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New Silurian-Devonian pseudophorid gastropods

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Abstract. Pseudophorid gastropods typically occur as warm-water (tropical to subtropical) elements in Late Ordovician-Permian strata. Silurian occurrences are known from the North Silurian Realm (North Atlantic Region) and Devonian occurrences are known only from the Old World Realm and Eastern Americas Realm. No occurrences are known from the cool- to cold-water Malvinokaffric Realm during the Silurian or Devonian. New Silurian-Devonian taxa of this biogeographically distinctive gastropod family include three new genera: *Gaspephorus*, based on the Late Silurian (Ludlow-Přídolí) *Euomphalopterus gasconensis* Northrop from Gaspé and northern Maine; *Peelophorus*, based on *Trochus astraliiformis* Lindström from the Silurian (Wenlock) of Gotland; and *Bergmadsenella*, based on *Pleurotomaria marklini* Lindström, also from the Late Silurian (Wenlock) of Gotland. In addition, a new species of *Astralites*, *A. gamblei*, from early Middle Devonian (Eifelian) strata of the Cheeneetnuk Limestone, McGrath A-5 quadrangle of west-central Alaska is established.

Key words: Gastropoda, Pseudophoridae, new taxa, Silurian, Devonian, Gaspé, Maine, Sweden, Alaska

Introduction

The family Pseudophoridae Miller, 1889, comprises a distinctive group of Paleozoic gastropods, characterized by a conical shell having a flat, concave, or weakly convex base within a surrounding frill. The oldest recognized member of the family is *Pseudophorus* cf. *P. profundus* (Lindström, 1884) of Rohr and Blodgett (1985) from the Ashgillian (late Late Ordovician) strata of the McGrath C-4 quadrangle, west-central Alaska (Farewell terrane). Members of this family were restricted to shallow, warm-water (tropical to subtropical) areas of the globe during their entire existence from Late Ordovician to Permian time. Silurian occurrences are known from the North Silurian Realm (North Atlantic Region) in both the North American and European provinces, and Devonian occurrences are known only from the Old World Realm and Eastern Americas Realm. The Pseudophoridae are totally absent from cool- to cold-water deposits of the Devonian Malvinokaffric Realm, recognized in central and southern South America, the Falkland Islands, South Africa, Ghana, and Antarctica. The gastropod fauna of the Malvinokaffric Realm is markedly impoverished and consists of only a handful of species, represented primarily by *Plectonotus* (*Plectonotus*) and the large species of *Tropidodiscus* (Blodgett et al. 1988, 1990).

Several new Devonian pseudophorid genera have previously been established since the publication of the Gastropod Treatise (Knight et al. 1960). *Taemasotrochus* was established by Tassell (1982) for his new species *T. giganticus* from the Emsian "Receptaculites" Limestone of New South Wales. Recently, Heidelberger (2001) established two new Middle Devonian pseudophorid genera (*Dentanitella* and *Devonoconica*) based on Givetian material from Germany. During a recent discussion of the importance of the Pseudophoridae in biogeographic reconstructions of the Middle Paleozoic, it became obvious to us that several new taxonomic entities were needed to make better known the taxonomic content and biogeographic patterns displayed by this group. These new taxic entities include three new Late Silurian genera: *Gaspephorus*, from Gaspé and Maine, and *Peelophorus* and *Bergmadsenella* from Gotland; as well as a new early Middle Devonian (Eifelian) species, *Astralites gamblei*, from the McGrath A-5 quadrangle of west-central Alaska (Farewell terrane).

Repositories: The herein figured and described specimens are deposited in the following museums: (1), Peabody Museum of Yale University (abbreviation YPM) in New Haven, Connecticut, USA, (2), University of Alaska Museum (abbreviation UAM) in Fairbanks, Alaska, USA, and (3), the Museum of Evolution, Palaeontology Section, Uppsala University (abbreviation UU) in Uppsala, Sweden.

Systematic paleontology

Subclass Archaeogastropoda Thiele, 1925
Superfamily Pseudophoroidea S. A. Miller, 1889
Family Pseudophoridae S. A. Miller, 1889

Remarks: The family Pseudophoridae Miller, 1889 comprises a distinctive group of Paleozoic gastropods characterized by a conical shell having a flat, concave, or weakly convex base within a surrounding frill. Knight et al. (1960) raised the taxonomic rank of the original family Pseudophoridae to that of a superfamily. Knight et al. (1960) recognized two families within this group: 1. the Planitrochidae Knight, 1956, containing representatives of Early Ordovician to Late Silurian age, and 2. the Pseudophoridae Miller, 1889, containing representatives of Silu-

