EARLY CAMBRIAN BRACHIOPODS FROM NORTH GREENLAND

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ABSTRACT. A silicified late Early Cambrian (early Toyonian) brachiopod assemblage is described from the Paralleldal Formation of Peary Land, central North Greenland. The fauna comprises *Acareorthis profunda* sp. nov., *Pelmanella borealis* gen. et sp. nov., *Kutorgina cingulata*, and *Agyrekia* aff. *obtusa*. The assemblage is comparable to faunas described from the Lower Cambrian (Botomian) of south Tien-Shan, Kirgizia, and the lower Middle Cambrian (Ordian) of New South Wales, Australia. Primitive articulatory structures are described for the first time in *Kutorgina cingulata*, suggesting a close affinity to the Nisusiidae and supporting the assignment of the latter family to the Kutorginida. *Acareorthis* is reported for the first time outside Australia; it is here referred to the Chileida in view of its strophic shell lacking all traces of articulatory structures. The new obolellid family Pelmanellidae is erected, comprising *Pelmanella* and the Australian genus *Bynguanoia*.

OUR knowledge of late Early to early Mid Cambrian calcareous-shelled brachiopods is based mainly on a few silicified faunas from New South Wales, Australia (Roberts and Jell 1990), south Tien-Shan, Kirgizia (Popov and Tikhonov 1990), and Israel and Jordan (Cooper 1976). New collections of Early Cambrian silicified calcareous brachiopods described here from North Greenland contain a total of four taxa. *Kutorgina cingulata* (Billings, 1861) is the most abundant species and represents about 72 per cent. of the total number of individuals, whereas *Agyrekia* aff. *obtusa* Koneva, 1979 (5 per cent.), *Acareorthis profunda* sp. nov. (10 per cent.) and *Pelmanella borealis* gen. et sp. nov. (13 per cent.) are relatively rare.

Finer details of morphology, such as micro-ornamentation and mantle canals, are not preserved in the available specimens, possibly due to the relatively coarse silicification of the shells. However, other characters including the main internal morphology and articulation, which otherwise remain poorly known in the majority of Cambrian brachiopod taxa, are well preserved. In particular, the primitive articulation can be studied for the first time in the type species of *Kutorgina*, *K. cingulata*. Previously, kutorginid articulation was known only from *Kutorgina catenata* from the Botomian of Kirgizia (Popov and Tikhonov 1990). An unusual pattern of articulation is described in the new obolellid *Pelmanella*.

GEOLOGICAL SETTING

All Greenland material described herein was collected in 1980 from the lower part of the Paralleldal Formation (Higgins *et al.* 1991; Ineson and Peel in press) by J. S. Peel and P. D. Lane during the North Greenland Project (1978–80; 1984–85) organized by the Geological Survey of Greenland (Grønlands Geologiske Undersøgelse). The collection (GGU 274907) was made on the north side of Paralleldal about 12 km north-east of the head of Jørgen Brønlund Fjord, southern Peary Land, central North Greenland (Text-fig. 1). At this locality, a diverse fauna includes archaeocyathids indicative of a late Early Cambrian (mid–late Toyonian) age (Debrenne and Peel 1986), olenellid trilobites, *Salterella*, the stenothecid *Cambridium*, helcionelloid molluscs (*Yochelcionella*, *Latouchella*) and the brachiopods described below. Originally calcareous organisms are generally coarsely silicified.

The Paralleldal Formation consists of about 140 m of cliff-forming dolomites which range in lithology from laminated, nodular dolomites (lower third) to oolitic and bioclastic dolomites; thick

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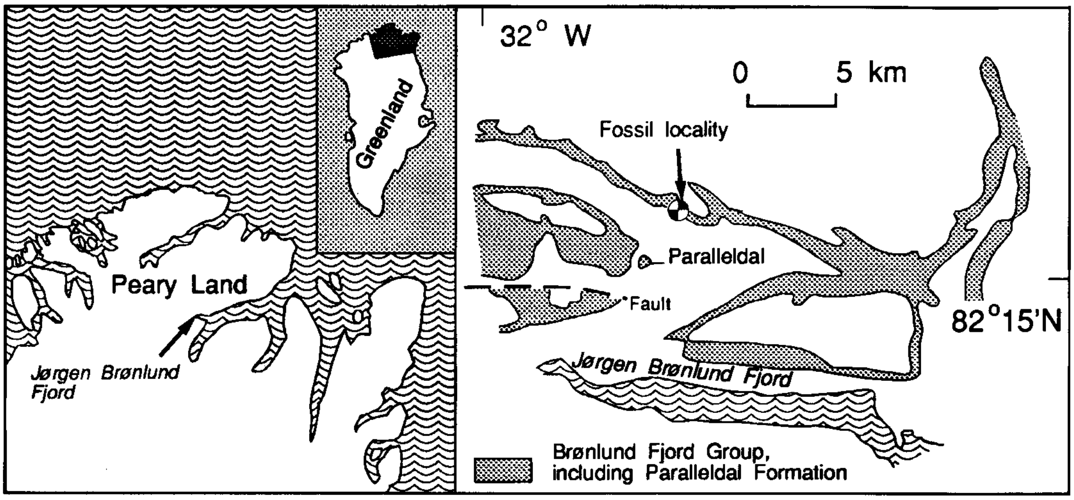


TEXT-FIG. 1. Position of the collection locality within the Paralleldal Formation (Brønlund Fjord Group), north of Jørgen Brønlund Fjord (JBF), Peary Land, North Greenland.

dolomite breccias are conspicuous in the middle and upper parts. The formation represents carbonate platform margin deposition within the southern shelf sequence of the Franklinian Basin succession of North Greenland and the Canadian Arctic Islands (Peel and Sønderholm 1991; Ineson and Peel in press). In the area north of Jørgen Brønlund Fjord, the Paralleldal Formation is the uppermost formation of the Brønlund Fjord Group; it is overlain unconformably by late early Ordovician dolomites of the Wandel Valley Formation (Ineson and Peel in press).

GENERAL AFFINITIES OF THE FAUNA

The described assemblage from the Paralleldal Formation includes genera of the Chileida, Obolellida (suborder Naukatidina) and Kutorginida, all of which became extinct at the end of the mid Cambrian. Surprisingly, no early orthides (Protorthidae or Eoorthidae) are present, although orthides are otherwise abundant in the late Early Cambrian brachiopod fauna of Israel (Cooper 1976) and the early Mid Cambrian (Ordian) fauna of New South Wales (Roberts and Jell 1990). *Nisusia* is also absent, but undescribed species of this genus were recovered in the underlying Sæterdal Formation, of late Botomian age.

The Greenland assemblage is most similar to that from New South Wales described by Roberts and Jell (1990). Of the forms documented from Australia, *Trematosia* sp. cf. *T. undulata* Cooper is here referred to *Kutorgina*, while *Kutorgina*? sp. (Roberts and Jell 1990, p. 285) is probably comparable to *Agyrekia* aff. *obtusa* Koneva in the Greenland assemblage. The chileide *Acareorthis* is known only from New South Wales and Greenland.

The presumably Botomian assemblage from Kirgizia (Popov and Tikhonov 1990) is also comparable; the cosmopolitian *Kutorgina* and *Nisusia* are the most abundant genera in Kirgizia, while the chileides (*Chile*) and naukatides (*Naukat*, *Oina*) are represented only by endemic genera. Pelman (1977) described a late Early Cambrian (Botomian and Toyonian) assemblage from Siberia, characterized mainly by *Kutorgina* and *Nisusia*, but lacking naukatides and protorthoids. The obolellides (*Siberia*, *Alisina* and *Trematobolus*) are also an important part of the Siberian fauna, but chileides (*Kotujella* and *Matutela*) are rare, appearing in the upper Toyonian and occurring also in the Amgian (Pelman 1977).

