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Cover: Idealized sketch of *Nipponites mirabilis* Yabe, a Late Cretaceous (Turonian) nostoceratid ammonite. Various reconstructions of the mode of life of this species have been proposed, because of its curiously meandering shell form (after T. Okamoto, 1988).

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Nautiloid and bactritoid cephalopods from the Carboniferous of the Jebel Qamar South area, United Arab Emirates

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Abstract. Nine species of cephalopods from the Ayim Formation of the Jebel Qamar South area, United Arab Emirates are described. They include orthoceratids: *Michelinoceras* sp. 1, *Michelinoceras*? sp. 2, *Temperoceras ayimense* sp. nov., *Mooreoceras*? sp. 1, *Mooreoceras*? sp. 2, *Mitorthoceras*? sp., Spyroceratinae, genus and species indeterminate; oncocerid: Poterioceratidae, genus and species indeterminate; and bactritid: *Bactrites* cf. *quadrilineatus* Girty. Based on the fauna, the Early Carboniferous age of the formation is first established herein.

Key words: Ayim Formation, Bactritida, Early Carboniferous, Oncocerida, Orthocerida, United Arab Emirates

Introduction

The cephalopods described herein were collected from the Ayim Formation of previously uncertain age, during field work in the Jebel Qamar South area, United Arab Emirates (Figure 1). Although preservation of the material is poor, we can provide new knowledge concerning age determination for the Ayim Formation and its paleobiogeographical implications for the situation of the Arabian Peninsula prior to the Neo-Tethys rifting.

The specimens studied are housed in the paleontological collections of the Geological Museum of Lausanne, Switzerland, and bear its registration numbers (prefixed MGL).

Geologic setting and fauna

The Jebel Qamar South area, situated in the northern Oman Mountains, is composed of the obducted Semail Ophiolite and allochthonous units of a large Paleozoic exotic block lying in the Hawasina Nappes (Pillevuit, 1993). The lithostratigraphy of this exotic block was first subjected to reconnaissance study by Hudson *et al.* (1954), who showed the distribution of the Ordovician and Permian rocks in the area. Robertson *et al.* (1990) subdivided this Paleozoic sediments into four formations, which are from base to top: Rann, Ayim, Asfar and Qamar Formations. Recently Pillevuit (1993) redefined those sequences as constituents of the Ramaq Group.

The cephalopods occur in sandy limestone and reddish shale located in the lower part of the Ayim Formation (Figure 2). Besides cephalopods, the fossils include serpulids (*Spirorbis* sp.), bryozoans, ostracodes, echinoderms, fish remains (Robertson *et al.*, 1990), and trace fossils (Pillevuit, 1993). An age between Ordovician and Early Permian for the Ayim Formation is not questionable because of its stratigraphic setting, *viz.* the Rann and Asfar Formations have been dated by trilobites (Hudson *et al.*, 1954) and brachiopods (Yanagida and Pillevuit, 1994), respectively. However, the lack of biostratigraphic study has left pending a precise age determination. A possible Devonian age has been suggested by Robertson *et al.* (1990) for this formation, based on lithologic similarities with the Devonian Griotte and Cephalopodenkalk of the Western European Variscan. Pillevuit (1993) stated that similar facies to the Ayim Formation are also recognized in Middle Ordovician to Upper Devonian deposits of the Middle East; i.e. the Middle to Upper Ordovician Qasim Formation in Saudi Arabia (Vaslet, 1990), and the Middle to Upper Silurian unnamed formation (Clark *et al.*, 1975) and the Upper Devonian Shishtu Formation (Stöcklin *et al.*, 1965) in Iran.

The cephalopod fauna of the Ayim Formation is dominated by orthoconic forms, and consists of nine species, including seven orthocerids (*Michelinoceras* sp. 1, *Michelinoceras*? sp. 2, *Temperoceras ayimense* sp. nov., *Mooreoceras*? sp. 1, *Mooreoceras*? sp. 2, *Mitorthoceras*? sp., Spyroceratinae, genus and species indeterminate) and two species of oncocerid (Poterioceratidae, genus and species indeterminate) and bactritid (*Bactrites* cf. *quadrilineatus* Girty). Although our

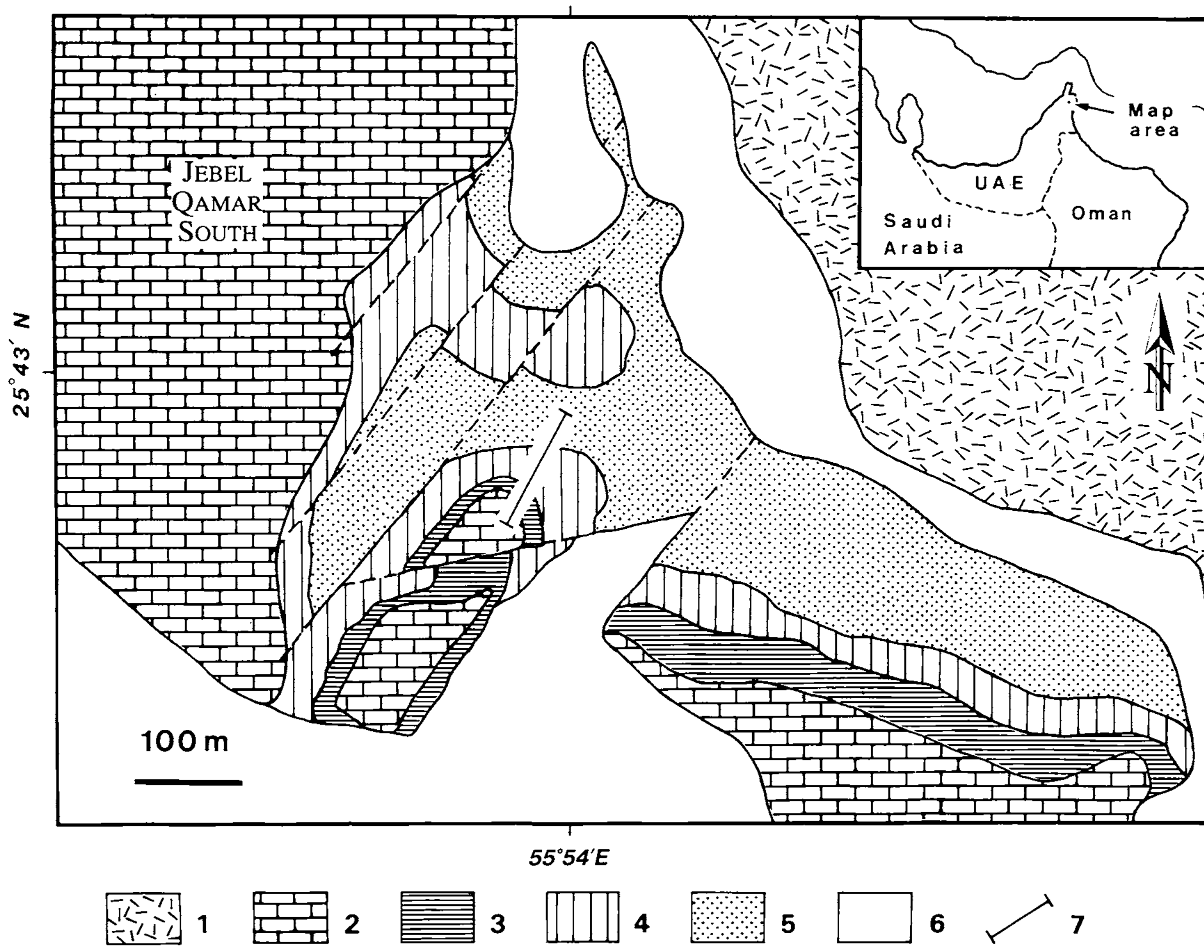

Figure 1. Map showing geology of the Jebel Qamar South area (modified from Pillevuit, 1993). **1**: Semail Ophiolite, **2-5**: exotic block (Ramaq Group), in descending order, 2, Qamar Formation; 3, Asfar Formation; 4, Ayim Formation; 5, Rann Formation, **6**: Alluvium, **7**: location of measured stratigraphic section given in Figure 2.

knowledge of the distribution of Late Paleozoic orthoconic cephalopods is not always sufficient, the cephalopods resemble species known from the North American Midcontinent region in overall aspect. The bactritid species from the Ayim Formation is comparable to that of *Bactrites quadrilineatus* Girty from the Chesterian of Oklahoma. The species *Michelinoceras* sp. 1 and *Mitorthoceras*? sp. also suggest affinities with the Late Mississippian species of the Midcontinent region. In addition, similar species to *Mooreoceras* ? sp. 1 is known to range from Morrowan to Atokan of North America. Documented range of the family Poterioceratidae and the genus *Temperoceras* extends to the Mississippian and the Triassic, respectively. Based on the evidence, the Ayim Formation is considered to be Early Carboniferous in age, with faunal exchange taking place through the seaway between Gondwana and Laurentia. Yanagida and Pillevuit (1994) indicated, however, that the Artinskian brachiopod fauna from the Asfar Formation, resting unconformably upon the Ayim Formation, shows affinity with the faunas of the Gondwana Tethyan and Cathaysia Tethyan provinces. This faunal transition may be caused by the closure of the seaway due to the amalgamation of Pangea during the Late Carboniferous to Early Permian (Scotese and McKerrow, 1990).

Systematic paleontology

Subclass Nautiloidea Agassiz, 1847
Order Orthocerida Kuhn, 1940
Superfamily Orthocerataceae M'Coy, 1844
Family Orthoceratidae M'Coy 1844
Subfamily Michelinoceratinae Flower, 1945
Genus ***Michelinoceras*** Foerste, 1932

Type species.—*Orthoceras michelini* Barrande, 1866.

Michelinoceras sp. 1

Figures 3-1—5

Description.—Orthocones with moderate shell expansion (approximately 5°), circular cross section; largest specimen

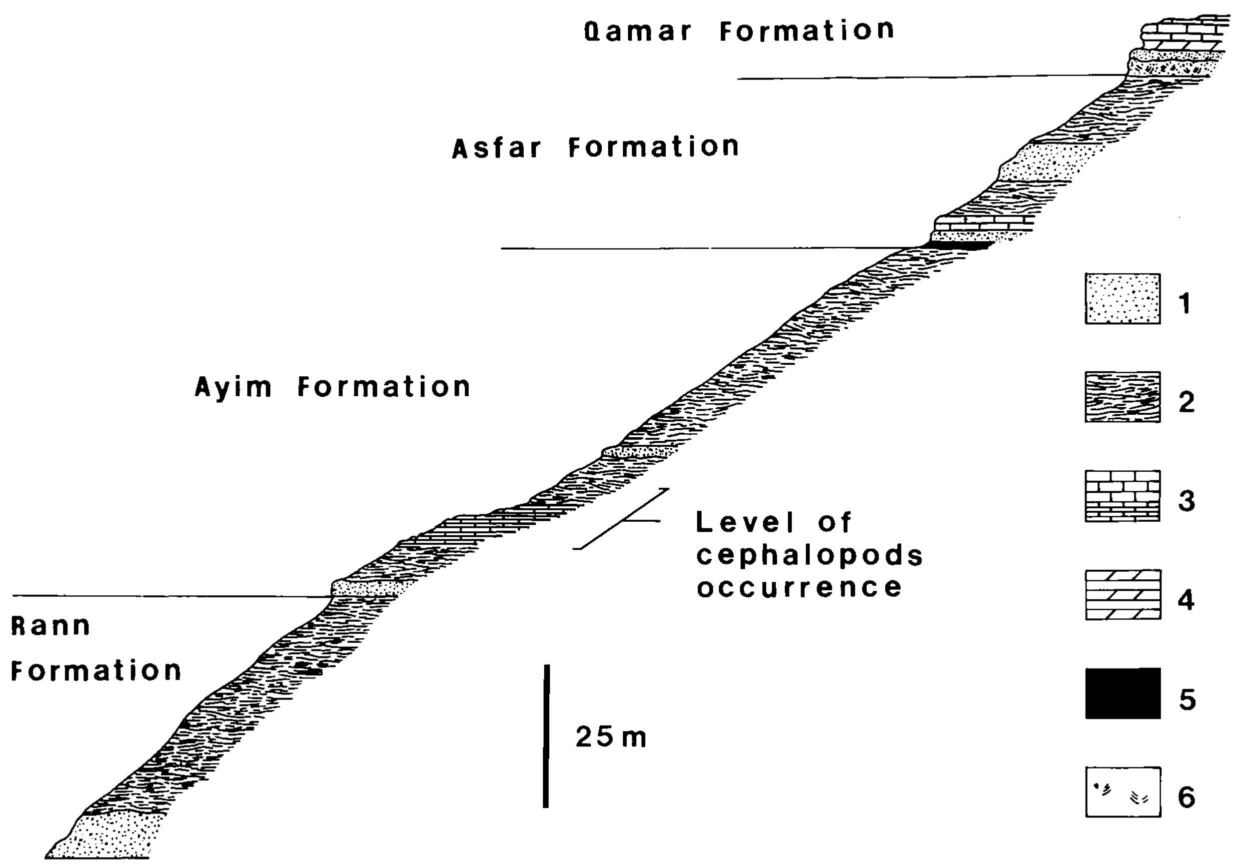

Figure 2. Stratigraphic section showing lithology of the Paleozoic formations of exotic block and stratigraphic position of cephalopods (modified from Pillevuit, 1993). **1**: sandstone, **2**: shale, **3**: limestone, **4**: dolomite, **5**: pillow lava, **6**: cross bedding.

of phragmocone attains 25 mm shell diameter; septal curvature moderate to relatively deep; cameral length somewhat variable, cameral ratio of apical shell 0.9-1.0, adorally camerae become short with 1.6-2.7 in this ratio; sutures straight, transverse; siphuncle central with weak constrictions at septal foramen, lacks endosiphuncular deposits; septal necks moderately long, orthochoanitic; connecting rings cylindrical; cameral deposits mural.

Discussion.—This species shows a superficial resemblance to *Michelinoceras wapanuckense* (Girty, 1909, pl. 6, figs. 11, 12) from the Mississippian (Chesterian) of Oklahoma. However, the internal structure of *M. wapanuckense*, shown by Gordon (1964, pl. 5, fig. 1), indicates longer camerae at the corresponding shell diameter.

Material.—Three specimens of incomplete phragmocones, MGL 72033-72035, were examined. In addition, a deformed specimen (MGL 72036) is questionably assigned to this species.

Michelinoceras ? sp. 2

Figures 3-8—10

Description.—Orthocones with gradual shell expansion (3-4°), circular cross section; largest specimen of phragmocone reaches 16 mm in diameter; septa deeply concave; cameral ratio approximately 2; sutures transverse, with broad lobes; siphuncle central with short orthochoanitic septal necks, cylindrical connecting rings.

Discussion.—This species differs from typical species of *Michelinoceras* in having short septal necks and lobate sutures. For these reasons it can be assigned only questionably to *Michelinoceras*.

Material.—Two specimens of incomplete phragmocones, MGL 72037 and 72038, were examined. In addition two ill-preserved specimens (MGL 72039, 72040) are questionably assigned to this species.

Family Geisonoceratidae Zhuravleva, 1959
Genus ***Temperoceras*** Barskov, 1960

Type species.—*Orthoceras temperans* Barrande, 1874.

Temperoceras ayimense sp. nov.

Figures 4-1—6, 10

Diagnosis.—Gradually expanding orthocones; siphuncle

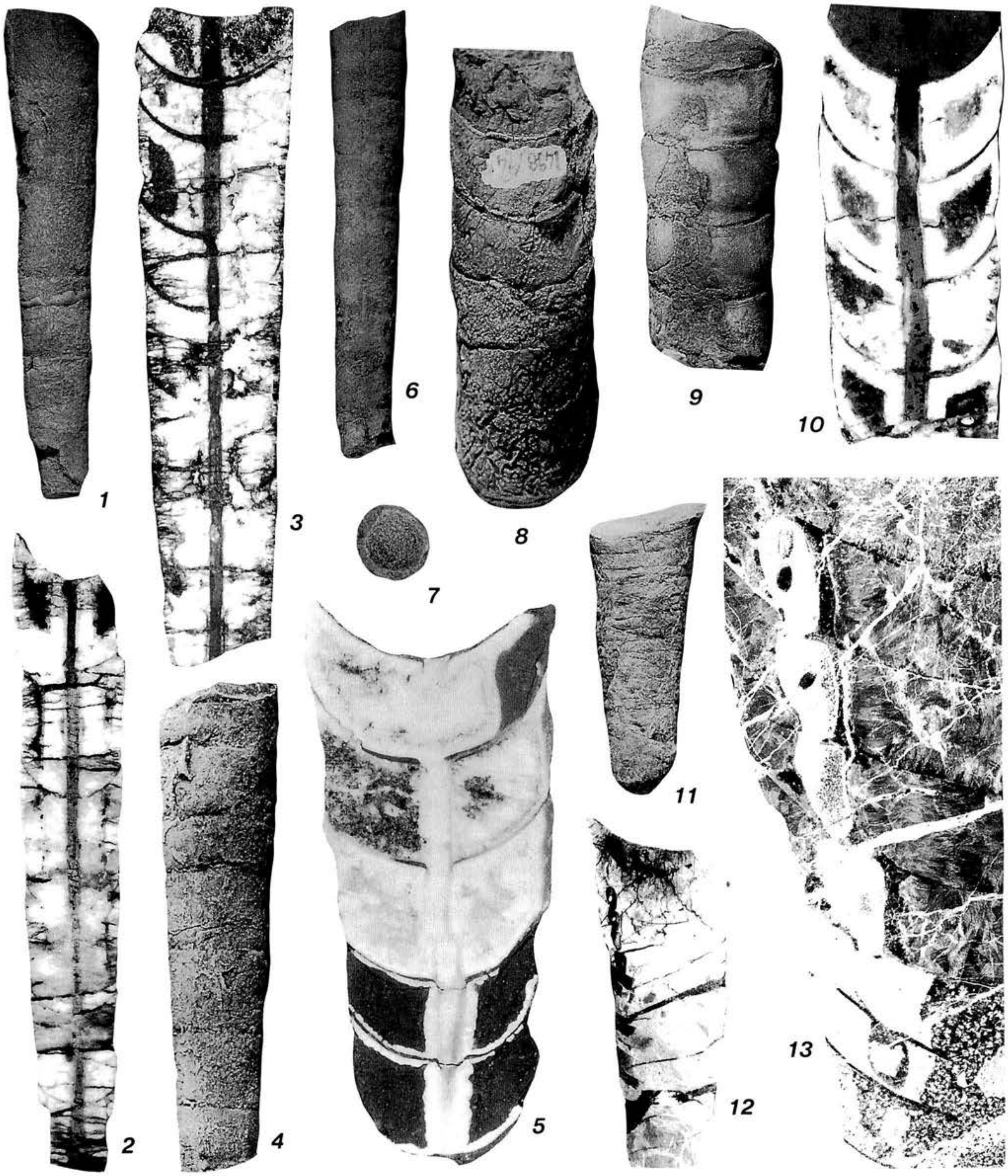

Figure 3. **1-5.** *Michelinoceras* sp. 1. **1, 2**: MGL 72034, 1, side view; 2, longitudinal polished section, **3, 4**: MGL 72033, 3, longitudinal polished section; 4, side view, **5**: MGL 72035, longitudinal polished section. **6, 7.** *Bactrites* cf. *quadrilineatus* Girty, MGL 72059, 6: ventral view, 7: septal view of adoral end, venter down. **8-10.** *Michelinoceras* ? sp. 2. **8**: MGL 72037, side view, **9, 10**: MGL 72038, 9, side view; 10, longitudinal polished section. **11-13.** Poterioceratidae, genus and species indeterminate, MGL 72058, 11: lateral view, venter on right, 12: dorsoventral thin section, venter on left, 13: details of siphuncle, negative print of thin section. 1, 4, 8, 9, 11 = ×1.5, 2, 3, 5-7, 10, 12 = ×2, 13 = ×10.

nearly central in position with suborthochoanitic to orthochoanitic septal necks and subcylindrical connecting rings; cameral deposits episeptal-mural, hyposeptal; small endosiphuncular deposits occur in apical septal foramen.

Description.—Moderately large-sized orthocones with gradual shell expansion (approximately 3°), circular cross section, largest paratype (MGL 72043) of phragmocone attains approximately 30 mm (reconstructed) in diameter; sutures straight, slightly oblique; camerae short, cameral length 3.3-5.0 mm in holotype, cameral ratio in paratype (MGL 72403) approximately 4; septal curvature moderately deep; siphuncle nearly central; siphuncular diameter/shell diameter approximately 0.1, septal necks suborthochoanitic in venter, orthochoanitic in dorsum; swollen portion of septal necks usually not preserved, thus they appear "loxochoanitic"; septal neck length short, 0.2-0.3 mm in suborthochoanitic neck in apical holotype; connecting rings subcylindrical, slightly inflated in segments; cameral deposits episeptal-mural, usually forming circumsiphuncular ridges, and hyposeptal, but adoral camera lacks hyposeptal deposits; endosiphuncular deposits of annuli weakly developed in apical septal foramen, not fusing.

Discussion.—The external shell ornamentation is not known, so that generic assignment of the species is tentative at present. However, the siphuncular morphology and the possession of endosiphuncular annuli are shared by the two geisonoceratid genera: *Temperoceras* Barskov (1960; type species, *Orthoceras temperans* Barrande, 1874) and *Protokionoceras* Grabau and Shimer (1910, type species, *Orthoceras medullare* Hall, 1868). The gradual shell expansion suggests the species belongs to *Temperoceras* rather than *Protokionoceras*.

The present species somewhat resembles *Pseudotemperoceras pulchrum* Stschastlivtseva (1986, pl. 1, fig. 1; type species of the genus) which occurs in the Lower Triassic of Verkhoyanye, Yakutia. The Triassic species has more inflated connecting rings than *Temperoceras ayimense* sp. nov. In the generic comparison *Pseudotemperoceras* differs from *Temperoceras* only in degree of development of endosiphuncular deposits, and is probably a junior synonym of *Temperoceras*.

Material.—The holotype, MGL 72041, is an incomplete phragmocone, 84.5 mm in length. Four paratypes of incomplete phragmocones, MGL 72042-72045, are assigned. In addition, a deformed specimen (MGL 72046) was also examined.

Etymology.—The specific name is taken from the Ayim Formation, where the type specimens occurred.

Superfamily Pseudorthocerataceae Flower and Caster, 1935
Family Pseudorthoceratidae Flower and Caster, 1935
Subfamily Pseudorthoceratinae Flower and Caster, 1935
Genus ***Mooreoceras*** Miller, Dunbar and Condra, 1933

Type species.—*Mooreoceras normale* Miller, Dunbar and Condra, 1933.

Mooreoceras ? sp. 1

Figures 4-7—9

Description.—Orthoconic shell with relatively rapid shell expansion (approximately 8°), laterally compressed cross section, dorsoventral shell diameter 15 mm in adoral end; sutures straight, slightly oblique; septa moderately deep; cameral length short, cameral ratio ranges from 4.8 to 6.5; siphuncle subcentral with cyrtochoanitic short septal necks.

Discussion.—This description is based on a single poorly preserved phragmocone. This species resembles *Mooreoceras normale* Miller, Dunbar and Condra (1933, pl. 2, figs. 5-10) from Middle Pennsylvanian of the Midcontinent region of United States, although until more material is obtained identification is pending. *Mooreoceras normale* is known to range from Morrowan to Atokan (Gordon, 1964).

Material.—MGL 72047.

Mooreoceras ? sp. 2

Figures 5-7—9

Description.—Orthoconic shells with relatively rapid shell expansion (approximately 7°), circular cross section, oblique and nearly straight sutures; largest specimen of phragmocone reaches approximately 22 mm (reconstructed) in diameter; septa moderately deep; cameral ratio 2.6-3.7; siphuncle subcentral with cyrtochoanitic to suborthochoanitic septal necks, connecting rings fusiform.

Discussion.—*Mooreoceras* ? sp. 2 is easily distinguished from *M.* ? sp. 1 by its partly suborthochoanitic septal necks. The available specimens are insufficient for adequate assignment.

Material.—Three specimens of incomplete phragmocones, MGL 72048-72050, were examined. In addition, two ill-preserved specimens (MGL 72051, 72052) are questionably assigned to this species.

Subfamily Spyroceratinae Shimizu and Obata, 1935
Genus ***Mitorthoceras*** Gordon, 1960

Type species.—*Mitorthoceras perfilosum* Gordon, 1960.

Mitorthoceras ? sp.

Figures 5-1—4

Description.—Weakly lirated orthocones with moderate to relatively rapid shell expansion (6-8°), circular cross section; largest specimen of phragmocone reaches approximately 10 mm in diameter; sutures straight, transverse; septal curvature moderate to relatively deep; camerae relatively long, cameral ratio approximately 1.6; siphuncle central with suborthochoanitic septal necks.

Discussion.—The available specimens are very poorly preserved, but the surface ornamentation, relatively long camerae, and suborthochoanitic septal necks indicate similarity to the Mississippian species *Mitorthoceras perfilosum* Gordon (1960, pl. 27, figs. 1-4, 8).

Material.—Four specimens of incomplete phragmocones,

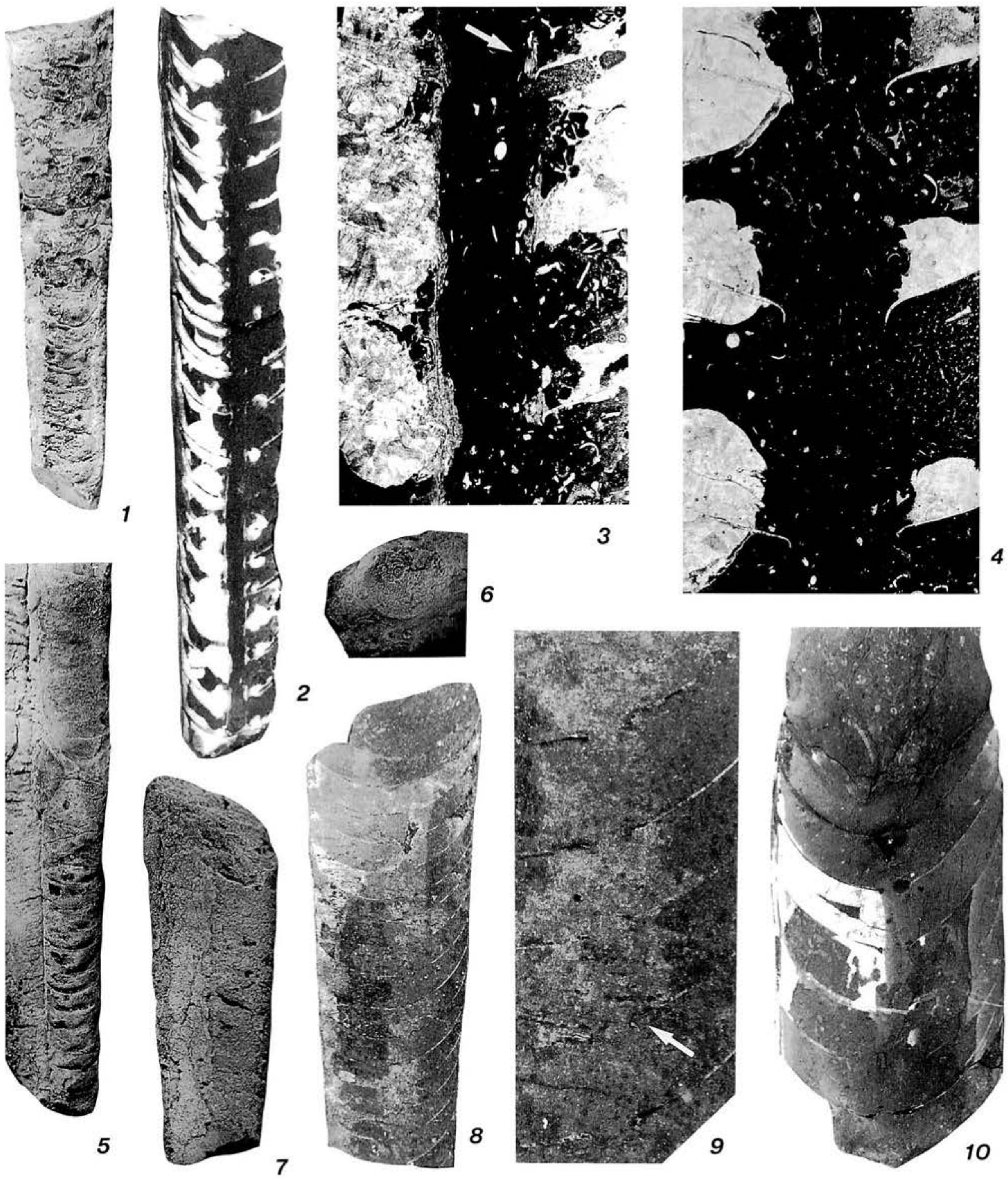

Figure 4. 1-6, 10. *Temperoceras ayimense* sp. nov.. 1-4 : holotype, MGL 72041, 1, dorsal view ; 2, dorsoventral polished section, venter on left ; 3, details of apical siphuncle, thin section, arrow indicates endosiphuncular deposits ; 4, details of adoral siphuncle, thin section, 5 : paratype, MGL 72042, side view, 6 : paratype, MGL 72044, septal view, 10 : paratype, MGL 72043, longitudinal polished section. **7-9.** *Mooreoceras* ? sp. 1, MGL 72047, 7 : lateral view, venter on right, 8 : dorsoventral polished section, venter on right, 9 : details of siphuncle, polished section, arrow indicates cyrtochoanitic septal neck. 1, 5, 6= ×1, 2, 7, 10= ×1.5, 3, 4, 9= ×8, 8= ×2.

MGL 72053-72056, were examined.

Genus and species indeterminate

Figures 5-5, 6

Discussion.—A single fragmentary specimen of a gently cyrtoconic phragmocone with circular cross section, nearly straight sutures, central siphuncular position is suggestive of a pseudorthoceratid rather than an oncocerid or nautilid. Furthermore, in siphuncular structure the specimen seemingly belongs to the Spyroceratinae. This species is unlike any known Late Paleozoic cephalopod, and may represent a new genus.

Material.—MGL 72057.

Order Oncocerida Flower in Flower and Kummel, 1950
Family Poterioceratidae Foord, 1888

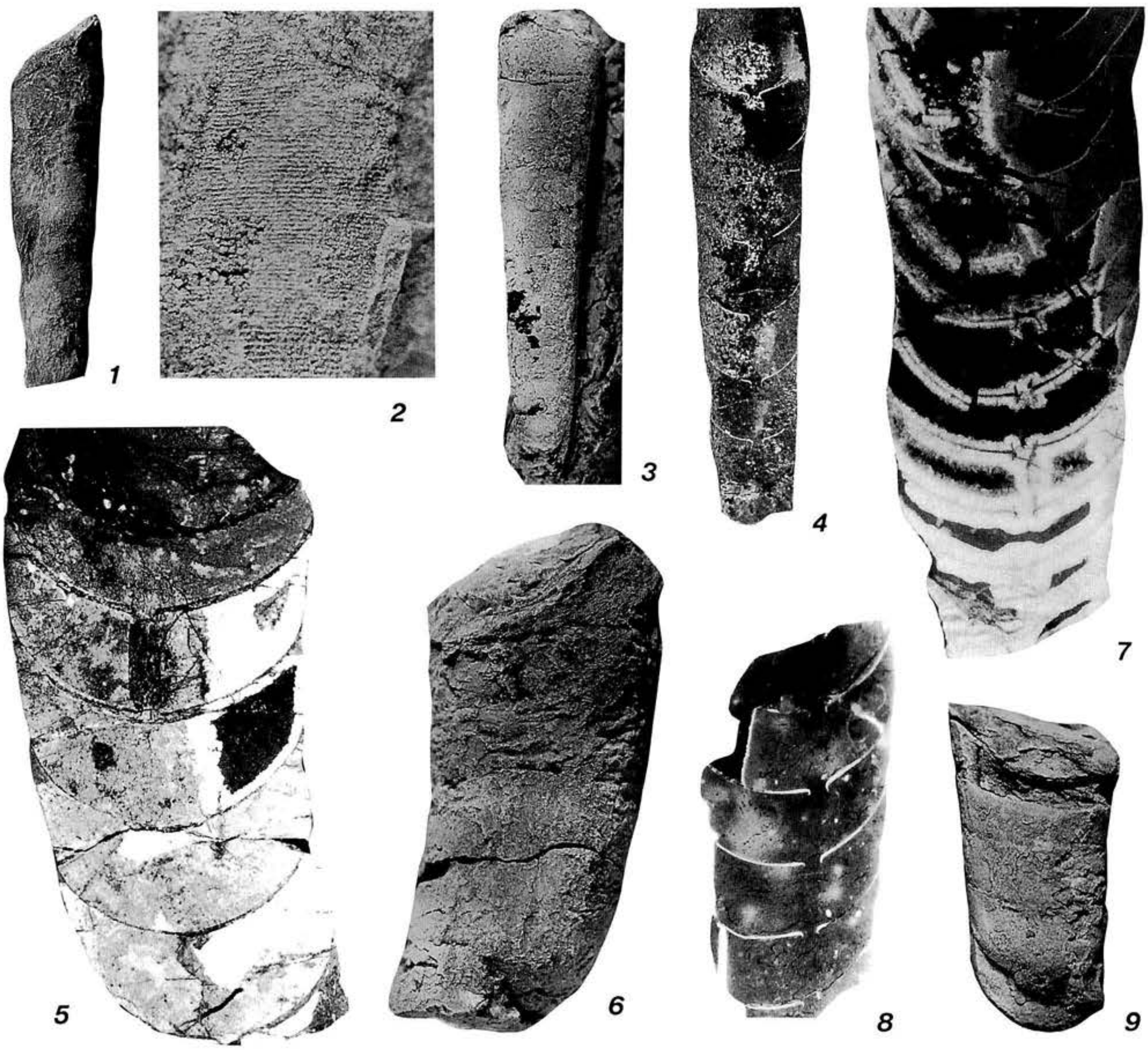

Figure 5. 1-4. *Mitorthoceras* ? sp., 1, 2 : MGL 72055, 1, side view ; 2, details of surface ornamentation, 3, 4 : MGL 72053, 3, side view ; 4, dorsoventral polished section. **5, 6.** Spyroceratinae, genus and species indeterminate, MGL 72057, 5 : dorsoventral polished section, 6 : side view. **7-9.** *Mooreoceras* ? sp. 2, 7 : MGL 72048, dorsoventral polished section, 8, 9 : MGL 72050, 8, dorsoventral polished section ; 9, lateral view. 1, 3, 6, 9 = ×1.5, 2 = ×10, 4, 5, 7, 8 = ×2.

Genus and species indeterminate

Figures 3-11—13

Discussion.—A single fragmentary and slightly deformed specimen is assigned to a poterioceratid genus and species indeterminate, based on the following morphology: exogastric cyrtocone, submarginal siphuncle with strongly curved dorsal septal necks and subquadrate connecting rings in longitudinal section.

The thick connecting rings of this species suggest relationship to the Early Devonian genus *Xenoceras* (Flower, 1951; type species, *X. oncoceroides* Flower) from New York. However, this species lacks the pendent deposits in septal foramen which are a diagnostic feature of *Xenoceras*.

Material.—MGL 72058.

Subclass Bactritoidea Shimanskiy, 1951
Order Bactritida Shimanskiy, 1951
Family Bactritidae Hyatt, 1884
Genus ***Bactrites*** Sandberger, 1843

Type species.—*Bactrites subconicus* Sandberger, 1843.

Bactrites cf. ***quadrilineatus*** Girty, 1909

Figures 3-6, 7

Compare with.—

Bactrites ? *quadrilineatus* Girty, 1909, p. 50-52, pl. 6, figs. 1-4.

Bactrites quadrilineatus Girty. Miller and Furnish, 1940, pl. 45, fig. 5; Mapes, 1979, p. 35, 36, pl. 1, figs. 6-9, pl. 2, figs. 7-9, pl. 3, figs. 1-3, 7-11, pl. 4, figs. 10, 12-16, pl. 12, fig. 3.

Description.—Single juvenile phragmocone of longiconic orthocone, 38.5 mm in length, with circular cross section; angle of expansion approximately 3°, adoral end attains 6.5 mm in diameter; sutures transverse, straight with ventral lobe; camera relatively long, cameral ratio approximately 1.4, marginal siphuncle has orthochoanitic septal necks and cylindrical connecting rings.

Discussion.—In the combination of numerical value of angle of shell expansion, straight sutures and cameral ratio, this specimen is strongly reminiscent of *Bactrites quadrilineatus* Girty known from the Mississippian (Chesterian) of the midcontinental United States. The outer shell wall with surface ornamentation and wrinkle-layer are eroded away making reliable specific assignment impossible.

Material.—MGL 72059.

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Middle Miocene-Pliocene freshwater gastropods of the Churia Group, west-central Nepal

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Abstract. In the Churia (Siwalik) Group of west-central Nepal fossil freshwater molluscs occur in relative abundance. No systematic study of these fossils has been done. Therefore, in this paper freshwater gastropods belonging to nine genera, including two new species, are described: *Bellamya celsispiralis*, sp. nov., *Bellamya* sp. A, *Bellamya* sp. B, *Angulyagra* sp., *Pila* sp., *Bithynia* sp., *Melanoides* sp., *Brotia palaeocostula*, sp. nov., *Brotia* sp. A, *Brotia* sp. B, *Brotia* sp. C, *Lymnaea* sp., *Indoplanorbis* sp., and *Gyraulus* sp. The genus *Angulyagra* is recorded for the first time from the Siwaliks.

Key words: Churia (Siwalik) Group, freshwater gastropods, Middle Miocene-Pliocene, Nepal.

Introduction

The Churia Group in west-central Nepal is of Middle Miocene to Plio-Pleistocene age and composed of molasse sediments, 5-6 km thick. It is considered equivalent to the Siwalik Group of India and Pakistan, which is well studied at the type locality of Northern Pakistan (Pilgrim, 1910; Johnson *et al.*, 1982, 1985). Recently, many geological studies were carried out in different areas of the Siwaliks of Nepal and these have resulted in the establishment of an independent lithostratigraphy (Glennie and Ziegler, 1964; Tokuoka *et al.*, 1986, 1988, 1990; Corvinus, 1994; Dhital *et al.*, 1995) for each area. These molasse sediments, showing a coarsening-upward sequence, are considered syntectonic deposits associated with the upheaval of the Himalayas. Various studies to decipher the geological history of the rising Himalayas and effects on the climate, environment, and distribution of the flora and fauna through time have been carried out in the Churia Group of Nepal (Awasthi and Prasad, 1990; Hisatomi and Tanaka, 1994; Quade *et al.*, 1995; Takayasu *et al.*, 1995). In the Churia Group of west-central Nepal, freshwater molluscs are locally abundant. The present study is an initial step in examining their relationship to changing environments through the time of uplift of the Himalayas. With this and one earlier paper (Takayasu *et al.*, 1995) we hope to record the number of genera of fossil molluscs from the Nepal Siwaliks, which could be of help for further comparison with similar faunas from other parts of the Siwaliks. In addition, the paleontological data can be of interpretive value to the reconstruction of paleoenvironments, paleobiogeographic distribution, and stratigraphic correlation.

The fossil specimens were collected from localities reported by Tokuoka *et al.* (1986, 1988, 1990) and from those added by us in subsequent field work. Part of the systematic description of these fauna was carried out in our earlier paper (Takayasu *et al.*, 1995), which reported on nine taxa belonging to four genera of Bivalvia. In the present paper fourteen gastropod taxa, including two new species, belonging to nine genera are described.

Geological Setting

The fossil localities cover the valleys of the Arungkhola, Binaikhola and Tinaukhola rivers, about 250 km southwest of Kathmandu in west-central Nepal (Figure 1). The lithostratigraphy of the Arung-Binaikhola area was established by Tokuoka *et al.* (1986), and was extended westward up to the Tinaukhola area by Tokuoka *et al.* (1988, 1990) (Figure 2). Due to lack of isotopically dateable beds, the age of the group is controlled by paleomagnetic polarity chrons. Magnetic polarity stratigraphy measured by Tokuoka *et al.* (1986) is compared with the La Brecque *et al.* (1981). In this report the same measured polarity chrons are correlated with the timescale of Cande and Kent (1992, 1994) (Figure 3). The formational boundaries therefore differ slightly from the previous report (Takayasu *et al.*, 1995) (Figure 3). The formational boundary between the Arung Khola Formation and Binai Khola Formation became older by 0.8 Ma and between the Binai Khola Formation and Chitwan Formation become younger by 0.3 Ma.