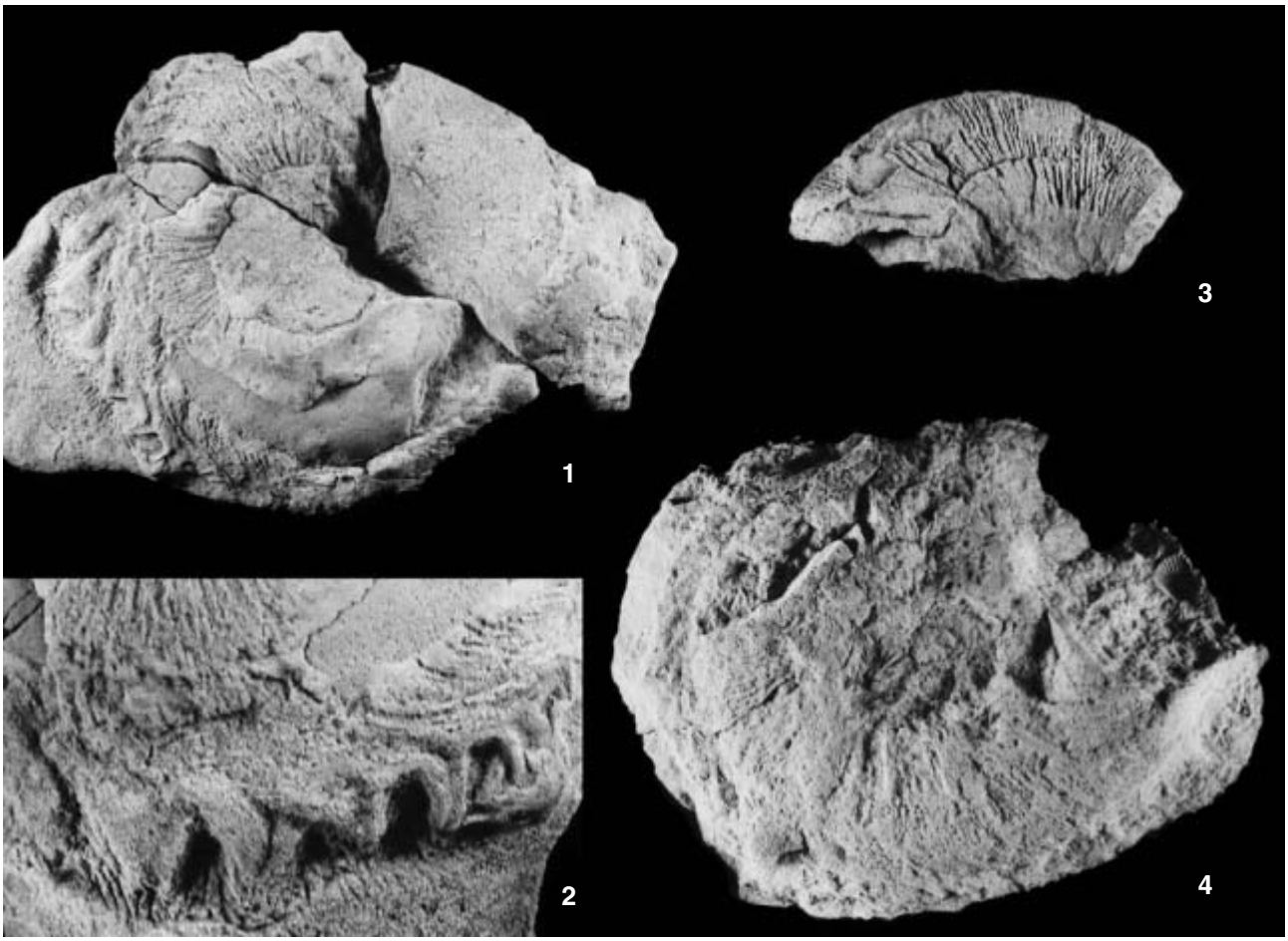

Fig. 1. *Gaspephorus gasconensis* (Northrop, 1939) from the Gascons Formation of southern Gaspé (Ludlow age). 1–2 – holotype, YPM 13310, basal view (× 1) and enlarged view of basal surface (× 2) to better show peripheral spines; 3 – hypotype, YPM 97373, basal whorl surface of fragmentary whorl (× 1); 4 – hypotype, YPM 13309, basal view of large shell (× 1).

rian to Middle Permian age (subsequently, a Late Ordovician representative was recognized by Rohr and Blodgett, 1985). We are not sure about the relationships between these families, and we presently do not have enough new data to re-evaluate this alliance. Knight et al. (1960) also mentioned the occurrence of a nacreous inner layer in some genera of each of these families. This fact places them within the order Vetigastropoda Salvini-Plawen and Haszprunar, 1987, belonging to the subclass Archaeogastropoda.