SYSTEMATIC PALAEONTOLOGY

Abbreviations in figures and text are as follows: Cl, length of cardinal muscle field; Cw and Clw, width of cardinal muscle fields; Il, length of pseudointerarea; Iw, width of pseudointerarea and width along posterior commissure; L, sagittal valve length; Lk, length of valve at commissure plane; max, maximum; min, minimum; N, number of specimens; Pw, width of dorsal median groove; S, standard deviation; Sl, length of median ridge; T, height of valve; VPl, length of ventral muscle platform; VPw, width of ventral muscle platform; W, maximum width; X, mean. Dimensions are in millimetres.

Figured and cited specimens from Greenland (prefixed by MGUH) are housed in the Geological Museum, University of Copenhagen. Other illustrated specimens are deposited in the Swedish Museum of Natural History (RM Br) and Central Scientific Research Geologic Exploration Museum, St Petersburg (CNIGR).

Order CHILEIDA Popov and Tikhonov, 1990
Superfamily MATUTELLOIDEA Andreeva, 1962
Family CHILEIDAE Popov and Tikhonov, 1990

Genus ACAREORTHIS Roberts *in* Roberts and Jell, 1990

Type species. Acareorthis jelli Roberts (*in* Roberts and Jell), 1990; from the early Mid Cambrian (Ordian) First Discovery Limestone, New South Wales, Australia.

Diagnosis. See Roberts and Jell 1990, p. 268.

Remarks. Roberts (*in* Roberts and Jell 1990) regarded *Acareorthis* as a primitive orthide because it has a strophic, bisulcate shell, with costellate radial ornamentation; it was referred provisionally to the family Nisusiidae. However, *Acareorthis* completely lacks articulatory structures with the exception of a weak transverse ridge along the straight dorsal posterior margin. Moreover, the perforation anterior to the ventral umbo suggests close affinity to the early Cambrian *Chile* (Popov and Tikhonov 1990). *Acareorthis* is referred here to the family Chileidae. It differs from *Chile* in having costate ornamentation covering the entire shell, a high ventral interarea with narrow, triangular delthyrium covered completely by a ridge-like pseudodeltidium, and in lacking a colleplax.

Acareorthis is somewhat similar to *Matutella* (Cooper 1951; Andreeva 1962) in having a pseudodeltidium, radial ornamentation covering all the shell, and a ventral umbonal perforation. It differs from the latter genus, however, in possessing a planoconvex shell in which the high ventral interarea is divided medially by a ridge-like pseudodeltidium, a rectimarginate anterior commissure, and in the absence of colleplax which is present in *Matutella*, although in a rudimentary form (Andreeva 1962, pl. 5, fig. 1*e*).

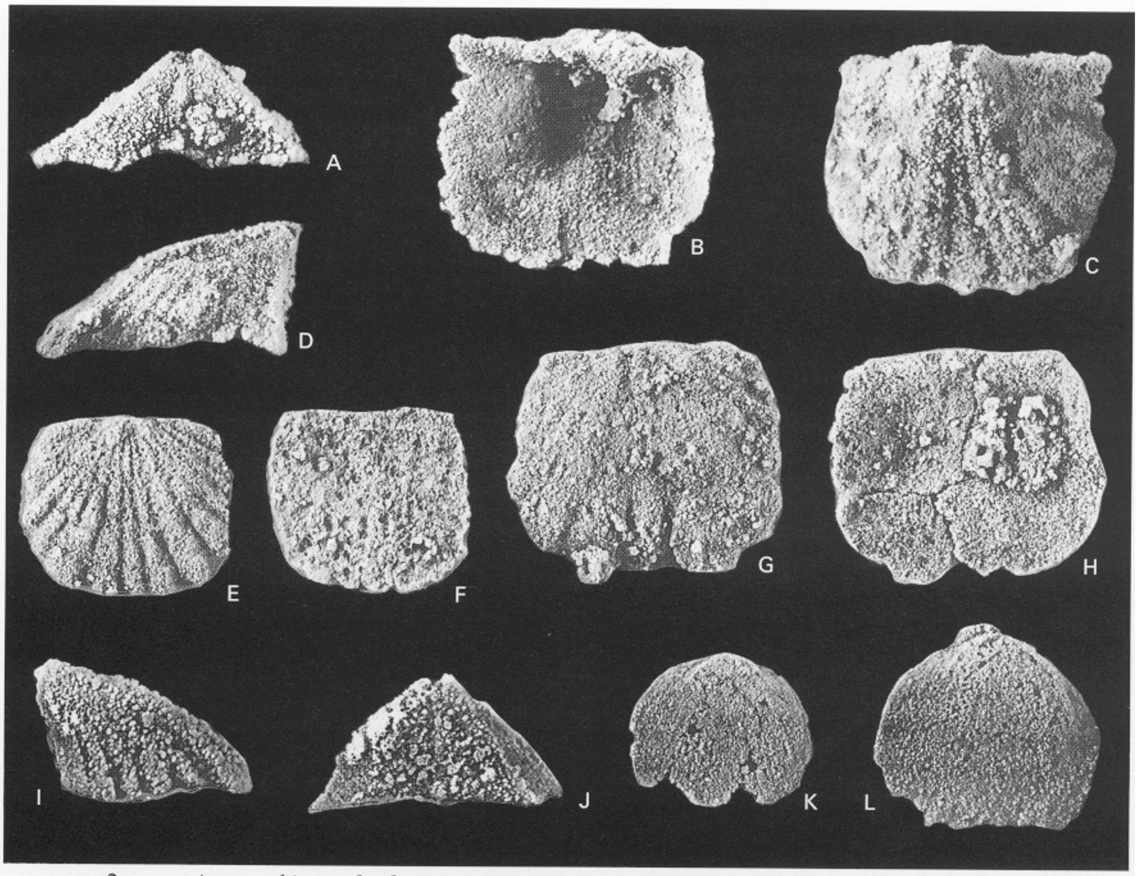
Acareorthis profunda sp. nov.

Text-figures 2A–J, 3

Derivation of name. From the Latin *profundus*, deep.

Holotype. Ventral valve, MGUH23740 (L 7·68, Lk 6·4, W 7·36, T 3·52) from the Paralleldal Formation (GGU collection 274907), Peary Land, central North Greenland.

Paratypes. Figured: ventral valves, MGUH23741 (L 6·24, Lk 6·08, W 6·4, T 3·84); dorsal valves, MGUH23745 (L 5·84, W 6·8, Iw 5·36); MGUH23746 (L 4·56, W 5·04, Iw 4·0). Unfigured; MGUH23742 (L 6·72, Lk 6·08, W 6·88, T 3·04); MGUH23744 (L 4·56, W 4·88, Iw 3·36). Total of one complete shell, nine ventral, and three dorsal valves. All specimens from the same collection and locality as the holotype.



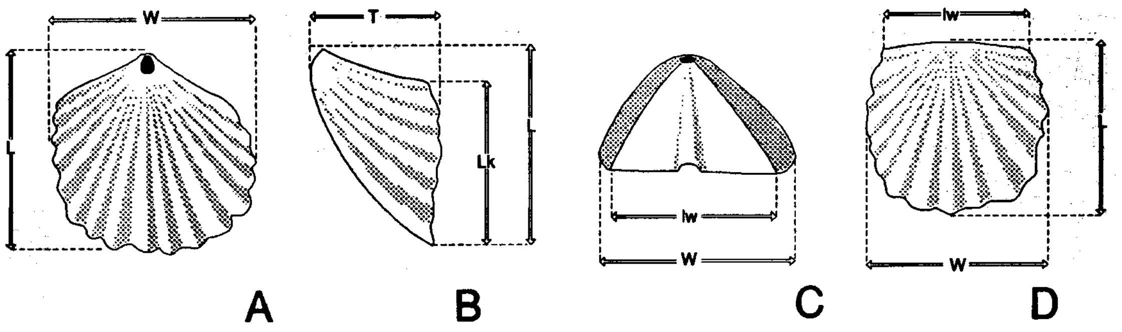
TEXT-FIG. 2. A–J, *Acareorthis profunda* sp. nov. A–D, holotype, MGUH23740; ventral valve in posterior, interior, exterior and lateral view respectively; ×5. E–F, MGUH23746; dorsal valve exterior, interior; ×5·2. G–H, MGUH23745; dorsal valve exterior, interior; ×5·2; I–J, MGUH23741; ventral valve lateral view, posterior view; ×7. K–L, *Pelmanella borealis* gen. et sp. nov.; dorsal valve exterior. K, MGUH23750; L, MGUH23751; both ×5·6. All specimens from the Paralleldal Formation (late Early Cambrian), Peary Land, central North Greenland (GGU collection 274907).