The Churia Group is divided into the Arung Khola, Binai

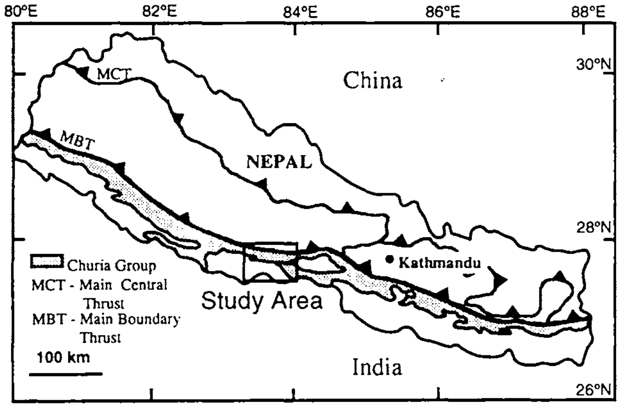


Figure 1. Index map of the study area.

Khola, Chitwan and Deorali Formations, in ascending order, and is divided into South and North Belts by the Central Churia Thrust (Figure 2). The group is separated from the northern older Midland Group by the Main Boundary Thrust (M.B.T.), and from the southern younger Gangetic Alluvium by the Frontal Churia Thrust (F.C.T.). The Arung Khola Formation (9.3-14 Ma) is composed mainly of alternating beds of variegated siltstone and sandstone with finer sediment dominating. It is divided into lower, middle and upper members. The sandstone beds become thicker toward the upper part. The Binai Khola Formation (2.7-9.3 Ma) is dominated by alternating beds of sandstone and siltstone, the sandstone beds being much thicker and the siltstone beds not variegated; it is further divided into lower, middle and upper members. The Chitwan Formation (1.3-2.7 Ma) is composed of clast-supported pebble to cobble conglomerates. The Deorali Formation (<1.3 Ma) is dominated by matrix-supported cobble to boulder conglomerates and alternating beds of coarse-grained sandstone.

The molluscan fossils are found from the upper member of the Arung Khola Formation, dated as about 10.5 Ma, to the upper part of the middle member of the Binai Khola Formation, about 3.5 Ma (Figure 3). The molluscan fossil occurrences are not continuous stratigraphically; they are wanting between 9 Ma to 8 Ma and 6 Ma to 5 Ma. Generally the fossil shells are better preserved in the younger localities than in the older ones. All of the gastropod taxa are aquatic prosobranchs and three are aquatic pulmonates (Table 1).

Systematic paleontology

All the specimens described here are deposited at the Toyohashi Museum of Natural History (TMNH), Toyohashi, 441-31 Japan.

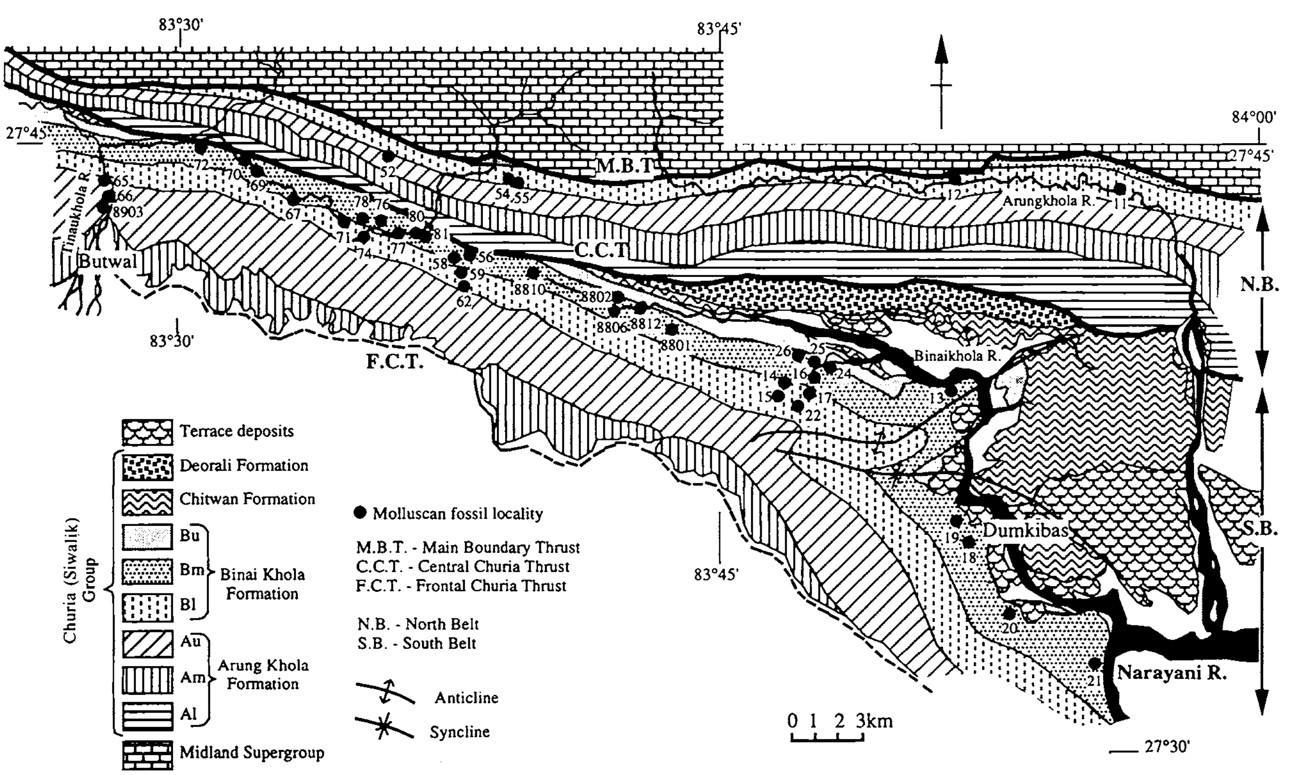


Figure 2. The generalized geologic map of the Arungkhola-Tinaukhola area, west-central Nepal after Tokuoka *et al.* (1986, 1988, 1992) with fossil localities. Locality numbers have prefix "F-".

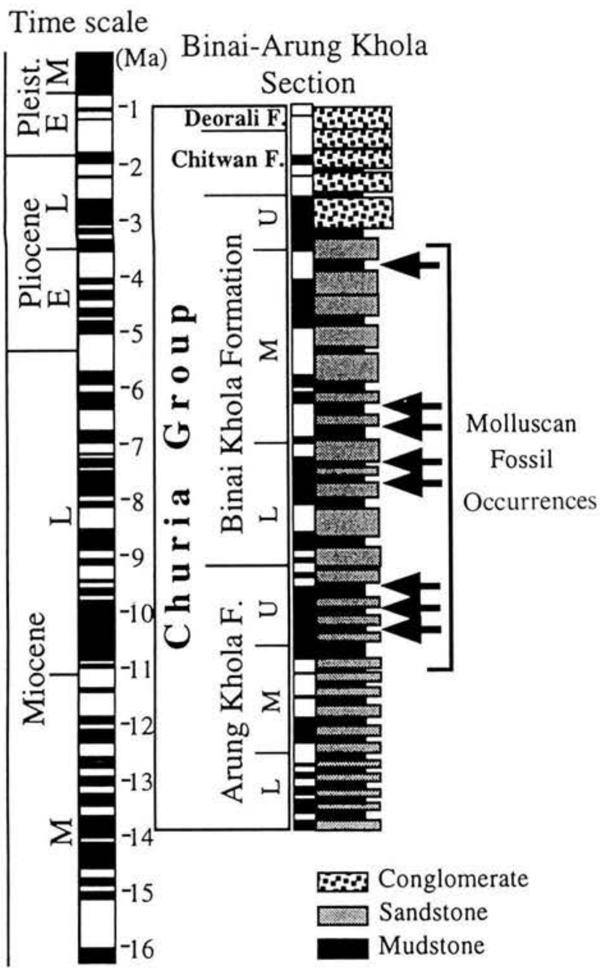


Figure 3. Generalized stratigraphic column of the Churia (Siwalik) Group with polarity chron of Tokuoka *et al.* (1986) correlated with the magnetic stratigraphy of Cande and Kent (1992) and the occurrences of the molluscan fossils.

Table 1. List of the Gastropoda taxa from the Churia (Siwalik) Group, west-central Nepal.

Class Gastropoda	Genus *Brotia*
Subclass Prosobranchia	*Brotia palaeocostula*
Order Mesogastropoda	*Brotia* sp. A
Family Viviparidae	*Brotia* sp. B
Subfamily Bellamyinae	*Brotia* sp. C
Genus *Bellamya*	Subclass Pulmonata
Bellamya celsispiralis	Order Basommatophora
Bellamya sp. A	Family Lymnaeidae
Bellamya sp. B	Genus *Lymnaea*
Genus *Angulyagra*	*Lymnaea* sp.
Angulyagra sp.	Family Planorbidae
Family Ampullariidae	Subfamily Bulininae
Genus *Pila*	Genus *Indoplanorbis*
Pila sp.	*Indoplanorbis* sp.
Family Bithyniidae	Subfamily Planorbinae
Genus *Bithynia*	Genus *Gyraulus*
Bithynia sp.	*Gyraulus* sp.
Family Thiaridae	
Genus *Melanoides*	
Melanoides sp.	

Class Gastropoda
Subclass Prosobranchia
Order Mesogastropoda Thiele, 1929
Family Viviparidae Gray, 1847
Subfamily Bellamyinae Rohrbach, 1937
Genus ***Bellamya*** Jousseaume, 1886

Type species.—*Paludina bellamyi* Jousseaume. Recent: Senegal, West Africa.

Distribution.—Africa, South, East and Southeast Asia.

Geologic range.—Jurassic to Recent.

Remarks.—The shell of the genus is turbiniform with ovately rounded aperture, pointed apex and rounded base. Whorls are rounded and almost smooth without traces of distinct spiral ridges or sculpture. Umbilicus narrow or closed.

This operculate gastropod from the Indian subcontinent was generally described under the generic name *Paludina* Lamarck and then later referred to by the senior name of *Viviparus* or *Vivipara* Lamarck. The genus *Idiopoma* established by Pilsbry (1901) with "*dissimilis*" as the type species was used as a subgenus of *Vivipara* by Preston (1915) but at present "*dissimilis*" is grouped in the genus *Bellamya* Jousseaume. According to Prashad (1928) the African species *B. unicolor* (Olivier) is very closely allied to the Indian species *V. dissimilis* (Müller). The name *Viviparus sensu lato* for the Asian and African species has been generally discarded following the anatomical study of Rohrbach (1937) which pointed out the differences from *Viviparus sensu stricto*. Yen (1943) also assigned *Viviparus* (s. l.) or the group called "*Vivipari dissimilis*" in *Bellamya*. Similarly, Subba Rao (1989) has grouped the Indian viviparids into *Bellamya* Jousseaume; *Cipangopaludina* Hannibal; *Angulyagra* Rao; and *Taia* Annandale. Common species of living viviparids in the Indian subcontinent are *Bellamya bengalensis* (Lamarck) and *B. dissimilis* (Müller), the second- and third-mentioned genera are distributed in Assam (Northeast India), Burma, and East Asia, and the last genus is considered to be endemic to Burma. Annandale and Seymour Sewell (1921) included all Indian forms with dark-banded shells into *V. bengalensis* (Lamarck) with one form *nepalensis* from "Nepal Valley". The present fossil specimens show close affinities with the recent genera *Bellamya* Jousseaume and *Angulyagra* Rao.

Hislop (1860) was the first to record fossil viviparids from the Indian subcontinent with materials from the Late Cretaceous Intertrappean Beds. He reported twelve species of *Paludina* Lamarck, but Annandale (1921b) found only *Paludina normalis* Hislop, to be a true viviparid, belonging to the group of *Vivipara dissimilis* (Müller). Fossil *V. bengalensis* was reported from the Pliocene Nerbuddah Gravel, India, by Annandale (1921b).

Bellamya celsispiralis sp. nov.

Figures 4-1—4

Materials.—TMNH02098, TMNH02099, TMNH02100, TMNH02101.

Diagnosis.—Shell elongated turbinate in shape, spire high, spire nearly equal to body whorl and whorls much rounded with impressed suture.

Description.—Shell medium in size for the genus, about 18 to 23 mm high, dextral, elongated turbinate in shape and moderately solid. Spire elevated, long, equal or slightly longer than the body whorl, apical angle about 50°, consisting of six whorls, gradually and regularly increasing in size. Apex not preserved. Whorls rounded and separated by impressed suture. Body whorl not greatly enlarged in size. Shell surface marked with coarse and fine slightly opisthoclined growth lines. Aperture (not completely preserved in the holotype but as observed in the paratypes) broadly ovate, small, thinly lipped, slightly angled on adapical side with continuous margin; inner lip thicker than the outer lip; umbilicus imperforate to narrowly perforate.

Type.—Holotype: Figures 4-1a, b, TMNH02098. Paratypes: Figures 4-2—4, TMNH02099, TMNH02100, TMNH02101.

Measurements (*in mm*).—

TMNH* coll. cat. no.	Height	Width	Height of body whorl	Height of aperture	Apical angle
02098 (Holotype)	21.8	13.3	12.7	7.8+	50°
02099 (Paratype-1)	19.2	14.3	–	–	50°
02100 (Paratype-2)	23.0	16.4	–	–	45°
02101 (Paratype-3)	18.4	15.7	10.0	–	50°

* Toyohashi Museum of Natural History

Etymology.—The name is given after its rather high spire.

Type Locality.—About 500 m west of Dumkibas along the Mahendra Highway (F-18 in Figure 2). Middle member of the Binai Khola Formation.

Stratigraphic range.—Middle member of the Binai Khola Formation.

Fossil Localities.—F-18, F-21.

Remarks.—The present fossil species has an elongated turbinate shape shell with smooth rounded whorls with a characteristically long spire. The recent and fossil species belonging to the genus *Bellamya* Jousseaume do not possess a spire longer than the height of the body whorl. The recent species of *Bellamya* common in the Indian subcontinent and Southeast Asia have spires shorter than the body whorl.

V. hasani Prashad which is considered to be from the Nerbuddah alluvial deposit (embedded in consolidated sandstone, which may have been derived from an older formation), India, is somewhat similar in shape and size, but has weak peripheral angulation and a spire shorter than the body whorl. *Paludina bugtica* Blanford, 1883, and *Vivipara atavia* Annandale, 1921b, from Oligo-Miocene beds of Gaj Stage, Bugti Hills, Baluchistan, differ from the present species in having less inflated whorl and a shorter spire. The present species differs from *Vivipara gregoriana* Annandale, 1924, and *V. dubiosa* Annandale, 1924, from the Pliocene Dawna Hills of Burma, in possessing more rounded whorls with a well impressed suture.

Bellamya sp. indet. **A**

Figures 4-5—8

Materials.—TMNH02158, TMNH02159, TMNH02160, TMNH02161.

Description.—The shell is small in size for the genus, about 12 to 15 mm in height, but, owing to deformation, the original size cannot be accurately determined. The shell is dextral, subconically turbinate and thin; spire short, less than half the shell height, apical angle about 75°, consisting of five to six whorls with rapidly increasing whorl diameter. Earlier whorls very small, slightly shouldered below suture. Later whorls almost flat or slightly rounded with a moderately strong angulation below the suture. Suture weakly impressed. Body whorl greatly enlarged. Shell surface smooth, glossy with fine growth lines, original shell probably thicker. Aperture poorly preserved.

Measurements (*in mm*).—

TMNH coll. cat. no.	Height	Width	Height of body whorl	Height of aperture	Apical angle
02158	12+	12	6+	–	70°
02159	9+	10	4+	–	75°
02160	12+	11	6+	–	–
02161	11+	12–	7+	–	–

Stratigraphic range.—Upper member of the Arung Khola Formation to lower member of the Binai Khola Formation.

Fossil Localities.—F-65, F-11, F-12 (Figure 2).

Remarks.—The present species is placed under the genus *Bellamya* based on its shell morphology with its smooth rounded whorls, turbinate shape and lack of surface sculpture. From its small size and a little rounded whorl with weakly developed angulation just below the suture, it is most similar to *Bellamya dissimilis* (Müller). Because of the lack of well preserved specimens, specific identification is deferred.

Bellamya sp. indet. B

Figures 4-9—12

Materials.—TMNH02102, TMNH02103, TMNH02104, TMNH02105.

Description.—Shell small in size for the genus, commonly ranging from 10 to 15 mm in height, dextral, turbinate and somewhat thick. Spire slightly elevated, short, less than half the height and consisting of rounded whorls. Apical angle about 70°. Apex small. Whorl diameter rapidly increasing. Body whorl much larger, inflated, with smooth and convex periphery and basally rounded. Suture between whorls impressed. Surface of the shell very smooth and glossy, marked with very fine growth lines. Aperture oval with a slight angulation on adapical side. Aperture margin continuous, of uniform thickness; inner lip with narrow parietal

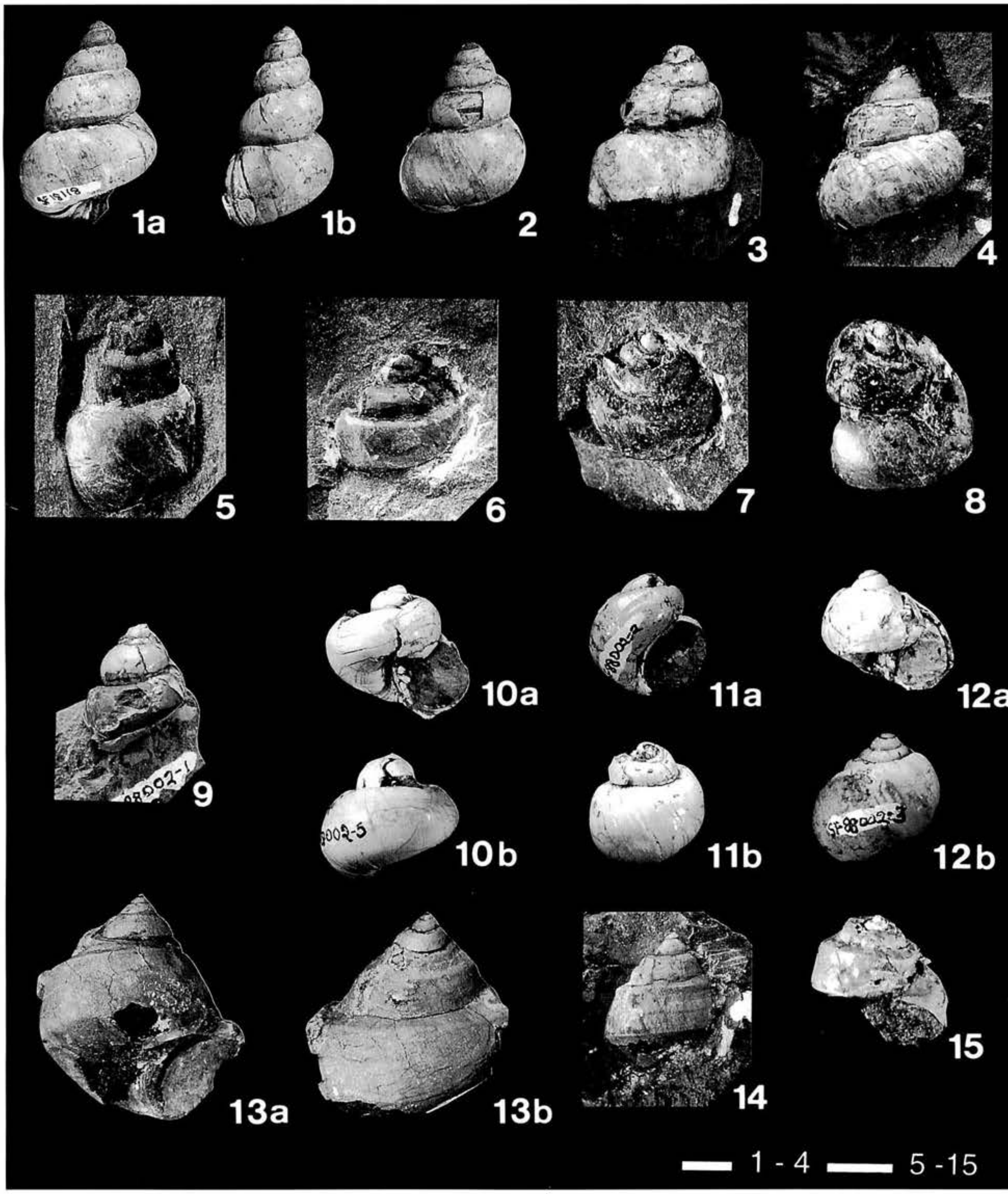


Figure 4. 1–4. *Bellamya celsispiralis* sp. nov., 1 : holotype, TMNH 02098, 1a : adapertural view, 1b : side view, 2 : paratype 1, TMNH 02099, 3 : paratype 2, TMNH 02100, 4 : paratype 3, TMNH 02101. **5–8.** *Bellamya* sp. indet. A, 5 : TMNH 02158, 6 : TMNH 02159, 7 : TMNH 02160, 8 : TMNH 02161. **9–12.** *Bellamya* sp. indet. B, 9 : TMNH 02102, 10 : TMNH 02103, 11 : TMNH 02104, 12 : TMNH 02105. **13–15.** *Angulyagra* sp. indet., 13 : TMNH 02110, 14 : TMNH 02106, 15 : TMNH 02109. All scale bars : 5 mm.

callus. Umbilicus imperforate.

Measurements (*in mm*).—

TMNH coll. cat no.	Height	Width	Height of aperture	Height of body whorl	Apical angle
02102	10.6	9.0	—	7.5	70°
02103	11.0+	11.0	7.5+	10.0+	70°
02104	10.0+	9.4	7.8+	8.5+	70°
02105	10.0+	9.0+	—	8.0+	70°

Stratigraphic range.—Middle member of the Binai Khola Formation.

Fossil Locality.—F-88002.

Remarks.—At present the specimens are collected from only one locality (F-88002) and are few in number. *Vivipara atavia* Annandale (1921b) from the Oligo-Miocene Bugti Hills, Baluchistan, resembles the present species in having a short spire and impressed suture but the latter is smaller in size, with more rounded whorls. The Recent species *Bellamya micron* described by Annandale (1921a) from Manipur, Northeast India, is similar in shape and size to the present species, but the former has a blunt peripheral angle. Until more specimens from other localities can be found a species level determination is deferred.

Genus ***Angulyagra*** Rao, 1931

Type species.—*Paludina oxytropis* Benson. Recent: Manipur Valley, Northeast India.

Distribution.—Assam, Burma and China.

Geologic Range.—Oligocene to Recent.

Remarks.—The shell of the genus is medium in size, thin, conical in shape with spiral ridges, peripheral keel well developed and base flattened.

The genus was initially described as *Dactylochlamys* by Rao (1925). However, as the name was preoccupied a new generic name *Angulyagra* was proposed in 1931. The present species shows close affinities to this Southeast Asian genus *Angulyagra* in shell shape and sculpture. Recent species of this genus *A. oxytropis* (Benson) and *A. microchactophora* (Annandale) are reported from Manipur, Assam by Annandale (1921a). Yen (1943) reported the following species from China: *Angulyagra costata* (Quoy and Gaimard), *A. thersites* (Reeve), *A. oxytropoides* (Heude), *A. polyzonata* (Frauenfeld), *A. quangdungensis* (Kobelt), *A. annulata* (Yen).

Angulyagra sp. indet.

Figures 4-13—15

Materials.—TMNH02106, TMNH02107, TMNH02108, TMNH02109, TMNH02110.

Description.—Shell medium in size, dextral, conically turbinate in shape and thin. Spire moderately elevated, less than half of the shell height with five whorls. Earlier whorls rounded to weakly shouldered and latter ones strongly shouldered just below the suture. Apical angle about 70°. Initial whorls very small. Body whorl large, comprising of two thirds of the shell height, sides broadly and obliquely flattened and obtusely angled at the periphery. Base of the body whorl only slightly convex. Suture with abutting whorls. Shell surface with fine growth lines and two or three lines of the spiral sculpture. Aperture only partly preserved in some specimens, rounded oval with weakly reflected lip. Umbilicus imperforate to narrowly perforate.

Measurements (*in mm*).—

TMNH coll. cat. no.	Height	Width	Height of body whorl	Height of aperture	Apical angle
02106	10.0+	9.0	7.0+	—	68°
02107	20.0+	15.6+	10.7+	—	—
02108	15.0+	14.0+	10.0+	—	70°
02109	15.0+	15.0	—	—	—
02110	18.0+	16.0+	13.0+	7.0+	70°

Stratigraphic range.—Middle member of the Binai Khola Formation.

Fossil Locality.—F-13.

Remarks.—The specimens belonging to this genus are collected from only one locality, F-13. Most are incompletely preserved. The fossil shell is characterized by a thin and subconical shell. The occurrence of the genus *Angulyagra* in a fossil state so far west from its Recent distribution indicates that its past distribution may have been much wider. The surface spiral sculpture of the fossil species is weaker than in the Recent taxa. However, at present well preserved samples with a complete aperture are not available, preventing species level identification.

Family Ampullariidae Gray, 1847

Genus ***Pila*** Röding, 1798

Type species.—*Helix ampullacea* Linné, 1758. Recent: Asia.

Distribution.—Asia and Africa.

Geologic range.—Lower Eocene to Recent.

Remarks.—The genus is characterized by a shell with an inflated body whorl with large aperture and a short spire. The operculum is thick with an inner calcareous layer and nacreous columnar side. Recent species of this genus are widely distributed in the tropical regions of Africa and Asia.

Pila sp. indet.

Figures 5-1—3

Materials.—TMNH02111, TMNH02112, TMNH02113

Description.—Shell medium in size for the genus, dextral, reversely conic in shape and thin. Spire short, obtuse, consisting of five whorls. Body whorl very large, inflated below the weakly convex periphery. Shell surface marked by fine growth lines. Aperture also deformed but probably elongate pyriform as inferred from the shape of the operculum. Umbilicus narrowly perforated. Operculum thick, calcareous, light brown in colour and pyriform in shape. The upper margin narrowly rounded and somewhat elongate, lower margin regularly rounded. Outer surface with small subcentral nucleus situated toward the inner margin, surrounded by concentric growth lines. Rim of the operculum slightly thickened. Inner surface with large muscle scar.

Measurements (*in mm*).—

TMNH coll. cat. no.	Height	Width	Height of body whorl	Height of aperture	Apical angle
02111	30.0+	36.0+	–	–	–
02112	24.4+	25.5+	24.4	21.7+	–
02113 (operculum)	21.6+*	15.7			

* Length

Stratigraphic range.—Middle member of the Binai Khola Formation.

Fossil Locality.—F-13 (Figure 2).

Remarks.—Few poorly preserved shells from locality F-13, with numerous fragmented shells. In all specimens the spire is depressed to the body whorl level due to deformation. Opercula are more numerous and better preserved than the shells. *Pachylabra* (=*Pila*) *prisca* Prashad, is the only fossil species of this genus reported from the Siwaliks. It is described by Prashad (1925) based on opercula collected from the Lower Siwalik (Chinji) series of Kashmir which are similar in size to the operculum of the present fossil specimen. However the latter is more elongate and thinner. As compared with the operculum of *Pila globosa* (Swainson), a Recent widely distributed species of the Indian subcontinent, the fossil one is narrower and elongated. Within the Recent species of the subcontinent, *P. virens* (Lamarck) has the most similar operculum to that of the present species. As most specimens are poorly preserved, the characters needed for species identification are insufficient.

Family Bithyniidae Walker, 1927
Genus ***Bithynia*** Leach, 1818

Type species.—*Helix tentaculata* Linné. Recent: Europe.

Distribution.—Europe and Asia.

Geologic range.—Miocene to Recent.

Remarks.—This genus is characterized by a small, ovate-conoidal shell with very delicate spiral lines; without a varix parallel to the peristome; calcareous operculum with a paucispiral nucleus.

Bithynia sp. indet.

Figures 5-4—10

Materials.—TMNH02114, TMNH02116, TMNH02117, TMNH02118, TMNH02121, TMNH02122, TMNH02123.

Description.—Shell small in size, ranging from 2 to 5 mm, dextral, ovate-conoidal in shape, somewhat thick. Composed of four regularly increasing whorls, rounded and convex. Body whorl larger than spire, periphery and base rounded. Suture distinct but shallow. Shell surface corneous, somewhat glossy and sculptured with delicate lines of growth only. Aperture partially observed, ovate in outline, lip slightly reflected. Umbilicus closed. Operculum calcareous, ovoidal in shape, white colour, concentric with large subcentral nucleus, internal surface convex with a flattened border on the outer margin with raised rim.

Measurements (*in mm*).—

TMNH coll. cat. no.	Height	Width	Height of body whorl	Height of aperture	Apical angle
02114	2.3+	1.8	1.2+	–	48°
02115	3.2+	3.0+	2.0+	–	–
02116	5.8+	3.5	3.6+	–	48°
02117	3.3+	2.3+	2.0+	–	–
02118	–	2.2	2.2+	1.5+	–
02119	–	2.0	2.2+	–	–
02120	–	2.0+	2.2+	1.5+	–
02121	2.3	1.8	1.2	–	50°
02122 (operculum)	1.8*	1.2	–	–	–
02123 (operculum)	1.9*	1.3	–	–	–

* Length

Stratigraphic range.—Upper member of the Arung Khola Formation to middle member of the Binai Khola Formation.

Fossil Localities.—F13 and F21 (shell and operculum); F65, F18, F19, F17 (only opercula).

Remarks.—According to Subba Rao (1989) and Annandale (1920) the subfamily Bithyniinae of the Indian subcontinent can be divided on the basis of shell characters into five genera: *Bithynia* Leach, *Sataria* Annandale, *Gabbia* Tryon, *Dignostoma* Annandale and *Hydrobioides* Nevill. Based on the shell morphology and its calcareous operculum with concentric growth lines and subcentral nucleus, the present specimens are identified as a species of *Bithynia* Leach. Shells of *Bithynia* sp. are found along with opercula at two localities only (F-13, F-21), although white calcareous opercula are found at most localities. The opercula are not found attached to the shell and they are of a different shape and size, probably belonging to two or more species. Most of the tiny shells are fragile and difficult to separate from the sediment containing them, so preventing specific identification.

Family Thiaridae Gray, 1847
Genus ***Melanoides*** Olivier

Type species.—*Melanoides fasciolata* Olivier=*Nerita tuberculata* Müller. Recent: India.

Distribution.—Paleotropic and subtropic.

Geologic range.—Paleocene to Recent.

Remarks.—This world-wide genus is characterized by its turreted shell with a long spire consisting of many whorls. The shell is sculptured with more or less strong spiral grooves and axial ribs and generally shows great variability within each species.

Regarding the taxonomy of melanians there are different opinions: Morrison (1954) regarded it as a genus of the family Thiaridae Gray and Brandt (1974) also treated it as a genus of the subfamily Thiarinae Gray; Subba Rao (1989), following Pace (1973), regarded *Melanoides* as a subgenus of genus *Thiara* Röding, of the subfamily Thiarinae Gray.

Melanoides cf. ***tuberculata*** (Müller, 1774)

Figures 5-11—16

Materials.—TMNH02124, TMNH02125, TMNH02126, TMNH02127, TMNH2128.

Description.—Shell small to medium in size for the genus, 20 to 24 mm long, dextral, moderately thin, elongate and turreted with eight remaining whorls. Spire elevated, long, apical angle about 21° to 25°. The early whorls including the apex eroded. Whorls increasing in diameter slowly and regularly, sides gently rounded in profile. Body whorl not very large and below the periphery only marked by spiral ridges. Suture shallow but distinct. Strongly sculptured with four to five spiral ridges crossed by closely spaced obtuse ribs. The ribs stronger than the spiral ridges in the early whorls, in later whorls it is formed into rows of tubercles. Aperture not well preserved.

Measurements (*in mm*).—

TMNH coll. cat no.	Height	Width	Height of body whorl	Height of aperture	Apical angle
02124	24.0+	10.5	13.0+	7.0+	–
02125	17.0+	9.0+	6.0+	–	–
02126	19.0+	11.0+	–	–	–
02127	18.0+	9.0+	–	–	–
02128	15.0+	5.0+	5.0+	–	25°
02129	25.0+	8.0+	–	–	25°

Stratigraphic range.—Upper member of the Arung Khola Formation to middle member of the Binai Khola Formation.

Fossil Localities.—F-65, F-12, F-17, F-18, F-19, F-13, F-21.

Remarks.—The present specimens are quite similar to the Recent species of *Melanoides tuberculata* (Müller). The fossil specimens have more prominent surface sculpture. However, the variability within the species is extremely great as pointed out by many authors (Van Benthem Jutting, 1956 ; Starmuhlner, 1974 ; Brandt, 1974). Therefore, we concluded that the fossil specimens belong to this species.

Genus ***Brotia*** H. Adams, 1866

Type species.—*Melania pagodula* Gould. Recent : Asia.

Distribution.—Southeast Asia.

Geologic range.—Pliocene to Recent.

Remarks.—The genus *Brotia* H. Adams is characterized by a long turreted shell, the spire being longer than the body whorl, which is smooth or sculptured with spiral ridges and/ or axial ribs and may be ornamented with tubercles or spines.

The genus was established with *Melania pagodula* Gould as the type species and subdivided into several subgenera (Preston, 1915 ; Brandt, 1974 ; Subba Rao, 1989) with Morrison (1954) treating the subgenus *Antimelania* Crosse and Fischer as a genus. The Indian subcontinent species are all grouped under the subgenus *Antimelania* Crosse and Fischer by Subba Rao (1989) with a regularly rounded aperture at the base as a characteristic feature. Brandt (1974) similarly subdivided the genus into two subgenera *Brotia* s.s. and *Senckenbergia* Yen, for Thai species, the former with protracted peristome at the base and in the latter not protracted. The same criteria is applied in an opposite manner for other species, for example, *Melania variabilis* Benson, which is the type species of the subgenus *Antimelania* Crosse and Fischer, is regarded as a synonym of *Brotia costula* (Rafinesque) which is placed into subgenus *Brotia* s.s. by Brandt (1974) but has a rounded aperture base. Hence, the use of the criteria for further subdivision is rather confusing. Furthermore, in the case of the present fossil specimens the base of the aperture is generally not preserved. Therefore, we are reluctant to divide the genus into subgenera for the present fossil species based on the above character.

Brotia palaeocostula sp. nov.

Figures 5-17—23

Materials.—TMNH02130, TMNH02131, TMNH02132, TMNH02133, TMNH02134, TMNH02135, TMNH02136, TMNH02137.

Diagnosis.—Suture banded, beltlike, shell marked with spiral and axial ridges, in the latter whorls with relatively widely spaced prominent axial ridges with blunt spines just above the periphery.

Description.—Shell medium in size for the genus, 30 to 50 mm long, dextral, turreted, narrowly conic and a little thick. Spire high and elongated with gradually increasing whorls. Apex and early whorls eroded. Shell generally with two to five remaining whorls. Body whorl rounded, shorter than the spire. Suture between the whorls distinct, not impressed but banded beltlike appearance due to a parallel groove below it. Surface of the shell distinctly marked with spiral and axial ridges. Surface of the early whorls cancellate. In the last two whorls axial ridges more prominent with blunt projecting spines just above the periphery, strongly developed in the last whorl. The spines more pronounced in larger matured specimens. Below the periphery of the body whorl the area is marked with spiral ridges only. Aperture incompletely preserved, probably elongated oval in outline with thin outer lip.

Type.—Holotype : Figures 4-17, TMNH02130. Paratypes : Figures 4-18-23, TMNH02131, TMNH02132, TMNH02133, TMNH02134, TMNH02135, TMNH02136.

Measurements (*in mm*).—

TMNH coll. cat. no.	Height	Width	Height of body whorl	Height of aperture	Apical angle
02130 (Holotype)	50.0+	23.4	26.0+	–	35°
02131 (Paratype-1)	36.0+	23.0+	18.0+	–	–
02132 (Paratype-2)	36.5+	15.4+	–	–	–
02133 (Paratype-3)	33.0+	30.0+	18.0+	–	–
02134	36.0+	16.0+	18.0+	–	–
02135	28.0+	24.0+	22.0+	–	–
02136	25.0+	20.0+	18.0+	–	–
02137	26.0+	18.0+	13.0+	–	–

Etymology.—The present fossil species shows some similarity to the Recent species *B. costula* (Rafinesque), hence the name 'old-costula'.

Type Locality.—At the right bank of the Jhumsakhola river about 600 m east of the confluence with the Tinaukhola river (F-72 in Figure 1). Middle member of the Binai Khola Formation.

Stratigraphic Range.—Upper member of the Arung Khola Formation to middle member of the Binai Khola Formation.

Fossil Localities.—F-65, F-72, F-17, F-20, F-18, F-16, F-13.

Remarks.—The species belonging to this genus are represented by many subgenera in Southeast Asia. The presently described species *Brotia palaeocostula* is most similar to *Brotia (Antimelania) costula* (Rafinesque) in shape but differs in surface sculpture, suture and size. The present species was collected from many localities and surface sculpture is consistent. Generally in large and mature specimens of the new fossil species, the sculpture is more pronounced. Due to its distinct surface sculpture and size we regard it as a new, extinct species.

Brotia sp. indet. **A**

Figures 6-1—3

Materials.—TMNH02138, TMNH2139, TMNH2140.

Description.—Shell medium in size for the genus, 30 to 40 mm long, dextral, turreted with elongated conic spire, moderately thick. Spire conical, high, nearly half the shell length. Apex and early whorls eroded. The shell consists of more than nine evenly increasing whorls. Early whorls nearly flat in outline but the later ones obtusely convex. Apical angle about 30° to 32°. Sutures shallow with area below it a flat and bandlike. Shell surface sculptured with prominent rounded axial ridges with three to four weak spiral threads. Axial ridges comparatively strongly developed, rounded, curved, and constricted at the narrow suture area. Body whorl larger, rounded, marked with eight to nine axial ribs; subequal with spire; and below the periphery marked with many prominent spiral ridges. Aperture is not well preserved.

Measurements (in mm).—

TMNH coll. cat. no.	Height	Width	Height of body whorl	Height of aperture	Apical angle
02138	37.0+	16.6	17.3+	–	32°
02139	30.6+	13.1	15.2+	–	30°
02140	39.0+	18.8	–	–	32°

Stratigraphic range.—Middle member of the Binai Khola Formation.

Fossil Localities.—F-19, F-8806, F8812.

Remarks.—There are only three slightly well preserved specimens and five poorly preserved ones. Although the shell surface as well as shape can be clearly seen, due to the lack of complete specimens characters such as the aperture cannot be observed. This species differs from *Brotia palaeocostula* in shell surface sculptures and size; the former has well developed axial ridges with weak spiral ridge and is smaller in size. It shows some similarity to fossil *Melania pseudepiscopalis* Blanford, 1883, but the present species has more closely placed axial ribs and is smaller in size. It is also somewhat similar in shell sculpture to *Thiara (Melanoides, 1876) herculea* (Hanley and Theobald, 1876) which is considered to be a synonym of *Brotia (Brotia) costula costula* by Brandt (1974). However, the present species is much smaller in size with weakly developed spiral threads and prominent axial ribs which do not develop spines. *Brotia* sp. B has more widely placed axial ridges with absence of spiral sculpture and *Brotia* sp. C has both spiral and axial sculpture more well developed than in *Brotia* sp. A. Due to lack of more well preserved specimens further identification is difficult.

Brotia sp. indet. **B**

Figures 6-4—7

Materials.—TMNH02141, TMNH02142, TMNH02143, TMNH02144.

Description.—Shell moderately large for the genus, 30 to 60 mm long, dextral, slender, elongated conic in shape, moderately thin. Spire long, more than two-thirds of the shell length, consisting of only six remaining whorls. Apex and early whorls eroded. Side of whorls obtusely rounded, slowly increasing in diameter. Suture impressed. In the early whorls shell surface sculptured with comparatively closely placed prominent axial ridges, slightly enlarged around the peripheral area. In the later whorls axial ridges more widely spaced and in the last two whorls ridges produced into short blunt tubercles. Axial ridges do not extend beyond the suture. Spiral sculpture absent. Body whorl a little larger and moderately rounded. Aperture not preserved.