The genus *Pseudophorus* Meek, 1873, the type genus of the family Pseudophoridae, is based on *Trochita antiqua* Meek, 1872, from the Eifelian Columbus Limestone of Ohio. Knight (1941) studied the type material of this genus and noted that "the holotype and paratype are very poorly preserved steinkerns." In addition, he noted that almost nothing is known concerning the shell base. On the other hand, Knight et al. (1960) used the shape of the shell base as one of two diagnostic characters for the family Pseudophoridae. We are in no doubt that gastropod genera united to the Pseudophoridae form a natural gastropod group, but we also feel that its family level diagnosis needs to be re-evaluated. Similarities in shell characters also exist between the members of the families Pseudophoridae and Euomphalopteridae, suggesting a close relationship between these groups. The family Euomphalopteridae Koken, 1896, was placed within the Pleurotomarioidea by Knight et al. (1960). This placement was later criticized by Linsley et al. (1978) who suggested its placement within the Euomphaloidea. However, we see much closer affinities between the Pseudophoridae and Euomphalopteridae than between the Euomphalopteridae and Euomphaloidea. Members of the Euomphaloidea never develop a peripheral frill or spines, and their protoconch morphology places them into a separate but distinct gastropod group (Bandel and Frýda 1998). It seems to be probable that the family Euomphalopteridae can be regarded as a junior synonym of the family Pseudophoridae.

Genus *Gaspephorus* gen. nov.

Type species: *Euomphalopterus gasconensis* Northrop, 1939.

Etymology: Combination of the geographic name Gaspé and the gastropod genus name *Phorus*.

Diagnosis: Large pseudophorid gastropods with prominent, short, scooplike spines open abaperturally with slightly basal declination, shell base broadly rounded, moderately phaneromphalous.

Remarks: Northrop (1939, p. 212) mentioned that *G. gasconsensis* had much shorter spines than the Ludlow

Pleurotomaria elora of Whiteaves (1895, p. 74, Pl. 11, figs 5–6), which may also be a pseudophorid. *Gaspephorus* gen. nov. markedly differs from all other members of the family Pseudophoridae by its prominent, short scooplike peripheral spines that open abaperturally (see Figs 1.1, 1.2, 2). Other pseudophorid genera bearing prominent peripheral spines include *Hystricoceras* Jahn, 1894 and *Peelophorus* gen. nov. *Hystricoceras* Jahn from the Silurian of the Czech Republic differs from the new genus in having much longer and thicker spines. *Peelophorus* gen. nov. from the Upper Silurian of Gotland differs from *Gaspephorus* gen. nov. in being much smaller and higher spired, and also in having much longer, non-scooplike spines.

Species assigned: Only the type species is known.

Gaspephorus gasconensis (Northrop, 1939)
Figs 1, 2

1939 *Euomphalopterus gasconensis* Northrop, p. 212, pl. 22, figs 3, 4; ?variety p. 212, pl. 23, fig. 4.
1966 "*Euomphalopterus*" *gasconensis* Northrop – Boucot and Yochelson, p. A13-A14, pl. 1, figs 19, 21, 22; text fig. 2.

Diagnosis: Because of monotypy see that of genus.

Description: See description of Northrop (1939) and Boucot and Yochelson (1966). We have re-illustrated Northrop's types so as to better show the characters of the shell base and peripheral spines.

Remarks: Northrop's type specimens of *Gaspephorus gasconensis* are deposited in the Peabody Museum of Yale University (abbreviation YPM) in New Haven, Connecticut, USA. Additional material described and illustrated by Boucot and Yochelson (1966) but not re-illustrated here is deposited in the U.S. National Museum in Washington, D.C.

Occurrence: *Gaspephorus* gen. nov. is based on the Late Silurian (Ludlow-Přídolí) *Euomphalopterus gasconensis* Northrop, 1939, recognized originally from Gaspé and later from northern Maine (Boucot and Yochelson 1966). *G. gasconensis* is present in the Ludlow Gascons Formation of southern Gaspé. It also occurs in the Lower Conglomerate Member of the Hobbstown Formation of Somerset County, Maine, where it is associated with brachiopods and ostracodes of Ludlow-Přídolí age (Boucot and Heath 1969, p. 40) that may have been reworked from the underlying Ludlow-Přídolí beds of the Hardwood Mountain Formation. Both the Gaspé and northern Maine locality are within the eastern confines of the North American Province of the North Silurian Realm. However, the paucity of data on Silurian pseudophorids should be noted, i.e., there might be non-North American Province occurrences yet to be discovered. The impoverished Silurian gastropod fauna of the cool-climate, Southern Hemisphere Malvinokaffric Realm makes occurrence there highly unlikely, as is the case of many Silurian taxa (Boucot 1975).

Types: Holotype, YPM 13310, hypotypes YPM 13309 and YPM 97373.

