravshan Range, southern Tyan Shan (Sapelnikov, 1985), and northern Urals (Baltica; see Beznosova, 2014).

*Other species included.*—*Proconchidium muensteri bisulcatum* Rukavishnikova and Sapelnikov, 1973, *Holorhynchus giganteus* zone, upper Katian, central Kazakhstan; *Proconchidium tchuilensis* Rukavishnikova and Sapelnikov, 1973, *Holorhynchus giganteus* zone, Upper Katian, Chu-Ili Mountains, southern Kazakhstan; *Proconchidium brodeurensis* Rong, Jones, and Nentwich, 1989, uppermost Katian, 8 m below the top of the Baillarge Formation, Brodeur Peninsula, Baffin Island, Arctic Canada.

*Proconchidium schleyi* new species  
Figures 7, 8

*Types.*—Holotype, MGUH 34049 (Fig. 7.6–7.11, relatively small, conjoined shell for the species; figured paratypes, MGUH 34050 (immature, conjoined shell, Fig. 7.1–7.5), MGUH 34051 and 34052 (Fig. 7.12, 7.13; naturally split



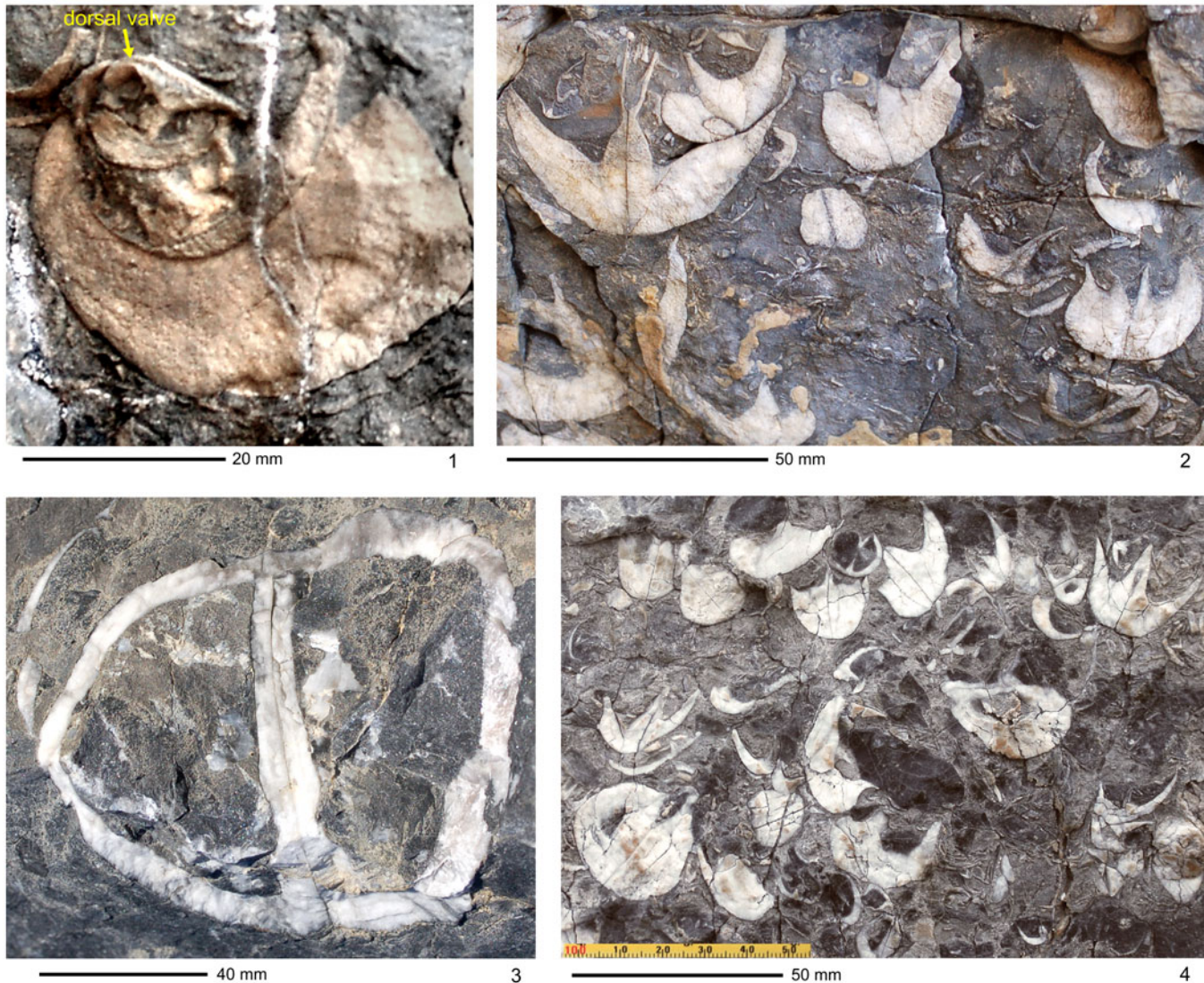
**Figure 7.** *Proconchidium schleyi* n. sp. from upper Katian strata equivalent to the lower Turesø and Alegatsiaq Fjord formations, G.B. Schley Fjord, North Greenland. (1–5) MGUH 34050, paratype, dorsal, ventral, lateral, posterior, and anterior views of small, immature shell; note presence of incipient ventral interarea (4). (6–11) MGUH 34049, holotype, dorsal, ventral, lateral, posterior, anterior, and enlarged umbonal views of moderate-sized shell; note relatively well-developed inner hinge plates (IHP) visible through partly abraded dorsal umbo (11, photographed with shell immersed in alcohol). (12, 13) MGUH 34051 and 34052, paratypes, two large ventral valves split medially, exposing long median septum extending to anterior margin.