TABLE 1. *Acareorthis profunda* sp. nov.; average dimensions of the ventral valves.

	L	Lk	W	T	L/W	Lk/W	T/L
N	5	5	5	5	5	5	5
X	6·4	5·7	7·0	3·6	114%	81%	88%
S	0·84	1·03	0·33	0·65	12·6	6·6	6·3
Min	5·6	4·5	5·8	3·4	95%	67%	46%
Max	7·7	6·4	7·4	4·3	129%	100%	75%

Diagnosis. Large for genus, ventral valve sub-pyramidal with maximum height at umbo; narrow sulcus originating near beak; umbonal perforation small, rounded; dorsal valve almost flat, lacking sulcus; radial ornament of 14–16 rounded costae.

Description. Shell planoconvex; transversely rectangular in outline; posterior margin straight, occupying about 82 per cent. of maximum shell width. Ventral valve strongly convex, with shallow, but well-defined sulcus



TEXT-FIG. 3. *Acareorthis profunda* sp. nov.; schematic drawings showing location of measurements. A, ventral valve exterior; B, ventral valve lateral view; C, ventral valve posterior; D, dorsal valve exterior.

originating near beak; sub-pyramidal, on average 114 per cent. as long as wide, and 55 per cent. as high as long, with maximum height at umbonal area; ventral beak pointed, with sub-circular perforation about 0·15–0·20 mm across, anterior to umbo; ventral interarea high, triangular, planar, apsacline, divided medianlly by narrow, ridge-like pseudodeltidium. Dorsal valve flat, plate-like, lacking sulcus. Shell coarsely costate with a maximum of 14–16 low, rounded costae.

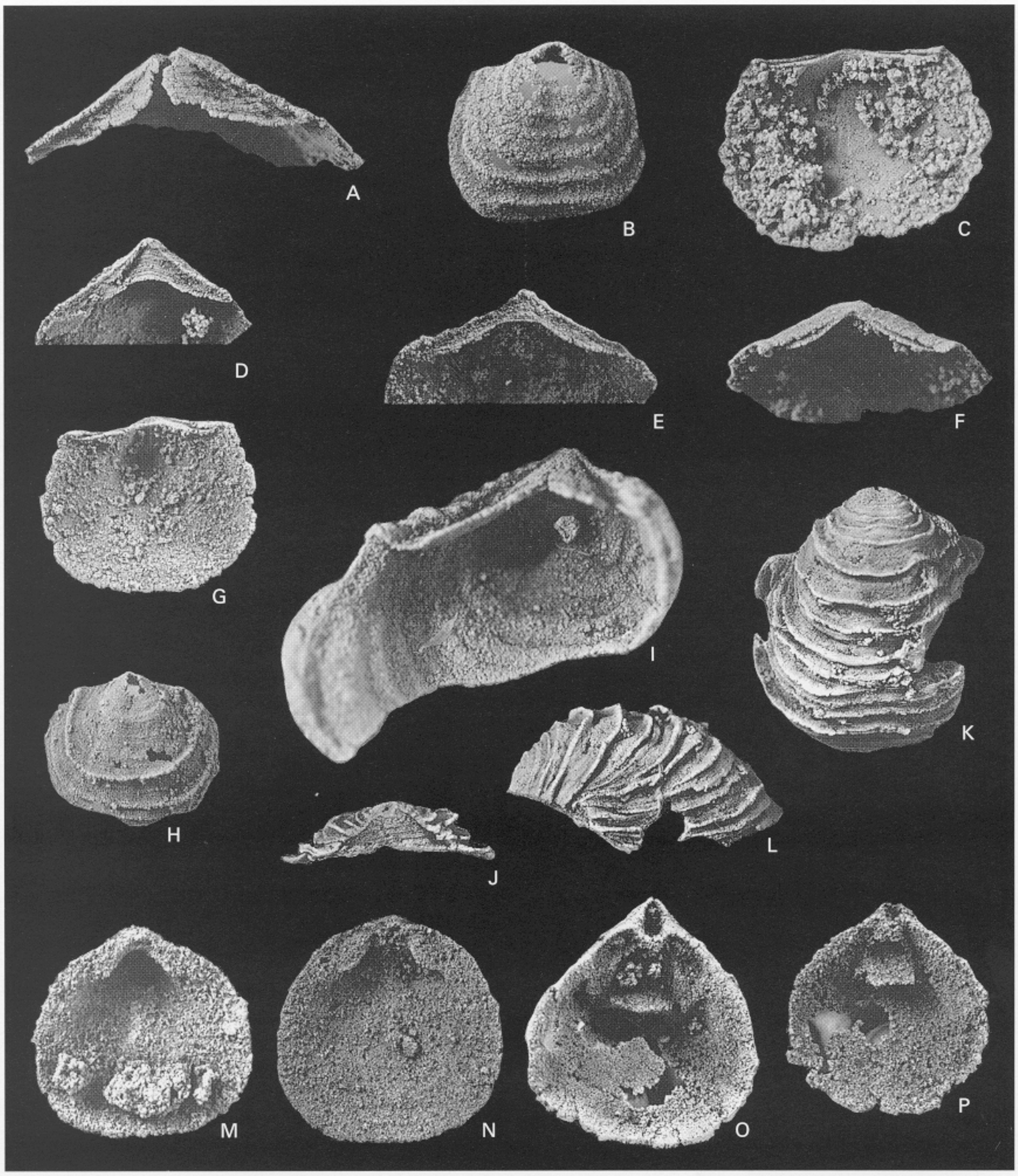
Ventral interior with thickened umbonal area. Dorsal interior with thickened ridge along posterior margin. Muscle scars and mantle canals of both valves not known.

Remarks. A. profunda is comparable to *A. jelli* Roberts (*in* Roberts and Jell 1990) in having a planoconvex shell with a sub-pyramidal ventral valve. In both species the high, apsacline interarea is divided medially by a narrow, convex pseudodeltidium. However, it can be distinguished from the type species by its much larger size, the well-defined radial ornamentation with fewer costae, and its well-defined ventral sulcus. In addition, the ventral umbonal perforation is relatively small and a dorsal sulcus is absent. Roberts (*in* Roberts and Jell 1990, p. 270) noted the presence of a low dorsal interarea in *A. jelli* but our observations on topotypes of this species (kindly supplied by J. Roberts), as well as comparisons with our specimens from Greenland, suggest that the dorsal valve of *Acareorthis* is characterized by hemipheral growth and seemingly lacks an interarea.

Order NAUKATIDA Popov and Tikhonov, 1990

Diagnosis. Shell biconvex, smooth or with radial ornament; ventral interarea with concave pseudodeltidium, which may be perforated by an elongate, sub-oval foramen; ventral visceral platform high, may be free peripherally; articulation with pair of closely spaced, ventral denticles in some genera, located on arcuate plate (anterise), and dorsal sockets on lateral sides of notothyrial platform; dorsal adductor scars arranged radially.

Remarks. Naukatida was established by Popov and Tikhonov (1990) as a separate order, based mainly on the presence of a highly raised ventral muscle platform, and the unusual articulation present in *Oina* and *Naukat*. The articulation of both these genera consists of an anterise (that is, an arcuate plate anterior to the delthyrial margins) bearing paired denticles and a pair of sockets on the lateral sides of a highly raised notothyrial platform (Text-fig. 5). *Pelmanella* gen. nov. and *Bynguanoia* Roberts (*in* Roberts and Jell 1990) also exhibit these distinctive naukatid features, but differ in details of articulation and in the arrangement of muscle scars; they are referred here to the new family Pelmanellidae, described below.