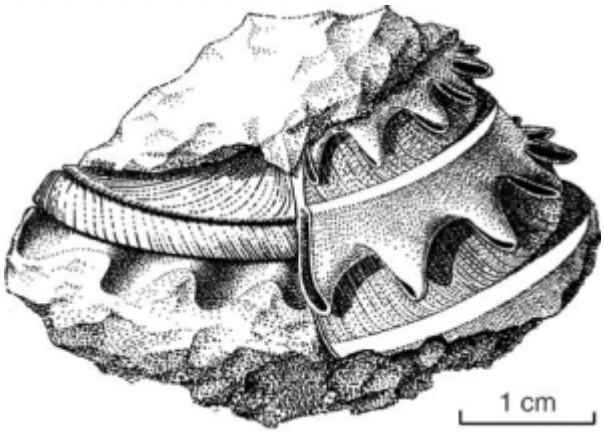

Fig. 2. Artist's rendering of *Gaspephorus gasconensis* (Northrop, 1939), shown with part of the shell removed to reveal the growth lines on the basal surface (from Boucot and Yochelson 1966, fig. 2).

Genus *Peelophorus* gen. nov.

Type species: *Trochus astraliiformis* Lindström, 1884 (*pars*).

Etymology: In honor of Prof. John S. Peel, Uppsala University, Uppsala, Sweden, Early Paleozoic gastropod worker.

Diagnosis: Medium-sized, moderately high-spired, trochiform pseudophorid gastropods with well developed peripheral keel bearing numerous, closely spaced, prominent, abaperturally open hollow spines that project slightly forward on mature whorls, but project downwards on earliest whorls; base anomphalous with numerous widely spaced growth lines.

Comparison: The relatively high-spired character of the shell, together with its numerous closely-spaced spines along the peripheral keel clearly distinguish this new genus from most other genera of the Pseudophoridae. Only two other spinose pseudophorid genera are known (both are of Silurian age), namely: *Hystricoceras* Jahn, 1894 and *Gaspephorus* gen. nov. *Hystricoceras* Jahn differs from *Peelophorus* gen. nov. in having very long, slightly arcuate spines. *Gaspephorus* gen. nov. differs from *Peelophorus* gen. nov. in being much larger, lower spired and in having shorter, scooplike spines.

Species assigned: Only the type species is known.

Peelophorus astraliiformis (Lindström, 1884)
Figs 3.1–3.5

1884 *Trochus astraliiformis* Lindström, p. 153, pl. 14, figs 54–55, 58 (*non* 56–57)

Diagnosis: Because of monotypy see that of genus.

Description: Lindström (1884, p. 153) provided the following description: "Shell conical, tapering to a narrow apex from a broad body whorl. Eight whorls. Their upper border lacerated, as it were, by thick, spinous projections, the base of which completely conceals the adjoining suture. These processes were formed by reflexed folds of the suc-

cessive lines of growth, as may best be seen on the umbilical surface of the shell. A little beneath this edge there is a longitudinal bulging out of the whorls. Between the lines of growth the convex surface of the shell is smooth or most finely, traversally striated. The aperture is nearly circular, apiculated in the superior corner, the lips thick and reflexed, the umbilicus is scarcely visible. The sculpture of the umbilical side consists in thick and coarse callous lines of growth at regular distance from each other."

Our examination of the designated lectotype indicates an additional comment on the character of the shell. We did not observe any trace of an umbilicus as noted by Lindström, no umbilicus is present in either of his two illustrated specimens (one being our designated lectotype, the other assigned here as "pseudophorid genus indet."). Our meaurements of the lectotype specimen are as follows: 13.0+ mm in height and 12.0+ mm in width.

Occurrence: Lindström (1884) reported the occurrence of this species at Klinteberg, illustrating two specimens. We designate the more complete specimen shown in Pl. 14, figs 54–55, and 58 as the lectotype. The incomplete specimen figured in Pl. 14, figs 56–57, representing only a final whorl fragment of a slightly larger shell, is herein assigned to a separate species, which we designate as pseudophorid genus indet. The rocks at Klinteberg are of late Wenlock age, Klinteberg Group.

Type: Lectotype, UU G1040.

Pseudophorid genus indet.
Figs 3.6–3.11

1884 *Trochus astraliiformis* Lindström, p. 153, pl. 14, figs 56–57 (*non* 54–55, 58)

Remarks: Lindström (1884) included a single final whorl fragment (his pl. 14, figs 56–57) in his new species *Trochus astraliiformis* (= *Peelophorus astraliiformis* in this paper). Our observation of both of his illustrated specimens of this species indicates that these two shells are probably not conspecific. This fragment differs from our designated lectotype (pl. 14, figs 54–55, 58 of Lindström) in having a much more convex whorl profile, less strongly inclined growth lines on outer whorl surface, and more numerous, stronger, and more closely spaced growth lines on basal whorl surface. Because this specimen is not generically distinct, we simply designate it here as "indeterminate pseudophorid."

Illustrated specimen: UU G1041.

Genus *Bergmadsenella* gen. nov.

