



Morphology and ecology of the bradoriid arthropods *Spinospitella* and *Nikolarites* from the Cambrian (Series 2, Stage 4) of North Greenland (Laurentia)

John S. Peel¹ · Christian B. Skovsted² · Elise Wallet¹

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Abstract

Tuberculate fragments referred to *Nikolarites spasskyi* are compared with a complete carapace and other material of *Spinospitella* from Cambrian Series 2, Stage 4 in North Greenland. The descriptions expand earlier brief records from Laurentia of the two bradoriids, originally described from Siberia and Australia, respectively. The mutually exclusive occurrences of the two taxa indicate ecological control of their distribution in North Greenland. Robust fragments of *Nikolarites spasskyi* occur in reworked higher energy deposits of the Aftenstjernesø Formation, while thin-walled carapaces of *Spinospitella* characterise deeper water mudstones within the Buen and Aftenstjernesø formations.

Keywords Bradoriida · Morphology · Ecology · Cambrian (Series 2 · Stage 4) · North Greenland · Laurentia

Introduction

Trilobites, with their heavily mineralised exoskeletons, are easily the most conspicuous arthropods in the Cambrian, although localities with exceptional preservation, such as the lagerstätten of Chengjiang, Sirius Passet and the Burgess Shale (Briggs et al. 1994; Ineson and Peel 2011; Peel and Ineson 2011; Hou et al. 2017), with a wealth of lightly sclerotised forms, present a more accurate picture of arthropodan diversity. Widespread small bivalved shields or valves (< 10 mm) grouped together as bradoriids also display high diversity evident through a variety of methods of preservation, although their position relative to other arthropod groups is largely unresolved (Hou et al. 2002, 2010;

Williams et al. 2007; Zhai et al. 2019; McMenemy 2020). Most older records concern macrofossils that are often preserved in three dimensions, indicating the presence of robust shields (Ulrich and Bassler 1931; Siveter and Williams 1997; Hou et al. 2002). More recent studies focus on recovering phosphatic Small Shelly Fossils by digesting carbonates in weak acids, a process that may yield pristine faunas often displaying exquisite details of surface structures (Skovsted et al. 2006; Zhang 2007; Peel 2017a). In addition, the acid residues often contain broken and distorted bradoriid specimens demonstrating variation in the degree of phosphate mineralisation, be it primary or secondary, or postmortal effects such as exuviation, crumpling following ingestion by predators (Peel 2015) or taphonomic degradation. Fine details of surface sculpture may also be preserved in bradoriid assemblages of Small Carbonaceous Fossils retrieved by maceration of siliciclastic sediments in hydrofluoric acid, although the organic remains are commonly fragmented (Slater et al. 2018; Wallet et al. 2020).

Assemblages of Cambrian Stage 4 bradoriids from Greenland have been recovered from all three of these preservational windows. The macrofauna from the shelf mudstones of the Buen Formation at Brillesø in south-eastern Peary Land (Fig. 1) includes specimens of the cambriid *Petrianna fulmenata* Siveter, Williams, Peel, and Siveter, 1996 almost 10 mm in length (Siveter et al. 1996; Peel and Willman 2018). It is associated with *Aluta siku* Peel and

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✉ John S. Peel
john.peel@pal.uu.se

Christian B. Skovsted
christian.skovsted@nrm.se

Elise Wallet
elise.wallet@geo.uu.se

¹ Department of Earth Sciences (Palaeobiology), Uppsala University, Villavägen 16, 75236 Uppsala, Sweden

² Department of Palaeobiology, Swedish Museum of Natural History, Box 50007, 10405 Stockholm, Sweden

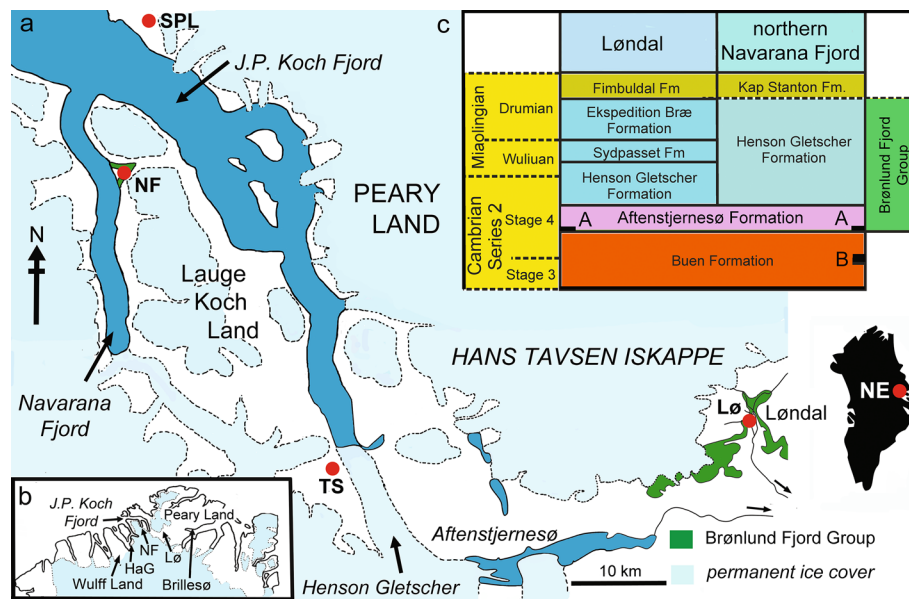


Fig. 1 Geography and geology. **a** Map of the western Peary Land–Lauge Koch Land area showing location of sample sites. Outcrop of Brønlund Fjord Group only shown at northern Navarana Fjord and Løndal: NE, North-East Greenland (inset map of Greenland); NF, Navarana Fjord locality; Lø, Løndal locality; SPL, Sirius Passet Lagerstätte; TS, type section of the Aftenstjernesø Formation. **b** Map of North Greenland showing sample localities in the Aften-

stjernesø Formation at Navarana Fjord (NF) and Løndal (Lø), in the Kap Troedsson Formation at Harder Gletscher (HaG) and in the Buen Formation at Brillesø. **c** Stratigraphic schemes at Løndal in the western Peary Land and southern Lauge Koch Land area compared to northern Navarana Fjord, showing derivation of material: A, Aftenstjernesø Formation assemblages at Navarana Fjord and Løndal; B, Buen Formation assemblage at Brillesø in Peary Land

Willman, 2018 and *Indota?* sp., the latter closer to *Indiana* Matthew, 1902 according to Streng and Geyer (2019), while fragments of several unidentified forms are also present (Peel and Willman 2018). Poorly preserved material assigned to *Petrianna?* sp. occurs in the highest beds of the Buen Formation (Peel and Willman 2018). Assemblages of Small Carbonaceous Fossils from the Buen Formation in the same outcrops contain fragments of several bradoriid taxa (Slater et al. 2018), including material recently assigned to *Spinospitella* Skovsted et al., 2006 (Wallet et al. 2020).

The Kap Troedsson Formation yielded well preserved phosphatised *Hipponicharion skovstedi* Peel, 2017a and *Beyrichona avannga* Peel, 2017a in assemblages of Small Shelly Fossils from southern Wulff Land (Fig. 1b). The fossils occur in a shallow ramp succession of lime mudstones and skeletal limestones that is equivalent to the more distal starved dolostone succession of the correlative lower member of the Aftenstjernesø Formation of the J.P. Koch Fjord area (Fig. 1; Ineson and Peel 1997; Peel 2017a).

Small Shelly Fossils from the upper Henson Gletscher Formation in Løndal (Fig. 1) include rare bradoriids in limestones from the youngest parts of Cambrian Stage 4. Peel et al. (2016) and Peel (2017a) described *Navarana pearylandica* Peel, 2017a, *Liangshanella? nivalis* Peel et al., 2016 and *Zepaera?* sp.