Measurements (in mm).—

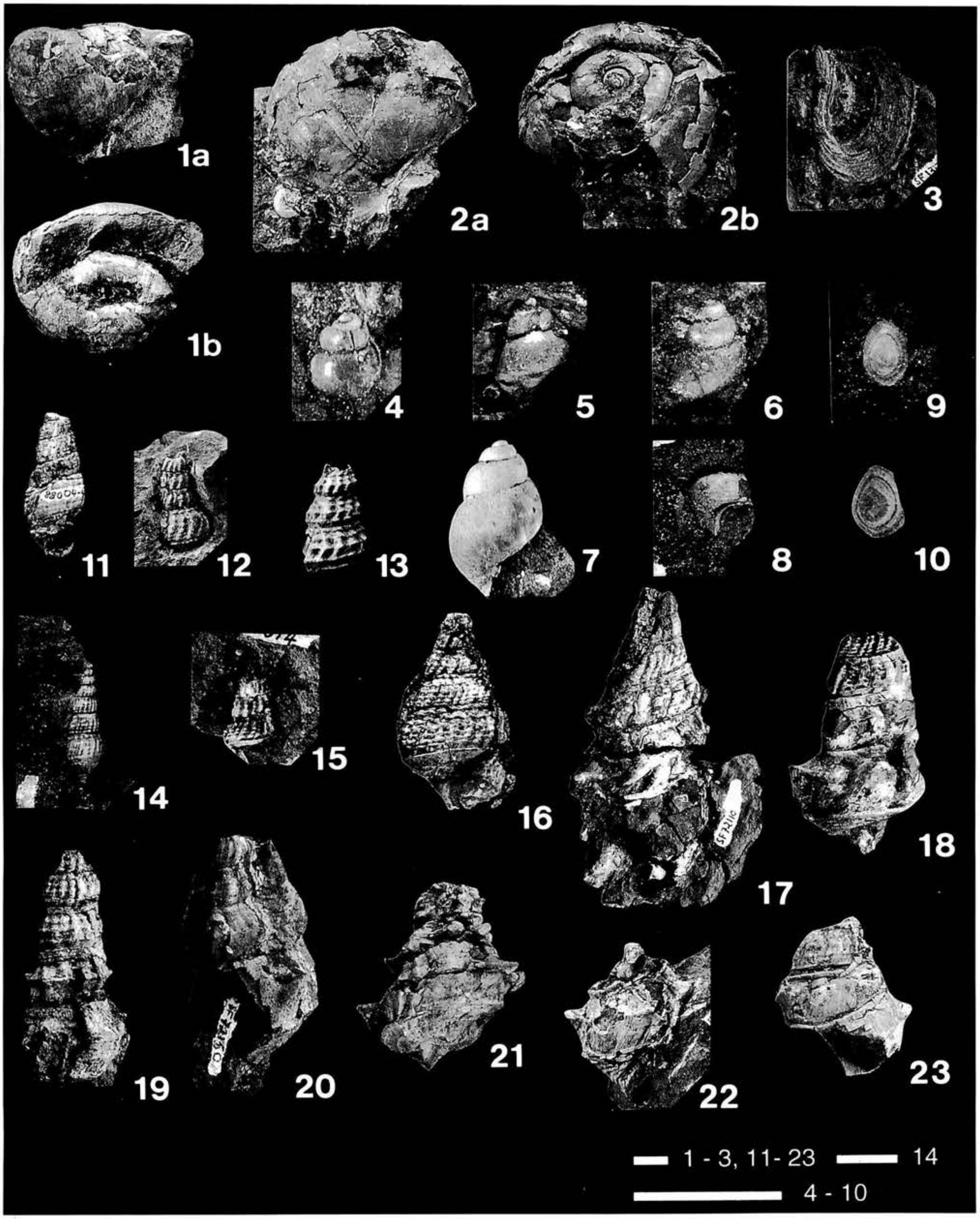
TMNH coll. cat no.	Height	Width	Height of body whorl	Height of aperture	Apical angle
02141	56.5+	21.2+	25.0+	–	32°
02142	33.2+	9.5+	11.0+	–	–
02143	20.0+	8.0+	8.0+	–	–
02144	23.8+	10.2+	13.2+	–	–

Stratigraphic range.—Middle member of the Binai Khola Formation.

Fossil Localities.—F-13, F-8806, F-8812.

Remarks.—Although the shell shape and the sculpture of the poorly preserved sample clearly indicate its relation to the genus *Brotia*, further identification is difficult. There are only three specimens so far, one each from localities F-8806, F-

Figure 5. **1-3.** *Pila* sp. indet., 1: TMNH 02112, 2: TMNH 02111, 3: Operculum, TMNH 02113. **4-10.** *Bithynia* sp. indet., 4: TMNH 02114, 5: TMNH 02117, 6: TMNH 02118, 7: TMNH 02116, 8: TMNH 02121, 9: TMNH 02122, 10: TMNH 02123. **11-16.** *Melanoides* cf. *tuberculata*, 11: TMNH 02124, 12: TMNH 02125, 13: TMNH 02126, 14: TMNH 02128, 15: TMNH 02127, 16: TMNH 02128. **17-23.** *Brotia palaeocostula* sp. nov., 17: holotype, TMNH 02130, 18: paratype 1, TMNH 02131, 19: paratype 2, TMNH 02132, 20: TMNH 02134, 21: paratype 3, TMNH 02133, 22: TMNH 02135, 23: TMNH 02136. All scale bars: 5 mm.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88012 and F-13. The present specimens differ from *Brotia palaeocostula, Brotia* sp. A, and *Brotia* sp. C in having simple surface sculpture consisting of comparatively widely spaced axial ribs with absence of spiral sculpture.

Brotia sp. indet. **C**

Figures 6-8—11

Materials.—TMNH02145, TMNH02146, TMNH02147, TMNH02148.

Description.—Shell small in size for the genus, 20 to 35 mm long, dextral, slender, narrowly conic in shape, moderately thin. Spire high, long, more than half the shell length, consisting of six remaining convex whorls. Apex and early whorls eroded. Whorls slowly increasing in diameter with obtusely rounded sides, later ones less rounded and angled due to more developed subsutural and subperipheral spiral ridges. Body whorl large, rounded with nearly straight flat side between upper and lower spiral sculpture. Suture distinct but shallow. Shell surface marked by four to five thin spiral threads crossing the stronger axial ridges, giving a beaded appearance to the axial ridges. The axial rib does not extend beyond the suture. Basal part of the body whorl with spiral ridges only. Aperture not observed.

Measurements (in mm).—

TMNH coll. no. cat.	Height	Width	Height of body whorl	Height of aperture	Apical angle
02145	31.8+	11.2+	18.6+	—	50°
02146	20.7+	8.0	8.2	—	50°
02147	31.8+	13.5+	12.4+	—	50°
02148	28.7+	12.0+	10.4+	—	—

Stratigraphic range.—Middle member of the Binai Khola Formation.

Fossil Localities.—F-25, F-8806, F-17.

Remarks.—The specimens of this species are also few and poorly preserved. However, in shell sculpture it is quite different from the previously described three forms. Although the present fossil species is small in size for the genus, its characteristic turreted shell with distinct axial and spiral sculpture shows its affinity to *Brotia,* H. Adams rather than *Melanoides* Olivier. It shows some similarity in surface sculpture to the Recent species *Brotia (B.) pseudoasparata* Brandt, 1968, distributed in Southeast Asia; but the former is much smaller in size and has a greater number of spiral ridges. Further identification is difficult until better preserved samples are found.

Subclass Pulmonata
Order Basommatophora Keferstein, 1864
Family Lymnaeidae Gray, 1842
Genus **Lymnaea** Lamarck, 1799

Type species.—*Limnaea stagnalis* (Linné)=*Helix stagnalis* Linné, 1758. Recent: Europe and Asia.

Distribution.—Worldwide.

Geologic range.—Palaeocene to Recent.

Lymnaea sp. indet.

Figures 6-12—13

Materials.—TMNH02149, TMNH02150.

Description.—Shell medium for the genus, dextral, elongate ovate in outline, rather thin. Spire small, acuminated, nearly equal in height with the width of the suture at the base of the spire. Body whorl much longer and larger than the spire, outer lip expanded and convex. Surface of the body whorl marked with fine growth lines. Aperture, columella and spire whorls not observed.

Measurements (in mm).—

TMNH coll. cat. no.	Height	Width	Height of body whorl	Apical angle
02149	11.4+	7.0+	9.4+	—
02150	3.2+	2.3	2.8	—

Stratigraphic range.—Middle member of the Binai Khola Formation.

Fossil Localities.—F-13, F-17.

Remarks.—So far only two specimens, incompletely preserved, have been collected from localities F-13 and F-17 (Figure 2). The shell is not completely preserved, but shell form is most like that of *Lymnaea* Lamarck. From its much larger body whorl, in comparison to the spire, and slightly expanded outer lip, the specimen from F-17 is distinguished as *Lymnaea* Lamarck. However, the second specimen from F-13 is of small size for the genus. Further identification can be done only if better preserved specimens can be collected. The rare occurrence of this species in the fossil assemblage is most probably due to the fragile nature of the shell of this group. Bhatia (1974) reported two species of *Lymnaea* from the Pleistocene of Upper Karewa, Kashmir, *L. (Galba) andersoniana* forma *similans* (Preston) and *L. (Pseudosuccinea) acuminata* (Lamarck) forma *hians* (Sowerby).

Family Planorbidae Gray, 1840
Genus **Indoplanorbis** Annandale and Prashad, 1921

Type species.—*Planorbis exustus* Deshayes. Recent: Malabar Coast.

Distribution.—South and Southeast Asia.

Geologic range.—Pliocene to Recent.

Remarks.—The genus *Indoplanorbis* Annandale and Prashad, differs from genus *Bulinus* Müller, in having a discoid shell and in certain minor anatomical characters (Hubendick, 1955).

Indoplanorbis cf. **exustus** (Deshayes, 1834)

Figures 6-14—15

Materials.—TMNH02151, TMNH02152.

Description.—Shell large in size for the family, discoidal and moderately thick. Upper and lower sides somewhat concave. The specimen consists of three to four whorls, rapidly increasing in size and rounded. All the whorls not

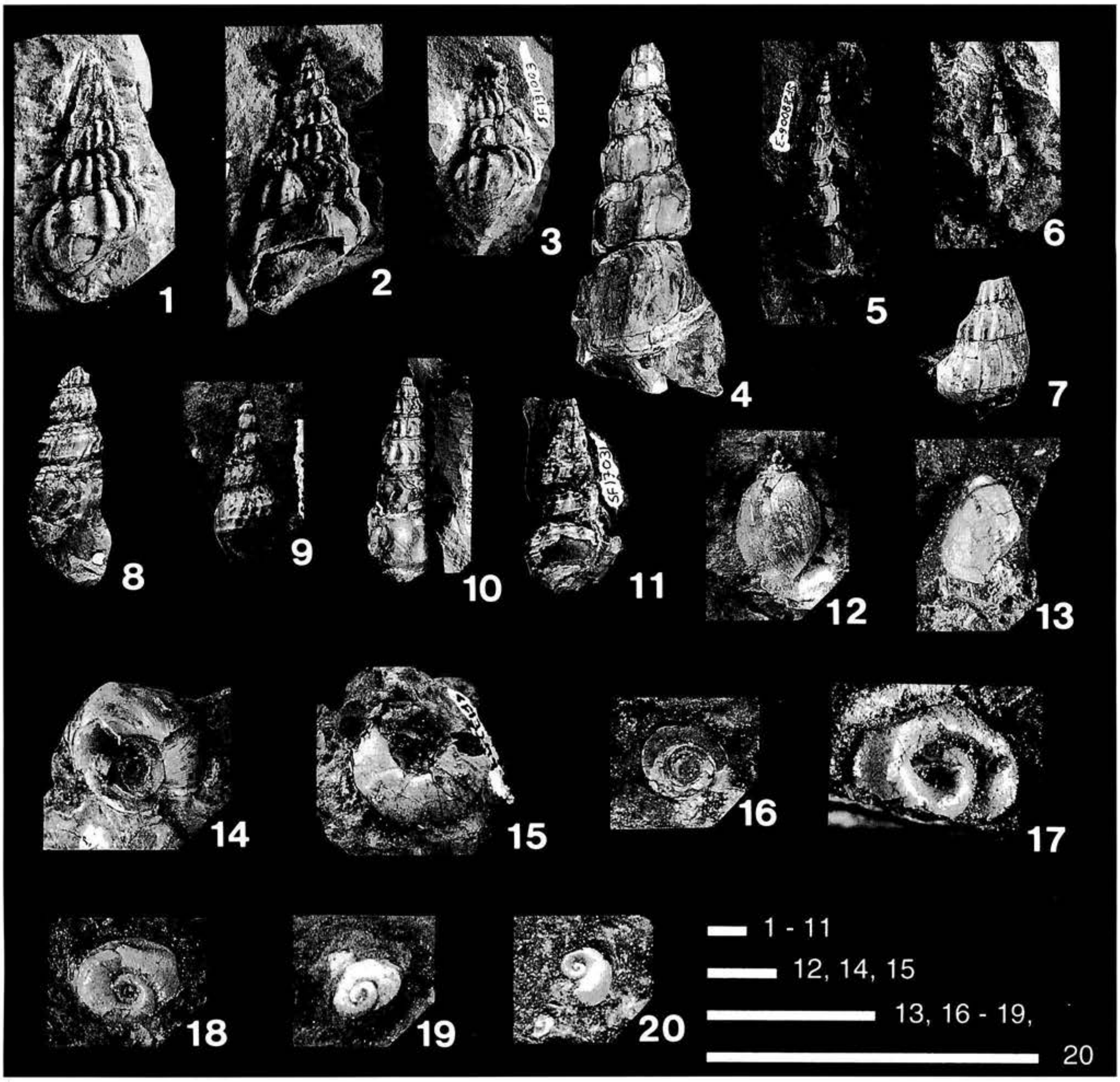

Figure 6. **1-3.** *Brotia* sp. indet. A, 1 : TMNH 02138, 2 : TMNH 02139, 3 : TMNH 02140. **4-7.** *Brotia* sp. indet. B, 4 : TMNH 02141, 5 : TMNH 02142, 6 : TMNH 02143, 7 : TMNH 02144. **8-11.** *Brotia* sp. indet. C, 8 : TMNH 02145, 9 : TMNH 02146, 10 : TMNH 02147, 11 : TMNH 02148. **12, 13.** *Lymnaea* sp. indet., 12 : TMNH 02149, 13 : TMNH 02150. **14, 15.** *Indoplanorbis* cf. *exustus*, 14 : TMNH 02151, 15 : TMNH 02152. **16-20.** *Gyraulus* sp. indet., 16 : TMNH 02154, 17 : TMNH 02155, 18 : TMNH 02153, 19 : TMNH 02156, 20 : TMNH 02157. All scale bars : 5 mm.

visible from basal side. Suture distinctly impressed. Surface of the shell marked with irregular but distinct growth striation. Aperture not preserved.

Measurements (*in mm*).—

TMNH col. cat. no.	Height	Diameter	Height of aperture
02151	6.0+	10.9+	–
02152	4.0+	10.0+	–

Stratigraphic range.—Middle member of the Binai Khola

Formation.

Fossil Locality.—F-13.

Remarks.—Large number of incomplete and broken specimens are collected from locality F-13, only two are more completely preserved. The aperture is not preserved and the shell is slightly compressed with only one side visible. The present specimen is most similar to the Recent widely distributed *Indoplanorbis exustus* (Deshayes) in shape, size and surface sculpture. Bhatia (1974) reported *I. exustus* from the Pleistocene Upper Karewa, Kashmir, India, his specimens are much larger than the presently reported specimens which may be immature shells.

Genus ***Gyraulus*** Charpentier, 1837

Type species.—*Planorbis albus* Müller=*Planorbis hispidus* Draparnaud. Recent: Switzerland.

Distribution.—Europe, Asia, Africa and North America.

Geologic range.—Jurassic? to Recent.

Remarks.—The discoidal shell of this genus is small, less than 10 mm in diameter.

Gyraulus sp. indet.

Figures 6-16—20

Materials.—TMNH02153, TMNH02154, TMNH02155, TMNH02156, TMNH02157.

Description.—Shell very small in size, ranging from 2 to 4 mm in diameter, discoidal, dextral and thin. All the whorls visible from above but apical part cannot be observed. Whorls increasing in diameter rapidly and consist of two and a half to three whorls. Body whorl larger and a little expanded around the aperture.

Measurements (in mm).—

TMNH coll. cat. no.	Height	Diameter	Height of aperture
02153	–	2.5+	–
02154	–	4.0+	–
02155	–	2.5+	–
02156	–	1.5+	–
02157	–	0.8+	–

Stratigraphic range.—Middle member of the Binai Khola Formation.

Fossil Localities.—F-13, F-72, F-21.

Remarks.—The shells of this species are abundant at few localities. Generally only one side of specimens can be observed, preventing accurate identification. These small, discoid and dextral shells are grouped into *Gyraulus* Charpentier. Due to the thin and fragile nature of the shell, preservation is poor, identification to species level is not possible at present. In the fossil state the genus is reported by Bhatia (1974) from the Pleistocene Upper Karewa, Kashmir.

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Two new *Nilssoniocladus* species from the Jurassic (Oxfordian) Tochikubo Formation, Northeast Honshu, Japan

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Abstract. **Two new *Nilssoniocladus* species are erected based on the well preserved specimens collected from the Tochikubo Formation (Oxfordian), Soma-Nakamura Group, Northeast Honshu, Japan. Both *Nilssoniocladus tairae* sp. nov. and *N. japonicus* sp. nov. are represented by long and short shoots terminally with a rosette of leaves. Detached leaves of *Nilssoniocladus* were piled up on the bedding planes, forming so-called '*Nilssonia*' mats which suggest that the leaves of both species are deciduous like those of the type species. The slender habit of long shoots suggests that *Nilssoniocladus* plants are climbers.**

Key words: Late Jurassic (Oxfordian), '*Nilssonia*', *Nilssoniocladus*, *Northeast* Japan, Ryoseki-type flora

Introduction

Instead of a leaf genus '*Nilssonia*', the genus *Nilssoniocladus* was established by Kimura and Sekido (1975) based on a much more complete specimen consisting of a slender long shoot and helically arranged short shoots. The short shoot gives off a terminal rosette of '*Nilssonia*' leaves. The type species is *Nilssoniocladus nipponensis* (Yokoyama) from the Lower Cretaceous Oguchi Formation in the Inner Zone of Japan. In the type specimen (KM-301U), a long shoot, several short shoots and rosettes of leaves are clearly in organic connection.

The leaves appear to be deciduous, because a number of detached leaves of *Nilssoniocladus nipponensis* proximally with expanded petiole base are seen piled up everywhere, forming thick mats. Judging from the slender habit of the long shoot, this plant was thought to be a climber.

Later, Spicer and Herman (1996) described two species of *Nilssoniocladus*, *N. alaskensis* and *N. chukotensis*, from uppermost Albian-lower Cenomanian beds in Alaska and Chukotka (Russia) respectively.

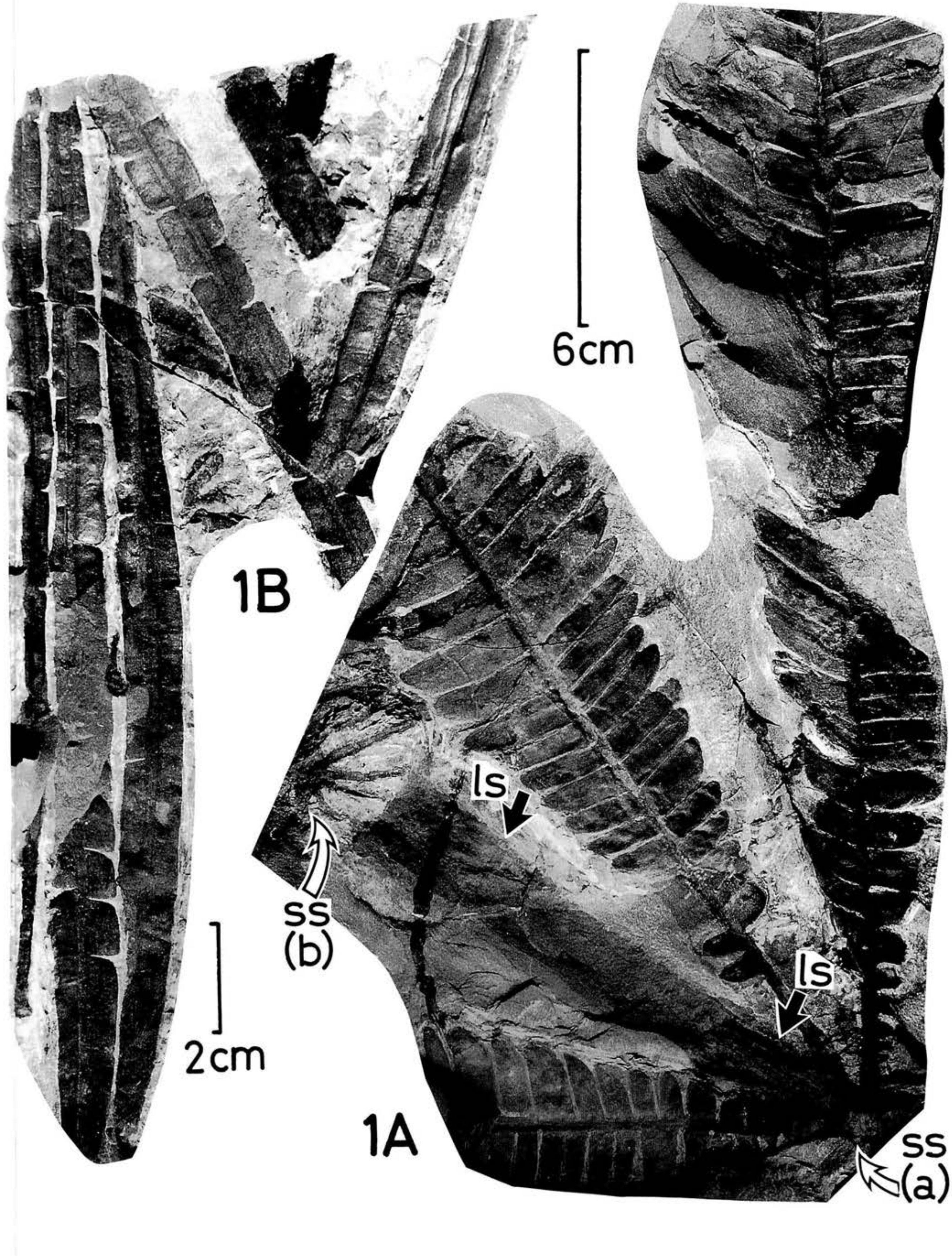
In this paper, we propose two new *Nilssoniocladus* species, *N. tairae* sp. nov. and *N. japonicus* sp. nov., based on newly collected specimens from the fossiliferous Tochikubo Formation, Northeast Honshu, Japan.

The shoots and leaves are sometimes preserved in organic connection. *Nilssoniocladus tairae* bears at least seven leaves terminally to the vertically compressed young short shoot. The leaves of *Nilssoniocladus japonicus* resemble those of '*Nilssonia*' *schaumburgensis* which has been provisionally regarded as '*Nilssonia*' ex gr. *schaumburgensis* (Kimura and Ohana, 1988b) or '*Nilssonia*' sp. cf. '*N*' *schaumburgensis* (Kimura, 1976). They are in organic connection terminally to the vertically compressed young short shoot. In both species, long shoots are poorly preserved, and thus their surface features are uncertain.

The present *Nilssoniocladus* species are associated with various thermophilic Ryoseki-type plant taxa. On the other hand, *Nilssoniocladus nipponensis* (Yokoyama), the type species, is associated with various temperate Tetori-type plant taxa (e.g. Ohana and Kimura, 1995).

Repository.—Specimens utilized and referred in this paper are housed in Kashima History and Folklore Museum, Fukushima Prefecture (KHFM) and Komatsu City Museum, Ishikawa Prefecture; type specimen of *Nilssoniocladus nipponensis* (Yokoyama); KM-301U (KM).

Figure 1. **1A.** *Nilssoniocladus tairae* sp. nov. A poorly preserved long shoot (ls) and two short shoots. The lower short shoot (ss-a) bears four terminally disposed leaves, and in the upper short shoot (ss-b), leaf-laminae are missing leaving six petioles (Holotype, KHFM-210007). **1B.** Detached *Nilssoniocladus Japonicus* leaves (formerly regarded as *Nilssonia* ex gr. *schaumburgensis*) (KHFM-210004).


1B
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Stratigraphy

The Upper Jurassic Tochikubo Formation is a nonmarine sequence belonging to the predominantly marine Soma-Nakamura Group. The Tochikubo Formation is about 350 m thick and intercalated between the marine Callovian Yamagami Formation and the marine Oxfordian-Kimmeridgian Nakanosawa Formation. Stratigraphical details of the Soma-Nakamura Group were given previously by Mori (1963) and a survey of its plant taxa was published by Kimura and Ohana (1988a, b).

This paper deals with the description of two *Nilssoniocladus* species discovered recently. A list of definite *Nilssoniocladus* species hitherto known is given in tabular form.

Systematic description

Class Cycadopsida
Order Cycadales
Family Nilssoniaceae Kimura and Sekido, 1975
Genus ***Nilssoniocladus*** Kimura and Sekido, 1975

Type species.—*Nilssoniocladus nipponensis* (Yokoyama) Kimura and Sekido: Lower Cretaceous Oguchi Formation, Itoshiro Group, Tetori Supergroup in the Inner zone of Japan.

Generic diagnosis.—Stem in ultimate parts slender, branched, consisting of long and short shoots, woody. Long shoot with long and smooth internodes, and bearing short shoots spirally. Short shoots covered with spirally placed rhomboidal leaf scars and at apex bearing a group of '*Nilssonia*' leaves. All leaf scars essentially similar, no scale leaf scars among them. Not possible to observe whether short shoots are in the axil of a leaf or of a scale leaf (Kimura and Sekido, 1975, p. 113).

Nilssoniocladus tairae sp. nov.

Figures 1A, 2A-D, 3A

Material.—Holotype : KHFM-210007. Paratype : KHFM-210006 (counterpart of the holotype). Other specimens : KHFM-210005, 210008, 210009, 210011, 210016.

Locus typicus.—Near Koyamada, Kashima-cho, Soma-gun, Fukushima Prefecture (roughly 37°41′46″N, 140°54′16″E).

Stratum typicum.—Tochikubo Formation (Oxfordian), Soma-Nakamura Group (Mori, 1963).

Derivatio nominis.—Specific epithet after Muneo Taira who collected the specimens described here.

Occurrence.—Locally common.

Specific diagnosis.—Long shoot slender, 1.2 cm wide, giving off short shoots, each terminally with a rosette of seven large-sized leaves. Leaf lamina regularly and deeply cut, forming more than 35 pairs of pinnae. Pinnae rectangular with pointed apices. Petiole shorter with 5-6 pairs of small-sized oval or semicircular pinnae. Veins numerous, simple, parallel, and not convergent at pinna apex.

Description.—Long and short shoots are present. Preserved part of long shoot is 16 cm long and 1.2 cm (partly 1.4 cm) wide, with roughly striated surface ; no other definite scars have been found on the surface.

Preserved part of short shoot is 1.5 cm in diameter, and about 5 mm long (or high). Crushed rhomboidal petiole scars are rarely observed on the surface of the short shoots (Figure 2B). Terminally, the short shoot gives off at least seven leaves, forming a leaf rosette. Estimated length of the internode between successive short shoots is 18-20 cm. Details of mode of arrangement of short shoots on the long shoot are, however, uncertain.

The leaves are large, oblanceolate, more than 30 cm long and up to 8 cm wide. The rachis is prominent, 3-4 mm wide, and has a short and thick petiole which is less than 1 cm long and 4 mm wide ; the base of the petiole is slightly expanded and in organic connection with the top of a short shoot. Leaf lamina is regularly and deeply cut, forming more than 35 pairs of pinnae. Pinnae are typically rectangular ; acroscopic margin is nearly straight, and basiscopic margin is rounded apically. The pinnae of the holotype are 41 mm long and 9 mm wide, rarely narrower ; those of the proximal 5-6 pairs are small and oval or semicircular (Figure 2A).

Veins are prominent, numerous, simple, parallel, and not convergent at pinna apex ; 18 in number in each pinna (22-23 per cm in density).

Leaf cuticle is not preserved, and reproductive organs are not observed.

Remarks.—This new locality of the Tochikubo Formation has yielded a new type of *Nilssoniocladus* leaves as described above. Some leaves are in organic connection to the short shoots of *Nilssoniocladus*, and form a leaf rosette. The leaves also occur as fragments of leaf rosettes in which short shoots are missing. Most parts occur as detached leaves, forming '*Nilssonia*' leaf-mats on the bedding plane. Therefore, the leaves of this species appear to be deciduous. Many leaves have expanded petiole bases. In our new collection, no detached scar of a short shoot has been found on the surface of a long shoot.

We suggest that the short shoots of *Nilssoniocladus tairae* probably belong to a younger development stage, possibly when the plants were two or three years old, because they are shorter in length and not so prominently elongated on the long shoot.

The surface of the long shoot and of the depressed short shoot, and the proximal portions of rachis and petiole are covered with a faded brownish substance. It is probable that these brown stains are due to some resinous substance oozing out from the woody part of the plant.

The abaxial side of the leaves may resemble leaves of bennettitalean *Pterophyllum* and *Ptilophyllum*, in some aspects because the present rachises are markedly exposed in abaxial view. However, laminae of the present leaves completely cover the rachises in adaxial view. This is a characteristic feature of the *Nilssoniocladus* and '*Nilssonia*' leaves.

So far as we know, the leaves of *Nilssoniocladus tairae* are unique in size, shorter petiole and small-sized proximal pinnae.

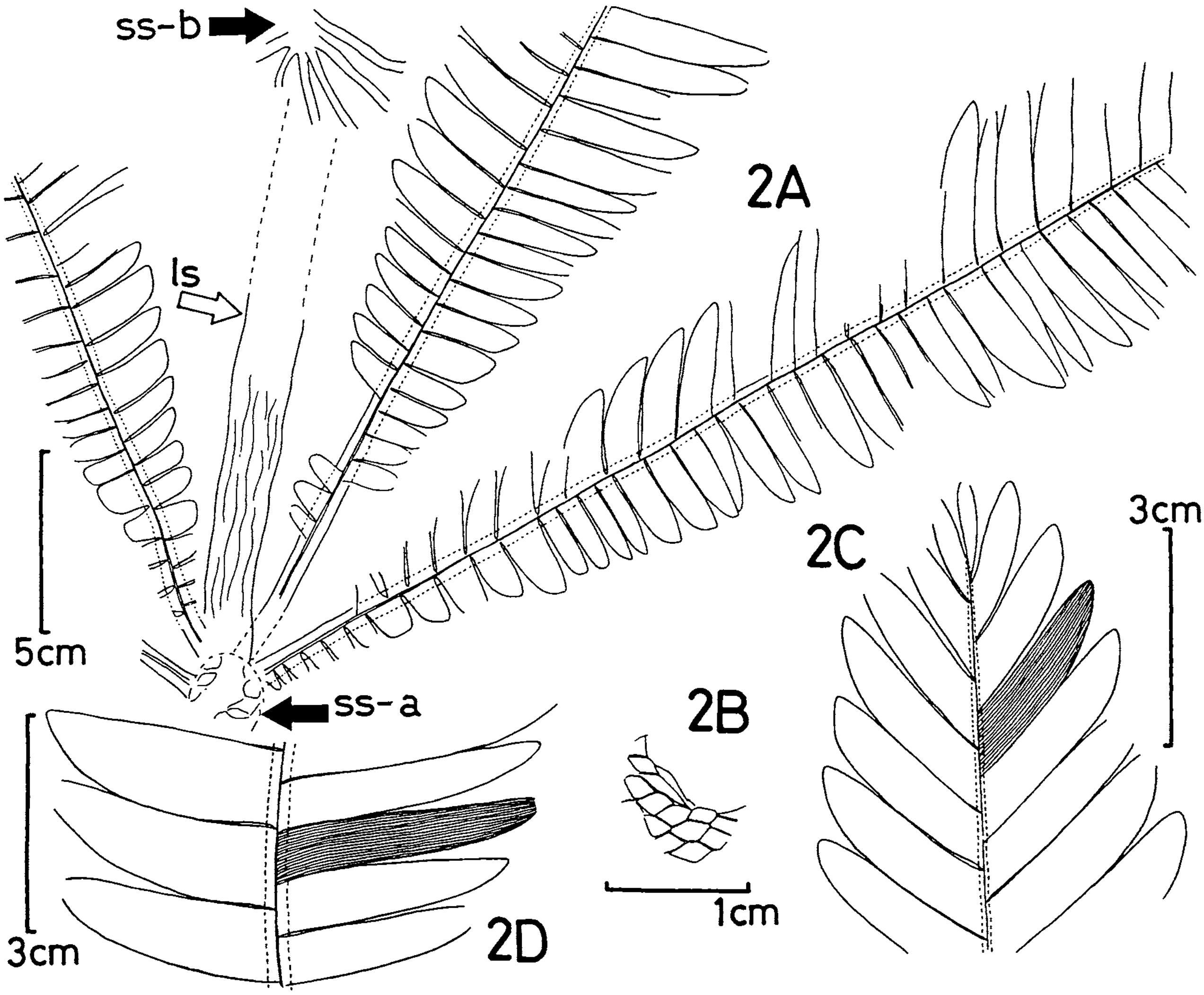


Figure 2. *Nilssoniocladus tairae* sp. nov. **2A.** Drawn on the basis of holotype and paratype. **2B.** Helically disposed rhomboidal petiole bases left around the lateral surface of a short shoot (KHFM210016). Vascular bundles are invisible. **2C.** Apical part of a leaf and venation (KHFM-210011). Pinnae are directed forward. **2D.** Typical pinnae, drawn from the holotype.

Nilssoniocladus japonicus sp. nov.

Figures 1B, 3B-C, 4A-F

Nilssonia ex gr. *schaumburgensis* (Dunker) Nathorst: Kimura and Ohana, 1988b, p. 164, pl. 12, fig. 3; pl. 13, figs. 2-6; pl. 14, figs. 4-5; figs. (text-figs.), 26a-h (Tochikubo Formation).

Material.—Holotype: KHFM-210003. Paratype: KHFM-210002 (counterpart of the holotype). Other specimens: KHFM-210001, 210004, 210018, 210019.

Locus typicus.—Same as *Nilssoniocladus tairae*.

Stratum typicum.—Same as *Nilssoniocladus tairae*.

Derivatio nominis.—After Japan.

Occurrence.—Long and short shoots are rare, but detached leaves formerly regarded as *Nilssonia* ex gr. *schaumburgensis* are quite abundant.

Specific diagnosis.—Each short shoot giving off at least seven leaves. Leaves closely helical at apex of a short shoot, forming a leaf rosette. Leaves long and narrow, nearly parallel-sided, variable in form and size.

Description.—Preserved long shoot is 8 cm long and 7 mm wide with poorly preserved ornamentation on its surface. Short shoot is 1 cm in diameter, and low cylinder-like. The internode between successive short shoots is estimated to be 3.5 cm long.

Leaves are long and narrow, more than 14 cm long and up to 1.3 cm wide, and have rather stout petiole which is 5.5 cm long and 4 mm wide. Seven helically arranged leaves are borne at the top of the short shoot, and form a leaf rosette. Leaf laminae are nearly parallel-sided, completely covering upper surface of prominent rachis. Leaves are variable in form. Some leaves are with entire or irregularly undulated or

Table 1. List of definite *Nilssoniocladus* species. In these species leaf-cuticles and inner anatomical features of the shoots are not preserved.

Nilssoniocladus species (occurrence)	Long shoot	Short shoot	Leaf-type	Reference and age
N. nipponensis (Yokoyama) Kimura and Sekido (Inner zone of Japan)	present	present	*'Nilssonia' nipponensis* Yokoyama (1889)	Kimura and Sekido, 1975; Lower Cretaceous
N. alaskensis Spicer and Herman (Alaska)	present	present	*'Nilssonia' alaskana* Hollick (1930)	Spicer and Herman, 1996; Upper most Albian-lower Cenomanian
N. Chukotensis Spicer and Herman (Chukotka, Russia)	not preserved	present	*'Nilssonia' serotina* Heer (1878)	Spicer and Herman, 1996; Upper most Albian-lower Cenomanian
N. tairae Takimoto, Ohana and Kimura sp. nov. (Northeast Honshu, Japan)	present	present	*Nilssoniocladus tairae* Takimoto, Ohana and Kimura sp. nov.	Takimoto, Ohana and Kimura, this work; Oxfordian
N. japonicus Takimoto, Ohana and Kimura sp. nov. (Northeast Honshu, Japan)	present	present	*'Nilssonia' schaumburgensis* (Dunker) Nathorst-like	Takimoto, Ohana and Kimura, this work; Oxfordian

shallowly dissected margins, some leaves are rather deeply dissected into rectangular segments with truncated distal margins, and some leaves are dissected into semicircular segments (pinnae) (e.g. Kimura, 1976; Kimura and Ohana, 1988b). These leaf-types are specifically inseparable, and may be included in a wide range of continuous intraspecific variation. The largest lamina is more than 17.5 cm long and 2.1 cm wide. Apex is broadly rounded or sometimes shallowly emarginate. The petiole base is expanded laterally. In some cases, several vascular bundle scars (?) are seen in a semicircular row (Figure 4F). Veins are densely crowded, simple, parallel and typically 44 per cm.

Cuticle is not preserved and the reproductive organs are not observed.

Remarks.—The leaves of *Nilssoniocladus japonicus* were found detached and piled up together on the same bedding plane, indicating that they were deciduous.

These detached leaves are similar in form to those originally described by Dunker (1846) as *Pterophyllum schaumburgense* from the Wealden beds of North Germany, and later transferred to *Nilssonia* by Nathorst (1890) based on specimens collected from Lower Cretaceous sites in the Outer Zone of Japan. However, it is still uncertain whether the Japanese leaves are really conspecific with the German leaves or not, because neither preserve cuticles. We provisionally described the detached Japanese leaves as *'Nilssonia'* ex gr. *schaumburgensis* (Dunker) Nathorst or *'Nilssonia'* sp. cf. *'N' schaumburgensis* (Dunker) Nathorst.

Generally, Late Jurassic *'Nilssonia' schaumburgensis*-like leaves in Japan are nearly twice as large as those of Early Cretaceous leaves in Japan. We propose *Nilssoniocladus japonicus* sp. nov. for the Jurassic specimens having larger leaves.

The surface of long and short shoots is also covered with a faded brownish substance of the same probable origin as suggested above.

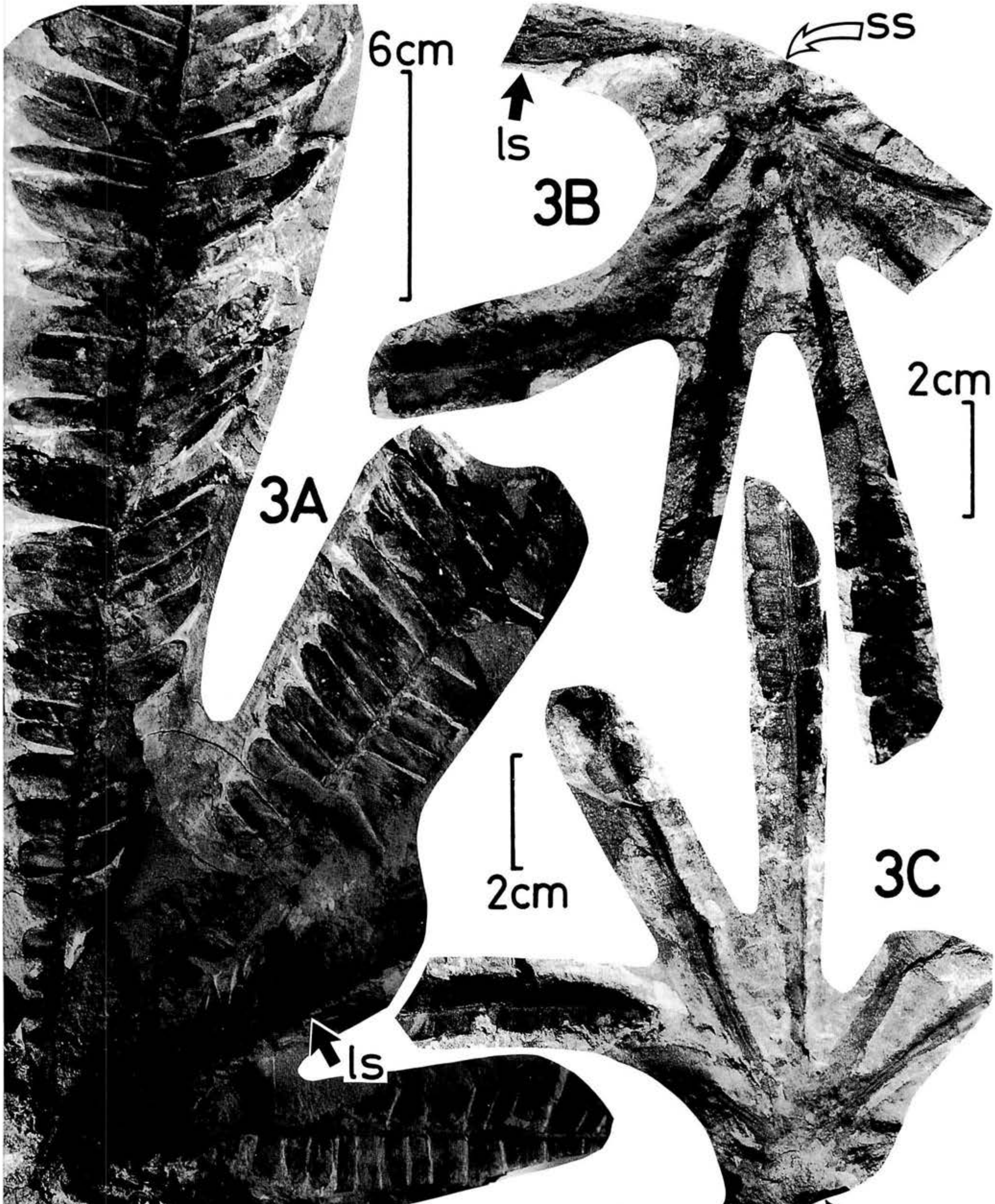
Comparison and discussion

As shown in the original line drawing, the type species *Nilssonicladus nipponensis* has a slender long shoot with a smooth surface (Kimura and Sekido, 1975, text-fig. 1). No surface ornamentation, such as longitudinal wrinkles, short shoot scars and growth increment boundary like those reported for *Nilssoniocladus alaskensis* Spicer and Herman (Spicer and Herman, 1996), has been observed. In *Nilssoniocladus chukotensis* Spicer and Herman, short shoots were shed together with the leaf rosettes (Spicer and Herman, 1996). Such a shedding of short shoots has so far not been recognized in the Japanese species.