ventral valves along median septum). All from upper Katian strata, G.B. Schley Fjord, North Greenland.

**Diagnosis.**—Large, elongate, ventribiconvex shells of *Proconchidium*, with strong, simple costae, incipient ventral interarea present at early growth stage; relatively long inner

hinge plates for genus, diverging anteriorly at very low angle along valve floor.

**Description.**—Shell relatively large for genus, elongate, ventribiconvex, attaining estimated length of 60 mm in large forms; equidimensional length and width with moderate



**Figure 8.** *Proconchidium schleyi* n. sp. (1–4) Field photographs of weathered rock surfaces, upper Katian strata equivalent to the lower Turesø and Alegatsiaq Fjord formations, G.B. Schley Fjord, North Greenland, showing strongly thickened posterior and median septa of ventral valves. Note near in situ preservation of large and heavy ventral valves and a rarely preserved dorsal valve in the shell beds (1).

biconvexity in small form, elongating to length/width ratio of  $\sim 1.5$  and becoming strongly biconvex in medium-sized form (Fig. 7.6–7.11). Maximum shell width located in anterior part of shell, and maximum thickness in posterior part of shell. Hinge line narrow, usually not exceeding one-third of shell width, with anterolaterally sloping cardinal extremities. Anterior commissure largely rectimarginate. Fold and sulcus absent. Costae simple, strong, with rounded crest and rare bifurcation, averaging 14 costae per 10 mm in anterior part of relatively large shells. Ventral umbo moderately convex, only slightly higher than opposite umbo in small form, with small beak tilted posteroventrally from commissural plane. At medium growth stage, ventral umbo becoming tumid, strongly arched, with prominent beak extending dorsally beyond commissural plane to hang over opposite umbo. Delthyrium open. Ventral interarea absent in large shells, but incipient interarea may be present in small forms (Fig. 7.4). Dorsal umbo moderately convex, with small beak bent over

commissural plane, most prominently in large shells (Fig. 7.12, 7.13).

Umbonal cavity of ventral valve prominently thickened to completely filled by secondary shell substance (Fig. 8.2, 8.4). Spondylium moderately long, deep, and narrow, with U-shaped cross section (i.e., with only slight widening toward spondylium opening), extending for about two-thirds of valve length; spondylium wall thickened in basal (ventral) portion close to junction with median septum, but unthickened in dorsal portion (Fig. 8.2, upper left valve in image). Median septum long, extending near anterior margin of valve, increasing in height gradually and gently from apex to more than three-fourths of valve length, then tapering and receding in height sharply toward anterior margin (Figs. 7.12, 7.13, 8.1), thickened by prismatic layer along entire length.