Elsewhere in Greenland, Poulsen (1932) noted *Bradoria* sp. from the Bastion Formation of North-East Greenland (Fig. 1a, inset map), while Skovsted (2006) described *Albrunnicola* sp., *Liangshanella sayutinae* (Melnikova, 1988) and *Indiana secunda* (Matthew, 1895) from the same area. Scale-bearing hollow spines of *Mongolitubulus henrikseni* Skovsted and Peel, 2001 from the Bastion Formation were shown to be part of the exoskeleton of a bradoriid by Skovsted (2005).

The present paper describes spinose bradoriids from the middle part of the Buen Formation and the lower member of the overlying Aftenstjernesø Formation of North Greenland (Fig. 1c). The material is referred to two genera originally proposed in distant Cambrian palaeocontinents, and expands earlier reports of their occurrence in Laurentia. *Spinospitella* was described from the Mernmerna Formation (Cambrian Stage 4) of South Australia (Skovsted et al. 2006), where it appears to be widespread in the *Dailyatia odyssei* shelly fossil Zone (Betts et al. 2017). *Spinospitella* has also been reported from the Shackleton Limestone in the Transantarctic Mountains of Antarctica (Betts et al. 2017; Claybourn et al. 2019, 2020). The recent description of *Spinospitella* from small carbonaceous fossil assemblages in the Buen Formation (Wallet et al. 2020) is confirmed by a complete individual from the basal Aftenstjernesø Formation at Navarana Fjord (Fig. 2). Its occurrence in North Greenland

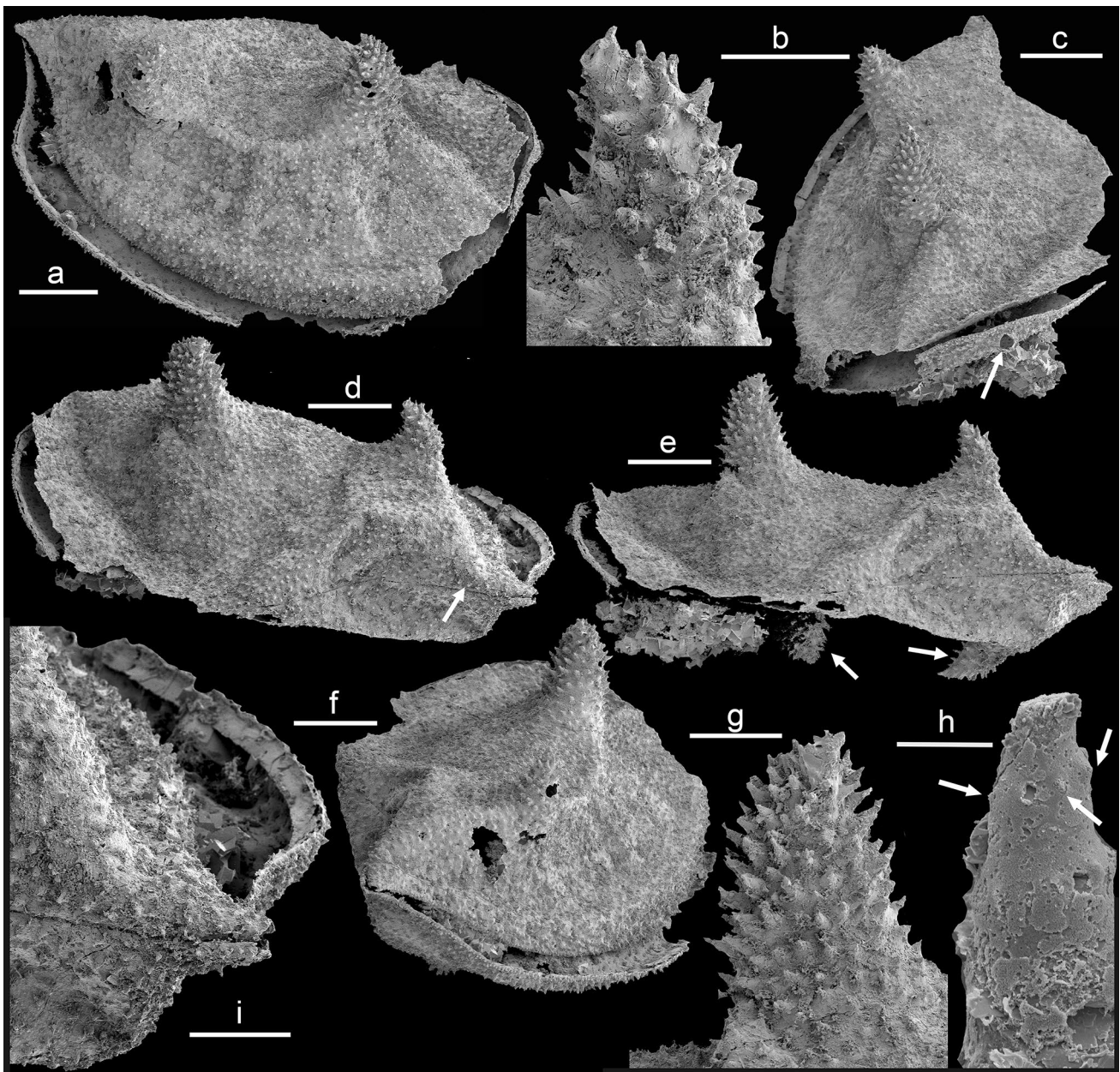


Fig. 2 *Spinospitella coronata* Skovsted et al., 2006, PMU 36980 from GGU sample 313012, Navarana Fjord, North Greenland, Aftenstjernesø Formation, Cambrian Series 2, Stage 4; **a** left valve in lateral view; **b** anterior first order spine with covering of second order spines; **c** oblique posterior view with base of broken marginal spine (arrow); **d** dorso-lateral view showing hinge line (arrow), enlarged

in **i**, anterior to right; **e** dorsal view showing spines on right valve (arrowed), anterior to right; **f** oblique anterior view; **g** posterior first order spine with covering of second order spines; **h** second order spine with corona of third order spines (arrows). Scale bars 10 μm (**i**), 200 μm (**b**, **g**, **h**), 500 μm (**a**, **c**–**f**)

adds to the similarity between East Gondwana (Australia and Antarctica) and Greenland Cambrian Stage 3–Stage 4 faunal assemblages of Small Shelly Fossils first noted by Skovsted (2006).

Nikolarites Vassiljeva (Vasilieva), 1994 is a poorly known genus based on fragmented specimens from the Pestrotsvet Formation, late Atdabanian Stage (Cambrian

Stage 3) in the Lena–Aldan region, Siberia (Vasilieva 1994, 1998). It was first reported as rare fragments from Greenland by Skovsted (2006) but the present abundant material adds support to its interpretation as a bradoriid, as suggested by Skovsted et al. (2006) and Kouchinsky et al. (2015). The current material clarifies the relationship between the two genera, focusing on their contrasting

preservation and distribution in different environments in the lower Cambrian shelf succession of North Greenland.

Geological background

Cambrian sediments in North Greenland accumulated on the present day southern margin of the transarctic Franklinian Basin (Higgins et al. 1991; Ineson and Peel 1997), a site that lay across the equator during the Cambrian (Torsvik and Cocks 2016). A southern shelf area is bounded to the north of the present study area (Fig. 1a) by a deep-water trough succession, which subsequently became the focus of Ellesmerian deformation (Higgins et al. 1991). Deposition of the Buen Formation (Cambrian Stages 3–4; thickness 325–500 m in the southern area) followed a major regional transgression across a karstified earliest Cambrian platform, and commenced with a sandstone-dominated lower member (Bryant and Pickerill 1990; Ineson and Peel 1997; Peel and Willman 2018). A second marine advance introduced an upper member of dark, richly fossiliferous mudstones (Peel and Willman 2018; Slater et al. 2018; Wallet et al. 2020).