There are many plant sites in the Tochikubo Formation, but the occurrence of *Nilssoniocladus tairae* and its detached leaves appears to be restricted to the new locality. Therefore, *Nilssoniocladus tairae* is considered to be a local or endemic species in the Tochikubo Formation.

Matsuo (1976) illustrated mature and developed short shoots terminally with a cluster of three leaves and two scar-like imprints on a slender long shoot from the Lower Cretaceous Oguchi Formation in the Inner Zone of Japan. In his paper (written in Japanese), he regarded these leaves as *Nilssonia nipponensis*, ignoring the established genus *Nilssoniocladus* (Kimura and Sekido, 1975). Although Ma-

Figure 3. **3A.** *Nilssoniocladus tairae* sp. nov. Counterpart of the holotype (paratype, KHFM-210006). **3B, 3C.** *Nilssoniocladus japonicus* sp. nov., **3B:** Long shoot (ls) is poorly preserved. Short shoot (ss) bears terminally seven disposed leaves (Holotype, KHFM-210003), **3C:** Counterpart of the holotype (paratype, KHFM-210002). The long shoot (ls) is hidden below the short shoot.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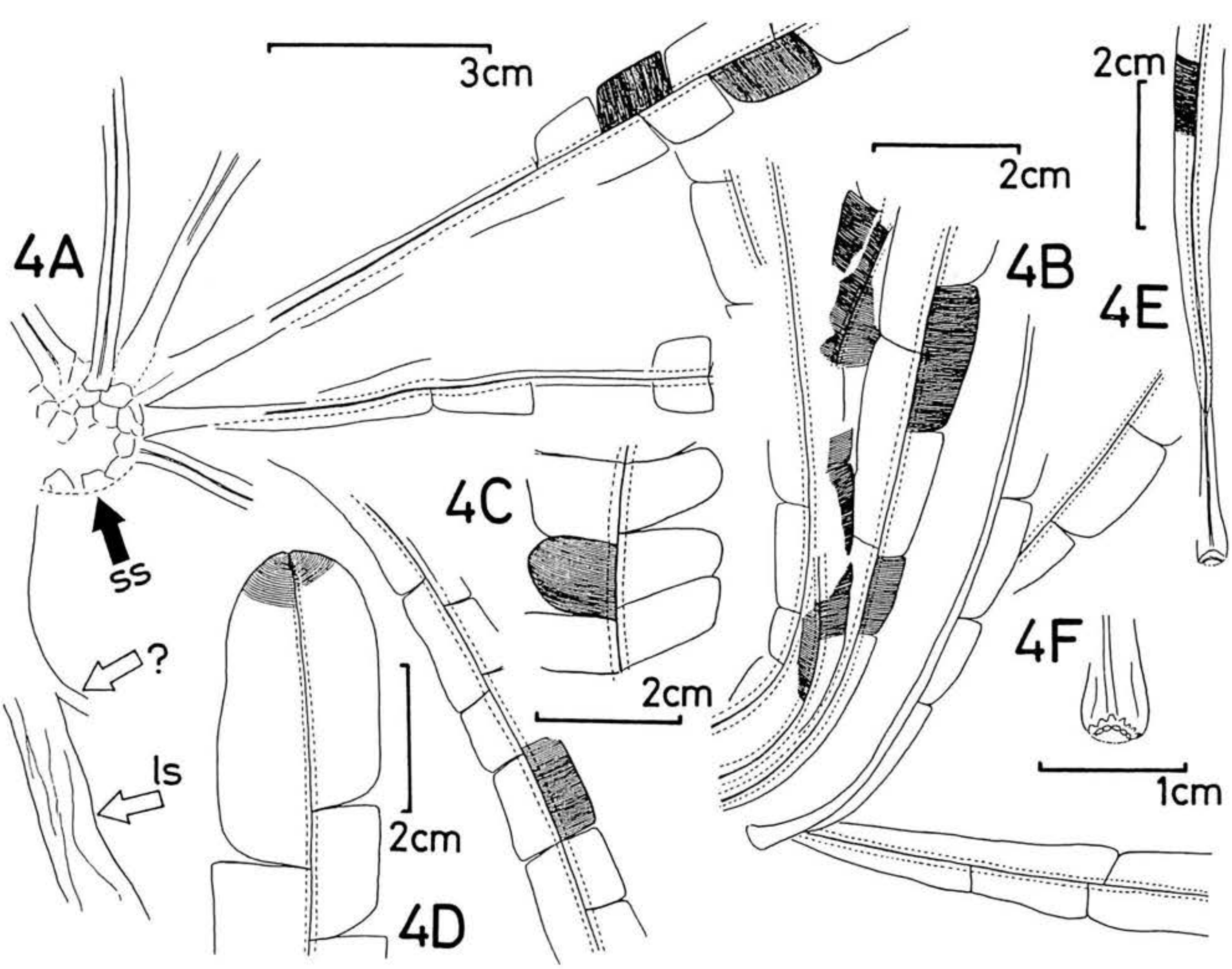

Figure 4. *Nilssoniocladus japonicus* sp. nov. **4A.** Drawn on the basis of holotype and paratype. A projection from the long shoot (arrow ?) is functionally uncertain. **4B.** Detached leaves (KHFM210018). **4C.** Regularly arranged semicircular pinnae of a detached leaf in association with Figure 4D. **4D.** Rounded leaf apex of a large-sized detached leaf and venation, drawn partly from KHFM-210001. **4E.** Lower part of a detached leaf. Lamina of this part is entire (KHFM-210019). Petiole base is expanded and with a clean-cut plane. **4F.** Enlarged from the proximal part of Figure 4E. Several vascular bundle scars (?) are in a semicircular row.

tsuo's line-drawing is simplified, the specimen might belong to *Nilssoniocladus*. The leaves have a characteristic toothed margin and are in our view probably assignable to *Nilssoniocladus lobatidentatus* (Vassilevskaja) known from the Lower Cretaceous of the Lena Basin (e.g. Vassilevskaja *et al*., 1972). Detached leaves with toothed margin also occur from the Lower Cretaceous of the Tetori Basin in the Inner zone of Japan (Kimura and Sekido, 1976a, b).

Krassilov (1975, fig. 18) illustrated a *Nilssoniocladus*-like shoot with a cluster of leaves, but there are no morphological details.

Nilssonia schaumburgensis (Dunker) described by Watson (1969) from the English Wealden beds includes leaf fragments with preserved cuticle. Its laminae are irregularly and shallowly dissected, and have an emarginate apex. Some leaves are regularly dissected, but the sinuses do not reach to the rachis and the venation is not crowded. Although such English leaves superficially resemble the Japanese leaves of '*Nilssonia*' ex gr. *schaumburgensis* or '*N*' sp. cf. '*N*' *schaumburgensis*, it is uncertain whether these English leaves are conspecific with the Japanese leaves described here.

The *Nilssoniocladus* plants are considered to be woody climbers, because their slender long shoots bearing the load of large-sized leaf rosettes could not have kept the plants upright.

It is likely that the number of *Nilssoniocladus* species will increase in future. Because we know a number of the tufts of '*Nilssonia*' leaves hitherto described, all of which seem to converge toward a common point.

An attached table shows a list of definite *Nilssoniocladus* species hitherto known.

Acknowledgments

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Further notes on the ammonoid genus *Parajaubertella*

(Studies of Cretaceous Ammonites from Hokkaido and Sakhalin-LXXX)

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Abstract. **On the basis of additional material, a revised diagnosis of *Parajaubertella kawakitana* Matsumoto, 1943 is given and *P. zizoh* sp. nov. is established. While the former is fairly large, the latter is small. The globose shell, consisting of much depressed whorls with a deep and narrow umbilicus and a subangular umbilical edge, occurs for a while in the ontogenetic development of *Parajaubertella*. In *P. kawakitana* this character occurs in an early substage (shell diameter from 5 mm to 35 mm), and is followed by a long-continued middle stage, whereas in *P. zizoh* it appears somewhat later and extends to an early part of the adult body chamber. The adult body chamber is characterized by the bandlike or low, foldlike, broad ribs separated by narrow grooves (=adult *sacya*-type ornament) in both species. Their common ancestor, if any, has not been found. On the basis of the characters of the two species, *Parajaubertella* is referred to the Gaudryceratidae instead of the Tetragonitidae. The two species occur commonly in the Lower Cenomanian, but the level of their first appearance has yet to be investigated.**

Key words: Cenomanian, dimorphism, Gaudryceratidae, *Parajaubertella, P. kawakitana, P. zizoh*

Introduction

The ammonite genus *Parajaubertella* was established by Matsumoto (1943) under the family Gandryceratidae on a species from South Sakhalin and Hokkaido. Because of its peculiar characters and probably because of the too short description in the original paper, its systematic position has been interpreted in different ways by authors (*e.g.* Wright, 1957, Wiedmann, 1962a, b; Murphy, 1967; Howarth, 1996).

P. kawakitana Matsumoto, 1943, the type species, was recently described in detail by Matsumoto (1995, p. 11-27, figs. 3-13) under the Gaudryceratidae, while the revised edition of the *Treatise on Invertebrate Paleontology*, Part L, vol. 4 (Cretaceous Ammonoidea) was under preparation. Matsumoto should have sent a preprinted copy of his manuscript to the editor, but regrettably he failed to do so. Howarth (1996, p. 8 in that revised edition) has assigned *Parajaubertella* to the subfamily Tetragonitinae of the family Tetragonitidae.

In this paper, *P. kawakitana* is redescribed in the light of additional material, and another new species is established on specimens we acquired from the Soeushinai area. To accommodate these two species, a revised diagnosis of *Parajaubertella* is given, along with some comments on the relationships between the species concerned.

We hope that this paper may settle the above systematic problem.

General remarks

Technical terms.—As to the morphological terms and their abbreviations, we follow those in the recently published paper by Matsumoto (1995, p. 7-9).

Repositories.—The specimens which are illustrated and/or measured in this paper are held in the following institutions or collections in the alphabetic order of their abbreviations;

- GK : Type Room, Department of Earth and Planetary Sciences, Kyushu University, Fukuoka
- UMUT : University Museum, University of Tokyo, Hongo, Tokyo
- YKC : Yoshitaro Kawashita Collection, temporarily housed in his residence, but eventually to be transferred to some institutions or museums

Localities.—The localities (abbreviated as loc. in the description below) where the described specimens were acquired are indicated by numbers under the heading KY (collected by K.Y.), R (collected by T. Nishida and others) or YKC (collected by Y. Kawashita). Their sites are shown in the route maps of the recently published papers by Nishida *et al.*, (1996; 1997). They are all in the Soeushinai area of northwestern Hokkaido. As to the Cretaceous stratigraphy of that area, readers may refer to the same papers, in which the scheme by Hashimoto *et al.* (1965) is considerably revised. A few specimens supplied by Takashi Yoshida are from Hirotomi of the Monbetsu area, south-central Hokkaido.

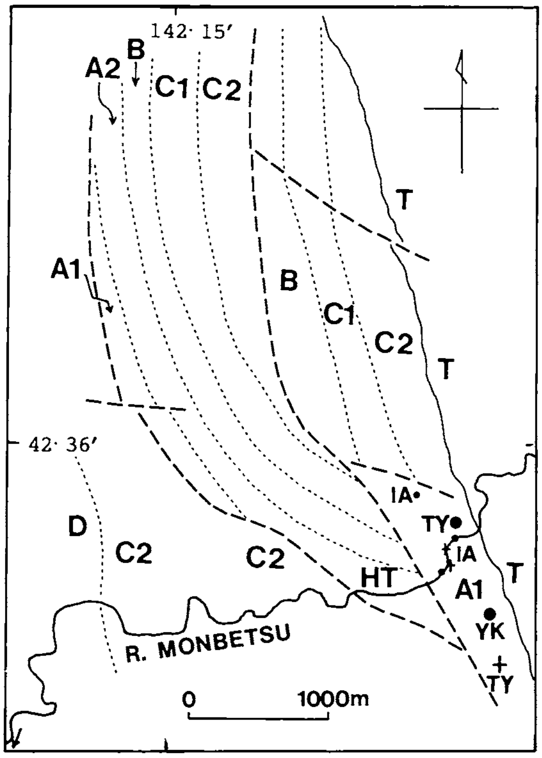


Figure 1. Geological sketch map of Hirotomi, Monbetsu area (courtesy of A. Inoma). The Upper Cretaceous is subdivided in ascending order from Units Al (Lower Cenomanian) through A2, B, C, to D (Campanian) and overlain by a mid-Tertary formation (T) with unconformity. A locality of early Cenomanian ammonite is indicated by a solid circle (in situ) or a cross-mark (transported). A solid circle with TY is BIU570228, and the one with YK is for *Sharpeiceras mexicanum* ; cross-mark with TY is BIU570298 and others with IA are for *Desmoceras* (*Pseudouhligella*) *japonicum* Yabe etc. The location of the mapped area is indicated as M in the general map of Hokkaido by Matsumoto (1995, fig. 2).

Their localities are indicated under the heading BIU and are shown in Figure 1 of this paper.

Paleontological descriptions

Superfamily Tetragonitaceae Hyatt, 1900
Family Gaudryceratidae Spath, 1927
Genus ***Parajaubertella*** Matsumoto, 1943

Type species.—*Parajaubertella kawakitana* Matsumoto, 1943 by original designation (Matsumoto, 1943, p. 666).

Diagnosis (revised).—Shell typically large and fairly involute, but may be small in some species. Whorls at some ontogenetic stage much depressed, with broadly rounded venter, inflated flanks, subangular umbilical edge and fairly narrow and deep umbilicus, resulting in small but globose shell form. Whorl of late growth stage, including the adult body chamber, suboval or subrounded in section and provided with flat-topped or low foldlike, broad ribs separated by narrow grooves as in those of adult *Anagaudryceras sacya* (Forbes) (Figure 2 and also Matsumoto, 1995, fig. 18). Lirae on the shell surface, periodic collars during growth and ribs of the adult body chamber subradial and gently flexuous on the flank and weakly or somewhat projected on the venter. Suture fundamentally similar to that of *Gaudryceras*, with formula E, L, U_2, U_1[=S], I. At the stage of small globose shell, the third lateral saddle situated on the umbilical edge.

Discussion.—One of us (Matsumoto, 1995, p. 10) has recently concluded that *Parajaubertella* is distinct from *Gabbioceras* Hyatt and that it is not a member of the subfamily Gabbioceratinae. Now, let us discuss the problem of whether it is more reasonable to ascribe *Parajaubertella* to the Tetragonitinae or to the Gaudryceratidae.

The suture of *Parajaubertella* is similar to that of *Eogaudryceras, Anagaudryceras* and *Gaudryceras* in the constituting elements, with a single main saddle in the internal part and symmetrically bifid saddles in the external part. That of Tetragonitinae has two or more internal saddles and asymmetric or even apparently tripartite saddles in the external part (see Wiedmann, 1962a, 1973 ; Matsumoto, 1959).

The type species and another new species of *Parajaubertella* are closely allied to *Anagaudryceras sacya* in having fine lirae on the surface of the outer shell layer and also the same type of ornament on the adult body chamber as described in generic diagnosis. In both genera the lirae, constrictions, collars and major ribs are gently flexuous on the flank and more or less weakly projected from the ventrolateral shoulder to the venter. In some individuals of *A. sacya* (Forbes) major ribs may appear for a short while at a middle growth stage as is illustrated by Kennedy and Klinger (1979, pl. 9, fig. 1) and shown by an example (Figure 2) from Hokkaido. This feature is somewhat similar to that of the middle-aged *P. kawakitana*.

In *Tetragonites* periodic constrictions and growth lines are generally prorsiradiate on the flank and more or less rursiradiate on the ventrolateral shoulder, crossing the venter with a weakly backward sinus. Howarth (1996, p. 8) attempted to compare *Parajaubertella* with *Takahashia* of the Tetragonitinae. The ribs of *Takahashia* Matsumoto, 1984 (p. 33, fig. 1) are rather rursiradiate on sides, crossing the venter with a backward sinus. They are analogous to those of a nautiloid genus *Cymatoceras* and not comparable with those of *Parajaubertella*.

These features evidently indicate that *Parajaubertella* belongs to the Gaudryceratidae.

Parajaubertella kawakitana Matsumoto, 1943

Figures 3—6

Synonymy.—See Matsumoto, 1995, p. 11.

Material.—The following specimens are added herein to the holotype and other specimens listed by Matsumoto (1995, p. 12) : YKC610608 (Figure 3-2) obtained in situ at loc. R518 and YKC060823 (Figure 4) at loc. R521p, on the eastern branch of the Suribachi-zawa ; YKC050609 from the Bishamon-zawa, YKC080621 (Figure 5) from loc. R909 of the Hotei-zawa ; YKC080615 and YKC081029 from the upper

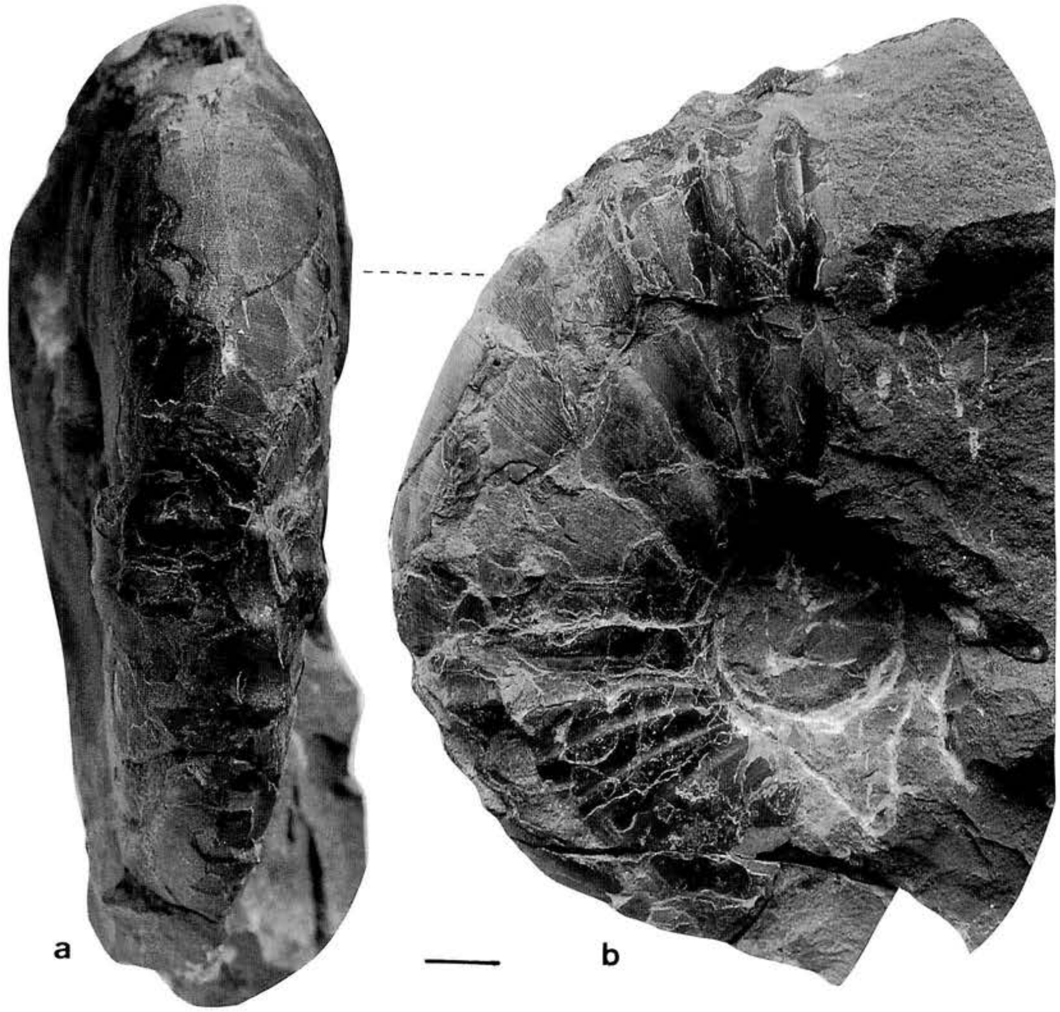


Figure 2. *Anagaudryceras sacya* (Forbes). YKC060825 from loc. R540p. Back (a) and side (b) views, x 1. An example in which major ribs appear for a short while at a distance adapically from the typical adult *A. sacya*-type ornament. Bar scale : 10 mm. (Photos by courtesy of Katsumi Shinohara.)

reaches of the Kyoei-sakin-zawa ; these are all from Member My3 of the Soeushinai area. YKC080914 (Figure 3-1) from loc. R987p, lower part of My5, upper reaches of the Kotanbetsu River.

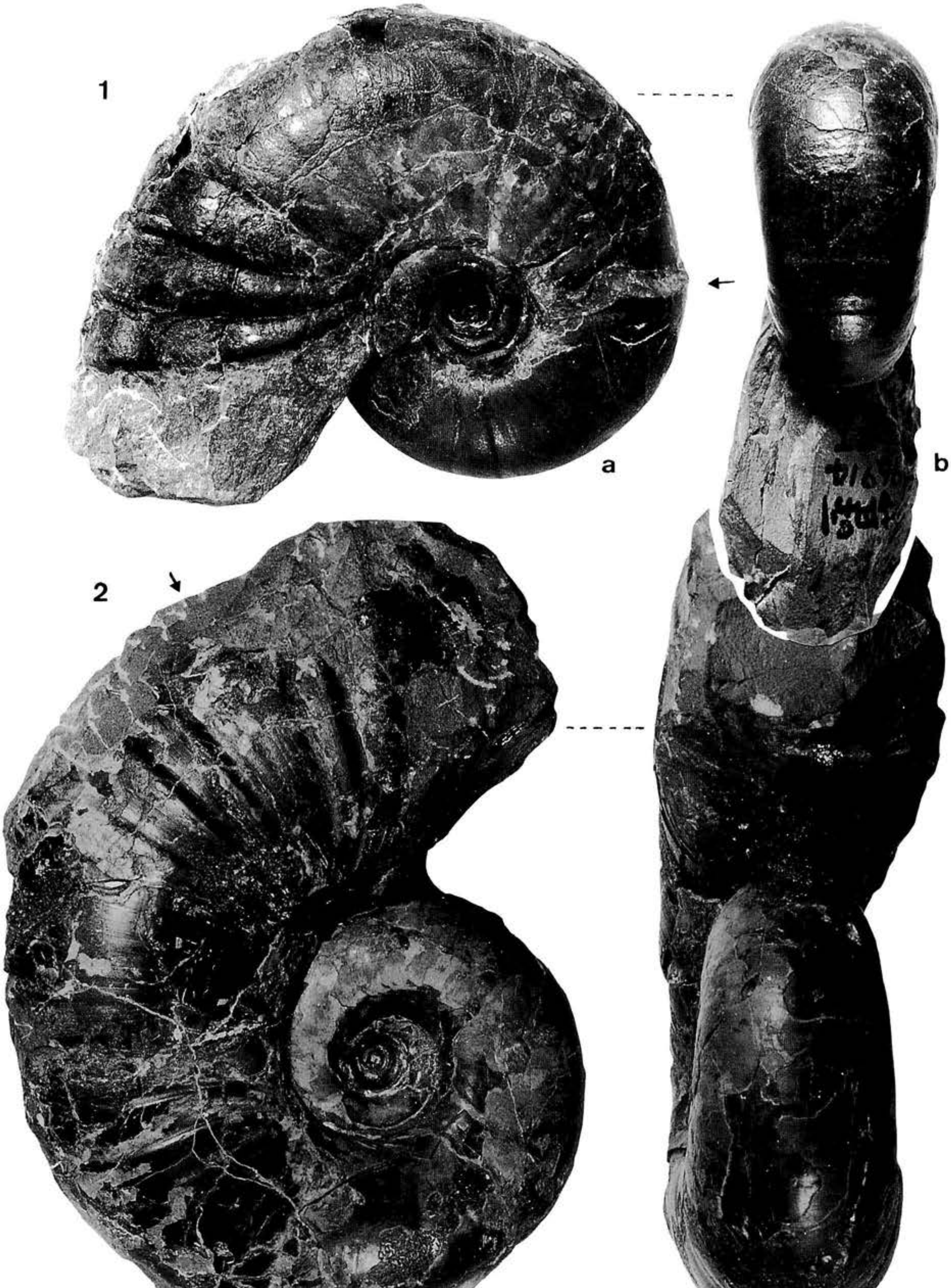
GK.H8479 (Figure 6) from loc. BIU570298, GK.H8480 and GK.H8481 from loc. BIU570228 [=BIU570235], near Hirotomi of the Monbetsu area, where an unnamed member of mudstone extends narrowly trending NNE-SSW along the Chennai-zawa, a branch rivulet of the Monbetsu River (see Figure 1).

Diagnosis.—Small shell of early growth stage globose, with narrow and deep umbilicus and depressed whorl section. Whorl of middle growth stage long continued, showing gradual change from subrounded to suboval section and ornament of several rhythmic furrows occurring in periodic segments, where a constriction with associated collar and faint, incipient major ribs may sometimes appear. Adult shell large, about 200 mm diameter on average ; its body chamber provided with the adult *A. sacya*-type ornament as described in the generic diagnosis.

Dimensions.—See Table 1.

Description.—The very young shell up to about 5 mm in diameter is similar to that of *Gaudryceras* and *Anagaudryceras* (see Matsumoto, 1995, fig. 5). The succeeding young

Figure 3. *Parajaubertella kawakitana* Matsumoto. **1a, b.** YKC080914, in a nodule obtained at loc. R987p. **2a, b.** YKC610608 from loc. R518 (in situ). Left lateral (a) and frontal (b) views, xl. In both specimens the body chamber is incomplete and secondarily compressed. Arrow mark indicates the position of the preserved last septum. Bar scale : 10 mm.


1
a
b
2
a
b

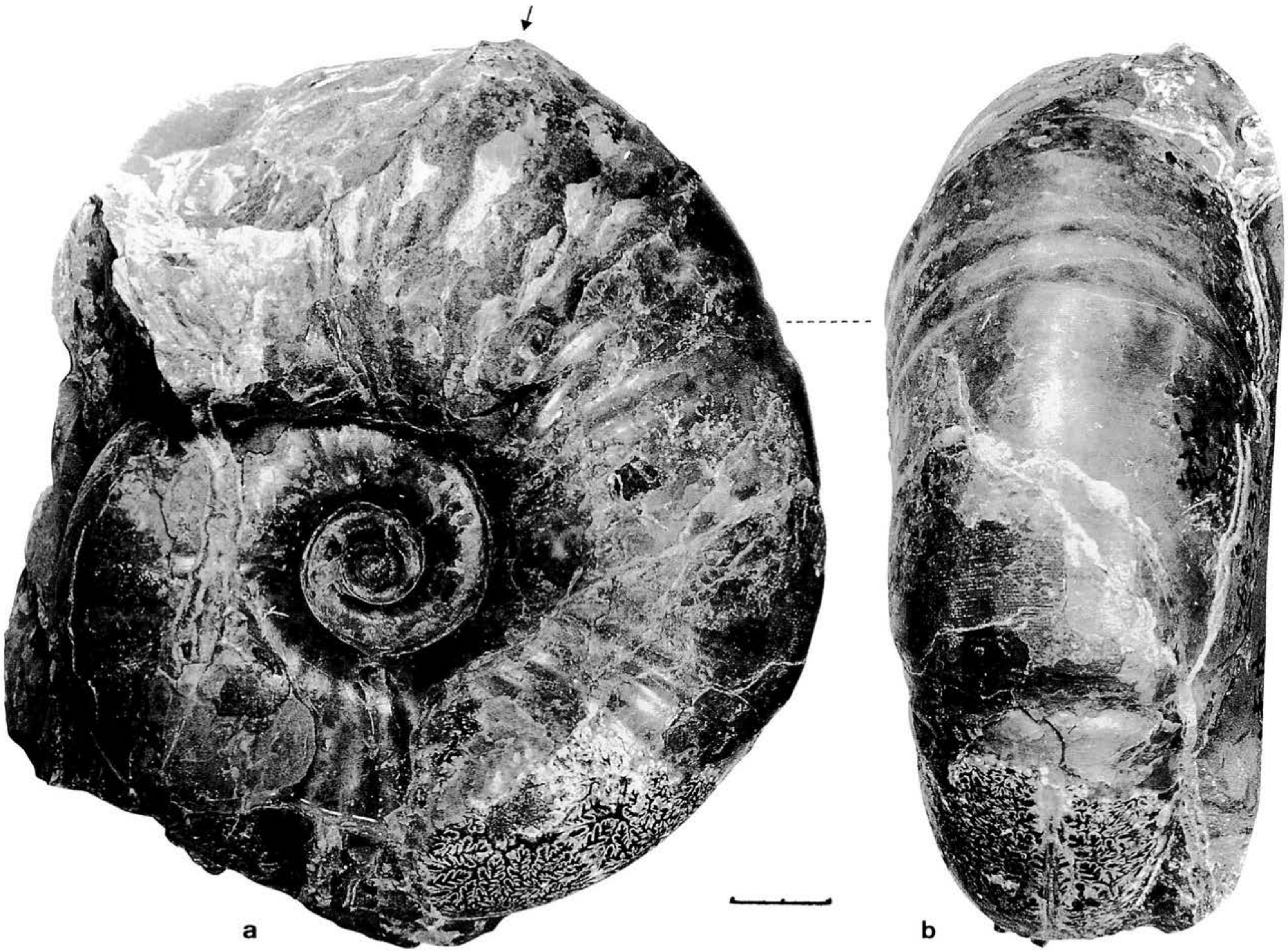


Figure 4. *Parajaubertella kawakitana* Matsumoto. YKC060823 from loc. R521p. Right lateral (a) and ventral (b) views of a nearly complete phragmocone, ×0.85. Note the fine lirae on the shell surface where the outer shell layer is preserved and also the intricate suture where the test is taken out. Bar scale : 20 mm.

Table 1. Measurements of *Parajaubertella kawakitana*.

Specimen	D	U	U/D	H	H/D	B	B/D	B/H	H/h
YKC060823 (LS+45°)	171.0	43.0	.25	78.0	.46	—	—	—	—
〃 〃 (LS−45°)	145.0	35.0	.24	68.0	.47	66.0	.46	0.97	1.62
YKC610608	76.0	20.0	.26	35.0	.46	36.0	.47	1.08	1.67
Holotype (LS)	73.0	19.7	.27	33.6	.46	36.0	.49	1.07	1.71
GK. H8480 (E′)	67.0	17.0	.25	30.0	.45	32.0	.48	1.07	1.50
〃 〃 (E′−180°)	—	—	—	20.5	—	23.0	—	1.12	—
GK. H8441	66.0	17.5	.27	31.0	.47	27.0	.44	1.07	—
YKC080914 (LS)	60.0	15.5	.26	28.0	.47	30.5	.51	1.09	1.70
GK. H8479 (E′)	59.0	16.5	.28	26.5	.45	26.5	.45	1.00	1.66
〃 〃 (E−180°)	—	—	—	18.5	—	21.0	—	1.14	—
GK. H8478 (inner)	56.0	15.7	.28	25.5	.45	25.8	.46	1.01	—
UMUT. MM19699 (E)	28.5	7.8	.27	13.0	.48	20.0	.72	1.51	1.69

For other previously measured specimens, see Matsumoto, 1995, table 1.
D=diameter, U=width of umbilicus, H=whorl-height, B=whorl-breadth, h=whorl-height at half a whorl (*i.e.* 180°) adapical from H; E=preserved end, E′=near the preserved end; LS=last septum, LS′=immediately behind LS, E-180°=at half a whorl adapical from E. Measurements of linear dimensions are in mm.

shell with diameter to about 35 mm is globose, with much depressed whorl, subangular umbilical edge and narrow and deep, steplike umbilicus. This is well exemplified by the specimens previously illustrated by Matsumoto (1995, fig. 7A-D).

The middle growth stage continues for fully one whorl or more, with, shell diameter from 35 or 40 mm to 100 or 130 mm in many cases, but there is a considerable size variation between individuals. Examples are shown in Matsumoto (1995, figs. 4, 9—11) and this paper (Figures 3-2, 4, 6). The shell of this growth stage is moderately involute, with a fairly narrow and moderately deep umbilicus; whorl expands with a fairly high ratio, but its cross section shows a gradual change from subrounded to suboval; in parallel to dense, subradial lines on the shell surface several rhythmic furrows occur in periodic segments; some of the furrows are deep enough to be called constrictions and accompanied behind by a weak collar or sometimes by faint, incipient major ribs.

The adult shell is fairly large; GK.H8456, obtained by Y.K. in the Suribachi-zawa of Soeushinai area and figured by Matsumoto (1995, fig. 13) represents the later half of a large body chamber, although in many cases the adult body chamber is partly preserved or distorted. The ornament of the adult body chamber is characterized by flat-topped, bandlike or low foldlike, broad major ribs with narrowly grooved interspaces. This is well observable even in partly preserved specimens (see Figures 3-1, 2; 6-1; also Matsumoto, 1995, figs. 4, 10, 11, 12).

Suture fundamentally similar to that of *Gaudryceras*; at the globose young stage the third lateral saddle inside of U2 situated at the umbilical edge, with descending auxiliaries on the umbilical wall; incisions fairly deep even at this stage, becoming progressively more intricate with growth (see Figure 5; also Matsumoto, 1995, fig. 3d).

Discussion.—Based on the diagnostic characters, this species is presumed to have close affinities with some species of *Anagaudryceras*, although its direct ancestor has not been found in the hitherto described species. For the reason of the peculiar characters of its globose immature shell, its separation in an allied but distinct genus is justified. The long-continued middle growth stage and the consequent large size of the adult shell are of specific rather than generic character.

The unusually small specimens as represented by YKC080914 (Figure 3-1) might be interpreted as a microconch of a dimorphic pair, but the evidence of sexual dimorphism is by no means sufficient. The apparent end of the septate stage does not always imply the beginning of the adult body chamber, as has been already explained (Matsumoto, 1995, p. 25). There is also considerable size variation as has been mentioned in the above description.

Occurrence.—The additional specimens came from the siltstone of Member My3 and lower part of Member My5 (Lower Cenomanian) of the Soeushinai area (see Nishida *et al*., 1996; 1997) and also from the unnamed mudstone member at Hirotomi of the Monbetsu area. The latter is referred also to the Lower Cenomanian on the ground of *Sharpeiceras mexicanum* (Böse) obtained by Y.K. from it.

The specimens described previously are from Member Kx and Ky of the Kawakita Group in the mid-valley of the Naibuchi [Naiba], South Sakhalin; upper part of Member

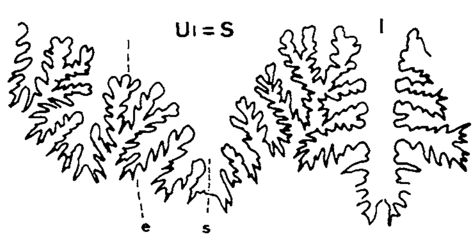


Figure 5. *Parajaubertella kawakitana* Matsumoto. Internal suture of YKC080621b8 from loc. R909. I: internal lobe, U_1=S: first umbilical lobe situated at s. e: umbilical edge, s: umbilical seam. Bar scale: 10 mm.

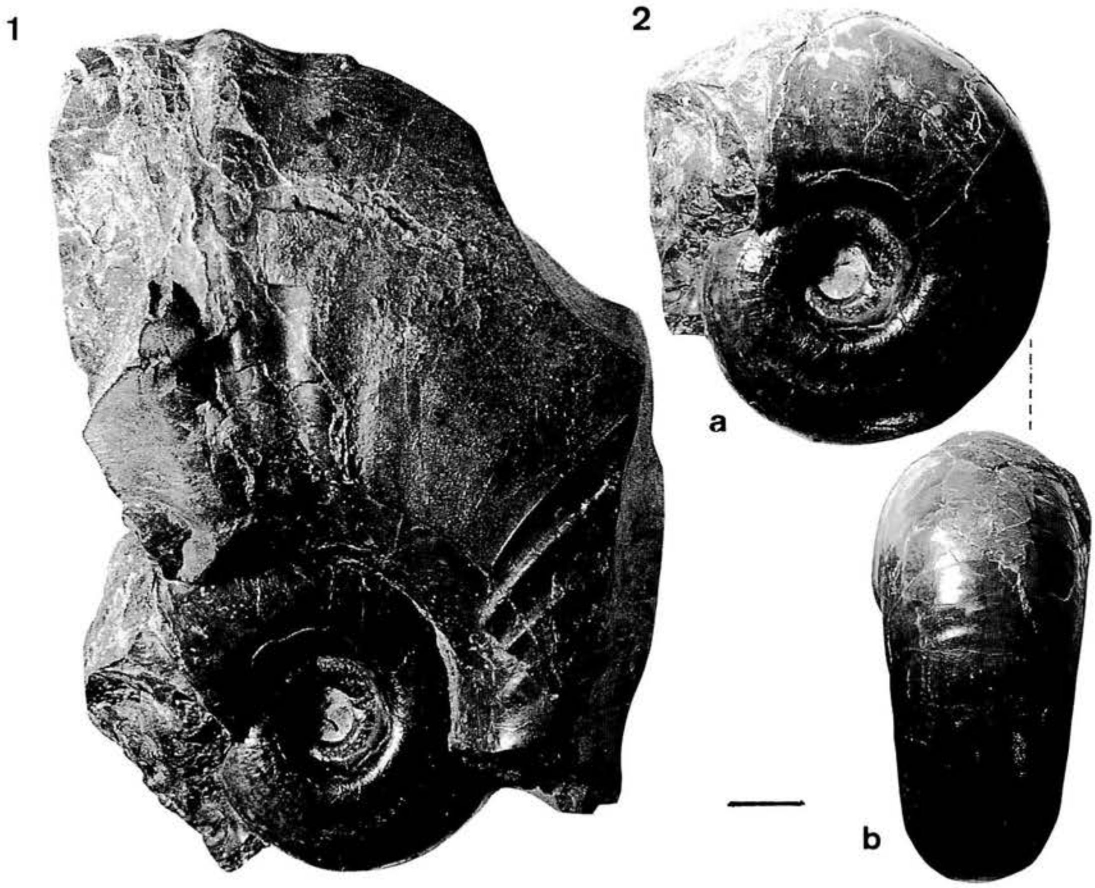


Figure 6. *Parajaubertella kawakitana* Matsumoto. GK.H8479 from loc. BIU570228 (T. Yoshida). 1 : Right lateral view of the whole specimen in which outer whorl is incomplete ; 2 : Lateral (a) and ventral (b) views of the inner whorl, ×1. Bar scale : 10mm.

IIa of the Abeshinai-Saku area northern Hokkaido ; Member My3 and lower part of Member My5 in the Soeushinai area ; Members IId and IIe of the Oyubari-Shuyubari area of central Hokkaido (Matsumoto, 1943, p. 667 ; 1995, p. 25). This species is, thus, common in the Lower Cenomanian of Hokkaido and South Sakhalin. It occurs also in the Chi'tina Valley of southern Alaska (Matsumoto, 1959 and Jones, 1967 under *P. imlayi*, which is a junior synonym of *P. kawakitana*), in the upper part of the Haida Formation of western British Columbia (McLearn, 1972), and in the Talovka Basin of western Korjak-Kamchatka (Alabushev, 1995).