TEXT-FIG. 4. A–H, *Kutorgina cingulata* (Billings, 1861). A, D–E, ventral valve pseudointerarea; A, MGUH23763; D, MGUH23753; E, MGUH23762; ×5. B, MGUH23760; juvenile ventral valve; ×5; C, F, MGUH23759; dorsal valve interior, posterior view showing dorsal hinge ridges and furrows; ×4; G, MGUH23754, dorsal valve interior; ×4. H, MGUH23761; juvenile ventral valve; ×5. I–L, *Kutorgina catenata* Koneva, 1979; I, PMKg3; ventral valve interior showing ventral hinge grooves on the lateral sides of pseudodeltidium; ×10. J, CNIGR 23/12589; ventral valve posterior view; ×3. K–L, CNIGR 22/12589; ventral valve exterior, lateral view; ×3. M–P, *Pelmanella borealis* gen. et sp. nov.; M–N, dorsal valve interior; M, MGUH23749; N, MGUH23747; both ×4. O–P, ventral valve interior; O, MGUH23743, holotype; P, MGUH23748; both ×4.

Superfamily NAUKATOIDEA Popov and Tikhonov, 1990
Family PELMANELLIDAE fam. nov.

Diagnosis. Shell with rudimentary dorsal interarea, lacking notothyrial platform; ventral interior lacking denticles on anterise; posterior adductor scars on separate paired cardinal muscle platforms in both valves.

Genera assigned. Pelmanella, Lower Cambrian (Toyonian), North Greenland; *Bynguanoia,* lower Middle Cambrian (Ordian), New South Wales, Australia.

Remarks. Pelmanella and *Bynguanoia* both possess an anterise and high ventral muscle platforms and can be referred to the naukatides. The genera differ, however, from *Oina* and *Naukat* (and the family Naukatidae) in having a rudimentary, undivided dorsal interarea, paired cardinal muscle platforms in both valves, and in lacking paired denticles on the anterise. It is likely that the anterise in *Pelmanella* and *Bynguanoia* may have served as an articulatory structure in fixing the inner margins of the raised dorsal cardinal platform. Dorsal muscle scars posterior to the rotational axis that may have served as diductors are unknown. Conceivably, the shell opening mechanism was hydraulic, and may have been activated by outside lateral muscles (on the outer parts of the ventral cardinal muscle platform; Text-fig. 5) attached to the anterior body wall. In contrast, members of the Naukatidae have paired denticles on the anterise and possessing a notothyrial platform with rudimentary, paired sockets, and may have had oblique muscles serving as diductors (Popov and Tikhonov 1990).

Bojarinovia Aksarina (*in* Aksarina and Pelman, 1978) and *Swantonia* Walcott (see Rowell 1977) may also belong within the Pelmanellidae, but their internal morphologies are unknown.

Genus PELMANELLA gen. nov.

Derivation of name. After the late Dr Ju. L. Pelman, a pioneer in the study of Early Cambrian brachiopods who died prematurely in a field accident.

Type species. Pelmanella borealis sp. nov.

Diagnosis. Shell slightly ventribiconvex, elongate, sub-oval to sub-circular in outline, smooth; anterior commissure rectimarginate; ventral valve with rudimentary apsacline interarea; delthyrium open, narrow, triangular, with distal margins joined by anterise; dorsal valve gently convex with rudimentary interarea; ventral interior with paired cardinal muscle platforms; ventral muscle platform separated from cardinal platforms by deep, oblique grooves; dorsal interior with paired cardinal muscle platforms, bearing medially located anterior adductor scars, divided by low median ridge.

Remarks. This genus resembles *Oina* (Popov and Tikhonov 1990) in having a smooth, slightly ventribiconvex, sub-circular shell. *Pelmanella* is distinguished from the latter in having an open delthyrium, paired cardinal muscle platforms in both valves, and a weak dorsal median ridge. In addition, a notothyrial platform and denticles are lacking. In the internal morphology of both valves *Pelmanella* is closely similar to *Bynguanoia* Roberts (*in* Roberts and Jell, 1990), but it differs

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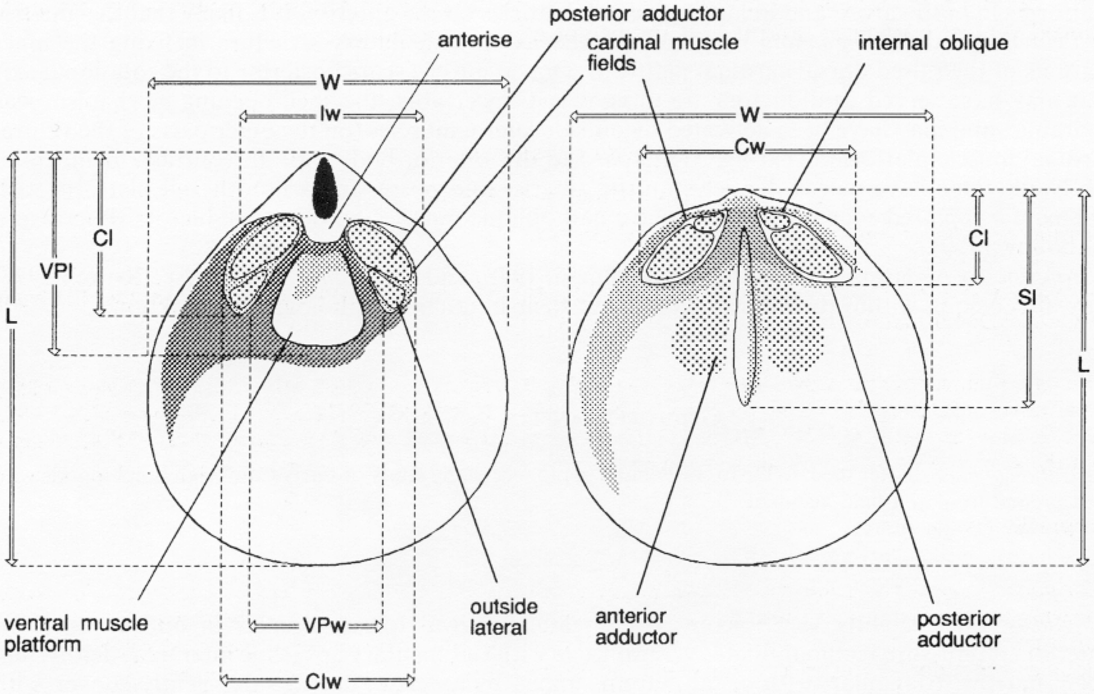
A–H, M–P from the Paralleldal Formation (late Early Cambrian), Peary Land, central North Greenland (GGU collection 274907); I–L from the Lower Cambrian (Botomian), south Tien-Shan, Alaj Range, Chachme River (locality 5069-8 of Popov and Tikhonov 1990).

TABLE 2. *Pelmanella borealis* gen. et sp. nov.; average dimensions of dorsal valves.

	L	W	Cl	Cw	Sl	L/W	Sl/L
N	8	8	4	4	5	8	5
X	4·9	5·2	1·6	3·3	3·2	94%	51%
S	1·71	1·61	0·56	1·02	1·38	5·4	13·5
Min	2·7	3·0	0·5	2·3	1·76	87%	41%
Max	8·0	8·0	2·2	4·6	4·46	100%	71%



TEXT-FIG. 5. *Pelmanella borealis* gen. et sp. nov.; schematic drawings showing location of measurements and position of muscle scars. A, ventral valve interior; B, dorsal valve interior.

TABLE 3. *Kutorgina cingulata* (Billings, 1861); average dimensions of ventral valves.

	L	W	T	Iw	Pw	L/W	T/L	Iw/W	Pw/Iw
N	20	20	20	19	17	20	20	19	17
X	8·68	9·82	2·89	7·68	5·74	88%	33%	80%	76%
S	1·847	1·981	0·871	1·632	1·247	4·9	8·5	6·8	8·2
Min	4·5	4·6	1·5	4·2	2·9	76%	24%	67%	62%
Max	12·4	13·0	4·8	11·5	8·5	97%	65%	90%	93%

TABLE 4. *Kutorgina cingulata* (Billings, 1861); average dimensions of dorsal valves.