The overlying Brønlund Fjord Group (Cambrian Series 2–Miaolingian Series; Fig. 1c) is a carbonate-dominated complex that prograded across the shelf towards the northern deep-water trough (Higgins et al. 1991; Ineson and Peel 1997). In the southern J.P. Koch Fjord area, the Brønlund Fjord Group (Fig. 1c) consists of an alternation of cliff-forming formations made up of prograding cross-bedded dolomitic grainstones with conspicuous debris flows, deposited during sea level highstands, and recessive mudstone–carbonate units that represent lowstand conditions (Higgins et al. 1991; Ineson and Peel 1997). This lithostratigraphic subdivision is not applicable in northern J.P. Koch Fjord, where the prograding carbonate units have thinned out, and the succession is dominated by outer shelf mudstones and carbonates assigned to the Henson Gletscher and Kap Stanton formations (Ineson et al. 1994; Fig. 1c).

The Aftenstjernesø Formation represents the first of these carbonate progradation events, overlying the siliciclastic shelf sediments of the Buen Formation (Ineson and Peel 1997; Peel and Willman 2018), and it can be traced north almost to the outer margin of the shelf. It is dominated by cliff-forming dolostone grainstones that attain a thickness of about 62 m (Ineson and Peel 1997) in its type area at the head of J.P. Koch Fjord (Fig. 1a, locality TS) but this value is reduced to only 18 m at the Navarana Fjord locality (Fig. 1a, locality NF). Fossils from the Aftenstjernesø Formation are restricted generally to the basal member (usually 3–5 m in thickness) of dolomitic grainstones rich in

glauconite, phosphorite bioclasts, pyrite and phosphatized hardgrounds, but limestones are present in Løndal (Frykman 1980; Peel 2017b). The lower member accumulated in a sediment-starved outer ramp setting and can be traced from southern to northern J.P. Koch Fjord, and in outcrops eastward to Løndal and across southern Peary Land, beyond.

Materials and methods

GGU sample 184004 was collected by J. S. Peel on 16 June 1974 from the lower part of the upper member of the Buen Formation at Brillesø (82°13' N, 29°58' W) in southern Peary Land (Fig. 1b; Peel and Willman 2018).

GGU samples 255501, 255502 and 255503 were collected by P. Frykman on 11 July 1979 in Løndal, western Peary Land (82°16'N, 37°03'W) from 10 cm, 50 cm and 90 cm, respectively, above the lowest exposed level of the lower member of the Aftenstjernesø Formation (Fig. 1a, locality Lø). GGU sample 255513 was collected by P. Frykman on 12 July 1979 about 150 m north-east of GGU samples 255501–255503, about 1.35 m above the junction between the Buen Formation and the overlying lower member of the Aftenstjernesø Formation.

GGU sample 313012 was collected by A.K. Higgins on 28 June 1984 from the lowest beds of the Aftenstjernesø Formation on the southern limb of the prominent Navarana Fjord anticline in Sect. 12 of Higgins et al. (1992) at 82°35.5'N, 42°14'W (Fig. 1a, locality NF). In this section the Aftenstjernesø Formation overlies dark mudstones of the Buen Formation and attains a thickness of 18 m, culminating in a 3–4 m thick debris flow. Overlying strata were assigned to the Henson Gletscher Formation by Higgins et al. (1992).

Small Carbonaceous Fossils from mudstones of GGU sample 184004 were extracted using techniques described by Butterfield and Harvey (2012), and subsequently mounted for SEM study (Wallet et al. 2020). Other samples were limestones and dolostones that were digested in weak acetic acid following the protocol established by Jeppsson et al. (1985) prior to mounting of selected specimens from the residues for SEM study.

Abbreviations and repositories. GGU prefix—indicates a sample collected by Grønlands Geologiske Undersøgelse (Geological Survey of Greenland), now part of the Geological Survey of Denmark and Greenland (GEUS), Copenhagen, Denmark. PMU prefix—denotes a specimen deposited in the palaeontological type collection of the Museum of Evolution, Uppsala University, Sweden.

Environmental control

The single, almost complete and only slightly deformed specimen of *Spinospitella coronata* was the only skeletal fragment recovered following acid digestion of a fine-grained dark carbonate sample (weight about 0.5 kg), interpreted as representing the ambient outer shelf environment and its autochthonous fauna from Navarana Fjord (Fig. 2). In contrast, several other samples from the Aftenstjernesø Formation, at and adjacent to the same locality at Navarana Fjord (Fig. 1a, locality NF), contain a rich small shelly fauna, with 50 species documented by Peel (2020, 2021); these assemblages are clearly allochthonous and have been transported down slope with disarticulation, sorting and erosion as a consequence.

Sample residues from Løndal, to the south-east (Fig. 1a, locality Lø), are also rich in Small Shelly Fossils and many elements in the fauna occur also in the allochthonous assemblages from Navarana Fjord (Peel 2021). The Løndal samples show clear evidence of erosion, disarticulation and other taphonomic changes, and contain numerous fragments of *Nikolarites* (Figs. 4, 5) that are not present in the Aftenstjernesø Formation samples from Navarana Fjord. Peel and Willman (2018: fig. 9H, I), however, illustrated robust spines, which they assigned to the bradoriid *Petrianna?* sp. from siltstones of the uppermost Buen Formation rich in comminuted transported shells at the same locality, immediately below the boundary with the overlying Aftenstjernesø Formation at Navarana Fjord.

Wallet et al. (2020) compared the distribution of *Spinospitella* in residues of Small Carbonaceous Fossils from the Buen Formation from Brillesø with that of *Isoxys volucris* Williams et al., 1996, which is extremely common in the slightly older macro fauna of the Sirius Passet Lagerstätte (Williams et al. 1996; Stein et al. 2009; Nielsen et al. 2017; Fig. 1a, locality SPL). The smooth-shelled *Isoxys*, although bivalved, is not a bradoriid but a stem-group arthropod (Legg and Vannier 2013) and has been interpreted as a pelagic hunter (Vannier and Chen 2000; Zhao et al. 2014). Entire specimens from Sirius Passet range in length from 5 mm to more than 20 mm, excluding the long terminal spines. Wallet et al. (2020) suggested that certain small broken spines in the Small Carbonaceous Fossil assemblage from Brillesø may be *Isoxys*, but Peel and Willman (2018) did not identify *Isoxys* or *Spinospitella* among macrofossils at that locality.

In discussing the *Spinospitella* specimens, Wallet et al. (2020) suggested that the absence of such spinose forms from the slightly older Sirius Passet Lagerstätte (Fig. 1a, SPL) might reflect environmental control in terms of oxygen or depth parameters of the distribution of bradoriids within the Buen Formation, with the epibenthic *Spinospitella*-like forms being restricted to the shelf environments. Wallet et al.

(2020) noted that *Spinospitella* and specimens of the much larger *Petrianna fulmenata* Siveter et al., 1996 were known only from outer shelf deposits of the Buen Formation in southern Peary Land (Peel and Willman 2020), whereas thin-walled pelagic species of the bivalved *Isoxys* Walcott, 1890 were common in the Sirius Passet Lagerstätte and elsewhere (Williams et al. 1996; Vannier and Chen 2000; Paterson et al. 2008; Stein et al. 2009; Nielsen et al. 2017).

Unlike the Buen Formation around Brillesø (Slater et al. 2018; Wallet et al. 2020), no Small Carbonaceous Fossils are known from the transitional Buen Formation at Sirius Passet due to high levels of regional metamorphism (Vidal and Peel 1993). In general, the Sirius Passet Lagerstätte is dominated by large arthropods and lobopods, some of which achieve sizes of 25 cm and 45 cm, respectively (Stein et al. 2013; Vinther et al. 2016). Fossil specimens less than about 5 mm are generally absent, suggesting that the absence of the small specimens of *Spinospitella*, if initially present, may result from a taphonomic or diagenetic filter. As noted above, *Spinospitella* is well represented in the small organic fossil fraction at Brillesø, but not in the described macrofauna (Peel and Willman 2018).

