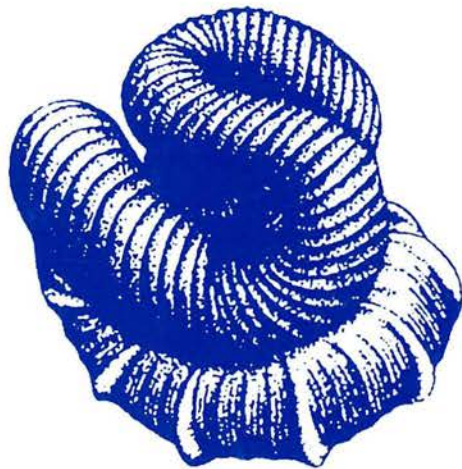


# Paleontological Research

ISSN 1342-8144

Formerly  
**Transactions and Proceedings  
of the  
Palaeontological Society of Japan**



**Vol. 4 No.3**  
**September 2000**

---

The Palaeontological Society of Japan

---

---

**Co-Editors Kazushige Tanabe and Tomoki Kase**

---

Language Editor **Martin Janal (New York, USA)**

**Associate Editors**

Jan Bergström (Swedish Museum of Natural History, Stockholm, Sweden), Alan G. Beu (Institute of Geological and Nuclear Sciences, Lower Hutt, New Zealand), Satoshi Chiba (Tohoku University, Sendai, Japan), Yoichi Ezaki (Osaka City University, Osaka, Japan), James C. Ingle, Jr. (Stanford University, Stanford, USA), Kunio Kaiho (Tohoku University, Sendai, Japan), Susan M. Kidwell (University of Chicago, Chicago, USA), Hiroshi Kitazato (Shizuoka University, Shizuoka, Japan), Naoki Kohno (National Science Museum, Tokyo, Japan), Neil H. Landman (American Museum of Natural History, New York, USA), Haruyoshi Maeda (Kyoto University, Kyoto, Japan), Atsushi Matsuoka (Niigata University, Niigata, Japan), Rihito Morita (Natural History Museum and Institute, Chiba, Japan), Harufumi Nishida (Chuo University, Tokyo, Japan), Kenshiro Ogasawara (University of Tsukuba, Tsukuba, Japan), Tatsuo Oji (University of Tokyo, Tokyo, Japan), Andrew B. Smith (Natural History Museum, London, Great Britain), Roger D. K. Thomas (Franklin and Marshall College, Lancaster, USA), Katsumi Ueno (Fukuoka University, Fukuoka, Japan), Wang Hongzhen (China University of Geosciences, Beijing, China), Yang Seong Young (Kyungpook National University, Taegu, Korea)

**Officers for 1999–2000**

President: Kei Mori

Councillors: Kiyotaka Chinzei, Takashi Hamada, Yoshikazu Hasegawa, Itaru Hayami, Hiromichi Hirano, Noriyuki Ikeya, Junji Itoigawa, Tomoki Kase, Hiroshi Kitazato, Itaru Koizumi, Haruyoshi Maeda, Ryuichi Majima, Makoto Manabe, Hiroshi Noda, Ikuwo Obata, Kenshiro Ogasawara, Terufumi Ohno, Tatsuo Oji, Tomowo Ozawa, Yukimitsu Tomida, Tsunemasa Saito, Takeshi Setoguchi, Kazushige Tanabe, Akira Yao

Members of Standing Committee: Hiroshi Kitazato (General Affairs), Tatsuo Oji (Liaison Officer), Makoto Manabe (Finance), Kazushige Tanabe (Editor in Chief, PR), Tomoki Kase (Co-Editor, PR), Ryuichi Majima (Planning), Hiromichi Hirano (Membership), Kenshiro Ogasawara (Foreign Affairs), Haruyoshi Maeda (Publicity Officer), Noriyuki Ikeya (Editor, "Fossils"), Yukimitsu Tomida (Editor in Chief, Special Papers), Tamiko Ohana (Representative, Union of Natural History Societies).

Secretaries: Masanori Shimamoto, Takao Ubukata (General Affairs), Hajime Taru (Planning), Tokuji Mitsugi (Membership), Shuko Adachi (Foreign Affairs), Kazuyoshi Endo, Yasunari Shigeta, Takenori Sasaki (Editors of PR), Akira Tsukagoshi (Editor of "Fossils"), Naoki Kohno (Editor of Special Papers), Hidenori Tanaka (Publicity officer)

Auditor: Nobuhiro Kotake

Notice about photocopying: In order to photocopy any work from this publication, you or your organization must obtain permission from the following organization which has been delegated for copyright for clearance by the copyright owner of this publication.

Except in the USA, Japan Academic Association for Copyright Clearance (JAACC), 41-6 Akasaka 9-chome, Minato-ku, Tokyo 107-0052, Japan. Phone: 81-3-3475-5618, Fax: 81-3-3475-5619, E-mail: kammori@msh.biglobe.ac.jp

In the USA, Copyright Clearance Center, Inc., 222 Rosewood Drive, Danvers, MA 01923, USA. Phone: (978)750-8400, Fax: (978)750-4744, [www.copyright.com](http://www.copyright.com)

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).

All communication relating to this journal should be addressed to the

**PALAEONTOLOGICAL SOCIETY OF JAPAN**

c/o Business Center for Academic Societies,

Honkomagome 5-16-9, Bunkyo-ku, Tokyo 113-8622, Japan

Visit our society website at

<http://ammo.kueps.kyoto-u.ac.jp/palaeont/index.html>

# The presence of an azhdarchid pterosaur in the Cretaceous of Japan

NAOKI IKEGAMI<sup>1</sup>, ALEXANDER W. A. KELLNER<sup>2</sup> and YUKIMITSU TOMIDA<sup>3</sup>

<sup>1</sup>Mifune Dinosaur Museum, 995-3 Mifune Mifune Town, Kamimashiki-gun, Kumamoto Prefecture 861-3207, Japan  
(e-mail: naokii@fa2.so-net.ne.jp)

<sup>2</sup>Museu Nacional, Rio de Janeiro, Quinta da Boa Vista, RJ 20.940-040, Brazil

<sup>3</sup>National Science Museum, 3-23-1 Hyakunincho, Shinjyuku, Tokyo 169-0073, Japan

Received 24 September 1999; Revised manuscript accepted 14 April 2000

**Abstract.** An incomplete pterosaur cervical vertebra from the “Upper” Formation (Late Cenomanian-Early Turonian) of the Mifune Group, Kumamoto Prefecture, Japan, is described. Although not complete, this vertebra is very elongated and has a reduced neural spine, allowing its assignment to the Azhdarchidae. It differs from other azhdarchids by being less constricted and by the morphology of the postzygapophyses. This Japanese occurrence extends the distribution of the Azhdarchidae during the Cretaceous to the easternmost part of Asia.

**Key words:** Azhdarchidae, Late Cretaceous, Mifune Group, Pterosauria, Southwest Japan

## Introduction

The occurrence of pterosaur remains in Japan is very limited. The first record of these volant archosaurs in Japan was the distal part of a femur and other associated bones that were found in Cretaceous sediments of Hokkaido (Obata *et al.*, 1972). Since then, a limited number of fragmentary material has been recovered from a few localities. These include an incomplete wing phalanx (Okazaki and Kitamura, 1996) and the proximal articulation of a left wing metacarpal (Ikegami and Tamura, 1996) both found in the “Upper” Formation of the Mifune Group, in Kumamoto Prefecture, an incomplete wing phalanx (Unwin *et al.*, 1996), and an incomplete cervical vertebra (Chitoku, 1996). To these we add the description of an incomplete cervical vertebra that can be referred to the Azhdarchidae, a long-necked pterodactyloid. The occurrence of this specimen was previously reported (Ikegami, 1997), and a full description and comparison of this material are presented here.

## Geological setting

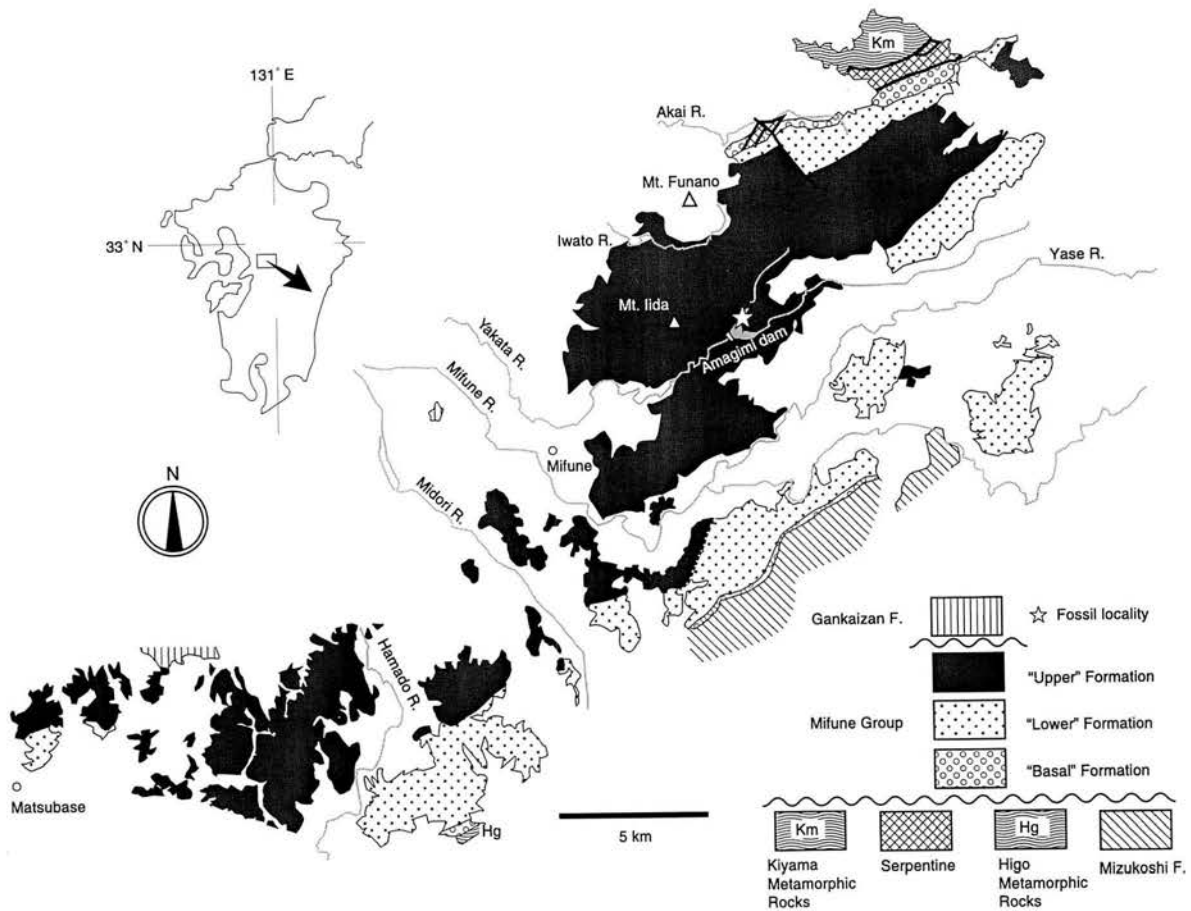
The pterosaur fossil described here was recovered from an outcrop near Amagimi dam, Mifune Town, Kamimashiki-gun, Kumamoto Prefecture, Japan (Figure 1), which is located approximately 20 km southeast of central Kumamoto City. The Mifune Group, broadly distributed in this area, was named by Matsumoto (1939), and was subdivided into three formations, namely the “Basal”, “Lower”, and “Upper”

Formations (Figure 2). Although the terms basal, lower, and upper should not be used for formation names, those names were given as official names by Matsumoto (1939) and have not been revised since then. Therefore, these terms are used here until a full revision is published. Tamura and Sawamura (1964), Tamura and Tashiro (1966), and Tamura (1970, 1976, 1977, 1979) further investigated and expanded the distribution of the group, and studied the pelecypod fauna from those strata. The stratigraphy of the group, however, has not markedly changed from the original study of Matsumoto (1939).

The “Upper” Formation is characterized by red mudstone, blue-green sandstone, and more than dozen tuff beds (Matsumoto, 1939). It reaches 800 to 1000 m in thickness, and vertebrate fossils have been found in several horizons (Tamura *et al.*, 1991).

The azhdarchid specimen described here was found in a coarse sandstone bed, about 30 cm thick and with muddy patches, which belongs to the middle part of the “Upper” Formation (Figure 2). This coarse sandstone is more or less lens-shaped, and appears at a distinct level between two tuff beds. The locality of the azhdarchid, as well as other sites from the same horizon, also yielded many fragmentary bones of various taxa, including dinosaurs, crocodiles, turtles, fishes, and mammals (Tamura *et al.*, 1991; Hirayama, 1998; Setoguchi *et al.*, 1999).

The “Upper” Formation is considered terrestrial based on the rock facies and fossil taxa. Although those fossils do not include taxa that are useful for identifying the age of the



**Figure 1.** Geological map of the area southeast of Kumamoto City (after Tamura, 1979), showing the locality of the azhdarchid pterosaur.

formation, *Eucalycoceras* sp. cf. *E. spathi* is known from the middle part of the "Lower" Formation, suggesting a middle Cenomanian age for this unit (Tamura and Matsumura, 1974). However, the Gankaizan Formation that overlies the "Upper" Formation, south of Kumamoto City, yielded *Inoceramus amakusensis*, which indicates the early Santonian (Tamura and Tashiro, 1966). These specimens suggest that the age of the "Upper" Formation lies between middle Cenomanian and early Santonian. However, the lower part of the Ohnogawa Group, which outcrops east-northeast of the Mifune Group, includes red beds and tuff beds that resemble the "Upper" Formation of the Mifune Group. The upper marine facies of the Ohnogawa Group has yielded *Inoceramus hobetsuensis*, indicating middle Turonian age (Noda, 1969). Therefore, the age of the "Upper" Formation of the Mifune Group can be estimated as late Cenomanian to early Turonian (Matsumoto *et al.*, 1982). Hirayama (1998) also suggested as the age of the "Upper" Formation late Cenomanian to early Turonian, based on the similarity between chelonian assemblages from this formation and those of Central Asia.

### Systematic description

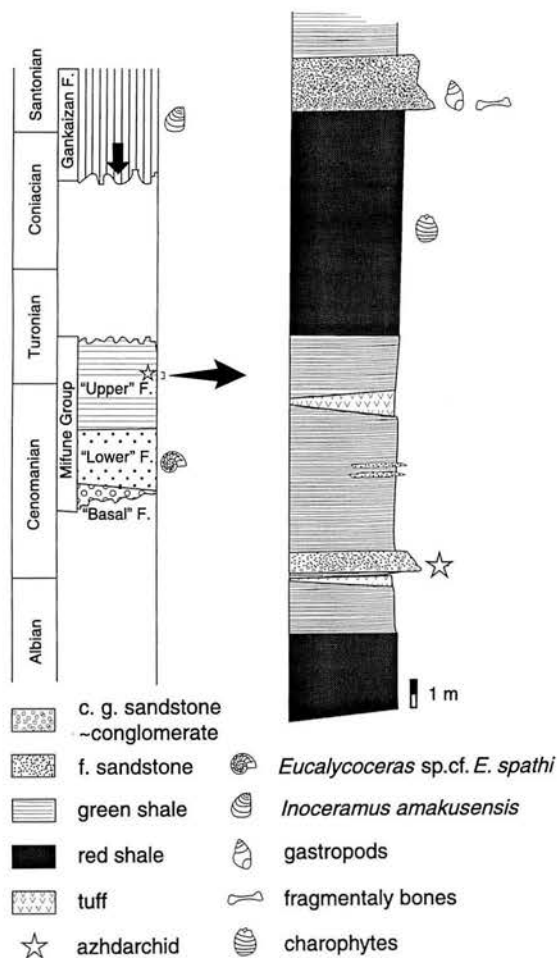
Family Azhdarchidae Nessov, 1984  
Azhdarchidae gen. et sp. indet.

Figure 3

**Material.**—MDM (Mifune Dinosaur Museum) 349, a cervical vertebra from the Mifune Group; a cast in Museu Nacional, Rio de Janeiro (MN 5022-V).

**Description.**—The specimen consists of an incomplete procoelous cervical vertebra, with the cranial part including the prezygapophyses missing (Fig. 3). The vertebra is compressed dorsoventrally, which causes distortion towards the left lateral side. Although this compression changed the natural shape of this bone, it is not completely flattened like many pterosaur specimens from the Niobrara Chalk of North America, but maintains some of its original three-dimensionality. Several breaks, cutting the vertebral body and some filled with matrix, are present, particularly on the dorsal surface (Figure 3 A, B). On the ventral side, the cortical bone is crushed, forming several bony plates in a "broken eggshell"-like pattern.





**Figure 2.** Stratigraphy of the Upper Cretaceous sediments in the area southeast of Kumamoto City (after Tamura and Matsumura, 1973; Tamura and Tashiro, 1966; Matsumoto *et al.*, 1982) on the left, and columnar section of the "Upper" Formation of the Mifune Group at the fossil locality on the right.

Near the caudal articulation, the neural spine is broken, but the preserved parts suggest that it was very low. Slightly away from the articulation, this structure almost disappears, being reduced to a very thin ridge that extends for most of the preserved vertebral length. On the right side, another ridge runs parallel to the neural spine, about 5 mm away from the midline. Evidence of a similar ridge is also observed about 6 mm from the midline on the left side, most of which was lost during the compaction of the specimen. This ridge is interpreted as the transverse process that, in this specimen, is very reduced and does not reach the postzygapophysis.

The postzygapophyses are set well apart from the vertebral body, with the left one better preserved. They are not parallel to each other, and each of them forms an estimated angle with the midline of the centrum of about 33° (based on the right side) in dorsal view.

Also in distal view, the postzygapophyses are set apart

from the vertebral body, although the angle relative to the ventral surface is very difficult to estimate (Figure 3 G,H).

The articular surface of the postzygapophysis is suboval; the dorsal part is constricted, and the ventral part is rounded. Above the dorsal margin, a small process is present.

The posterior condyle is not very well preserved in this specimen. Apparently, it had a suboval outline, with the major axis directed lateromedially. The dorsal margin is rounded, and the ventral margin is flattened. On each side of the condyle, the postexapophyses are observed, of which the left side is better preserved. It forms a small process that is directed laterocaudally.

Two pneumatic openings are observed lateral to the neural canal; the right one is better preserved. Both pneumatic openings are slightly smaller than the neural canal and occupy a relatively high position in the posterior surface of the vertebra. There is no evidence of a third pneumatic foramen above the neural canal.

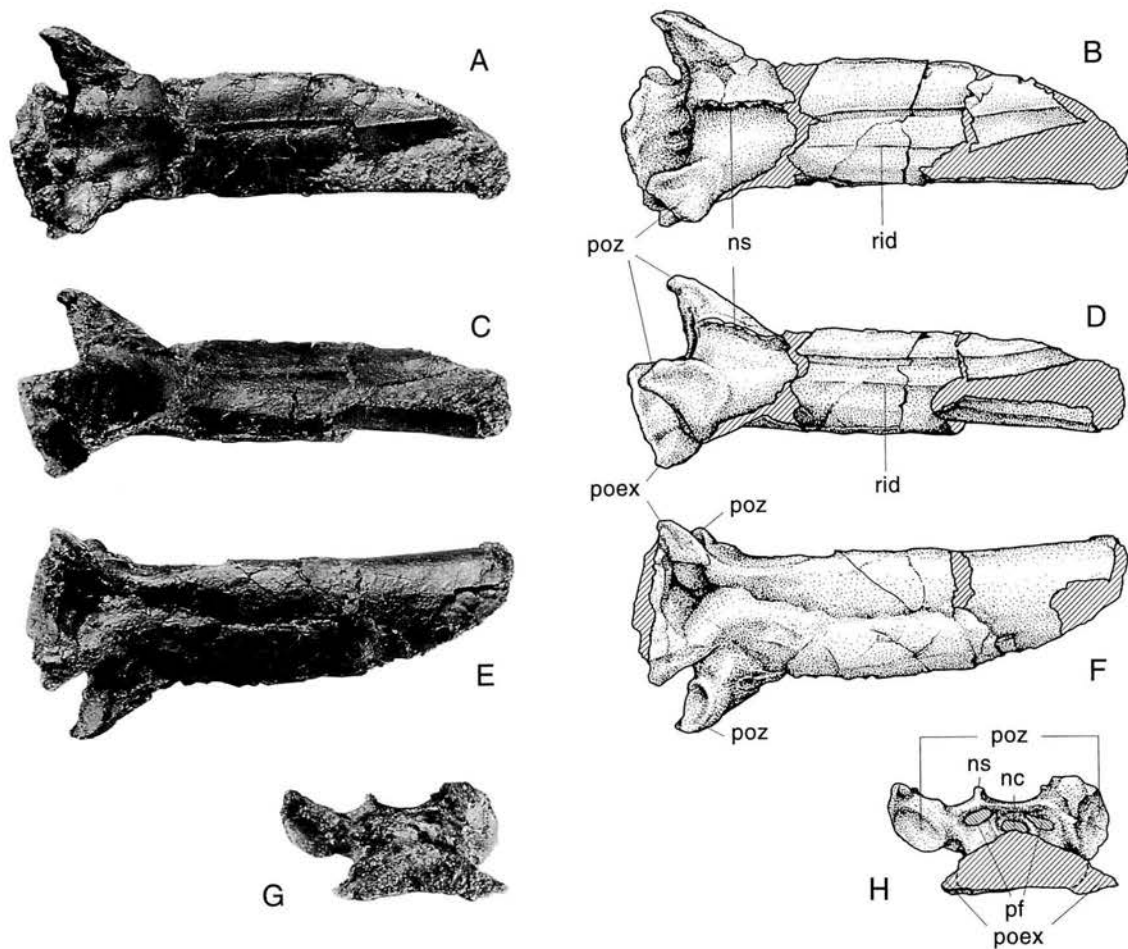
The reconstruction of the middle part for this cervical vertebra indicates that the transverse section was oval and slightly wider than high (see Table 1). Based on the preserved part, this vertebra was very elongate, with a minimum length/width ratio of 4.3, but likely over 5. The exact length, however, is unknown.

*Comparisons and discussion.*—Comparisons of this specimen with other pterosaur cervical vertebrae show that it shares one feature with the Azhdarchidae: its relative length. Elongated mid-cervical vertebra with a low neural spine is one of the synapomorphies of azhdarchids (Howse, 1986), indicating that this specimen represents a member of this pterosaur clade. Padian (1984, 1986) refined the diagnosis of Nessov (1984), showing among other things that the vertebra centrum enclosed the neural canal, a situation nearly unique in vertebrates.

As far as comparisons are possible, this cervical vertebra shows some differences from other azhdarchids. In dorsal view, the postzygapophyses are thinner and set apart at a greater angle relative to the vertebra's midline, as compared to *Quetzalcoatlus* sp. (Howse, 1986) and to *Azhdarcho* (Nessov, 1984; cast MN 4692-V). The position of the pneumatic foramina lateral to the neural canal is similar to the condition in *Quetzalcoatlus* (TMM 42422-24, cast MN 4699-V), and also of *Azhdarcho*. In the cranial articulation of some cervical vertebrae attributed to the latter, there is an extra pneumatic opening above the neural canal (Nessov, 1984). Whether a similar opening was present in the Japanese specimen is unknown.

This specimen further differs from all known azhdarchids by having a well developed ridge parallel to the neural spine, by being less constricted with comparatively straighter lateral margins, and by having the process above the postzygapophyses smaller but comparatively more pointed.

So far, only two azhdarchids with a complete or nearly complete neck are known: *Quetzalcoatlus* sp. from the USA and *Zhejiangopterus linhaiensis* from China. The former, unfortunately, is still undescribed. The latter was originally regarded as a nyctosaurid (Cai and Wei, 1994), but Unwin and Lü (1997) reclassified this taxon in the Azhdarchidae, based on the low position of the orbit relative to the nasoantorbital fenestra, which is an azhdarchid



**Figure 3.** Azhdarchidae gen. et sp. indet. (MDM 349), cervical vertebra from the Mifune Group. **A, B:** dorsal; **C, D:** right lateral; **E, F:** ventral; **G, H:** posterior views. Natural size. Abbreviations: nc, neural canal; ns, neural spine; pf, lateral pneumatic foramen; poex, postexapophysis; poz, postzygapophysis; rid, lateral ridge.

**Table 1.** Measurements of Azhdarchidae gen. et sp. indet. (MDM 349), cervical vertebra from the Mifune Group (in mm).

preserved length	65
width of postzygapophyses	25.5
width of the centrum (preserved)	15.5
width of the centrum (reconstructed)	≈ 13
height of middle part (preserved)	7
height of middle part (reconstructed)	≈ 11

synapomorphy (Kellner and Langston, 1996). Because the cervical vertebrae of *Z. linhaiensis* were not sufficiently described and illustrated without any detail (Cai and Wei, 1994), a detailed comparison with Japanese specimen cannot be made. Therefore, some of the variations described above could be related to the position of the cervical vertebrae in the neck (e.g. lateral margins, directions of the postzygapophyses).

The Azhdarchidae have been known to occur from the Cenomanian deposits of Morocco (Kellner and Mader, 1996); Turonian-Coniacian strata of Uzbekistan (Nesov, 1984); the Campanian Judith River Formation of Alberta, Canada (Currie and Russell, 1982); Campanian Two Medicine Formation of Montana, USA (Padian, 1984; Padian and Smith, 1992; Padian *et al.*, 1995); Campanian-Maastrichtian deposits of Senegal (Monteillet *et al.*, 1982); the Maastrichtian Javelina Formation of Texas, USA (Lawson, 1975; Kellner and Langston, 1996); Maastrichtian deposits in Jordan (Arambourg, 1959); and in late Maastrichtian deposits of Méridon, France (Buffetaut *et al.*, 1997). Along with the Chinese specimens mentioned above (*Z. linhaiensis*, late Cretaceous), the occurrence of Azhdarchidae in Japan extends the distribution of those pterosaurs during the Cretaceous to the easternmost part of Asia.

### Acknowledgments

The specimen described here was collected by an excavation managed by the Mifune Board of Education with the cooperation of a number of people in 1996. That excavation was financially supported by the Mifune Board of Education and the Kumamoto Prefectural Board of Education. We would like to thank Minoru Tamura for many helpful comments during the field research. Also, we thank Yasuko Okamoto for the illustrations of figures 3 B, D, F, and H.

### References

- Arambourg, C. 1959: *Titanopteryx philadelphiae* nov. gen., nov. sp., ptérosaurien géant. *Notes et Mémoires du Moyen Orient*, 7, p. 229-234.
- Buffetaut, E., Laurent, Y., Le Loeuff, J. and Bilotte, M. 1997: A terminal Cretaceous giant pterosaur from the French Pyrenees. *Geological Magazine*, vol. 134, no. 4, p. 553-556.
- Cai, Z. and Wei, F., 1994: On a new pterosaur (*Zhejiangopterus linhaiensis* gen. et sp. nov.) from Upper Cretaceous in Linhai, Zhjiang, China. *Vertebrata Palasiatica*, vol. 32, p. 181-194, pls. I-II. (in Chinese with English summary)
- Chitoku, T. 1996: Pterosaur bone from the Upper Cretaceous of Enbetsu, Hokkaido. *Bulletin of the Hobetsu Museum*, No. 12, p. 17-24. (in Japanese with English abstract)
- Currie, P. J. and Russell, D. A., 1982: A giant pterosaur (Reptilia: Archosauria) from the Judith River (Oldman) Formation of Alberta. *Canadian Journal of Earth Sciences*, vol. 19, no. 4, p. 894-897.
- Hirayama, R. 1998: Fossil turtles from the Mifune Group (Late Cretaceous) of Kumamoto Prefecture, Western Japan. In, Report of the research on the distribution of important fossils in Kumamoto Prefecture, "Dinosaurs from the Mifune Group, Kumamoto Prefecture, Japan", p. 85-99. (in Japanese with English abstract)
- Howse, S. C. 1986: On the cervical vertebrae of the Pterodactyloidea (Reptilia: Archosauria). *Zoological Journal of the Linnean Society*, vol. 88, p. 307-328.
- Ikegami, N. 1997: An azhdarchid pterosaur from the Mifune Group, Kumamoto Prefecture, Japan. *Abstracts of the 104th Annual Meeting of the Geological Society of Japan*, p. 350. (in Japanese)
- Ikegami, N. and Tamura, M., 1996: New dinosaurs and a pterosaur from the Mifune Group. *Proceedings of the Nishinohon branch Geological Society of Japan*, No. 108, p. 9-10.
- Kellner, A. W. A. and Langston, W., Jr. 1996: Cranial remains of Quetzalcoatlus (Pterosauria, Azhdarchidae) from the Late Cretaceous sediments of Big Bend National Park, Texas. *Journal of Vertebrate Paleontology*, vol. 16, no. 2, p. 222-231.
- Kellner, A. W. A. and Mader, B. J. 1996: First report of Pterosauria (Pterodactyloidea, Azhdarchidae) from Cretaceous rocks of Morocco. *Journal of Vertebrate Paleontology*, vol. 16, suppl. to no. 3, p. 45A.
- Lawson, D. A. 1975: Pterosaur from the Latest Cretaceous of West Texas. Discovery of the largest flying creature. *Science*, vol. 187, p. 947-948.
- Matsumoto, T., 1939: Geology of Mifune district, Kumamoto Prefecture, Kyusyu (with special reference to the Cretaceous system). *The Journal of the Geological Society of Japan*, vol. 46, no. 544, p. 1-12, pl. 1. (in Japanese with English résumé)
- Matsumoto, T., Obata, I., Tashiro, M., Ohta, Y., Tamura, M., Matsukawa, M., and Tanaka, H., 1982: Correlation of marine and non-marine formations in the Cretaceous of Japan. *Fossils (Kaseki)*, no. 31, p. 1-26. (in Japanese with English abstract)
- Monteillet, J., Lappartient, J. R., and Taquet, P. 1982: Un ptérosaurien géant dans le Crétacé supérieur de Pake (Sénégal). *Comptes rendus de l'Académie des Sciences, de Paris*, 295, p. 409-414.
- Nessov, L. A. 1984: Pterosaurs and Birds from the Upper Cretaceous of Middle Asia. *Paleontological Journal*, vol. 1, p. 47-57.
- Noda, H., 1969: Biostratigraphic study of the Onogawa Group, Kyushu. *Science Reports, Department of Geology, Kyushu University*, Vol. 10, No. 1, p. 1-10. pls. 1-3. (in Japanese with English Abstract)
- Obata, I., Hasegawa, Y., and Otsuka, H., 1972: Preliminary report on the Cretaceous reptile fossils from Hokkaido. *Memoirs of National Science Museum*, vol. 5, p. 213-222. (in Japanese with English abstract)
- Okazaki, Y. and Kitamura, N., 1996: The first discovery of a pterosaur from the Cretaceous Mifune Group, Kyushu, Japan. *Bulletin of the Kitakyushu Museum of Natural History*, No. 15, p. 133-136.
- Padian, K., 1984: Large pterodactyloid pterosaur from the Two Medicine formation (Campanian) of Montana. *Journal of Vertebrate Paleontology*, vol. 4, no. 4, p. 516-524.
- Padian, K., 1986: A taxonomic note on two pterodactyloid families. *Journal of Vertebrate Paleontology*, vol. 6 no. 3, p. 289.
- Padian, K. and Smith M., 1992: New light on late Cretaceous pterosaur material from Montana. *Journal of Vertebrate Paleontology*, vol. 12, no. 1, p. 87-92.
- Padian, K., de Ricqlés A. J. and Horner, J. R., 1995: Bone histology determines identification of new fossil taxon of pterosaur (Reptilia: Archosauria). *Comptes rendus de l'Académie des Sciences de Paris, Séries II*, no. 320, p. 77-84.
- Setoguchi, T., Tsubamoto, T., Hanamura, H., and Hachiya, K., 1999: An early Late Cretaceous mammal from Japan, with reconsideration of the evolution of tribosphenic molars. *Paleontological Research*, vol. 3, no. 1, p. 18-28.
- Tamura, M., 1970: The hinge structure of *Trigonioides*, with description of *Trigonioides mifunensis*, sp. nov. from Upper Cretaceous Mifune Group, Kumamoto Pref., Japan. *Memoirs of the Faculty of Education, Kumamoto University*, no. 18, Natural Science, p. 38-53
- Tamura, M., 1976: Cenomanian bivalves from the Mifune Group, Japan Part 1. *Memoirs of the Faculty of Education, Kumamoto University*, no. 25, Natural Science, p. 45-59. pls. I-III.
- Tamura, M., 1977: Cenomanian bivalves from the Mifune Group, Japan Part 2. *Memoirs of the Faculty of Education, Kumamoto University*, no. 26, Natural Science, p. 107-144. pls. I-XIII.
- Tamura, M., 1979: Cenomanian bivalves from the Mifune Group, Japan Part 3. *Memoirs of the Faculty of Education, Kumamoto University*, no. 28, Natural Science, p. 59-74. pls. I-III.

- Tamura, M. and Matsumura, M., 1974: On the Age of the Mifune Group, Central Kyushu, Japan. *Memoirs of the Faculty of Education, Kumamoto University*, no. 23, Natural Science, p. 47-56, pl. I.
- Tamura, M., Okazaki, Y., and Ikegami, N., 1991: Occurrence of carnosaurian and herbivorous dinosaurs from Upper Formation of Mifune Group, Japan. *Memoirs of the Faculty of Education, Kumamoto University*, no. 40, Natural Science, p. 31-45. (*in Japanese with English abstract*)
- Tamura, M. and Sawamura, M., 1964: Upper Cretaceous Mitake-yama Formations in central Kyushu. *Memoirs of the Faculty of Education, Kumamoto University*, no. 12, Natural Science, p. 15-22. (*in Japanese with English abstract*)
- Tamura, M. and Tashiro, M., 1966: Upper Cretaceous system south of Kumamoto. *Memoirs of the Faculty of Education, Kumamoto University*, no. 14, Natural Science, p. 24-35. (*in Japanese with English abstract*)
- Unwin, D. M. and Lü J., 1997: On Zhejiangopterus and the relationships of pterodactyloid pterosaurs. *Historical Biology*, vol. 12, p. 199-210.
- Unwin, D. M., Manabe, M., Shimizu, K., and Hasegawa, Y., 1996: First record of pterosaurs from the Early Cretaceous Tetori Group: a wing-phalange from the Amagodani Formation in Shokawa, Gifu Prefecture, Japan. *Bulletin of National Science Museum, Tokyo, Ser. C*, vol. 22, nos. 1-2, p. 37-46.

# The suprageneric classification of the foraminiferal genus *Murrayinella* and a new species from Japan

RITSUO NOMURA<sup>1</sup> and YOKICHI TAKAYANAGI<sup>2</sup>

<sup>1</sup>Foraminiferal Laboratory, Faculty of Education, Shimane University, Matsue, 690–8504, Japan  
(e-mail: nomura@edu.shimane-u.ac.jp)

<sup>2</sup>c/o Institute of Geology and Paleontology, Faculty of Science, Tohoku University, Sendai, 980–8578, Japan

Received 29 November 1999; Revised manuscript accepted 24 April 2000

**Abstract.** Japanese species of the foraminiferal genus *Murrayinella* have a rotaliid aperture that is defined by a foraminal plate and umbilical coverplate. Our observations suggest that this genus must be transferred from the family Glabratellidae to the family Rotaliidae. Its morphological similarity to the genus *Schackoinella*, as shown by the presence of a peripheral spine on each chamber, must be a result of homeomorphic convergence. *Murrayinella* never possesses apertural grooves like those of glabratellids. We give a detailed description of the apertural structure of the Japanese species of *Murrayinella* and formally describe a new species, *M. bellula*.

**Key words:** benthic foraminifera, *Murrayinella*, Rotaliidae, suprageneric taxonomy.

## Introduction

Species of the foraminiferal genus *Murrayinella* are common in shallow-water sediments of both the Sea of Japan and the Pacific Ocean. The following are well known species: *Murrayinella minuta* (Takayanagi, 1955), *Murrayinella globosa* (Millett, 1903), and *Murrayinella takayanagii* (Matoba, 1967), all of which have been reported from the late Pleistocene to Recent. Among them, *Murrayinella minuta* is the most common species in Japan. A *Murrayinella* species has also been reported from the early middle Miocene of Southwest Honshu, Japan (Nomura, 1990). The earliest appearance of the genus is thus not from the Pliocene (Loeblich and Tappan, 1987), but from the middle Miocene.

Despite its common occurrence, the systematic position of this genus is still confused. Heron-Allen and Earland (1915) originally described *Murrayinella murrayi* as a *Rotalia* species, while the allied form *M. globosa* was described as a *Discorbina* species by Millett (1903). Subsequently, other species now allocated to *Murrayinella* were placed in the genus *Pararotalia*, except for some other generic allocations such as “*Eponides*” (Ujié, 1963) and *Praeglobotruncana* (McCulloch, 1977). Thus, many workers regarded *Murrayinella* as closely related to the Rotaliidae. However, Loeblich and Tappan (1987) placed *Murrayinella* in the Glabratellidae, referring to their earlier systematic review (Loeblich and Tappan, 1964), on the basis of Heron-Allen and Earland’s observation that suggested a different mode of reproduction from the Rotaliidae, and an apparent

similarity to the genus *Schackoinella* from the late Miocene of Austria (Weinhandl, 1958). Indeed, Haman and Christensen (1971) regarded *Murrayinella* as a synonym of *Schackoinella*.