	L	W	Iw	Pw	L/W	Iw/W	Nw/Iw
N	7	7	7	6	7	7	6
X	7·02	9·34	6·94	5·48	75%	75%	79%
S	1·628	1·760	1·470	1048	7·2	12·7	4·6
Min	4·5	6·5	4·6	3·8	64%	59%	74%
Max	8·9	11·4	8·8	6·6	86%	95%	86%

from the latter in having a smooth shell with a rectimarginate anterior commissure, strongly reduced ventral propareas, and in the absence of a pseudodeltidium.

Pelmanella borealis sp. nov.

Text-figures 2K–L, 4M–P, 5

Derivation of name. From the Latin *borealis*, northern.

Holotype. MGUH23743, ventral valve (L 7·27, W 7·12, Cl 2·56, Cw 3·36, MPl 2·88, MPw 2·48, Iw 3·04) from the Paralleldal Formation (GGU collection 274907), Peary Land, central North Greenland.

Paratypes. Figured: ventral valve, MGUH23748 (L 7·12, W 6·8, Cl 2·4, Cw 3·44, MPl 3·36, MPw 2·24, Iw 2·08); dorsal valves, MGUH23747 (L 8·0, W 8·0, Cl 2·24, Cw 4·64, Sl 4·96); MGUH23751 (L 5·44, W 5·52, Cl 1·92, Cw 2·72, Sl 3·36); MGUH23749; MGUH23750. Total of three ventral and 14 dorsal valves. All specimens from the same collection and locality as the holotype.

Diagnosis. As for genus.

Description. Ventral valve moderately and evenly convex, about 102–105 per cent. as long as wide, with somewhat acuminated beak; ventral interarea rudimentary, apsacline, occupied mainly by narrow, triangular delthyrium, with distal margins joined by anterise. Dorsal valve gently convex, sub-circular, about 94 per cent. as long as wide; dorsal interarea rudimentary, divided medially by narrow, shallow groove.

Ventral interior with strongly raised, solid, antero-median muscle platform, occupying about 40–48 per cent. of maximum valve length; ventral cardinal muscle platform with scars of the posterior adductors and, possibly, oblique lateral muscles; ventral cardinal muscle field separated from anterior muscle platform by deep oblique groove. Dorsal interior with posterior adductors situated on elevated posterolateral muscle platforms; dorsal anterior adductor scars large, elongate sub-oval, weakly impressed; dorsal median ridge low, extending anteriorly to mid-valve.

Order KUTORGINIDA Kuhn, 1949

Diagnosis. Shell inequibiconvex to planoconvex, anterior margin rectimarginate, rarely sulcate; posterior margin wide, straight, with large median opening; delthyrium widely triangular, covered by convex pseudodeltidium, bounded laterally by furrows; beak with small, rounded apical foramen; dorsal interarea divided by wide notothyrium; both valves with slightly thickened, weakly defined visceral area, situated close to posterior margin; dorsal diductor scars placed on floor of notothyrial cavity; cardinal process absent; articulation without teeth and dental sockets; digestive tract probably open with anus placed posteromedianly.

Superfamily KUTORGINOIDEA Schuchert, 1893

Diagnosis. Shell with articulation characterized by two triangular plates formed by dorsal propareas and bearing oblique ridges on the inner sides, which seat into deep furrows formed by ridges along inner sides of ventral propareas and lateral extensions of pseudodeltidium.

Family KUTORGINIDAE Schuchert, 1893
(incl. Yorkiidae Rowell, 1962 and Agyrekiidae Koneva, 1979)

Diagnosis. As for superfamily.

Remarks. Recent studies of the articulation of *Kutorgina* and *Nisusia* (Rowell and Caruso 1985; Popov and Tikhonov 1990) suggest that kutorginids may represent one of the most primitive types of articulate brachiopod. Their hinge mechanism is simple and quite different from that present in most other Palaeozoic brachiopods; it consists of two narrowly triangular propareas in the dorsal valve, fitting into two deep furrows bounding the margins of the pseudodeltidium in the ventral valve. This type of articulation is also present in the Agyrekiidae and Yorkiidae, and there seems to be little reason to keep these families separated from the Kutorginidae.

Genus KUTORGINA Billings, 1861

Type species. Kutorgina cingulata Billings, 1861, p. 8; Lower Cambrian, L'Anse au Loup (Belleisle), Labrador.

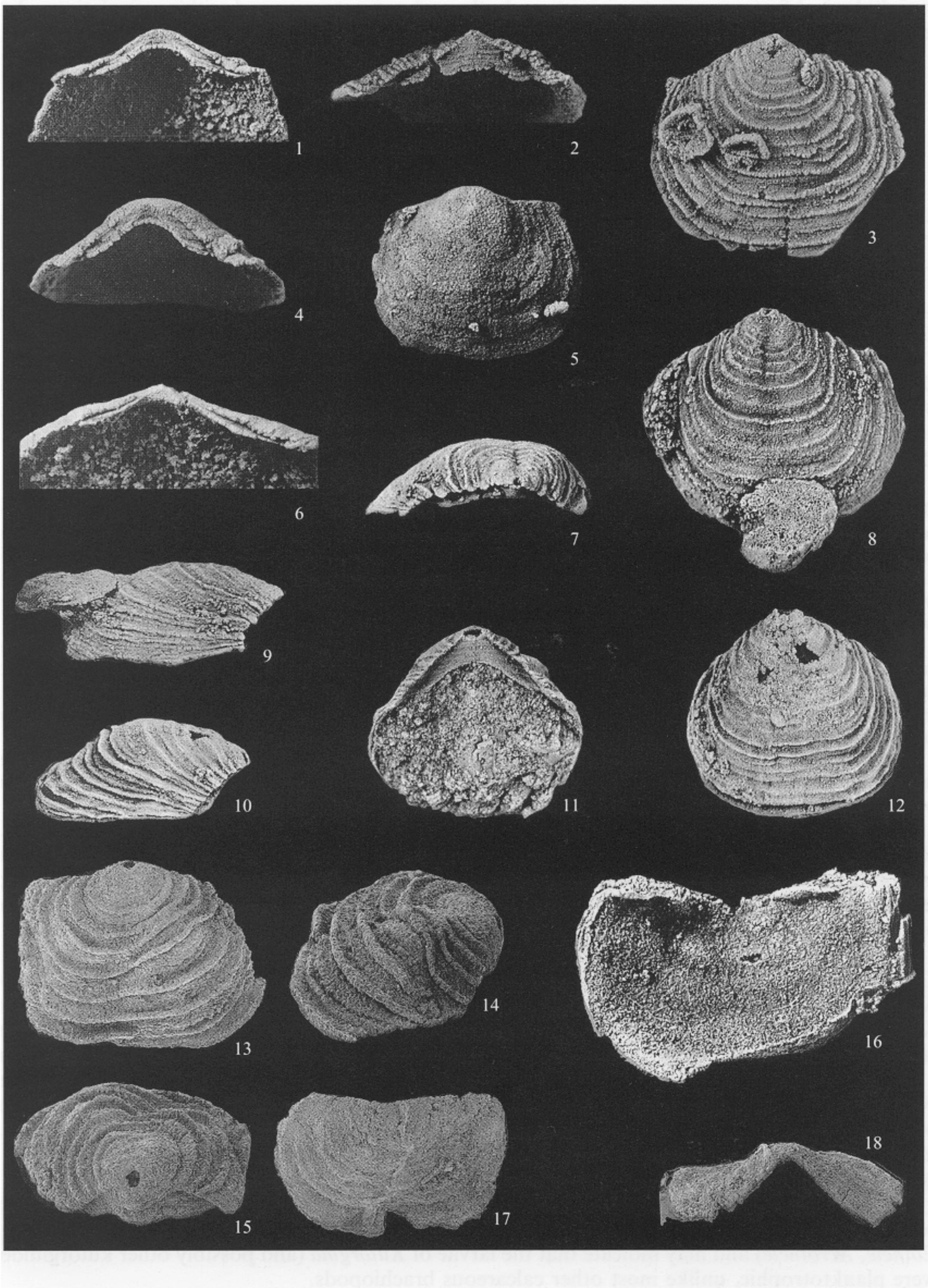
Diagnosis. Shell strongly ventribiconvex to planoconvex; strongly lamellose peripherally, with granular micro-ornament; ventral interarea apsacline to orthocline, occupied mainly by broad, convex pseudodeltidium, bordered by deep hinge grooves; dorsal propareas narrowly triangular with deep dorsal hinge grooves and strong hinge ridges on the inner sides; dorsal interior with radially arranged adductor scars and diductor scars situated on low, transversely sub-triangular notothyrial platform; dorsal mantle canals pinnate.