While the evidence regarding comparison of *Spinospitella* and *Isoxys* is equivocal, the thesis of environmental control put forward by Wallet et al. (2020) is supported by the present material. Robust fragments of thick, multi-layered, shield and associated spines of *Nikolarites spasskyi* are common in the Aftenstjernesø Formation in Løndal (Fig. 1a). The fragments are often rounded and exfoliated, indicating erosion and transport in a relatively high energy setting; large sections of shield are absent. In contrast, the single specimen of the thinner shelled *Spinospitella coronata* from the outer shelf setting, at Navarana Fjord to the north, is articulated, almost complete and well preserved; fragments of shields of *Spinospitella* or *Nikolarites* are not known from this or other samples from the Aftenstjernesø Formation at Navarana Fjord. These other samples from the Aftenstjernesø Formation (exclusive of GGU sample 313012 with the complete *Spinospitella* specimen) clearly preserve allochthonous fossil material transported down slope, whereas the described complete specimen of *Spinospitella coronata*, the only fossil specimen recovered from a sample lacking comminuted shell material, is interpreted as representing the ambient environment and autochthonous fauna of the outer shelf. Although not specifically studied, the distribution of *Spinospitella* in South Australia seems to follow a similar pattern. In South Australia, *Spinospitella* is most common in the Mernmerna Formation, representing a carbonate ramp-slope facies and is less common in the older Wilkawillina and Wirrapowie Limestones, which represent more shallow environments than the Mernmerna Formation (Betts et al. 2017).

While the fragments of *Spinospitella* sp. from the Buen Formation are derived from geographically southern areas of North Greenland at Brillesø, they accumulated in mudstones at the deepest point of the major regional transgression in the middle Buen Formation prior to the upwards shallowing trend that continued up to the basal Aftenstjernesø Formation (Ineson and Peel 1997). Environmentally, these outer shelf mudstones from the medial Buen Formation are akin to the outer shelf fine grained sediments at Navarana Fjord, and both yield *Spinospitella*. The robust shields of *Nikolarites spasskyi* in the Aftenstjernesø Formation from Løndal characterize higher energy inner shelf conditions than *Spinospitella*, which favoured a quieter, outer shelf environment.

Peel (2017a) described a different assemblage of bradoriids from the Kap Troedsson Formation near Harder Gletscher (Fig. 1b, HaG), stratigraphically continuous with the basal member of the Aftenstjernesø Formation. Well preserved specimens of *Beyrichona avannga* Peel, 2017a and *Hipponicharion skovstedii* Peel 2017a occur in a shallow carbonate ramp succession (Ineson and Peel 1997), which lacks the robust ornamented spines of *Nikolarites*. Neither are *Beyrichona avannga* and *Hipponicharion skovstedii* known from the basal Aftenstjernesø Formation, suggesting the differentiation of a third bradoriid community in addition to the *Nikolarites* and *Spinospitella* faunas from the inner to outer shelf.

Systematic palaeontology

Euarthropoda sensu Walossek, 1999

Order **Bradoriida** Raymond, 1935

Family uncertain

Discussion. Rozanov (1986: 89) suggested that a new family Mongolitubulidae might be erected within hyolithelminths to include *Mongolitubulus*, at that time considered to be tubular rather than spinose, but it was later discussed also as a “conodontomorph” by Rozanov and Zhuravlev (1992). Topper et al. (2013) proposed Mongolitubulidae as a new family of Bradoriida to include the eponymous genus, *Tubuterium* Melnikova, 2000, *Spinospitella* and possibly *Rushtonites* Hinz, 1987. However, it is apparent that *Mongolitubulus*, as currently recognised, is a form genus for similar ornamented spines (Skovsted and Peel 2001; Skovsted 2005). A variety of spinose shield morphologies is included in the genus, ranging from *Mongolitubulus unispinosa* Topper et al., 2007 to the multi-spined *Mongolitubulus henrikseni* Skovsted and Peel, 2001. The polyphyletic nature of spines referred to *Mongolitubulus* was discussed by Li et al., (2012) and Caron et al. (2013) who noted that material from Greenland assigned to *Mongolitubulus squamifer*

Missarzhevsky 1977 by Skovsted and Peel (2001) could be interpreted as the spines of a hallucigeniid lobopodian. The lobopodian hypothesis concerning *Mongolitubulus* was earlier put forward by Dzik (2003) on the basis of specimens from the early Cambrian Shabatky Formation of Kazakhstan. Taxonomically, the issue is confused, since material described by Meshkova (1985), Skovsted and Peel (2001), Dzik (2003) and Wrona (2004, 2009), and discussed by Caron et al. (2013), is referred by these authors to the type species, *Mongolitubulus squamifer* Missarzhevsky, 1977 from Mongolia. While other species referred to *Mongolitubulus* by Skovsted and Peel (2001), Skovsted (2005), Skovsted et al. (2006), Topper et al. (2007), Kouchinsky et al. (2015) are demonstrably bradoriids, the status of Missarzhevsky’s (1977) type material from Mongolia remains equivocal, as is that of the family.

McMenamin (2020) did not discuss Mongolitubulidae, but assigned *Mongolitubulus*, *Nikolarites* (as *Nicolarites*) and *Spinospitella* to the Family Duibianellidae Shu, 1990, together with *Duibianella* Shu, 1990 (inadvertently spelt *Dubianella*), *Neoduibianella* Shu, 1990, *Spinella*, Zhang 2007 (which he considered to be a synonym of *Mongolitubulus unispinosa* Topper et al., 2007) and *Kazakhstanotubulus* Gridina, 1991. Topper et al. (2013: 73) commented that spines of *Duibianella* differ from those of *Mongolitubulus* and *Spinospitella* by being ornamented with lower nodes rather than elongated spines, but they are compared here to *Nikolarites*.

At this time, *Mongolitubulus* and *Spinospitella* are left unassigned at family level, while *Nikolarites* is assigned tentatively to Duibianellidae.

Genus *Spinospitella* Skovsted et al., 2006

Type species. *Spinospitella coronata* Skovsted et al., 2006 from the Mernmerna Formation of South Australia, Cambrian Series 2, Stage 4.

Discussion. Skovsted et al. (2006) described *Spinospitella* from the Mernmerna Formation (Cambrian Stage 3–4) of South Australia based on collections containing a juvenile valve and partially broken bradoriid shields showing exquisite details of the ornamentation.

The distinctive ornamentation of a fine net draped around spines and tubercles characteristic of *Spinospitella* to form a honeycomb pattern has been described also in *Nikolarites spasskyi* Vassiljeva [Vasilieva], 1994 from the Atdabanian of the Lena–Aldan region of Yakutia, Siberia (Vasilieva 1994), and in bradoriids such as *Duibianella* and *Neoduibianella* superbly illustrated by Zhang (2007) from the Cambrian of China. While the fragmentary nature of the Siberian specimens (Vasilieva [Vassiljeva 1998]: pls. 39, 40) inhibits unequivocal interpretation, they represent almost certainly fragments of a bradoriid that can be differentiated from

Spinospitella in terms of the micro-ornamentation of the shield.