Dorsal internal structures only partially known. Inner hinge plates relatively long, about 6 mm long along valve floor in moderate-sized shell (Fig. 7.11). Outer hinge plates and rod-like

crura well developed, observed only from field photos of naturally weathered, massive rock surfaces (Fig. 8.1)

*Etymology*.—Named after G.B. Schley, one of the founding members of the Peary Arctic Club (New York), as well as G.B. Schley Fjord—the type locality of the new species—which was named in his honor by Robert E. Peary in 1900.

*Materials*.—See Materials and methods section.

*Remarks*.—The affinity of the G.B. Schley Fjord material to *Proconchidium* is based on the relatively long inner hinge plates that can be observed in the only two available conjoined shells. As summarized by Sapelnikov (1985), other internal characters of these shells are largely identical to those of *Tcherskidium*, such as its extremely thickened ventral valve posterior and long and thickened median septum extending almost to the anterior margin. By contrast, the unthickened part (especially the distal portion) of the spondylium appears rather delicate, which has been observed in various forms of both *Proconchidium* and *Tcherskidium* (e.g., Nikolaev and Sapelnikov, 1969, fig. 1; Sapelnikov and Rukavishnikova, 1975, p. 59, fig. 16; Jin and Blodgett, 2020, figs. 7.5).

Among the known congeneric species, *Proconchidium schleyi* n. sp. attains the largest maximum shell length of about 60 mm, based on the measured length of 57.5 mm of ventral valve with slightly damaged anterior (Fig. 7.12, 7.13). The type species, *P. muensteri*, rarely has shells that exceed 30 mm long. *P. brodeurensis* attains a maximum length of 40 mm. *P. tchuilensis* is the closest to the new species, with a reported maximum size of ~50 mm. Apart from its larger maximum shell size, *P. schleyi* is the only species of *Proconchidium* known to have an incipient ventral interarea.

#### Genus *Holorhynchus* Kiær, 1902

*Type species*.—*Holorhynchus giganteus* Kiær, 1902. Langåra Formation (uppermost Katian), Oslo Region, Norway (St. Joseph, 1938; Cocks, 1982; Brenchley et al., 1997).

*Occurrence*.—Upper Katian to lower Llandovery; Balto-Scandia, Urals, Kazakhstan, Tien Shan, North China, Yukon, Alaska, and Kolyma.

*Remarks*.—Rong et al. (2004) emended the diagnosis of *Holorhynchus* to include typical forms that lack a ventral median septum, as well as atypical forms that have an incipient ventral median septum; the atypical forms are from the upper Katian Badanjilin Formation of Inner Mongolia (Alxa tectonic clock), North China. It is one of the small number of pentameride genera that survived the Hirnantian mass extinction but occurred only sporadically during the earliest Silurian.

In addition to the type species, the following species or subspecies have been considered valid with a high degree of confidence (Rong et al., 2004): *Holorhynchus giganteus latisulcifer* Rukavishnikova and Sapelnikov, 1973, Tolen beds, central and eastern Kazakhstan; *Holorhynchus cinghizicus* Borissiak, 1955, Alpeis horizon, lower–middle Llandovery, eastern and

southern Kazakhstan. *Holorhynchus sinicus* Fu, 1982, Zhao-huajing Formation, upper Rhuddanian–lower Aeronian, Ningxia, North China.

Several species that were originally or subsequently regarded as *Holorhynchus* have been excluded from the genus (see Rong and Boucot, 1998; Rong et al., 2004).

#### *Holorhynchus giganteus* (Kiær, 1902)

##### Figure 9

1902 *Holorhynchus giganteus* Kiær, 1902, p. 63, figs. 1–7.

1938 *Holorhynchus giganteus*; St. Joseph, p. 292, pl. 4, figs. 1–5; text-fig. 9.

1971 *Holorhynchus giganteus*; Boucot et al., 1971, p. 277, pl. 5, figs. 1–9; pl. 6, figs. 1–5.

1987 *Holorhynchus* n. sp. Blodgett et al., p. 56, fig. 3A.

2004 *Holorhynchus giganteus*; Rong et al., p. 293, figs. 5.1–5.18, 5.22–5.25, 6, 7 (and comprehensive synonymy therein up to 2004).

2008 *Holorhynchus giganteus*; Beznosova, p. 34, fig. 3.1.2.