Type species: *Pleurotomaria marklini* Lindström, 1884.

Etymology: In honor of Vivianne Berg-Madsen, Curator of Palaeontology, Uppsala University, Uppsala, Sweden, who was of great assistance in recognizing and then loaning Lindström's originals.

Diagnosis: Medium-sized, trochiform pseudophorid gastropod with well developed flattened, weakly undulose peripheral frill weakly inclined downwards; shell base distinctly phaneromphalous with deep umbilicus, bearing very strong, closely spaced, opisthocyrt cords.

Comparison: The subquadrate whorl profile with a nearly flat, overhanging frill and deep umbilicus clearly separate this new genus from all other genera previously placed in the Pseudophoridae. In terms of general shell form, the new genus resembles *Euomphalopterus* Roemer, 1876, the type genus of the family Euomphalopteridae Koken, 1896, but differs from the latter genus in its lack of a well-developed channel. As noted above, the close morphological resemblance between some members of the Pseudophoridae and the Euomphalopteridae indicates that the latter family is probably a junior synonym.

Species assigned: Only the type species is known.

Bergmadsenella marklini (Lindström, 1884)
Fig. 4

1884 *Pleurotomaria marklini* Lindström, p. 121, pl. 11, figs 24–26.

Diagnosis: Because of monotypy see that of genus.

Description: Lindström (1884, p. 121) provided the following original description: "Shell trochiform, nearly flat on umbilical side. Whorls six with even sides. Slit band placed a little above the median line of the whorls, thin and folded in irregular wavy curves. The sculpture consists in transverse, oblique lines, which on the umbilical side are coarse, callous ridges. Aperture obliquely ovate, umbilicus open, but narrow."

Our examination of the herein designated lectotype specimen indicates that the feature that Lindström describes as a "slit band" is not in reality a selenizone, but rather a flat, slightly declined subhorizontal, undulose frill (see Figs 4.1, 4.7). The aperture is subquadrate in outline. Ornamentation consists of nearly orthocline growth lines on outer whorl face and very strong, closely spaced opisthocyrt cords on base. Cords are approximately equal in width to intervening interspaces. Our measurements of the lectotype specimen are as follows: 13.2+ mm in height and 18.1+ in width.

Occurrence: Lindström (1884) reported that the occurrence of this species was based on three specimens (one of which was illustrated) found in the limestone at Klinteberg. This corresponds to the late Wenlock Klinteberg Group. We designate the illustrated specimen shown in Pl. 11, figs 24–26 as the lectotype.

Type: Lectotype, UU G1042.

Genus *Astralites* Whiteaves, 1892

Type species: *Astralites fimbriatus* Whiteaves, 1892.

Astralites gamblei sp. nov.
Fig. 5

Diagnosis: *Astralites* with horizontal lirae, lacking collabral swellings or spines.