In contrast to *Spinospitella*, Skovsted et al. (2006: 14) noted that the network pattern in the ornamentation continued over the summit of second order spines and tubercles in *Nikolarites*, a feature visible in some of the illustrations in Vasilieva (1994, 1998) and Kouchinsky et al. (2015). This observation is confirmed here in material from North

Greenland and provides a more solid base for the recognition of *Nikolarites*. It is stressed, however, that gross features of the shield of *Nikolarites* are not known. Future study may determine that shields with dissimilar gross morphology may simply share similar ornamentation, a situation reminiscent of that in *Mongolitubulus*, where several species are recognised, mainly on the nature of the prominent spines. Given the interpreted defensive function of the

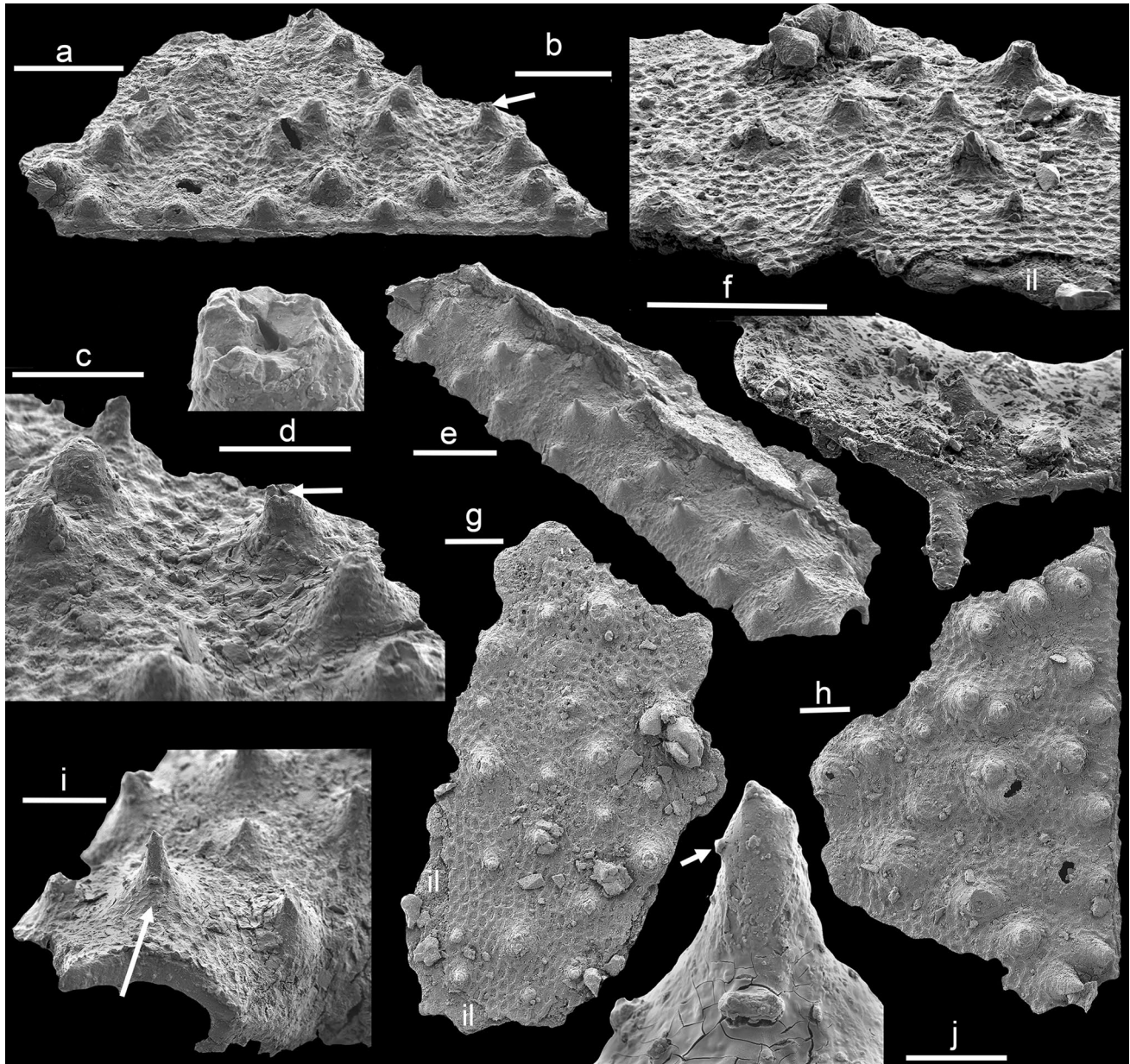


Fig. 3 Small Carbonaceous Fossils of *Spinospitella* cf. *coronata* from GGU sample 184004, Brillesø, southern Peary Land, North Greenland, Buen Formation, Cambrian Series 2, Stage 4; **a, c, d, h** PMU 36,304, preserving a straight margin (**c, h**), arrow points to broken hollow spine enlarged in **c** and **d**; **e, i, j** PMU 36,303, showing gentle curvature, lower-right termination enlarged (**i**) to show detail of orna-

mentation of second-order spines; arrow points to spine enlarged in **j**; **j** detail of spine showing incomplete corona of third-order spines (arrow); **f** PMU 36,306 showing rounded margin bearing a spine; **b, g** PMU 36,305, showing inner layer (il) overlain by ornamented outer layer enlarged in **b**. Scale bars 5 μm (**j**), 10 μm (**d**), 50 μm (**b, c, f-i**) and 100 μm (**a, e**)

Mongolitubulus spines (Skovsted and Peel 2001), it is not unlikely that similar structures were developed on otherwise dissimilar shields.

Amphikeropsis myklosis Topper et al., 2007 from the Mernmerna Formation of South Australia (Topper et al. 2007: figs. 7D–K, 8) resembles *Spinospitella* in terms of the two prominent spines on each shield, but lacks the hollow second order spines. Topper et al. (2007) suggested that *A. myklosis* may have belonged to the same group of bradoriids as *Spinospitella*, *Duibianella* and *Mongolitubulus*, and by inference *Nikolarites*, but this hypothesis is presently difficult to test.

Spinospitella coronata Skovsted et al., 2006

Figures 2, 3

2006 *Spinospitella coronata* Skovsted, Brock and Paterson: 21, figs. 6–9.

2007 *Spinospitella coronata*—Topper, Skovsted, Brock and Paterson: 85, fig. 9.

2011 *Spinospitella coronata*—Topper, Skovsted, Brock and Paterson: fig. 7N.

2016 *Spinospitella coronata*—Betts, Paterson, Jago, Jacquet, Skovsted, Topper and Brock, fig. 20L–P.

2018 bradoriid fragments (cf. *Spinospitella*)—Slater et al.: fig. 2Q–AI.

2020 *Spinospitella coronata*—McMenamin: 24.

2021 (bradoriids)—Wallet et al.: fig. 4.

Material. PMU 36,980 from GGU sample 313012, eastern side of Navarana Fjord, Lauge Koch Land, North Greenland (Fig. 1a, locality NF); lower Aftenstjernesø Formation. PMU 36,303–PMU 36,306 from GGU sample 184004, middle Buen Formation, Brillesø, Peary Land (Fig. 1b). All specimens from Cambrian Series 2, Stage 4.

Occurrence. Mernmerna Formation (Skovsted et al. 2006; Topper et al. 2007; Betts et al. 2017), of South Australia; Cambrian Series 2, Stages 3–4. Buen Formation and Aftenstjernesø Formation of North Greenland; Cambrian Series 2, Stage 4. *Spinospitella* sp. was reported from the Holyoake Formation of East Antarctica (Claybourn et al. 2019; Claybourn 2020); Cambrian Series 2, Stage 4. Rare specimens were also reported from the older Wilkawillina Limestone and Wirrapowie Limestone (Betts et al. 2016) of South Australia; Cambrian Series 1, Stage 2, but these occurrences need to be confirmed by further studies.