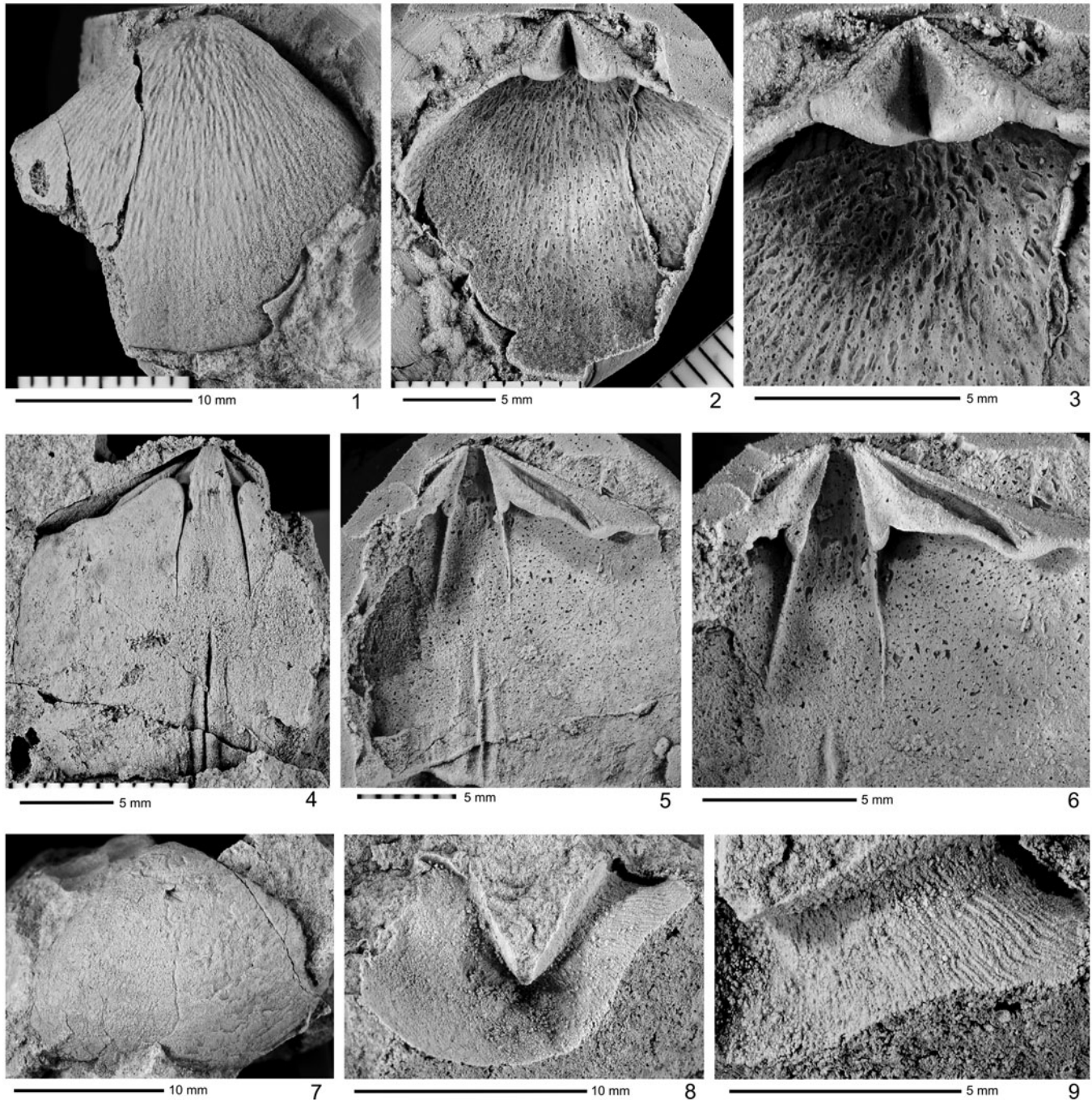
2015 *Holorhynchus giganteus*; Shiino et al., p. 28, figs. 3A–L, 4A–E.

*Types*.—Lectotype (PMO 12431), formalized and figured by St. Joseph (1938, pl. 4, figs. 1–3), uppermost Katian, Asker, Oslo district, Norway.