Previous investigations lacked detailed comparative observations on the foraminal structure of these small taxa that were beyond the resolution power of binocular microscopes. We carried out detailed anatomical observations of the inner test by scanning electron microscope, using a method of Nomura (1983). As a result, all the species of this genus are shown to be devoid of radiating apertural grooves as in the glabratellids, instead their apertures have the foraminal plate and umbilical coverplate typical of the rotaliids. We now describe the Japanese species, including a new species, in detail and discuss the suprageneric position of the genus *Murrayinella*.

## Foraminal structures of *Murrayinella*

In general, the apertural structures of the genus *Murrayinella* resemble those of *Ammonia* or *Pararotalia* species which have a foraminal plate and umbilical coverplate. These basic features of the rotaliid aperture are well shown in several species from Eocene sediments of the Paris Basin (Hottinger *et al.*, 1991) and from the Red Sea (Hottinger *et al.*, 1993; Revets, 1993) and Japan (Nomura and Takayanagi, 2000). The final aperture of *Murrayinella* is an umbilical to extraumbilical slit usually covered with numerous small spines. The penultimate and antepenultimate foramina are a high arch or rounded openings with the



foraminal plate on the proximal side and with the umbilical coverplate closing up the umbilical side of the slit-shaped aperture.

The foraminal structure of *Murrayinella* species fundamentally resembles the *Pararotalia*-type rather than the *Ammonia*-type (Nomura and Takayanagi, 2000). *Murrayinella minuta* and *M. bellula* deviate little from the *Pararotalia*-type foramen. However, the foraminal plate of *M. globosa* is variable, ranging from the *Pararotalia*-type foramen to a form which is close to the *Ammonia* type. A quite different type is found in *M. takayanagii*. The *Ammonia*- or *Pararotalia*-type foramen can be distinguished by the position of the foraminal plate. The base of the foraminal plate in the *Ammonia*-type foramen is formed on the umbilical side of the previous whorl and thus the foramen is arch-shaped, while that of the *Pararotalia*-type foramen bends towards the inner side of the apertural opening, forming a lip-like structure in its lower side (or proximal side). Thus, the foraminal plate of the *Pararotalia*-type foramen is called a lower lip in order to distinguish from a toothplate of Hottinger *et al.* (1991). This difference of foraminal structure is significant for the discrimination of larger forms of rotaliid taxa when discussing their phylogenetic relationships. However, we regard this difference in *Murrayinella* as a less significant criterion for the suprageneric classification of this genus, because of the situation in *M. takayanagii*. The foramen of *M. takayanagii* is exceptional for rotaliid taxa, because the foraminal plate and chamber flap are poorly developed in contrast to the well developed umbilical coverplate observed from the outside of the test. We consider that this aperture has no systematic significance for the phylogenetic reconstruction of the rotaliid taxa. We would retain all these kinds of foramina in the genus *Murrayinella*.

### Discussion

The most recent suprageneric classification of the genus *Murrayinella* places it within the family Glabratellidae, superfamily Discorbacea, although knowledge of both its external and internal structures is imperfect (Loeblich and Tappan, 1987). Farías (1977) proposed that *Murrayinella* should include *M. murrayi* and *M. globosa* (= *Rotalia erinacea* Heron-Allen and Earland), but the latter species has been regarded by some authors to be better placed in *Schackoinella* (Quilty, 1975). According to our observations, *Murrayinella* never shows the umbilical features, such as radial grooves, that aid attachment during plastogamy, the type of reproduction found in the Glabratellidae. The aperture of the Glabratellidae is a low interiomarginal slit on the umbilicus without additional internal structures. The observation reported by Heron-Allen and Earland (1915) for *M. murrayi* showing "double (budded) specimens" must be questioned. The aperture of *M. murrayi* and *M. globosa* is an umbilical to extraumbilical slit, which must make plastogamic reproduction impossible. We believe that Heron-Allen and Earland's budded specimens do not belong to *Murrayinella*. The external morphology of *Schackoinella* is similar to *Murrayinella*, but its aperture is mostly umbilical and has radial striations, typical of the Glabratellidae. These features clearly show that *Murrayinella* and

*Schackoinella* have a different phylogenetic origin. The most obvious way to distinguish *Murrayinella* and *Schackoinella* is provided by the internal structure of the aperture. The foraminal plate and the umbilical coverplate in *Murrayinella* are never found in *Schackoinella*.

Through our examination, we have found that the structure of the aperture in *Murrayinella* resembles that found in the Rotaliidae and the foraminal structure is similar to the *Pararotalia*-type foramen. Exceptionally, there is the intermediate form between the *Ammonia* type and the *Pararotalia* type and one more type of foramen that does not belong to either of them. In view of these varied foramina, it was difficult to decide whether this genus should be placed in the subfamily Pararotaliinae or subfamily Ammoniinae in the scheme of Loeblich and Tappan's (1987) suprageneric classification. Loeblich and Tappan (1987) defined the foramen of the subfamily Pararotaliinae as having a "single interiomarginal slitlike aperture, converted into areal intercameral foramen" that is the typical *Pararotalia*-type foramen. They did not refer to the foraminal structure in the subfamily Ammoniinae, but instead to structures associated with the aperture such as radial canals, fissures, and umbilical cavities. However, these structures are not restricted to the Ammoniinae. Members of the Pararotaliinae also have these structures (Hottinger *et al.*, 1991, 1993; Nomura and Takayanagi, 2000). A strict usage of these structures would not help to discriminate between the Ammoniinae and the Pararotaliinae. Instead, the distinction between the *Pararotalia*-type and the *Ammonia*-type foramen provides the best character for deciding on the subfamily placement (Nomura and Takayanagi, 2000). A supplementary structure, the labial aperture, is sometimes found in the *Ammonia*-type foramen but is never associated with the *Pararotalia* one. The foraminal structures of *Murrayinella* are rather simple and lack labial apertures. We are of the opinion that the difference between the Ammoniinae and the Pararotaliinae can be found in the foraminal structure and that this feature is most helpful for the subfamily-level classification. Therefore, we suggest that the placement of this genus in the subfamily Pararotaliinae and in the family Rotaliidae is valid.

### Systematic descriptions

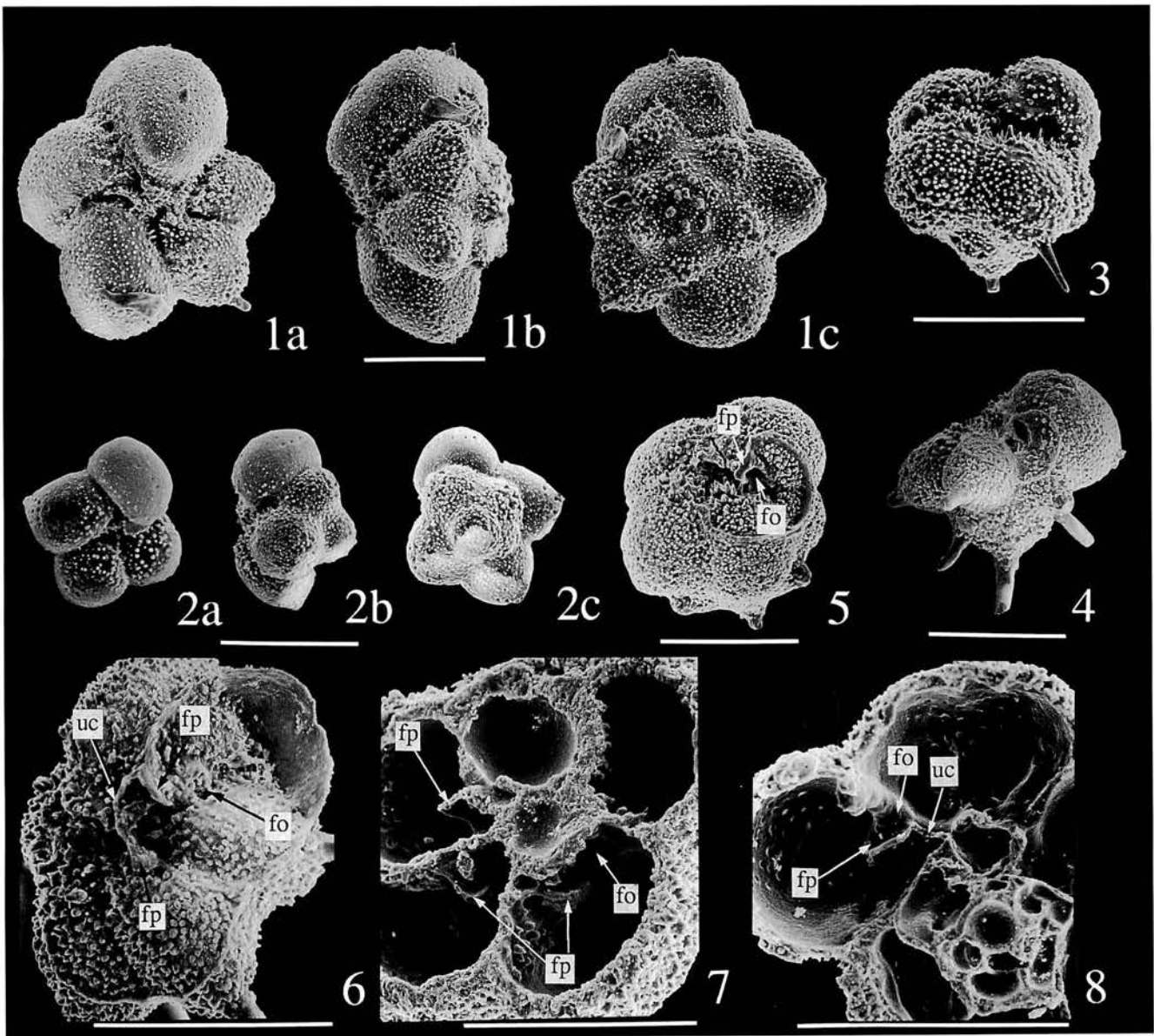
Order Rotaliida Lankester, 1885  
 Superfamily Rotaliacea Ehrenberg, 1839  
 Family Rotaliidae Ehrenberg, 1839  
 Subfamily Pararotaliinae Reiss, 1963  
 Genus *Murrayinella* Farías, 1977

*Type species.*—*Rotalia murrayi* Heron-Allen and Earland, 1915.

*Emended description.*—Test small, low trochospiral to high trochospiral with depressed or opened umbilicus; inflated to globular chambers usually rough with numerous small spines, four to six in the final whorl; sutures depressed to deeply depressed; periphery rounded to angled, usually lobulate; aperture a low interiomarginal slit located extraumbilically; apertures in preceding chambers rounded; walls hyaline, rough and translucent.

**Remarks.**—Loeblich and Tappan (1987) placed this genus in the family Glabratellidae Loeblich and Tappan (1964), based on their interpretation of Heron-Allen and Earland's claim to have observed double (or budded) specimens in the type species. *Rotalia erinacea* Heron-Allen and Earland and *Discorbina imperatoria* var. *globosa* Millett were placed in the genus *Schackoinella* Weinhandl by Quilty (1975), which also belongs to the family Glabratellidae.

These observations strongly influenced Loeblich and Tappan's (1987) decision to place this genus in the glabratellids. However, Whittaker and Hodgkinson (1979) once considered *Murrayinella* to be conspecific with *Schackoinella*, but they immediately changed their opinion after examining Quilty's description of the type species *Schackoinella sarmatica* Weinhandl. In the postscript of their monographic paper, they suggested that the difference



**Figure 1.** *Murrayinella globosa* (Millett) from Holocene bay-floor muds of Tateyama, Chiba Prefecture. Scale bar: 100  $\mu\text{m}$ . **1a-c.** Mature specimen. **2a-c.** Immature specimen. **3.** Obliquely viewed specimen showing the marginal slit of the aperture. **4.** Peripheral view of specimen without the final chamber showing the arched opening of the penultimate foramen. **5.** Oblique view of specimen without the final chamber showing the foraminiferal plate. **6.** Oblique view of the penultimate and antepenultimate foraminiferal plates (fp) and the penultimate umbilical coverplate (uc). fo = foramen. **7.** Specimen with dorsal chambers removed showing the foraminiferal plate (fp) protruded from each foramen (fo). **8.** Specimen with ventral chambers removed showing the foraminiferal plate (fp) from the penultimate foramen (fo) and the umbilical coverplate (uc).

in the aperture and the ventral feature formed a basis for discriminating between *Murrayinella* and *Schackoinella*. As observed herein, the basic structure of the *Murrayinella* aperture is the same as that of the rotaliids. Both are characterized by the foraminal plate and umbilical coverplate. The final aperture of *Murrayinella* is always an umbilical to extraumbilical slit, but the previous foramina are rounded to oval openings as a result of the umbilical side-slit being partly closed up by the umbilical coverplate. This apertural structure can only be explained by the rotaliid aperture and foraminal model (Hansen and Reiss, 1971; Nomura and Takayanagi, 2000).

### *Murrayinella globosa* (Millett)

Figure 1.1–1.8

- Discorbina imperatoria* (d'Orbigny) var. *globosa* Millett, 1903, p. 701, pl. 7, figs. 6a–c.
- Rotalia erinacea* Heron-Allen and Earland, 1915, p. 720, pl. 53, figs. 23–26.
- "*Eponides*" *globosa* (Millett). Ujiie, 1963, p. 233, pl. 1, figs. 27a–29 (part).
- Pararotalia* cf. *imperatoria globosa* (Millett). Chiji and Lopez, 1968, pl. 12, figs. 5a–c.
- Pararotalia murrayi* (Heron-Allen and Earland). Chiji and Lopez, 1968, pl. 12, figs. 6a, b.
- Pararotalia minuta* (Takayanagi). Matoba, 1967, p. 256, pl. 27, figs. 5a, b.
- Pararotalia?* *globosa* (Millett). Matoba, 1970, p. 57, pl. 6, figs. 8a–c.
- Schackoinella sarmatica* Weinhandl. Haman and Christensen, 1971, p. 44, text-figs. 1–3.
- Schackoinella globosa* (Millett). Quilty, 1975, p. 331; Loeblich and Tappan, 1994, p. 142, pl. 294, figs. 1–10.
- Murrayinella erinacea* (Heron-Allen and Earland). Farias, 1977, pl. 1, figs. 7–10.
- Schackoinella* (?) *dissensa* McCulloch, 1977, p. 317, pl. 169, figs. 5, 10a–c, 11a, b, 12a–c.
- Ammonia globosa* (Millett). Zheng *et al.*, 1978, p. 49, pl. 5, figs. 7a–11c.
- "*Schackoinella*" *globosa* (Millett). Whittaker and Hodgkinson, 1979, p. 63, pl. 5, figs. 11, 12a, b, pl. 10, fig. 6 (transferred to the genus *Murrayinella* in postscript).
- Pararotalia* aff. *globosa* (Millett). Oki, 1989, p. 133, pl. 15, figs. 9a–d.
- Murrayinella globosa* (Millett). Matoba and Fukasawa, 1992, fig. 9, nos. 16a–c.

**Examined specimens.**—Specimens from Holocene bay-floor muds (7400–4100BP) of Tateyama, southern part of the Boso Peninsula. Sample locality is given by Fujiwara *et al.* (1997) as in the cliff of the Heguri-gawa River, approximately 139°52'55"E and 35°0'27"N.

**Description.**—Test rather small, planoconvex with a convex ventral side and flat to slightly inflated dorsal side; periphery lobulate and with a short transparent spine on each chamber; sutures distinct, radiate, deeply depressed on ventral side, and curved on dorsal side; chambers four to five on ventral side, inflated; aperture indistinct with a covering of small spines, but apparently an umbilical to extraumbilical slit; wall rough and hispid, usually transparent; pores present, but usually indistinct with small spines on walls, opti-

cally indistinctly radial.

**Apertural structure.**—The final aperture is an umbilical to extraumbilical slit and is covered with small spines (Figure 1.1–1.3). The foramen is arch-shaped (Figure 1.4, 1.5), with an umbilically extended foraminal plate and umbilical coverplate (Figure 1.6–1.8). The foraminal plate obliquely protrudes from the apertural face and its proximal part continues to the umbilical coverplate. The umbilical flap is distinct and adheres to the preceding ones. It has a narrow slit, but does not connect with the labial aperture.

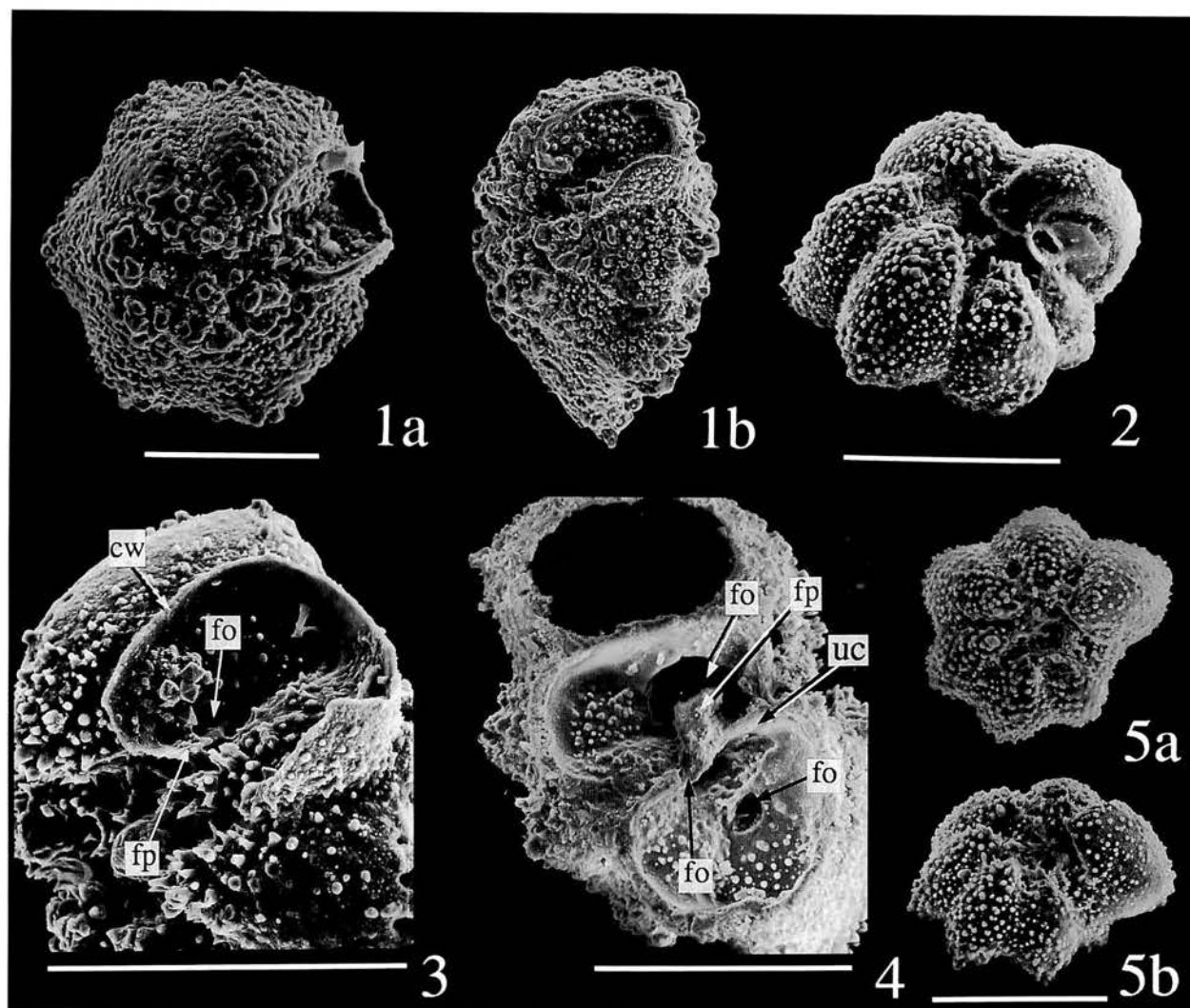
**Geographic occurrences.**—Mostly limited to the Indo-Pacific region. In Japan, this species is widely distributed in the coastal areas of both the Sea of Japan and the Pacific.

**Stratigraphic occurrences.**—Known from the late Miocene (Whittaker and Hodgkinson, 1979) to the Recent.

**Size and measurements.**—Maximum test width is 250  $\mu\text{m}$ , maximum test length is 171  $\mu\text{m}$ ; minimum test width is 99  $\mu\text{m}$ , minimum test length is 63  $\mu\text{m}$ ; averaged test width is 166  $\mu\text{m}$ , averaged test length is 114  $\mu\text{m}$ .

**Remarks.**—Heron-Allen and Earland (1915) placed this species in *Rotalia*, and erroneously renamed it *Rotalia erinacea*, since they believed that the original name was preoccupied by *Rotalia globosa* (Hantken) (see Whittaker and Hodgkinson, 1979 for further discussion). However, later workers suggested the placement in *Rotalia* was invalid, because of its rather different test morphology. This species is characterized by a small test and rough test surface totally covered with small spines, which obscure the details of the apertural structure. Ujiie (1963) considered it to belong to the genus *Eponides*, but he also questioned this generic placement, because of the different nature of the undeveloped inframarginal sulcus around the aperture, the wall lamellarity, and other subordinate external differences of test. Based on our detailed observation, however, the aperture of this species is an extraumbilical slit similar to the rotaliid one. The foraminal plate and the umbilical coverplate, which are basic components in the rotaliid aperture, are present but the foraminal plate is very variable. In general, these structures resemble the *Pararotalia*-type foramen. However, some specimens have the *Ammonia*-type foramen proposed by Nomura and Takayanagi (2000). Nevertheless, the base of the foraminal plate is not well developed in comparison with typical form of the *Ammonia*-type foramen that shows a hook-like structure. As far as the apertural structure is concerned, this species conforms to the *Pararotalia*-type foramen. Otherwise, it is usually characterized by a depressed umbilicus, where the chamber flaps are closely imbricated and fused to make a more rough umbilicus surface. Such features, and the covering of small spines, are enough to separate this species from both *Ammonia* and *Pararotalia* and to warrant a separate genus *Murrayinella*.

*Murrayinella globosa* has been confused with *M. murrayi* (Heron-Allen and Earland, 1915) by some workers. Hatta and Ujiie (1992) considered these two species to be conspecific, based on the opinion that there are gradational changes between the peripheral spines of *M. globosa* and the acute papillae of *M. murrayi*. However, *M. murrayi* has six chambers in the final whorl and a more convex umbilical side of the test (Heron-Allen and Earland, 1915) and surface



**Figure 2.** *Murrayinella minuta* (Takayanagi) from Holocene bay-floor muds of Tateyama, Chiba Prefecture. Scale bar: 100  $\mu$ m. **1a, b.** Mature specimen **2.** Obliquely viewed specimen showing the penultimate foramen with broken foraminiferal plate. **3.** Penultimate foramen with final chamber wall removed showing the basal part of the foraminiferal plate (fp) extended from the inside of the penultimate foramen (fo). cw = chamber wall. **4.** Obliquely sectioned specimen showing the preceding foramen with the foraminiferal plate (fp) and the umbilical coverplate (uc). fo = foramen. **5a, b.** Immature specimen.

rugosity (Whittaker and Hodgkinson, 1979), while *M. globosa* has four to five chambers in the final whorl and a depressed umbilical center without a distinct protrusion.

#### ***Murrayinella minuta* (Takayanagi)**

Figure 2.1–2.5

*Rotalia?* *minuta* Takayanagi, 1955, p. 45, 52, text-figs. 29a–c.

*Pararotalia murrayi* (Heron-Allen and Earland). Ujiie, 1963, p. 239, pl. 3, figs. 3a–9.

*Pararotalia?* *minuta* (Takayanagi). Matoba, 1970, p. 58, pl. 6, figs. 5a–c, 6a–c, 7a–c.

*Praglobotruncana* (?) *wordeni* McCulloch, 1977, p. 424, pl. 178, figs. 7, 10, pl. 179, figs. 7, 8.

*Pararotalia minuta* (Takayanagi). Huang, 1980, p. 55, pl. 1, figs.

1–6, pl. 2, figs. 1–6, pl. 3, figs. 1–6, pl. 4, figs. 1–6.

*Pararotalia globosa* (Millett). Hatta and Ujiie, 1992, p. 198, pl. 43, figs. 5a–c.

*Murrayinella minuta* (Takayanagi). Matoba and Fukasawa, 1992, fig. 9, nos. 17a–c; Kamemaru, 1996, pl. 20, figs. 3, 4.

**Examined specimens.**—Specimens from Holocene bay-floor muds (7400–4100BP) of Tateyama, southern part of the Boso Peninsula. Sample locality is given by Fujiwara *et al.* (1997) as in the cliff of the Heguri-gawa River, approximately 139°52'55'E and 35°0'27"N.

**Emended description.**—Test small, planoconvex with a strongly convex ventral side and nearly flat dorsal side; su-

tures distinct, nearly straight, radiate, slightly depressed in mature specimens and depressed in immature specimens on ventral side, and oblique and curved on dorsal side; chambers five to six on ventral side, slightly inflated, but more inflated on ventral side in immature stage; umbilicus nearly closed and with protruded plug in mature, but slightly open in immature specimens; aperture indistinct with small covering spines, but appears to be an umbilical to extraumbilical slit; wall rough and hispid, usually translucent; pores present, but indistinct with small spines on the walls, optically indistinctly radial.

**Apertural structure.**—The final aperture is an umbilical to extraumbilical slit with a poorly developed umbilical flap (Figure 2.1–2.3, 2.5). The foramen is oval and oblique to the base of the apertural face, with an umbilically extended foraminal plate (Figure 2.4). The protruded foraminal plate is close to the umbilicus and much inclined to the apertural face. The base of the foraminal plate extends onto the distal side of the foramen, forming a lip-like structure (Figure 2.2). The umbilical coverplate is formed, but it does not cover the labial aperture in the preceding foramen.

**Geographic occurrences.**—This species is widely distributed in the coastal areas of both the Sea of Japan and the Pacific. Huang (1980) reported it from the Taiwan Strait at depths ranging from 5.5 to 100 m.

**Stratigraphic occurrences.**—Known from the Late Quaternary to the Recent.

**Size and measurements.**—Maximum test width is 218  $\mu\text{m}$ , maximum test length is 193  $\mu\text{m}$ ; minimum test width is 133  $\mu\text{m}$ , minimum test length is 81  $\mu\text{m}$ ; averaged test width is 177  $\mu\text{m}$ , averaged test length is 124  $\mu\text{m}$ .

**Remarks.**—*Murrayinella minuta* (Takayanagi) was originally tentatively placed in the genus *Rotalia* because it had a closed umbilicus different from that of *Rotalia* as well as hispid walls. Later Ujiie (1963) considered this species to be synonymous with *Rotalia murrayi* and placed it in *Pararotalia* on account of the apertural and foraminal structures. However, Matoba (1970) separated it from *murrayi*, stating that *minuta* has a strongly convex ventral side and flat dorsal side, while *murrayi* has a subglobular test with convex dorsal side and rounded periphery. We support his suggestion that *minuta* is different from *murrayi*.

The variable form of this species is similar to *M. globosa* in having a more lobulate periphery and the incipient spines in earlier chambers of the last whorl. McCulloch (1977) regarded one such variant as a new species that she tentatively assigned to the genus *Praeglobotruncana*. However, these characters fall within the range of *minuta*'s variation.

Ujiie (1963) was the first to discuss the apertural structure of this species and mentioned that it has a toothplate (= the foraminal plate and umbilical coverplate) connected with the preceding foramen. His observation follows the result of Loeblich and Tappan (1957) who studied the type species of the genus *Pararotalia* [i.e., *P. inermis* (Terquem)]. Thus, he put this species in the genus *Pararotalia*. On the basis of observations of the internal structure of *P. inermis* given by Reiss and Merling (1958), he further mentioned that the anterior side of the foraminal plate of *M. minuta* is abruptly cut off at a distance of half a chamber length. Ujiie's observations are important for understanding the true nature of this

apertural structure. The foraminal plate of the *Pararotalia*-type foramen looks like a lip in the lower side of the foramen, resulting from the inward extension of the basal part of the foraminal plate to the distal side of the aperture (Nomura and Takayanagi, 2000). We agree that the aperture and foramen of *minuta* are therefore the same as in *Pararotalia*. The foraminal structure seen by us was also noted by Huang (1980) who showed the foraminal plate (his lip) associated with the one side of the foramen (e.g., Huang, 1980, pl. 2, figs. 2–4). This feature suggests the close phylogenetic relation of *minuta* to *Pararotalia* species. Except for the apertural similarity, however, the small test and the rough test surface are diagnostic enough to separate *minuta* from *Pararotalia* and keep it in *Murrayinella*.

### *Murrayinella takayanagii* (Matoba)

Figure 3.1–3.3

*Pararotalia minuta* (Takayanagi) var.. Matoba, 1967, p. 256, pl. 27, figs. 6a, b.

*Pararotalia ? takayanagii* Matoba, 1970, p. 63, pl. 6, figs. 9a–c, 10 a–c.

*Murrayinella takayanagii* (Matoba). Takayanagi and Hasegawa, 1986, pl. 2, figs. 3a–c.

**Examined specimens.**—Four specimens from the Pleistocene of Well Kashimaoki SK-1, donated by Prof. S. Hasegawa, Hokkaido University; three specimens from the Recent sediment of Matsushima Bay (paratypes), donated by Prof. Y. Matoba, Akita University.

**Emended description.**—Test very small, low trochospiral, planoconvex to concave-convex; spiral side of test gently concave due to the inflation of chambers of the last whorl; periphery subrounded and strongly lobulate becoming stellate; umbilical side deeply concave, usually open without a plug; chambers five to five and one half in final whorl, inflated on periphery; sutures depressed on both umbilical and spiral sides; wall calcareous, thin, very finely perforate, covered with small pustules, peripheral area in each last whorl chamber with blunt spines; aperture arch-shaped and large for test, opened to umbilicus with narrow overturned lip.

**Apertural structure.**—The foraminal plate is poorly developed, but each umbilical coverplate is clearly shown around the umbilicus (Figure 3.1–3.3). The umbilical coverplate is inflated toward the umbilicus, thus it looks like a part of the chamber wall.

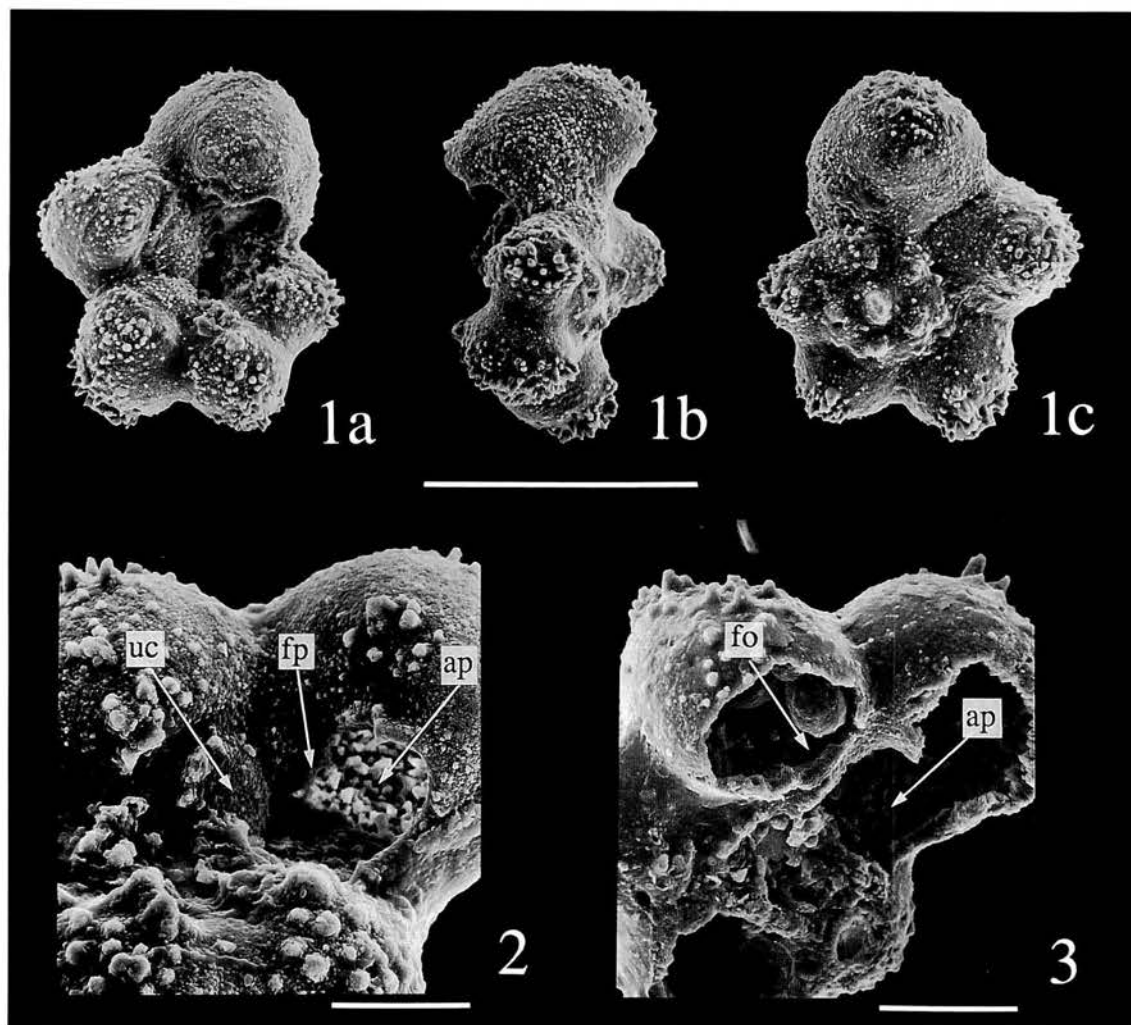
**Geographic occurrences.**—This species is known in the northern Pacific coast of Honshu Island, Japan.

**Stratigraphic occurrences.**—Known from the Pleistocene to the Recent.

**Size and measurements.**—Maximum test width is 135  $\mu\text{m}$ , maximum test length is 69  $\mu\text{m}$ ; minimum test width is 119  $\mu\text{m}$ , minimum test length is 53  $\mu\text{m}$ ; averaged test width is 127  $\mu\text{m}$ , averaged test length is 59  $\mu\text{m}$ .

**Remarks.**—The well developed final aperture, and the widely opened and depressed umbilicus are characteristics of this species. Matoba (1970) placed it in the genus *Pararotalia*, based on the similarity of the aperture to that of *Pararotalia minuta*. However, the systematic position of this species has been questioned, because it lacks the umbilical





**Figure 3.** *Murrayinella takayanagii* (Matoba) from the Pleistocene of Well Kashimaoki SK-1. **1a-c.** Mature specimen. Scale bar: 100  $\mu\text{m}$ . **2.** Enlargement of aperture (ap) showing the small foramininal plate (fp) and a completely covered umbilical coverplate (uc). Scale bar: 20  $\mu\text{m}$ . **3.** Umbilical section of no. 2 specimen showing the internal rim of the penultimate foramen (fo). ap = aperture. Scale bar: 30  $\mu\text{m}$ .

plug that is a characteristic feature of *Pararotalia*. After examining these systematic problems, we are of the opinion that the aperture of *takayanagii* is fundamentally comparable to the foramininal plate and umbilical coverplate concept of the rotaliids, but these features at the same time are somewhat different from their expression in *Pararotalia*. The aperture of *takayanagii* is usually rounded, without special developments such as the umbilical flap, while that of *Pararotalia* is an extraumbilical slit with a development of both the foramininal plate (=lower lip of Nomura and Takayanagi, 2000) and an umbilical coverplate. Because the chamber flap is poorly developed in *takayanagii*, the umbilical coverplate that partly conceals the umbilical side of the foramen is clearly shown in the umbilical view. The foramininal plate itself is less developed and is not clearly differentiated from the chamber wall. These apertural characters, and the ab-

sence of the umbilical plug, both strongly suggest that the placement of this species in *Pararotalia* is inappropriate.