Description. Equivalved bradoriid arthropod, postplete in large specimens but almost bilaterally symmetrical in juveniles. Hinge line gently convex in lateral view, marked by a narrow groove (Fig. 2d, arrow). Antero-cardinal angle

produced into a short but distinct spine (Fig. 2a); postero-cardinal termination seemingly angular. Ventral margin in lateral view initially concave below the antero-cardinal spine, but thereafter uniformly convex (Fig. 2a). Ventral margin of right valve (left not visible for comparison) with acute transition from spinose outer surface to a smooth inward sloping rim on the interior (Fig. 2d, i). Outer margin of shield flattened with a narrow brim in juvenile (Skovsted et al. 2006: fig. 9D) but inflated to form a broad, convex, comarginal ramp in adult, widest posteriorly (Fig. 2a). Each valve in the adult ornamented by two prominent, robust, first order spines located at one third of the distance from the hinge to the ventral margin; posteriormost spine is larger (Fig. 2e, spines arrowed on right valve). Anterior spine located at about one quarter of the length; broadly based, tapering, and curved towards the posterior (Fig. 2a, d, e). Posterior spine located at about two thirds of valve length, with its tip curved anteriorly (Fig. 2e, g). Shape of inner valve area seemingly with a broad comarginal ridge connecting the two first order spines and with three obscure radial folds in the posterior half of the shell connecting this to the marginal ramp (Fig. 2a).

External shield surface, including the first order spines, covered by closely spaced, pointed, second order spines; the intervening polygonal network obscured by encrustation. Second order spines slender, smooth, but with circlets of short, stubby, third order spines (Fig. 2h). Internal surface of the shield with circular pits corresponding to the hollow second order spines. A broken spine base indicates a large spine close to the posterior margin of the right valve, absent from the left valve (Fig. 2c, arrow).

Discussion. *Spinospitella coronata* was fully described by Skovsted et al. (2006) whose description placed particular emphasis on the nature of the spinose ornamentation. A circlet of third order spines was considered a diagnostic character for *Spinospitella coronata* by Skovsted et al. (2006). These fine structures are not always present in specimens from Australia (Skovsted et al. 2006; Topper et al. 2007; Betts et al. 2016, 2017), presumably due to preservational factors such as abrasion and/or coating by secondary minerals. However, we note that the best preserved specimens in the type lot are juveniles (see discussion below) and until more complete and well preserved larger specimens are known from Australia the taxonomic implications of presence/absence of the third order spines will remain uncertain. Fine details of the outer surface sculpture are partly obscured in the Navarana Fjord specimen by a thin, crystalline or flaky, diagenetic coating, presumably of phosphate, although poorly preserved circlets of third order spines (Fig. 2h, arrows) can be recognized on the second order spines that cover the shield surface. A similar spine is preserved on a carbonaceous fragment from Brillesø (Fig. 3i, j, arrows).

The single specimen from Navarana Fjord is a slightly crushed, almost complete individual 3.4 mm long (Fig. 2a), with height about half of length. It is twice the height of the holotype (Skovsted et al. 2006: fig. 9A), whereas the largest specimen figured by Topper et al. (2007) had a length of 2.1 mm. Thus, the Navarana Fjord specimen is the largest specimen of *Spinospitella coronata* so far described and the great size difference between this and the complete juvenile, length 750 µm, figured by Skovsted et al. (2006: fig. 9D–F), together with specimens from the Buen Formation (Waller et al. 2020), is reflected in morphological changes during ontogeny. The most notable ontogenetic changes include the enhanced postplete shape and greater prominence of the antero-dorsal spine. The relief of the first order spines is also increased in the adult and their tips turn in towards each other. Second order spines are more strongly developed and acute, reflecting an ontogenetic trend observed by Skovsted et al. (2006).

Fragments from the middle Buen Formation tentatively assigned to *Spinospitella coronata* more clearly show the network between the second order spines. The latter preserve third order spines (Fig. 3j) and often appear to be perforated (Fig. 3d, arrow). However, this reflects corrosion of the thin walls at their tips so as to penetrate the outer ornamented layer (Fig. 3b). One fragment displays a marginal spine (Fig. 3f) that can be compared to the broken marginal spine in the specimen from Navarana Fjord (Fig. 2c, arrow).

? Family **Duibianellidae** Shu, 1990

Genus **Nikolarites** Vassiljeva [Vasilieva, 1994]

Type species. *Nikolarites spasskyi* Vassiljeva [Vasilieva], 1994, Pestrotsvet Formation, late Atdabanian Stage (Cambrian Stage 3), Lena–Aldan region, Siberia.

Diagnosis. Seemingly a bradoriid with two or more large, hollow, first order spines of variable form on each shield; their placement unknown. Shield surface covered by closely spaced, conical tubercles about 50 µm in diameter with a distinct apical node. Tubercles varying in shape and inclination from conical to inclined, becoming spinose on the first order spines (Fig. 5a, e, k). Outer surface ornamented by a raised network of four to six sided cells which drapes over the tubercles, rising up their sides (Fig. 4k); inner surface smooth, with depressions corresponding to the hollow inner surface of the tubercles on the outer surface (Fig. 4e). Shield composed of several laminated layers, with the spines notably robust.

Discussion. In the literature, the genus is variously referred to as *Nikolarites* or *Nicolarites*, combined with the specific epithet *spasskyi* or *spasskii*, and its author as Vassiljeva, Vasilieva or Vasil'eva (1994). In the original

publication (1994), the author of the paper is transliterated as Vasilieva, N.I., but the taxon itself is described as *Nikolarites spasskyi* Vassiljeva. In 1998, Vasilieva is stated to be the author of the publication, but the taxon is referred to *Nikolarites spasskii* Vasil'eva (1994), 1998: 113).

Vasilieva (1994, 1998) assigned *Nikolarites* to the cambroclavate Family Zhijinitidae Qian, 1978 but there is little similarity in form and structure to cambroclavids as described by Conway Morris and Menge (1991). Comparison of the fragments from North Greenland with material illustrated from the Pestrotsvet Formation of Yakutia by Vasilieva (1994, 1998) and from the Emyaksin Formation of the Anabar uplift by Kouchinsky et al. (2015) leaves little doubt that *Nikolarites* is a bradoriid.

Nikolarites differs from *Spinospitella* in terms of the ridges of the honeycomb pattern network extending onto the lower sides (Fig. 4i, k) of the tubercles (equivalent to the secondary spines of *Spinospitella*). The upper parts of tubercles are often smooth, in part due to exfoliation (Fig. 4a). The tubercles (Fig. 4f, i, k, l) and even the large spines (Fig. 5b, g) of *Nikolarites* also terminate in a swollen, smooth node not seen in *Spinospitella*, whereas second order spines of *Spinospitella* carry circlets of small third order spines (Figs. 2h, 3j) absent in *Nikolarites*.

Capricambria Hinz, 1991 from the Miaolingian Series (late Wuliuan Stage) of Queensland has a pair of prominent spines on each shield. The surface of the shields is covered by a raised network of ridges, but the abundant small tubercles of *Nikolarites* are lacking.

The terminal nodes on tubercles of *Nikolarites* invite comparison with *Duibianella* from the Yu'an shan Formation (late Cambrian Stage 3) in China, but the shields of the latter are covered with numerous, large and closely packed, globose nodes, some of which carry circlets of minor nodes or spines and the inflated termination (Zhang 2007: pl. 8, figs. 11–15). *Neoduibianella* from the Shuijingtuo Formation (late Cambrian Stage 3) has three or four, widely spaced, large, globose, first order spines covered with small tubercles (Zhang 2007: pl. 9, figs. 7–12) that may be compared to the first order spines of *Spinospitella* and *Nikolarites*. Intervening shield areas of *Neoduibianella* are covered by a honeycomb pattern raised network similar to that seen in both *Spinospitella* and *Nikolarites*, but small tubercles of varying size are unequally scattered across the shield surface. These small tubercles often carry a swollen apical node as in *Nikolarites* (Zhang 2007: pl. 9, fig. 7). *Nikolarites* differs from *Neoduibianella* in possessing long, slender first order spines (Fig. 5a, b) compared to the barrel-shaped spines of the latter genus, and more abundant tuberculation of the shields. Overall similarities suggest, however, that *Nikolarites* and *Neoduibianella* are closely related.