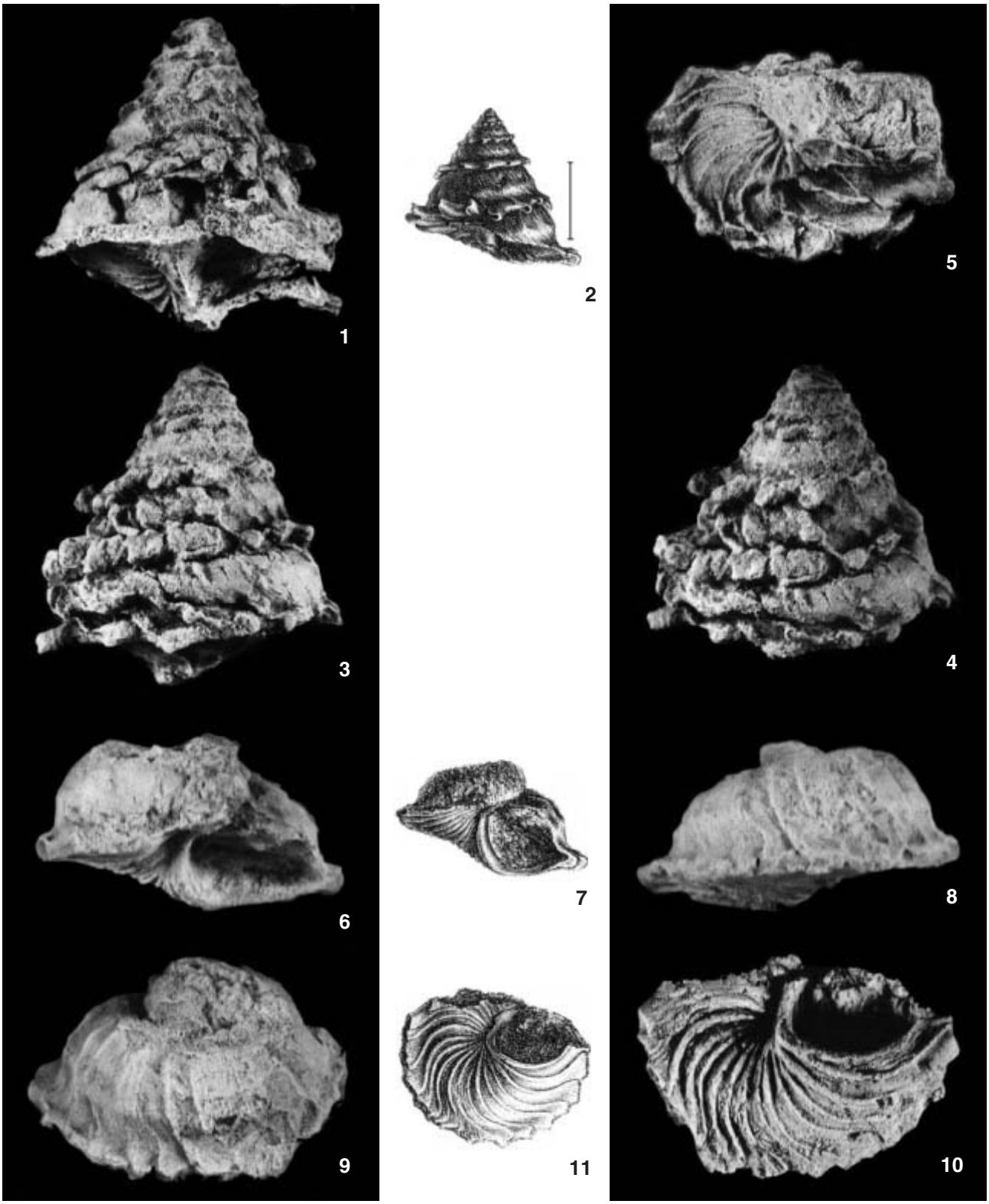

Fig. 3. *Peelophorus astraliiformis* (Lindström, 1884 *pars*) from Klinteberg beds, Gotland Island, Sweden. Lectotype, UU G1040. 1–2 – apertural views (× 4 and × 2; 2 from Lindström, pl. 14, fig. 54); 3 – abapertural, × 4; 4 – oblique abapertural, × 4; and 5 – basal view, × 4. Pseudophorid genus indet. (*Trochus astraliiformis* Lindström, 1884 *pars*) from Klinteberg beds, Gotland Island, Sweden. UU G1041. 6–7 – apertural views, (× 4 and × 2; 7 – from Lindström, 1884, pl. 14, fig. 57); 8–9 – abapertural and oblique abapertural views, × 4; and 10–11 – basal views, (× 4 and × 2; 11 from Lindström, 1884, pl. 14, fig. 56).

Description: Medium-sized trochiform shell, whorls numbering 4-5, juvenile portion of shell more high-spired than more adult portion; protoconch not preserved; upper whorl surface weakly convex, suture moderately incised; final and penultimate whorls with strongly digitate frill, each digitation strongly arched with convex apical surface and concave basal surface (Figs 5.5–5.6); interdigitations recessed; ornament on upper whorl surface composed of