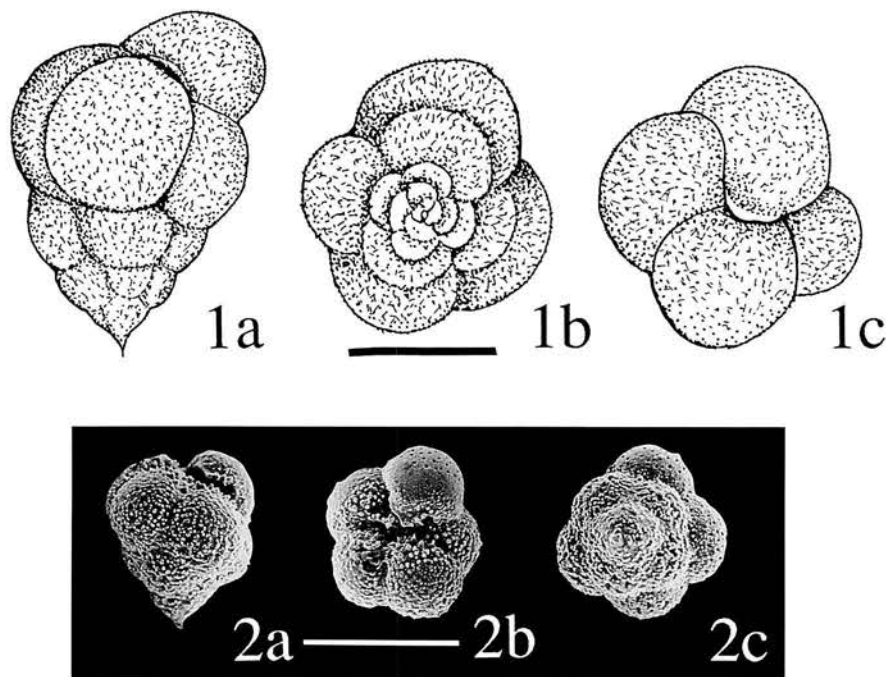
On the basis of the basically trochospiral nature of the test, and taking the hispid nature of the test surface and the basic apertural structure of this species into consideration, we have put *takayanagii* in the genus *Murrayinella*.

***Murrayinella bellula* sp. nov.**

Figures 4.1-4.2; 5.1-5.6; 6

"*Eponides*" *globosa* (Millett). Ujiie, 1963, p. 233, pl. 1, fig. 26 (part).

**Diagnoses.**—Highly trochospiral test with inflated globular chambers; walls hispid; one spine usually in the earliest portion of the test; aperture an umbilical slit; foramen associated with a lip-like foramininal plate and an umbilical coverplate.



**Figure 4.** 1a–c. Holotype (NFL 9901) of *Murrayinella bellula* sp. nov. from Holocene bay-floor muds of Tateyama, Chiba Prefecture. 2a–c. Paratype (NFL 9902) of *Murrayinella bellula* sp. nov. Scale bar: 100  $\mu$ m.

*Holotype and paratypes.*—Holotype (registered number, NFL 9901), Figure 4. 1a–c, Holocene bay-floor muds (7400–4100BP) in Tateyama, Chiba Prefecture; paratypes (registered number, NFL 9902), Figure 4. 2a–c, from the same deposits. Sample locality is given as number 7 by Fujiwara *et al.* (1997) in the cliff of the Heguri-gawa River, approximately 139°52'55"E and 35°0'27"N.

*Depository.*—Holotype, paratypes and figured specimens are deposited in Nomura Foraminiferal Laboratory, Shimane University (NFL).

*Description.*—Test small, cone-shaped, with a strongly convex ventral side and nearly flat dorsal side; sutures distinct, radiate, and depressed on ventral side; chambers four to five on ventral side, inflated; periphery lobulate in final whorl; aperture indistinct and covered with small spines, but an umbilical slit; wall rough and covered with very small pustules; pores present, but indistinct due to rough surface, optically indistinctly radial.

*Apertural structures.*—The final aperture is an umbilical slit and is covered with small spines (Figure 5.3). The foramen is elongate, oval and obliquely arranged to the plane of the whorl (Figure 5.2). The foraminal plate is formed at the base of the foramen and protruding from it (Figure 5.1, 5.4–5.6). The umbilical coverplate is continued from the foraminal plate and conceals the umbilical side of the foramen (Figure 5.4, 5.5).

*Geographic occurrence.*—This species is common in the Holocene bay-floor muds (tsunami deposits) in Tateyama, southern part of the Boso Peninsula. Ujiie (1963) recorded

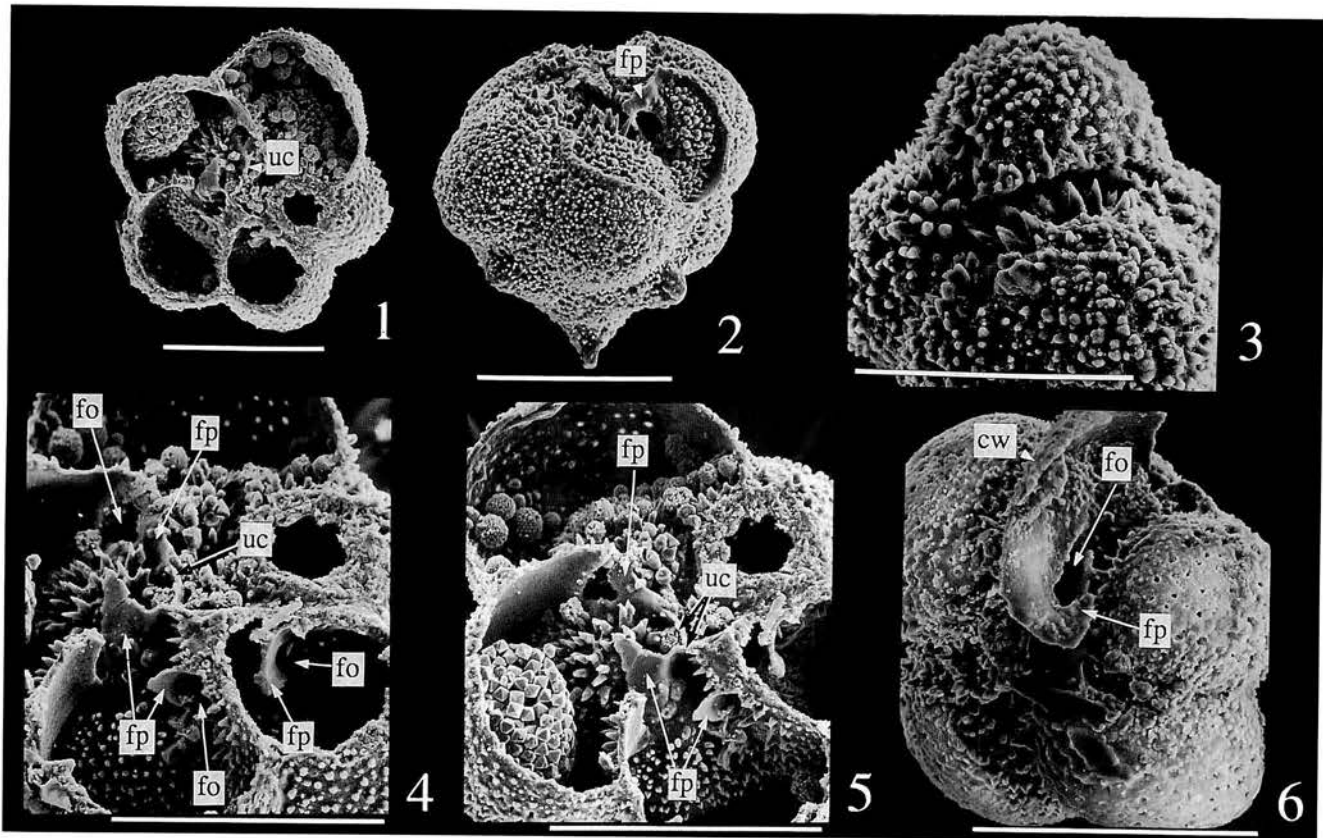
this species from Tokyo. Thus, the known geographic distribution is limited to the Kuwanto area.

*Stratigraphic occurrences.*—Known only from the Holocene.

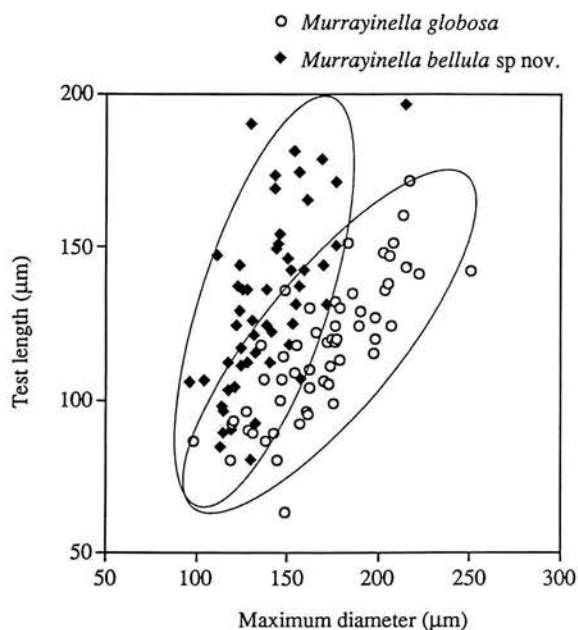
*Size and measurements.*—Maximum test width is 215  $\mu$ m and maximum test length is 196  $\mu$ m; minimum test width is 97  $\mu$ m and minimum test length is 80  $\mu$ m; averaged test width is 139  $\mu$ m and averaged test length is 129  $\mu$ m.

*Remarks.*—This new species is characterized by its high trochospiral coil and rough test surface. The foraminal structure is of the rotaliid type consisting of foraminal plate and umbilical coverplate. The foraminal plate is much inclined to the previous whorl and forms a prominent plate in the lower side of the foramen, whose structure is the same as the *Pararotalia*-type foramen described by Nomura and Takayanagi (2000).

The umbilical view of this species is similar to that of *M. globosa* in having four to five globular chambers in the final whorl and suggests a close phylogenetic relationship with the latter. Ujiie (1963) regarded this form as a variant of *M. globosa*. However, the size distribution (test length and maximum width) indicates the isolated position of this new species from *M. globosa*, particularly for mature individuals (Figure 6). A discriminant analysis also indicates statistically significant differences between the two species. Moreover, this species possesses a short spine in the initial chamber, but is usually devoid of spines in subsequent chambers. This spine is one of the characteristics of the new species.



**Figure 5.** Details of *Murrayinella bellula* sp. nov. Scale bar: 100  $\mu\text{m}$ . 1. Sectioned specimen with ventral chambers removed. uc = umbilical coverplate. 2. Oblique view of specimen showing the small spines and foraminiferal plate (fp) with oval opening of penultimate foramen. 3. Mature specimen showing the slit aperture with hispid crystals. 4. Closeup of no. 1 showing the protruded foraminiferal plates formed in the lower side of the foramen. fo = foramen, fp = foraminiferal plate, uc = umbilical coverplate. 5. Another view of no. 4. fp = foraminiferal plate, uc = umbilical coverplate. 6. Oblique view of penultimate foramen (fo) with foraminiferal plate (fp) and the remains of final chamber wall (cw).



*Murrayinella bellula* occurs in sand and sandy gravel beds in association with abundant *Ammonia japonica*, *Pseudononion japonicum* and miliolids, an assemblage apparently indicative of shallow marine conditions with some influence of brackish water. The assemblage containing this new species also includes planktic and some offshore species such as *Uvigerina proboscidea*, *Planocassidulina helena*, *Bulimina marginata*, and *Brizalina striata*. These offshore-cum-brackish assemblages may derive from the Pleistocene Kazusa Group, which contains a well preserved offshore and shallow-water foraminiferal assemblage. However, Fujiwara *et al.* (1997) proposed that such a mixed occurrence of bay to offshore foraminiferal assemblages in the bay-floor muds could be explained by a tsunami event based on the analyses of the sedimentary facies and sequence. This species possibly came from the shallower

← **Figure 6.** Size distribution of *Murrayinella globosa* (Millet) and *M. bellula* sp. nov. plotted against axes of maximum diameter and test length. Ellipsoids indicating a 95% confidence region for each species.

coastal environment.

*Etymology.*—The specific name is derived from Latin *bellulus*, pretty, referring to its small and delicate test.

### Conclusions

We described four Japanese species of *Murrayinella*, including one new species, from the Late Quaternary tsunami deposits in Tateyama, in the southern part of the Boso Peninsula. Detailed observations of the *Murrayinella* aperture indicate that the grooves radiating from the aperture that are so diagnostic of the glabratellids are never developed. Instead, *Murrayinella* has a foramen associated with a foraminal plate and umbilical coverplate, which is typical of rotaliids. We therefore suggest that the suprageneric placement of *Murrayinella* is not in the family Glabratellidae, but the Rotaliidae.

### Acknowledgements

We express our appreciation to Y. Matoba (Akita University) and S. Hasegawa (Hokkaido University) for sharing *Murrayinella takayanagii* specimens. We are deeply indebted to John E. Whittaker of the Natural History Museum, London, for the improvement of the manuscript and Stefan A. Revets of the University of Western Australia, for his critical review.

### References

- Chiji, M., and Lopez, S. M., 1968: Regional foraminiferal assemblages in Tanabe Bay, Kii Peninsula, central Japan. *Publication from the Seto Marine Biological Laboratory*, vol. 16, no. 2, p. 85–125, pls. 6–16.
- Ehrenberg, C. G., 1839: Über die Bildung der Kreidelfelsen und des Kreidemergels durch unsichtbare Organismen. *Physikalische Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin*, 1838: separate 1839, p. 59–147. (fide Loeblich and Tappan, 1987)
- Fariás, J. R., 1977: *Murrayinella*: taxa nuevo para la ciencia de foraminíferos del Reciente de Agua Somera. *Revista Española de Micropaleontología*, vol. 9, p. 343–345.
- Fujiwara, O., Masuda, F., Sakai, T., Fuse, K. and Saito, A., 1997: Tsunami deposits in Holocene bay-floor muds and the uplift history of the Boso and Miura Peninsula. *The Quaternary Research*, vol. 36, no. 2, p. 73–86.
- Haman, D. and Christensen, E. W., 1971: *Schackoinella* from Recent sediments of the northern Asiatic Shelf. *Journal of Foraminiferal Research*, vol. 1, p. 43–44.
- Hansen, H. J. and Reiss, Z., 1971: Electron microscopy of Rotaliacean wall structure. *Bulletin of the Geological Society of Denmark*, vol. 20, part 4, p. 329–346, pls. 1–21.
- Hatta, A. and Ujié, H., 1992: Benthic foraminifera from coral seas between Ishigaki and Iriomote Islands, southern Ryukyu Island Arc, northwestern Pacific. Part 2. Systematic description of Rotaliina. *Bulletin of the College of Science, University of the Ryukyus*, no. 54, p. 163–287, pls. 20–51.
- Heron-Allen, E. and Earland, A., 1915: The foraminifera of the Kerimba Archipelago (Portugese East Africa). Part II, *Transactions of the Zoological Society of London*, vol. 20, no. 17, p. 543–794.
- Hottinger, L., Halicz, E. and Reiss, Z., 1991: The foraminiferal genera *Pararotalia*, *Neorotalia*, and *Calcarina*: Taxonomic revision. *Journal of Paleontology*, vol. 65, no. 1, p. 18–33.
- Hottinger, L., Halicz, E. and Reiss, Z., 1993: Recent foraminifera from the Gulf of Aqaba, Red Sea. *Opera / Academia Scientiarum et Artium Slovenica, Class IV: Historia naturalis*, 33 and *Znanstvenoraziskovalni Tsentor SAZU. Paleontoloski Institut Ivana Rakovca*, 3, p. 1–179, pls. 1–230.
- Huang, T., 1980: Morphology and taxonomy of *Rotalia? minuta* Takayanagi, 1955. *Petroleum Geology of Taiwan*, no. 17, p. 53–57, pls. 1–4.
- Kamemaru, A., 1996: Changing composition of benthic foraminiferal thanatocoenoses in Matsushima Bay, north-east Japan, from 1960's to 1970's. *Fossils (Kaseki)*, no. 61, p. 1–20. (in Japanese with English abstract)
- Lankester, E. R., 1885: Protozoa, In, *Encyclopaedia Britannica*, vol. 19, 9th ed., p. 830–866. (fide Loeblich and Tappan, 1987)
- Loeblich, A. R., Jr. and Tappan, H., 1957: Morphology and taxonomy of the foraminiferal genus *Pararotalia* Le Calvez, 1949. *Smithsonian Miscellaneous Collections*, vol. 135, no. 2, p. 1–24., pls. 1–5.
- Loeblich, A. R., Jr. and Tappan, H., 1964: Sarcodina Chiefly "Thecamoebians" and Foraminiferida, vol. 1 and 2. In, Moore, R. C., ed., *Treatise on Invertebrate Paleontology, Protista 2 Part C*. The Geological Society of America and the University of Kansas Press, p. 1c–900c.
- Loeblich, A. R., Jr. and Tappan, H., 1987: *Foraminiferal Genera and their Classification*. Van Nostrand Reinhold Company, New York, 970 p., 847 pls.
- Loeblich, A. R., Jr. and Tappan, H., 1994: Foraminifera of the Sahul Shelf and Timor Sea. *Cushman Foundation for Foraminiferal Research, Special Publication* no. 31, p. 1–661, pls. 1–393.
- Matoba, Y., 1967: Younger Cenozoic foraminiferal assemblages from the Choshi District, Chiba Prefecture. *Science Reports of the Tohoku University, 2nd Series (Geology)*, vol. 38, no. 2, p. 221–263, pls. 25–30.
- Matoba, Y., 1970: Distribution of Recent shallow water foraminifera of Matsushima Bay, Miyagi Prefecture, Northeast Japan. *Science Reports of the Tohoku University, 2nd Series (Geology)*, vol. 42, p. 1–85.
- Matoba, Y. and Fukasawa, K., 1992: Depth distribution of Recent benthic foraminifera on the continental shelf and uppermost slope off southern Akita Prefecture, northeast Japan (the eastern Japan Sea). In, Ishizaki, K. and Saito, T., eds., *Centenary of Japanese Micropaleontology*, p. 207–226. Terra Scientific Publishing Company, Tokyo.
- McCulloch, I., 1977: *Qualitative Observations on Recent Foraminiferal Tests with Emphasis on the Eastern Pacific*. Pts. 1–3. pls. 49–248. Allan Hancock Foundation, University of Southern California, Los Angeles, 676 pp.,
- Millett, F. W., 1903: Report on the Recent foraminifera of the Malay Archipelago collected by Mr. A. Durrand, F. R. M. S. Part XIV. *Journal of Royal Microscopical Society*, p. 253–275.
- Nomura, R., 1983: An embedding technique for observation of internal microfossil structure by scanning electron microscopy. *Micropaleontology*, vol. 29, p. 1–5, pl. 1.
- Nomura, R., 1990: Late middle Miocene foraminifera from the Matsue Formation, Shimane Prefecture. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 158, p. 459–484.

- Nomura, R. and Takayanagi, Y., 2000: Foraminiferal structures of some Japanese species of the genera *Ammonia* and *Pararotalia*, family Rotaliidae (Foraminifera). *Paleontological Research*, vol. 4, no. 1, p. 16-30.
- Oki, K., 1989: Ecological analysis of benthonic foraminifera in Kagoshima Bay, south Kyushu, Japan. *South Pacific Study (Kagoshima University Research Center for the South Pacific)*, vol. 10, no. 1, p. 1-191, pls. 1-22.
- Quilty, P. G., 1975: A new species of *Schackoinella* from the Eocene of Western Australia with comments on the Glabratellidae. *Journal of Foraminiferal Research*, vol. 5, p. 326-333.
- Reiss, Z., 1963: Reclassification of perforate foraminifera. *Bulletin of the Geological Survey of Israel*, vol. 35, p. 1-111, pls. 1-8.
- Reiss, Z. and Merling, P., 1958: Structure of some Rotaliidae. *Bulletin of the Israel Geological Survey*, no. 21, 1-19, pls. 1-5.
- Revs, S. A., 1993: The foraminiferal toothplate, a review. *Journal of Micropalaeontology*, vol. 12, no. 2, p. 155-169, pls. 1-3.
- Takayanagi, Y., 1955: Recent foraminifera from Matsukawaura and its vicinity. *Contribution from the Institute of Geology and Paleontology, Tohoku University*, no. 45, p. 18-52, pls. 1-2.
- Takayanagi, Y. and Hasegawa, S., 1986: Pleistocene benthic foraminifera in Well Kashimaoki SK-1. In, Matoba, Y. and Kato, M. eds., *Studies on Cenozoic benthic foraminifera in Japan*. Akita University, Akita, p. 95-104, 2 pls.
- Ujiié, H., 1963: Foraminifera from the Yurakucho Formation (Holocene), Tokyo City. *Science Reports of the Tokyo Kyoiku Daigaku, Section C*, vol. 8, no. 79, p. 229-243.
- Weinhandl, R., 1958: *Schackoinella*, eine neue Foraminiferengattung. *Verhandlungen der Geologischen Bundesanstalt, Wien*, 1958, p. 141-142.
- Whittaker, J. E. and Hodgkinson, R. L., 1979: Foraminifera of the Togopi Formation, eastern Sabah, Malaysia. *Bulletin of the British Museum (Natural History), Geology Series*, vol. 31, no. 1, p. 1-120.
- Zheng, S., Cheng, T., Wang, X. and Fu, Z., 1978: The Quaternary foraminifera of the Dayuzhang irrigation area, Shandong Province, and a preliminary attempt at an interpretation of its depositional environment. *Studia Marina Sinica*, no. 13, p. 16-78, pls. 1-10.



# Upper premolar dentitions of *Deperetella birmanica* (Mammalia: Perissodactyla: Deperetellidae) from the Eocene Pondaung Formation, Myanmar

TAKEHISA TSUBAMOTO<sup>1</sup>, PATRICIA A. HOLROYD<sup>2</sup>, MASANARU TAKAI<sup>3</sup>, NOBUO SHIGEHARA<sup>3</sup>,  
AYE KO AUNG<sup>4</sup>, TIN THEIN<sup>5</sup>, AUNG NAING SOE<sup>6</sup> and SOE THURA TUN<sup>4</sup>

<sup>1</sup>Department of Geology and Mineralogy, Graduate School of Science, Kyoto University, Kyoto 606-8502, Japan (e-mail: tsuba@kueps.kyoto-u.ac.jp)

<sup>2</sup>Museum of Paleontology, University of California, Berkeley, CA 94720, USA

<sup>3</sup>Primate Research Institute, Kyoto University, Inuyama 484-8506, Japan

<sup>4</sup>Department of Geology, Dagon University, Yangon, Myanmar

<sup>5</sup>Department of Geology, University of Patheingyi, Patheingyi, Myanmar

<sup>6</sup>Department of Geology, University of Yangon, Yangon, Myanmar

Received 20 October 1999; Revised manuscript accepted 8 May 2000

**Abstract.** Discovery of upper premolar dentitions of *Deperetella birmanica* (Mammalia: Perissodactyla: Deperetellidae) from the Eocene Pondaung Formation, central Myanmar (= Burma) throws a new light on previously confused species- and genus-level systematics of *Deperetella* and its related genus *Diplolophodon*. Clarification of the relationship among the *Deperetella* species is particularly important for correlation of Eocene mammal faunas in Asia. The newly discovered material show the characteristics of the previously unknown upper premolar dentition of *D. birmanica*, demonstrating that *Deperetella similis* (the type species of the genus *Diplolophodon*) from China is a junior synonym of *Deperetella birmanica* and that *D. birmanica* is clearly distinguishable from all other species of *Deperetella*. The genus *Diplolophodon*, to which *D. birmanica* has often been allocated, is regarded conventionally as a junior synonym of *Deperetella* because this genus is not sufficiently distinct from *Deperetella* to warrant generic separation. The presence of *D. birmanica* and its comparable species in several Eocene deposits of Myanmar, China and Mongolia suggests that these deposits are roughly contemporaneous.

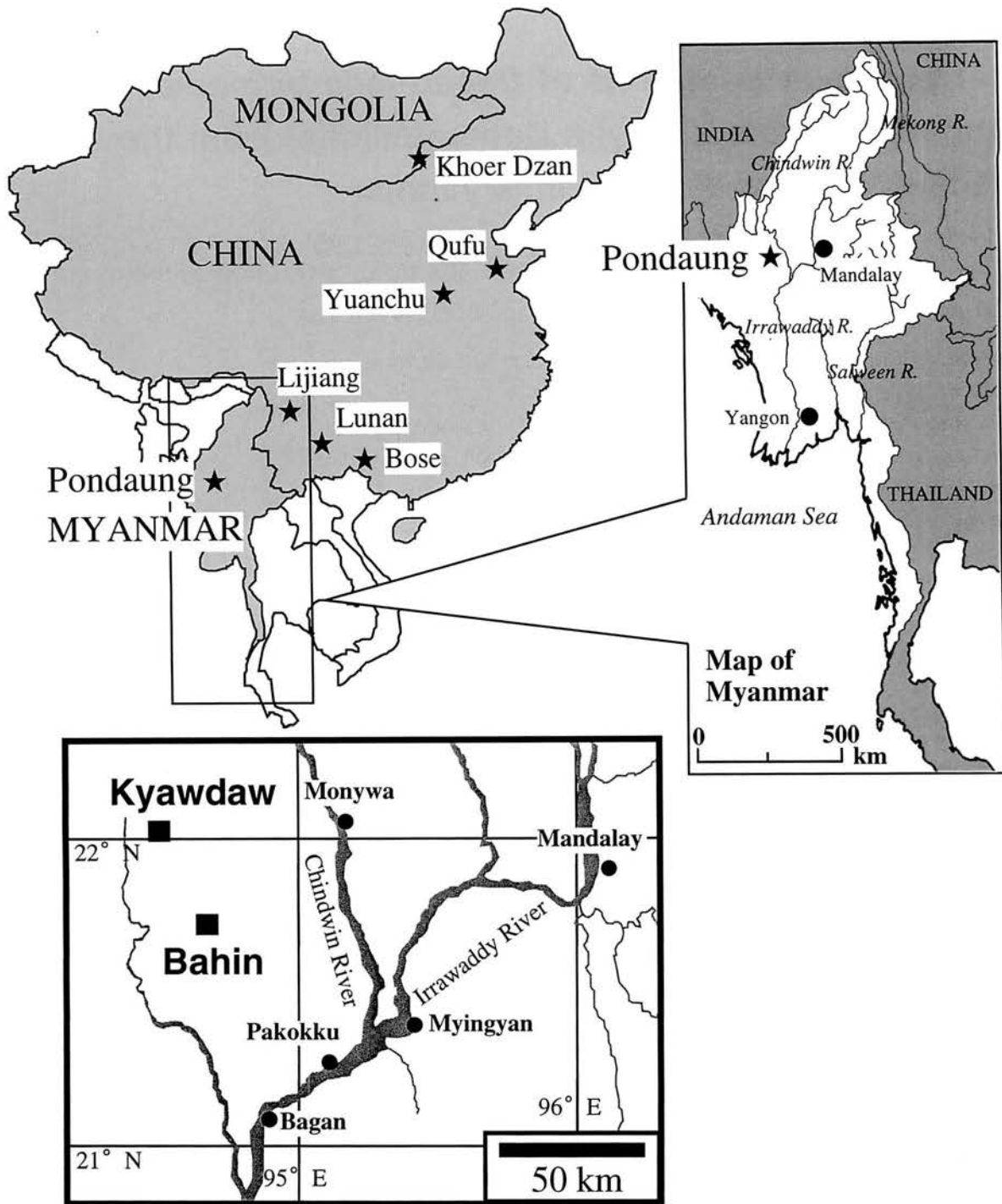
**Key words:** *Deperetella*, Deperetellidae, *Diplolophodon*, Eocene, Myanmar, Pondaung Formation

## Introduction

*Deperetella* is an Asian Eocene tapiroid perissodactyl genus and was proposed by Matthew and Granger (1925a) based on *Deperetella cristata* Matthew and Granger, 1925a as the type species. This genus and *Teleolophus* Matthew and Granger, 1925b, which together constitute the family Deperetellidae Radinsky, 1965, are among the most common elements of the middle to late Eocene mammal fauna in Asia and important for correlation of Eocene mammal faunas in this area. Zdansky (1930) proposed *Diplolophodon* and described *Diplolophodon similis* as the type species. Of several species in the genus *Deperetella*, *Deperetella birmanica* (Pilgrim, 1925) from the Pondaung Formation, Myanmar has been sometimes referred to the genus

*Diplolophodon* based on their small dental size and several of their dental characteristics (e.g. Ding *et al.*, 1977).

Previous classification of *Deperetella birmanica* and its related species has been much confused because these species were described on the basis of different parts of dentitions. *D. birmanica* was originally described by Pilgrim (1925) as *Chasmotherium? birmanicum* based on two mandibular rami of a single individual from the Eocene Pondaung Formation, central Myanmar. This was the only species of the Deperetellidae from the Pondaung Formation, and was questionably referred to the genus *Deperetella* by Colbert (1938). On the other hand, *Diplolophodon similis* was described based on an upper dentition from the Heti Formation in the Yuanchu Basin of the Shanxi and Henan Provinces, China (Zdansky, 1930). Young (1937) reported



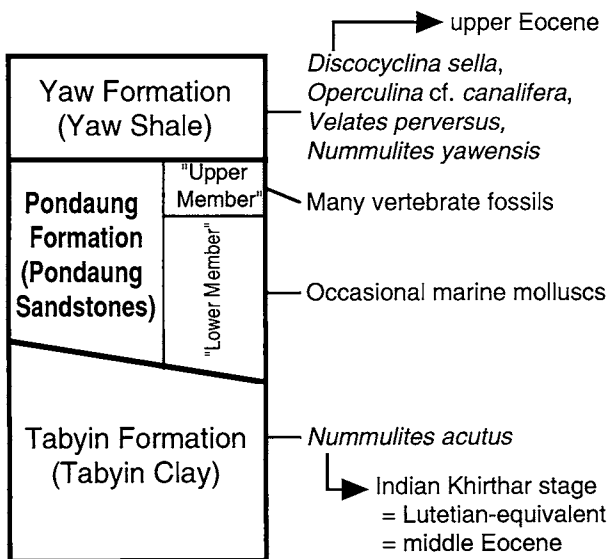
**Figure 1.** Maps showing distribution of several deperetellid-bearing deposits in Asia, names of place mentioned in this paper, and collecting sites of NMMP-KU 0005 and 0006. **Upper left map** showing locations of deposits that yielded *Deperetella birmanica* (Pilgrim, 1925) or *Deperetella* sp. cf. *D. birmanica* (black stars). Data from Colbert (1938), Li and Ting (1983), Russell and Zhai (1987), Shi (1989), Dashzeveg and Hooker (1997), and Huang (1999). **Upper right map** is topographic map of Pondaung area in central Myanmar, showing some major cities (black circles). **Lower map** showing collecting sites (black squares) of NMMP-KU 0005 and 0006 in the Pondaung Formation.

an additional upper dentition of *D. similis* from the same formation. Radinsky (1965) referred both *Chasmothereium? birmanicum* and *Diplolophodon similis* to the genus *Deperetella*, and established a new family Deperetellidae. He mentioned that *D. birmanica* was related to *D. similis*. Chow *et al.* (1974) first reported the lower and additional upper dentitions of *D. similis* from the Lumeiyi Formation in the Lunan Basin of Yunnan Province, China, distinguishing *D. similis* from *D. birmanica* on the basis of several morphological differences in the lower dentitions.

The upper dentition of *D. birmanica* was discovered in Pondaung Formation during paleontological field research by Myanmar researchers in 1997 (Pondaung Fossil Expedition Team, 1997). In this study, we describe two maxillary fragments with premolars of *D. birmanica*. This discovery provides new information on the relationship of *D. birmanica* and *D. similis*.

**Geological setting**

The Pondaung Formation (Pondaung Sandstones) distributed in the central part of Myanmar (Figure 1) can be divided into "Lower" and "Upper" members for convenience: the "Lower Member" is mainly composed of greenish sandstone and is about 1,500 m thick in the type section; and the "Upper Member" is dominated by variegated-colored mudstone, about 500 m thick in the type section, and yields many mammalian and other vertebrate fossils (13 genera belonging to three orders; see Pilgrim and Cotter, 1916; Colbert, 1938; Holroyd and Ciochon, 1995; Jaeger *et al.*, 1999), indicative of a freshwater lagoonal environment (Colbert, 1938; Aye Ko Aung, 1999; Aung Naing Soe, 1999; Figure 2). The present material was recovered from the middle part of the "Upper Member" of the Pondaung



**Figure 2.** Generalized stratigraphy of middle to late Eocene deposits in central Myanmar and representative fossil species. Compiled from Stamp (1922), Eames (1951), Bender (1983), Holroyd and Ciochon (1994), and Aye Ko Aung (1999).

Formation. The Pondaung Formation grades downward into the Tabyin Formation (Tabyin Clay), and the two formations partially interfinger (Figure 2; Stamp, 1922; Bender, 1983). The Pondaung Formation is overlain by the Yaw Formation (Yaw Shale) with a distinct lithological break (Figure 2; Stamp, 1922; Bender, 1983). The Pondaung Formation is considered to date from middle to late Eocene based on the microfossil dating of the Tabyin Formation and the Yaw Formation (Bender, 1983; Figure 2). On the basis of the mammal fauna, the "Upper Member" of the Pondaung Formation has been considered most likely to be Bartonian age (late middle Eocene) (e.g. Russell and Zhai, 1987; Holroyd and Ciochon, 1994, 1995).

**Systematic paleontology**

Family Deperetellidae Radinsky, 1965  
Genus *Deperetella* Matthew and Granger, 1925a

*Diplolophodon* Zdansky, 1930, p. 35.

*Type species.*—*Deperetella cristata* Matthew and Granger, 1925a.

*Other species included.*—*Deperetella birmanica* (Pilgrim, 1925); *Deperetella depereti* (Zdansky, 1930) Radinsky, 1965; *Deperetella dienensis* Chow *et al.*, 1974; *Deperetella khaitchinulensis* Reshetov, 1979; *Deperetella sichuanensis* (Xu *et al.*, 1979) Tong and Lei, 1983.

*Distribution and age.*—Asia. Middle to late Eocene.

*Diagnosis.*—"Deperetellids with premolar series longer than molars and posterior premolars molariform. P<sup>2-4</sup> protolophs and metalophs slightly convergent to parallel, and separated lingually. P<sub>1</sub> and especially P<sub>2</sub> lengthened into shearing blades; P<sub>3-4</sub> with complete hypolophids. Molars relatively shorter and wider than those of *Teleolophus*. Manus tridactyl" (Radinsky, 1965, p. 222).

*Remarks.*—The genus *Diplolophodon* was proposed by Zdansky (1930) based on an upper dentition of *Diplolophodon similis* from the Heti Formation in China. Radinsky (1965) regarded *Diplolophodon* as a junior synonym of *Deperetella*, although he recognized some characteristics that distinguished *Diplolophodon* from *Deperetella*. Ding *et al.* (1977), in contrast, viewed *Diplolophodon* as a distinct genus, in which *Diplolophodon major* Young, 1937 and *Diplolophodon birmanicum* were included. We follow Radinsky's (1965) view, because it is difficult to judge based on such a scanty fossil record whether the above-mentioned differences are intra- or intergeneric variations.