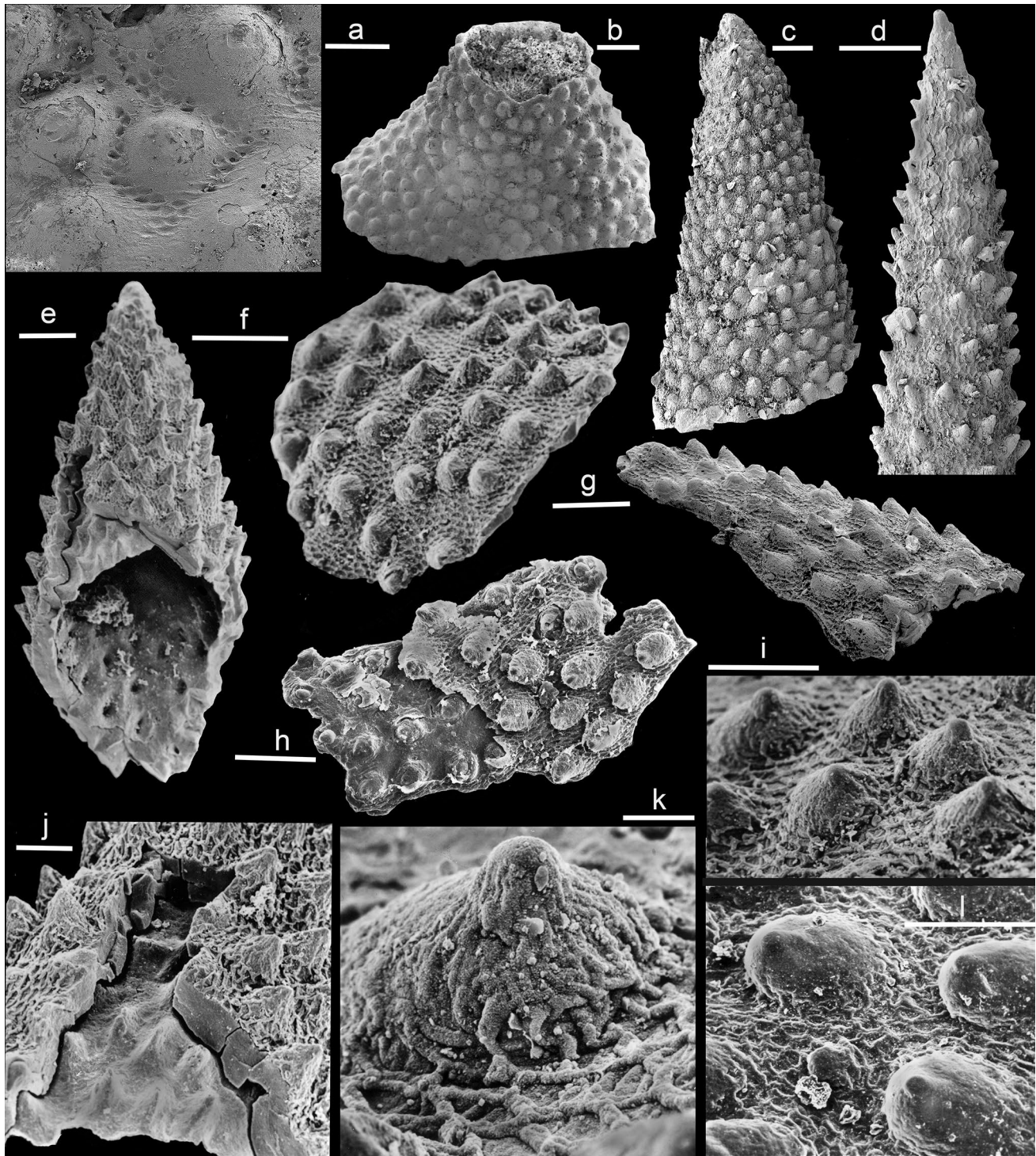


Fig. 4 *Nikolarites spasskyi* Vassiljeva, 1994, Aftenstjernesø Formation, North Greenland, Cambrian Stage 4. All samples from Løndal, Peary Land, North Greenland. **a, b** PMU 38,139 from GGU sample 255503, expanded base of major spine with detail of exfoliated surface (**a**); **c** PMU 38,140 from GGU sample 255503; **d** PMU 38,141 from GGU sample 255503; **e, j** PMU 38,142 from GGU sample 255502 broken spine showing layered, thick, shield with conical depressions on interior producing spines on the upper surface of the inner layer (**j**); **f, i, k** PMU 38,143 from GGU sample 255502, shield

fragment showing conical tubercles with apical nodes and detail of honeycomb network on sides of tubercle (**k**); **g** PMU 38,144 from GGU sample 255502; **h** PMU 38,145 from GGU sample 255501, shield fragment with outer layer with honeycomb network (right) partly exfoliated (left); **l** PMU 38,146 from GGU sample 255513, detail of asymmetric tubercles with apical nodes set in honeycomb network. Scale bars 10 μm (**k**), 50 μm (**a, i, j, l**), 100 μm (**c-h**), 200 μm (**b**)