The above records indicate that this species occurs commonly in the lower part of the Cenomanian, but its first and last datum levels have yet to be worked out.

Parajaubertella zizoh sp. nov.

Figures 7-9

Material.—The holotype is GK.H8482 (Figure 7-4) contained in a nodule (loc. R575 pl) which had fallen directly from the outcropping siltstone at loc. R575 of Member My3 on the right side of a small branch gully of the middle course of the Suribachi-zawa, a tributary of the River Sounnai. That locality was examined by Y.K. and T.M. The nodule contains *Marshallites rotundatus* Matsumoto and Takahashi among others. From another fallen nodule at a nearby locality, R575 p4, a specimen of *Graysonites* cf. *adkinsi* Young, YKC030728, was acquired by Y.K. In addition to the holotype, the specimens which show the adult body chamber at least partly are GK.H8445 (Figure 9-3) from loc. KY307, GK.H8446 (Figure 9-1) from loc. KY617, GK. H8447 (Figure 9-2), from loc. KY807, GK.H8485 (Figure 7-6) from loc. R518 p5 and YKC060619 (Figure 7-5) from the Bishamon-zawa, a branch of the Nakamata-zawa.

Among the phragmocones, mostly without body chamber, measured specimens are GK.H8484 (loc. R518 p5), GK. H8486 (Figure 7-2) (loc. R519 p2), GK.H8487 (Figure 7-3) (loc. R567p) and YKC050610. GK.H8488 and YKC060825 were collected *in situ* at loc. R456a and R575, respectively. GK. H8489 (Figure 7-1) from R519 p3 is tiny but shows fairly intricate sutures. The above specimens are all from Mem-

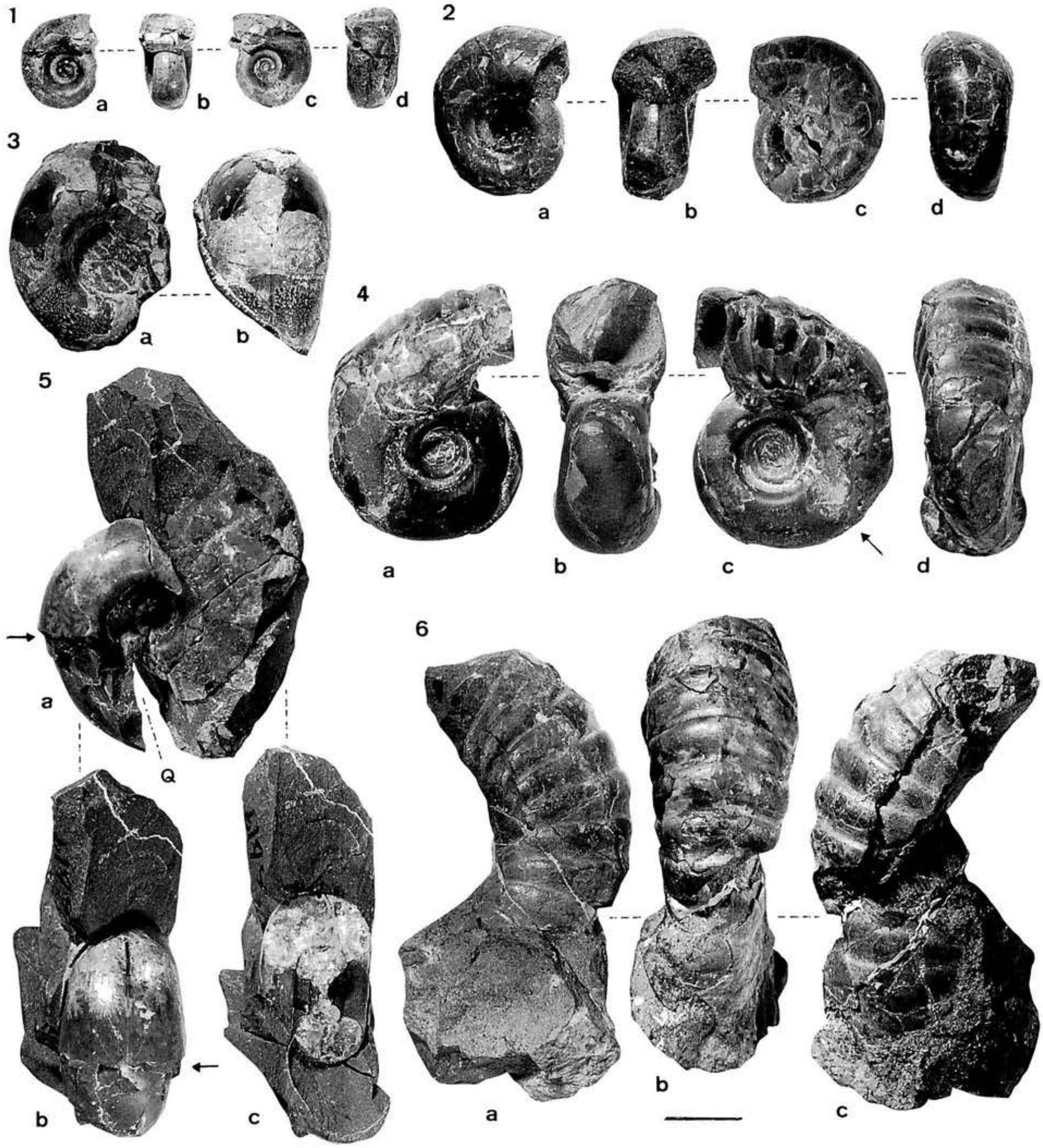


Figure 7. *Parajaubertella zizoh* sp. nov. **1a-d.** GK.H8489 from loc. R519p3 (four views of a juvenile). **2a-d.** GK.H8486 from loc. R519p2 (four views of a distorted phragmocone). **3.** GK.H8487 from loc. R567p ; left lateral (a) and ventral (b) views of an incomplete specimen that represents last part of phragmocone and early part of body chamber. **4.** GK.H8482 (holotype) from loc. R575p in four views, i.e. left side (a), front (b), rlght side (c) and back (d). **5.** YKC060619, from the Bishamon-zawa, showing right side (a), venter (b) and cross-section (c). **6.** GK. H8485 from loc. R518p5 ; right side (a), venter (b) and left side (c) of body chamber. *Marshallites* sp. crops out along a fissure. All from Member My3 of Soeushinai area. The views of a-d in 1 and 2 are similar to those in 4. All × 1.2. Bar scale : 10 mm.

Table 2. Measurements of *Parajaubertella zizoh.*

Specimen		D	U	U/D	H	H/D	B	B/D	B/H	H/h
GK. H8445	(LS+180°)	59.5	16.5	.28	27.5	.46	30.0	.34	1.09	1.77
〃 〃	(LS′)	38.5	10.5	.27	18.0	.48	22.5	.58	1.25	—
GK. H8446	(LS)	39.0	10.6	.27	17.0	.44	19.6	.58	1.15	—
GK. H8482	(E′)	34.0	10.7	.31	14.7	.43	—	—	—	—
〃 〃	(LS)	24.0	7.7	.32	9.2	.38	14.6	.61	1.59	1.42
YKC060619	(LS)	—	—	—	11.0	—	16.8	—	1.53	—
GK. H8447	(LS′)	—	—	—	10.4	—	15.2	—	1.46	—
GK. H8484		22.4	7.2	.32	8.2	.37	12.6	.56	1.54	1.11
GK. H8486		17.8	6.0	.34	6.6	.37	9.4	.53	1.42	1.27
YKC050610	(E)	17.0	5.8	.34	7.2	.42	10.0	.59	1.39	—

Abbreviations as for Table 1.

ber My3 of the Soeushinai area, except for GK.H8445.

Diagnosis.—Shell small, normally about 40 to 45 mm in diameter and not exceeding 70 mm even in extreme cases. Whorls in the main growth stage depressed, with fairly narrow and deep umbilicus, becoming subrounded in section in the adult body chamber. Broad, flat-topped major ribs of *Anagaudryceras sacya* type appears earlier at diameter of 30 mm.

Dimensions.—See Table 2.

Description.—Early whorls less than 10 mm diameter are reniform in section. In the succeeding main part of the septate stage, the whorl is much broader than high, with broadly arched venter, much inflated flanks and fairly deep umbilicus.

The umbilical ratio (U/D) is somewhat variable (see Table 2). This may be due partly to the effect of secondary deformation, but in general the ontogenetic change is noted, namely, the umbilicus is moderately wide in youth and becomes fairly narrow later. At the substage with shell diameter about 20 to 25 mm, the umbilicus is fairly deep and encircled by a nearly vertical or slightly overhanging, high wall. At this substage the whorl is broadest at the inner end of the flank, showing the ratio B/H about 1.5 ($\pm$0.1), and then, the flank slopes down for a short distance to the subangular edge of the umbilicus.

In the septate stage fine and dense lirae are discernible on the surface of the outer shell layer; constrictions are infrequent, except for several approximated ones on the last portion of the phragmocone.

The ornament of the adult body chamber is characterized by more or less wide, bandlike or low but asymmetrically wavy major ribs, with narrowly grooved interspaces. They are gently flexiradiate on the flank and somewhat projected on the venter. The lirae on the external surface of the body chamber are fine or very fine, showing some variation in density.

For some reasons the adult body chamber is often incompletely preserved, but its length can be estimated from the trace of the umbilical seam. The size of the complete adult shell, thus measured, is generally 40 to 45 mm in diameter. Only one specimen, GK.H8445 (Figure 9-3), with an original diameter of 70 mm, is exceptionally larger than that. It was obtained from a transported nodule at locality KY307, which is a considerable distance from the other localities. It may have been derived from some part of Member My5, which is fairly higher than My3 but still somewhere in the Cenomanian. That specimen is, however, referred to this species at least provisionally, because it shows nearly all the specific characters described above.

The suture is as for the genus, following the fundamental pattern of *Anagaudryceras* and *Gaudryceras*. In the late septate stage, with shell diameters from 25 to 30 mm, the middle of U_2 is situated at about the point of maximum whorl breadth and the "third saddle" (here called for the sake of convenience) is at the umbilical edge, with somewhat but not much broadened stem; the auxiliaries are descending on the umbilical wall (Figure 8).

Specific name.—It is taken from Zizoh-Bosatsu in Japanese, i.e., Ksitigarbha in Sanskrit, a Buddhist deity often represented by a small statue and worshipped by country people.

Discussion.—On the grounds of the specific characters described above, this species is certainly assigned to *Parajaubertella*. It is, however, much smaller than *P. kawakitana*. In *P. zizoh* the long continued middle growth stage of the

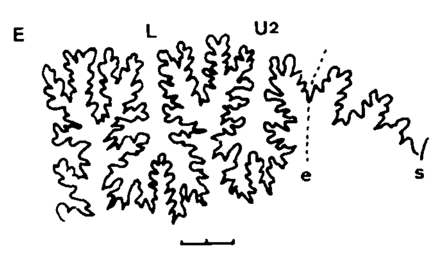


Figure 8. *Parajaubertella zizoh* sp. nov. External suture of GK.H8487 (Figure 7-3) at H=10.8, B=16.0. E: external lobe, L: lateral lobe, U_2: second umbilical lobe, e: umbilical edge, s: umbilical seam. Bar scale: 2 mm.

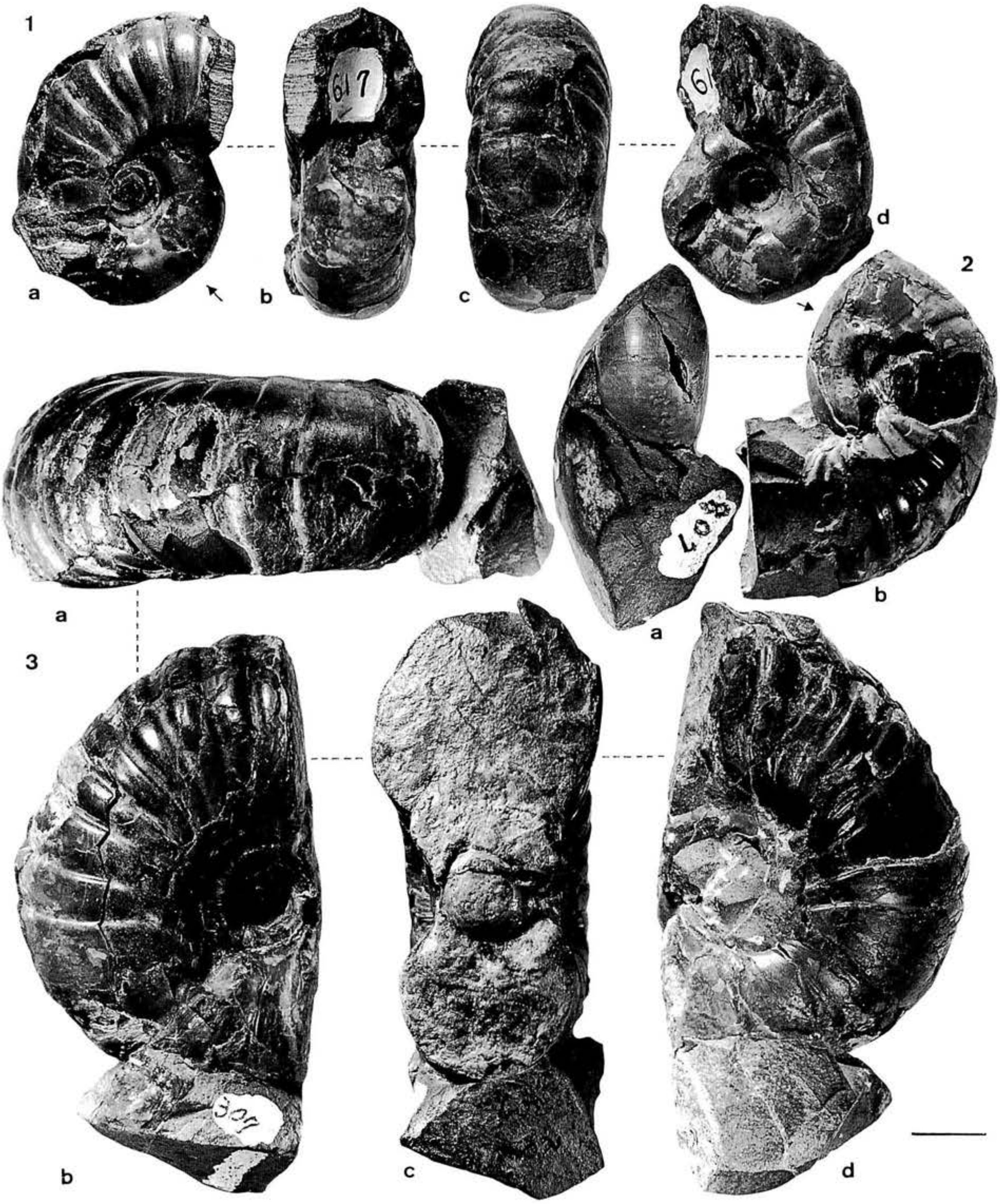


Figure 9. *Parajaubertella zizoh* sp. nov. **1a-d.** GK.H8446 from loc. KY617 (four views of an adult specimen). **2.** GK.H8447 from loc. KY807 ; ventral (a) and lateral (b) views of an incomplete specimen, in which the last part of the phragmocone is well-preserved, with sutures partly exposed, but the body chamber is much distorted and incomplete. **3.** GK.H8445 from loc. KY307 ; ventral (a), left side (b), sectional (c) and right side (d) views. It is exceptionally large for this species. All ×1.2. Bar scale : 10 mm. (Photos in Figures 3, 4, 6, 7 and 9 by courtesy of Naoko Egashira.)

latter is omitted and a gradual change of whorl shape and ornament does not occur. As maturity comes early in *P. zizoh*, the adult body chamber is still somewhat broader than high, although it is subrounded in the late part. In adult *P. kawakitana* the whorl section is suboval and higher than broad. Even in youth the two species can be discriminated; specifically the young shell of *P. zizoh* has a wider umbilicus than does *P. kawakitana* (see U/D in Tables 1 and 2).

It might be claimed that small specimens of *P. zizoh* are merely microconchs of *P. kawakitana*. In the case of a sexual dimorphic pair, however, the morphological differences between the paired shells are normally minor in early growth stages and become clearer later, with much distinction in the adult. The observed young shells of *P. zizoh* show a dissimilar shape from those of *P. kawakitana*. We are, hence, inclined to deny the idea of regarding *P. zizoh* and *P. kawakitana* as a dimorphic pair of one species.

Furthermore, in the hitherto described species of Gaudryceratidae there are little or almost no examples of undoubted dimorphic pairs. There should be of course anatomical differences between males and females in this ammonoid group. *Gaudryceras denseplicatum* (Jimbo) and *G. intermedium* Yabe were once interpreted as a sexual dimorphic pair (Hirano. 1978). As Matsumoto (1995, p. 116) has recently commented, this interpretation is unnatural, if not impossible, because the two species do not have the same stratigraphic range, although their ranges partly overlap, and because they show dissimilar styles of ornament from a fairly young stage onward. On the contrary, no noticeable difference in the shell is recognized between a number of couples of one species, as exemplified by *Anagaudryceras limatum* (Yabe) (see Matsumoto, 1995, p. 53, 62, fig. 31).

In these circumstances and for the reason mentioned above, we regard for the moment *P. zizoh* as specifically distinct from *P. kawakitana* (see also discussion under that species).

As another possible interpretation, the above comparison seems to suggest that *P. zizoh* may be a result of acceleration of heterochronic shell growth and that *P. kawakitana* may exemplify retardation. We have found yet no common ancestor which could give rise to such evolutionary differentiation.

So far as the early substage (about 10 mm diameter) is concerned, *P. zizoh* appears to be similar to certain species of *Anagaudryceras*. In later growth stages *P. zizoh* has a deeper and narrower umbilicus surrounded by a more angular edge and a broader whorl, as compared with any known species of *Anagaudryceras*.

There are two incomplete specimens collected at locs. R527 and R302 from the Upper Albian Member My2 of the Soeushinai area. Regrettably they have lost their septate whorls, but their body chamber resembles that of *P. zizoh* in size, shell shape and ornament. Hence they could be referred to *P. zizoh* with a query or cf.. There are, however, small adult specimens which have been reported under *Anagaudryceras sacya* from the Albian of South Africa (see Kennedy and Klinger, 1979, pl. 10, figs. 3, 4). The latter does not show a depressed whorl or globose shell shape of *Parajaubertella* fashion. The two specimens mentioned above might be merely fragmentary body chambers of a small form of *Anagaudryceras*. In *A. sacya*, which is long ranging, the variation in size seems to be considerable, but dimorphic pairs of this species have not been reported with sufficient evidence.

If the general shell shape alone is considered, *P. zizoh* appears to be similar to some small examples of certain species of *Tetragonites*, e.g., a form of *T. rectangulatus* Wiedmann (1973, pl. 7, figs. 1, 2) or that of *T. balmensis* Breistroffer (see Wiedmann, 1973, pl. 7, fig. 3), but this is quite superficial. *P. zizoh* has sutural elements which are the same as those of *Gaudryceras* and *Anagaudryceras*. In *Tetragonites*, constrictions normally have a backward sinus on the venter (see also the general discussion of the genus).

We have found some examples of *Gabbioceras* sp. from Member My3 of the Soeushinai area and correlatable units of other areas, although we do not intend to describe that species definitively on this occasion. It is small, about 25 mm in diameter at the beginning of the adult body chamber, and much globose. It seems to be similar to *G. yezoense* Shigeta, 1996 in shell shape. It has more depressed whorls and a narrower umbilicus as compared with *P. zizoh*. It has periodic constrictions accompanied behind by well raised flares, which are rursiradiate on the outer flank and show a slightly backward sinus as in *Tetragonites*. Its internal suture has U_1 between I and U_3=S. Its well preserved specimens have riblets at rhythmic intervals around the umbilicus but do not show the lirae of *Anagaudryceras*. The body chamber, which is preserved under crushed state in some specimens, does not show adult *A. sacya* type ribbing. Thus, this species of *Gabbioceras*, can be clearly distinguished from *P. zizoh*. We are inclined to refer this *Gabbioceras* sp. to the Tetragonitidae. The similarity between *P. zizoh* and *Gabbioceras* sp. can be stated as an example of homeomorphy, though within the same superfamily Tetragonitaceae.

Occurrence.—As for Material. Even in the case of the fallen or transported nodules, the examined specimens came almost certainly from the fine-sandy siltstone of Member My3, Lower Cenomanian Zone of *Graysonites adkinsi* of the Soeushinai area, as is evidenced by the sites of localities also by some associated species (see Nishida *et al.*, 1996). One exceptional specimen is presumed to have been derived from Member My5.

To know the true stratigraphic range and geographic distribution of this species, further investigations are required.

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Permian bryozoans from the exotic formations in Oman

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Abstract. Thirty bryozoan species in nineteen genera are described from the exotic formations in Oman. The bryozoans include one new species, *Rugofenestella omanica*, eighteen previously described species and eleven indeterminable species. These bryozoan faunas indicate an early Murgabian to early Midian age (Permian). They show relationships to bryozoan faunas of the northern, central, and southern Tethyan realm.

Key words: Bryozoans, Exotic formation, Oman, Paleontology, Permian

Introduction

Permian bryozoan faunas in the Middle East are still poorly known. Pillevuit (1993), engaged in a geological field survey of the exotic formations in Oman, studied and sampled autochthonous, para-autochthonous and allochthonous Permian to Cretaceous units in the Oman Mountains. He collected many different Permian fossils. Some brachiopods were described by Yanagida and Pillevuit (1994), some trilobites by Becq-Giraudon and Pillevuit (1995), and some cephalopods by Niko, *et al.* (1996). The present study identifies the bryozoan fauna and extends our knowledge of the distribution and paleogeographic relations of Permian bryozoans in the Middle East.

Geological Setting

The Oman mountains are composed of five main structural units (Glennie *et al*., 1974) as follows:

1) The Autochthonous A and B units form the lowest outcropping tectonic units in Oman. The Autochthonous A is composed of folded Proterozoic to Paleozoic rocks, and the Autochthonous B is composed of Permian to Cretaceous carbonate platform and deeper-water marine sediments, typical of the southern Neotethyan passive margin.

2) The Sumeini Nappe is represented by Neotethyan slope deposits of Permian to Cretaceous age.

3) The Hawasina Nappes are subdivided into six groups comprising Permian to Cretaceous sediments; they are the Ramaq Group (Pillevuit, 1993), the Al Buda'ah Group (Pillevuit, 1993), the Hamrat Duru Group (Glennie *et al*., 1974 ; Béchennec, 1988 ; Béchennec *et al*.,1992b), the Kawr Group (Béchennec, 1988 ; Béchennec *et al*., 1992b ; Pillevuit, 1993) and the Umar Group (Béchennec, 1988). Each group is defined by lithologic, sedimentologic and biostratigraphic criteria. They were derived from part of the Neotethys, which we refer to here as the Hawasina basin (Béchennec, 1988), and transported onto the Arabian margin during the Late Cretaceous (Campanian-Maastrichtian) obduction of the Semail ophiolite.

4) The Semail ophiolite is composed of a thick Cretaceous oceanic lithospheric slab.

5) The Mesoautochthonous unit is composed of a platform sequence ranging from Campanian-Maastrichtian to Miocene age, overlying unconformably the older units. This sedimentary sequence postdates the obduction of the Semail ophiolite.

The bryozoans were collected from all units except the Mesoautochthonous unit and the Semail ophiolite.

Bryozoan Localities and their Faunas

The detailed geological sequence at each locality (Figure 1) is described in Pillevuit (1993) and Pillevuit *et al*. (1997, MS). In the following list, an asterisk(*) denotes described and illustrated species in this report (Table 1).

Wadi Tayin (Samples 60-64); Lat. 23°03′10″N, Long. 58°17′50″E

The samples examined in the present article are from a 10m-thick limestone block of Permian age. This block belongs to a series of breccia exposed along the road of the Wadi Tayin, some 10 km to the east of the bifurcation from the Muscat-Sur road. According to Béchennec *et al*. (1992a, in map), this unit of breccia belongs to the Matbat Formation and is considered to have been deposited during the Triassic Period.

60- Fragments of fenestellids: *Polypora* ? sp.
61- Fragments of fistuliporids: *Fistulipora* ? sp., associated with fusulinaceans (*Pseudofusulina, Verbeekina, Neoschwagerina, Codonofusiella*)
64- Fragments of Goniocladiidae: *Goniocladia* ? sp., associated with fusulinaceans (*Minojapanella*)

Table 1. Distribution of the described bryozoans from the exotic formations in Oman.

Locality / Species	Wadi Maqam					Nackl	Qarari	Fath	
	479	484	497	498	499	631	1028	1620	1621
Fistulipora cf. *F. wanneri*	○								
Eridopora parasitica							○		
Hexagonella kobayashii	○					○			
Goniocladia timorensis	○								
Dyscritella tenuirama	○								
Dyscritella sp. *indet.*						○			
Paralioclema eplicatum								○	○
Rhombopora aff. *R. lepidodendroides*	○								
Rhombopora sp. indet.	○								
Streblascopora delicatula	○	○				○			
Streblascopora exillis	○	○							
Timanodictya cf. *T. dichotoma*			○	○					
Girtypora cf. *G. ramosa*					○				
Alternifenestella cf. *A. horologia*	○								
Alternifenestella sp. indet. A	○								
Alternifenestella sp. indet. B	○								
Alternifenestella sp. indet. C	○								
Alternifenestella sp. indet. D	○								
Minilya duplaris	○								
Minilya sp. indet.	○								
Laxifenestella lahuseni	○								
Fabifenestella subpermiana	○								
Rugofenestella basleoensis	○								
Rugofenestella omanica, n. sp.	○								
Penniretepora sp. indet.	○								
Septopora sp. indet.	○								
Polypora cf. *P. elliptica*	○								
Polypora cf. *P. gigantea*	○								
Polypora sp. indet.	○								
Protoretepora ? sp. indet.						○			

Jebel Qamar (Samples 1507-1508 and 355-415)

The samples from Jebel Qamar belong to the Permian Qamar Formation of the Ramaq Group. The Ramaq Group is an allochthonous unit of the Hawasina Nappes and interpreted as a tilted block of the Oman margin of Permian age.

Jebel Qamar South section 1 (Samples 1507-1508); Lat. 25°43′32″N, Long. 55°53′50″E

1507- *Fistulipora* sp., *Ramipora* ? sp., *Polypora* ? sp.

1508- *Fistulipora* ? sp., *Streblascopora* sp., "Fenestellid" sp.

Jebel Qamar South section 6 (Samples 355-369); Lat. 25°42′48″N, Long. 55°54′23″E

355- *Pseudobatostomella* sp., *Rhombopora* ? sp., "Fenestellid" sp.

359- *Dyscritella* sp.

369- *Dyscritella* sp.

Jebel Qamar South section 7 (Samples 375-379); Lat. 25°42′48″N, Long. 55°53′43″E

375- *Hexagonella* ? sp., "Fenestellid" sp.

376- "Fenestellid" sp.

379- "Fenestellid" sp.

Jebel Qamar North (Samples 412-415); Lat. 25°42′48″N, Long. 55°54′08″E

412- *Rhombopra* ? sp., *Streblascopora* ? sp., "Fenestellid" sp., *Penniretepora* sp.

413- *Dyscritella* sp. "Fenestellid" sp., *Polypora* sp.

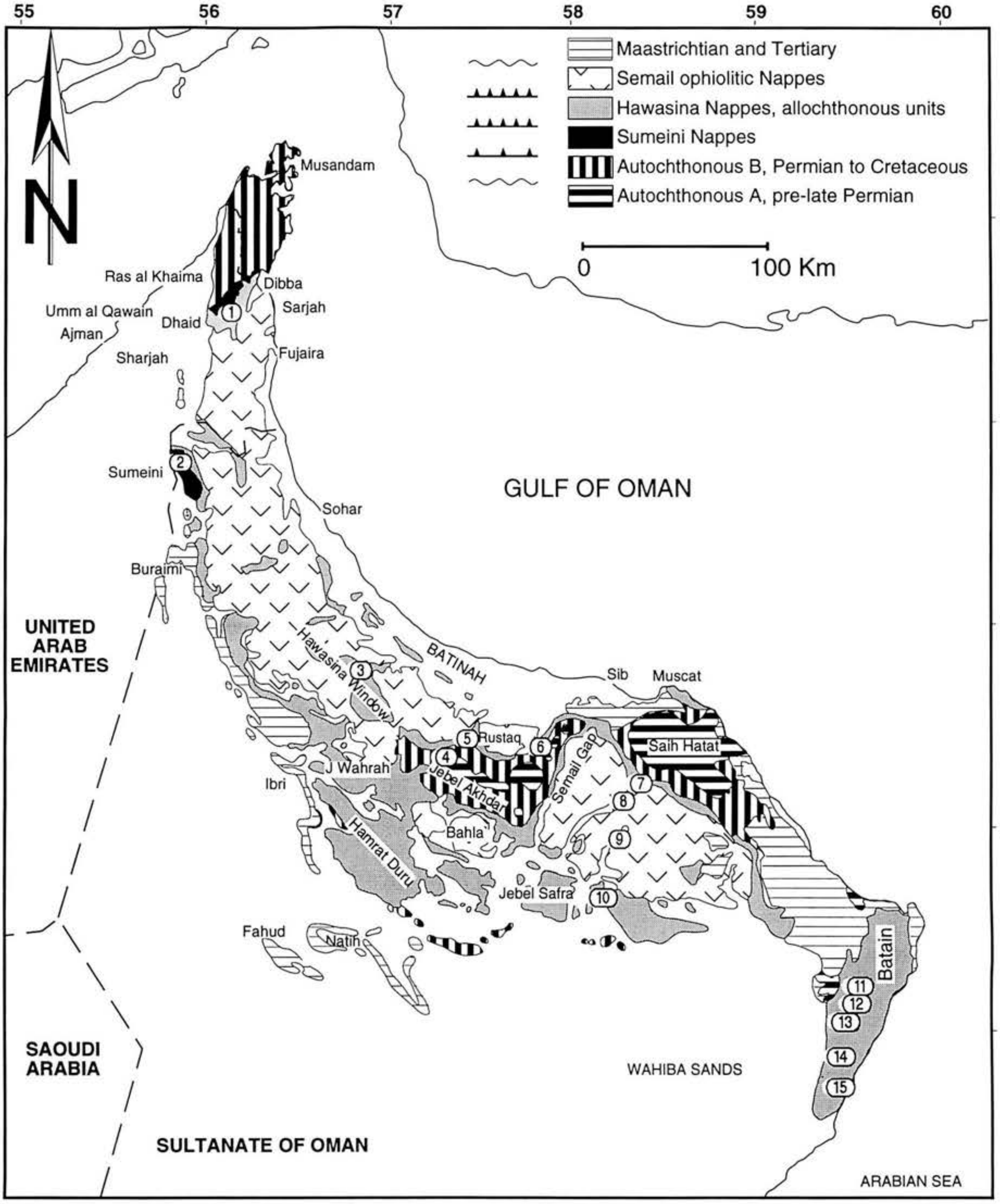
414 "Fenestellid" sp.

415- *Dyscritella* ? sp. "Fenestellid" sp., *Polypora* sp.

Wadi Maqam (Samples 479-499); Lat. and Long. not exactly.

The samples from Wadi Maqam are from the Member A of the Maqam Formation (Watts, 1985) that corresponds to the base of the Sumeini Group (Watts, 1985; Pillevuit, 1993). This member begins with 70 to 80 m of black dolomitized schists followed by grey-colored limestones bearing spicules and ostracods.

These limestones are interbedded with nodular marls, argillaceous beds, and more rare beds of bryozoan- and echinoid-bearing calcirudites. The upper part of this member is composed of grey decimetric limestones interstratified



(1) Jebel Qamar South and North
(2) Sumeini Wadi Maqam
(3) Lihban
(4) Wadi Sahtan
(5) Rustaq West
(6) Nackl
(7) Jebel Rahbah
(8) Wadi Wasit and Wadi Tayin
(9) Wadi Musjah
(10) Fath
(11) Locality A37
(12) Locality A39
(13) Locality A36 and Locality A32
(14) Jebel Qarari and Locality 941
(15) Locality 754 and Locality A10

Figure 1. Geological map of the Oman Mountains region, showing the localities of bryozoan faunas.

with argilaceous beds. The limestones include some ammonoids and trilobites indicative of Murgabian age (Becq-Giraudon and Pillevuit, 1995).

*479- *Fistulipora* cf. *F. wanneri, Hexagonella kobayashii, Goniocladia timorensis, Dyscritella tenuirama, Rhombopora* aff. *R. lepidodendroides, Rhombopora* sp. indet., *Streblascopora delicatula, Streblascopora exillis, Alternifenestella* cf. *A. horologia, Alternifenestella* sp. indet. A, *Alternifenestella* sp. indet. B, *Alternifenestella* sp. indet. C, *Alternifenestella* sp. indet. D, *Minilya duplaris, Minilya* sp. indet., *Laxifenestella lahuseni, Fabifenestella subpermiana, Rugofenestella basleoensis, Rugofenestella omanica*, n. sp., *Penniretepora* sp. indet., *Polypora* cf. *P. elliptica, Polypora* cf. *P. gigantea, Polypora* sp. indet.

480- *Streblascopora* sp.

*484- *Fistulipora* sp., *Goniocladia* sp., *Rhombopora* sp., *Streblascopora delicatula, Streblascopora exillis*, "Fenestellid" sp., *Polypora* sp.

*497- *Timanodictya* cf. *T. dichotoma*

*498- *Timanodictya* cf. *T. dichotoma*

*499- *Girtypora* cf. *G. ramosa*

Nackl (Samples 631-632 and 1222-1234); Lat. 23°22′40″N, Long. 57°48′50″E

The samples examined in the present article came from blocks of polygenetic breccia 20 m thick and from the overlying stratified calcarenites. This breccia mapped as the Ba'id Formation (Béchennec *et al*., 1992b; Rabu *et al*., 1986) is interpreted as sediments of the Permian Arabian platform redeposited at the foot of the Arabian margin (Pillevuit, 1993). Fusulinaceans such as *Yangchenia* sp., *Sumatrina* sp., and *Neoschwagerina* sp. are found in the Samples 1222-1234 and indicate Murgabian age.

* 631- *Fistulipora* sp., *Hexagonella kobayashii* ? sp., *Goniocladia* ? sp., *Dyscritella* sp. indet., *Rhabdomeson* sp., *Streblascopora delicatula, Protoretepora* ? sp. indet. "Fenestellid" sp.

632- Fragments of Fistuliporidae, gen. et sp. indet.

1222- *Sulcoretepora* sp., *Dyscritella* sp., *Rhombopora* sp., "Fenestellid" sp.

1223- *Fistulipora* sp., *Rhombopora* sp., "Fenestellid" sp., *Polypora* sp.

1226- *Fistulipora* sp., Hexagonellidae: *Hexagonella* sp. or *Meekopora* sp., *Sulcoretepora* sp., *Streblascopora* sp., "Fenestellid" sp., *Polypora* sp.

1231- *Fistulipora* sp., *Sulcoretepora* sp., "Fenestellid" sp., *Polypora* sp.

1234- Hexagonellid gen. et sp. indet.

Wadi Wasit (Samples 665-683); Lat. 23°06′40″N, Long. 58°21′00″E

This series is characterized by the thick Upper Permian volcanosedimentary sequence composed of pillow lavas, tuffites and calcirudites of the Permian reefal limestones. All samples examined are from the blocks of limestones interpreted as being deposited at the foot of the Arabian margin (Pillevuit *et al*. 1997, MS).

665- Bryozoans indeterminable

670- Fragments of fenestellids

671- *Fistulipora* sp., "Fenestellid" sp.

672- Bryozoans indeterminable

677- Bryozoans indeterminable

683- Bryozoans indeterminable

Jebel Rahbah (Samples 1279-1280); Lat. 23°11′00″N, Long. 58°20′50″E

The samples examined are from a large block 100 m thick in a polygenetic breccia. The block is composed of fusulinaceans (*Nankinella* sp., *Verbeekina* sp., *Neoschwagerina* sp.) and bryozoan-bearing Permian platform limestones, ammonoid-bearing Triassic red limestones (Hallstatt) and volcanic rocks. The fusulinaceans indicate Murgabian age.

1279- *Streblascopora* sp., "Fenestellid" sp.

1280- *Streblascopora* sp., "Fenestellid" sp.

Wadi Sathan (Sample 1362); Lat. 23°20′00″N, Long. 57°18′50″E

This locality falls in the autochthonous units of the Jebel Akhdar. The sample is found 60 m above the transgressive unit of the Saiq Formation in Wadi Sahtan, and may be of Permian age.

1362- *Rhombopora* ? sp., *Rhabdomeson* sp.

Rustaq West (Sample 1371); Lat. 23°23′46″N, Long. 57°22′28″E

This locality is situated some kilometers west of Rustaq. Lithofacies suit noted in this locality is considered a product of collapsing Permian platform into the Carnian-Norian Neotethyan basin. It is represented by a thick breccia composed mainly of the blocks of Permian platform limestones with some Triassic Hallstatt facies limestones reworked in sandstones and *Halobia*-bearing cherts of the Matbat Formation.

1371- *Fistulipora* sp.

Lihban (Sample 1587); Lat. 23°46′20″N, Long. 56°52′30″E

This locality is situated near the village of Lihban in the Wadi Hawasina. The outcrop is represented by a breccia of the Permian platform limestone overlying a thick sequence of pillow lavas and tuffites of probable Upper Permian age.

1587- *Fistulipora* sp., "Fenestellid" sp., *Polypora* sp.

Fath (Samples 1620-1621); Lat. 22°40′00″N, Long. 58°08′00″E

The locality is situated six kilometers north of the village of Fath. The outcrop is represented by an olistolith of Permian platform limestone (Murgabian) embedded in the grainstone of the Matbat Formation. The bryozoans and fusulinaceans (*Yangchenia* sp., *Chusenella* sp., *Neoschwagerina* sp., *Yabeina* sp.) are found in the limestone olistolith.

*1620- *Paralioclema eplicatum*

*1621- *Paralioclema eplicatum*, Bryozoans, gen. et sp. indet.

Wadi Musjah (Samples 1626-1631); Lat. 22°58′40″N, Long. 58°15′40″E.

The locality is situated in the Wadi Musjah. The samples of this section comes from blocks of Permian platform limestones in turbidites. The bryozoans and fusulinaceans (*Codonofusiella* sp., *Paraboultonia* sp., *Yangchenia* ? sp., *Neoschwagerina* sp., *Yabeina* sp.) indicate Murgabian-Midian age.

1626- *Girtyporina* ? sp.

1631- *Fistulipora* sp., Girtyporidae gen. et sp. indet.

Batain Jebel Qarari (Samples 1027-1033 and 1461-1462); Lat. 21°53′40″N, Long. 59°28′20″E

The locality is situated 10 km west of Al Ashkarah. This summit is a large block of Permian limestone found in association with Upper Cretaceous radiolarites and turbiditic sediments. From Beds 1027 to 1033, some fusulinaceans such as *Parafusulina* or *Pseudofusulina* are found associated with bryozoans.

1027- *Prismopora*? sp., Trepostomata, gen. et sp. indet., "Fenestellid" sp., *Polypora* sp.

*1028- *Eridopora parasitica*, *Hexagonella* sp., *Streblascopora* sp., "Fenestellid" sp.

1033- Fistuliporid bryozoans, *Streblascopora* sp., "Fenestellid" sp., *Penniretepora* sp., *Polypora* sp.

1461- "Fenestellid" sp.

1462- *Fistulipora* sp., *Rhombopora* sp., *Streblascopora* sp. (in association with fusulinaceans: *Codonofusiella* sp.)

Batain, Loc. 753 (Samples 1602-1604); Lat. 21°43′31″N, Long. 59°21′13″E

The locality is in the vicinity of Ras Al Jifan. The outcrop is composed of a block of platform limestones resedimented in calcarenites that overlies red radiolarites of probably Cretaceous age.

1602- *Fistulipora* sp., *Sulcoretepora*? sp., Trepostomata, gen. et sp. indet., *Streblascopora* aff. *S. diaphragma*, "Fenestellid" sp., *Polypora* sp., in association with fusulinaceans: *Boultonia* sp., *Codonofusiella* sp., Schwagerinidae gen. et sp. indet., which were noted briefly and illustrated by Sakagami (1994) in Yanagida and Pillevuit (1994). The fauna was referred to the upper Artinskian to lower Guadalupian by them.

1604- *Penniretepora*? sp.

Batain Loc. 941 (Samples 1463-1464); Lat. 21°51′08″N, Long. 59°27′44″E

This outcrop is represented by a breccia composed mainly of Permian platform limestone blocks. It overlies the grainstones of the Matbat Formation, probably indicating a Triassic age for the breccia. The constituent limestone blocks themselves contain Artinskian fusulinaceans, such as *Parafusulina* sp. and/or *Pseudofusulina* sp.)