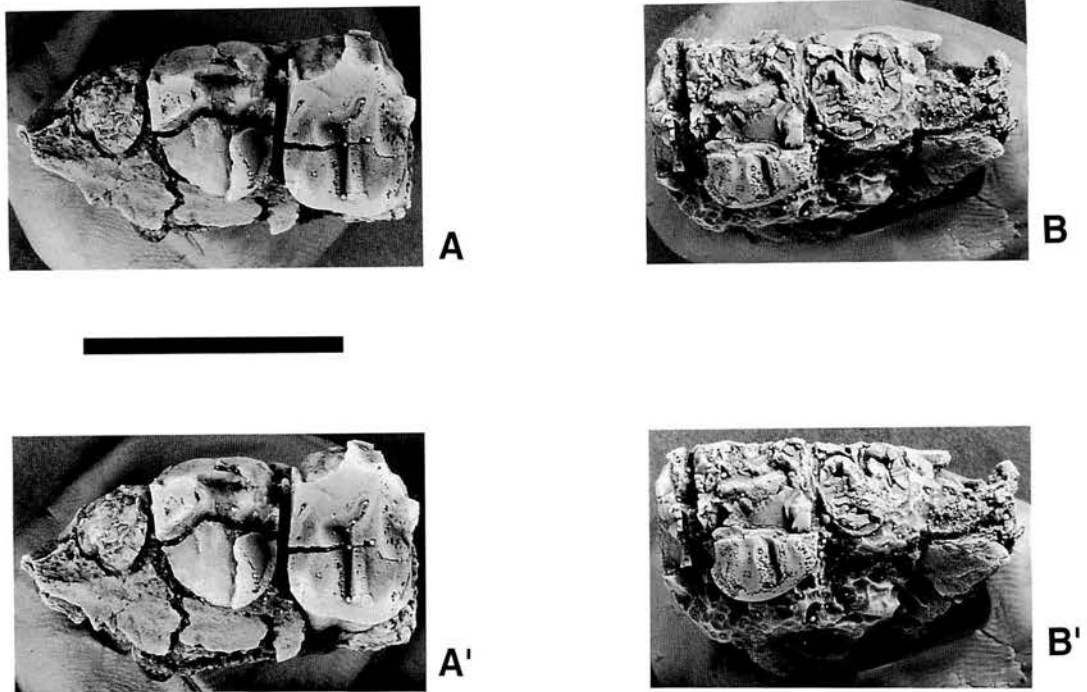
***Deperetella birmanica* (Pilgrim, 1925)**

Figures 3, 4C–D

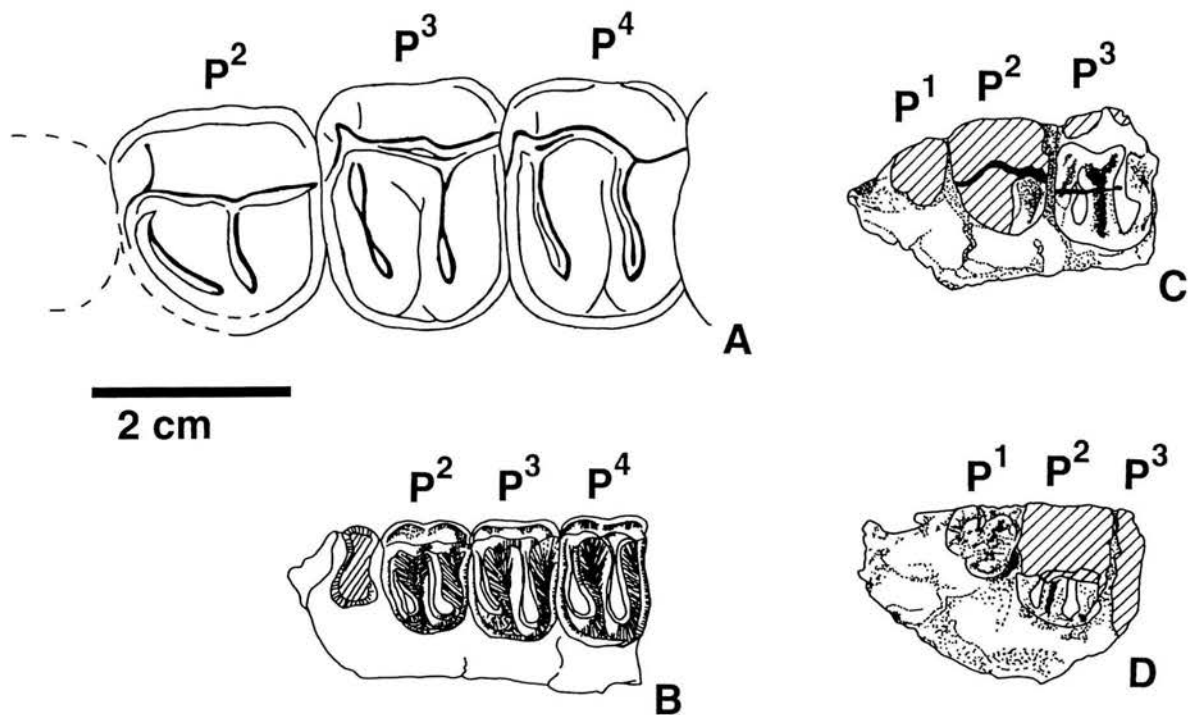
*Chasmothereium? birmanicum* Pilgrim, 1925, p. 25, pl. 2, fig. 9.  
*Diplolophodon similis* Zdansky, 1930, p. 35, pl. 1, fig. 35; Young, 1937, p. 419, fig. 5; Zong *et al.*, 1996, p. 83, pl. 32, fig. 4; Huang, 1999, p. 129.

*Diplolophodon major* Young, 1937, p. 421, fig. 6.

*Deperetella? birmanicum* (Pilgrim, 1925). Colbert, 1938, p. 348, fig. 40. [sic]



**Figure 3.** *Deperetella birmanica* (Pilgrim, 1925). **A, A'**. NMMP-KU 0005, stereo pair of fragmentary left upper jaw with broken  $P^{1-3}$  in occlusal view. **B, B'**. NMMP-KU 0006, stereo pair of fragmentary right upper jaw with broken  $P^{1-3}$  in occlusal view. Scale bar = 2 cm.



**Figure 4.** Upper premolar dentitions of *Deperetella cristata* Matthew and Granger, 1925a, "*Deperetella similis*" (Zdansky, 1930) and *Deperetella birmanica* (Pilgrim, 1925) in occlusal view. **A.** *D. cristata*, American Museum of Natural History (AMNH) No. 20290 with 20293,  $P^{2-4}$ , after Radinsky (1965, fig. 14). **B.** "*D. similis*" (Shanxi specimen),  $P^{2-4}$ , after Young (1937, fig. 5) and Radinsky (1965, p. 222, footnote 1). **C.** *D. birmanica*, NMMP-KU 0005,  $P^{1-3}$ . **D.** *D. birmanica*, NMMP-KU 0006,  $P^{1-3}$  (reversed). Scale bar = 2 cm.

*Deperetella similis* (Zdansky, 1930). Radinsky, 1965, p. 226; Chow *et al.*, 1974, p. 263, 272, pl. 1, fig. 3, 5–7.

*Deperetella birmanicum* (Pilgrim, 1925). Radinsky, 1965, p. 227. [sic]

*Diplophodon cf. similis* Zdansky. Ding *et al.*, 1977, p. 38, pl. 1, fig. 4.

*Diplophodon birmanicum* (Pilgrim, 1925). Ding *et al.*, 1977, p. 44, 45.

*Diplophodon qufuensis* Shi, 1989, p. 91, 99, pl. 1, fig. 7.

**Material.**—National Museum of the Union of Myanmar No. NMMP-KU 0005, a left maxillary fragment with roots of P<sup>1</sup>, very heavily damaged P<sup>2</sup> and relatively complete P<sup>3</sup>; NMMP-KU 0006, a right maxillary fragment with roots of P<sup>1</sup>, lingual one-third of P<sup>2</sup> and mesial margin of P<sup>3</sup>.

**Locality.**—NMMP-KU 0005 was from Bahin, Myaing Township, central Myanmar; NMMP-KU 0006 was from Kyawdaw, Palé Township, central Myanmar (Figure 1).

**Horizon and age.**—Middle part of the "Upper Member" of the Pondaung Formation (Figure 2), middle to late Eocene (most probably late middle Eocene).

**Revised diagnosis.**—A small-sized *Deperetella* with half the size of the type species *D. cristata*. The dental morphology is most derived in the genus. The molar cingulum is absent or weakly developed. P<sup>2</sup> is relatively shorter and wider than that of *D. cristata*. On P<sup>2-4</sup>, the protoloph and metaloph are nearly parallel to each other, nearly perpendicular to the tooth row, and separated lingually.

**Description.**—P<sup>1</sup> has two buccolingually widened roots. The distal root is larger than the mesial one. Judging from

the roots, P<sup>1</sup> is longer than wide, and as long as and much narrower than P<sup>2</sup>. No P<sup>1</sup> crown is preserved in the present material.

The crown of submolariform P<sup>2</sup> of each specimen is very poorly preserved. The protoloph and metaloph appear to be nearly parallel to each other and nearly perpendicular to the tooth row. These two are separated lingually by a groove. The distal cingula are present. There seems to be no lingual cingulum, although the tooth of each specimen is heavily worn. The existence of mesial and buccal cingula, and the characteristics of buccal structures in the tooth are uncertain.

P<sup>3</sup> is relatively better preserved in NMMP-KU 0005 than in NMMP-KU 0006, where only the broken anterior part of the tooth is preserved. P<sup>3</sup> is more molariform and transversely larger than P<sup>2</sup>. The protoloph and metaloph are nearly parallel to each other, nearly perpendicular to the tooth row, and separated lingually by a groove. The mesial and distal cingula are present. There seems to be no lingual cingulum, although the tooth of each specimen is heavily worn. The buccal structures are not preserved. The protoloph, paracone and metaloph form a slightly oblique, inverted U-shape, and the metacone is located as buccally as the paracone.

Dental measurements and comparison with other species are given in Table 1.

## Discussion

NMMP-KU 0005 and 0006 possess submolariform premo-

**Table 1.** Measurements (in mm) of upper premolars of NMMP-KU 0005 and 0006 and some other species of *Deperetella*. Henan and Shanxi specimens are those described by Zdansky (1930) and Young (1937), respectively. Data for "*Deperetella similis*", *D. cristata* and *D. dienensis* are from Ding *et al.* (1977), Radinsky (1965) and Chow *et al.* (1974), respectively. Abbreviations: L, anteroposterior length; W, buccolingually width; AMNH, American Museum of Natural History; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology in Beijing, China.

Specimen	P <sup>1</sup>	P <sup>1</sup>	P <sup>2</sup>	P <sup>2</sup>	P <sup>3</sup>	P <sup>3</sup>	P <sup>4</sup>	P <sup>4</sup>
	L	W	L	W	L	W	L	W
<i>Deperetella birmanica</i> (Pilgrim)								
NMMP-KU 0005	7.2 <sup>1</sup>	6.9 <sup>1</sup>	9.8	12.2	9.9	14.1		
NMMP-KU 0006	7.4 <sup>1</sup>	7.1 <sup>1</sup>	9.4 <sup>2</sup>					
" <i>Deperetella similis</i> (Zdansky, 1930)"								
Henan specimen (Zdansky, 1930)					9.0	11.5	9.4	13.4
Shanxi specimen (Young, 1937)			9.0	10.8	9.0	12.3	9.5	13.0
IVPP V29					10.0	12.8	10.7	14.3
<i>Deperetella cristata</i> Matthew & Granger								
AMNH 20290			19.9	21.8				
AMNH 20293					18.7	24.4		
<i>Deperetella dienensis</i> Chow <i>et al.</i>								
IVPP V31.1							13.0	20.0

<sup>1</sup> The measurements are based on the roots, not on the crown.

<sup>2</sup> Estimated value.



lars ( $P^{2-3}$ ) which are much wider than long and have a U-shaped crista that consists of a protoloph, paracone and metaloph. The protoloph and metaloph are arranged nearly parallel and lingually separated (Figures 3 and 4C–D). These characteristics of NMMP-KU 0005 and 0006 agree well with those of the upper premolar series of *Deperetella* diagnosed by Radinsky (1965). In *Deperetella*, the lower dentitions bear a diastema anterior to  $P_1$  (Matthew and Granger, 1925a, fig. 5; Radinsky, 1965, fig. 14). Based on this fact, the presence of a diastema anterior to  $P^1$  in its upper dentitions can be expected, though  $P^1$  and anterior part to  $P^1$  have not yet been discovered in any species of the genus. The presence of a diastema anterior to the most anterior tooth or tooth roots of both NMMP-KU 0005 and 0006 strongly suggests that these tooth or tooth roots are identifiable as  $P^1$ .

NMMP-KU 0005 and 0006 are referred to the nominal species *Deperetella similis* from China, based on the similar size and dental morphology of the protoloph and metaloph that are nearly parallel to each other and nearly perpendicular to the tooth row on  $P^2$  (Figure 4B–D and Table 1). *Deperetella cristata* has upper premolar dentitions much larger than the present specimens, and its protoloph and metaloph on  $P^2$  are not parallel (Figure 4A). *Deperetella khaitchinulensis* and *Deperetella depereti* are similar to *D. cristata* in dental morphology (Dashzeveg and Hooker, 1997). The dental size of *D. khaitchinulensis* and *D. depereti* is larger than that of the present specimens. *Deperetella dienensis* is also similar to *D. cristata* in terms of dental morphology (Chow *et al.*, 1974), and its dental size is intermediate between those of *D. cristata* and the present specimens. *Deperetella sichuanensis* is similar in dental size to the present specimens, but the dental morphology of the former is the most primitive among the genus (Tong and Lei, 1984).

The only deperetellid previously recorded from the Pondaung Formation is *D. birmanica*, which has so far been represented only by lower dentitions. Radinsky (1965) noticed that *D. birmanica* is more closely related to *D. similis* than to other species of *Deperetella* based on the followings; the dentitions in *D. birmanica* and *D. similis* are nearly the same size, and lack the molar cingula, which are present in *D. cristata* and *D. depereti*. He did not synonymize *D. similis* to *D. birmanica*, because *D. birmanica* was represented only by a lower dentition, while *D. similis* was represented only by upper dentitions at that time. Ding *et al.* (1977) and Dashzeveg and Hooker (1997) also recognized the dental similarity between *D. similis* and *D. birmanica*. Chow *et al.* (1974) clearly distinguished *D. similis* from *D. birmanica* because *D. similis* lacks the posterior spur on  $P_4$  and has broadly and posteriorly convex lophids on  $M_{1-3}$  in the lower dentition. However, these differences indicated by Chow *et al.* (1974) are not useful characteristics for separating the two species, since such are probably caused only by dental abrasion: the lower dentition in *D. birmanica* (Geological Survey of India (GSI) C348) is heavily worn, while the lower dentitions in *D. similis* (IVPP V713, V31) are almost intact (see Chow *et al.*, 1974, pl. 1, figs. 3, 5–7). *Diplophodon major* Young, 1937 from the Heti Formation in China was synonymized to *Deperetella similis* by

Radinsky (1965), and *Diplophodon qufuensis* Shi, 1989 from the Huangzhuang Formation in China was synonymized to *Diplophodon similis* (= *Deperetella similis*) by Zong *et al.* (1996) and Huang (1999). Zong *et al.* (1996) and Huang (1999) did not discuss the relationship between *D. birmanica* and *D. similis*, despite the fact that the two species are very similar. Our discovery of the upper premolar dentitions of this form strongly suggests that *D. similis* and *D. birmanica* are conspecific.

*Deperetella birmanica* is distinguished from the other species of *Deperetella* by its smaller dental size, by the absence or weak development of molar cingula, and by the high degree of molarization in its premolar series (the lingually separated and nearly parallel protoloph and metaloph are present both on  $P^{3-4}$  and  $P^2$ ) (Figure 4). This high degree of molarization in its premolar series suggests that *D. birmanica* is the most derived species among the genus *Deperetella*. Radinsky (1965), however, interpreted this fact as a result of a greater elongation of the anterior premolars in *Deperetella cristata* in contrast to the higher degree of molarization of the premolars in *Deperetella similis* (= *D. birmanica*).

The new synonymy enables us to correlate the Pondaung fauna with local middle to late Eocene mammal faunas in China, which yield *D. birmanica*, and Mongolia, which yield *D. sp. cf. D. birmanica*: Dongjun fauna of the Bose Basin, Guangxi Province, China; Lumeiyi fauna of the Lunan Basin and Xiangshan fauna of the Lijiang Basin, Yunnan Province, China; Heti fauna (from the Rencun Member) of the Yuanchu Basin, Shanxi and Henan Province, China; Huangzhuang fauna of Qufu County, Shandong Province, China; Ergilin Dzo fauna (from the Sevkhul Member) of Khoer Dzan, Mongolia (Figure 1; Li and Ting, 1983; Russell and Zhai, 1987; Shi, 1989; Zong *et al.*, 1996; Dashzeveg and Hooker, 1997; Huang, 1999). The occurrences of *D. birmanica* and *D. sp. cf. D. birmanica* suggest that these deposits are roughly contemporaneous to each other, and that these mammal faunas were mutually interchanged among them during middle to late Eocene.

#### Acknowledgments

We are grateful to the Myanmar Government for granting our study of the specimens. We thank Colonel Than Tun, Major Bo Bo and other personnel of the Office of Strategic Studies, Ministry of Defence, Union of Myanmar for guidance and help in the field, and curators of the National Museum of the Union of Myanmar for assisting of our work at that institution. The first author is indebted to Takeshi Setoguchi, Department of Geology and Mineralogy, Kyoto University for his kind help in studying at the laboratory of the department. This manuscript was improved by two anonymous referees and Tomoki Kase, one of the editors of this journal.

This research was supported by the Overseas Scientific Research Funds (No. 09041161 to N. Shigehara) and by the Grant-in-Aid for JSPS Fellows (No. 9714 to T. Tsubamoto), both from the Ministry of Education, Science, Sports and Culture of Japan (Monbusho).

## References

- Aung Naing Soe, 1999: Sedimentary facies of the upper part of the Pondaung Formation (in central Myanmar) bearing late Middle Eocene anthropoid primates. *In*, Pondaung Fossil Expedition Team *ed.*, *Proceedings of the Pondaung Fossil Expedition Team*, p. 152–178. Office of Strategic Studies, Ministry of Defence, Yangon.
- Aye Ko Aung, 1999: Revision on the stratigraphy and age of the primates-bearing Pondaung Formation. *In*, Pondaung Fossil Expedition Team *ed.*, *Proceedings of the Pondaung Fossil Expedition Team*, p. 131–151. Office of Strategic Studies, Ministry of Defence, Yangon.
- Bender, F., 1983: *Geology of Burma*, viii + 293 p. Gebrüder Borntraeger, Berlin.
- Chow, M., Chang, Y. and Ting, S., 1974: Some early Tertiary Perissodactyla, from Lunan basin, E. Yunnan. *Vertebrata Palasiatica*, vol. 12, no. 4, p. 262–273, pls. 1–3. (*in Chinese with English summary*)
- Colbert, E. H., 1938: Fossil mammals from Burma in the American Museum of Natural History. *Bulletin of the American Museum of Natural History*, vol. 74, p. 255–436.
- Dashzeveg, D. and Hooker, J. J., 1997: New ceratomorph perissodactyls (Mammalia) from the Middle Eocene of Mongolia: their implications for phylogeny and dating. *Zoological Journal of the Linnean Society of London*, vol. 120, p. 105–138.
- Ding, S., Zheng, J., Zhang, Y. and Tong, Y., 1977: The age and characteristic of the Liuniu and the Dongjun Faunas, Bose basin of Guangxi. *Vertebrata Palasiatica*, vol. 15, no. 1, p. 35–45, pls. 1–2. (*in Chinese with English summary*)
- Eames, F. E., 1951: A contribution to the study of the Eocene in western Pakistan and western India: D. Discussion of the faunas of certain standard sections, and their bearing on the classification and correlation of the Eocene in western Pakistan and western India. *Quarterly Journal of the Geological Society of London*, vol. 107, p. 173–200.
- Holroyd, P. A. and Ciochon, R. L., 1994: Relative ages of Eocene primate-bearing deposits of Asia. *In*, Fleagle, J. G. and Kay, R. F. *eds.*, *Anthropoid Origins*, p. 123–141. Plenum Press, New York.
- Holroyd, P. A. and Ciochon, R. L., 1995: A new artiodactyl (Mammalia) from the Eocene Pondaung Sandstones, Burma. *Annals of Carnegie Museum*, vol. 64, no. 3, p. 177–183.
- Huang, X., 1999: Middle Eocene mammals of Lijiang Basin, Yunnan. *In*, Wang, Y. and Deng, T. *eds.*, *Proceedings of the Seventh Annual Meeting of the Chinese Society of Vertebrate Paleontology*, p. 125–138. China Ocean Press, Beijing.
- Jaeger, J.-J., Tin Thein, Benammi, M., Chaimanee, Y., Aung Naing Soe, Thit Lwin, Than Tun, San Wai and Ducrocq, S., 1999: A new primate from the middle Eocene of Myanmar and the Asian early origin of anthropoids. *Science*, vol. 286, p. 528–530.
- Li, C. and Ting, S., 1983: The Paleogene mammals of China. *Bulletin of Carnegie Museum of Natural History*, no. 21, p. 1–98.
- Matthew, W. D. and Granger, W., 1925a: New mammals from the Shara Murun Eocene of Mongolia. *American Museum Novitates*, no. 196, p. 1–11.
- Matthew, W. D. and Granger, W., 1925b: The smaller perissodactyls of the Irdin Manha Formation, Eocene of Mongolia. *American Museum Novitates*, no. 199, p. 1–9.
- Pilgrim, G. E., 1925: The Perissodactyla of the Eocene of Burma. *Palaeontologica Indica, New Series*, vol. 8, memoir no. 3, p. 1–28, pls. 1–2.
- Pilgrim, G. E. and Cotter, G. de P., 1916: Some newly discovered Eocene mammals from Burma. *Records of the Geological Survey of India*, vol. 47, p. 42–77, pls. 1–6.
- Pondaung Fossil Expedition Team, 1997: *Report on Work Achieved by the Pondaung Fossil Expedition Team*. Office of Strategic Studies, Ministry of Defence, Yangon. (*in Burmese, partly in English*)
- Radinsky, L. B., 1965: Early Tertiary Tapiroidea of Asia. *Bulletin of the American Museum of Natural History*, vol. 129, p. 181–264.
- Reshetov, V. Yu., 1979: Early Tertiary Tapiroidea of Mongolia and the USSR. *Trudy Sovmestnaya Sovetskogo-Mongolskaya Paleontologicheskaya Ekspeditsiya*, vol. 11, p. 1–141. (*in Russian*)
- Russell, D. E. and Zhai, R., 1987: The Paleogene of Asia: mammals and stratigraphy. *Mémoires du Muséum National d'histoire Naturelle, Ser. C, Sciences de la Terre*, vol. 52, p. 1–488.
- Shi, R., 1989: Late Eocene mammalian fauna of Huangzhuang, Qufu, Shandong. *Vertebrata Palasiatica*, vol. 27, no. 2, p. 87–102, pls. 1–3. (*in Chinese with English summary*)
- Stamp, L. D., 1922: An outline of the Tertiary geology of Burma. *The Geological Magazine*, vol. 59, no. 11, p. 481–501.
- Tong, Y. and Lei, Y., 1984: Fossil tapiroids from the upper Eocene of Xichuan, Henan. *Vertebrata Palasiatica*, vol. 22, no. 4, p. 269–280, pls. 1–2. (*in Chinese with English summary*)
- Xu, Y., Yan, D., Zhou, S., Han, S. and Zhong, Y., 1979: Subdivision of the Red Beds of Li-Guan-Qiao Basin with description of fossil mammals therefrom. *In*, Chinese Academy of Sciences, Institute of Vertebrate Paleontology and Paleoanthropology, and Nanking Institute of Geology and Paleontology *eds.*, *Mesozoic and Cenozoic Red Beds of South China*, p. 416–432, pl. 1. Science Press, Beijing. (*in Chinese*)
- Young, C. C., 1937: An early Tertiary vertebrate Fauna from Yuanchü. *Bulletin of the Geological Society of China*, vol. 17, nos. 3 and 4, p. 413–438.
- Zdansky, O., 1930: Die alttertiären Säugetiere Chinas nebst stratigraphischen Bemerkungen. *Palaeontologia Sinica, Ser. C*, vol. 6, fasc. 2, p. 1–87, pls. 1–5.
- Zong, G., Chen, W., Huang, X. and Xu, Q., 1996: *Cenozoic Mammals and Environment of Hengduan Mountains Region*, 279 p. China Ocean Press, Beijing. (*in Chinese with English abstract*)

# Late Oligocene larger foraminifera from the Komahashi-Daini Seamount, Kyushu-Palau Ridge and their tectonic significance

MIA MOHAMMAD MOHIUDDIN<sup>1</sup>, YUJIRO OGAWA<sup>2</sup> and KUNITERU MATSUMARU<sup>3</sup>

<sup>1</sup>Marine Geology Department, Geological Survey of Japan, Tsukuba 305–8567 Japan; on study leave from Department of Geology and Mining, the University of Rajshahi, Rajshahi 6205 Bangladesh (e-mail: mohi@gsj.go.jp)

<sup>2</sup>Institute of Geoscience, University of Tsukuba, Tsukuba 305–8571 Japan

<sup>3</sup>Department of Geology, Faculty of Education, Saitama University Urawa, 338–8570 Japan

Received 26 August, 1999; Revised manuscript accepted 1 June 2000

**Abstract.** A larger foraminiferal assemblage consisting of *Miogypsinella ubaghsi* (Tan), *Spiroclypeus margaritatus* (Schlumberger) and other species is described from limestone blocks dredged at two sites on the Komahashi-Daini Seamount of the Kyushu-Palau Ridge. The fauna dates the limestone samples as Late Oligocene and is correlatable with the younger part of the Minamizaki Limestone on the Ogasawara (Bonin) Islands. These shallow-water benthic foraminifera give evidence for the shallow-water attitude of the Kyushu-Palau Ridge during the Oligocene, which has been rifted, submerged, and finally subsided to the present water depth.

**Key words:** Komahashi-Daini Seamount, Kyushu-Palau Ridge, larger foraminifera, Late Oligocene

## Introduction

The Kyushu-Palau Ridge is an about 3,000 km long submarine ridge with a general N-S trend which divides the sea floor into the Nankai Trough on the east and the Ryukyu Trench on the west (Figure 1). On the Kyushu-Palau Ridge, a series of isolated seamounts were discovered during the 1970's (Shiki *et al.*, 1974; Shiki *et al.*, 1975). The Komahashi-Daini Seamount is located near the northern margin of this ridge. During the R/V Tansei-Marukou KT94-10 Cruise, which operated July 5-12, 1994, we dredged limestone samples along with many intrusive, hypabyssal and volcanic rocks such as tonalite, andesite, tuff and pumice from the Komahashi-Daini Seamount. In this study, we describe the larger foraminifera in the limestone samples and discuss the age assignment based on the foraminiferal data and their tectonic significance.

## Material

During the KT94-10 cruise, samples were dredged at two sites of the Komahashi-Daini Seamount. DG-04 site is located on the northeastern slope of the north peak, and DG-05 site on the eastern slope of the major peak (Table 1 and Figure 2). Among the rock samples, one limestone sample (DG-04-01) from the northern site and two (DG-05-01 and DG-05-02) from the southern site were studied.

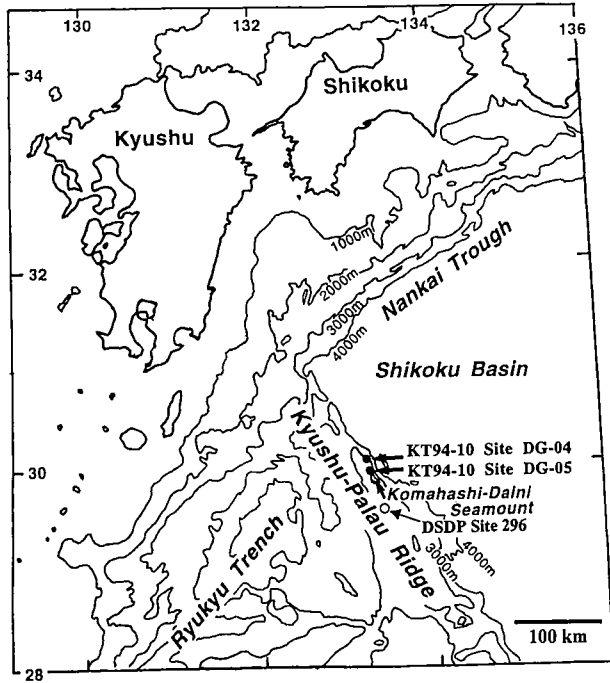
The limestone samples are indurated packstone or

packstone to wackstone. All these samples are moderately hard to compact, and white to creamy white in color. They contain abundant larger and smaller benthic foraminifera, together with coral biolithite, calcareous algae and mollusks.

All of the described larger foraminiferal specimens are kept in the Geological Survey of Japan, under catalogue numbers GSJF 15418 to GSJF 15427.

## Results

Thirteen foraminiferal species were identified (Figures 3–8). Dominant species are *Spiroclypeus margaritatus*, *Nephrolepidina praejaponica*, *N. angulosa*, *N. marginata*, *Eulepidina ephippiooides*, *Heterostegina borneensis*, *Miogypsinella ubaghsi* and *Austrotrillina howchini*. No distinct difference in species composition was found among the three samples. This assemblage was assigned an age of Te 1–4 (Tertiary e 1–4) according to the system of Far East Letter Stages, equivalent to Late Oligocene (Hashimoto *et al.*, 1980; Hashimoto and Matsumaru, 1984; Mohiuddin, 1997). Coexistence of *M. ubaghsi* and *S. margaritatus* along with *H. borneensis*, *Eulepidina*, *Miogypsinoides* and *Spiroclypeus* is indicative of a Late Oligocene age as seen in the Melinau Limestone of Sarawak, North Borneo (Adams, 1965). Moreover, Adams and Belford (1974) suggested that the association of *S. margaritatus*, *H. borneensis* and *E. ephippiooides* is indicative of the Tertiary lower e, which is believed to be equivalent to the Upper Oligocene (Chattian) of Europe.

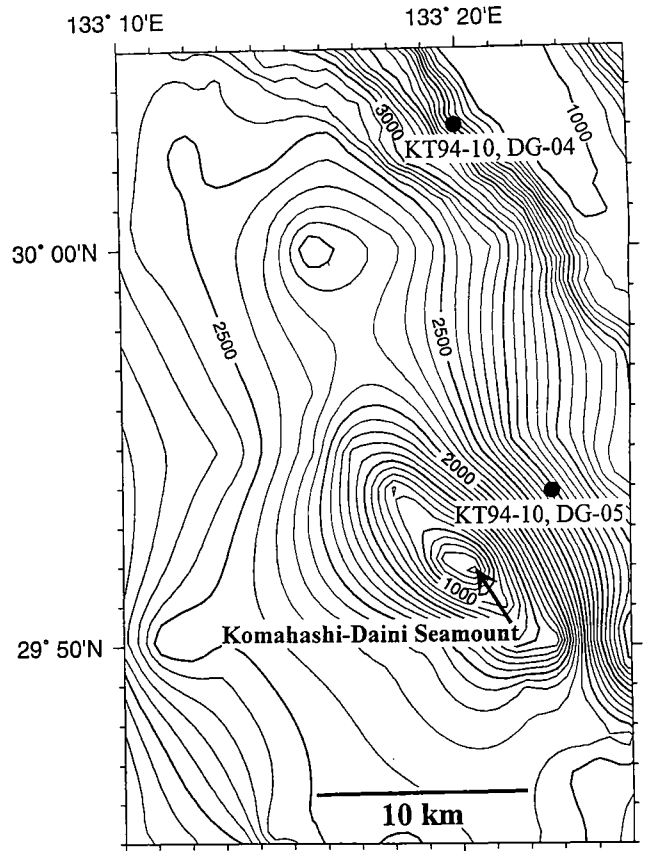


**Figure 1.** Index map of dredged samples used for this study.

The *M. ubaghsi* -*S. margaritatus* assemblage can be correlated with the fauna of the upper member of the Minamizaki Limestone in Chichi-Jima and Minami-Jima, Bonin Islands. *Miogypsinella boninensis* (Matsumaru, 1996) described from the Bonin Islands is thought to be a junior synonym of *Miogypsinella ubaghsi* (Tan, 1936). This assemblage may be correlated with the assemblage of Te Stage limestones from 1210 to 1599 feet depth in Enewetok Atoll Drill Hole and with those from 1597.5 to 1671 feet depth in Bikini Atoll Drill Hole. The *M. ubaghsi* -*S. margaritatus* assemblage is also correlated with the fauna of the Bubton Limestone, Mindoro, Philippines (Hashimoto and Matsumaru, 1984). The Te Stage is regarded as corresponding to Zone P. 21 of Blow's (1969, 1979) planktonic foraminiferal zonation.

**Discussion**

Konda (1975) reported larger foraminifera in limestone samples dredged from the eastern slope near a peak of the



**Figure 2.** Location of dredge sites KT94-10 on Kyushu-Palau Ridge. Adopted from Ohara *et al.* (1999). Contours in meters.

Komashashi-Daini Seamount, Kyushu-Palau Ridge and assigned to the samples an age younger than Middle Miocene based on the foraminiferal assemblage. The northern half of the Kyushu-Palau Ridge was dated around 48 Ma by Ar-Ar dating of volcanoclastic and granitic rocks (Ozima *et al.*, 1977). A similar age was also obtained from K-Ar age of augite-orthopyroxene andesite rocks in Haha-Jima of the Bonin Islands (Kaneoka *et al.*, 1970). These age data suggest that the Izu-Ogasawara arc was juxtaposed with the northern Kyushu-Palau Ridge before the initiation of back-arc spreading in the Shikoku Basin. Moreover, larger foraminiferal age data in this study gave a Late Oligocene age for the limestone blocks of the Komahashi-Daini

**Table 1.** Location of dredged samples on the Kyushu-Palau Ridge.

Sample No.	Location	Latitude	Hit bottom Longitude	Water depth (m)	Latitude	Off bottom Longitude	Water depth (m)	Dredged materials
DG-04-01	KPR, Unnamed Seamount	30°02.983'N	133°19.880'E	3800	30°02.074'E	133°18.465'E	2632	tuff, pumice and limestone
DG-05-01 and DG-05-02	KPR, Komahashi-Daini Seamount	29°53.983'N	133°22.656'E	3334	29°53.160'N	133°20.992'E	2500	tonalite, andesite and limestone

Sample No.			Larger foraminiferal species
DG-04-01	DG-05-01	DG-05-02	
X	X	X	<i>Spiroclypeus margaritatus</i> (Schlumberger)
X	X		<i>Heterostegina borneensis</i> van der Vlerk
X	X		<i>Nephrolepidina praejaponica</i> Matsumaru
X	X		<i>Nephrolepidina angulosa</i> (Provale)
X	X		<i>Nephrolepidina marginata</i> (Michelotti)
X		X	<i>Miogypsinella ubaghsi</i> (Tan)
X		X	<i>Austrotrillina howchini</i> (Schlumberger)
X			<i>Eulepidina dilatata</i> (Michelotti)
	X	X	<i>Eulepidina ephippioides</i> (Jones and Chapman)
	X		<i>Amphistegina radiata</i> (Fichtel and Moll)
X			<i>Eulepidina</i> sp.
X			<i>Ammonia</i> sp.
X		X	<i>Heterostegina</i> sp.

Figure 3. Occurrence of larger foraminiferal species in dredged samples.

Seamount, which is consistent with the oldest age of the basement rocks in the Shikoku Basin (Watts and Weissel, 1975).

The association of Late Oligocene coral-bearing limestone with benthic foraminifera of shallow-sea nature and igneous rocks recognized at the Komahashi-Daini Seamount has also been reported at DSDP Site 296, south of the seamount, at a depth of 2,920m (Figure 1). This evidence suggests that volcanogenic-calcareous sedimentary sequences of Oligocene age are rather widely distributed in the northern part of the Kyushu-Palau Ridge, including the Komahashi-Daini Seamount.

In view of the paleoenvironmental nature of the larger foraminiferal assemblage consisting of *Miogypsinella*, *Spiroclypeus*, *Austrotrillina*, *Eulepidina*, *Amphistegina* and *Heterostegina*, an environment of the shallow open ocean at the shelf edge was suggested for the deposition of limestone beds of the Komahashi-Daini Seamount, as in the case of the limestone beds of the Minamizaki Limestone, Chichi-Jima (Matsumaru, 1996). Moreover, the presence of several species of *Lepidocyclina* (*Eulepidina*) associated with pyroclastic sediments in cores 56 and 57 at DSDP Site 296 indicates a neritic environment (Ujiié, 1975).

In contrast to the cases of the Komahashi-Daini Seamount and of Chichi-Jima, where the Late Oligocene sediments are exposed near the seamount surface, a drill hole at DSDP Site 296 displays a considerably continuous sequence from in situ volcanic rocks through Late Oligocene shallow-water sediments. It includes larger foraminifera and pelagic calcareous ooze, suggesting a subsidence of the Kyushu-Palau Ridge (Ujiié, 1975).

It is noteworthy that the northern parts of the Kyushu-Palau Ridge and the Izu-Bonin Arc resemble each other in the timing of the cessation of volcanic activity and in the final

paleoenvironment reaching a shallow-water depth. Since Uyeda and Ben-Avraham (1972) many authors have supposed that both ridges formed a single arc at the initial stage and then were divided into two arcs owing to the spreading of the Shikoku and Parece Vella Basins. This study offers a new line of supporting evidence for this hypothesis.

### Conclusion

The oldest age of the Kyushu-Palau Ridge is Late Oligocene based on larger foraminifera. The benthic foraminiferal assemblage in the limestone samples is correlated with that from the upper part of the Minamizaki Limestone exposed on the Ogasawara (Bonin) Islands of the Izu-Bonin Arc. This fact suggests that the Kyushu-Palau Ridge and the Izu-Bonin Arc initially formed a single arc. Afterward the arc may have split by a spreading of the Shikoku and Parece Vella Basins.

### Systematic descriptions

Family Lepidocyclinidae Scheffen, 1932

Genus *Nephrolepidina* Douvillé, 1911

*Nephrolepidina praejaponica* Matsumaru, 1989

Figures 6.1–6.4, 6.6, 6.7, 6.9, 6.10, 7.1, 7.6–7.9

*Nephrolepidina praejaponica* Matsumaru. In Matsumaru and Kimura, 1989, p. 265, 267, figs. 6.1–6.13; Matsumaru *et al.*, 1993, p. 8, figs. 2.4, 3.6–3.8.

*Material*.—Thirteen specimens (GSJF 15420-1–13) including one megalospheric specimen in a vertical section (GSJF 15420-1; Figure 6.1).