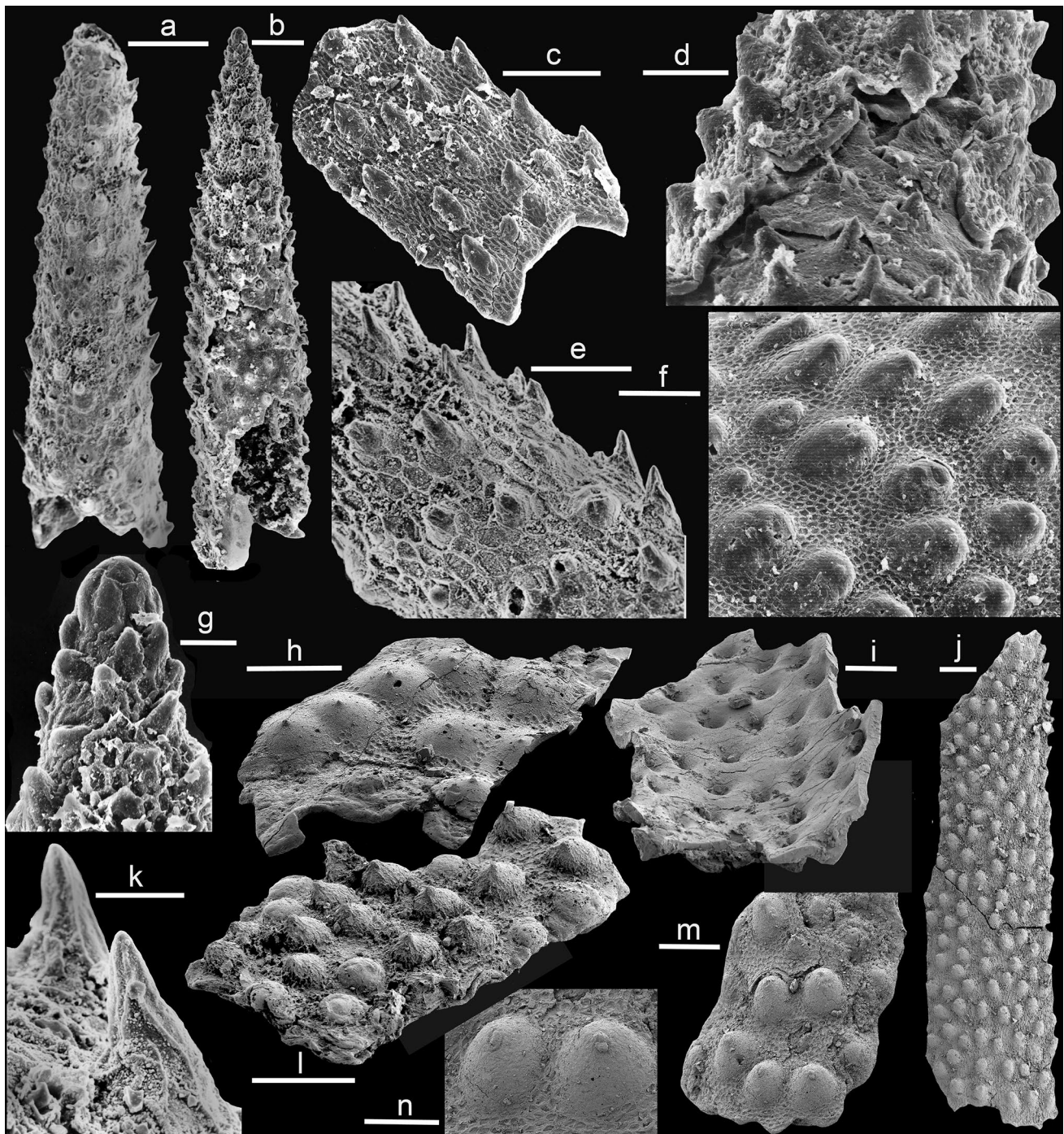


Fig. 5 *Nikolarites spasskyi* Vassiljeva, 1994, Aftenstjernesø Formation, North Greenland, Cambrian Stage 4. All samples from Løndal, Peary Land, North Greenland. **a, e, k** PMU 38147 from GGU sample 255513, broken first order spine with detail of second order spines (**e, k**); **b, d, g** PMU 38,148 from GGU sample 255501, first order spine showing partially exfoliated outer layer (**d**) and rounded tip (**g**); **c** PMU 38,149 from GGU sample 255501, curved fragment showing inclined tubercles; **f** PMU 38,150 from GGU sample 255502, detail

of outer surface showing rounded, inclined, tubercles; **h** PMU 38,151 from GGU sample 255502, corroded and partially exfoliated fragment; **i** PMU 38,152 from GGU sample 255502, inner surface showing conical depressions; **j** PMU 38,153 from GGU sample 255502; **l** PMU 38,154 from GGU sample 255502; **m, n** PMU 38,155 from GGU sample 255502, fragment showing detail of honeycomb network exfoliated from rounded tubercles, detail in (**n**). Scale bars 20 μm (**g, k**), 50 μm (**d, e, i, n**), 100 μm (**a-c, f, h, j, l, m**)

Nikolarites spasskyi Vassiljeva [Vasilieva], 1994

Figures 4, 5

1994 *Nikolarites spasskyi* Vassiljeva [Vasilieva]: 7, pl. 2, fig. 1.

1998 *Nikolarites spasskii* Vassiljeva—Vasilieva: 113, pl. 39, figs. 1–6; pl. 40, figs. 1–5.

2001 *Nikolarites spasskyi*—Skovsted and Peel: 146.

2006 *Nikolarites spasskyi*—Skovsted: 1104, fig. 10.20, 10.21.

2020 *Nikolarites*—McMenamin: 21.

Material. PMU 38,139, PMU 38,140, PMU 38,141 from GGU sample 255503; PMU 38,142, PMU 38,143, PMU 38,144, PMU 38,150, PMU 38,151, PMU 38,152, PMU 38,153, PMU 38,154, PMU 38,155 from GGU sample 255502; PMU 38,145, PMU 38,148, PMU 38,149 from GGU sample 255501; PMU 38,146, PMU 38,147 from GGU sample 255513. All samples from the Aftenstjernesø Formation, Cambrian Stage 4. Løndal, Peary Land, North Greenland.

Occurrence. Pestrotsvet Formation (Vasilieva 1994, 1998), late Atdabanian Stage (Cambrian Stage 3), Lena–Aldan region, Siberia. Bastion Formation (Cambrian Stage 4), North-East Greenland (Skovsted 2006). Aftenstjernesø Formation (Cambrian Stage 4), North Greenland.

Discussion. The gross morphology of the shields, including the number and distribution of large spines, is not known. The holotype figured by Vasilieva (1994, 1998) is a triangular fragment of a shield, 1.5 mm long but broken on all sides, bearing two prominent spines joined by a low swelling. The larger spine has been broken away from its raised base but reveals its circular cross section. The smaller spine has a low conical shape and pointed apex. No equivalent fragment is known in the current material from North Greenland, but a single large fragment from North Greenland (Fig. 4b, length 2 mm) preserves the conical base of a large circular spine about 700 µm in diameter. The surface of the fragment and of the low conical spine is covered with a honeycomb pattern, a network of approximately 6-sided cells with sharply raised cords and depressed centres (Vasilieva 1998: pl. 39, fig. 4).

Conical tubercles with convex sides occur within the honeycomb pattern (Fig. 4f); individual tubercles are variable in width relative to height and culminate in an apical node (Fig. 4f, i, k). Interspaces between tubercles vary from one to two diameters of the tubercles, which is the area occupied by about three or four of the cells of the network (Vasilieva 1998: pl. 39, fig. 4). The tuberculate surfaces in Vasilieva's (1998) illustration

appear identical to the pattern on gently curved fragments from North Greenland (Fig. 4f), where variation in spacing of the tubercles is more apparent. In pristine specimens (Fig. 4k), the ridges from the network rise towards the apex of the tubercles and the apical node is rounded. However, the ridges on the tubercles may be obscure or missing, often as a result of exfoliation or possibly corrosion of the outer shield surface (Fig. 5m), although the apical node remains distinct (Fig. 5h, n). Individual tubercles may be radially symmetrical (Fig. 4f, i, k) or with their axis inclined (Figs. 4g, l, 5f), the latter usually parallel to the axis of curvature of the fragments (Fig. 5c, j).

Vasilieva (1998: pl. 40) illustrated a slightly curved fragment of a slowly tapering spine (length about 1 mm), circular in cross section but broken at each extremity. While the surface network is clearly expressed, the tubercles are pointed, thorn-like, slightly taller than wide, and widely spaced, with six or more cells between each spine. The apices of the thorn-like tubercles are directed distally from the broken base of the spine, and inclined at about 45 degrees to its surface; their sides are ornamented with irregular ridges. Closely similar spines from North Greenland vary from almost cylindrical with increased tapering towards the more uniformly tapering apex (Fig. 5b), to more uniformly narrow cones (Figs. 4d, 5a). While the honeycomb network may be somewhat coarser than in the specimen illustrated by Vasilieva (1998), the tubercles on the spines show similar shape, inclination and ornamentation (Fig. 5a, e, k), becoming narrower and more acute as the apex is approached. Where preserved, the apex of the spines is formed by a globose node (Fig. 5b, g). One illustrated spine (Fig. 4c) is a wider, slightly curved cone, with closely spaced inclined tubercles more similar in shape to the equidimensional tubercles of the shallowly convex fragments (Figs. 4g, 5l). Its form and curvature suggest that it may represent the type of spine attached to the large spine base (Fig. 4b). Vasilieva (1994) commented that the shield had three shell layers, and several layers are clearly seen in the robust Greenland material (Figs. 4e, j; 5d).

Skovsted (2006) assigned to *Nikolarites* two thick-shelled, cone-shaped, fragments with densely spaced tubercles from the Bastion Formation of North-East Greenland (Fig. 1c) that compare well with the robust base of a spine from North Greenland (Fig. 4b). A similar blunt spine was described as ‘‘Nodose cap’’ by Landing et al. (2002: 302, fig. 4.12) from the latest Early Cambrian ‘‘Anse Maranda Formation’’ of Ville Guay, Québec.

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