Remarks. The genus is in need of revision, but this is outside the scope of this paper, even though we assign specimens to the type species. A major problem is that species of *Kutorgina* have very few distinctive characters, and details of ornamentation, outline, and shell profile, as well as other

EXPLANATION OF PLATE 1

Figs 1–12. *Kutorgina cingulata* (Billings, 1861). 1, MGUH23753; ventral pseudointerarea; ×5. 2–3, MGUH23752; ventral valve, posterior view, exterior; ×4. 4–5, MGUH23757, dorsal valve; 4, posterior view, ×5; 5, exterior, ×3. 6, MGUH23755; dorsal pseudointerarea showing dorsal hinge ridges and hinge furrows; ×5. 7–9, MGUH23756; ventral valve; 7, posterior view, 8, exterior, 9, lateral view; all ×3. 10–12, MGUH23758; ventral valve; 10, lateral view, 11, ventral interarea, 12, exterior; all ×3. All from the Paralleldal Formation (late Early Cambrian), Peary Land, central North Greenland (GGU collection 274907).

Figs 13–18. *Kutorgina catenata* Koneva, 1979. 13–15, PMKg1; ventral valve, 13, exterior, 14, lateral view, 15, oblique posterior view; all ×11. 16, PMKg2; dorsal valve interior; ×10. 17–18, PMKg4; juvenile dorsal valve; 17, exterior, ×9; 18, posterior view, ×10. All from the Lower Cambrian (Botomian), south Tien-Shan, Alaj Range, Chachme River (locality 5069-8 of Popov and Tikhonov 1990).



POPOV *et al.*, *Kutorgina*

morphological features seem to vary strongly throughout ontogeny and within populations. As a result, the majority of the species described is not well-defined.

Kutorgina cingulata (Billings, 1861)

Plate 1, figures 1–12; Text-figure 4A–H

1912 *Kutorgina cingulata* (Billings) Walcott, p. 580, pl. 5, figs 1, 1*a*–*e* [see for synonymy].

Lectotype. Selected here from the syntypes (deposited in the Geological Survey of Canada, Ottawa) described by Billings (1861), GSC 384a, ventral valve (L 15·8, W 17·3, T 5·0); from the Lower Cambrian of L'Anse au Loup, Labrador.

Material. Figured, from the Paralleldal Formation (GGU collection 274907), Peary Land, central North Greenland; MGUH23752–23763. Total of 74 ventral and 29 dorsal valves.

Diagnosis. Shell transversely sub-rectangular in outline; ventral interarea strongly apsacline to orthocline in adults; ventral sulcus narrow, originating near umbo, shallowing anteriorly; dorsal valve flat with convex umbonal area; notothyrium broadly triangular with vestigial apical chilidium; ventral interior characters poorly known.

Description. Shell ventribiconvex to planoconvex, transversely sub-rectangular in outline, on average 89 per cent. as long as wide, with maximum width at mid-length. Ventral valve moderately to strongly and evenly convex, on average 33 per cent. as high as long; shallow sulcus originating at umbonal area, usually disappearing anterior to mid-valve; ventral interarea apsacline in juveniles, orthocline in adults, with broadly triangular, convex pseudodeltidium and rudimentary propareas, separated from pseudodeltidium by deep, widely divergent grooves; umbo pointed, bearing small apical foramen.

Dorsal valve flattened with raised umbonal area; notothyrium forming broad triangular notch, bordered laterally by grooved triangular propareas and covered apically by rudimentary chilidium (Text-fig. 7A–C); dorsal hinge furrows on inner sides of propareas bordered by hinge ridges which, in some large specimens, are comparable to the socket plates of *Nisusia*. Ornamented with numerous, slightly irregular, imbricating lamellae, strongly developed in ventral valve, but usually weakly defined in dorsal valve.

Muscle scars and mantle canals weakly impressed in both valves. Dorsal umbonal area with short, slightly raised notothyrial platform; dorsal anterior and posterior adductor scars radially arranged. Mantle canals poorly defined; proximal parts of pinnate mantle canals observed in one dorsal valve.

Remarks. The Greenland specimens are indistinguishable from the types of *K. cingulata* in most morphological characters. However, they are generally smaller than those from North America (maximum width 30 mm; Walcott 1912, p. 580) and lack the distinctive granular micro-ornamentation, but this is probably due to the secondary silicification of the shell.

K. reticulata Poulsen, 1932, from the Early Cambrian Ella Island Formation of north-east Greenland, seems to differ from *K. cingulata* mainly in the absence of a dorsal median fold. *K. cingulata* is distinguished from *K. catenata* Koneva, 1979, from the Lower Cambrian of Kazakhstan and Kirgizia, in having a ventral sulcus, a well-defined notothyrial platform, and strongly developed ridges bounding the inner sides of the grooves in the dorsal pseudointerarea.

Trematosia undulata (Cooper, 1976), from the Early Cambrian Nimra Formation of southern Negev, Israel, is also similar to *K. cingulata* in its strongly lamellose shell, minute apical foramen, broadly triangular, convex pseudodeltidium, and poorly defined propareas on an apsacline ventral interarea. *T. undulata* is here re-assigned to *Kutorgina*, but it differs from *K. cingulata* in having a gently convex ventral valve lacking a sulcus.

The wide geographical distribution of *Kutorgina* in the late Early Cambrian is comparable to the cosmopolitan distribution of acrotretoids (e.g. *Hadrotreta*, *Linnarssonia*) and acrothelids (e.g. *Eothele*, *Acrothele*) and may indicate that the larvae of *Kutorgina* (and possibly other kutorginides) were planktotrophic, unlike most other calcareous brachiopods.

Kutorgina catenata Koneva, 1979

Plate 1, figures 13–18; Text-figure 4I–L

1979 *Kutorgina catenata* Koneva, p. 58, pl. 23, figs 2–8; pl. 24, figs 1–5.
1990 *Kutorgina catenata* Koneva; Popov and Tikhonov, p. 45, pl. 3, figs 13–16; pl. 4, figs 7–9.

Holotype. Ventral valve (2138/226, Institute of Geological Sciences, Alma-Ata); from an Early Cambrian limestone olistolith, Agyrek Mountains, Kazakhstan.

Remarks. Silicified specimens of *Kutorgina catenata* from the Lower Cambrian of south Tien-Shan, Kirgizia are illustrated here for comparison with *K. cingulata*.

Genus AGYREKIA Koneva, 1979

Type species. *Agyrekia alata* Koneva, 1979; Lower Cambrian, Agyrek Mountains Kazakhstan, by original designation.

Diagnosis. Shell sub-equibiconvex, ornamented by concentric rugellae; ventral interarea catacline to procline, with well-defined narrow, flattened propareas; pseudodeltidium broad, gently convex; poorly defined ventral hinge grooves on lateral sides of pseudodeltidium; dorsal valve moderately convex; ventral mantle canals pinnate.

Remarks. In the original diagnosis of *Agyrekia* (Koneva 1979, p. 60) the dorsal valve was described as being high, sub-conical, with a well-developed homeochilidium. However, nearly all illustrated 'dorsal' valves of the type species *A. alata* (Koneva 1979, pl. 26, fig. 4; pl. 27, figs 2, 4; pl. 28, fig. 2; pl. 29, figs 2–3) are indistinguishable from the ventral valves in the morphology of the interarea, and clearly show shallow, but distinctive, hinge grooves on the lateral sides of the 'homeochilidium', thus indicating that they are ventral valves. Consequently, the dorsal valve of *A. alata* is known only from a single incompletely preserved specimen (Koneva 1979, pl. 26, fig. 1). *Agyrekia* differs from *Kutorgina* in having a much more strongly convex dorsal valve, with the maximum height anterior to the umbo. The morphology of the dorsal interarea is unknown in the type species, but it is likely that the dorsal valve of *Agyrekia* had a broad, sub-triangular, open notothyrium and short, triangular grooved propareas like other kutorginids. In particular, this type of morphology can be observed in the dorsal valves from Greenland which are assigned here to *Agyrekia* aff. *obtusa* Koneva.