*Description*.—Tests of megalospheric specimens, GSJF

15420–1–8, are small lenticular with diameter of 3.5 to 5.5 mm and thickness of 1.5 to 2 mm. Conical pillars are from 80 µm to 100 µm in diameter, and distributed in the central part of the test surface. The embryonic chambers are of nephrolepidine type. The protoconch is subcircular with a diameter of 240 µm. The second large chamber, the deuteroconch embraces the protoconch and has an internal diameter of 320 µm. The ratio of the inner diameter of the deuteroconch (II) to that of the protoconch (I) is 1.3. The outer wall of the embryonic chambers is more than 25 mm thick. The equatorial chambers of arcuate form near the perie embryonic chambers change from ogival to short hexagonal near the periphery. The height of the equatorial layer near the center is about 200 µm and at the periphery less than 100 µm. The lateral chambers are rectangular in shape and are arranged in a tier of 10 to 12 layers over the center. Chambers over the central area of the test have a length of more than 160 to 200 µm, a height of 45 to 60 µm, and floors and roofs 20 to 25 µm thick.

**Remarks.**—The present specimen has the same features of small embryonic chambers and short hexagonal equatorial chambers in as *N. praejaponica* Matsumaru from the Lower Member of the Misaki Formation, Tosa Shimizu City, Kochi Prefecture, Shikoku (Matsumaru and Kimura, 1989) and the Early Miocene (Aquitania) Shimizu Formation (Matsumaru *et al.*, 1993), Shikoku Island. *Nephrolepidina praejaponica* is similar to *N. japonica* (Yabe) in overall morphology, but differs from the latter in having a small test and small embryonic chambers, primitive form of the embryonic chambers, short hexagonal equatorial chambers, rectangular lateral chambers and wavy floors and roofs.

*Nephrolepidina* species have been reported from Zones N. 8 and N. 9 of Blow (1969) in the Japanese mainland (Yabe, 1906; Yabe and Hanzawa, 1922; Hanzawa, 1931a, b; 1964; Matsumaru, 1967, 1971a) except the Izu Peninsula and Shikoku Island (Matsumaru, 1971a; Matsumaru and Kimura, 1989).

#### *Nephrolepidina angulosa* (Provale, 1909)

Figure 6.5

*Lepidocyclus tournoueri* Lemoine and R. Douvillé var. *angulosa* Provale, 1909, p. 28, pl. 3, figs. 13–15.

*Lepidocyclus angulosa* Provale. Rutten, 1912, p. 21, figs. 1–4.

*Lepidocyclus (Nephrolepidina) angulosa* Provale. Hanzawa, 1957, p. 76, 77, pl. 20, figs. 1–9, pl. 21, fig. 5, pl. 22, figs. 4, 14.

*Nephrolepidina angulosa* (Provale). Matsumaru, 1992, p. 259, 260, figs. 1.6, 1.7.

**Material.**—One megalospheric specimen in a vertical section, GSJF 15421.

**Remarks.**—This species is characterized by having a flat-

topped central boss with stout pillars; equatorial chambers in the mature stage are hexagonal in shape; the roof and floor of the lateral chambers are straight; and the chamber cavities are narrow and long. External appearance of the shell is similar to that of *Nephrolepidina praejaponica* Matsumaru, but it differs from the latter in possessing several conical pillars formed on the flat top of the central boss.

Family Nummulitidae de Blainville, 1827

Genus *Spiroclypeus* H. Douvillé, 1905

#### *Spiroclypeus margaritatus* (Schlumberger, 1902)

Figures 4.1, 4.2, 4.4, 4.5, 4.7, 4.9, 4.10, 5.1–5.13, 8.1

*Heterostegina margaritata* Schlumberger, 1902, p. 152, 153, pl. 7, fig. 4.

*Spiroclypeus orbitoideus* H. Douvillé, 1905, p. 460–462, pl. 14, figs. 1–6; Tan, 1937, p. 183, 184, pl. 1, figs. 2–4, pl. 2, figs. 1–13, pl. 3, figs. 1–7; Cole, 1957a, p. 332–333, pl. 95, figs. 6–12; Matsumaru, 1976a, p. 200, pl. 1, figs. 1, 8, 10; Hashimoto, Matsumaru and Sugaya, 1981, p. 59, pl. 13, fig. 8.

*Spiroclypeus leupoldi* van der Vlerk, 1925, p. 14, 15, pl. 2, fig. 16; pl. 5, figs. 41, 48; Yabe and Hanzawa, 1929, p. 188, pl. 24, fig. 9; Cole, 1954, p. 577, 578, pl. 208, figs. 1–19; Hanzawa, 1957, p. 45, 46, pl. 5, figs. 7–13; Matsumaru, 1974, p. 108, pl. 15, figs. 1–4, 10, 13–15, 21–23, 28; Matsumaru, 1976a, p. 199, 200, pl. 1, figs. 4–7, 14, 15, 21, 23, 4.

*Spiroclypeus yabei* van der Vlerk, 1925, p. 16, pl. 2, fig. 19, pl. 5, figs. 40, 50; Tan, 1937, p. 183, pl. 1, figs. 5, 6, pl. 3, figs. 10, 11, pl. 4, figs. 8–10, text-fig. 1; Cole, 1954, p. 580–581, pl. 207, figs. 1–14, pl. 208, figs. 20–26; Cole, 1957b, p. 764, pl. 239, figs. 9–10.

*Spiroclypeus tidoenganensis* van der Vlerk, 1925, p. 16, 17, pl. 1, fig. 12, pl. 5, figs. 42, 47; Tan, 1937, p. 183, pl. 1, fig. 10, pl. 2, figs. 4–5, pl. 3, fig. 12, pl. 4, figs. 2–5, 19–21; Hanzawa, 1957, p. 46, 47, pl. 3, figs. 1–6, pl. 4, figs. 1, 8–10; Cole, 1957a, p. 332, pl. 95, figs. 13–15; Matsumaru, 1976a, p. 200, pl. 1, figs. 3, 9, 12, 18–20, 22, pl. 6, fig. 15; Hashimoto, Matsumaru and Sugaya, 1981, p. 60, 61, pl. 13, figs. 9, 12.

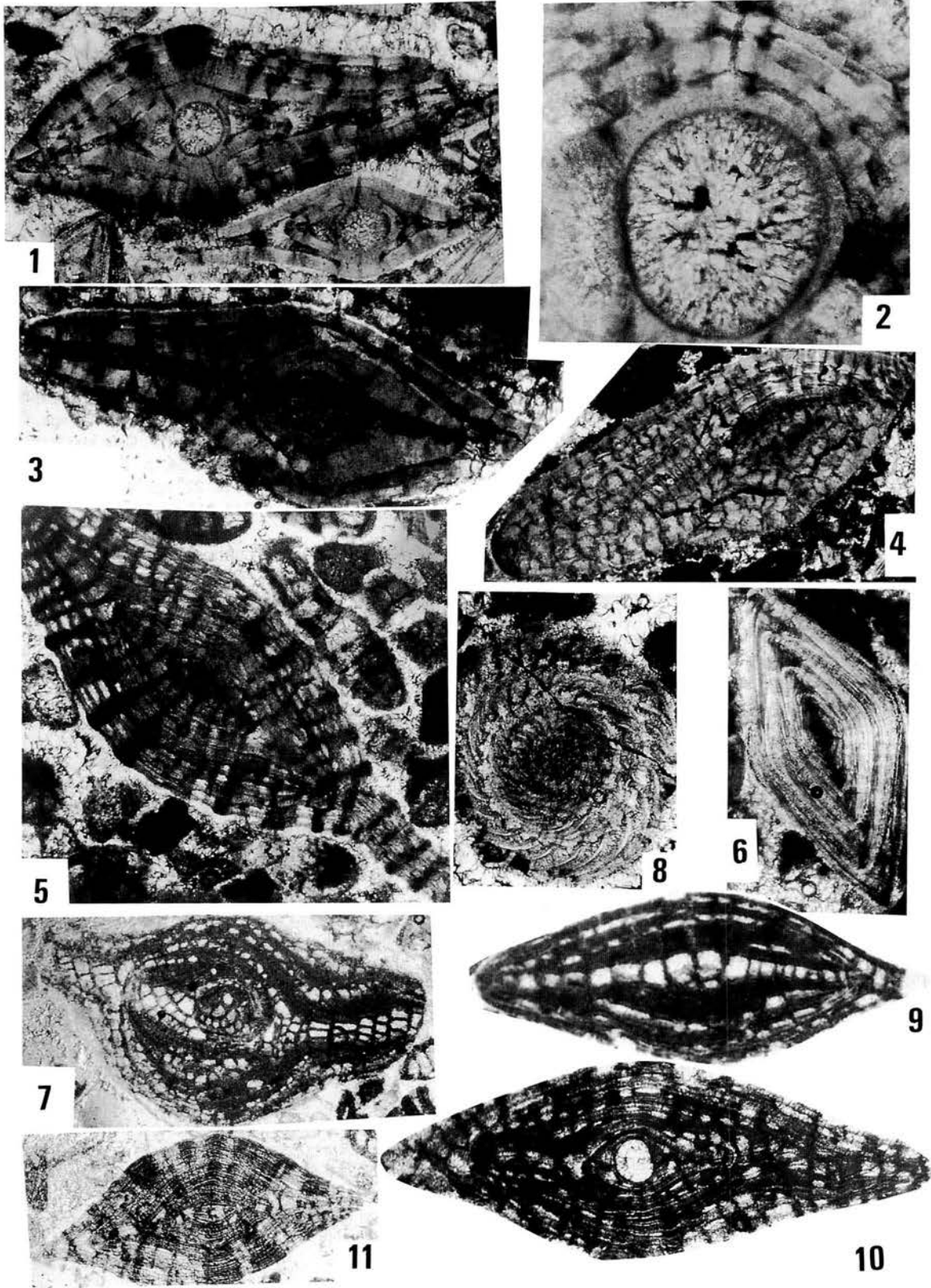
*Spiroclypeus margaritata* (Schlumberger). Yabe and Hanzawa, 1925, p. 627–630, pl. 2, fig. 10, pl. 3, figs. 8, 9, pl. 4, figs. 3–8, text-figs. 1–4; Krijnen, 1931, p. 89, pl. 1, figs. 1–3; Tan, 1937, p. 182, 183, pl. 2, fig. 12, pl. 3, fig. 9, pl. 4, figs. 6, 7; Hanzawa, 1940, p. 789, 790, pl. 42, figs. 3–9; Cole, 1954, p. 578–580, pl. 206, figs. 10–25, pl. 207, figs. 15, 16; Matsumaru, 1974, p. 108, pl. 15, figs. 16, 24, 26; Hashimoto and Matsumaru, 1975, p. 122, pl. 13, figs. 11, 12; Hashimoto, Matsumaru and Sugaya, 1981, p. 59, 60, pl. 13, fig. 3; Matsumaru, Myint Thein and Ogawa, 1993, p. 10, 11, figs. 2–1–9, 3–1.

*Spiroclypeus margaritata* (Schlumberger) var. *umbonata* Yabe and Hanzawa, 1929, p. 187, 188, pl. 124, figs. 5–8.

*Spiroclypeus higginsii* Cole. Hanzawa, 1957, p. 45, pl. 5, figs. 1–6, 14; Cole, 1957a, p. 332, pl. 95, figs. 1–5, pl. 109, fig. 16; Cole,

➔ **Figure 4.** 1, 2, 4, 5, 7, 9, 10. *Spiroclypeus margaritatus* (Schlumberger), 1 (upper), 5, 9, 10: vertical sections, x 30, (GSJF 15418–1–4) 4, 7: oblique sections, x 30, (GSJF 15418–5–6), 2: megalospheric protoconch x 200, (GSJF 15418–7). 3. *Heterostegina* sp. vertical section, x 30. 6, 8. *Amphistegina radiata* (Fichtel and Moll), 6: vertical section, x 20, (GSJF 15427–1) 8: median section, x 20, (GSJF 15427–2) 11. *Heterostegina borneensis* van der Vlerk, vertical section, x 30, (GSJF 15419).





1957b, p. 763, 764, pl. 239, figs. 11, 12, 14; Matsumaru, 1974, p. 108, pl. 15, figs. 1, 5, 8, 12, 18, 19; Matsumaru, 1976a, p. 199, pl. 1, figs. 2, 11, 16, 17.

*Spiroclypeus margaritatus* (Schlumberger). Matsumaru, 1996, p. 104–108, pl. 32, figs. 1–8, pl. 33, figs. 1–9.

**Material.**—Twenty specimens, GSJF 15418–1–20.

**Description.**—Test small, inflated to lenticular, bordered by a rather thin flange, central area more than 3.5 mm in diameter and 1.5 mm in thickness. Low raised pustules distributed in umbonal portion of the test having a diameter of less than 100  $\mu\text{m}$ . The megalospheric embryonic chambers consist of a spherical protoconch followed by a reniform deuteroconch. The inner diameters of protoconch (DI) and deuteroconch (DII) vary from 200 to 250  $\mu\text{m}$  and 450 to 550  $\mu\text{m}$ , respectively with a (DII/DI) ratio of 2.2.

**Remarks.**—Tan (1937) divided the species of *Spiroclypeus* into the pustulate and the reticulate group. The former group is characterized by prominent pillars on the umbonal portion of the test, the later one by the development of an external reticulation of the septa at the central part of the test. *Spiroclypeus margaritatus* belongs to the pustulate group and is characterized by large and heavy pillars, thick roofs and floors in lateral chambers, and moderate sized operculine chambers.

According to Matsumaru (1996), all the *Spiroclypeus* species reported from the West Pacific region are junior synonyms of *Spiroclypeus margaritatus* (Schlumberger). This species, known from Chichi-Jima, is restricted in occurrence to the Upper Member of the Minamizaki Limestone. It has a comparatively short stratigraphic range in Te, from the top of the *Heterostegina borneensis* Zone to the base of the *Miogypsinoides dehaartii* Zone, in the Eniwetok Atoll Drill Holes (Cole, 1957b).

Genus *Heterostegina* d'Orbigny, 1826

*Heterostegina borneensis* van der Vlerk, 1929

Figure 4.11

*Heterostegina borneensis* van der Vlerk, 1929, p. 16, figs. 6a–c, 25a–b; Cole and Bridge, 1953, p. 23, pl. 2, figs. 1–3, 5; pl. 4, figs. 16–18; Hanzawa, 1957, p. 95, pl. 26, figs. 11, 19; pl. 27, figs. 4–8; Matsumaru, 1976a, p. 199, pl. 3, figs. 17–19, 21–22; Matsumaru, 1996, p. 94–96, pl. 28, figs. 1–7.

**Material.**—One microspheric specimen in a vertical section, GSJF 15419.

**Description.**—Test small, initial part evenly lenticular with a moderately wide, thin flange on distal part. Test diameter ranges from 2.2 mm to 2.7 mm; test thickness ranges from 1.0 to 1.2 mm; thickness of pillars varies from 120  $\mu\text{m}$  at umbo to 100  $\mu\text{m}$  at tip of flange. In vertical section, embryonic apparatus biloculine; initial protoconch subcircular; its diameter less than 100  $\mu\text{m}$ . Prominent pillars are present on the central boss of the test. Pillars penetrating to outer

wall of embryonic apparatus and equatorial layer.

**Remarks.**—*Heterostegina borneensis* and *Spiroclypeus margaritatus* co-occur in the Lower and Upper members of the Minamizaki Limestone. In the Komahashi-Daini Seamount Limestone, *H. borneensis* is associated with *Spiroclypeus margaritatus*, the latter species being the more abundant one. *H. borneensis* has also been recognized as a marker species to distinguish Te1–4 from Te5 (Cole, 1957a; Adams, 1965; Matsumaru, 1974, 1978), since van der Vlerk (1925) regarded it to be a useful species for delimiting Te1–4.

Family Austrotrillinidae Loeblich and Tappan, 1986

Genus *Austrotrillina* Parr, 1942

*Austrotrillina howchini* (Schlumberger, 1893)

Figure 8.11

*Trillina howchini* Schlumberger, 1893, p. 119, 120, text-figs. 1–2, pl. 3, fig. 6; Hanzawa, 1940, p. 791–793, pl. 42, figs. 1, 2.

*Austrotrillina howchini* (Schlumberger). Cole and Bridge, 1953, p. 20, pl. 14, fig. 12; Cole, 1954, p. 573, pl. 210, figs. 6–9; Hanzawa, 1957, p. 38, pl. 22, figs. 12, 13; pl. 34, figs. 1, 2; Matsumaru, 1996, p. 214–216, pl. 84, figs. 3–7.

**Material.**—One microspheric specimen in a longitudinal section, GSJF 15424.

**Remarks.**—*Austrotrillina howchini* originally described from Saipan is also found in the Bikini Atoll Drill Holes associated with *Spiroclypeus* and *Eulepidina* in Te Stage (Cole, 1954). The stratigraphic range of this species has been given as Te through Tf1–2 (Glaessner, 1943) and as Te and Tf1 (van der Vlerk, 1948). Hanzawa (1940) stated that this species is found only in the Aquitanian stage in the Western Pacific. Hashimoto and Matsumaru (1984) suggested that *A. howchini* ranged from Te4 to Te5–Tf1. This species occurs in association with *Miogypsinella boninensis* and *Spiroclypeus margaritatus* in the Minamizaki Limestone, Chichi-Jima, assigned to Te 1–4 of the Far East Letter Stages (Hashimoto *et al.*, 1980; Hashimoto and Matsumaru, 1984).

Family Lepidocyclinidae Scheffen, 1932

Subfamily Eulepidininae Matsumaru, 1991

Genus *Eulepidina* H. Douvillé, 1911

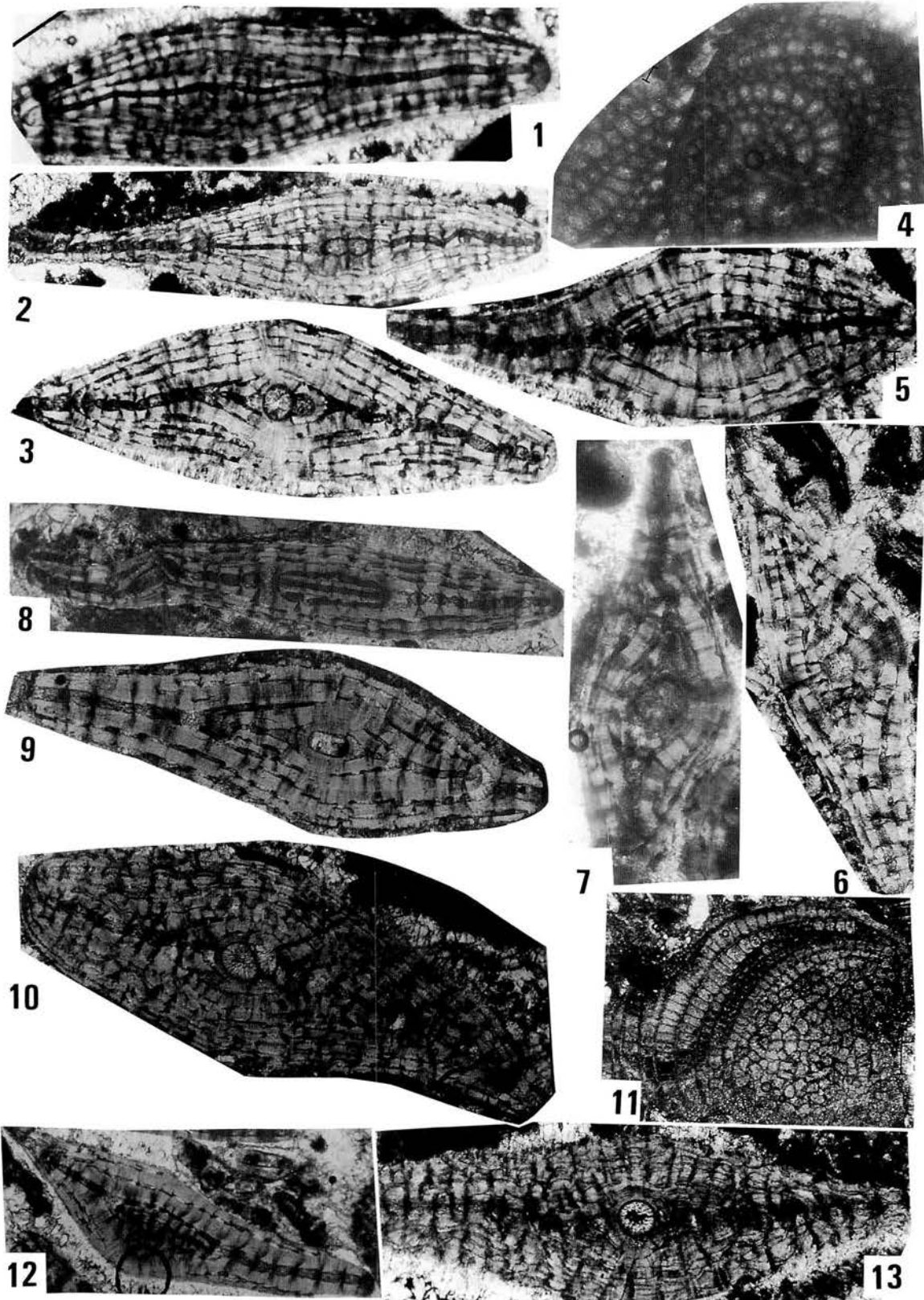
*Eulepidina ehippioides* (Jones and Chapman, 1900)

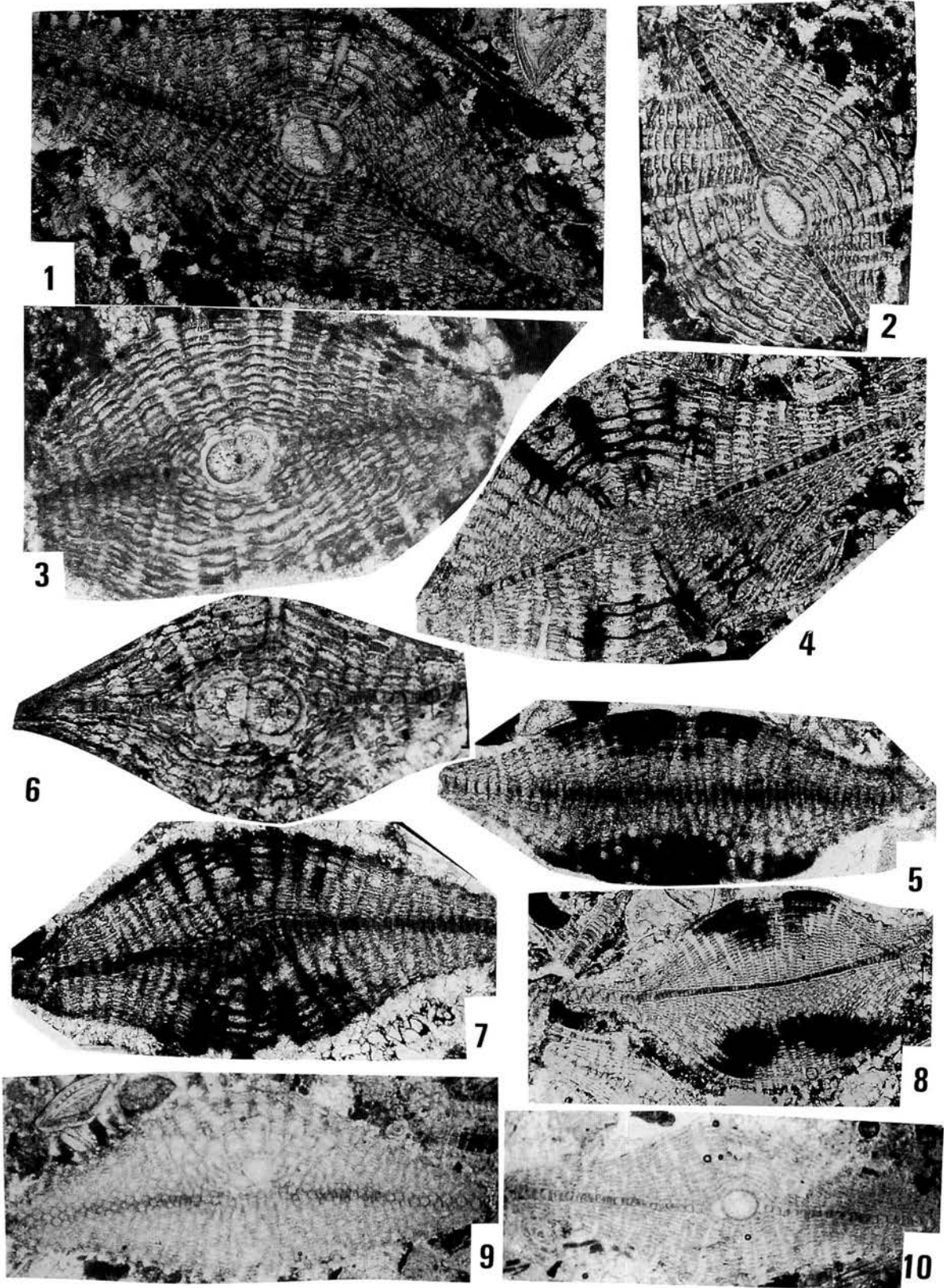
Figures 6.8, 7.3, 7.4

*Orbitoides* (*Lepidocyclina*) *ehippioides* Jones and Chapman, 1900, p. 251, 252, pl. 20, fig. 9. *Lepidocyclina ehippioides* Jones and Chapman. Grimsdale, 1952, p. 240–244, pl. 23, figs. 8, 17, 18. *Lepidocyclina* (*Eulepidina*) *formosa* Schlumberger. Cole, 1954, p. 594–597, pl. 216, figs. 1–16; pl. 217, figs. 9–11, pl. 218, figs. 1, 3, 4.

*Lepidocyclina* (*Eulepidina*) *gibbosa* Yabe. Cole, 1954, p. 597, pl. 217, figs. 9–11.

→ **Figure 5.** 1–13. *Spiroclypeus margaritatus* (Schlumberger). 1–3, 5–10, 12, 13: vertical sections, x 30, (GSJF 15418–8–18), 4, 11: oblique sections, x 30, (GSJF 15418–19–20).







*Lepidocyclus* (*Eulepidina*) *planata* Oppenoorth. Cole, 1954, p. 597, 598, pl. 217, figs. 7, 8; pl. 218, figs. 5, 6.

*Lepidocyclus* (*Eulepidina*) *ephippioides* Jones and Chapman. Cole, 1957b, p. 346–337, pl. 108, figs. 4–13; pl. 109, figs. 11–15.

*Eulepidina ephippioidea* (Jones and Chapman). Matsumaru, 1996, p. 178–181, pl. 65, figs. 1–6, pl. 66, figs. 1–3; pl. 67, figs. 1–6; pl. 68, figs. 1–3; pl. 69, figs. 1–4; pl. 70, figs. 1–5, text-fig. 20–5.

**Material.**—Three megalospheric specimens (GSJF 15426–1–3).

**Remarks.**—*Eulepidina ephippioidea* is characterized by the possession of a small nucleocoenoch and hexagonal or spatulate equatorial chambers. The earliest name of this species was thought to be *Orbitoides* (*Lepidocyclus*) *ephippioides* Jones and Chapman. According to Grimsdale (1952), the American Oligocene species *L. (E.) favosa* Cushman should be a synonym of *L. ephippioidea* (Jones and Chapman).

***Eulepidina dilatata*** (Michelotti, 1861)

Figure 8.1 (lower)

*Orbitoides dilatata* Michelotti, 1861, p. 17, pl. 1, figs. 1–2.

*Eulepidina dilatata* (Michelotti). Matsumaru, 1971b, p. 184, 185, pl. 22, figs. 28–38; Hashimoto and Matsumaru, 1975, p. 114, 115, pl. 12, figs. 10, 11; Matsumaru, 1996, p. 162–178, pl. 60, figs. 1–6; pl. 61, figs. 1–6; pl. 62, figs. 1–7; pl. 63, figs. 1–6; pl. 64, figs. 1–2, text-figs. 20–2, 4, text-fig. 30.

**Material.**—One obliquely sectioned megalospheric specimen, GSJF 15425.

**Remarks.**—The present species is characterized by having a lenticular shape, polygonal outline, large nucleocoenoch, hexagonal equatorial chambers, low and long lateral chambers and thin roofs and floors. It differs in general shell shape from *Eulepidina ephippioidea* (Jones and Chapman). Recently, Matsumaru (1996) investigated the size of the embryonic chambers of *E. dilatata* and *E. ephippioidea* from the Minamizaki Limestone, Chichi-Jima and concluded that microspheric *E. dilatata* slightly differs in chamber budding formation from microspheric *E. ephippioidea*.

Family Miogypsinidae Vaughan, 1928

Genus ***Miogypsinella*** Hanzawa, 1940

***Miogypsinella ubaghsi*** (Tan, 1936)

Figures 7.2, 8.2, 8.3

*Miogypsinoides ubaghsi* Tan, 1936, p. 47, 48, pl. 1, figs. 1–7; Cole, 1954, p. 603, 604, pl. 221, figs. 5, 9–18; pl. 222, figs. 13, 15.

*Miogypsinella ubaghsi* (Tan). Hanzawa, 1940, p. 767, 768, text-fig. 4.

**Material.**—Three melalospheric specimens; one in an

equatorial section, GSJF 15423–3 (Figure 8.3), one in an axial section, GSJF 15423–1 (Figure 8.2), and one in a vertical section, GSJF 15423–2 (Figure 8.2).

**Description.**—Test small, slightly wider than long, fan-shaped; 1.5 to 1.8 mm in diameter and 0.65 to 0.75 mm in thickness. Surface ornamentation consists of large pustules over the initial portion and finer, closer-spaced pustules over the distal portion. Embryonic chambers are bilocular, first chamber is nearly spherical and second chamber is reniform. Initial chambers are followed by subquadrate periembrionic chambers arranged so that they form virtually two coils. Periembrionic chambers gradually increase in length as they are added for about 1.5 volutions at which point they decrease gradually in length to the end of the coil.

**Remarks.**—The present species differs from *Miogypsinella borodinensis* Matsumaru, 1996, described from Minamizaki Limestone, Chichi-Jima, in having fewer equatorial and embryonic chambers and a small apical angle.

Family Amphisteginidae Cushman, 1927

Genus ***Amphistegina*** d'Orbigny, 1826

***Amphistegina radiata*** (Fichtel and Moll, 1798)

Figures 4.6, 4.8, 8.1

*Nautilus radiatus* Fichtel and Moll, 1798, p. 58, pl. 8, figs. 8a–d.

*Amphistegina lessoni* d'Orbigny. Yabe and Hanzawa, 1925, p. 48, 49, pl. 8, figs. 9, 10; Hanzawa, 1931b, p. 156, pl. 24, fig. 7; pl. 25, figs. 5–8; pl. 10, fig. 4.

*Amphistegina radiata* (Fichtel and Moll). Yabe and Hanzawa, 1929, p. 179, 180, pl. 18, fig. 6; Matsumaru, 1976b, p. 408, pl. 1, figs. 1–3, 5–13, 17, 23, 26–27, text-figs. 6–8. Matsumaru, 1996, p. 188, pl. 74, figs. 1–5.

**Material.**—Three microspheric specimens (GSJF 15427–1–3)

**Remarks.**—The present specimens show a close similarity with those of *A. radiata* described from the Minamizaki Limestones (Matsumaru, 1996) and are characterized by many chambers in the last whorl, curvature of the spiral suture and septa and a large protoconch.

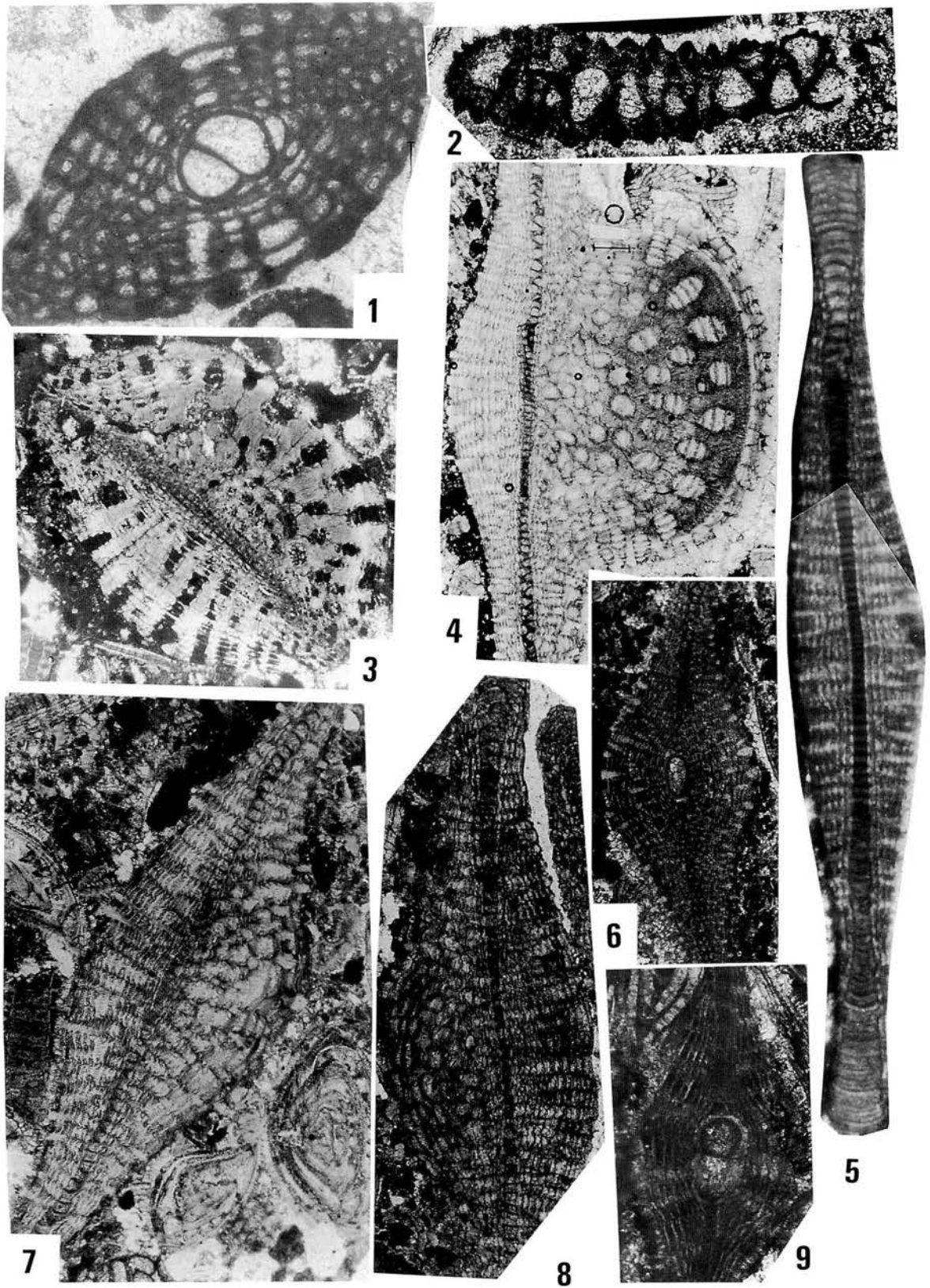
**Acknowledgments**

We acknowledge the help of the crew and scientific party on board the R/V Tansai Maru KT94–10 cruise, particularly T. Ishii. Thanks are also due to H. Ujiié, Takushoku University, for discussion on some larger foraminifera taxonomy and for critical reading of the manuscript. We would like to thank A. Nishimura, Geological Survey of Japan, for extensive and fruitful discussions regarding geologic history of the Kyushu-Palau Ridge.