1463- *Streblascopora* sp., "Fenestellid" sp., *Polypora* sp.

1464- *Streblascopora* sp., "Fenestellid" sp., *Polypora* sp.

Batain Loc. A10 (Sample 1731); Lat. 21°43′52″N, Long. 59°24′56″E

This outcrop is characterized by a sequence of Anisian-Ladinian radiolarite and grainstone with thinly bedded limestones overlain by a breccia of Permian platform limestone blocks containing fusulinaceans (*Parafusulina*-like), sponges, corals, bryozoans, brachiopods, crinoids. The associated fusulinaceans may indicate an Artinskian age.

1731- *Goniocladia* sp., *Dyscritella* sp., *Polypora*? sp.

Batain Loc. A32 (Sample 2506); Lat. 22°04′52″N, 59°30′38″E

The sample was collected from the limestone blocks that belong to a breccia of indeterminable age. The bryozoans, however, may indicate a Permian age.

2506- *Sulcoretepora* sp., *Rhombopora* sp., *Streblascopora* sp., "Fenestellid" sp., *Polypora* sp.

Batain Loc. A36 (Samples 2521-2531); Lat. 22°01′16″N, Long. 59°29′42″E

The samples were collected from limestone blocks that belong to a breccia of indeterminable age. The bryozoans, however, may indicate a Permian age.

2521- *Streblascopora* sp., "Fenestellid" sp.

2524- "Fenestellid" sp.

2531- *Fistulipora* sp., "Fenestellid" sp.

Batain Loc. A37 (Sample 2537); Lat. 22"12′30″N, Long. 59"34′44″E

The samples were collected from limestone blocks that belong to a breccia of indeterminable age. The bryozoans, however, may indicate a Permian age.

2537- *Goniocladia*? sp., *Rhombopora* sp., *Streblascopora* sp., "Fenestellid" sp., *Polypora* sp.

Batain Loc. A39 (Samples 2557-2566); 22°09′51″N, Long. 59°36′29″E

The samples were collected from the limestone blocks that belong to a breccia of indeterminable age. The bryozoans, however, may indicate a Permian age.

2557- Hexagonellidae, gen. et sp. indet., *Streblascopora* sp., "Fenestellid" sp., *Polypora* sp.

2566- *Rhombopora* sp., *Streblascopora* sp., "Fenestellid" sp., *Polypora* sp.

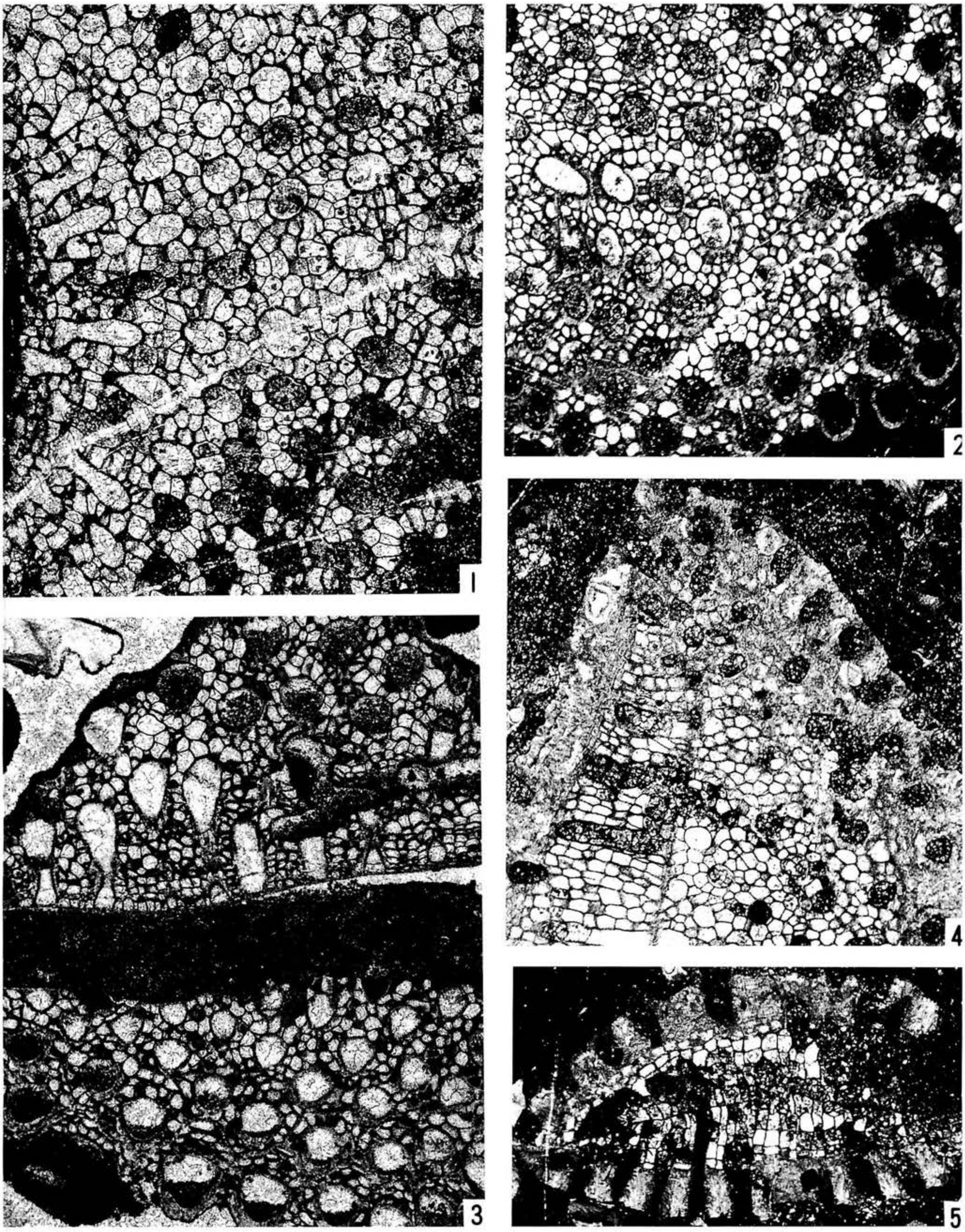
As a whole, the following 24 genera of Permian Bryozoa are identified mainly from the allochthonous formations and a few from autochthonous formations in the Oman Exotics (Permian to Cretaceous): *Fistulipora, Eridopora, Hexagonella, Meekopora*?, *Goniocladia, Prismopora*?, *Sulcoretepora, Dyscritella, Pseudobatostomella, Paralioclema, Rhombopora, Rhabdomeson, Streblascopora, Timanodictya, Girtypora, Alternifenestella, Minilya, Laxifenestella, Fabifenestella, Rugofenestella, Penniretepora, Septopora, Polypora* and *Protoretepora*.

All 18 species, except for one new and 11 indeterminable species, are common in the northern, central, and southern Tethys region. In addition, a small element of the fauna, for example *Timanodictya*, is similar to faunas on the Russian Platform and in the Uralian Sea. The bryozoans were deposited under agitated conditions because most of them are fragmentary. The present study provides an additional datum for bryozoan paleobiogeography in the Permian.

Systematic paleontology

All specimens treated in the present study are stored in the Geological Museum, University of Lausanne (MGL).

Figure 2. **1, 2.** *Fistulipora* cf. *F. wanneri* Bassler, tangential sections, MGL74509 and 74516a, respectively. **3.** *Eridopora parasitica* (Waagen and Wentzel), tangential (lower part) and oblique (upper part) section, MGL74532a. **4, 5.** *Hexagonella kobayashii* Sakagami, 4: oblique section, MGL74505c, 5: transverse section, MGL74503d. (All figures are ×20)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Phylum Bryozoa Ehrenberg, 1831
Order Cystoporata Astrova, 1964
Suborder Fistuliporina Astrova, 1964
Family Fistuliporidae Ulrich, 1882
Genus ***Fistulipora*** McCoy, 1850

Fistulipora cf. ***F. wanneri*** Bassler, 1929

Figures 2-1, 2

Compared.—
Fistulipora wanneri Bassler, 1929, p. 43, pl. 233(9), figs. 1-5.

Material and Locality.—MGL74508a, 74509, 74516a (Maqam).

Description.—Only three tangential sections were examined. Shape of zoarium uncertain. Zooecial tube broadly ovate or subcircular, longer diameter excluding lunarium ranges from 0.333 to 0.500 mm and shorter diameter ranges from 0.321 to 0.358 mm. Usually 3 to 4 zooecia per 2 mm diagonally. Lunarium well developed but thin, occupying nearly one half of zooecial circumference, its thickness less than 0.030 mm. Vesicular tissue regularly arranged, usually one to three vesicles between adjacent zooecia and 6 to 8 vesicles per mm horizontally.

Remarks.—Although present only in tangential sections, the present form may be compared with *Fistulipora wanneri* described by Bassler (1929) from the Permian of Timor Island in essential characters and measurements.

Genus ***Eridopora*** Ulrich, 1882

Eridopora parasitica (Waagen and Wentzel), 1886

Figures 2-3

Fistulipora parasitica Waagen and Wentzel, 1886, p. 923, pl. 45, fig. 6 ; pl. 105, figs. 1-4.
Eridopora parasitica (Waagen and Wentzel), Xia, 1986, p. 232, pl. 132, figs. 8, 9, pl. 15, figs. 5, 7.
Eridopora cf. *parasitica* (Waagen and Wentzel), Sakagami, 1980, p. 273, pl. 31, figs. 7-9.
Eridopora major Bassler, 1929, p. 52, pl. 225(1), figs. 1-4 ; Gorjunova, 1975, p. 45, 46, pl. 3, fig. 1 ; Xia, 1991, p. 189, pl. 7, figs. 8, 9.

Material and Locality.—MGL74532a (Qarari).

Description.—A single tangential, partly obliquely longitudinal section shows an encrusting zoarium, in life the animal may have been attached to a foreign object such as soft body tissue.

In tangential section, zooecial tubes rounded triangular with moderately developed lunarium. Diameters of zooecial tubes becoming larger from inner to outer : inside longitudinal diameter of tubes excluding lunarium ranges from 0.256 to 0.321 mm in inner part and from 0.385 to 0.462 mm in outer part, inside transverse diameter ranges from 0.256 to 0.321 mm in inner part and from 0.385 to 0.449 mm in outer part. Usually 3.5 to 4 zooecia per 2 mm diagonally. V-shaped lunarium disposed at proximal end of zooecial tube. Thickest part of lunarium reaching 0.090 mm in outer part of zooecial tube, but very thin in inner part. A pair of small projections deposited at opposite side of lunarium in a tube. Vesicular tissue well developed, not so regular in size and arrangement, usually one to three vesicles between adjacent zooecia, and 7 to 10 vesicles per mm diagonally.

Because of the imperfect specimen, the longitudinal section cannot be sufficiently observed. Diaphragms may be abundant but the interval is indistinct. Interzooecial tissue consists of regularly arranged vesicles which are usually quadrate or scale-shaped in inner zone but are not observable in outer zone.

Remarks.—The present species was originally described from the Middle *Productus* Limestone in the Salt Range of Pakistan, and it is characterized by the existence of a pair of small projections at the opposite side of the lunarium in the tangential section of the tube. As mentioned by Sakagami (1980), such a pair of projections is also recognized in *Eridopora major* Bassler (1929) from the Permian of Timor Island. Therefore, *Eridopora major* may be a junior synonym of *E. parasitica*. The present species has been known from the Xarla Formation (Kazanian) of Xainza, Northern Xizang in China by Xia (1986) and another comparable form from the lower part of the Abadehian in the Abadeh region of Central Iran. Bassler (1929), Gorjunova (1975) and Xia (1991) described *Eridopora major* from the Permian of Timor Island, Central Pamir and Tibet, respectively.

Family Hexagonellidae Crockford, 1947
Genus ***Hexagonella*** Waagen and Wentzel, 1886

Hexagonella kobayashii Sakagami, 1968

Figures 2-4, 5 ; 3-1-3

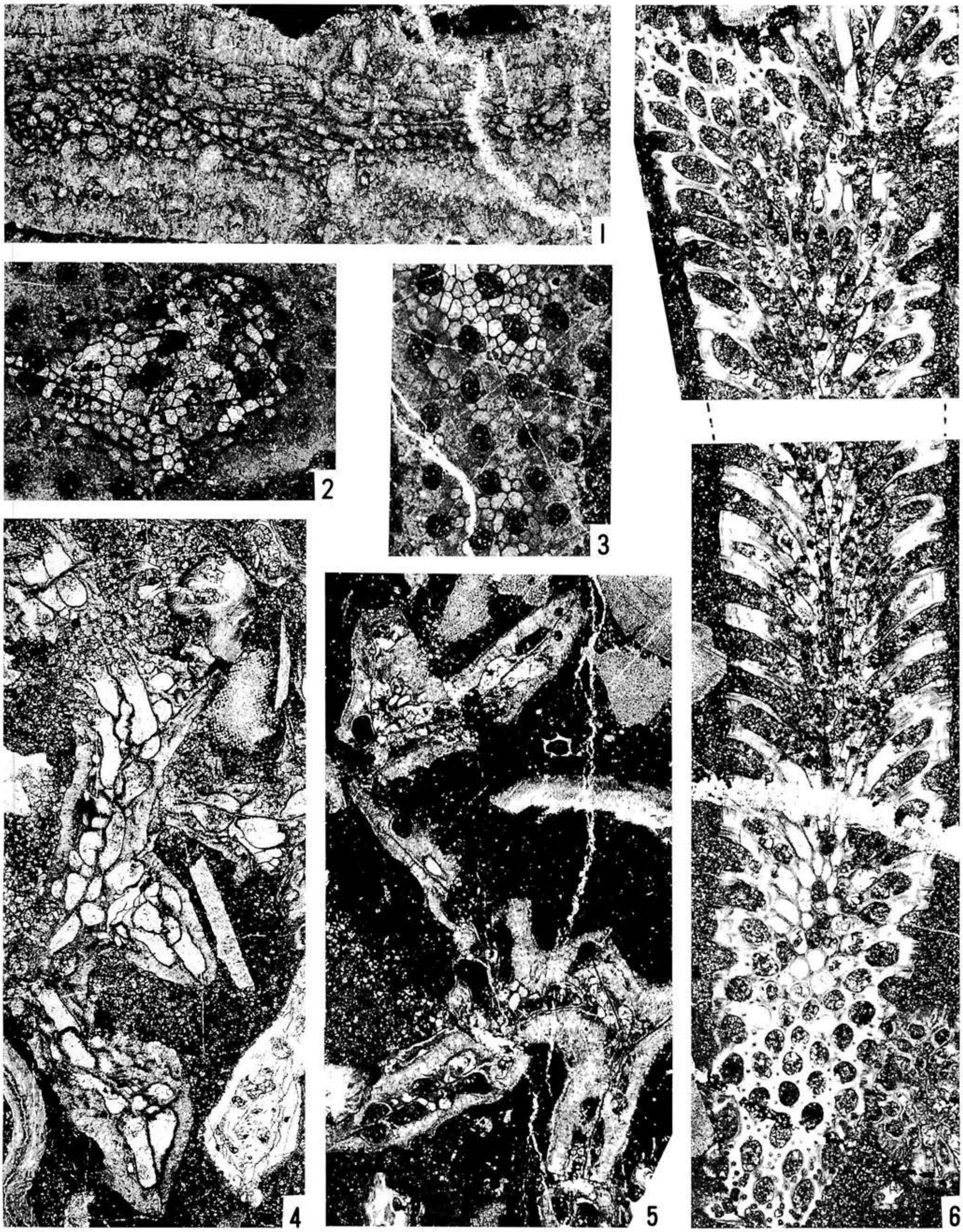
Hexagonella kobayashii Sakagami, 1968a, p. 50, 51, pl. 9, figs. 3-5.

Material and Locality..—MGL74503a, 74503d, 74505c, 74507a, 74511a, 74511b, 74513a, 74513b, 74519a, 74519b, 74522a, 74522b (Maqam) ; MGL74530a (Nackl).

Description.—Zoarial features only seen in thin sections, exact mode of bifurcation not known. Probably broad, parallel-sided, flattened, bifurcating frond, more than 2 mm in thickness.

In tangential section, zooecial tubes nearly circular to oval, diameter from 0.154 to 0.205 mm, occasionally 0.244 at a maximum, usually 4 to 4.5 zooecia per 2 mm diagonally. Lunarium horseshoe-shaped,occupying about one-third to one-fourth of zooecial circumference, but in many cases obliterated by secondary alteration. Interzooecial tissue fine and regularly arranged, 8 to 10 vesicles per mm horizonally in

Figure 3. 1-3. *Hexagonella kobayashii* Sakagami, 1 : longitudinal section, MGL74530a. 2, 3 : tangential sections (showing the hexagonellid ridges, especially in Fig. 3-2), MGL74522b and 74503a, respectively. **4, 5.** *Goniocladia timorensis* Bassler, oblique sections, MGL74520b and 74507b, respectively. **6.** *Dyscritella tenuirama* Crockford, longitudinal section, MGL74515. (All figures are ×20)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inner zone. Hexagonellid ridges are observed in thin sections cut close to the surface but their form is unknown.

In longitudinal section, zooecial tubes proximally parallel to mesotheca for a short distance, afterwards curving gradually upward and then extending directly to outer surface of zoarium at an angle of about 90°. Single diaphragm occasionally observed in inner zone of tube. Interzooecial tissue consisting of elongated quadrate vesicles arranged regularly in longitudinal series in inner zone, usually covered by dark dense fibrous materials in outer zone.

Remarks.—*Hexagonella kobayashii* was originally described from the Rat Buri Limestone cropping out at Khao Phrik near the neck of the peninsular part of Thailand. Although the surface in the present specimens is not observed, the present form can be identified with *Hexagonella kobayashii* described from Thailand by the horseshoe-shaped lunaria being relatively well developed and by its measurements. A specimen from Sample 631 in Nackl is questionably identified with *H. kobayashii*. The geological age is considered to be Middle Permian (Artinskian).

Family Goniocladiidae Waagen and Pichl, 1885
Genus ***Goniocladia*** Etheridge, 1876

Goniocladia timorensis Bassler, 1929

Figures 3-4, 5

Goniocladia timorensis Bassler, 1929, p. 89, pl. 247(23), figs. 8-15; Crockford, 1944a, p. 157, pl. 5, fig. 8; Crockford, 1957, p. 38; Sakagami, 1966, p. 153, text-figs. 4a, b; Morozova, 1970, p. 80, 81, pl. 4, fig. 3.
Goniocladia timorensis var. *afghana* Termier and Termier, 1971, p. 32, pl. 16, figs. 1-9.

Material and Locality.—MGL74507b, 74520b (Maqam).

Description.—Owing to the fact that only a few fragmentary specimens were examined, zoarial form is unknown but probably consits of anastomosing branches. Branch width ranges from 0.7 to 0.8 mm. Zooecial tubes circular in tangential section near surface, diameter ranging from 0.154 to 0.179 mm, parallel to coenelasma for a short distance and curved gradually upward, meeting outer zoarial surface at an angle of about 90°. Diaphragm lacking. Interzooecial tissue consisting of vesicles in inner zone and dark fibrous material from 0.13 to 0.19 mm thick in outer zone.

Remarks.—Although these specimens are poorly preserved, the present form is quite similar to *Goniocladia timorensis* Bassler (1929) from the Permian of Timor Island in its main characters and measurements. The present species has been reported also from the Permian of Western Australia by Crockford (1944a, 1957), Thailand by Sakagami (1966), Afghanistan by Termier and Termier (1971) and Primorye region of Russia by Morozova (1970).

Order Trepostomata Ulrich, 1882
Family Dyscritellidae Dunaeva and Morozova, 1967
Genus ***Dyscritella*** Girty, 1911

Dyscritella tenuirama Crockford, 1957

Figures 3-6

Dyscritella tenuirama Crockford, 1957, p. 52, 53, pl. 13, figs. 1, 2; Sakagami, 1968c, p. 54, 55, pl. 8, figs. 4-8; Sakagami, 1995, p. 256-258, figs. 18-5, 6.
Dyscritella cf. *tenuirama* Crockford. Sakagami, 1970, p. 50, 51, pl. 7, fig. 7.

Material and Locality.—MGL74503c, 74515, 74517a (Maqam).

Description.—Zoarium slender, cylindrical ramose branches, diameter ranges from 1.9 to 2.5 mm, averaging 2.1 mm measured on 3 specimens.

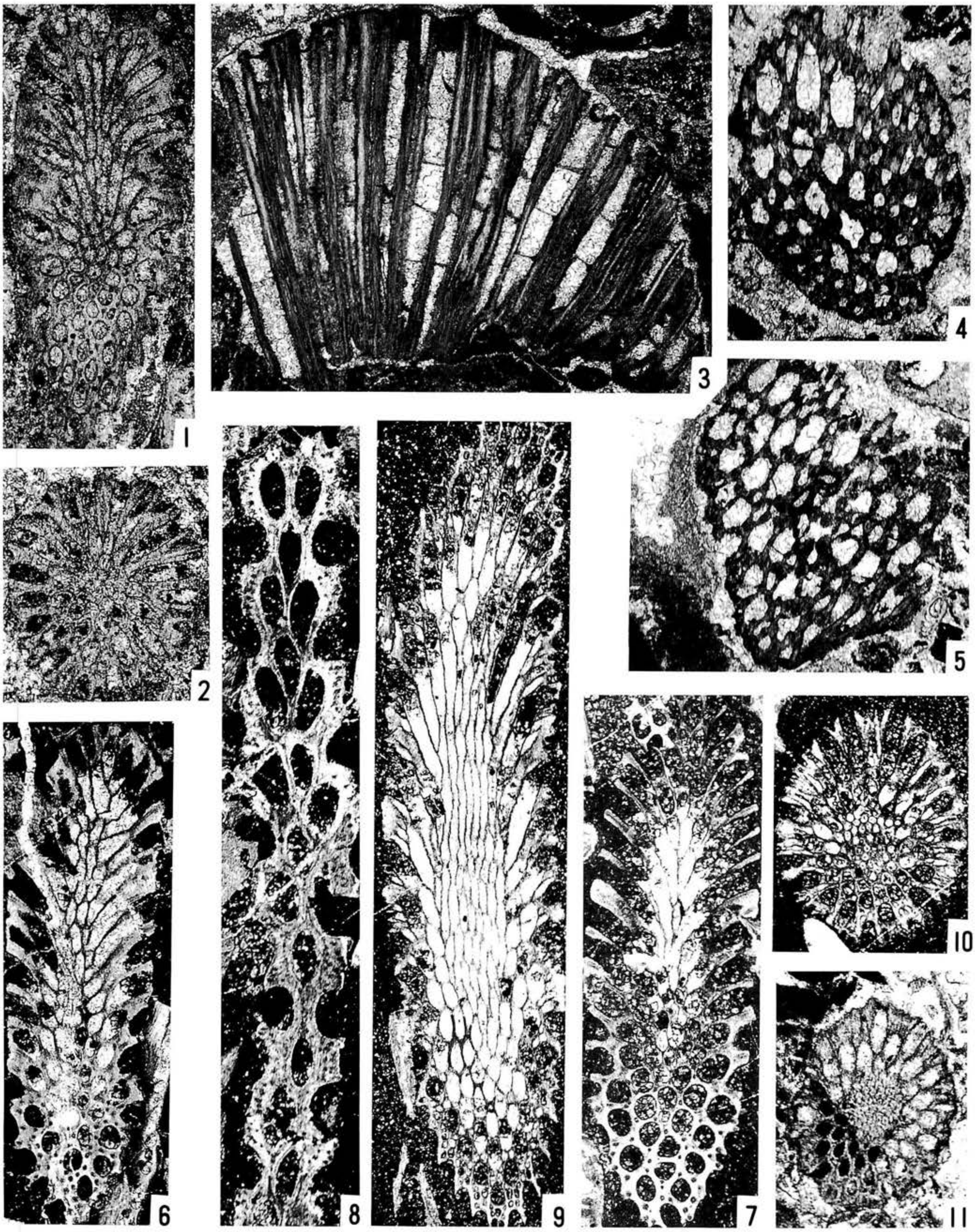
In longitudinal section, zooecial tubes parallel to longitudinal direction of zoarium in inner part of endozone, but gradually curve outward to meet outer surface of zoarium at an angle of about 90°. Zooecial walls straight, thin with a central black line in endozone, and rapidly thickening with finely laminated fibers in exozone. Diaphragms lacking.

In tangential section near the surface, zooecial apertures regularly arranged in substance in longitudinal and diagonal directions, about 3 and 4 in 1 mm in the respective directions. Zooecial tubes oval, longer diameter ranges from 0.231 to 0.282 mm; shorter diameter ranges from 0.140 to 0.167 mm. Mesozooecia circular and rare, 0.050 to 0.070 mm. Well developed acanthostyles usually located at intersection of zooecial walls in inner part of exozone, increasing in number in outer part, surrounded by concentric dark dense fibers. Outside and inner diameters ranging from 0.050 to 0.060 mm and 0.006 to 0.010 mm, respectively.

In transverse section, zooecial tubes thin-walled, polygonal in central part of endozone. The other characters observed in transverse section are the same as in longitudinal section.

Remarks.—*Dyscritella tenuirama* was originally described from the Noonkanbah and Liveringa Formations of the Fitzroy basin, Western Australia by Crockford (1957), and later from the Permian of the peninsular part of Thailand by Sakagami (1968c, 1970) and very recently from the upper part of the Copacabana Group (*Eoparafusulina* zone) in Bolivia, South America by Sakagami (1995). The present form quite agrees with the originally described specimens from Australia in the measurements and essential characters of the internal structure.

Figure 4. **1, 2.** *Dyscritella* sp. indet., obliquely longitudinal and transverse sections, MGL74531a and 74531b, respectively. **3-5.** *Paralioclema eplicatum* Morozova, 3: longitudinal section, MGL74534. 4, 5: oblique sections, MGL74537 and 74533, respectively. **6, 7.** *Rhombopora* aff. *R. lepidodendroides* Meek, obliquely longitudinal sections, MGL74505a and 74505b, respectively. **8.** *Rhombopora* sp. indet., tangentially longitudinal section, MGL74506c. **9-11.** *Streblascopora delicatula* Sakagami, 9: longitudinal section, MGL74520a, 10, 11: transverse sections, MGL74514b and 74530b, respectively. (All figures are ×20)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Dyscritella sp. indet.

Figures 4-1, 2

Material and Locality.—MGL74531a, 74531b (Nackl).

Descriptive remarks.—Obliquely longitudinal and transverse sections examined. Zoarium slender, cylindrical ramose branches, diameter 1.6 to 1.7 mm. The present form is not unlike *Dyscritella tenuirama*, described above, but differs distinctly from the latter species by the smaller size of zooecial tubes and less developed and smaller acanthostyles. Because of the poor preservation of the thin section, specific identification must be postponed until better specimens are accumulated.

Family Araxoporidae Morozova, 1970
Genus ***Paralioclema*** Morozova, 1961

Paralioclema eplicatum Morozova, 1965

Figures 4-3—5

Paralioclema eplicatum Morozova, 1965, in Ruzhentsev and Sarycheva, p. 184, 185, pl. 25, fig. 3; Morozova, 1970, p. 135, pl. 21, fig. 4, pl. 22, fig. 1; Sakagami, 1973a, p. 69, 70, pl. 9, figs. 3-5.

Material and Locality.—MGL74533, 74534, 74535, 74536, 74537, 74538 (Fath).

Description.—Several fragments of encrusting zoarium, these may have been attached to some soft body tissue. Thickest part of zoarium reaching 5.5 mm.

In longitudinal section, zooecial tubes seem to run for a very short distance along coenelasma, then curve rapidly upward, making a right angle to surface. Usually thin and straight or slightly concave diaphragms in zooecial tubes, spaced at intervals of usually 0.30 to 0.50 mm, 4 to 5 in 2 mm length of zooecial tubes. Diaphragms in mesozooecia present but indistinct owing to poor preservation. Wall sides very smooth. Zooecial wall laminae trend approximately parallel to longitudinal direction of zooecia for a short distance before curving into zooecial boundaries. In longitudinal section of acanthoecia, laminae are sharply swelled out to surface.

In tangential section, zooecial tubes irregularly circular with polygonal margin effected by well developed acanthostyles. Diameter of zooecia 0.154 to 0.192 mm in inner zone and 0.192 to 0.231 mm in outer zone. Mesozooecia circular, commonly present, usually 0.077 to 0.103 mm, but occasionally 0.128 mm in outer zone. Acanthostyles numerous and well developed, covered with coarse concentric fibrous materials varying from 0.10 to 0.20 mm in diameter. Inside diameter of acanthostyles very small, less than 0.020 mm.

Remarks.—Except for being slightly different in the microscopic measurements, the present form is identical with *Paralioclema eplicatum*, which was originally described by Morozova (1965, 1970) from the Gnishik horizon (lower part of Guadalupian stage, Upper Permian) of Transcaucasia, Armenia, Russia, and later by Sakagami (1973a) from the upper part of the Guadalupian of Kampong Awah Quarry and Jenka Pass in Pahang, Malaya, in all of the essential characters.

Order Cryptostomata Vine, 1883
Suborder Rhabdomesina Astrova and Morozova, 1956
Family Rhomboporidae Simpson, 1895
Genus ***Rhombopora*** Meek, 1872

Rhombopora aff. ***R. lepidodendroides*** Meek, 1872

Figures 4-6, 7

Compared.—

Rhombopora lepidodendroides Meek, Newton 1971, p. 28, 29, 31-35, pl. 1, figs. 1-6, 11, 12, pl. 2, figs. 1-8, 11, 16 (see also the synonym list); Sakagami, 1995, p. 261-262, figs. 1-1-6.

Material and Locality.—MGL74505a, 74505b (Maqam).

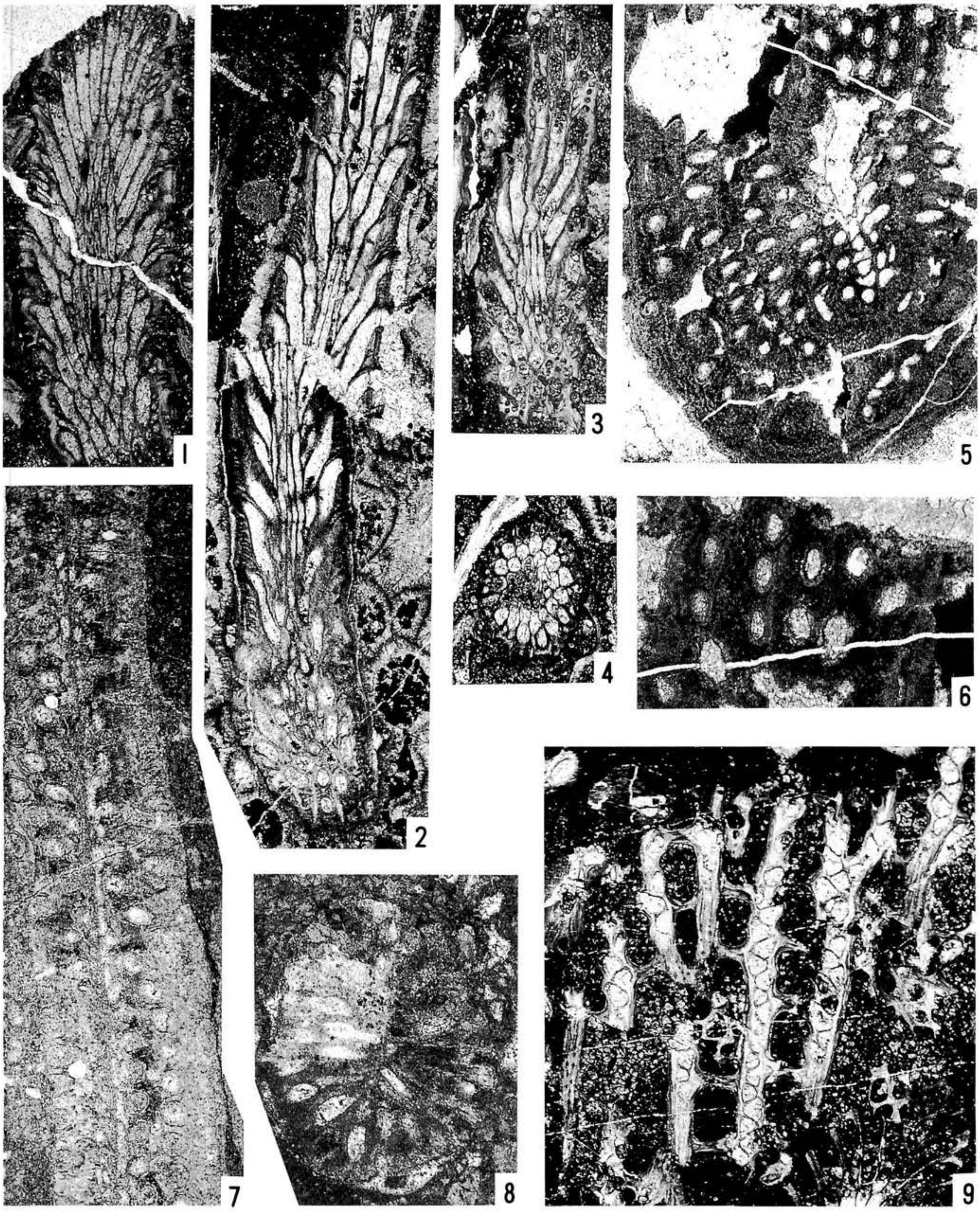
Description.—Zoarium consisting of slender, cylindrical stem, diameter 1.3 mm and 1.5 mm, respectively.

In longitudinal section, axial region consists of a nearly straight axis and straight zooecial tubes making a small angle with longitudinal direction in endozone, bending slightly and gradually outward to meet outer surface of zoarium at an angle of about 50 degrees. Zooecial walls thin and nearly straight in endozone and gradually thickened, consisting of finely laminated fibers in exozone. Diameter of endozone about 0.5 mm and width of exozone 0.4 to 0.5 mm.

In tangential section of exozone, zooecial tubes oval, longer diameter 0.192 to 0.231 mm and shorter diameter 0.141 to 0.179 mm, probably regularly arranged in longitudinal and diagonal directions; their detailed arrangement is, however, indistinct owing to badly oriented thin sections. Usually one, occasionally two acanthostyles at each corner of zooecial tube, surrounded by concentric dark fibers; outside diameter ranges varies from 0.030 to 0.060 mm, inside diameter less than 0.010 mm. Paurostyles not visible.

Remarks.—Because only two obliquely oriented thin sections are available, detailed comparisons are difficult, but the present form appears identical with *Rhombopora lepidodendroides* in essential characters. Newton (1971) discussed *R. lepidodendroides* in detail, and he concluded that its variation in time (from Early Pennsylvanian to Late Permian) and space (in worldwide distribution) lacked any systematic pattern. For the present, the Omani specimens described here are placed in a relationship of affinity.

Figure 5. 1. *Streblascopora delicatula* Sakagami, longitudinal section, MGL74525a. **2-4.** *Streblascopora exillis* Sakagami, 2, 3: longitudinal sections, MGL74512a and 74525b, respectively, 4: transverse section, MGL74526a. **5-7.** *Timanodictya* cf. *T. dichotoma* (Stuckenberg), 5: obliquely tangential section, MGL74529, ×10, 6: enlarged tangential part of Fig. 5-5, 7: longitudinal section, MGL74528, ×10. **8.** *Girtypora* cf. *G. ramosa* Morozova, transverse section, MGL74529. **9.** *Alternifenestella* cf. *A. horologia* (Bretnall), tangential section, MGL74505d. (All figures are ×20, except for **5**-5 and **5**-7)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Rhombopora sp. indet.

Figures 4-8

Material and Locality.—MGL74506c (Maqam).

Descriptive remarks.—A single tangentially longitudinal section was examined. Zoarium consisting of nearly straight, slender, cylindrical stem, having small diameter: about 1.0 mm. The present form is not unlike *Rhombopora lepidodendroides* in general mode, but it can be distinguished from the latter species by the larger diameter of the zooecial tubes. The specific identification must be postponed until better specimens are accumulated.

Family Hyphasmoporidae Vine, 1886
Genus ***Streblascopora*** Bassler, 1952

Streblascopora delicatula Sakagami, 1961

Figures 4-9—11; 5-1

Streblascopora delicatula Sakagami, 1961, p. 52, pl. 25, figs. 7-10, pl. 26, figs. 1-18, pl. 27, figs. 1-5; Sakagami, 1973b, p. 84, 85, pl. 8, figs. 1-4; Yang and Lu, 1984, p. 53, 54, pl. 1, fig. 5b, pl. 2, figs. 3a, b.

Material and Locality.—MGL74503b, 74514b, 74516b, 74518a, 74518b, 74520a, 74525a (Maqam); MGL74530b (Nackl).

Description.—Zoarium consists of cylindrical ramose branches, varying from 1.3 to 1.9 mm in diameter.

In longitudinal section, diameter of central bundle 0.5 to 0.7 mm, ratios of zoarial diameter to central bundle ranging from 2.5 : 1 to 3.1 : 1, and number of tubes in central bundle 7 to 8. Zooecial tubes arise from central bundle at an angle of about 25°, straight in endozone and curving rapidly at inner edge of exozone. Metapores arise from base of exozone, approximately parallel to endozone wall for a very short distance, then curving rapidly outward and parallel to zooecial tubes in exozones.

In tangential section of exozone, zooecial tubes oval, longer diameter 0.154 to 0.179 mm and shorter diameter 0.090 to 0.115 mm. Zooecial apertures arranged regularly in longitudinal rows with about 4.5 zooecia in 2 mm measuring lengthwise and almost 10 in the same space transversely. Superior and inferior hemisepta may be present but are rarely observable. Metapores usually circular but irregular in shape and size, diameter ranging from 0.013 to 0.038 mm, usually two or three rows with 2 to 3 in each row longitudinally. Total number of metapores disposed between zooecial tubes in one series usually 7, occasionally 10.

In transverse section, number of tubes in central bundle were counted as more than 40 in one typical section. The other characters observed in transverse section are the same as in longitudinal section.

Remarks.—Many species included in the genus *Streblascopora* are widely distributed in the Tethys and Tasman Geosyncline provinces in Middle Permian time. Among these, the present form agrees with *Streblascopora delicatula* which was described originally by Sakagami (1961) from the Upper Permian of several localities in Japan in its essential features, especially size of zoarium and mode of central bundle. The present species is characterized and can be distinguished from the already described species by the larger diameter of the central bundle, having about 40 or more tubes. This species has been reported also from the Lower Permian (most probably late Artinskian) of the Rat Buri Limestone in Khao Raen at the neck of the peninsular part of Thailand by Sakagami (1973b) and the Maokou Formation (Permian) of Kueichou, South China by Yang and Lu (1984).

Streblascopora exillis Sakagami, 1970

Figures 5-2—4

Streblascopora exillis Sakagami, 1970, p. 64, 65, pl. 12, figs. 4-8.

Material and Locality.—MGL74511c, 74512a, 74523b, 74523c, 74525b, 74526a (Maqam).

Description.—Zoarium nearly straight, slender, cylindrical stem, 0.9 to 1.2 mm in diameter.

In longitudinal section, diameter of central bundle 0.3 to 0.5 mm, ratio of zoarial diameter to central bundle ranging from 3.0 : 1 to 4.0 : 1, and number of tubes in central bundle 4 to 6. Zooecial tubes arise from central bundle at an angle of about 20°, straight in endozone and curving rapidly at inner edge of exozone. Metapores arise from base of exozone, approximately parallel to endozone wall for a very short distance, then curving rapidly outward and parallel to zooecial tubes in exozone.

In tangential section, zooecial tubesoval, larger diameter 0.141 to 0.167 mm and shorter diameter 0.103 to 0.128 mm. Zooecial apertures arranged regularly in longitudinal rows. Number of zooecia indistinct but probably 3 to 4 per 2 mm longitudinally. Superior and inferior hemisepta seem to be undeveloped. Metapores circular and regular in shape and size, usually two rows with four to five in each longitudinal row, total number of metapores disposed between zooecial tubes in one series 8 to 10. One straight diaphragm disposed near surface of tube.

In transverse section, number of tubes in central bundle counted as nearly 10. The other characters observed in transverse section are the same as in longitudinal section.

Remarks.—The present form may be identical with *Streblascopora exillis* which was described by Sakagami (1970) from Ko Muk on the west coast of Thailand in all essential characters, especially its small zoarial diameter and number of metapores between zooecial tubes. The Ko Muk bryozoan fauna is thought to be most probably late Artinskian. The present form seems to resemble *Streblascopora biserialis* (Bassler) which was originally described by Bassler (1929) from Timor, but a detailed comparison between them is impossible, because the Timor species depends on a brief description with only one illustration of the surface of a specimen.