*Materials*.—Calcareous and moldic specimens, 14 ventral valves and 1 dorsal valve (internal mold), localities 86ABd5 and 86ABd60A, uppermost beds of the Fossil Creek Volcanics, White Mountains, Livengood C-1 1:63,360 scale quadrangle, east-central Alaska.

*Remarks*.—The Alaskan shells from the uppermost Fossil Creek Volcanics stratigraphic unit were initially reported by Blodgett et al. (1987) as “*Holorhynchus* n. sp.,” with one dorsal internal mold (same as Fig. 8.4–8.6 herein) illustrated but without accompanying description. In this study, the affinity of the Alaskan material to *Holorhynchus* can be confirmed on the basis of their transversely elliptical, smooth shells, small (relative to shell size), free-hanging, V-shaped spondylium (Fig. 9.8), absence of a ventral median septum (Fig. 9.2, 9.3, 9.8), and presence of long, slender, anterolaterally diverging hinge sockets (Fig. 9.4, 9.5). The longitudinal striations on the inner surface of the ventral valve of *H. giganteus*, illustrated in specimens from the Oslo region (Boucot et al., 1971, pl. 6, fig. 5) and from the Siljan district (Shiino et al., 2015, fig. 3I), are well developed also in the Alaskan material (Fig. 9.1–9.3, 9.8, 9.9). The pair of long, slender adductor muscle scars, separated by a low, rounded medial ridge in the dorsal valve, located anterior of the distal ends of the inner hinge plates, is present in both the type species (Boucot et al., 1971, pl. 6, fig. 2) and the Alaskan material (Fig. 9.4, 9.5).

The Alaskan form differs from the typical specimens of *H. giganteus* in having longer inner hinge plates. For the type species, Boucot et al. (1971) reported that the inner hinge plates (= “outer plates”) vary from 3 to 10 mm long in large shells, commonly diverging anterolaterally along the valve floor but



**Figure 9.** *Holorhynchus giganteus* Kiær, 1902. Four disarticulated valves from the uppermost beds (locality 86ABd5 = 86ABd 60A) of the Fossil Creek Volcanics, upper Katian, White Mountains, Livengood C-1 1:63,360 scale quadrangle, east-central Alaska. (1–3) GSC 131848, internal mold, silicon rubber cast, and further enlarged posterior of incomplete ventral valve, small (anteriorly missing) spondylium, and longitudinally striated valve floor, locality 86ABd60A. (4–6) GSC 131849, internal mold, silicon rubber cast, and further enlarged cardinalia of incomplete dorsal valve, locality 86ABd5. (7) GSC 131850, partly exfoliated ventral valve showing smooth outer surface, locality 86ABd60A. (8, 9) GSC 131851, interior of broken ventral valve showing V-shaped spondylium in transversal cross section and longitudinal striations on valve floor, locality 86ABd60A.

tilted slightly basomedially toward the valve floor. These authors also reported variants with anteromedial and basomedially converging inner hinge plates (e.g., Boucot et al., 1971, pl. 6, fig. 3) that, in a rare specimen, form an incipient cruralium. In the relatively small, well-preserved dorsal valve from Alaska, the inner hinge plates appear longer in their proportion anterior of the hinge-line level compared with those in the type material

from the Oslo region illustrated by Boucot et al. (1971) but are comparable to the long inner hinge plates in relatively small shells of *H. giganteus* from the Siljan district of Sweden (Shiino et al., 2015, figs. 4D, E).

The Alaskan shells mostly have incomplete preservation; however, judging from the preserved parts, the available specimens are generally smaller than the maximum shell size of



typical *H. giganteus* but are comparable to the specimens from the Boda Limestone of Sweden (Shiino et al., 2015).

*H. giganteus* has been widely reported from the upper Katian of Siberia and Kazakhstan and has been used commonly for tracking the Ordovician–Silurian boundary interval in these regions (Sapelnikov, 1985; Kovalevskiy et al., 1991).

## Acknowledgments

Fieldwork in North Greenland (2006) was funded by the Danish Natural Science Research Council (DATH) and the Natural Sciences and Engineering Research Council of Canada (JJ). DATH thanks the Leverhulme Trust for additional support. Topotype specimens of *Tcherskidium unicum* used in this study were collected by M. Churkin Jr. Journal reviewers G. Baarli and J.Y. Rong provided invaluable information and comments, which helped improve the paper immensely.

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Accepted: 8 June 2022