**References**

Adams, C.G., 1965: The foraminifera and stratigraphy of the

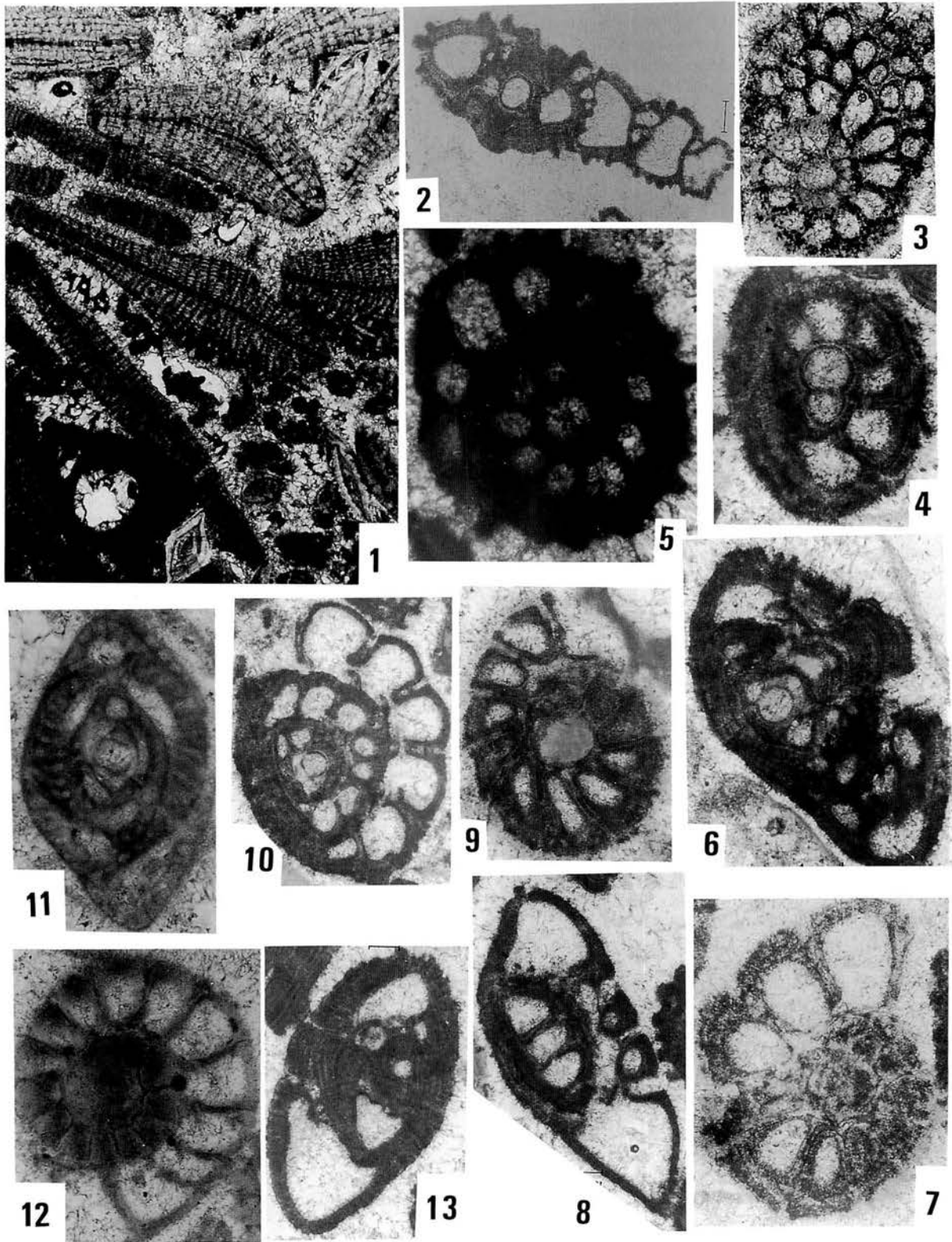
◀ **Figure 6.** 1–4, 6, 7, 9, 10. *Nephrolepidina praejaponica* Matsumaru, vertical sections, x 30, (GSJF 15420–1–8). 5. *Nephrolepidina angulosa* (Provale), vertical section, x 30, (GSJF 15421). 8. *Eulepidina ephippioidea* (Jones and Chapman), vertical section, x 20, (GSJF 15426–1).





- Melinau Limestone, Sarawak, and its importance in Tertiary correlation. *Quarterly Journal of the Geological Society of London*, vol. 121, p. 283-338, pls. 21-30.
- Adams, C.G. and Belford, D.J., 1974: Foraminiferal biostratigraphy of the Oligocene-Miocene limestones of the Christmas Island (Indian Ocean). *Palaeontology*, vol. 17, p. 475-506.
- Blainville, H.M.D. de, 1827: *Manuel de malacologie et de conchyliologie* (1825). Paris: F.G. Levraut, 664pp., 87pls.
- Blow, W.H., 1969: Late Middle Eocene to Recent planktonic foraminiferal biostratigraphy. In Brönnimann, P. and Renz, H. H., eds., *Proceedings of the First International Conference on Planktonic Microfossils*, Geneva, 1967, vol. 1, p. 199-421. E. J. Brill, Leiden.
- Blow, W.H., 1979: *The Cainozoic Globigerinida*, 3 vols. 1413pp., E.J. Brill, Leiden.
- Cole, W.S., 1954: Larger foraminifera and smaller diagnostic foraminifera from the Bikini Drill Holes. *U. S. Geological Survey Professional Papers*, 260-O, p. 569-608.
- Cole, W.S., 1957a: Larger foraminifera of Saipan. *U.S. Geological Survey Professional Papers*, 280-I, p. 321-360.
- Cole, W.S., 1957b: Larger foraminifera from Eniwetok Atoll Drill Holes. *U.S. Geological Survey Professional Papers*, 260-V, p. 743-784.
- Cole, W.S. and Bridge, J., 1953: Geology and larger foraminifera of Saipan Island. *U.S. Geological Survey Professional Papers*, 253, p. 1-45, pls. 2-15.
- Cushman, J.A., 1927: An outline of a reclassification of foraminifera. *Contributions from the Cushman Laboratory for Foraminiferal Research*, vol. 3, 105 pp., 25 pls.
- Douvillé, H., 1905: Les foraminifères dans le Tertiaire de Borneo. *Bulletin de la Société Géologique de France, Série 4*, vol. 6, no. 2, p. 435-464.
- Douvillé, H., 1911: Les foraminifères dans le Tertiaire des Philippines. *Philippine Journal of Science, series D*, vol. 6, p. 53-80, pl. A-D.
- Fichtel, L. and Moll, J.P.C., 1798: *Testacea microscopica, aliaque minuta ex generibus Argonauta et Nautilus, ad naturam picta et descripta*. Vienna: Camesina, xii+123 pp., 1-24 pls.
- Glaessner, M.F., 1943: Problem of stratigraphic correlation in the Indo-Pacific region. *Royal Society Victoria Proceedings, New Series*, vol. 55, pt. 1, p. 41-80.
- Grimsdale, T.F., 1952: Cretaceous and Tertiary foraminifera from the Middle East. *British Museum (Natural History) Bulletin*, vol. 1, no. 8, p. 223-247, pls. 20-25.
- Hanzawa, S., 1931a: Notes on Tertiary foraminiferous rocks from the Kwanto Mountainland, Japan. *Science Reports of the Tohoku Imperial University, Second Series (Geology)*, vol. 12, no. 2, p. 141-157.
- Hanzawa, S., 1931b: On some Miocene rocks with *Lepidocyclus* from the Izu and Boso Peninsulas. *Science Reports of the Tohoku University, Second Series (Geology)*, vol. 12, p. 157-170, pls. 27, 28.
- Hanzawa, S., 1940: Micropaleontological studies of drill cores from a deep well in the Kita-Daito-Zima (North Borodino Island). *Jubilee Publication of Prof. H. Yabe's 60th Birthday*, p. 755-802 pls. 39-42.
- Hanzawa, S., 1957: Cenozoic foraminifera of Micronesia. *Geological Society of America Memoir*, 66, p. 1-63.
- Hanzawa, S., 1964: The phylomorphogenesis of the Tertiary foraminiferal families, Lepidocyclinidae and Miogypsiniidae. *Science Reports of the Tohoku University, 2nd Series (Geology)*, vol. 35, p. 295-313.
- Hashimoto, W. and Matsumaru, K., 1975: Larger foraminifera from the Philippines, Part III. Limestone from eastern coastal ranges of north and central Luzon. *Geology and Paleontology of Southeast Asia*, vol. 16, p. 117-125, pl. 13.
- Hashimoto, W. and Matsumaru, K., 1984: Mesozoic and Cenozoic larger foraminifera of the Philippine and a reference to those found from Borneo by the APRSA's paleontological reconnaissance. *Geology and Paleontology of Southeast Asia*, vol. 25, p. 147-166.
- Hashimoto, W., Matsumaru, K. and Fuchimoto, H., 1980: Consideration on the stratigraphy of the Caraballo Range, northern Luzon: Larger foraminiferal ranges on the Cenozoic of the Philippines. *Proceedings of First International Congress on Pacific Neogene Stratigraphy*, vol. 20, p. 119-134.
- Hashimoto, W., Matsumaru, K. and Sugaya, M., 1981: Larger foraminifera from the Philippines. Part XI. On the Coal Harbor Limestone, Cagraray Island, Batan Island Group, Albay Province. *Geology and Paleontology of Southeast Asia*, vol. 22, p. 55-62, pl. 13.
- Jones, T.R. and Chapman, F., 1900: On the foraminifera of the Orbitoidal limestones and reef rocks of Christmas Island. In, Andrews, C.W. ed., *A Monograph of Christmas Island (Indian Ocean)*, British Museum (Natural History), London, p. 226-264. pls. 20, 21.
- Kaneoka, I., Isshiki, N. and Zashu, S., 1970: K-Ar ages of the Izu-Bonin Islands. *Geochemical Journal*, vol. 4, p. 53-60.
- Konda, I., 1975: Some paleontological results and problematic subjects on GDP Research Cruise. *Marine Science/Monthly*, vol. 7, no. 7, p. 465-470. (in Japanese with English abstract)
- Krijnen, W.F., 1931: Het Genus Spiroclypeus in het Indo-Pacifische Gebied. *Geologisch-Mijnbouwkundig Genootschap Nederlanden Kolonien, Verhandelingen, Geology Series*, vol. 9, p. 77-111.
- Loeblich, A.R.Jr. and Tappan, H., 1986: Some new and redefined genera and families of Textulariina, Fusuliniina, Involutiniina and Miliolina (Foraminiferida). *Journal of Foraminiferal Research*, vol. 16, p. 334-346.
- Matsumaru, K., 1967: Geology of the Tomioka area, Gunma Prefecture, with a note on "*Lepidocyclus*" from the Abuta Limestone Member. *Science Reports of the Tohoku University, Second Series (Geology)*, vol. 39, p. 113-147.
- Matsumaru, K., 1971a: Studies of the Genus *Nephrolepidina* in Japan. *Science Reports of the Tohoku University, Second Series (Geology)*, vol. 42, p. 97-185, pls. 9-26.
- Matsumaru, K., 1971b: The genera *Lepidocyclus* and *Eulepidina* from New Zealand. *Transactions and*

← **Figure 7.** 1, 6-9. *Nephrolepidina praejaponica* Matsumaru, 1: oblique section, x 20, 6-9: vertical sections, x 30, (GSJF 15420-9-13). 2. *Miogypsiniella ubaghsi* (Tan), vertical section, x 80, (GSJF 15423-1). 3, 4. *Eulepidina ehippioides* (Jones and Chapman), vertical sections, x 20, (GSJF 15426-2-3). 5. *Eulepidina* sp., vertical section, x 10.



- Proceedings of the Paleontological Society of Japan, New Series*, no. 84, p. 179–189, pls. 22, 23.
- Matsumaru, K., 1974: Larger foraminifera from east Mindanao, the Philippines. *Geology and Paleontology of Southeast Asia*, vol. 14, p. 101–115, pls. 14–19.
- Matsumaru, K., 1976a: Larger foraminifera from the islands of Saipan and Guam, Micronesia. In Takayanagi, Y. and Saito, T. eds., *Progress in Micropaleontology*, p. 190–213. Micropaleontology Press, New York.
- Matsumaru, K., 1976b: Larger foraminifera from the Ryukyu Group, Nansei Shoto Islands, Japan. *First International Symposium on Benthonic Foraminiferal Margins. Pt. B. Maritime Sediment, Special Publication 1*, p. 401–424.
- Matsumaru, K., 1978: Biostratigraphy and paleoecological transition of larger foraminifera, Minamizaki Limestone, Chichi-Jima, Japan. *Proceedings of Second Working Group Meeting Biostratigraphic Datumplane of the Pacific Neogene, IGCP Project 114*, p. 63–88, Bandung.
- Matsumaru, K., 1991: On the evolutionary classification of the Family Lepidocyclinidae (Foraminiferida). *Transactions and Proceedings of the Paleontological Society of Japan, New Series*, no. 164, p. 883–909.
- Matsumaru, K., 1992: Some Miocene *Nephrolepidina* (Family Lepidocyclinidae) from the Shimoshiroiwa Formation, Izu Peninsula, Japan. In Ishizaki, K. and Saito, T. eds., *Centenary of Japanese Micropaleontology*, p. 257–265.
- Matsumaru, K., 1996: Tertiary larger foraminifera (Foraminiferida) from the Ogasawara Islands, Japan. *Paleontological Society of Japan, Special Papers*, no. 36, 239p.
- Matsumaru, K. and Kimura, K., 1989: Larger foraminifera from the Eocene Shumizu and Miocene Misaki Formations in Tosa Shimizu City, Kochi Prefecture, Shikoku, Japan. *Transactions and Proceedings of the Paleontological Society of Japan, New Series*, no. 156, p. 156–169.
- Matsumaru, K., Myint Thein and Ogawa, Y., 1993: Early Miocene (Aquitian) larger foraminifera from the Shimizu Formation, Ashizuri Cape, Kochi Prefecture, Shikoku, Japan. *Transactions and Proceedings of the Paleontological Society of Japan, New Series*, no. 169, p. 1–14.
- Michelotti, G., 1861: Études sur le Miocene inférieur de l'Italie septentrionale. *Natuurkundige Verhandlingen Hollandsche Maatschappij der Wetenschappen*, vol. 2, pt. 15, p. 1–183, pls. 1–16.
- Mohiuddin, M.M., 1997: Biostratigraphic and tectonic significance of the Paleogene to Early Miocene carbonate rocks: Mineoka Tectonic Belt and Kyushu-Palau Ridge. Unpublished Ph. D. Thesis, University of Tsukuba, 160p., Japan.
- Ohara, Y., Kasuga, S., Kato, Y., Okino, K., Taira, A., Arima, M., Haraguchi, S., Ishii, T. and Katsura T., 1999: Continental crust formation in an oceanic island arc: drilling proposal at the Kyushu-Palau Ridge. *Chikyū Monthly*, Special No. 23, p. 133–140. (in Japanese)
- Orbigny, A.d., 1826: Tableau méthodique de la classe des Céphalopodes. *Annales des Sciences Naturelles*, vol. 7, p. 96–314, pls. 10–17.
- Ozima, M., Kaneoka, Y. and Ujiie, H., 1977:  $^{40}\text{Ar}$ – $^{39}\text{Ar}$  age of rocks and development mode of the Philippine Sea. *Nature*, vol. 267, p. 816–818.
- Parr, W.J., 1942: New genera of Foraminifera from the Tertiary of Victoria. *Mining and Geological Journal*, vol. 2, p. 361–363, 5 figs.
- Provale, I., 1909: Di alcune Nummulitine e Orbitoidine dell'Isola di Borneo. *Rivista Italiana de Paleontologia*, vol. 15, p. 65–96, pls 2–3.
- Rutten, L.M.R., 1912: Studien über foraminiferen aus Ost-Asien. *Sammlungen des geologischen Reichsmuseum in Leiden, Folge 1*, vol. 9, p. 202–224, pls. 2, 13.
- Scheffen, W., 1932: Zur Morphologie und Morphogenese der "Lepidocyclinen". *Paläontologische Zeitschrift*, vol. 14, p. 233–256, pls. 9–10.
- Schlumberger, C., 1893: Note sur les genres Trillina et Linderina. *Bulletin de la Société Géologique de France, Série 3*, vol. 21, p. 118–123, pl. 3.
- Schlumberger, C., 1902: Note sur un *Lepidocyclina* nouveau de Borneo. *Sammlungen des Geologischen Reichsmuseums in Leiden, Folge 1*, vol. 6, p. 250–253, pl. 7.
- Shiki, T., Aoki, H., Suzuki, M., Musashino, M. and Okuda, Y., 1974: Geological and petrographical results of the GDP 8th cruises in the Philippine Sea. *Marine Sciences/Monthly*, no. 6, p. 555–560. (in Japanese)
- Shiki, T., Tokuoka, H., Aoki, H., Misawa, Y., Konda, I. and Nishida, S., 1975: Some geological results of the GDP cruises in the Philippine Sea, with special references to bottom sampling of the GDP-8, 11. In *Geological Problems of the Philippine Sea*, Geological Society of Japan, p. 67–74.
- Tan, S.H., 1936: Zur Kenntnis der Miogypsiniden. *De Ingenieur in Nederlandsche-Indië, Afd. IV, Mijnbouw en Geologie*, Jaarg. 3, no. 3, p. 45–61, pls. 1–2.
- Tan, S.H., 1937: On the genus *Spiroclypeus* H. Douvillé with a description of Eocene *Spiroclypeus vermicularis* nov. sp. from Koetai in east Borneo. *De Ingenieur in Nederlandsche-Indië, Afd. IV, Mijnbouw en Geologie*, Jaarg. 4, no. 10, p. 177–193.
- Ujiie, H., 1975: Planktonic foraminiferal biostratigraphy in the Western Philippine Sea. In Karig, D.E., Ingle, J.C. et al., eds. *Initial Reports of the Deep Sea Drilling Project*, vol. 31, p. 677–691. U.S. Government Printing Office, Washington, D.C.
- Uyeda, S. and Ben-Avraham, Z., 1972: Origin and development of the Philippine Sea. *Nature*, vol. 240, p. 176.
- Vaughan, T.W., 1928: Subfamily Miogypsinidae Vaughan. In Cushman, J.A., 1928, Foraminifera their classification and economic use, *Special Publication of Cushman Laboratory for Foraminiferal Research*, vol. 1, 401p.
- Vlerk, I.M. van der, 1925: A study of Tertiary foraminifera from the "Tidoengsche Landen" (E. Borneo). *Dutch East Indies, Dienst van der Mijnbouw, Wetenschappelijke Mededelingen. Dienst van den Mijnbouw in Nederland*

◀ **Figure 8.** 1. Bioclastic packstone containing diagnostic species such as *Spiroclypeus margaritatus* (Schlumberger) (GSJF 15418–20), *Nephrolepidina marginata* (Michelotti) (GSJF 15422), *Eulepidina dilatata* (Michelotti) (GSJF 15425) and *Amphistegina radiata* (Fichtel and Moll) (GSJF 15427–3) x 20. 2, 3. *Miogypsinella ubaghsi* (Tan). 2: axial section, x 20, GSJF 15423–2, 3: equatorial section, x 20, (GSJF 15423–3). 4–10, 12, 13. *Ammonia* sp., 4, 7, 9, 10, 12: oblique sections, x 20, 5: equatorial section, x 20, 6, 8, 13: axial sections, x 20. 11. *Austrorillina howchini* (Schlumberger), longitudinal section, x 20, (GSJF 15424).

- sch-Indie*, no. 3, p. 13-32, pls. 1-6.
- Vlerk, I.M. van der, 1929: Groote foraminiferen van N.O. Borneo. *Wetenschappelijke Mededelingen Dienst van der Mijnbouw in Nederlandsch-Indie* no. 9, p. 5-30.
- Vlerk, I.M. van der, 1948: Stratigraphy of the Cenozoic of the East Indies based on Foraminifera. *International Geological Congress, Report of 18th Session, Great Britain*, pt. 15, p. 61-63.
- Watts, A. B. and Weissel, J.K., 1975: Tectonic history of the Shikoku marginal basin. *Earth and Planetary Science Letters*, vol. 25, p. 239-250.
- Yabe, H., 1906: On the orbitoid limestone from Nakakosaka and from Kuboi on the Lake Kawaguchi. *Journal of Geological Society of Japan*, vol. 13, no. 156, p. 317-320.
- (*in Japanese*)
- Yabe, H. and Hanzawa, S., 1922: *Lepidocyclina* from Naka-Kosaka, Province of Kodzuke, Japan. *Japanese Journal of Geology and Geography*, vol. 1, no.1 p. 45-50, pls. 5-8.
- Yabe, H. and Hanzawa, S., 1925: A *Lepidocyclina*-Limestone from Klias Peninsula, B. N. Borneo. *Gedenkboek Verbeek, Verhandelingen Geologisch-Mijnbouw Genootschap Nederland en Kolonien, Geology Series*, vol. 8, p. 617-631, pls. 1-4.
- Yabe, H. and Hanzawa, S., 1929: Tertiary foraminiferous rocks of the Philippines. *Science Reports of the Tohoku University, Second Series (Geology)*, vol.11, no. 3, p. 137-190, pls. 15-27.

# ***Kheraiceras* Spath (Ammonoidea)—new forms and records from the Middle Jurassic sequence of the Indian Subcontinent**

SUDIPTA K. JANA, SUBHENDU BARDHAN and SUBRATA K. SARDAR

Department of Geological Sciences, Jadavpur University, Calcutta 700-032, India  
(corresponding author: Bardhan, s\_bardhan01@yahoo.co.uk)

Received 5 January 2000; Revised manuscript accepted 21 July 2000

**Abstract.** *Kheraiceras* Spath reached its peak during the Late Bathonian-Early Callovian and achieved a wide biogeographic distribution during that interval. The genus speciated rapidly and is represented in the fossil record by many species. The present endeavour provides a full taxonomic account of six species, of which five are from Kutch, western India. The sixth, *K. noetlingi* sp. nov., is based on the specimen described as '*Sphaeroceras*' cf. *bullatum* d'Orbigny by Noetling (1896) from Baluchistan, Pakistan. Among the five Kutch species one has also been found in Baluchistan. We know little about specific dimorphism in *Kheraiceras*. In at least three instances dimorphic pairs have been matched. Of the six species of *Kheraiceras* described herein three are new and two are new records. They are: *Kheraiceras cosmopolitum*, *K. bullatum*, *K. cf. hannoveranum*, *K. spathi* sp. nov., *K. sp. A*, and *K. noetlingi* sp. nov. Like many other biota, including other ammonites, *Kheraiceras* speciation is marked by a high degree of endemism in the Kutch Sea, which extended up to Baluchistan. The endemism in this newly opened basin is due to the transgressions resulting from the fragmentation of Gondwanaland.

**Key words:** *endemism, Indian Subcontinent, Kheraiceras, Middle Jurassic, migration, sexual dimorphism*

## **Introduction**

The genus *Kheraiceras* Spath, 1924 of the family Tullitidae has been thought to evolve from *Bullatimorphites* Buckman, 1921. Unlike its probable ancestor, *Kheraiceras* has a wide biogeographic distribution along the margins of the Tethys and the Pacific including Indonesia, Mexico and South America (Donovan *et al.*, 1981; Mangold, 1984; Riccardi *et al.*, 1989; Sandoval *et al.*, 1990; Westermann, 1993). The genus has not been reported, however, from the Boreal or Subboreal Provinces. From the distribution patterns it appears that *Kheraiceras* is longitudinally widespread and latitudinally more restricted to the palaeotropics and subtropics (see also Westermann and Callomon, 1988). It shows strong facies control, since most of its species are found mainly in calcareous facies deposited in shallow seas (Arkell, 1952; Bardhan *et al.*, 1988). *Kheraiceras* is of great stratigraphic value because of its short temporal distribution, although its biostratigraphic potentialities have not been fully explored (see Bardhan *et al.*, 1999). *Kheraiceras* ranges in age from Late Bathonian to Late Callovian (Hahn, 1969, 1971), but was at its peak during the Late Bathonian and Early Callovian when many other biostratigraphically impor-

tant taxa, e.g. *Macrocephalites* Zittel, 1884 and *Reineckeia* Bayle, 1878 also flourished.

In the present endeavour, we have made a taxonomic study of six *Kheraiceras* species, among which three are new and two have not been described previously from the subcontinent. Dimorphism is now considered to be very important in understanding evolution within a lineage and must be taken into account in phylogeny. Although dimorphism in *Kheraiceras* is evident, little is known about specific dimorphic pairs (for details see Bardhan *et al.*, 1994, 1999). In the present study we have distinguished dimorphic pairs in three species. Besides, there are two new microconchs and one macroconch species whose counterparts are still unknown. So far *Kheraiceras* is described in the literature mainly by macroconchs and microconchs are often rare. We have plentiful microconch specimens with a well preserved peristome showing apertural modifications. They are described herein.

The measurements of the types and other specimens of the present collection (abbreviated as below) are in mm. D=diameter; H=whorl height; W=whorl width; U=umbilical diameter.

*Repository.*—Curatorial Division, Geological Survey of

India, Calcutta (GSI); The Indian Museum, Calcutta; Department of Geological Sciences, Jadavpur University, Calcutta, India (JUM).

### Previous Study

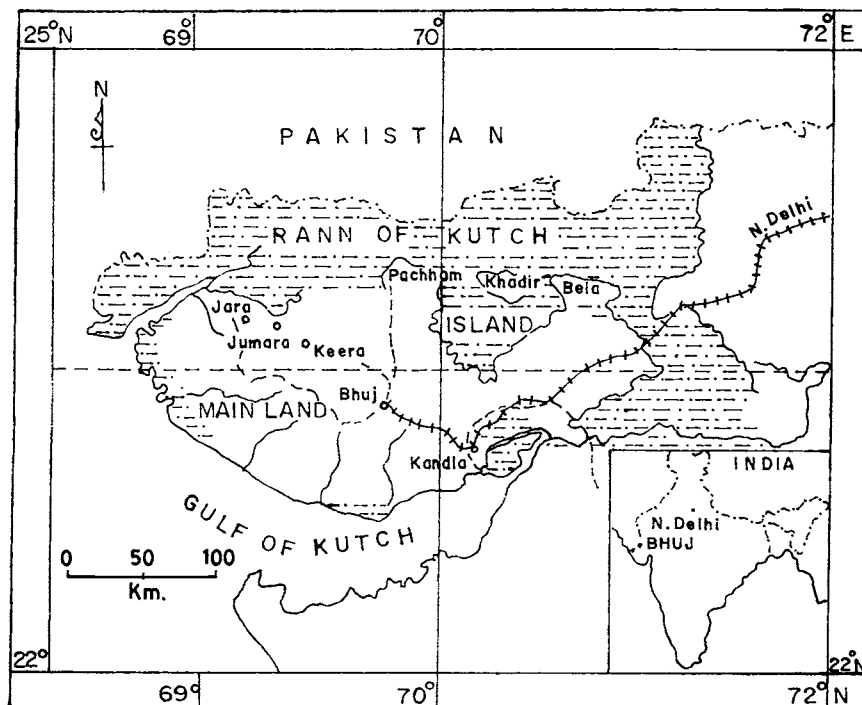
There are only a few reports of *Kheraiceras* from the Indian subcontinent. Waagen's (1875) "*Stephanoceras bullatum*" d'Orbigny, 1846 which Spath (1924) subsequently made the type species of *Kheraiceras*, i.e., *K. cosmopolitum*, comes from the Golden Oolite of Keera, Kutch. Recently many specimens of this species have been collected from Kutch, and the intraspecific variability and dimorphism of this species have been firmly established (Bardhan *et al.*, 1994). Noetling (1896) described a large single specimen as '*Sphaeroceras*' cf. *bullatum* (pl. 6, figs. 2, 2a) from the Polyphemus Limestone bed of Mazardrik, Baluchistan. Although it resembles *Kheraiceras hannoveranum* (Roemer, 1911) from the Late Bathonian of Europe (Westermann and Callomon 1988), novel traits distinguish it and is described here as a new species. Spath (1931) reported *K. aff. cosmopolitum* from his Macrocephalus Zone of Jumara, Kutch, which is represented by a complete microconch resembling closely the one of our present species, *K. spathi* <m> and has been synonymised with it. Kanjilal (1978) reported *Kheraiceras probullatum* from Kutch which is now considered to be a variant of *Macrocephalites formosus* (Sowerby, 1840) (see Pandey and Westermann, 1988). *K. ex. gr. platystoma* reported by Bardhan and Datta (1987) from Jumara is now considered to be an extreme depressed variant of *K. cosmopolitum*. Krishna *et al.* (1987) il-

lustrated but did not describe a specimen as a microconch of *K. cosmopolitum* from the Golden Oolite of Keera. It appears, however, from the figure to be an adult macroconch of *K. bullatum* with a partially preserved body chamber. Bardhan *et al.* (1988) described *Bullatimorphites* sp. from Jumara which is in fact a *Kheraiceras* species with a less depressed inner whorl and strong, coarse ribbing persisting on the adult body chamber. It has been redesignated here as *K. cf. hannoveranum* (see also Callomon, 1993; Jain *et al.*, 1996). Panday and Westermann (1988) reported a single specimen of *Bullatimorphites (Kheraiceras?)* n. sp. A from the Middle (?) Bathonian of Patcham 'island', Kutch. It has peculiar *Bullatimorphites*-like inner whorls and a *Kheraiceras*-like eccentrically coiled body chamber.

The spatio-temporal distribution of *Kheraiceras* reveals its relatively narrow stratigraphic but wide biogeographic distributions. Yet little attention has been paid to its biostratigraphic potentialities except in Submediterranean France. In a previous attempt we have proposed a new biozonation scheme of the Upper Bathonian-Lower Callovian sequence of Kutch based on different stratigraphic ranges of *Kheraiceras* and other important time-diagnostic taxa such as *Macrocephalites*, *Reineckeia* etc. (Bardhan *et al.*, 1999). An attempt has also been made for regional standard chronostratigraphy and interprovincial correlation.

### Stratigraphy

Species of *Kheraiceras* are distributed throughout the entire Callovian sequence of the basal Chari Formation in Kutch. One species straddles into the uppermost Batho-



**Figure 1.** Geographic location of Kutch with Keera and Jumara, the type area of the Chari Formation. The patterned area is the Rann of Kutch.



nian bed in Jumara. The Chari Formation is a regionally persistent, highly fossiliferous unit and constitutes one of the four principal divisions of the Kutch Mesozoic (for details see Biswas, 1977; Mitra *et al.*, 1979; Krishna, 1984). It represents a near-continuous section ranging from the Upper Bathonian through the entire Callovian and Oxfordian. There are, however, reports of condensation of the se-

quence and time-averaging of fauna during the Oxfordian (Fürsich *et al.*, 1992; Halder and Bardhan, 1996). The Chari Formation represents a heterolithic facies consisting of shale, limestone and sandstone. The carbonate facies which yields the present *Kheraiceras* specimens is occasionally oolitic and is more dominant in the lower part of the sequence. The partially exposed, underlying Patcham Formation at Jumara is on the other hand predominantly calcareous, consisting of coral biostromes and limestone-marl alternations. Judging from the faunal associations and sedimentological evidence, these two formations are considered to be the product of a shallow-marine environment (Biswas, 1991; Datta, 1992; Fürsich and Oschmann, 1993).

The present *Kheraiceras* species have been systematically collected from different limestone beds of Jumara and Keera in the mainland of Kutch (Figure 1). Jumara is the stratotype of the Chari Formation and Keera is the type locality of *Kheraiceras cosmopolitum*. Stratigraphic occurrences of *Kheraiceras* species in the Jumara and Keera sections is shown in Figure 2.

All species of *Kheraiceras* described herein restrictedly occur within the zones spanning Upper Bathonian to Lower Callovian (Figure 3). Although these zones are based mainly on endemic Kutch ammonites, discoveries (e.g., Kayal and Bardhan, 1998) of some well time-diagnosed short-ranging taxa have made possible broad interprovincial correlation with other *Kheraiceras*-bearing provinces (for detailed discussion on age and correlation see Bardhan *et al.*, 1999).

*Kheraiceras cf. hannoveranum* is also known from

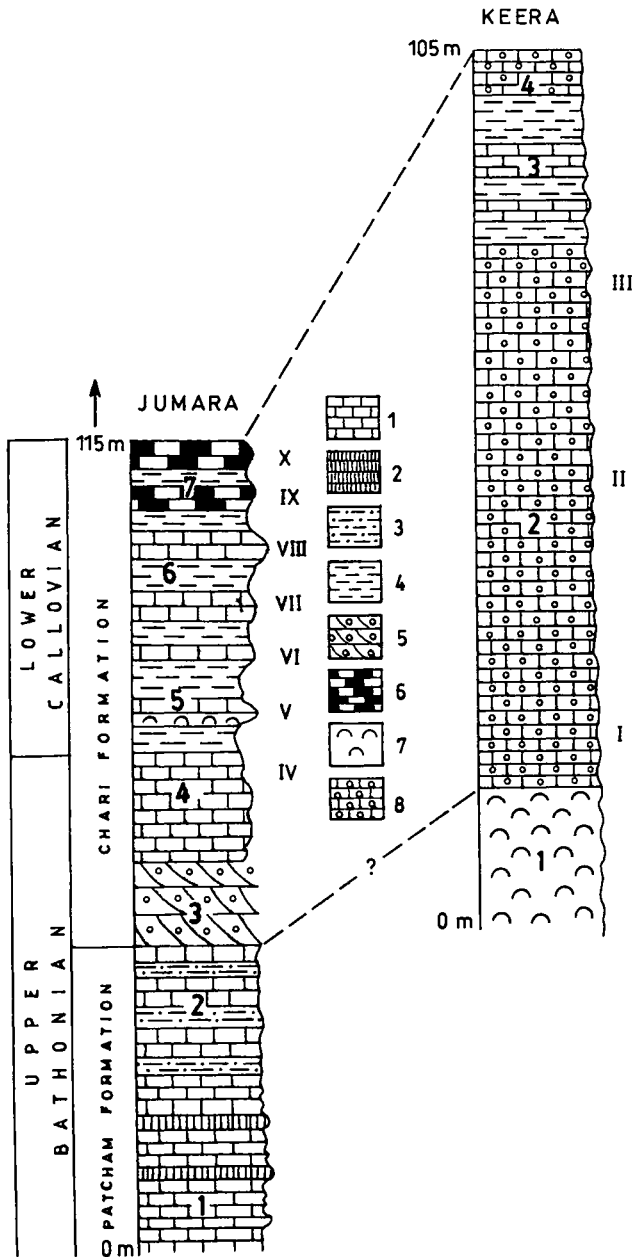


Figure 2. Stratigraphic sections at Jumara and Keera. Key. 1. white, cream or brown-coloured limestone; 2. coral biostrome; 3. marl; 4. shale; 5. cross-stratified, lenticular, green, oolitic limestone; 6. grey shelly limestone with thin alternating bands of red or white limestone and grey shale; 7. bioclastic grainstone; 8. oolitic limestone. Occurrences of different *Kheraiceras* species are indicated by horizon nos. (I-X).

AGE	ZONE	SUBZONE	FAUNAL HORIZON	SPECIES			
EARLY CALLOVIAN	FORMOSUS	SEMILAEVIS	Nothocephalites semilaevis	K. sp.A.			
			M. formosus				
		FORMOSUS	Kamptokephalites lamellosus				
			Kampt. dimerus				
		DIADEMATIS	K. bullatum				
			I. diadematus				
		TRANSITORIUS	Kheraiceras cosmopolitum				
			I. transitorius				
		LATE BATHONIAN	CHRYSOOLITHICUS		MADAGASCARIENSIS	M. madagascariensis	K. cosmopolitum K. bullatum K. cf. hannoveranum K. spathi
					CHRYSOOLITHICUS	Sivajiceras congener	
TRIANGULARIS	TRIANGULARIS		Indocephalites chrysoolithicus				
	HIANS		Macrocephalites triangularis				
			Procerites hians				

Figure 3. Range chart of different species of *Kheraiceras* in Kutch. Zones and Subzones are after Bardhan *et al.* (1999).

Baluchistan. Another new species described here, *Kheraiceras noetlingi*, has been found only in Baluchistan. Both come from the Polyphemus Limestone, Mazardrik, Baluchistan.

**Kheraiceras Faunal Associations**

*Kheraiceras*, though it ranges from Late Bathonian to Late Callovian (Hahn, 1969), is more diverse in Early Callovian, when other biostratigraphically important genera e.g., *Macrocephalites* Zittel and *Reineckeia* Bayle, also underwent adaptive radiation. In Submediterranean France *Kheraiceras* is closely associated with reineckeids in the Lower Callovian beds, but macrocephalitids are rare (Cariou, 1984). In England, this part is marked by diverse macrocephalitid species but *Kheraiceras* and reineckeids are absent (Callomon *et al.*, 1988). Kutch, on the other hand, includes ammonites of all these three groups and thus provides a unique opportunity for high resolution of biostratigraphic zonation and interprovincial chronostratigraphic correlation.

Recently Bardhan *et al.* (1999) proposed biostratigraphic zonations within the Bathonian-Callovian Stages of Kutch (Figure 3). The faunal horizons are not found in every section, but the subzones are regionally persistent and can be easily recognised for their characteristic ammonite assemblages in all the sections in the mainland of Kutch.

*Kheraiceras* species are distributed throughout these assemblages except for the lowest one, i.e., the Triangularis Subzone. Different *Kheraiceras* species have different

biostratigraphic ranges and like macrocephalitids, they are more diverse in the lowest Early Callovian. A brief summary of the faunal association of each *Kheraiceras* species is given here (Figure 4). The relative abundance of other important ammonite species is discussed and a possible age correlation based on time-diagnostic or equivalent taxa is indicated.

The only *Kheraiceras* species described from outside Kutch is *K. noetlingi* sp. nov. It comes from the Polyphemus Limestone, Mazardrik, Baluchistan (Noetling, 1896). It is associated with *Macrocephalites triangularis* 'group', *Clydoniceras baluchistanense* (Spath) and *Choffatia* (*Homeoplanulites*) (Spath). This faunal association indicates a Late Bathonian age (see also Westermann and Callomon, 1988).