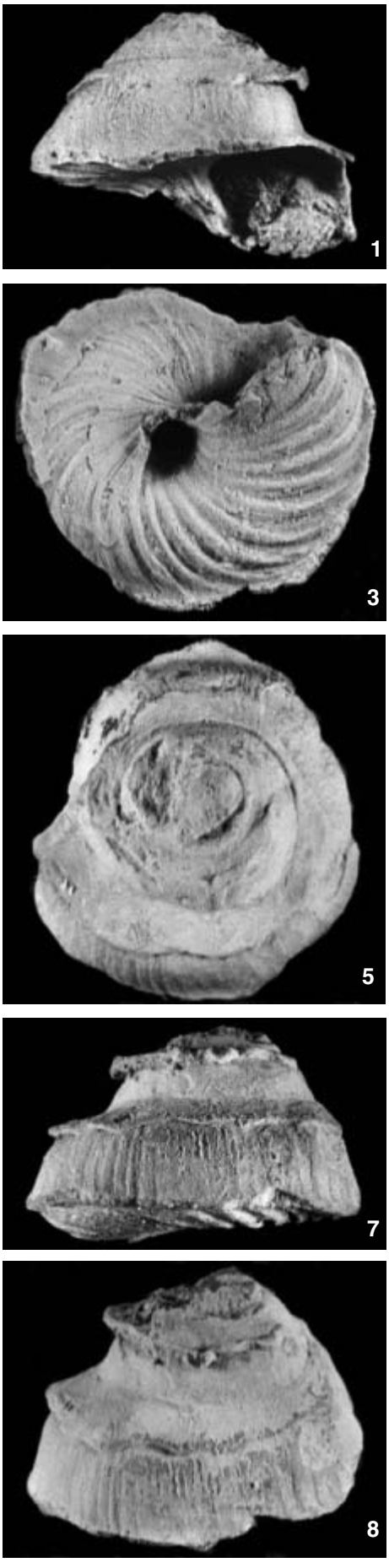

Fig. 4. *Bergmadsenella marklini* (Lindström, 1884) from Klinteberg beds, Gotland Island, Sweden. Lectotype, UU G1042. 1–2 – apertural views (× 3 and × 2; 2 from Lindström, 1884, pl. 11, fig. 24); 3–4 – basal views, (× 3 and × 2; 4 from Lindström, 1884, pl. 11, fig. 25); 5–6 – apical views (× 3 and × 2; 6 from Lindström, pl. 11, fig. 26); 7 – abapertural, × 3; and 8 – oblique abapertural, × 3.

numerous, horizontal spiral lirae; base cryptomphalous, convex on outer half and concave on inner half, the boundary between these two areas occupied by a strong spiral angulation; columellar lip prosocline, with a single, strong, rounded tooth which continues internally as a thickened, rounded spiral ridge; parietal lip or inductura absent; outer lip not preserved; ornamentation on base composed of strongly arched threads directed obliquely backwards, primarily restricted to the lowermost part of the basal whorl, but some continuing abaxially onto the basal surface of the frill. The most complete specimen (holotype) has the following measurements: height 11.5 mm; width approximately 16.0 mm.

Comparison: *Astralites gamblei* sp. nov. differs from the type species, *Astralites fimbriatus* Whiteaves, 1892, from Givetian age strata of the Winnipegosis Formation of Manitoba in lacking collabral swellings and in having revolving spiral lirae that are horizontal (parallel to sutures), not weakly declined forward as in *A. fimbriatus*. The new species also differs from the European representatives of the genus (see discussion and illustrations in Heidelberger 2001) *Astralites sublimbatus* (d'Orbigny, 1850) and *Astralites muelleri* Heidelberger, 2001 from the Givetian of Germany. *A. sublimbatus* (d'Orbigny) most closely approaches the new species from the Cheeneetnuk Limestone, but is distinguished from the Alaskan species in having stronger spiral lirae. *A. muelleri* Heidelberger differs in having strong, well developed spinose projections along the frill. A species similar to *A. gamblei* is also present in coeval strata of the Wadleigh Limestone of southeast Alaska (see Blodgett et al. 2003), however, additional material is necessary to determine whether they belong to the same or to different species.

Etymology: The species is named in honour of Bruce M. Gamble, U.S. Geological Survey, Anchorage, Alaska.

Occurrence: *Astralites gamblei* sp. nov. comes from the Cheeneetnuk Limestone (Blodgett and Gilbert 1983), a 457 m thick carbonate unit exposed in the McGrath A-4 and A-5 quadrangles of west-central Alaska. The upper third of this formation bears a diverse, silicified fauna and flora of early Eifelian age (Blodgett 1983, Blodgett and Gilbert 1983) that occurs in richly fossiliferous