Suborder Timanodictyoidea Morozova, 1966
Family Timanodictyidae Morozova 1966
Genus ***Timanodictya*** Nikiforova, 1938

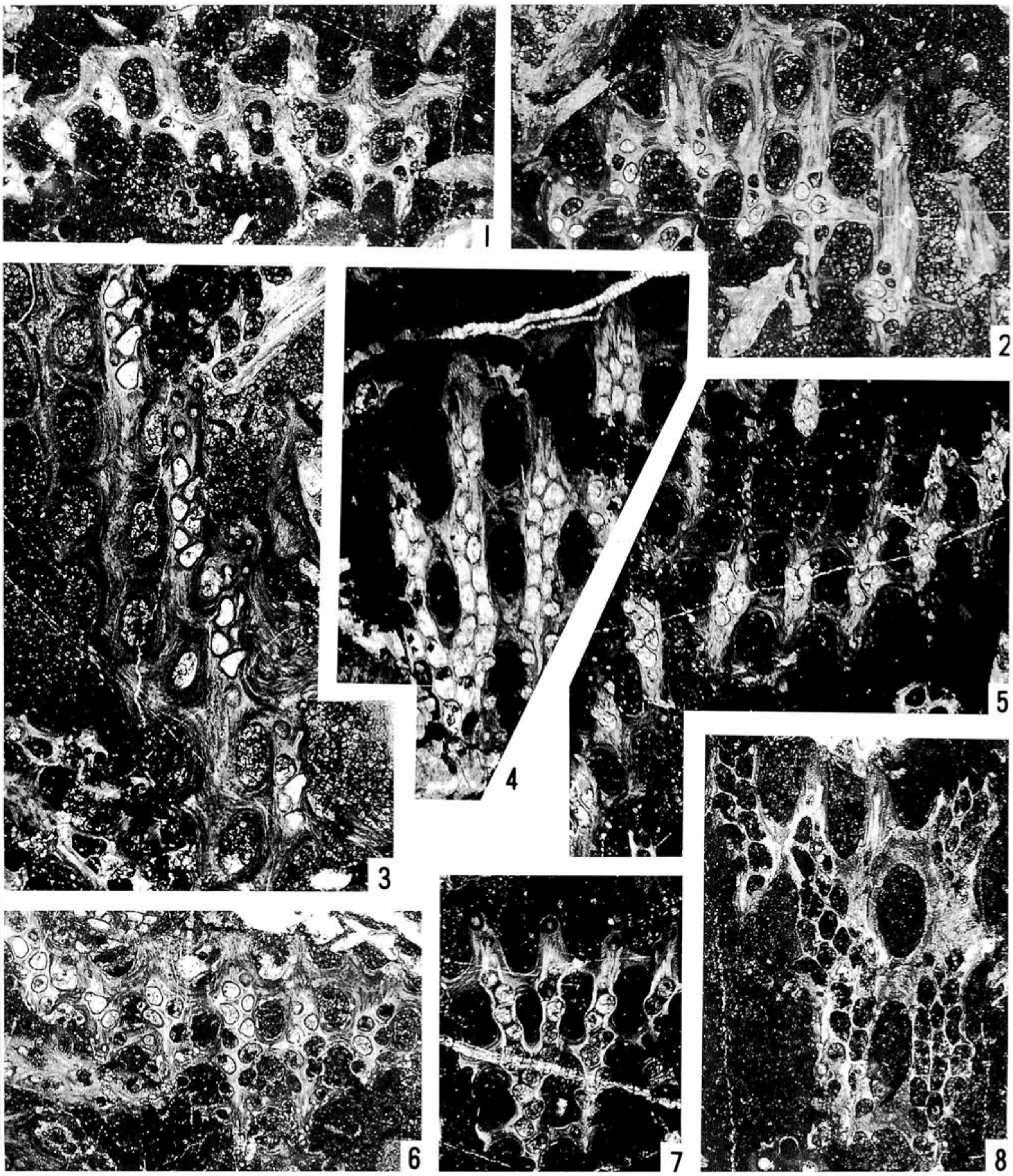


Figure 6. **1.** *Alternifenestella* sp. indet. A, tangential section, MGL74506b. **2.** *Alternifenestella* sp. indet. B, tangential section, MGL74508b. **3.** *Alternifenestella* sp. indet. D, tangential section, MGL74502. **4.** *Laxifenestella lahuseni* (Stuckenberg), tangential section, MGL74512b. **5.** *Minilya duplaris* Crockford, tangential section, MGL74517b. **6.** *Minilya* sp. indet., tangential section, MGL74524a. **7.** *Alternifenestella* sp. indet. C, tangential section, MGL74508c. **8.** *Polypora* cf. *P. elliptica* Rogers, tangential seciton, MGL74510. (All figures are ×20)

Timanodictya cf. ***T. dichotoma*** (Stuckenberg, 1895)

Figures 5-5—7

Compared.—
Coscinium dichotoma Stuckenberg, 1895, p. 173, pl. 24, fig. 3.
Timanodictya dichotoma (Stuckenberg), Nikiforova, 1938, p. 185-188, 269-271, pl. 48, figs. 1-4, pl. 49, figs. 1-10, pl. 50, figs. 1-4, pl. 51, figs. 1-6, pl. 52, figs. 5-7.
Timanodictya cf. *T. dichotoma* (Stuckenberg), Ross and Ross, 1962, p. 60-62, pl. 18, figs. 1-6.

Material and Locality.—MGL74527, 74528 (Maqam).

Description.—Only obliquely tangential and obliquely longitudinal sections were examined. Zoarium consists of broad, bifoliate branch, estimated to be about 8 mm in width and about 3 mm in thickness. The growth system is not observed in the present specimens.

In tangential section, zooecial tubes oval, usually 3.5 to 4 zooecia per 2 mm in longitudinal direction. Shorter diameter of zooecial tubes ranges from 0.128 to 0.167 mm, and longer diameter from 0.192 to 0.231 mm. Zooecial tubes surrounded by rather thick, light-colored partition. Interzooecial tissue consisting of fine, dark laminae and pierced by numerous small rods or tubes.

In longitudinal section, zooecial tubes proximally parallel to mesotheca, curved rapidly outward, and making a right angle with outer surface of zoarium.

Remarks.—Because of the secondarily altered, fragmentary specimens at hand, a detailed comparison with the type specimens of *Timanodictya dichotoma* described by Nikiforova (1938) from the '*Schwagerina*' beds (Lower Permian) of Timan, Russia is impossible. The present form, however, may be conspecific with the Timan species. The comparable species was described by Ross and Ross (1962) from the Wolfcampian ? of Holm Land, northeast Greenland.

Genus ***Girtypora*** Morozova, 1966

Girtypora cf. ***G. ramosa*** Morozova, 1966

Figures 5-8

Compared.—
Girtypora ramosa Morozova, 1966, p. 36, 37, pl. 5, fig. 2 ; Morozova, 1970, p. 248, 249, pl. 60, fig. 2, pl. 61, fig. 1 ; Liu, 1980, p. 253, pl. 111, figs. 5, 6.

Material and Locality.—MGL74529 (Maqam).

Description.—A single transverse section of zoarium was examined. Zoarium consisting of cylindrical branch, having a small diameter : about 2 mm. Zooecial tubes arise directly from median laminae to zoarial surface and range from 0.141 to 0.167 mm in diameter. Interzooecial tissue consists of dark, fine fibers with spicule-like structure.

Remarks.—Despite there being available only one transverse section of zoarium, the present form seems to be identical with *Girtypora ramosa* which was originally described by Morozova (1966) from the lower Kazanian (Upper Permian) of the Russian Platform in its essential characters, but the zooecial tubes are slightly narrower than in the Russian specimens. Accordingly, the present form is only compared with *Girtypora ramosa* although it may be conspecific with the Russian species. The present species was also described by Liu (1980) from the upper part of the Lower Permian of northeast China.

Order Fenestrata Elias and Condra, 1957
Family Fenestellidae King, 1849
Genus ***Alternifenestella*** Termier and Termier, 1971

Alternifenestella cf. ***A. horologia*** (Bretnall, 1926)

Figures 5-9

Compared.—
Fenestella horologia Bretnall, 1926, p. 15, pl. 1, fig. 6 ; Hosking, 1931, p. 13, pl. 4, fig. 3 ; Crockford, 1957, p. 57 ; Wass, 1966, p. 92-94, pl. 2, fig. 1, 3, not 2, 4-7 ; Wass, 1967, p. 16 ; Sa-

Table 2. Measurements of the species of *Alternifenestella, Minilya,*

Species	*Specimen No. (MGL)*	*No. per 10 mm*		*No. of zooecia*		*No. of nodes per 5 mm*
		branches (horizontally)	*fenestrules (longitudinally)*	*per 5 mm*	*per fenestrule*	
Alternif. cf. *A.horologia*	74505d	18	18	18	2	—
Alternif. sp. indet. A	74506b	18-20	16	16	2	indistinct
Alternif. sp. indet. B	74508b	16	14	14	2-3	indistinct
Alternif. sp. indet. C	74508c	18	16	16	2	indistinct
Alternif. sp. indet. D	74502	ca. 16	13	13	2-3	—
Minilya duplaris	74517b	20	18	18	2	36
Minilya sp. indet.	74524a	18	20	20	2	40
Laxif. lahuseni	74512b	16	10	ca. 20	4	indistinct
Fabif. subpermiana	74521a	12	9	18	4	indistinct
Rugof. basleoensis	74521b	13	9	18	4	—
Rugof. omanica sp. nov.	74514a, 74517c	15	8-9	16-18	4-5	16-18

kagami, 1968b, p. 69-71, text-fig. 3A.
Fenestella cf. *horologia* Sakagami, 1970, p. 55, 56, pl. 9, fig. 6.
Fenestrellina horologia (Bretnall), Crockford, 1943, p. 266 ; Crockford, 1944a, p. 158 ; Crockford, 1944b, p. 167, pl. 1, figs. 3, 6 ; Crockford, 1944c, p. 189, pl. 1, fig. 1 ; pl. 2, fig. A ;
Fenestella parviuscula Bassler, 1929, p. 76, pl. 241(17), figs. 8-13 ; Fritz, 1932, p. 99 ; Elias, 1937, p. 314.

Material and Locality.—74505d (Maqam).

Description.—A single tangential section. Zoarium probably fan-shaped, consists of straight, nearly parallel branches connected by dissepiments at regular intervals. Branches bifurcated at long intervals. Width of branch as wide as that of fenestrule, ranging from 0.256 to 0.282 mm ; 18 branches per 10 mm horizontally. Fenestrules quadrate with rounded corners ; width ranges from 0.231 to 0.321 mm, length ranging from 0.385 to 0.449 mm ; about 18 fenestrules per 10 mm of branch length. Dissepiments narrow, about 0.128 mm in width. Zooecial tubes arranged in strongly alternating longitudinal series ; trigonal or rhomboidal in lower to middle levels of branch, curved outward and circular at upper level of branch, 0.090 to 0.103 mm in diameter. Distance between zooecial apertures from center to center ranges from 0.256 to 0.321 mm ; about 18 zooecia per 5 mm longitudinally, consistently spaced in relation to dissepiment, 2 apertures per fenestrule. Nodes unobservable. Stereom thin, covering reverse side of branch, consists of inner semitransparent layer of colonial plexus and outer sclerenchyma of darker coarse fibers with well developed fine spicules.

Meshwork formula.—18/18//18/? (The meshwork formula used for fenestellids refers to the number of branches per 10 mm/number of fenestrules per 10 mm//number of zooecia per 5 mm/number of nodes in 5 mm).

Remarks.—The present form agrees well with *Fenestella horologia*, the neotype of which was revised by Crockford (1944b) in its microscopic measurements, meshwork formula and all essential characters, except for the arrangement of nodes, which was unobsevable. This species has been known from the Permian of Australia, Thailand, and also from Timor Island and Vancouver Island as *Fenestella parviuscula*.

Alternifenestella sp. indet. A

Figures 6-1

Material and Locality.—MGL74506b (Maqam).

Meshwork formula..—18-20/16//16/?.

Descriptive remarks.—This single tangential section of fragmentary zoarium consists of straight, parallel branches connected by dissepiments at regular intervals. Bifurcation of branches unknown. A detailed comparison with previously described species cannot be made at present because the one fragmentary specimen at hand is too poor for specific identification.

Alternifenestella sp. indet. B

Figures 6-2

Material and Locality.—MGL74508b (Maqam).

Meshwork formula.—16/14//14/?.

Descriptive remarks.—A single tangential section of fragmentary zoarium, consists of straight, parallel branches connected by dissepiments at regular intervals. Bifurcation of branches unknown. The one fragmentary specimen is insufficient for a specific discrimination.

Alternifenestella sp. indet. C

Figures 6-7

Material and Locality.—MGL74508c (Maqam).

Meshwork formula.—18/16//16/indistinct.

Descriptive remarks.—A single tangential section of fragmentary zoarium, consists of fan-shaped, fine meshwork with straight branches connected by dissepiments at regular intervals. Branches bifurcated frequently, as wide as that of

Laxifenestella, Fabifenestella and *Rugofenestella* (in mm).

Width of			Length of fenestrules	Diameter of zooecia near surface	Distance between zooecia	Outside diameter of nodes	Distance between nodes
branches	fenestrules	dissepiments					
.256-.282	.231-.321	.128	.385-.449	.090-.103	.256-.321	—	—
.231-.295	.205-.321	.154-.205	.321-.385	.080-.103	.256-.321	ca. .030	indistinct
.256-.385	.256-.321	.218-.296	.449-.513	.115-.128	192-.256	?	indistinct
.231-.256	.192-.256	.167-.192	.385-.513	.060-.070	.295-.359	—	indistinct
.321-.416	.189-.231	.321-.384	.385-.513	.120	.231-.256	—	—
.282-.321	.231-.256	.154-.192	.385-.449	.064-.077	.256-.321	.051-.064	.128-.192
.321-.385	.192-.231	.192-.256	.256-.321	.077-.090	.192-.231	.051-.064	.115-.128
.320-.352	.288-.320	.384-.416	544-.704	.103-.115	.256-.295	—	indistinct
.385-.449	.321-.385	.321-.385	.769-.833	.077-.090	.282-.308	indistinct	—
.321-.385	ca. .385	.231-.256	.769-.833	.064-.077	.256-.321	—	—
.384-.448	.288-.416	.480-.576	.512-.800	.115-.128	.256-.308	.077 ?	?

fenestrules. The present form seems to be similar to *Fenestella macronodata* Sakagami (1964) originally described from the Permian of the Akiyoshi Limestone, however, specific identification must be postponed until better specimens are accumulated.

Alternifenestella sp. indet. D

Figures 6-3

Material and Locality.—MGL74502 (Maqam).

Meshwork formula.—ca.16/13//13/?.

Descriptive remarks.—A single tangential section. Zoarium consists of straight, parallel branches connected by dissepiments at regular intervals. Branches bifurcate at long intervals and are wider than fenestrule. The present form is close to *Fenestella* cf. *retiformis* which was described from the *Parafusulina kaerimizensis* zone of the Akiyoshi Limestone Group, Japan, in its general appearance. However, specific identification must be postponed until better specimens can be accumulated.

Genus ***Minilya*** Crockford, 1944

Minilya duplaris Crockford, 1944

Figures 6-5

Minilya duplaris Crockford, 1944b, p. 173, 174, pl. 1, figs. 5, 7, text-fig. 1C, D; Crockford, 1946, p. 132; Crockford, 1957, p. 67, 68.

Material and Locality.—MGL74517b (Maqam).

Description.—A single tangential section was examined. Zoarium consists of straight, parallel branches connected by dissepiments at regular intervals. Branches bifurcate at very long intervals. Branches wider than fenestrules, ranging from 0.282 to 0.321 mm; about 20 branches per 10 mm horizontally. Fenestrules hourglass-shaped because zooecial apertures intrude at their sides, width ranging from 0.231 to 0.256mm, length ranging from 0.385 to 0.449 mm; about 18 fenestrules per 10 mm of branch length. Dissepiments narrow, 0.154 to 0.192 mm in width. Zooecial tubes alternately intersecting longitudinal series, triangular to pentagonal at lower level of branch, curved outward, pentagonal at middle and circular at upper levels of branch. Zooecial diameters near surface range from 0.064 to 0.077 mm. Distance between zooecial apertures from center to center ranges from 0.256 to 0.321 mm; about 18 zooecia per 5 mm longitudinally, consistently spaced in relation to dissepiment, 2 apertures per fenestrule, two rows of zigzag nodes prominent on well developed broad carina. Total number of nodes about 36 per 5 mm of branch length. Nodes range from 0.051 to 0.064 mm in outside diameters spaced at same interval as apertures, namely one node to each zooecial aperture. Stereom covering reverse side of branch consists of inner semitransparent layer of colonial plexus and outer sclerenchyma of darker fibers with very small granules.

Meshwork formula.—20/18//18/36.

Remarks.—The present form is nearest to *Minilya duplaris* in the meshwork formula and essential characters. This species was originally described by Crockford (1944b) as the type species of the newly established genus *Minilya* from the Noonkanbah series of Western Australia. Later, Wass (1966) discussed the specimens of *Fenestella horologia* and *Minilya duplaris* Crockford and concluded that those two species are conspecific and therefore, because of priority, *Minilya duplaris* is invalid. However, these two species seem to be different in the number of nodes per 5 mm of branch length as shown in Table 1 of Wass (1966). The genus *Minilya* is now recognized widely and is treated here as a valid genus.

Minilya sp. indet.

Figures 6-6

Material and Locality.—MGL74524a (Maqam).

Meshwork formula.—18/20//20/40.

Descriptive remarks.—A single tangential section of fragmentary zoarium consisting of straight branches connected by dissepiments at regular intervals. Bifurcation of branch not observed. The present form is very near to the above-described species *Minilya duplaris* in the meshwork formula, but it can be distinguished from the latter form by the microscopic measurements, namely the width of branches is narrower than that of the fenestrules in *M. duplaris* but wider in the present form, and by the shapes of the zooecial tubes in the middle level of the branch in tangential section. The specific denomination, however, must be reserved because of the poorly preserved specimen.

Genus ***Laxifenestella*** Morozova, 1974

Laxifenestella lahuseni (Stuckenberg), 1895

Figures 6-4

Fenestella lahuseni Stuckenberg, 1895, p. 148, 149, pl. 21, fig. 14; Nikiforova, 1938, pp. 80, 81, 231, pl. 14, figs. 1-5, text-figs. 41-43.

Fenestella lahuseni, forma A, Shulga-Nesterenko, 1936, p. 260,

Table 3. Measurements of the species

Species	Specimen No. (MGL)	No. per 10 mm		No. of zooecia	
		branches (horizontally)	fenestrules (longitudinally)	per 5 mm	per fenestrule
Polypora cf. *P. elliptica*	74510, 74524b	(13)-15	10	18-20	4
Polypora cf. *P. gigantea*	74516c	7?	2.5-3	12-13	ca. 10
Polypora sp. indet.	74504	10	4.5	14-15	(4?)-5

261, 281, text-figs. 25, 26.
Fenestella lahuseni var. *monoseriata*, Shulga-Nesterenko, 1941, p. 55, 56, pl. 3, fig. 3.

Material and Locality.—MGL74512b (Maqam).

Description.—A single tangential section of fragmentary zoarium, consisting of nearly straight branches connected by dissepiments at regular intervals. Branches may bifurcate frequently because zooecial tubes arranged in 3 rows just before bifurcation are observed often. Width of branch about as wide as or slightly wider than that of fenestrule, ranging from 0.320 to 0.352 mm, about 16 branches per 10 mm horizontally. Fenestrules elongate, quadrate with rounded corners, width ranging from 0.288 to 0.320 mm, length 0.544 to 0.704 mm ; about 10 fenestrules per 10 mm of branch length. Dissepiments rather wide, range from 0.384 to 0.416 mm in width. Zooecial tubes form very limited alternating longitudinal series, elongate quadrate or deformed pentagonal at middle level of branch, and circular at upper level, range from 0.103 to 0.115 mm in diameter. Zooecial apertures about 20 per 5 mm in a range, usually 4 zooecia per fenestsrule. Nodes indistinct. Stereom covering reverse side of branch consists of inner semitransparent layer of colonial plexus and outer sclerenchyma of darker fibers with small granules.

Meshwork formula.—16/10//20/?.

Remarks.—Although the nodes are indistinct, the present form is nearest to *Fenestella lahuseni* var. *monoseriata* in the meshwork formula, and the shape and arrangements of zooecial tubes at the middle level of the tangential section. Shulga-Nesterenko's specimens from the Lower Permian of the middle Pechora region of the Northern Urals, Russia, may be included in *Fenestella lahuseni*. The original specimen of this species was described by Stuckenberg (1895) from the Lower Permian (Artinskian) of the Kolva river region in Russia and was reexamined by Nikiforova (1938).

Genus ***Fabifenestella*** Morozova, 1974

Fabifenestella subpermiana (Shulga-Nesterenko), 1952

Figures 7-1

Fenestella subpermiana Shulga-Nesterenko, 1952, p. 31, pl. 3, fig. 1, text-figs. 10, 11 ; Gorjunova, 1975, p. 71, pl. 13, fig. 1.

Material and Locality.—MGL74521a (Maqam).

Description.—A single tangential section was examined. Zoarium consists of nearly straight branches connected by dissepiments at regular intervals. Branches bifurcated at long intervals. Branch width ranges from 0.385 to 0.449 mm and about 12 branches per 10 mm horizontally. Fenestrules elongate, quadrate with rounded corners, width ranges from 0.321 to 0.385 mm, length ranges from 0.769 to 0.833 mm, about 9 fenestsrules per 10 mm of branch length. Dissepiments moderate, width ranging from 0.321 to 0.385 mm. Zooecial tubes in limited alternating longitudinal series, usually kidney-shaped at middle level of branch, curved outward and circular at upper level, range from 0.077 to 0.090 mm in diameter. Zooecial apertures about 18 per 5 mm in a range, consistently positioned in relation to dissepiment, 4 zooecia per fenestrule. Nodes indistinct. Stereom covering reverse side of branch consists of inner semitransparent layer with three to four fine striations of colonial plexus and outer sclerenchyma of coarser fibers with very small granules.

Meshkwork formula.—12/9//18/indistinct.

Remarks.—The present form is similar to *Rugofenestella basleoensis*, described in the present report, in microscopic measurements, but it differs from the latter by the shape of the zooecial tubes in tangential section and the internal structure of the reverse side of the branch. The present form agrees with *Fenestella subpermiana*, especially as described by Gorjunova (1975) from the upper part of the '*Schwagerina*' horizon of the Lower Permian of the Bashkirian ASSR, Pamir in microscopic measurements.

Genus ***Rugofenestella*** Termier and Termier, 1971

Rugofenestella basleoensis (Bassler), 1929

Figures 7-2

Fenestella basleoensis Bassler, 1929, p. 74, pl. 240(16), figs. 5-9 ; Fritz, 1932, p. 99 ; Shulga-Nesterenko, 1936, p. 253-254, 277, text-fig. 16 ; Shulga-Nesterenko, 1939, p. 70, pl. 12, fig. 3 ; Shulga-Nesterenko, 1941, p. 102, pl. 19, fig. 4 ; pl. 20, figs. 1-3 ; Crockford, 1957, p. 58 ; Sakagami, 1968b, p. 73, text-fig. 3G ; Xia, 1986, p. 218, pl. 6, figs. 13, 14 ; Xia, 1991, p. 173, pl. 1, fig. 3.

Material and Locality.—MGL74521b (Maqam).

Description.—A single tangential section was examined. Zoarium consists of straight branches connected by dissepiments at regular intervals. Branches bifurcate at long intervals. Branch width ranges from 0.321 to 0.385 mm with about 13 branches per 10mm horizontally. Fenestrules elongate, quadrate with rounded corners, width about 0.385 mm, length ranging from 0.769 to 0.833 mm, about 9 fenestrules per 10 mm of branch length. Dissepiments moderate, width ranging from 0.231 to 0.256 mm. Zooecial tubes

of *Polypora* (in mm).

No. of rows of zooecia	Width of branches	Width of fenestrules	Width of dissepiment	Length of fenestrules	Diameter of zooecia near surface	Distance between zooecia
(2)-3	.416-.480	.256-.320	.320-.480	.480-.704	.115-.128	.256-.321
(5)-6-(8)	.960-1.216	ca. .500	ca. .640	ca. .300	ca. 115	.385-.410
4	ca. .640	ca. .480	.640-.704	1.120-1.280	.115-.128	.385-.449

arranged in strongly alternating longitudinal series, usually triangular at middle level, curved outward and circular at upper level of branch. Openings of zooecial tubes near surface rather small, ranging from 0.064 to 0.077 mm in diameter. Zooecial apertures about 18 per 5 mm in a range, consistently positioned in relation to dissepiment, usually 4 zooecia per fenestrule. Nodes indistinct. Stereom covering reverse side of branch consists of inner semitransparent layer of colonial plexus and outer sclerenchyma of coarser fibers with small granules.

Meshwork formula.—13/9//18/indistinct.

Remarks..—As the original specimen of *Fenestella basleoensis* from Timor Island was described on the basis of only a surface specimen by Bassler (1929), the internal structures are not distinct. However, the present form is identical with the Timor specimens in the meshwork formula and measurements. This species is widely distributed in the Tethyan region, being found in Timor, Thailand, China and the Ural region of Russia.

The present form is almost identical with *Fabifenestella subpermiana* (MGL74521a) described in the present report in measurements, but it can be distinguished distinctly from the latter form by the arrangement of zooecial tubes in the middle level of the branch in tangential section, namely, the strongly alternating intercalated zooecial tubes in the present form instead of the usually kidney-shaped zooecial tubes in the latter form.

Rugofenestella omanica sp. nov.

Figures 7-4, 5

Material and Locality.—MGL74514a (holotype), 74517c (paratype) (Maqam).

Description.—Zoarium consists of nearly straight, parallel branches connected by dissepiments at regular intervals. Branches bifurcate at long intervals. Branch width ranges from 0.384 to 0.448 mm with 13 to 15 branches per 10 mm horizontally. Fenestrules oval or quadrate with rounded corners; width ranges from 0.288 to 0.416 mm, length ranges from 0.512 to 0.800 mm; 8 to 9 fenestrules per 10 mm of branch length. Dissepiments range from 0.480 to 0.576 mm in width. Zooecial tubes arranged in strongly alternating longitudinal series, usually trigonal at middle level of branch, curved outward and circular at upper level of branch, 0.115 to 0.128mm in diameter. Distance between zooecial apertures from center to center ranges from 0.256 to 0.321 mm; 16 to 18 zooecia per 5 mm longitudinally, probably consistent in position in relation to dissepiment, usually 4 apertures per fenestrule. Nodes well developed, arranged in one row on straight carina, ranging from 0.077 to 0.103 mm in outside diameter; spaced at about the same intervals as apertures, namely 16 to 18 nodes per 5 mm of branch length. Stereom covering reverse side of branch consists of inner semitransparent layer of colonial plexus and outer sclerenchyma of darker fibers with very fine granules and some well developed spicules.

Meshwork formula.—13-15/8-9//16-18/16-18.

Remarks.—The present form seems to be nearest to the preceding species *Rugofenestella basleoensis*, especially the specimen described by Shulga-Nesterenko (1941) from the Lower Permian of the Ural region, Russia, in the meshwork formula except for the number of nodes in 5 mm branch length. The present form can be distinguished from the type *basleoensis* by Bassler (1929) from Timor by the wider dissepiments and smaller number of nodes in 5 mm branch length.

Genus ***Penniretepora*** d'Orbigny, 1849

Penniretepora sp. indet.

Figures 8-3

Material and Locality.—MGL74506a (Maqam).

Descriptive remarks.—A single tangential section of zoarium consisting of a pinnate, broad, straight main branch and short lateral branches. Width of main branch ranging from 0.650 to 0.700 mm. Lateral branch about 0.320 mm in width, extending alternately at about 70 degrees to main branch and at intervals of about 1.00 mm with about 3 lateral branches per 5 mm length of main branch. Zooecial tubes arranged in alternately longitudinal series, triangular with rounded corners at middle level of branch, oval in tangential section near surface, 10 to 11 zooecia per 5 mm length of one range and spaced regularly in pairs per interval between lateral branches.

The present form resembles *Penniretepora granulosa* which was described by Crockford (1944a) from the Callytharra series (Permian) of Western Australia in the measurements of the zoarium, however, a detailed comparison of them cannot be made at present, because Crockford (1944a) described and illustrated the type specimens by surface observation.

Family Septoporidae Morozova, 1962
Genus ***Septopora*** Prout, 1859

Septopora sp. indet.

Figures 8-2

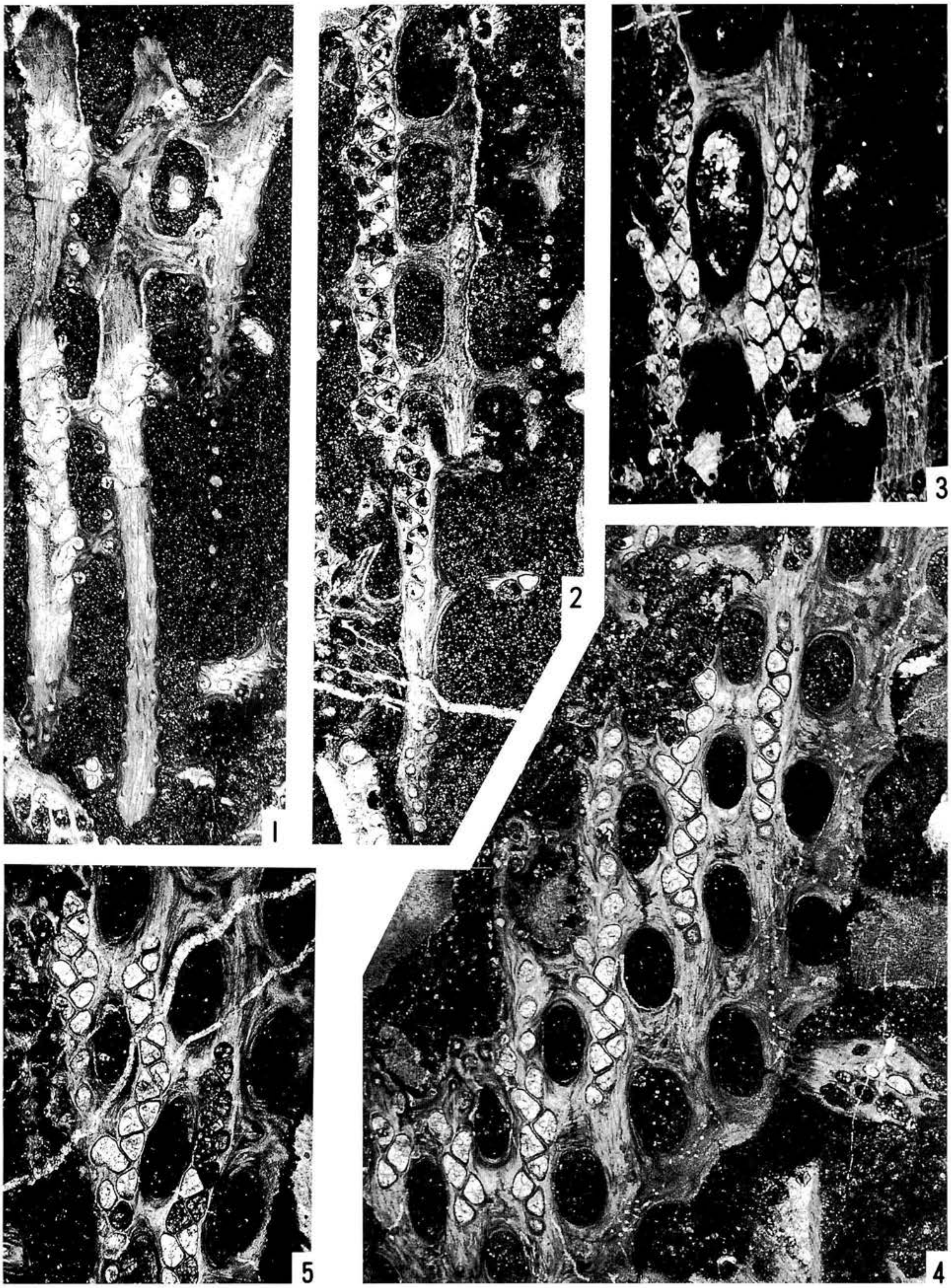
Material and Locality.—MGL74520c (Maqam).

Meshwork formula.—10/7//18/?

Descriptive remarks.—Form of zoarium unknown but probably fan-shaped based on the single fragment examined. Zoarium consists of straight, parallel branches connected by dissepiments at regular intervals.

The present form is identical with *Septopora ivanovi*

Figure 7. **1.** *Fabifenestella subpermiana* (Shulga-Nesterenko), tangential section, MGL74521a. **2.** *Rugofenestella basleoensis* (Bassler), tangential section, MGL74521b. **3.** *Polypora* sp. indet., tangential section, MGL74504. **4, 5.** *Rugofenestella omanica*, n. sp., tangential sections, MGL74514a (holotype) and 74517c (paratype). (All figures are ×20)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described by Shishova (1952), but Shishova's species was from the Mjachkovsky to Kasimovsky horizons (Middle to Upper Carboniferous) of the Moscow region, Russia, in the meshwork formula. The present form seems to be nearest to *Septopora regulata* by Yang and Lu (1962) from the Bayinhe Formation (Lower Permian) of Qilianshan, China in essential characters but the meshwork measurements are different, the meshwork formula of the Chinese specimens being 10.5/11//12.5/20. Specific identification is not possible because only one poorly preserved specimen is at hand.

Family Polyporidae Vine, 1883
Genus ***Polypora*** McCoy, 1844

Polypora cf. ***P. elliptica*** Rogers, 1900

Figures 6-8; 8-1

Compared.—
Polypora elliptica Rogers, 1900, p. 7, 8, pl. 4, fig. 2, Moore, 1929, pp. 23, 24, pl. 3, figs. 7, 8, 20; Sakagami, 1995, p. 270, figs. 4-4; 5-1.
Polypora elliptica (s.s) Rogers. Elias, 1937, p. 327, 328, fig. 3 m.

Material and Locality.—MGL74510, 74524b (Maqam).

Description.—Two tangential sections were examined. Zoarium consists of straight, parallel branches connected by dissepiments at regular intervals. Branches bifurcate infrequently. Branch width wider than width of fenestrule, ranging from 0.416 to 0.480 mm, usually about 15 branches per 10 mm horizontally. Fenestrules elongate, oval in outline; width ranges from 0.385 to 0.480 mm, length from 0.385 to 0.704 mm, usually about 10 per 10 mm of branch length. Dissepiment broad, ranges from 0.320 to 0.480 mm in width. Zooecial tubes usually 3 rows but before bifurcation of branch 4 rows, after bifurcation 2 rows; elongate quadrate or elongate hexagonal at middle level of branch because of slightly alternating intercalated zooecial tubes in longitudinal series. Zooecial tubes circular in tangential section near surface, ranging from 0.115 to 0.128 mm in diameter. Number of zooecial apertures ranges from 18 to 20 per 5 mm length of one range, usually 3 to 4 apertures per fenestrule. Distance between zooecial apertures ranges from 0.250 to 0.321 mm longitudinally. Stereom covering reverse side of branch consists of semitransparent layer of colonial plexus with some capillary canals and outer sclerenchyma of darker fibers with well developed fine granules.

Meshwork formula.—13-15/10//18-20/3(2) (The meshwork formula used for *Polypora* and *Protoretepora* refers to the number of branches per 10 mm/number of fenestrules per 10 mm//number of zooecia per 5 mm/number of rows of zooecia).

Remarks.—The present form resembles *Polypora elliptica*, originally described by Rogers (1900) from the Kereford Limestone of the Oread Formation, dated now as middle Virgilian in the meshwork formula and internal structures. This species was described by Sakagami (1995) also from the lower to middle part of the *Eoparafusulina* zone of the Copacabana Group in Bolivia.

Polypora cf. ***P. gigantea*** Waagen and Pichl, 1885

Figures 8-4

Compared.—
Polypora gigantea Waagen and Pichl, 1885, p. 786-789, pl. 89, figs. 1, 2; Sakagami, 1963, p. 208, 209, pl. XII, figs. 15, 16.

Material and Locality.—MGL74516c (Maqam).

Description.—A single tangential section of fragmentary zoarium consisting of straight, parallel, robust branches connected by dissepiments with long intervals. Branch width ranges from 0.960 to 1.216 mm; probably about 7 branches per 10 mm horizontally. Fenestrules very elongate, about 0.500 mm in width and about 3.00 mm in length; 2.5 to 3 per 10 mm length of branch. Width of dissepiments is about 0.640 mm. Zooecial tubes arranged in strongly alternating longitudinal series, usually rhomboidal at middle level of branch, 6 rows of each branch, before bifurcation 8 rows, after bifurcation 5 rows; 12 to 13 per 5 mm length of one range, probably about 10 zooecial apertures per fenestrule. Zooecia circular in tangential section near surface, about 0.115 mm across. Distance between zooecial apertures from center to center ranges from 0.385 to 0.410 mm, longitudinally. Stereom covering reverse side of branch consists of inner semitransparent layer of colonial plexus with many capillary canals and outer sclerenchyma of dark coarse fibers with fine granules.

Meshwork formula.—7 ?/2.5-3//12-13/(5)-6-(8).

Remarks.—The present form may be identical with *Polypora gigantea* which Waagen and Pichl (1885) described from the Middle *Productus* Limestone of Pakistan, however, detailed comparisons cannot be made based on the one poorly preserved specimen at hand.

Polypora sp. indet.

Figures 7-3

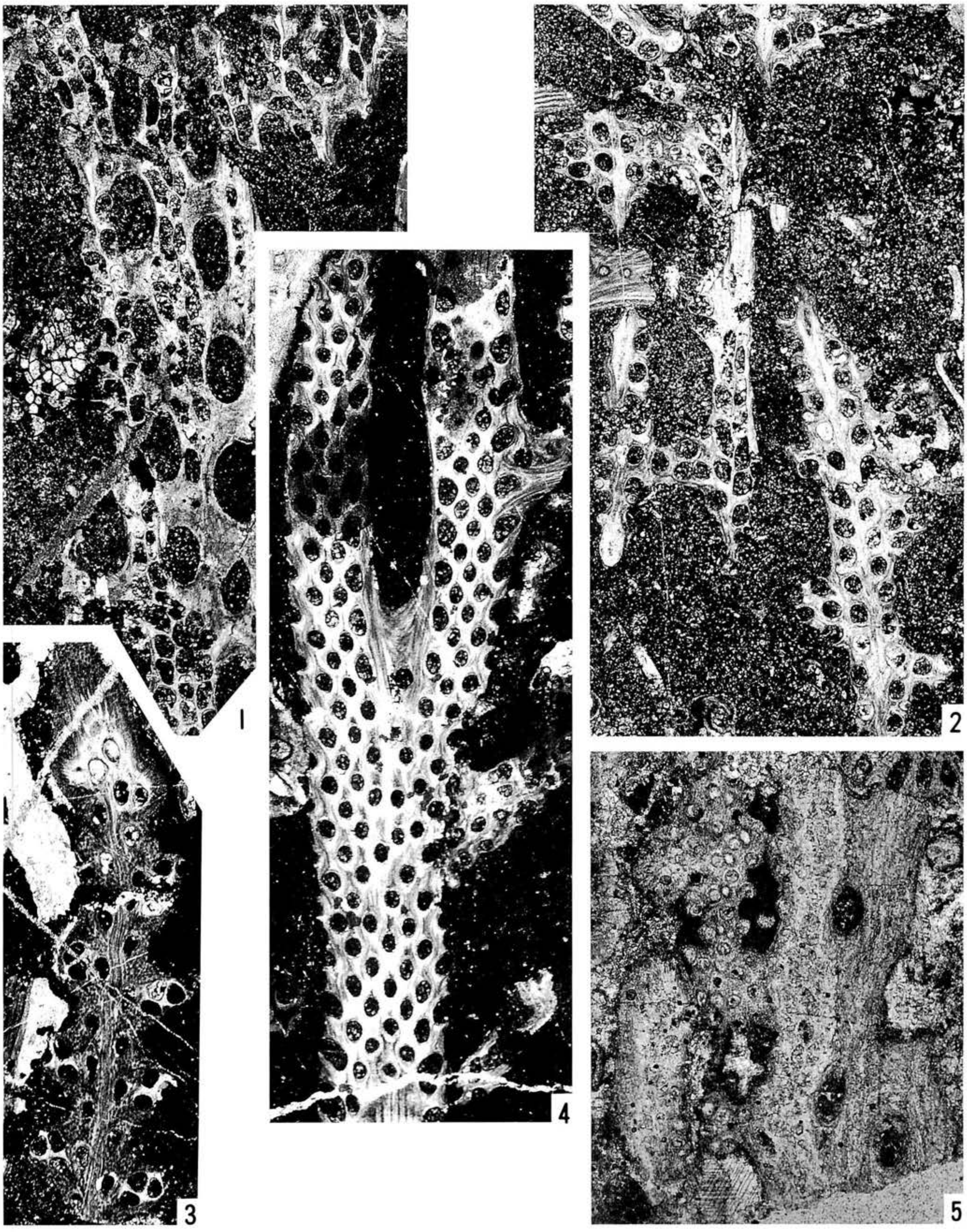
Material and Locality.—MGL74504 (Maqam).