*K. cf. hannoveranum* first appeared in the Madagascariensis Subzone of the Chrysoolithicus Zone in Kutch. It resembles the lectotype coming from the Upper Bathonian Orbis Zone of Germany. In the Madagascariensis Subzone, *Macrocephalites madagascariensis* is particularly abundant. It resembles *M. verus* (Buckman) in Europe which comes from the lowermost Callovian (Cariou, 1984; Callomon *et al.*, 1988). Another abundant macrocephalitid species is *Indocephalites chrysoolithicus* (Spath). *Sivajiceras congener* is also abundant while *Choffatia* sp. and *Oxyerites* (*Paroxyerites?*) sp. are less common. *K. cf. hannoveranum* also continues to the next assemblage, i.e., the Transitorius Subzone of the lowest Early Callovian where it co-occurs with diverse macrocephalitids, e.g., *Indocephalites transitorius*, *I. kheraensis*, *I. diadematus*, *Pleurocephalites elephantinus*, *Kamptokephalites lamellosus* and

Ammonite association	Kheraiceras species	Other important ammonite species																								
		<i>Macrocephalites madagascariensis</i>	<i>Macrocephalites formosus</i>	<i>Indocephalites transitorius</i>	<i>Indocephalites kheraensis</i>	<i>Indocephalites chrysoolithicus</i>	<i>Indocephalites diadematus</i>	<i>Pleurocephalites elephantinus</i>	<i>Dolkephalites subcompressus</i>	<i>Kamptokephalites lamellosus</i>	<i>Kamptokephalites dimenus</i>	<i>Kamptokephalites magnumbilicatus</i>	<i>Nothocephalites semilaevis</i>	<i>Nothocephalites asaphus</i>	<i>Eucyloceras eucyclum</i>	<i>Subkossmatia opis</i>	<i>Reineckeia tyrantiformis</i>	<i>Reineckeia anceps</i>	<i>Colokia oxyptycha</i>	<i>Choffatia codra</i>	<i>Choffatia pardagatus</i>	<i>Choffatia recuperoi</i>	<i>Choffatia</i> sp.	<i>Sivajiceras congener</i>	<i>Oxyerites</i> ( <i>Paroxyerites?</i> ) sp.	
Nothocephalites semilaevis	<i>K. cosmopolitum</i>	●		○	○	×	×	○	○	○	×	●	×	×	×	×	×	×	○	○	●					
Macrocephalites formosus	<i>K. cosmopolitum</i> <i>K. sp. A</i>	●			●	○	○	○	●	●	●	×					×					×				
Macrocephalites diadematus	<i>K. cosmopolitum</i> <i>K. bullatum</i>		○		○	○	●	●	○	○	●	×										×	×			
Indocephalites transitorius	<i>K. cosmopolitum</i> <i>K. bullatum</i> , <i>K. spathi</i> <i>K. cf. hannoveranum</i>		○	●	○	○	○	○	○	○	○												×			
Macrocephalites madagascariensis	<i>K. cf. hannoveranum</i>	●				●																	×	●	×	

● abundant, ○ common, × rare

Figure 4. Biostratigraphic distribution of *Kheraiceras* species in Kutch in association with other important ammonites.

*Dolikephalites subcompressus*, *Macrocephalites formosus*. Besides, other *Kheraiceras* species e.g., *K. cosmopolitum*, *K. bullatum*, *K. spathi* are also found from this level.

*K. cosmopolitum* is the most abundant species of *Kheraiceras* and an endemic form. It has a longer stratigraphic distribution spanning the entire Formosus Zone of the Lower Callovian. This zone can be approximately correlated with the Lower Callovian *Macrocephalus* and *Gracilis* Zones of France (see also Krishna and Westermann, 1987; Bardhan *et al.*, 1999). It is more frequent in the Formosus Subzone, where it is associated with abundant *Macrocephalites formosus*, *Indocephalites kheraensis*, *Kamptokephalites dimerus*, *Kamptokephalites lammellosus*, *Dolikephalites subcompressus*, and rare *Choffatia recuperoi*, *Reineckeia tyranniformis*. In the superjacent Semilaevis Subzone, *K. cosmopolitum* is associated with abundant *Nothocephalites semilaevis*, *Choffatia recuperoi*. *Collotia oxyptica*, *Eucyclocers eucyclum*, *Subkossmatia opis* and *Nothocephalites asaphus* are rare at this level. Judging by this faunal association, the upper limit of *K. cosmopolitum* can reasonably be placed at the uppermost Early Callovian. *K. spathi* sp. nov. comes from the level immediately above the Bathonian-Callovian boundary. This horizon yields diverse *Kheraiceras* species e.g., *K. cosmopolitum*, *K. cf. hannoveranum*, *K. bullatum*. The important macrocephalitids are *I. transitorius*, *I. chrysoolithicus*, *I. diadematus*, *P. elephantinus* etc.

*K. bullatum* appeared slightly above the base of the Lower Callovian, spanning the upper part of the Transitorius and the entire Diadematus Subzones. Here it is associated with *K. cosmopolitum* and typical members of the faunal assemblage such as *I. diadematus*, *P. elephantinus*, *K. dimerus*, etc. This faunal association indicates a late appearance of *K. bullatum* in Kutch because it is already known from the Late Bathonian of Europe as well as South America (see Riccardi *et al.*, 1989; Sandoval *et al.*, 1990). We agree with Krishna and Cariou (1990) who correlated *K. bullatum*-bearing horizons of Kutch approximately with the upper Herveyi Zone and Bullatus Zone of France on the basis of common associated taxa.

*K. sp. A* is represented by a single microconchiate specimen from the Formosus Subzone, which marks the disappearance of *K. bullatum*. It is associated with *K. cosmopolitum* and abundant *M. formosus*, *K. dimerus*, *K. lamellosus* and *D. subcompressus*.

### Systematic Palaeontology

Superfamily Perisphinctaceae  
Family Tullitidae Buckman, 1921  
Genus *Kheraiceras* Spath, 1924

*Type species*.—*Sphaeroceras cosmopolitum* Parona and Bonarelli 1895; original designation.

#### *Kheraiceras cosmopolitum* (Parona and Bonarelli, 1895)

Figures 5.1–5.4; 6c

*Holotype*.—GSI Type No. 2009. Internal mould with par-

tial shell remains, adult macroconch with last quarter of body chamber missing, from Golden Oolite of Keera.

*Material*.—In addition to the holotype, one macroconch (JUM/J/5) and two microconchs (JUM/J/2 and JUM/J/6) have been studied. All of them come from Jumara. The macroconch is an adult specimen with thin shell and last quarter of the body chamber missing, from Horizon V, Bed 5. The microconchs are almost complete, both coming from Bed 7; JUM/J/2 with terminal constriction present at flank and abraded on one side, from Horizon IX; JUM/J/6 with thin shell, from Horizon X.

*Diagnosis*.—Sphaeroconic, whorls extremely depressed and to a maximum in phragmocone, W/H ratio=2.8; body chamber occupies more than three-fourths of last whorl; beginning of body chamber marked by sudden whorl contraction and umbilical uncoiling following first a straight centrifugal line and then turning suddenly inwards; ribbing feeble in internal mould, disappears more rapidly near umbilicus than venter on body chamber, last seen at a diameter of 58 mm; umbilicus small, deep, umbilical wall gradually becomes steeper; flanks extremely short; septal suture with typically shallow tultid U<sub>2</sub>.

*Description*.—Detailed systematic description of macroconch, microconch, their synonymy and stratigraphic distribution have already been given in Bardhan *et al.* (1994).

*Occurrence*.—*Kheraiceras cosmopolitum* is an endemic Kutch species. The holotype comes from the Golden Oolite (Bed 2), Keera. JUM/J/5 is collected from Horizon V, Bed 5, Jumara. JUM/J/2 and JUM/J/6 come from Horizon IX and X respectively of Bed 7, Jumara.

#### *Kheraiceras bullatum* (d'Orbigny, 1846)

Figures 5.5a,b; 6a,b; 7.1–7.6; 8.1a–c; 9

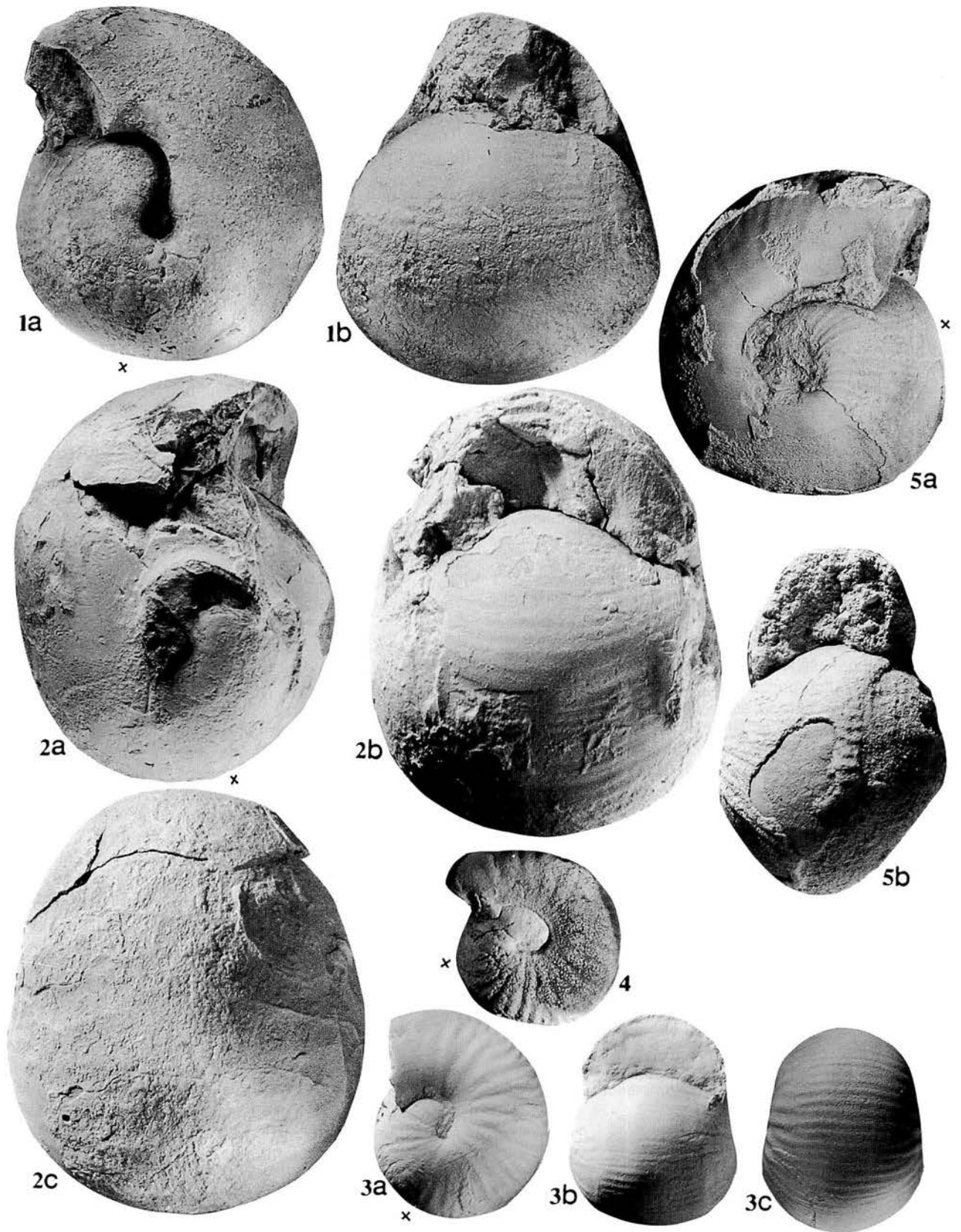
##### *Macroconch*.—

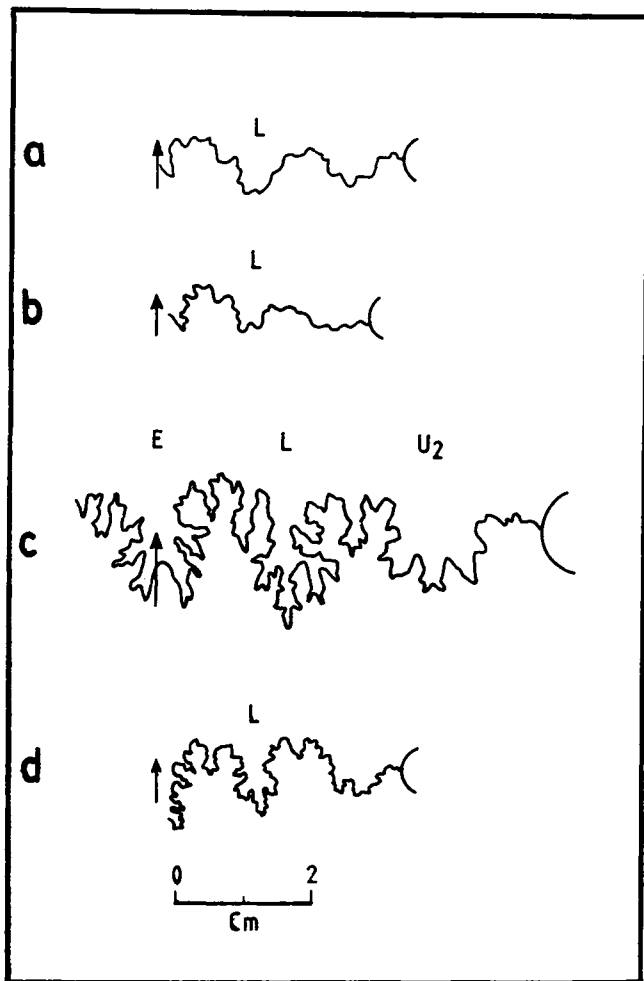
- 1846 *Ammonites bullatus* d'Orbigny, pl. 142, fig. 1, 2.  
1954 *Bullatimorphites bullatus* (d'Orbigny). Arkell, text-fig. 34.  
1958 *Kheraiceras bullatus* (d'Orbigny). Westermann, pl. 22, fig. 1a–b.  
1984 *Bullatimorphites (Kheraiceras) bullatus* (d'Orbigny). Westermann, Corona and Carrasco, pl. 2, fig. 8a–b.  
1987 *Kheraiceras cosmopolita* Krishna, Cariou and Enay, p. 4, pl. 1, fig. 6.  
1990 *Kheraiceras bullatum* (d'Orbigny). Krishna and Cariou, p. 112.

##### *Macroconch and microconch*.—

- 1999 *Kheraiceras bullatum* (d'Orbigny). Bardhan, Sardar and Jana, pl. 1, figs. 5–6.

*Material*.—Seven macroconch specimens, mostly adults, internal moulds with aperture missing. All come only from Bed 2, Keera; JUM/K/8–12, JUM/K/17 from lower horizon (Horizon I) and a near complete small variant, JUM/K/13, from upper level (Horizon II). Four microconchs with shell remains come only from Jumara; JUM/J/12 and JUM/J/13 with flared collar from Bed 6 (Horizon VII); JUM/J/14 with last quarter of body chamber missing, from Bed 5 (Horizon VI); JUM/J/11 near complete, abraded on one side, from basal part of Bed 7 (Horizon IX).





**Figure 6.** Septal sutures of *Kheraiceras*. **a, b.** Adult septal sutures of *Kheraiceras bullatum* (d'Orbigny) <M>, **a:** JUM/K/17 and **b:** JUM/K/9. **c.** Penultimate septal suture of the holotype (GSI type no. 2009) of *Kheraiceras cosmopolitum* (Parona and Bonarelli) <M>, after Spath 1928. **d.** Adult septal suture of *Kheraiceras* cf. *hannoveranum* (Roemer) <M>, JUM/J/10.

**Measurements.**—To record the remarkable modification of the adult body chamber, multiple measurements at different positions are given for a few specimens (Table 1).

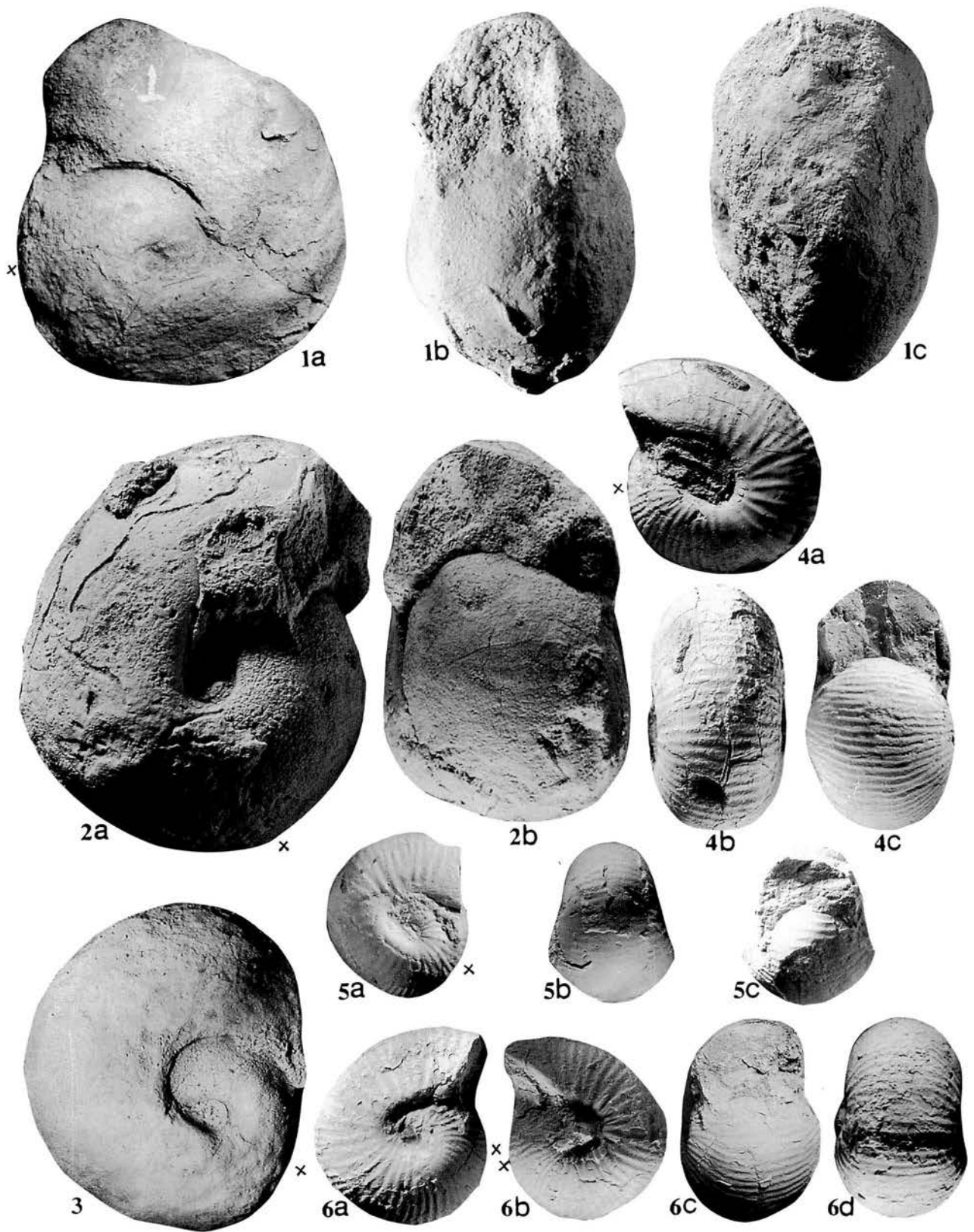
**Description.**—Macroconch<M>: Mostly internal mould, thin shell remains are rarely preserved. Body chamber

**Table 1.** Measurements for *Kheraiceras bullatum* (d'Orbigny, 1846) (in mm)

Specimen		D	U	H	W
Holotype	aperture	78	31	25	40
<M> JUM/K/8	body chamber	61	20	24	33
		56(ca)	13	26	32
		52	8	28	38
<M> JUM/K/9	body chamber	57	18	23	33
		54	17	24	32
<M> JUM/K/10	end-phragmocone	42(ca)	9	26	36
	body chamber	59(ca)	13	21	22
<M> JUM/K/11	body chamber	49	11	24	28
		57	20	22	23(ca)
<M> JUM/K/12	end-phragmocone	41	12	23	38(ca)
	aperture	60	20	24	32
<M> JUM/K/13	end-phragmocone	40	12	22	40
	aperture	47	14	18	27.5
	body chamber	43	10.5	19	26
<M> JUM/K/17		37	8	19	30
	end-phragmocone	34(ca)	8	14	23
	aperture	67	20	29	38
<M> JUM/J/11	end-phragmocone	53(ca)	12	28	42
	aperture	41	11	14	19
<M> JUM/J/12	body chamber	34	10	16	21
	aperture	43	14	15	23
<M> JUM/J/13	body chamber	36	10	15	21
		34	9	16	21
	aperture	35	12	16	20
<M> JUM/J/14	body chamber	30	7	13	19
		29	—	14	19
	body chamber	28	8	11	17
	26	8	11.5	17	
	23	5	11.5	19	

ellipticonic, phragmocone spindle-shaped. Early whorls involute, relatively depressed ( $W/H=1.04-1.65$ ), one inflated variant (JUM/K/12) having  $W/H=1.8$ . Maximum diameter observed is 67 mm, the specimen (JUM/K/17, Figure 7-2a,b) was still larger as evident from the trace of the last quarter of body chamber. Body chamber occupying almost whole of the last whorl. It partially occludes umbilicus at diameter 41 mm–55 mm immediately after end-phragmocone stage and shows a strong deviation from regular spiral, where it becomes straight initially and then egresses out ec-

← **Figure 5.** Dimorphs of *Kheraiceras*. (All natural size). **1-4.** *Kheraiceras cosmopolitum* (Parona and Bonarelli). **1a, b.** Holotype <M> 2009, from Golden Oolite of Keera Bed 2, mostly internal mould, adult with incompletely preserved body chamber, highly depressed variant, lateral (a) and frontal (b) views. **2a-c.** Adult <M> with last quarter of body chamber missing, from Horizon V, Bed 5, Jumara, JUM/J/5, lateral (a), frontal (b) and ventral (c) views. **3a-c.** Almost complete <M>, from Horizon X, Bed 7, Jumara, JUM/J/6, lateral (a), frontal (b) and ventral (c) views. **4.** Adult <M>, body chamber fully preserved, but broken near venter, from Horizon IX, Bed 7, Jumara, JUM/J/2, note terminal constriction preserved at the flank, lateral view. **5a, b.** *Kheraiceras bullatum* (d'Orbigny), <M>, mostly internal mould with shell remains. Adult with almost completely preserved body chamber, from Horizon I, Bed 2, Keera, JUM/K/12, lateral (a) and frontal (b) views. x: base of body chamber.





centrally, resulting in a wider umbilicus near peristome. Umbilicus varies ontogenetically ( $U/D=0.22-0.35$ ), holotype being more evolute ( $U/D=0.40$ ) relatively narrow, shallow to moderately deep in inner whorls; umbilical margin distinct and wall steeper throughout adult body chamber. Flanks short to slightly wide, flat to gently curved with rounded ventrolateral margin. Venter rounded, broad. Adult phragmocone diameter ranges from 40 to 53 mm and even less in a small variant, where the figure is about 34 mm. Maximum width of shell attained just at beginning of adult body chamber. Width of body chamber contracts maximally at middle part from where it gradually increases again. Whorl height on the other hand gradually decreases with increasing shell diameter. Aperture missing. Whorl depressed, semicircular to semielliptical in apertural outline.

Ribbing not well discernible as shell is mostly internal mould. Ribs appear to be dense and fine on inner whorls, while broad, distant and restricted on venter and seen at least up to diameter 57 mm in the adult body chamber. The number of secondaries on first half of outer whorl is about 24.

Both lobes and saddles not deeply incised. Both external and lateral lobes are frilled, but former are more slender. Incipient internal lobes less frilled. External saddle weakly bifid, first lateral saddle shallow, broad (Figure 6-a, b).

Microconch <m>: Mostly shell remains, strongly resembles macroconch in many morphological features (Figure 9) except being smaller in size ( $M : m \sim 1.42$ ). Beginning of adult body chamber is marked by sudden egression of umbilical seam and maximum inflation ( $W/H=1.25-1.65$ ) occurs just after it. Body chamber occupies nearly entire last whorl. Diameter of adult shell ranges from 35 to 43 mm. Apertural shape variable, elliptical to ovate. Peristome with slightly flared collar followed immediately by terminal constriction which cuts ribs obliquely. At middle part of body chamber of diameter 29 mm to 35 mm, apertural contraction is maximum, after which shell width again gradually increases towards aperture. Venter broad, strongly curved in inner whorls, becoming narrow and gently curved in body chamber. Laterals highly reduced, rounded up to end-phragmocone but widens and flattens later.

Both primary and secondary ribs are conspicuous, persistent up to peristome. Ribs fine and closely spaced in the early stage, becoming coarse and distant in outer whorl. Primaries rising from umbilical wall slightly rursiradiately, bifurcate irregularly at mid-flank or slightly higher. Secondaries and occasional solitaires go straight over venter. Number of secondaries in half whorl varies from 27 to 30.

Septal suture not discernible.

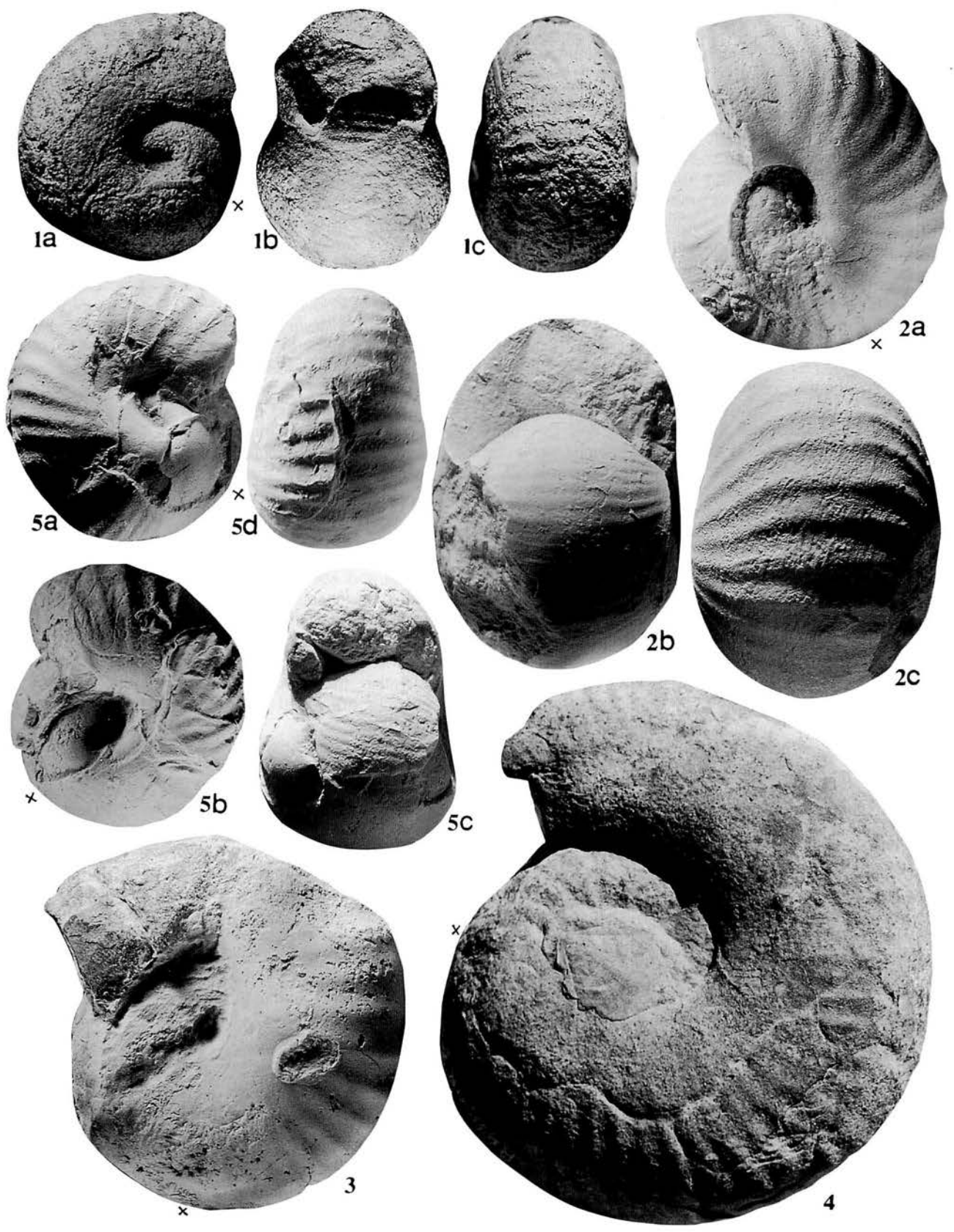
*Discussion.*—Macroconchs of the present form are closely

allied to the type specimens of *K. bullatum* (d'Orbigny, 1846) (see Arkell, 1954, text-fig. 34). They show strong resemblance in shell shape, whorl outline and nature of uncoiling of the umbilical seam. Ribbing pattern and the number of secondaries in the Kutch variant also agree more closely with the Lower Callovian *K. bullatum* s.s. The ribbing in the present macroconchs, however, is less conspicuous since most of them are internal moulds, and Arkell (1954) also pointed out that it is exaggerated in d'Orbigny's figure. However, d'Orbigny's species differs by its slightly larger adult shell diameter and relatively more inflated form. The stratigraphic and geographic distribution of *K. bullatum* is now better known. It is found in Europe, South America and Mexico, and ranges in age from Late Bathonian to Early Callovian (Cariou, 1984; Westermann *et al.*, 1984; Riccardi *et al.*, 1989; Sandoval *et al.*, 1990). The stratigraphic distribution of *K. bullatum* both in Kutch and France shows a phyletic size decrease (see also Krishna and Cariou, 1990). The relatively smaller adult size of the Kutch forms in comparison to those of Europe may, therefore, actually represent a smaller variant of a higher stratigraphic level or may be due to geographic variation (Bardhan *et al.*, 1999).

The microconch described here under the present species strongly resembles the macroconch of *K. bullatum* of both Kutch and European forms. Its phragmocone is similarly cadiconic but not much inflated like that of *K. cosmopolitum*, body whorl with typical *bullatum*-like uncoiling. The microconch, however, is characterised by much smaller adult size and apertural modification. In the microconch ribs are fine, dense, continuing all through the body whorl. Interestingly, in Kutch, although both dimorphs come from coeval stratigraphic horizons, they do not occur together. Macroconch specimens come from different stratigraphic levels within the Golden Oolite of Keera whereas the microconchs are found in different but coeval horizons of Jumara.

Microconch shows strong resemblance to different species of *Bomburites*. *B. devauxi* (de Grossouvre, 1891) (see Arkell, 1952, text-fig. 27), though similar in nature of shell shape and uncoiling, differs mainly by its smaller size, more depressed aperture and presence of strongly flared collar behind the terminal constriction. *B. globuliforme* (Gemmellaro, 1872) (see Arkell, 1952, text-fig. 27) has a shell size comparable to one of the variants of the present form (Figures 7-4a-c), but it is coarsely ornate and characterized by a peristome with a much flared collar. *K. prahecuense* of France also resembles the present form in shell diameter and *K. bullatum*-like other features. In Kutch both dimorphs are found at the same stratigraphic levels, but *K. prahecuense* appears only after the disappearance of *K.*

← **Figure 7.** *Kheraiceras bullatum* (d'Orbigny). (All natural size). **1a-c.** Adult <M>, internal mould, body chamber fully preserved, from Horizon I, Bed 2, Keera, JUM/K/8, lateral (a) frontal (b) and ventral (c) views. **2a, b.** Adult <M>, internal mould, almost completely preserved body chamber, from Horizon I, Bed 2, Keera, JUM/K/17, lateral (a) and frontal (b) views. **3.** Almost completely adult <M>, internal mould, aperture missing, from Horizon I, Bed 2, Keera, JUM/K/9, lateral view. **4a-c.** Adult <m>, with terminal constriction preserved near the flank, from Horizon VII, Bed 6, Jumara, JUM/J/12, lateral (a), ventral (b) and frontal (c) views. **5a-c.** Almost completely adult <m>, with partially preserved body chamber, from Horizon VI, Bed 5, Jumara, JUM/J/14, lateral (a), ventral (b) and frontal (c) views. **6a-d.** Complete adult specimen <m>, from Horizon VII, Bed 6, Jumara, JUM/J/13, lateral (a,b), frontal (c) and ventral (d) views. Note terminal constriction in 6b. x: base of body chamber.



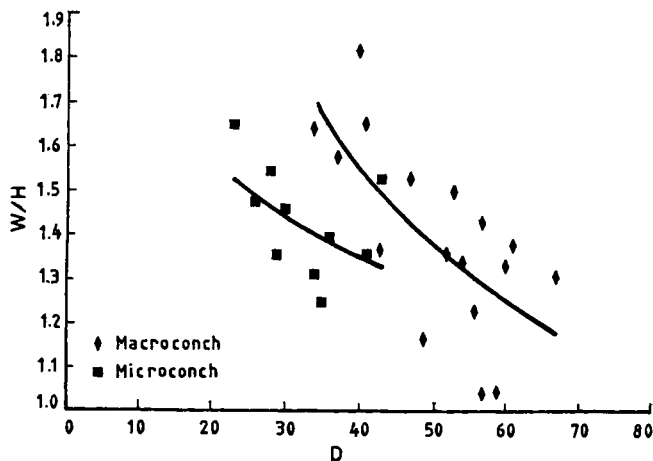


Figure 9. Best-fit growth curves of whorl section of macroconch and microconch of *Kheraiceras bullatum* (d'Orbigny).

*bullatum*, thus making two distinct subzones (Cariou, 1984). Recently, *Ammonites microstoma* d'Orbigny (see Arkell, 1954, text-fig. 35) has been considered as a possible microconch of *K. bullatum* (Westermann and Riccardi, 1979 and Westermann and Callomon, 1988). *A. microstoma*, though, with a less depressed phragmocone, has a gradual *Bullatimorphites*-like uncoiling of the body chamber. It appears that the present microconchiate forms are the better candidates to match to the true, i. e., macroconchiate form of *K. bullatum*.

The present macroconch closely resembles *K. cf. hannoveranum* <M>, described here, but the latter is larger and strongly ornate. Detailed comparison, however, is given in the discussion part of *K. cf. hannoveranum*.

Noetling's (1896) '*Sphaeroceras*' cf. *bullatum* is a giant *Kheraiceras* and considered as *K. cf. bullatum* by Pandey and Westermann (1988) and Westermann and Callomon (1988). Arkell (1954) also compared it with the European *K. bullatum* s.s. Noetling described the species from the Upper Bathonian Polyphemus Limestone, Baluchistan. We have inspected the only monotypic specimen reposit in the Geological Survey of India, Calcutta (Type No. 2915). Admittedly it is comparable with the European *K. bullatum* in coiling and ribbing pattern, but it is exceptionally large for the genus, having a diameter of 158 mm. Its body whorl is highly contracted and the aperture is barely in contact with the ventral surface of the preceding whorl. Besides, the

phragmocone does not become depressed as much as in *K. bullatum* and ribs disappear much earlier in the inner flank on the body chamber. The Baluchistan specimen is described here as a new species, *K. noetlingi* sp. nov.

*K. cosmopolitum* (Parona and Bonarelli, 1895), the type species, comes also from Kutch and stratigraphically overlaps the present species in the lower part of its range. This species and *K. bullatum* are closely related and their microconchs are also known. The nature of dimorphism is quite distinct and speaks for their specific separation. Both morphs of *K. cosmopolitum* have much inflated phragmocone, more depressed aperture and more eccentrically coiled body chamber than those of the present species. Microconchs of the two species are ornate to the end and characterised by apertural modification, but the microconch of *K. bullatum* has relatively fine, denser ribbing and more secondaries in the outer whorl than in *K. cosmopolitum*. Septal sutures are well discernible in macroconchs only, which are mainly represented by internal moulds. *K. cosmopolitum* has a more complex sutural pattern (Figure 6-c) at the same growth stage. Interestingly, both the species differ in macroconch-microconch size ratio which is greater in *K. cosmopolitum* ( $M : m \approx 2.05$ ).

*Kheraiceras spathi* sp. nov. <m> described later, is readily distinguishable from the microconch of the present species by its elliptically coiled body chamber, less depressed and less evolute early whorls, and pronounced terminal constriction.

Microconch of the present species differs from *Kheraiceras* sp. A <m>, described later, in being larger with coarse ornamentation and widely spaced ribbing.

Westermann *et al.* (1984) described *B. (K.) bullatum* from Mexico based on a full-grown and almost complete specimen (pl. 2, fig. 8a-b). Its obsolete ribbing on the body chamber and number of secondaries agree closely with some of our specimens of the present species. However, this Mexican form is slightly larger and may be an older geographic variant since it comes from the Upper Bathonian horizon. *Bullatimorphites (Kheraiceras) v-costatus* from the Upper Bathonian of Caracoles, Chile is a large and coarsely ornate form (Riccardi *et al.*, 1989, pl. 8, figs. 3, 4). This form is even larger than true *K. bullatum* <M> (d'Orbigny, 1846) of Europe and the Kutch form. Its ribbing is strong, distant and seems to persist on most of the outer whorl, and thus perhaps agrees closely with contemporary *K. hannoveranum* (Roemer).