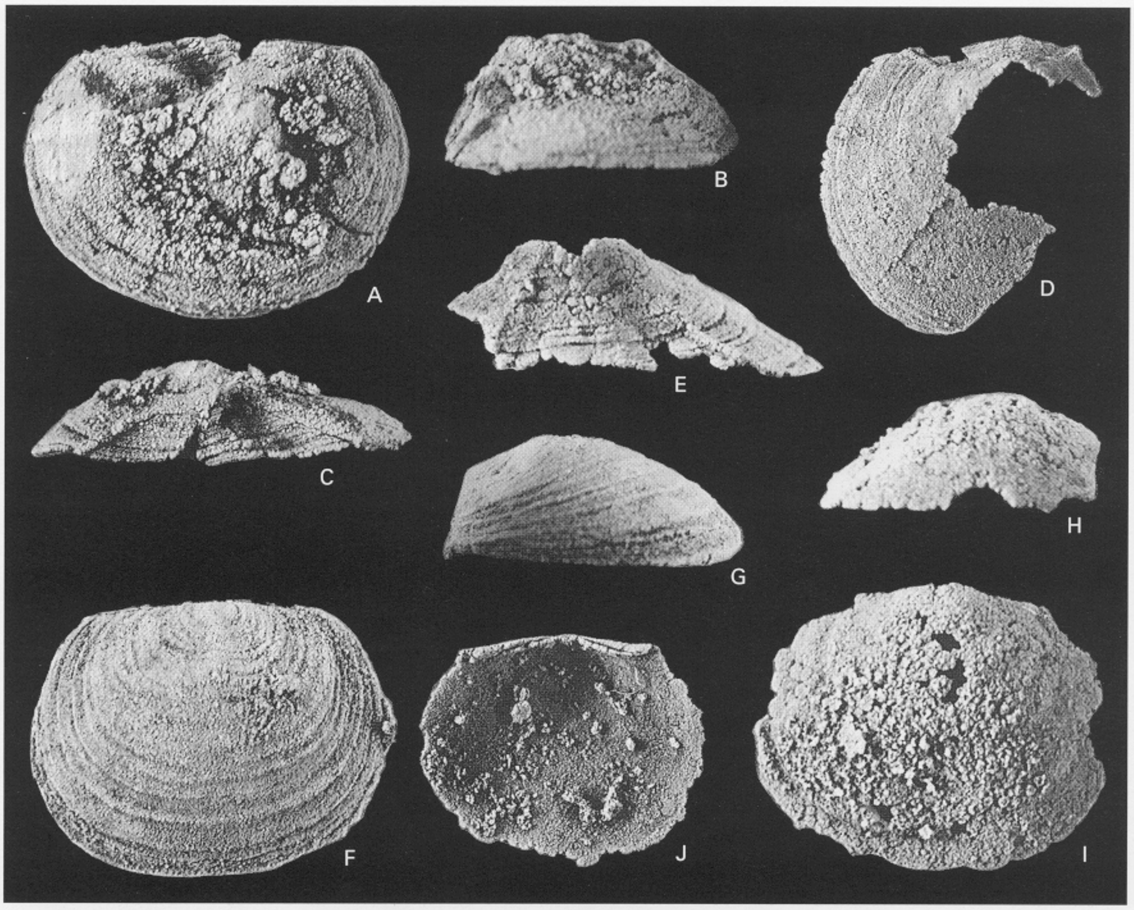
Agyrekia is closely similar to *Kutorgina* in the morphology of the ventral and dorsal interareas which have primitive articulatory structures. In *Agyrekia* aff. *obtusa*, however, the ventral hinge grooves on the lateral sides of the pseudodeltidium are weakly developed, the axis of rotation is fixed by the outer margins of the pseudodeltidium and the ventral propareas fit into furrows on the inner sides of the dorsal propareas. This pattern of the articulation is somewhat comparable to that of nisusiides, and the dorsal hinge ridges and furrows of *Agyrekia* aff. *obtusa* may be homologous to the socket plates and sockets of *Nisusia*.

Agyrekia aff. *obtusa* Koneva, 1979

Text-figure 6

Material. Figured: from the Paralleldal Formation (GGU collection 274907), Peary Land, central North Greenland; MGUH23766, ventral valve (L 11·5, W 14·6, T 4·2, Iw 10·4), MGUH23767; dorsal valves: MGUH23768 (L 7·4, W 9·0, T 2·3, Iw 6·4); MGUH23764 (L 7·7, W 10·0, T 2·96, Iw 6·6); MGUH23765 (L 7·4, W 9·2, Iw 5·2). Total of three ventral and five dorsal valves.

Description. Shell slightly ventribiconvex; transversely sub-oval in outline, with maximum width at mid-length. Ventral valve sub-conical, with posterior and lateral slopes gently convex in cross section; about 79 per cent.



TEXT-FIG. 6. *Agyrekia* aff. *obtusa* Koneva, 1979. A–C, MGUH23766; ventral valve exterior, lateral view, posterior view; all ×2·8. D–E, MGUH23767; ventral valve. D, exterior; ×2·8; E, pseudointerarea; ×4·2. F–G, MGUH23764; dorsal valve exterior, lateral view; ×4·2. H–I, MGUH237688; dorsal valve lateral view, exterior; both ×5·6. J, MGUH23765; dorsal valve interior; ×4·2. All specimens from the Paralleldal Formation (late Early Cambrian), Peary Land, central North Greenland (GGU collection 274907).

as long as wide, and 37 per cent. as high as long, with maximum height at apex; perforated by small, rounded foramen; ventral interarea high, planar, procline, with broad, sub-triangular, gently convex pseudodeltidium, bordered by widely divergent grooves; ventral propareas narrow, flattened, well-defined.

Dorsal valve moderately and evenly convex, about 80 per cent. as long as wide; ventral interarea rudimentary anacline, with narrow hinge ridges and furrows on inner sides of propareas; notothyrium broadly triangular, occupying about 81 per cent. of width of posterior margin. Shell smooth with fine, slightly irregular growth lamellae; micro-ornamentation not preserved.

Muscle scars and mantle canals weakly impressed in both valves.

Remarks. Our specimens are closely similar to *A. obtusa* Koneva (1979, p. 62) with respect to the obtusely sub-conical ventral valve, the procline ventral interarea with gently convex pseudodeltidium, bordered by widely divergent grooves, and the narrow, flattened propareas. As noted above, all but one of the dorsal valves of *A. obtusa* illustrated by Koneva (1979, pl. 31, figs 3–4) are probably ventral valves.

The type specimens of *Kutorgina catenata*, which come from the same locality as *A. obtusa*, include dorsal valves representing two different morphologies. In particular, one specimen illustrated by Koneva (1979, pl. 24, fig. 5) represents a typical *Kutorgina*, having a flattened dorsal valve, with the maximum height at the pointed, slightly elevated beak, whereas another specimen (pl. 24, fig. 3) has a moderately convex dorsal valve with the maximum height near mid-valve. The latter specimen is closely similar to the dorsal valves of *A.* aff. *obtusa* in our collection and most probably represents a dorsal valve of *A. obtusa.*

Another similar species is *Kutorgina pyramidalis* Aksarina (see Aksarina and Pelman 1978, p. 86, pl. 8, figs 1–9) from the Lower Cambrian (Toyonian), Batenev Ridge, south-western Siberia. It has a subequally biconvex shell with a moderately convex dorsal valve and a procline ventral interarea. *A.* aff. *obtusa* differs from the latter species, however, in having a weakly developed lamellose ornamentation. *K. pyramidalis* differs from other species of *Kutorgina* in having a convex dorsal valve with the maximum height slightly posterior to mid-length, as well as a sub-pyramidal ventral valve with a procline interarea and well-defined propareas. It is provisionally re-assigned here to *Agyrekia.*

A. aff. *obtusa* is also comparable to *Kutorgina*? sp. described by Roberts and Jell (1990, p. 285) from the early Mid Cambrian (Ordian) First Discovery Limestone of New South Wales, Australia. The Greenland species differs in having poorly developed concentric lamellae and in lacking a ventral sulcus.