Meshwork formula.—10/4.5//14-15/4.

Descriptive remarks.—A single tangential section of fragmentary zoarium consisting of straight, parallel branches connected by dissepiments at regular intervals. Bifurcation of branches not observed in this specimen. Only one poorly preserved specimen is available and this is insufficient for specific identification.

Genus ***Protoretepora*** de Koninck, 1876

Figure 8. **1.** *Polypora* cf. *P. elliptica* Rogers, tangential section, MGL74524b. **2.** *Septopora* sp. indet. tangential section, MGL74520c. **3.** *Penniretepora* sp. indet., tangential section, MGL74506a. **4.** *Polypora* cf. *P. gigantea* Waagen and Pichl, tangential section, MGL74516c. **5.** *Protoretepora* ? sp. indet., tangential section, MGL74531c. (All figures are ×20)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Protoretepora ? sp. indet.

Figures 8-5

Material and Locality.—MGL74531c (Nackl).

Meshwork formula.—ca. 12/ca. 8//ca. 18/4-5.

Descriptive remarks.—A single tangential section of fragmentary zoarium consisting of straight, parallel branches connected by broad dissepiments with zooecial tubes at regular intervals. Bifurcation of branches not observed in this specimen. The present form seems to belong to the genus *Protoretepora* in having zooecial apertures in the dissepiments, however, only one poorly preserved specimen is available and this is insufficient for a specific identification.

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Morphology and systematics of the Recent Japanese brachiopod *Shimodaia pterygiota* gen. et sp. nov. (Laqueidae : Terebratulida)

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Abstract. A small, brightly coloured brachiopod, *Shimodaia pterygiota* n. gen. and n. sp., presently restricted to waters of less than 100 m depth off Shimoda, Izu Penninsula, and parts of Sagami Bay, Honshu, Japan, is described and illustrated. Previously mistaken for *Frenulina sanguinolenta* (Gmelin), *S. pterygiota* is shown to differ from all other known laqueid brachiopods in its unique combination of adult cardinalial and brachidial features. Investigation of the loop ontogeny of *S. pterygiota* reveals that, whereas juvenile axial, cucullate and annular loop phases are comparable to those in other laqueids, the adult phase is unusual in consisting of an incomplete annular phase resulting from resorption of the transverse band. Only one adult specimen from over 200 recovered to date shows resuturing of previously discrete (resorbed) ascending loop branches to form a conventional annular phase.

Key words : Brachiopod, Japan, Laqueidae, loop ontogeny, Recent, *Shimodaia pterygiota* gen. et sp. nov.

Introduction

In 1986, a number of dead brachiopod shells were dredged from a depth of between 65 m and 71 m, about 3 km SSE of Shimoda, Izu Penninsula, Honshu, at localities close to an earlier reported occurrence (Harada and Mano, 1960) of the distinctive laqueid brachiopod, *Frenulina sanguinolenta* (Gmelin) (Figure 1 ; Table 1). While the shells of the 1986 collection exhibited a red/white, variegated pattern similar to that occurring in *Frenulina sanguinolenta*, they were generally somewhat smaller, and more rounded in shape (Figures 2-1—2-4). In addition, examination of dorsal valve interiors (Figures 2-5—2-6, Figure 3, Figure 7-1) revealed a morphology distinctly different from that occurring in *Frenulina* specimens of comparable size (Figure 4) and unlike that of any other previously described laqueid genus (MacKinnon, pers. comm., in Endo *et al.*, 1994). Inspection by Saito (1996) of the original illustrations of the brachiopods described by Harada and Mano (1960), revealed that, morphologically, the specimens they collected were indistinguishable from the later collection, and it was concluded that Harada and Mano had misidentified the material they had collected. Consequently a restudy of the problematic brachiopod has been undertaken with a view to its formal naming, describing, and illustrating. A comparison of *S. pterygiota* to morphologically similar juveniles of other Recent laqueid brachiopods from the same region has also been undertaken in an attempt to establish evolutionary relationships of *S. pterygiota* to those other taxa.

Materials and methods

Over 200 specimens of *S. pterygiota* have been collected from 8 localities (Table 1). After opening the conjoined valves with a scalpel blade, valves were then placed in bleach solution and constantly monitored under a binocular microscope. Soft tissues were removed using domestic grade bleach (sodium hypochlorite : approximately 5% (v/v)), as described by Mackay *et al.* (1994). Immediately all tissue was dissolved, each specimen was then washed, allowed to dry, and then mounted on a SEM stub. Specimens were then coated with gold, or Pt-Pd alloy, prior to observation by scanning electron microscope (Leica Stereoscan 440 or Hitachi S-2400S). Apart from one specimen of *Laqueus rubellus* which is housed in the National Museum of Natural History, Washington D.C. (USNM 550341), all specimens are housed in the University Museum of the University of Tokyo (UMUT). Lengths of dorsal and ventral valves are indicated by the abbreviations L_{dv} and L_{vv} respectively.

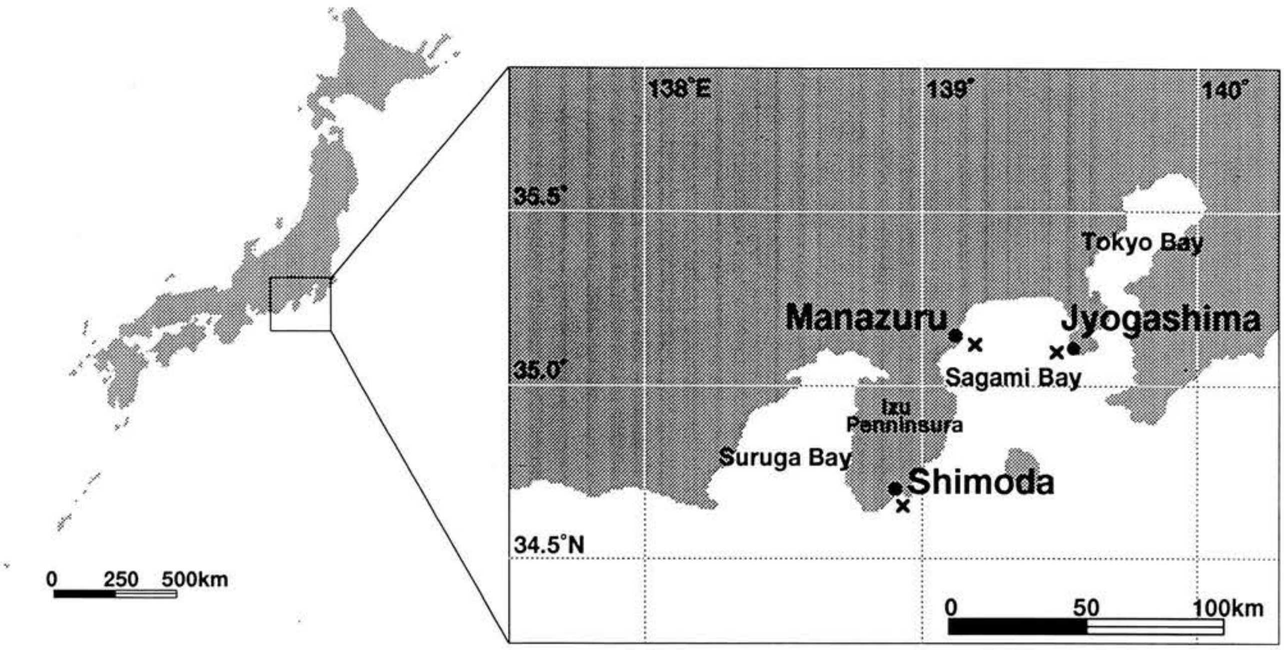

Figure 1. Locality map; localities at which *Shimodaia pterygiota* gen. et sp. nov. has been dredged indicated by (×).

Table 1. Locality data for *Shimodaia pterygiota* gen. et sp. nov.

Locality	Date	Station	Latitude	Longitude	Depth Range (m)
Off Shimoda	09.12.86	St. 4	N34°37.68′	E138°57.70′	65-71
	28.05.94	St. 4	N34°38.11′	E138°56.94′	52-57
		St. 7	N34°37.42′	E138°58.17′	73-98
		St. 8	N34°37.71′	E138°57.84′	67-81
	26.11.96	St. 1	N34°38.27′	E138°56.72′	36.8-45.5
		St. 2	N34°38.12′	E138°56.74′	46.0-47.3
Off Jyogashima	27.07.93	St. 3	N35°07′36′	E139°35′02′	80
Off Manazuru	05.09.94	St. 11	N35°08′12.5″	E139°11′20.7″	75-77

Systematics

Order Terebratulida Waagen, 1883
Family Laqueidae Thomson, 1927

Shimodaia gen. nov.

Type species.—*Shimodaia pterygiota* MacKinnon, Saito and Endo, sp. nov.

Diagnosis.—Small (<7.5 mm), ovate, commissure rectimarginate; beak erect, attrite; foramen submesothyrid; deltidial plates disjunct; dental plates present, pedicle collar broad; cardinal process inconspicuous, septal pillar arising (in adults) about midvalve, very long and narrow, strongly inclined anteroventrally, sometimes spinose distally, extending posteriorly as low ridge to unite with excavate inner hinge plates; adult loop annular with descending branches attached to septal pillar and ascending branches commonly incomplete, rarely forming a complete ring; juvenile axial loop phase with well developed septal flanges

Discussion.—*Shimodaia* resembles *Frenulina* in possessing red/white colour markings of the shell, but is readily distinguished from the latter genus (Figure 4) by its distinctive adult (incomplete) annular loop form (Figure 3) with prominent septal pillar, sessile septalium, and generally smaller adult size. Both the loop and cardinalia of *Shimodaia* are readily distinguishable from those in similar-sized juveniles of other larger sympatric laqueid brachiopods such as *Pictothyris picta* (Dillwyn) and *Laqueus rubellus* (Sowerby) (Figure 7). Juveniles of *S. pterygiota* and *Laqueus rubellus* are similar in

Figure 2. **1-8** *Shimodaia pterygiota,* gen. et sp. nov., 1-4: Ventral, dorsal, lateral, and anterior views of exterior of holotype, UMUT RB27390 (L_w7.05 mm), ×100. 5-6: Lateral and dorsal interior views of UMUT RB27394 (L_{dv}=6.2 mm), ×130 and ×100 respectively. 7: ventral interior view of UMUT RB27394b (counterpart of UMUT RB27394a) (L_w=6.4 mm), ×125. 8: Anterior oblique view of dorsal interior of UMUT RB27394a (L_w=6.4 mm), ×130.

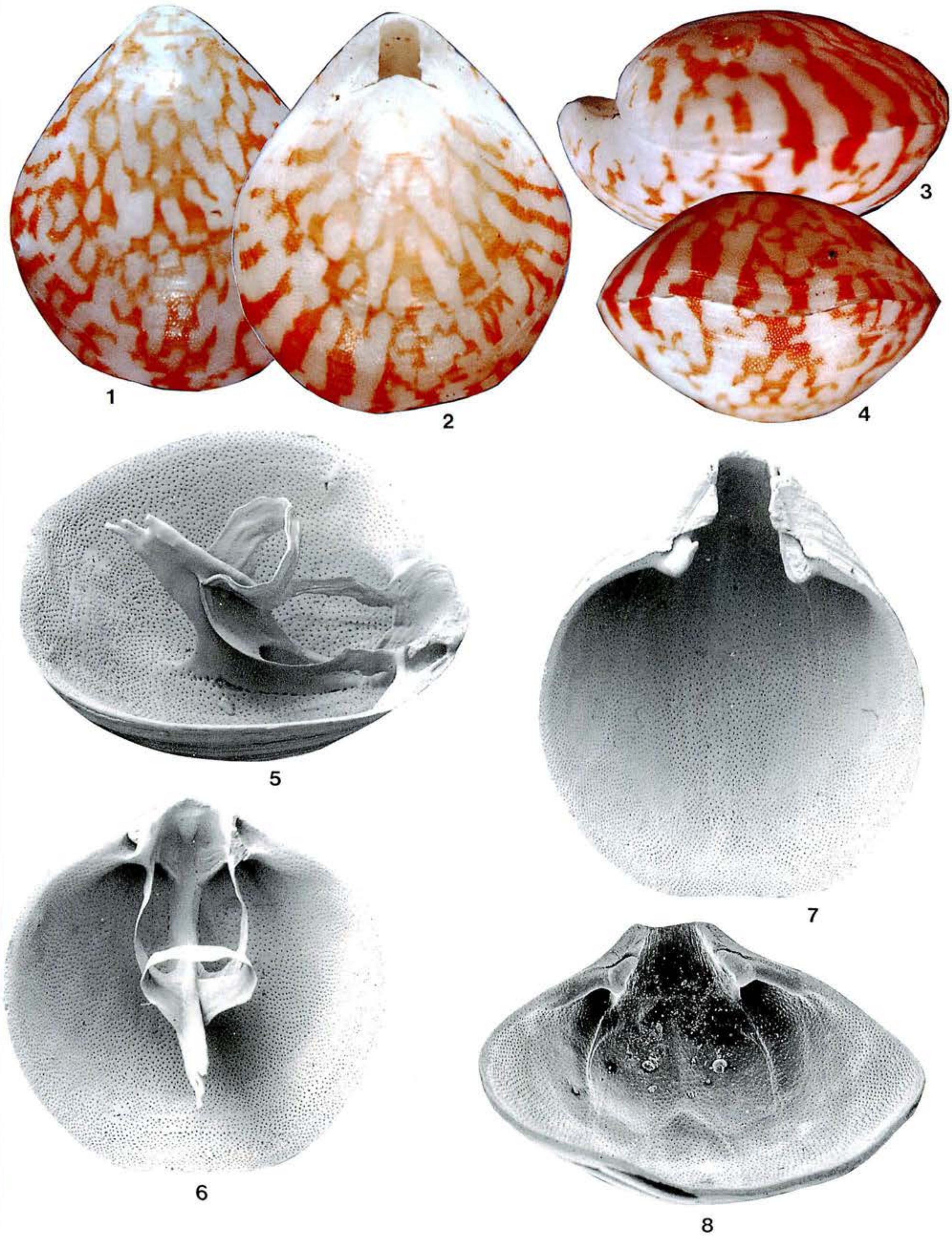
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Figure 3. Stereophotograph showing the incomplete annular (adult) loop phase of *Shimodai pterygiota*, gen. et sp. nov., UMUT RB19862 (L_{dv}=4.7 mm).

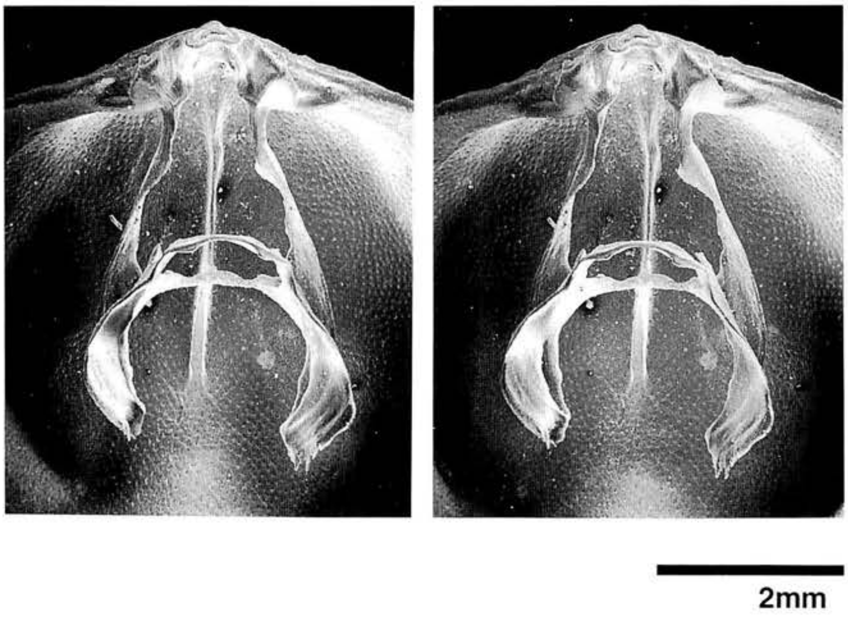


Figure 4. Stereophotograph showing the adult bilateral loop phase of *Frenulina sanguinolenta* (Gmelin), UMUT RB27395 (L_{dv}=6.6 mm).

that both share an inconspicuous cardinal process and sessile septalium, but the post-juvenile loop ontogeny of *L. rubellus* is much more extensive and complicated. As noted by Saito (1996), Harada and Mano (1960) observed mature gonads in specimens between 5 mm to 7 mm in ventral valve length, and Saito (1996) also noted crowding of growth lines around shell margins in specimens with a ventral valve length greater than 5 mm, thus the possibility that *Shimodaia* might represent the juvenile stage of some larger brachiopod is discounted.

Etymology.—Named after the town of Shimoda, Izu Peninsula, Honshu, Japan.

Shimodaia pterygiota sp. nov.

Figures 2-1—8, 3, 7-1

Frenulina sanguinolenta, Harada and Mano, 1960, p. 37-39, fig. 1-7.
'Frenulin' sp., Endo *et al*., 1994, tables 1, 3, 6 and text-fig. 7.
'Frenulina' sp., Saito 1996, p. 492, fig. 6-1—8.

Material.—Holotype: UMUT RB27390. Paratypes: UMUT RB27391, UMUT RB27392.

Diagnosis.—As for genus.

Description.—Small, moderately biconvex, with subcircular dorsal valve and subelliptical ventral valve; maximum width and thickness around midvalve; commissure straight. Beak attrite, suberect; pedicle foramen submesothyrid; deltidial plates no wider than teeth, subtriangular and disjunct. Exterior shell surface smooth; strongly mottled colouration consisting of a median and two lateral bands that are dominantly red-mottled, with intervening bands of white mottling.

Ventral valve interior with strong teeth supported by well developed dental plates; lateral umbonal cavities deep. Floor of delthyrial cavity lined by wide, impunctate, pedicle collar. Weakly to moderately impressed ventral muscle field, posterolaterally confined by dental plates, extending anteriorly from front edge of pedicle collar to about midvalve.

Dorsal valve interior with high, narrow, but robust, anteroventrally projecting septal pillar. Anteroventral extremity of septal pillar either blade-shaped or spinose and may reach to ventral valve floor. Descending lamellae extending between crura and septal pillar. Ascending lamellae arising from posterodorsal edge of septal pillar as two curved, wing-like processes. Processes widest proximally at attachment to septal pillar, and tapering distally; distal extremities rarely reuniting to form a ring. Septal pillar extending posteriorly as low ridge to merge with, steeply inclined, and dorsally convergent, inner hinge plates which do not quite fuse together medially, thus forming a sessile septalium. Prominent inner socket ridges and narrow outer socket ridges defining deep sockets. Crura short, with indistinct crural bases. Dorsal pedicle adjustor muscle scars well impressed on inner hinge plates. Low boss developed in some gerontic specimens just anterior of posteromedianly located myophore. Indistinct, elongate oval, adductor muscle scars located on valve floor on either side of septal pillar.

Dimensions (mm).—

Specimen	Length	Width	Thickness
UMUT RB27390(Holotype)	7.05	6.0	5.15
UMUT RB27391(Paratype)	6.65	5.75	4.70
UMUT RB27392(Paratype)	6.55	5.85	3.25

Scatter diagrams showing length/width and thickness/width differences between *Shimodaia pterygiota* sp. nov. and *Frenulina sanguinolenta* are shown in Figures 5A and 5B.

Occurrence.—A list of localities at which *S. pterygiota* has been collected is given in Table 1. *S. pterygiota* is especially abundant off Shimoda where it occurs with *Pictothyris picta*. At other stations in and near Sagami Bay, off Manazuru and off Jyogashima, *S. pterygiota* was collected along with *P. picta* and *Laqueus rubellus*.

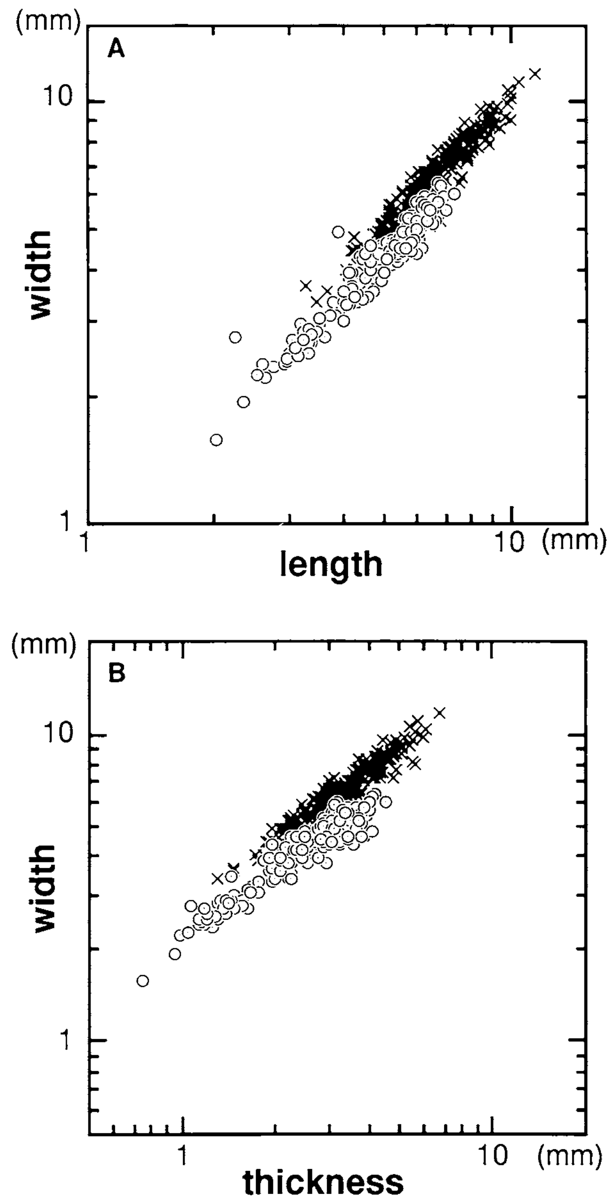


Figure 5. Scatter diagrams of **A**: length to width, and **B**: thickness to width, in *Shimodaia pterygiota* (×) (n=259), and *Frenullna sanguinolenta* (⊙) (n=230). Specimens of *F. sanguinolenta* used in this study were collected from "Tori-ike" cave, off Shimoji Islet, Miyako Island, Okinawa, at between 12 m and 40 m depth.

Etymology.—From the Greek *pterygion*, wing, referring to the wing-like ascending loop branches of the brachidium in adult forms.

Loop ontogeny

In order to clarify the taxonomic position of the present

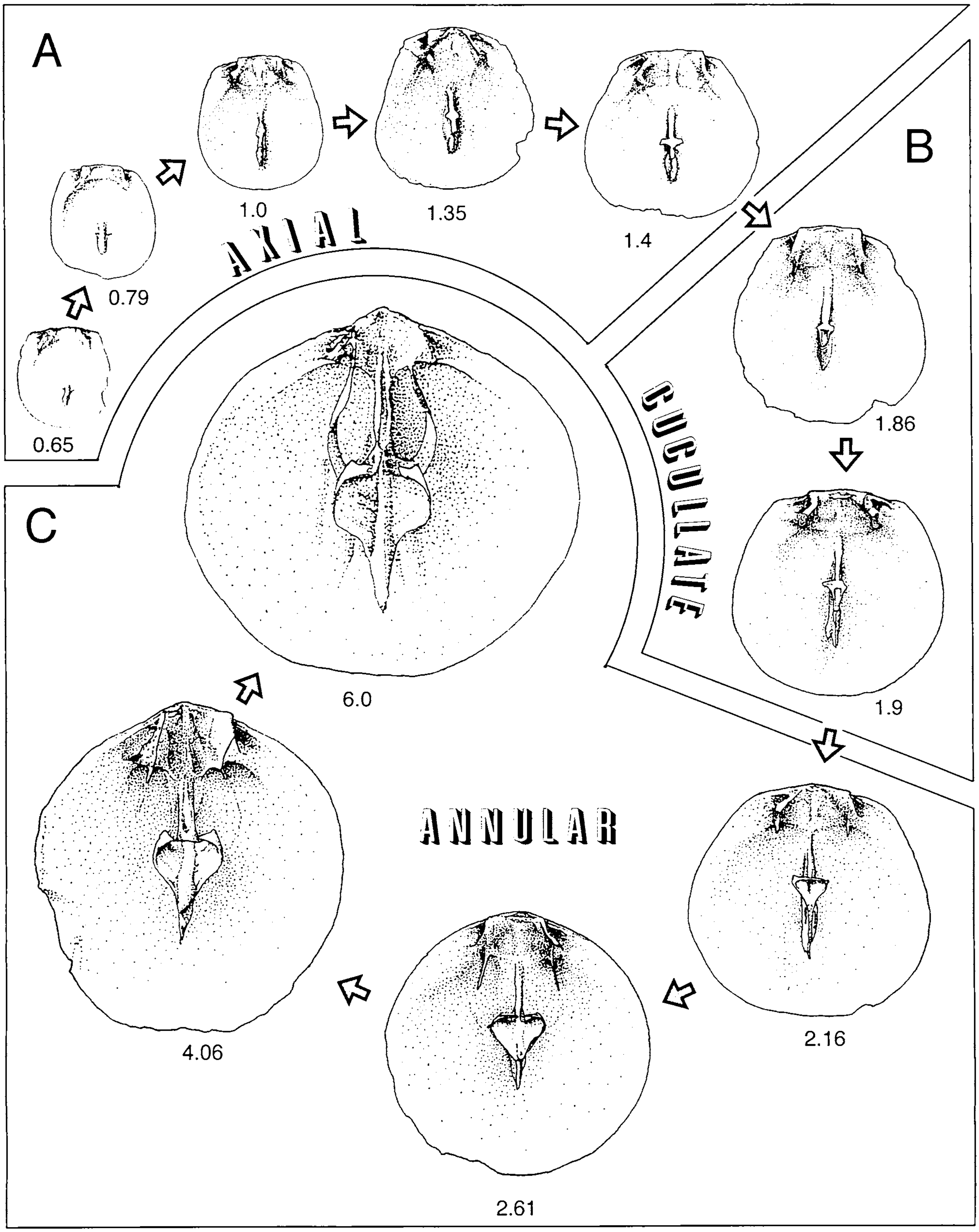


Figure 6. *Shimodaia pterygiota*, gen. et sp. nov. Ontogenetic series showing axial (A), cucullate (B), and annular (C) phases of loop development. Lengths of dorsal valves given in mm. beside each specimen.

species, loop ontogeny was investigated. The terminology applied by Richardson (1975), MacKinnon (1993), and Saito (1996) to transient loop phases is used herein. An ontogenetic series is shown in Figure 6A-C.

Axial Phase (early): In the smallest specimen investigated (dorsal valve length = 0.65 mm) the only distinctive features of the dorsal valve interior are sockets, defined by strong inner socket ridges, a narrow, peg-like, septal pillar that projects at a low angle toward the anterior commissure, and sporadic punctae; no muscle scars are discernible at this stage. The septal pillar, at this stage around 130 μm in length and 50 μm wide, arises at about 0.6 valve length, is antero-ventrally directed, and is composed of nonfibrous calcite.

Axial Phase (late): At 0.79 mm length, the rudiments of the septal flanges appear at the posterior basal margin of the septal pillar; the flanges are nonfibrous. At the distal end of the septal pillar a dense cluster of very small fibrous terminal faces, indicative of vigorous localised epithelial cell generation, is recognisible.

Between lengths 1.0 mm and 1.4 mm, the septal pillar becomes larger and more blade-like, and the septal flanges have migrated anteriorly to reach about halfway along the posterior edge of the septal pillar. The zone of very small fibres at the distal end of the septal pillar becomes elongated in the sagittal plane, and secondary layer fibres begin to extend from the valve floor up both sides of the septal pillar. In the median depression between the strong socket ridges, a pair of subquadrate dorsal pedicle adjustor muscle scar are discernible, and larger but less well-defined adductor impressions appear on the valve floor on either side of the septal pillar.

Cucullate Phase: Between lengths 1.4 mm and 1.9 mm, a shallow groove forms in that part of the distal edge of the septal pillar just anterior of the septal flanges. As growth proceeds, the laterally extended, wing-like septal flanges (which are migrating anteriorly) overlap the groove, thereby forming a narrow hood with a V-shaped cavity and flat-topped roof.

Annular Phase: By length 2.2 mm, differential growth along the anterodorsal edges, and resorption of the posterior section, of the hood gives rise temporarily to a ring. In addition, a pair of very small, anterior projecting crura emerge from the anteriormost edges of the inner socket ridges.

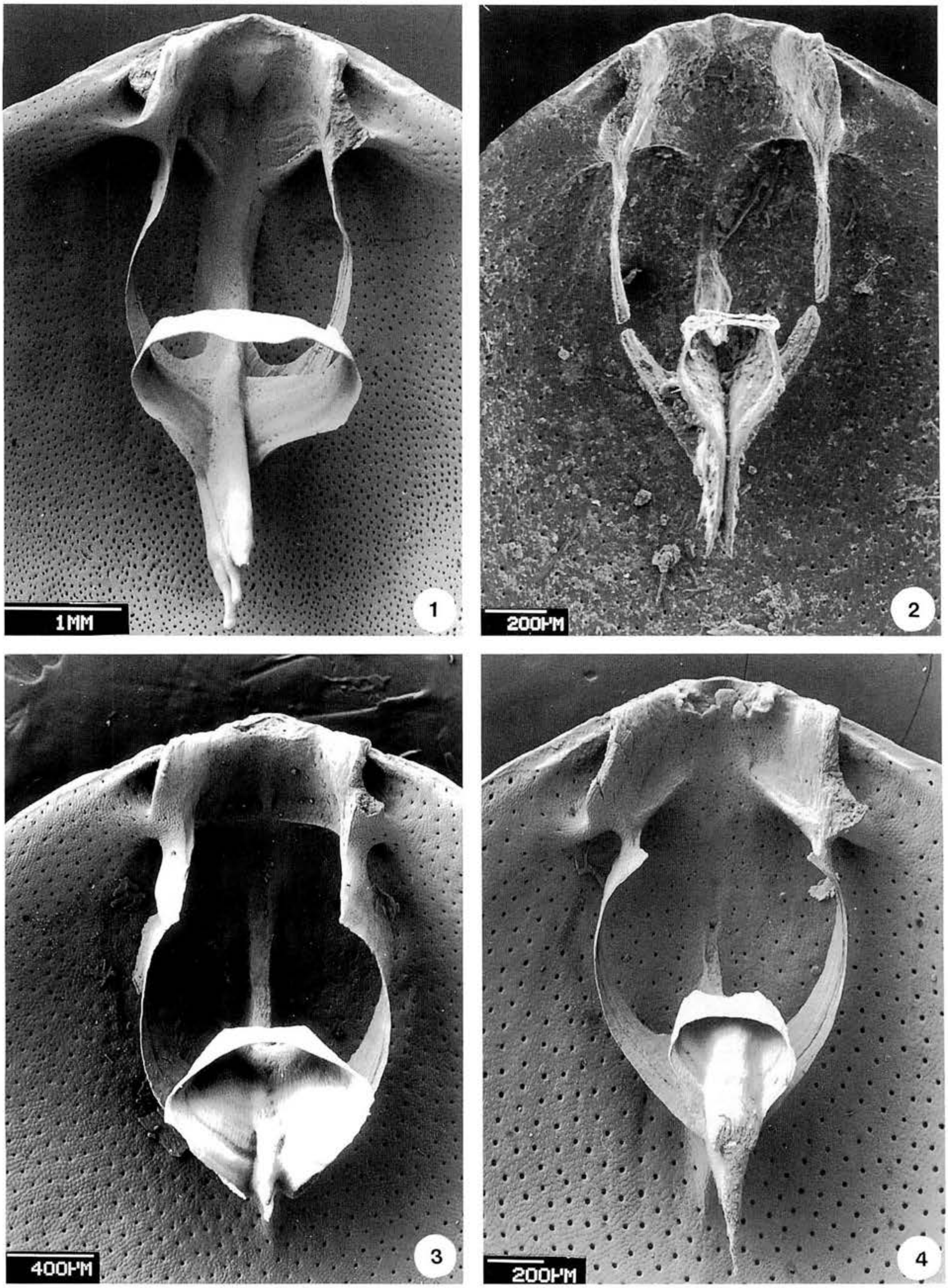
Incomplete Annular Phase: By length 2.6 mm the brachidial ring is broken due to resorption (not breakage) of the very narrow transverse band. The crural outgrowths continue to lengthen and beneath the crura, a pair of excavate inner hinge plates appear. From length 2.6 mm, and larger, the remaining ventrally curved parts of the ascending elements of the brachidium, and the septal pillar to which they are attached, continue to grow. The distal extremity of the septal pillar may become spinose, but it remains nonbifurcate. By about length 4.0 mm, the descending branches of *Shimodaia* are fully formed, running as arcuate branches from crura to septal pillar.

In one large specimen of dorsal valve length 6.0 mm (Figure 2-6, Figure 7-1), the ascending loop branches were observed to have reunited ventrally, but this specimen is, so far, unique. Usually, in adult specimens, the distal extremities of the ascending lamellae are separated by a gap. Similar incomplete annular loop phases have been reported by MacKinnon, *et al.* (1993) in the New Zealand mid-Cenozoic terebratellids *Praemagadina campbelli* and *Magadina squiresi*. Likewise an incomplete annular loop is found in Cretaceous *Magas* Sowerby, and in Cenozoic *Bouchardia*. However, all four taxa display various fundamental morphological dissimilarities to *Shimodaia* and, consequently, are not considered to be closely related to the latter.

Discussion

On external characteristics alone (in particular red/white variegated shell coloration, shell size, and shape), *Shimodaia pterygiota* most closely resembles *Frenullna sanguinolenta* and has in the past been confused with the latter species (e.g. Harada and Mano, 1960), however the present-day geographic distributions of the two species do not overlap. While *Shimodaia pterygiota* appears to be confined to the Izu Penninsula/Sagami Bay area, Honshu, *Frenulina sanguinolenta* is very widely distributed in tropical or near-tropical waters of the Pacific Ocean, including the Hawaiian Islands, Ryukyu and Ogasawara Islands of Japan, the Philippines, Sulu Archipelago, the Moluccas, New Caledonia, Tahiti, Tonga, and parts of northeastern, western, and southern Australia (Richardson, 1973). The largest specimen of *S. pterygiota* yet collected is about 7 mm in length (ventral valve), whilst the largest specimen of *F. sanguinolenta* currently available for study (from Japanese waters) is about 12 mm in length. Bivariate scatter diagrams showing the relationships between length/width, and thickness/width in over 200 specimens of both species reveal distinct differences in relative growth proportions (Figure 5). While there is close correspondence in the plots of length/width in both species, the plots of width/thickness (and length/thickness) reveal some discrepancy between the two species. Juvenile *F. sanguinolenta* are ovate in outline, whereas adult specimens tend to become subcircular; specimens of *S. pterygiota*, however, tend to remain ovate in outline throughout ontogeny.

Certain aspects of loop development in *S. pterygiota* have already been discussed by Saito (1996), as '*Frenulina*' sp., and compared with loop development in other Japanese laqueoid brachiopods, including *Frenulina sanguinolenta, Pictothyris picta*, and *Laqueus* sp. All three taxa pass through juvenile axial and annular loop phases comparable to those occurring in juvenile *Shimodaia*, but they do not then proceed to the adult (incomplete) annular phase characteristic of *Shimodaia*, and their later phases of loop ontogeny extend well beyond the axial and annular phases which they have in common with *Shimodaia*. As pointed out by Saito (1996), *Shimodaia* possesses a confusing mix of morphological characters in the dorsal valve interior. In the possession of steeply dipping inner hinge plates which converge on a low median septum to form a sessile septalium, and an inconspicuous dorsal diductor muscle attachment site (myophore), the cardinalia of *Shimodaia* (Figure 7-1) resemble those occurring in young *Laqueus rubellus* (Figure 7-2), as well as *Laqueus* sp. studied by Saito (1996). However, the septal pillar of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both juvenile *Laqueus* species becomes distinctly bifurcate along the anteroventral, growing edge by early in the axial loop phase (Figure 7-2), whereas the septal pillar of *Shimodaia* remains nonbifurcate throughout life (Figure 7-1). On the other hand, the septal pillars of both *Frenulina sanguinolenta* (Figure 7-3) and *Pictothyris picta* (Figure 7-4) remain essentially nonbifurcate throughout ontogeny, as occurs in *Shimodaia* but, in adult specimens of both *P. picta* and *F. sanguinolenta* (Figure 4), the cardinalia bear disjunct, subhorizontal, inner hinge plates elevated well above the valve floor. In addition, at the adult stage, the cardinal process is strongly differentiated in *Pictothyris*, and rather less well so in *Frenulina*. Thus, in summary, *Shimodaia* differs from juvenile *Laqueus* principally in the nonbifurcation of the septal pillar, whereas the main differences between *Shimodaia* and juveniles of both *Frenulina* and *Pictothyris* lie in the cardinalia, particularly the size and disposition of the inner hinge plates and the extent of definition of the cardinal process.

Because the foregoing morphological data concerning differences between *Shimodaia* and the other three taxa is so limited, there is little point in speculating as to which of the three, if any, is the most likely ancestor. Theoretically any one of the three taxa under consideration, i.e. *Laqueus, Frenulina*, or *Pictothyris*, could be the direct ancestor of *Shimodaia* but the issue could be resolved in the near future through appropriate molecular studies.

Acknowledgments

We wish to acknowledge the assistance of University of Canterbury personnel Neil Andrews (SEM), Kerry Swanson and Albert Downing (photography), Craig Jones (pen and ink drawings of ontogenetic series in Figure 6), and Lee Leonard (draughting of Figure 6). We acknowledge the help of the late Dr. Dick Grant, Rex Doescher, and Walter Brown of the National Museum of Natural History, Washington, D.C., for providing one of us (D. MacK.) with access to that museum's magnificent brachiopod collections, bibliographic databases, and scanning electron microscope facility. Thanks are also due to Eiji Tsuchida of the Ocean Research Institute, University of Tokyo for kindly providing us with brachiopod specimens, and to the staff members of the Shimoda Marine Research Center, University of Tsukuba for their help in collecting brachiopod samples.

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Figure 7. 1-4. Comparative views of cardinalia and axial loop phases in 1 : *Shimodaia pterygiota* gen. et sp. nov., UMUT RB27394a (L_{dv} = 6.2 mm). 2 : *Laqueus rubellus* (Sowerby) USNM 550341 (L_{dv} = 2.4 mm). 3. *Frenulina sanguinolenta* (Gmelin) (L_{dv} = 4.0 mm). 4. *Pictothyris picta* (Dillwyn) (L_{dv} = 2.7 mm).

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Palaeontological Society of Japan (JSP) Standing Committee Actions

During its meeting on March 8, the JSP Standing Committee enacted the following changes to its membership.

New members elected;

Hisako Doi,	Takashige Kawano,	Seiko Orita,
Natsume Sagawa,	Norihiko Sakakura,	Yutaro Suzuki,
Kiminori Taguchi,	Akio Takahashi,	Sumie Takeda,
Gengo Tanaka,	Cheol-Soo Yun.	

Resigned members;

Emiko Hayakaze, Koji Nakamura.

Deceased member;

Jiro Katto.

行事予定

◎1998年年会・総会は1998年1月30日（金）〜2月1日（日）に，神奈川県立生命の星・地球博物館で開催します．一般講演の申し込み締切は12月5日です．シンポジウムとして1月30日に「復元科学としての古生物学」（世話人：大野照文，小泉　格，濱田隆士，松島義章）が予定されています．

◎第148回例会は1998年6月27日（土）〜6月28日（日）に，北海道大学で開催が予定されています．一般講演の申し込み締切は5月10日です．現在，「ユニバシティミュージアム」と「復元科学としての古生物学」の2件のシンポジウムの申し込みがあります．夜間小集会などの企画がありましたら，行事係までご連絡下さい．

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