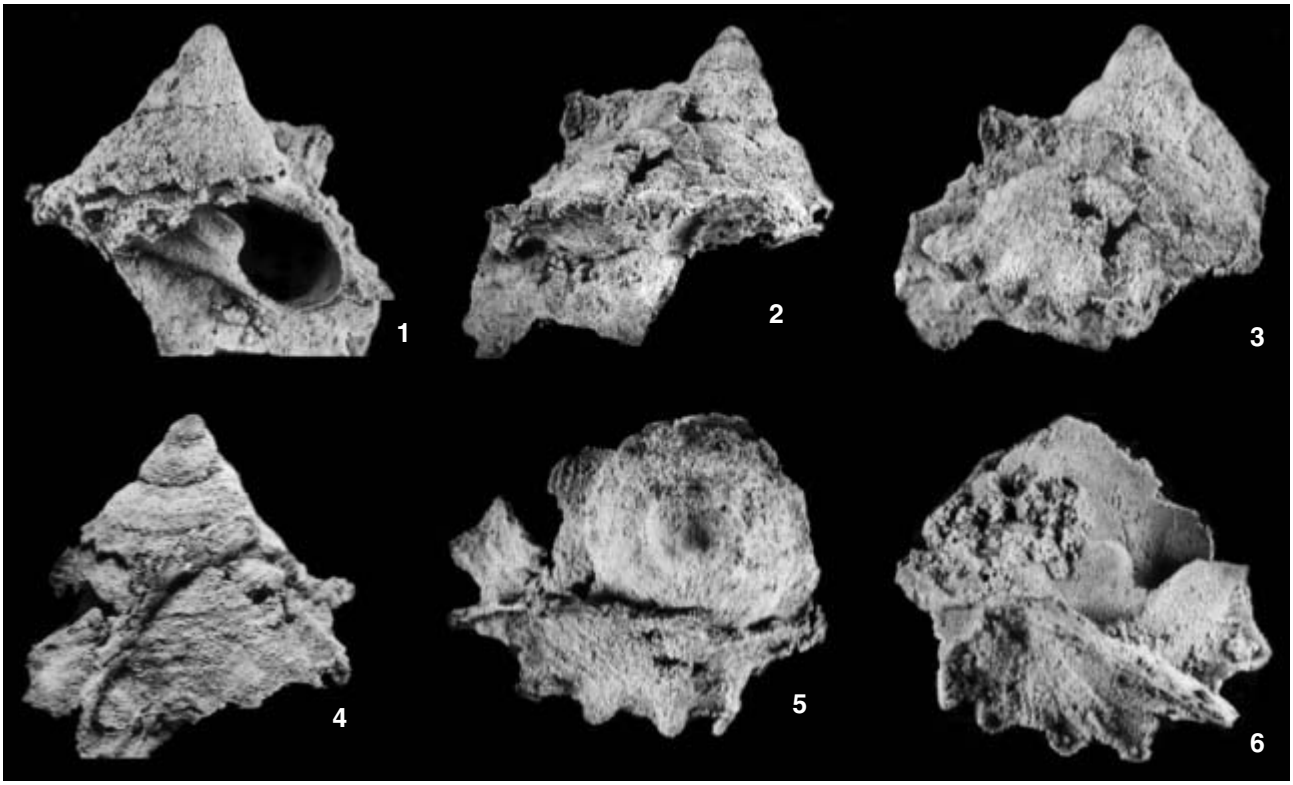

Fig. 5. *Astralites gamblei* sp. nov. from the early Eifelian age strata of the upper part of the Cheeneetnuk Limestone of the McGrath A-5 quadrangle, west-central Alaska. All views × 3. 1–6. Holotype, UAM 2658, apertural, abapertural, oblique abapertural, oblique side, apical and basal views. Specimen contains a large, markedly obvious veinlet of siliceous material which obliquely transects the shell.

lenses separated by much thicker, poorly fossiliferous intervals. Gastropods from the Cheeneetnuk Limestone have already been described in Blodgett and Rohr (1989), Blodgett and Johnson (1992), Blodgett (1993), and Blodgett and Cook (2002). These strata belong to the Nixon Fork subterrane of the Farewell terrane (Blodgett and Gilbert 1983). The Farewell terrane was established by Decker et al. (1994) to unite three previously defined tectonostratigraphic terranes (Nixon Fork, Dillinger, and Mystic) situated in southwestern and west-central Alaska that subsequently were recognized to be genetically linked with one another. Recent studies of the Devonian brachiopod faunas of this terrane indicate that the Farewell terrane probably originated as a continental margin sequence that was rifted from the Siberian paleocontinent (Blodgett and Brease 1997, Blodgett 1998, Blodgett and Boucot 1999, Garcia-Alcalde and Blodgett 2001, Blodgett et al. 2002, Boucot and Blodgett 2001, Frýda and Blodgett 2003 and in print).

The newly described species occurs at locality 79RB8 (=USGS locality 10061-SD), an approximately 3 m thick, richly fossiliferous, silicified shell horizon in the upper part of the type section of the Cheeneetnuk Limestone. The top of this horizon lies 101 m below the top of the Cheeneetuk Limestone. Conodonts associated with this bed suggest a *costatus* Zone (early Eifelian) age (Norman Savage, pers. commun., 1979). Further detailed description of the locality and an index map showing its occurrence can be found in Rigby and Blodgett (1983, fig. 1) and Blodgett and Rohr (1989, fig. 2).

The genus *Astralites* is restricted to the Middle Devonian and is known from the Old World Realm. It is known from two Eifelian localities in Alaska: 1. the new Cheeneetnuk Limestone species described here from the Farewell terrane of west-central Alaska, and 2. a single collection (field number 68AEs596; = USGS locality M1299-SD) made by J. Evans of the U.S. Geological Survey in 1968 from the Wadleigh Limestone of the Alexander terrane of southeastern Alaska. The southeastern Alaskan occurrence may well represent the same species, but further preparation of the silicified material that contains it is necessary. The genus is also known from the Givetian, including the occurrence of the type species, *Astralites fimbriatus* Whiteaves, 1892 from the Winnipegosis Formation of Manitoba and several occurrences in the Givetian of Germany, represented by *Astralites sublimbatus* (D'Orbigny, 1850) and *Astralites muelleri* Heidelberger, 2001.

The type specimens of *Astralites gamblei* sp. nov. are deposited in the University of Alaska Museum (abbreviation UAM) in Fairbanks, Alaska, USA.

Material: Seven silicified specimens of variable preservation from locality 79RB8 (= USGS locality 10061-SD).

Type: Holotype, UAM 2658.

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