REMARKS ON ARTICULATION IN EARLY CALCAREOUS BRACHIOPODS

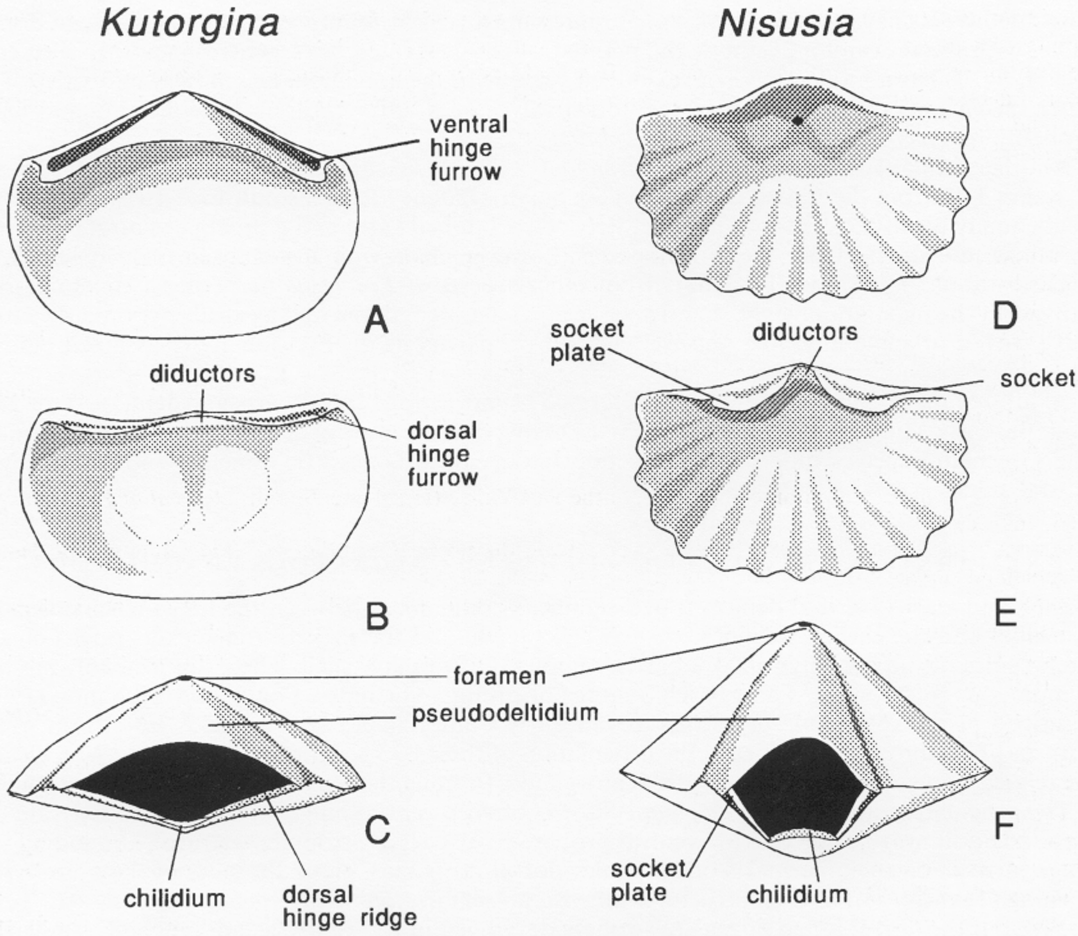
Rowell and Caruso (1985) demonstrated significant differences between the hinge mechanisms of nisusiides and the earliest orthides. *Nisusia* lacks teeth, and the sockets and sockets ridges on the lateral sides of the notothyrium are partly composed of primary shell. These are probably are not homologous to the sockets and brachiophores of primitive orthides. Popov and Tikhonov (1990) described primitive articulatory structures in Early Cambrian *Kutorgina* and *Nisusia* from south Kirgizia. They noted similarities in the articulation of these two genera and re-assigned *Nisusia* and the related genus *Eoconcha* to the order Kutorginida, forming the separate superfamily Nisusioidea.

The articulation in *Kutorgina cingulata* consists of deep ventral hinge furrows which separate the pseudodeltidium from the narrow ventral propareas, as well as strong hinge ridges, bounding the hinge furrows on the inner parts of triangular dorsal propareas, along the sides of the notothyrial opening (Text-fig. 7). All these structures are also present in *Kutorgina catenata* (Pl. 1, fig. 16; Text-fig. 4I), but the dorsal hinge ridges are strongly developed in *K. cingulata* and have some similarity to the socket plates of *Nisusia* (Pl. 1, fig. 6; Text-fig. 4F–G).

The axis of rotation between the valves in *Kutorgina* was fixed at two points by the distal parts of narrowly triangular dorsal propareas, which served as 'teeth', fitting into the deep ventral hinge furrows, essentially functioning as 'sockets'. The dorsal hinge ridges and furrows served as supporting structures in restricting the lateral movements of the valves.

In *Nisusia* (Rowell and Caruso 1985; Popov and Tikhonov 1990), the rotation axis coincides with the posterior commissure; it is fixed by the lateral margins of the pseudodeltidium which fit into the deep sockets on the inner margins of dorsal interareas (Text-fig. 7). The socket plates and sockets in *Nisusia* are probably homologous in *Kutorgina* to the dorsal hinge ridges and furrows respectively. These structures are situated on the inner margins of dorsal propareas and are composed partly of primary shell. The main difference between the two genera is that the dorsal hinge ridges and furrows in *Kutorgina* have supplementary articulatory functions, whereas the socket plates and sockets in *Nisusia* are the main articulatory structures in the dorsal valve. The articulation in *Kutorgina* seems to be more primitive and may be present in a rudimentary state in juvenile shells of *Nisusia* (Popov and Tikhonov 1990, pl. 3, figs 23–24).

The pattern of articulation in kutorginides (including nisusioids) was probably not ancestral to that of the early orthides (superfamily Protorthoidea). The earliest known protorthoidean genera (e.g. *Glyptoria* and *Israeleria*) completely lack structures comparable to the socket plates and sockets of *Nisusia*. The primitive brachiophores and sockets are composed entirely of secondary shell, and may have evolved later in relatively more derived taxa such as *Arctohedra.*



TEXT-FIG. 7. Schematic illustration of the articulation in kutorginids. A–C, *Kutorgina*, ventral valve interior, dorsal valve interior, posterior view. D–F, *Nisusia*, ventral valve interior, dorsal valve interior, posterior view (see also Holmer and Popov 1996, p. 13).

The presence of hinge groves on the lateral sides of the pseudodeltidium together with narrow, triangular propareas in the dorsal valve of *Yorkia wanneri* (see Rowell 1962), suggests an articulation pattern similar to that of *Kutorgina*. The specimens of *Trematosia* sp. 1 figured by Cooper (1976, pl. 1, figs 39–41), as well as some specimens of *Trematosia radifer* (Cooper 1976, pl. 1, figs 19–26), are probably not congeneric with the holotype of *Trematosia radifer* because they have a minute apical foramen, along with a kutorginide-like morphology; possibly they may be referred to *Yorkia*.

The holotype and several paratypes of *Trematosia radifer* (Cooper 1976, pl. 3, figs 1–6, 32) differ significantly from the other specimens referred to *Trematosia* in that they have a large foramen anterior to the apex, along with a poorly defined ventral interarea and a different dorsal interarea, probably with some primitive hinge structures. These features are unknown in kutorginides, and the affinities of these taxa with other early calcareous brachiopods remain uncertain.

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