Recently Géczy and Galacz (1998) described a new Late Bathonian species *Bullatimorphites (Bullatimorphites) dietli* from South Hungary. The paratype of the species (Géczy

← Figure 8. Dimorphs of *Kheraiceras*. (All natural size). 1a-c. *Kheraiceras bullatum* (d'Orbigny) <M>, internal mould, small variant, complete adult specimen, from Horizon II, Bed 2, Keera, JUM/K/13, lateral (a), frontal (b) and ventral (c) views, note obsolete ribbing restricted on the venter. 2-5. *Kheraiceras cf. hannoveranum* (Roemer) <M> and <m>. 2a-c. Adult <M> with last 1/3 of the body chamber missing, from Horizon IV, Bed 4, Jumara, JUM P-2, lateral (a), frontal (b) and ventral (c) views. 3. Adult <M>, one half is damaged, last part of the body chamber crushed, from Horizon V, Bed 5, Jumara, JUM/J/10, lateral view. 4. Almost complete adult specimen <M>, one side damaged, from the Polyphemus Limestone, Mazardrik, Baluchistan, kept in Indian Museum, Calcutta, type no. H. 48.607, lateral view. 5a-d. Almost complete adult specimen <m>, peristome missing, from Horizon I, Bed 2, Keera, JUM/K/7, lateral (a,b), frontal (c) and ventral (d) views. Note retention of coarse, distant ribbing to the end. x: base of body chamber

and Galacz, 1988, pl. III, fig. 7) resembles our smaller, younger variant (Figure 8.1a-c) from the late Early Callovian in nature of umbilical uncoiling and adult body whorl length.

Sandoval *et al.* (1990) recently established dimorphism in *K. bullatum* from the Upper Bathonian of Mexico. They synonymised their microconch with *Bomburites microstoma*, but the Mexican form differs from that of d'Orbigny. It, in fact, is very closer to the present microconch and one Mexican variant (*ibid.* pl. 9, 3a-c) is barely distinguishable.

**Occurrence.**—*Kheraicerias bullatum* has a wide biogeographic distribution. Besides Kutch, it occurs in Europe, South America and Mexico from the Late Bathonian to Early Callovian. In Europe the species is abundant in France. The lectotype (see Arkell, 1954, text-fig. 34) comes from the Upper Bathonian. The species is common in the Bullatum Subzone of the Lower Callovian (Cariou, 1984). *K. cf. bullatum* is reported from the East Pacific faunal province. In Mexico it appears in the lower part of the Steinmanni Zone (=upper part of Restrocostatum Zone or Aspidoides Zone of Europe), and is associated with *Epistrenoceras histricoides*, indicating a Late Bathonian age (Westermann *et al.*, 1984; Sandoval *et al.*, 1990). In Argentina it comes from the Vergarensis Zone, which is equivalent to the Macrocephalus Zone of Submediterranean France (Riccardi *et al.*, 1989).

All seven macroconchs from Kutch localities come from different horizons within Bed 2, Keera. JUM/K/8–12, JUM/K/17 from Horizon I and JUM/K/13 from Horizon II. Four microconchs come from Jumara. JUM/J/14 from Horizon VI, Bed 5; JUM/J/12–13 from Horizon VII, Bed 6 and JUM/J/11 from Horizon IX, Bed 7.

#### ***Kheraicerias cf. hannoveranum* (Roemer)**

Figures 6d; 8.2–8.5

##### **Macroconch.—**

- 1911 *Sphaeroceras quenstedti* var. *hannoverana* n.v. Roemer, p. 42, pl. 7, figs. 16, 21, pl. 8, fig. 1.  
 1915 *Sphaeroceras bullatum* d'Orbigny. Lóczy, p. 351, text-fig. 79.  
 1925 *Kheraicerias ? stansfieldi* Spath, pl. I, fig. 2a–b.  
 1952 *Bullatimorphites hannoveranus* (Roemer). Arkell, p. 108.  
 1958 *Bullatimorphites bullatus hannoveranus* (Roemer). Westermann, p. 65, pl. 21, figs. a–b.  
 1970 *Bullatimorphites (Bullatimorphites) cf. hannoveranus* (Roemer). Mangold, p. 303, figs. 96–97.  
 1971 *Bullatimorphites cf. hannoveranus* (Roemer). Hahn, pl. 7, fig. 3.  
 1988 *Bullatimorphites* sp. Bardhan, Datta, Khan and Bhaumik, pl. 1, fig. 1a–c.  
 1993 *Kheraicerias* sp. nov. A. Callomon, p. 235.  
 1994 *Bullatimorphites (Kheraicerias) hannoveranus* (Roemer). Dietl, p. 10, pl. 1, fig. 2.  
 1997 *Bullatimorphites (Kheraicerias) hannoveranus* (Roemer). Mangold and Rioult, pl. 18, fig. 6.  
 1998 *Bullatimorphites (Bullatimorphites) hannoveranus* (Roemer). Géczy and Galacz, pl. III, figs. 1a–b, 2a–b, text-fig. 9.

##### **Macroconch and microconch.—**

- 1999 *Kheraicerias cf. hannoveranum* (Roemer). Bardhan, Sardar and Jana, pl. 1, figs. 7–9.

**Material.**—The present collection includes three macroconchs and one microconch. Two macroconchs (JUM P-2, JUM/J/10) are collected from Beds 4 and 5 of Jumara (Horizons IV and V in Figure 2), Kutch, and the other one is from the Polyphemus Limestone, Mazardrik, Baluchistan, and now kept in the Indian Museum (H 48.607), Calcutta. The only microconch, JUM/K/7, comes from the lower part of the Golden Oolite (Bed 2, Horizon I in Figure 2) of Keera.

**Measurements.**—See Table 2.

**Description.**—Macroconch <M>: Shell ellipsoconic, moderately inflated, involute up to adult phragmocone stage and then becomes evolute with rapid uncoiling of umbilical seam. Whorl section depressed, ovate. Adult phragmocone diameter ranges from 45 to 60 mm. Adult body chamber covering more than 3/4 of the last whorl. Maximum shell diameter observed is about 100 mm. Maximum inflation (W/H=1.27–1.76) occurs at or just after end-phragmocone; both width and height show negative allometry afterwards.

Umbilicus shallow and umbilical margin is steep up to end-phragmocone diameter or early part of body chamber but later gradually becoming less inclined. Sudden egression of umbilical seam coincides with beginning of body chamber; first it goes straight up to about 18 mm length occluding partially umbilicus of inner whorl, then turns inwards eccentrically towards aperture resulting in a 'hook-shaped' body chamber. Flank short, barely existing in inner whorl but with ontogeny becomes broad and gently curved. Venter broad, highly curved at early stage but becomes gently rounded on adult body chamber. Ventrolateral margin is always rounded.

Shell coarsely ornate on body chamber. Phragmocone with relatively fine and dense secondaries; primaries short, regular and bifurcating on inner flank, and originating from umbilical margin. They disappear, resulting in smoothening of inner flank of body chamber while secondaries suddenly become coarse, distant and traced up to end of body chamber. Secondaries assume a broad, convex pattern aborally and then flex forward near ventrolateral margin and go over venter with slight forward projection. Number of secondaries on first half of outer whorl is 24.

Both external and lateral saddles are large, frilled.

**Table 2.** Measurements for *Kheraicerias cf. hannoveranum* (Roemer) (in mm).

Specimen	D	U	H	W
<M> JUM/J/10 body chamber	72(ca)	19	27	38
	61	20	34	44
<M> JUM P-2 body chamber	51	—	26	40
	60	14	24	40
<M> JUM/J/10 end-phragmocone	49	7	25	44
	45	7	24	40
<M> H 48.607 aperture	99(ca)	33	27(ca)	—
	60(ca)	—	24	34
<m> JUM/K/7 aperture	48	12	17	27
	42	13	22	28
	35(ca)	5	23	33

External saddle bifid with deeply incised secondary lobes, lateral lobe deep, narrow (Figure 6-d).

Microconch <m>: It replicates macroconch in all major aspects barring size. Body chamber occupies almost whole of last whorl. Maximum diameter observed is 48 mm. Maximum inflation ( $W/H \approx 1.59$ ) occurs on adult body chamber at diameter 35 mm followed by sudden contraction with decrease of both height and width. Aperture missing. Body chamber, initially after deviating from the regular spiral, goes straight for a distance of about 12 mm and then turns centrifugally towards the aperture.

Ornamentation similar to that on macroconch but both primaries and secondaries retained without losing strength up to end of preserved body chamber. Number of secondaries on first half of outer whorl is about 30.

**Discussion.**—The present species can be readily distinguished from other Kutch forms by its coarsely ornate ribbing which persists to the end of adult conch, sutural pattern and nature of dimorphism. However, it occupies morphometrically an intermediate position between highly depressed *K. cosmopolitum* and relatively compressed *K. bullatum* (see Figure 10).

The present species differs from *K. cosmopolitum* by its less contracted body chamber and less inflated phragmocone, relatively simple sutural pattern and more distant, coarse ribbing persistent up to the end of the body chamber. Moreover, in *K. cosmopolitum*, the growth of shell width relative to shell diameter shows negative allometry, while in the present species both width and height of the body chamber decrease with increasing shell diameter. Flanks are wider than in *K. cosmopolitum*. Moreover, dimorphic size ratio between these two species also differs.

The lectotype of *K. hannoveranum* from the Upper Bathonian Orbis Zone of Germany matches well with the macroconchs of the present species in having a less inflated phragmocone and coarse ribbing which persists to the end. Jain *et al.* (1996) also compared one of the variants (JUM P-

2, Figures 8-2a-c) of the present Kutch form with *Bullatimorphites* cf. *hannoveranus* (Roemer, 1911, pl. 8, fig. 1; Hahn, 1971, pl. 7, fig. 3) and *B. (Bullatimorphites)* cf. *hannoveranus* (Mangold, 1970, p. 303, figs. 96-97) from the Upper Bathonian Restrocostatum Zone of the Southern Jura. Callomon (1993) also noticed a similarity between the same Kutch specimen (JUM P-2) and *B. costatus* Arkell (Lissajous, 1923, p. 18, fig. 2), and *K. suivecum* (Roemer) (pl. 7, fig. 21). The latter species has now been regarded as a microconch of the present species (Géczy and Galacz, 1998) and the type specimens of *K. suivecum* (see Arkell, 1952, text-fig. 36) are quite comparable with the microconch of the present species (JUM/K/7) described herein (Figure 8-5a-d). All of them are characterised in having strongly ornate outer whorl and ribbing which continues to the end without losing strength.

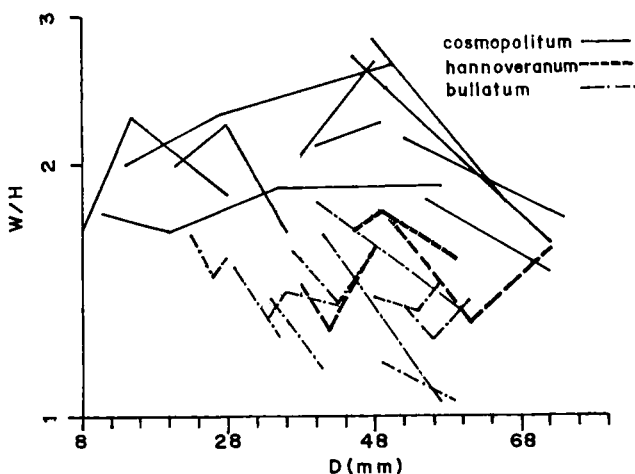
The European macroconchs of the present species are larger in size and come from the older stratigraphic horizons. The present forms come from beds ranging in age from Late Bathonian to earliest Callovian. It appears that their smaller adult size may be due to geographic variation as well as younger stratigraphic age, since phyletic size decrease is found in many species of *Kheraiceras*.

The macroconch of the present species is a close ally of that of *K. bullatum*, but differs in relatively large adult size and less contracted and less aberrantly coiled body chamber. Besides, in *K. bullatum* ribs are finer, more numerous, restricted mainly on the venter, and disappear finally near the aperture, while coarse, distant ribs which persist throughout the last whorl characterise the present species. Remarkably, these differences are also observed in microconchs.

*Kheraiceras? stansfieldi* described by Spath (1925, pl. 1, fig. 2a-b) from the 'Lower Callovian' Macrocephalus Zone of Madagascar, which is represented by an adult steinkern with crowded septal sutures and an incomplete body chamber, matches well with one of our specimens (Figures 8-2a-c) coming from the Madagascariensis Horizon. Both Kutch and Madagascan forms are similarly less depressed in apertural outline and have a rounded umbilical margin, and prorsiradiate ribs. Interestingly, the Madagascan form comes from the same locality and horizon which yield *Macrocephalites madagascariensis*. We believe that *Kheraiceras? stansfieldi* and the present *K. cf. hannoveranum* are conspecific.

**Occurrence.**—The lectotype of *K. hannoveranum* comes from the Upper Bathonian Orbis Zone of Germany. It closely resembles the Kutch form. The other Upper Bathonian specimens of the present species e.g., *Bullatimorphites* cf. *hannoveranus* (Roemer, 1911, pl. 8, fig. 1; Hahn, 1971, pl. 7, fig. 3), and *B. (Bullatimorphites)* cf. *hannoveranus* (Mangold, 1970, figs. 96-97, cited in Jain *et al.*, 1996) come from the Upper Bathonian Restrocostatum Zone of the Southern Jura.

Among our three macroconchs, JUM P-2 comes from Horizon IV, Bed 4, Jumara and JUM /J/10 from Horizon V, Bed 5, Jumara. The other one (H 48.607) comes from the Polyphemus Limestone, Mazardrik, Baluchistan. The only microconch (JUM/K/7) comes from Horizon I, Bed 2, Kerra.



**Figure 10.** Growth curve of whorl section of both macroconch and microconch of three species of *Kheraiceras* in Kutch. Continuous line graph shows developmental change in a specimen.



I



2a



2b



3b



3a



3c



***Kheraiceras spathi* sp. nov.**

Figures 11.2a, b

**Microconch.**—1931 *Kheraiceras* aff. *cosmopolita*, Spath, pl. XCVI, fig. 8a-b.1999 *Kheraiceras* sp. B. Bardhan, Sardar and Jana, pl. 1, fig. 12.

**Material.**—The present species is represented only by the holotype specimen (JUM/J/15) collected from Horizon V, Bed 5 of Jumara.

**Diagnosis.**—Shell small, compressed; inner whorls evolute, umbilical wall overhanging, depressed phragmocone, much contracted body chamber; width decreases during ontogeny, while height remains constant on outer whorl; retaining ancestral *Bullatimorphites*-like gradual uncoiling of body chamber, but characterised by flared peristome and highly contracted body chamber.

**Etymology.**—In honour of L.F. Spath, England, who first studied this species.

**Measurements.**—See Table 3.

**Description.**—Microconch <m>: Mostly internal mould, small, slender in shape (W/D=0.84 to 0.41, during ontogeny of outer whorl). Inner whorl sphaeroconic, gradually uncoiled to ellipticonic outer whorl. Body chamber occupies almost whole of last whorl. Maximum diameter observed is 36 mm. Beginning of body chamber at about 22 mm, marked by slightly inward curving of outer whorl, thus occludes partially inner umbilicus (U/D=0.21) and followed thereafter by gradual eccentric coiling, so that at aperture body chamber is in contact only with ventral surface of preceding whorl (U/D=0.33). Inner whorl relatively evolute, depressed with laterals barely existing. Venter broad, strongly curved. Umbilical margin sharp, angular with overhanging umbilical wall. Inner flanks gradually flatten and umbilical margin becomes rounded near aperture. Maximum inflation (W/H≈1.9) of shell is attained after beginning of adult body chamber. Width decreases from the early part of adult body chamber with increase of shell size, but height remains almost unchanged. Laterals widen and venter narrows ontogenetically on body chamber; whorl section depressed, ovate (at aperture, W/H=1.5). Aperture with deep, broad terminal constriction which rises very sharply in rursiradial

manner near inner margin, then proceeds with a broad forward projection towards outer margin. Peristome projected forward at venter. Aperture immediately next to the constriction appears to be slightly flared in internal mould.

Ribbing fine, feeble on internal mould but appears to be persistent up to aperture. Suture not well discernible.

**Discussion.**—The microconchiate affinity of the present specimen is obvious in its smaller size and contracted adult body chamber with modifications at the peristome.

The present species strongly recalls '*Bomburites*', a genus which is now considered as microconchs of *Kheraiceras*. It is a close match of the holotype of the type species *Bomburites devauxi* (de Grossouvre, 1891) (Arkell, 1954, text-fig. 27). However, the present species differs mainly by its gradual uncoiling of the body chamber, fine ribbing, relatively larger adult size and absence of any prominent flared collar at peristome.

Spath's (1931) *Kheraiceras* aff. *cosmopolita* (pl. XCVI, figs. 8a-b) which comes from the same stratigraphic horizon (Bed 5) and same locality at Jumara, resembles so strikingly the present species that they appear to be conspecific.

The present species differs from microconchs of all other *Kheraiceras* spp. of Kutch by its compressed form, gradual uncoiling of umbilical seam and inwardly sloping umbilical wall. It differs from *K. bullatum* <m> by its gradual uncoiling of umbilical seam, ellipticonic body chamber and less ornate shell.

*K. cosmopolitum* <m> is the most tumid species (W/D=0.69-1.03) of the present group, with an eccentrically coiled body chamber. It has a more depressed phragmocone and aperture than those of *K. spathi*. Besides, ribs in *K. cosmopolitum* are coarser and more distant.

Microconch of *K. cf. hannoveranum* is readily distinguishable from the present form in having larger shell diameter, strong ornamentation, highly contracted and aberrantly uncoiled body chamber.

The original figure of *Ammonites microstoma* described by d'Orbigny (1846, pl. 142, figs. 3-4) which was refigured by Arkell (1954, text-fig. 35) is closely comparable with the present form, particularly with respect to gradual uncoiling of the body chamber and presence of a deep terminal constriction. *A. microstoma* d'Orbigny, 1846 is now considered as a microconch of *Kheraiceras*. It, however, differs from the present form in its larger size, strongly ornate shell and distinct collar.

Spath (1931) compared the present form with *K. globuliformi* (Gemmellaro, 1872) (Parona and Bonarelli, 1895, pl. VI, fig. 1) but the latter species is larger in size and characterized by coarse ribbing, more eccentrically coiled body chamber and highly flared peristome.

**Occurrence.**—The monotypic holotype (JUM/J/15) comes from a horizon (Horizon V, Bed 5, Jumara) which lies just

**Table 3.** Measurements for *Kheraiceras spathi* sp. nov. (in mm).

Specimen	D	U	H	W
<m> Holotype, aperture	36	12	10	15
JUM/J/15 body chamber	29	8	10	17
near end-phragmocone	23	5	10	19.5

← **Figure 11.** Dimorphs in *Kheraiceras*. (All natural size). **1.** *Kheraiceras noettingi* sp. nov. <M>, holotype, (type no. 2915), complete adult, from the Polyphemus Limestone, Mazardrik, Baluchistan, now kept in Curatorial Division, Geological Survey of India, Calcutta, lateral view. **2a, b.** *Kheraiceras spathi* sp. nov. <m>, holotype, internal mould, complete adult specimen with deep terminal constriction from Horizon V, Bed 5, Jumara, JUM/J/15, lateral (a) and frontal (b) views. **3a-c.** *Kheraiceras* sp. A. <m>, adult with almost completely preserved body chamber, abraded near the last part, from Horizon III, Bed 2, Keera, JUM/K/16, lateral (a), frontal (b) and ventral (c) views; note fine, dense ribbing. x: base of body chamber.

above the Bathonian-Callovian boundary.

***Kheraiceras* sp. A**

Figures 11.3a–c

*Microconch.*—

1999 *Kheraiceras* sp. A. Bardhan, Sardar and Jana, pl. 1, fig. 11.

*Material.*—Only one specimen (JUM/K/16) collected from the Golden Oolite (Bed 2, Horizon III in Figure 2), Keera.

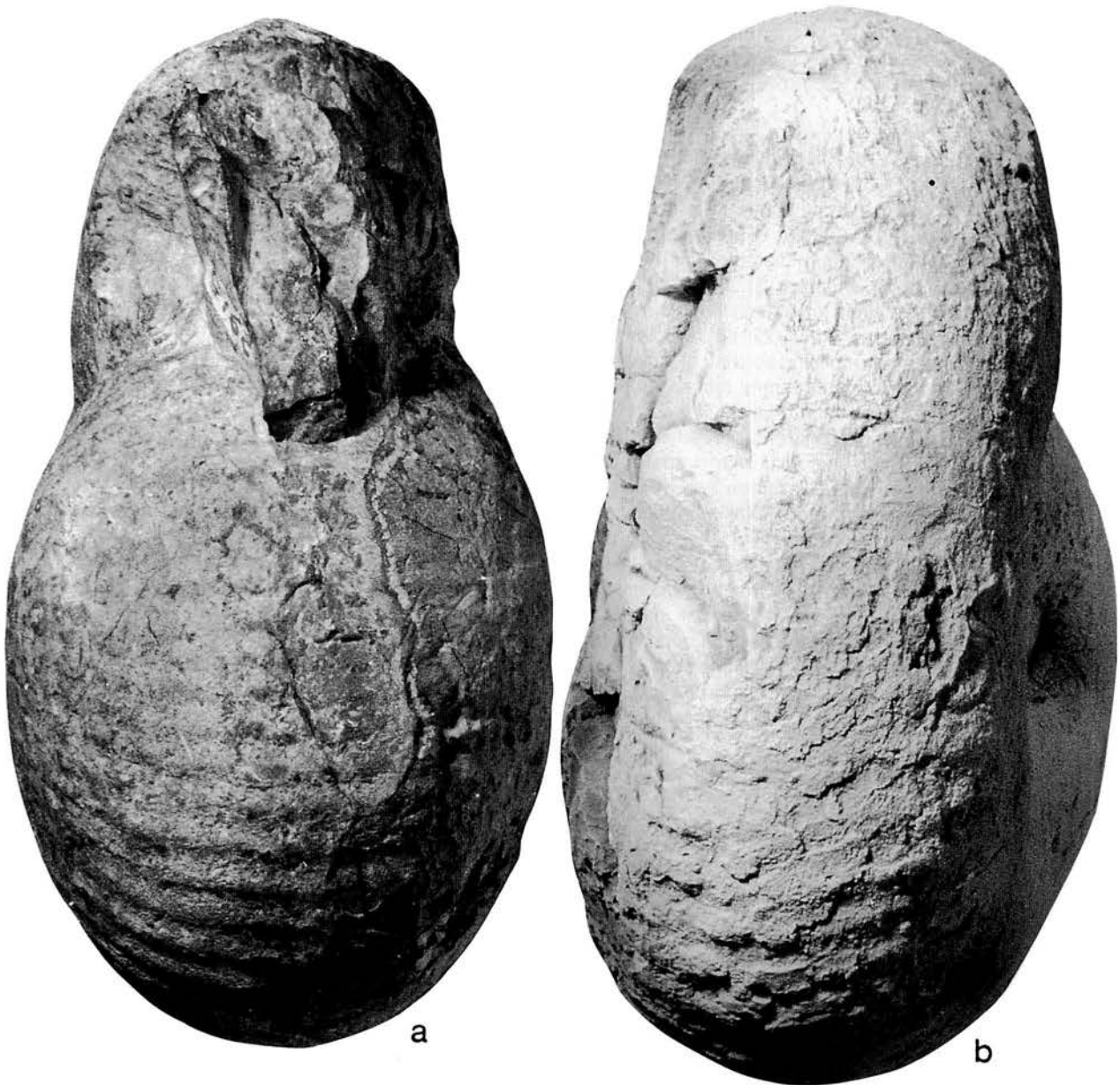
*Measurements.*—See Table 4.

*Description.*—Microconch <m>: Shell small, ellipsoconic?

**Table 4.** Measurements for *Kheraiceras* sp. A (in mm).

Specimen	D	U	H	W
<m> JUM/K/16 aperture	?30	7(ca)	11.5	14
body chamber	31	7(ca)	12	19
	26	4.5	11	20

( $W/D \approx 0.46$ ); strongly involute inner whorls. Adult phragmocone at about 21 mm. Maximum inflation ( $W/H = 1.8$ ) is attained after beginning of body chamber at 26 mm. Width of body whorl decreases rapidly with ontogeny while height



**Figure 12.** *Kheraiceras noettingi* sp. nov. <M>, same as figure 11.1, frontal (a) and ventral (b) views. (All natural size).

remains more or less same. Body chamber occupies more than 3/4 of last whorl, largest shell diameter being 31 mm, which occurs near middle part of body chamber. Afterwards shell diameter decreases slightly which may be due to secondary crushing of specimen. Aperture missing. Initially, umbilical seam deviates from regular spiral and goes straight in direction of largest shell diameter; then it suddenly turns inward and barely touches ventral surface of penultimate whorl. Venter broad, rounded and narrows down gradually towards aperture. Flanks short, less curved near mature phragmocone; both ventrolateral and umbilical margins gradual.

Ribs fine, dense, persisting till end. Primaries originating from umbilicus, straight to slightly rursiradiate near inner margin, and furcate irregularly either at or slightly above mid-flank. Secondaries feebly sinuous or straight across venter, about 34 on first half of outer whorl.

Septal suture not discernible.

**Discussion.**—The present species differs from *K. cosmopolitum* <m> by its smaller size, less depressed early whorls and more fine and dense ribbing.

It is smaller than *K. bullatum* <m> and body chamber is more contracted and aberrantly uncoiled. Besides, they differ in ribbing pattern and number of ribs per half whorl.

The described specimen also strongly recalls the holotype of '*Bullatimorphites*' *uhligi* (Popovichi-Hatzeg, 1905, pl. 6, fig. 7) (see Arkell, 1954, text-fig. 36). They both are characterised by fine dense ribbing and strongly involute phragmocone and may be conspecific if enough material is available. Unfortunately, the holotype of '*B.*' *uhligi* has an incomplete body chamber.

The unique holotype of *K. spathi* sp. nov. has a comparable adult shell diameter and fine, dense ribbing. It has, on the other hand, characteristic *Bullatimorphites*-like gradual uncoiling of body chamber and compressed shell shape. Besides, the present form differs also by its strongly involute inner whorls and less contracted aperture.

**Occurrence.**—Single specimen (JUM/K/16) from Horizon III of Bed 2, Keera.

### *Kheraiceras noetlingi* sp. nov.

Figures 11.1; 12a, b

#### **Macroconch.**—

1896 '*Sphaeroceras*' cf. *bullatum* d'Orbigny, Noetling, pl. 6, fig. 2, 2a.

1933 *Kheraiceras quenstedti* (J. Roemer). Spath, p. 808.

1999 *Sphaeroceras bullatum* Bardhan, Sardar and Jana, pl. 1, fig. 10.

**Material.**—The holotype, a unique specimen described by Noetling (1896, pl. 6, fig. 2, 2a) from the Polyphemus Limestone, Mazar Drik, now repositied in GSI (Type No. 2915) and refigured here (Figures 11.1; 12a, b).

**Diagnosis.**—Unusually large for the genus; less cadiconic phragmocone, aperture highly contracted, inner whorls involute, body chamber eccentrically uncoiled and barely in contact with the ventral surface of the preceding whorl, apertural whorl section elliptical; ribbing coarse, distant, becoming obsolete in the first half of the body chamber.

**Table 5.** Measurements for *Kheraiceras noetlingi* sp. nov. (in mm).

Specimen		D	U	H	W
<M> Holotype,	aperture	158	49	55	60
GSI Type	body chamber	132	34	51	60
No.2915	end-phragmocone	127	17	50	90

**Etymology.**—In honour of F. Noetling, who first studied this species.

**Measurements.**—See Table 5.

**Description.**—Macroconch <M>: Internal mould, large, relatively compressed ( $W/D \approx 0.7$ ). Complete adult specimen with maximum diameter 158 mm. Shell involute in early whorls, but becoming evolute in last whorl. Umbilical seam turns inward occluding partially umbilicus of inner whorls, end-phragmocone diameter 103 mm. Thereafter adult body chamber, which occupies more than 3/4 of last whorl, coils eccentrically and becomes very narrow at aperture, resulting in a wide umbilicus. Maximum inflation attained at end-phragmocone stage ( $W/H=1.8$ ) followed by rapid contraction of body chamber which is maximum at about diameter 132 mm ( $W/H=1.17$ ), thereafter height increases relative to width and at aperture  $W/H=1.09$ . In inner whorls, umbilical wall steep with umbilical margin relatively sharp to rounded but gradually becomes inclined with rounded umbilical margin on outer whorl. Flanks short and rounded in inner whorls, increase and tend to become less curved ontogenetically. Venter relatively broad and gently rounded up to end phragmocone, narrowing and arching strongly during later ontogeny. Apertural whorl section strongly depressed, ovate near beginning of body chamber and at aperture relatively compressed and elliptical.

Primary ribs prominent up to end phragmocone stage. They originate from umbilical wall slightly rursiradiately and furcate below midflank. Secondaries strong and distant, become gradually indistinct and restricted near venter and persist up to 3/4 of last whorl. Number of secondaries in first half whorl is about 30.

**Discussion.**—As far as we know the present species represents the largest *Kheraiceras* in the world. From its size alone it matches many *Bullatimorphites* species. *Bullatimorphites* and *Kheraiceras* form an evolving lineage and there exist several species which show morphologic overlapping (Sandoval, 1983; Pandey and Westermann, 1988). The affinity of the present species towards *Kheraiceras* is nevertheless unequivocal, based on its inflated phragmocone, eccentric coiling of umbilical seam and rapidly contracted body chamber. Although it comes from the Upper Bathonian sequence of Baluchistan (Noetling, 1896; Arkell, 1956), it is known that both *Bullatimorphites* and *Kheraiceras* overlap stratigraphically in the Upper Bathonian. *Bullatimorphites* has a very restricted geographic distribution and comes mainly from the Mediterranean Province.

Both Noetling (1896) and Arkell (1952) found the present holotype conspecific with the European *Kheraiceras bullatum* (d'Orbigny, 1846). Admittedly, the present species

resembles *K. bullatum* which ranges from the Late Bathonian to the earliest Callovian (Riccardi *et al.*, 1989), but the adult size difference between them is remarkable. Besides, d'Orbigny's type specimen of *K. bullatum* (see Arkell, 1952, text - fig. 34) has a more eccentrically coiled and less contracted adult body chamber and more depressed phragmocone. The present species also differs from the Indian form of *K. bullatum* <M>, described here, mainly by its adult size and coarser and distant ribbing.

*Bullatimorphites* cf. *hannoveranus* (Roemer, 1911) <M>, now known from both Europe and India, is also a larger form with coarser ornament and strongly recalls the present species. The present species, however, differs in having cadiconic, spindle-shaped inner whorls, highly contracted body chamber and less strong ribbing on the body whorl which becomes indistinct in the first half of body chamber and disappears thereafter. Study of *K.* cf. *hannoveranus* <M> reported here, makes the difference more apparent. Its body chamber is strongly ribbed and ribbing persists to the end without losing strength.

**Occurrence.**—The holotype comes from the Polyphemus Limestone bed, Mazardrik, Baluchistan. Judging from the faunal association which includes *Macrocephalites triangularis* 'group', *Clydoniceras baluchistanense* (Spath) and *Choffatia* (*Homeoplanulites*) (Spath), a Late Bathonian age of *K. noetlingi* is certain (see also Westermann and Callomon, 1988).

#### Remarks

*Kheraicerias* is a stratigraphically important genus of near circum-global distribution. The genus evolved from *Bullatimorphites*, presumably during the Middle Bathonian. It underwent a speciation burst during the Late Bathonian to Early Callovian. After this peak, the genus declined and was reduced to a few stragglers by the Middle and Late Callovian (Hahn, 1969, 1971). Its early radiation was accompanied by a spectacular dispersion of *Kheraicerias* species to almost all biogeographic provinces. The Upper Bathonian of Europe yielded at least seven species including both micro- and macroconchs (Arkell, 1952). Among them, two important macroconchiate species, i.e., *K. hannoveranus* and *K. bullatum* had wide biogeographic distributions. *K. bullatum*, besides Europe, is also reported from Mexico (Westermann *et al.*, 1984; Sandoval *et al.*, 1990), South America (Riccardi *et al.*, 1989) and India (Bardhan *et al.*, 1999). *K. hannoveranus* on the other hand, is so far known to occur only in Europe and India. However, a specimen reported as '*Bullatimorphites* (*Kheraicerias*) *bullatus*' by Sandoval *et al.* (1990, pl. 9, fig. 4a-c) is known from South Mexico. It comes from the Upper Bathonian Steinmanni Zone. It has a marked similarity to the macroconch of Indian *K.* cf. *hannoveranus* (for details see Bardhan *et al.*, 1999). *Bullatimorphites* (*Kheraicerias*) *v-costatus* from the Upper Bathonian of Caracoles, Chile is a large and similarly coarsely ornate form (Riccardi *et al.* 1989, pl. 8, figs. 3, 4). It is larger in size than true *K. bullatum* <M> of Europe and Kutch. Its ribbing is strong, distant and seems to persist on the body chamber for a greater distance and thus agrees more closely with contemporary *K. hannoveranus* of

Europe.

Both *K. hannoveranus*, the putative ancestor, and the descendant *K. bullatum* continued to the Lower Callovian beds in Europe. While the former is restricted to the basal Lower Callovian horizon in Southern Germany and the Northern Jura (*Kepplerites keppleri* horizon of Callomon *et al.*, 1988), *K. bullatum* proceeded further up to the *Cadoceras suevicum* fannal horizon of Subtethyan France (Cariou, 1984). Subsequently six new species of *Kheraicerias* appeared during the Early Callovian in these parts of Europe.

This paper describes six species of *Kheraicerias* of which three are new and four are endemic to Kutch and adjoining areas. Besides, Pandey and Westermann (1988) reported another Bathonian species of this genus from Kutch 'island'. The diversity falls in line with the Late Bathonian-Early Callovian radiation of the genus elsewhere, but a high degree of endemism may be attributed to the newly opened-up basin which was yet to establish well developed sea routes with other faunal provinces. Kutch was a pericratonic basin developed at the northwestern margin of the Indian plate with the beginning of fragmentation of Gondwanaland during the Bathonian (Biswas, 1991). The newly formed Kutch basin was immediately occupied by organisms which migrated from other areas and the basin acted as a cradle of evolution. The organisms that migrated here evolved rapidly to colonise the virgin ecospace (Halder, in press) and gave birth to a distinct faunal assemblage unique to India, Madagascar, East Africa and Baluchistan, all of which constitute what is known as the Indo-Madagascan or Ethiopian faunal province. Endemism and speciation events are all pervasive, affecting all major taxa. For example, corals showed a spectacular radiation; about seventy new species appeared in Kutch during Late Bathonian time (Gregory, 1900; Pandey and Fürsich, 1993). Many new gastropods (Das *et al.*, 1999), brachiopods (Mukherjee *et al.*, in press) and nautiloids (Halder, in press) originated. Among ammonites, another circum-global genus, *Macrocephalites* Zittel, 1884, was also a product of Bathonian innovation and followed a course of spectacular Late Bathonian-Early Callovian radiation and migration (Datta *et al.*, 1996; Jain *et al.*, 1996). Kutch macrocephalitids are diverse and marked similarly by a high degree of endemism (Spath, 1927-33). However, in both cases, ecologically better adapted species spread to various faunal provinces in a fleeting manner (sensu Ager, 1984) and their first appearances seem to be isochronous everywhere. Such bioevents are of great value in intercontinental chronostratigraphic correlation and in establishing stage boundaries (Callomon, 1993).

The precise place of origin of *Kheraicerias* is unclear. The oldest species known until recently, *K. hannoveranus*, appears to be isochronous everywhere during the Late Bathonian. It is now generally believed that *Kheraicerias* evolved from *Bullatimorphites* through a complex heterochronic process involving neoteny (for details see Bardhan *et al.*, 1994). Evolutionary novelties were introduced, for example, sudden increase in degree of involution, inflation of phragmocone and occlusion of umbilicus by aberrantly-coiled, highly contracted body chamber, etc. (see also Westermann and Callomon, 1988). Two *Kheraicerias* species older than *K. hannoveranus* have been reported from

Kutch. The *Kheraiceras* species from Baluchistan, *K. noetlingi*, is associated with some time-diagnostic ammonites indicating Late (? basal) Bathonian age (Westermann and Callomon, 1988). It is already a fully realised *Kheraiceras* with the synapomorphies (sensu Eldredge and Cracraft, 1980) such as inflated phragmocone, occluded umbilicus, excentrically coiled and contracted body chamber without ribbing towards the aperture. *K. noetlingi* nonetheless still has a *Bullatimorphites*-like large adult size. Unfortunately little is known about its inner whorls. Interestingly, inner whorls are *Bullatimorphites* - like in another Kutch species, *Bullatimorphites* (? *Kheraiceras*) sp. A described from the (?) Middle Bathonian by Pandey and Westermann (1988). It is a remarkable species showing a curious combination of many symplesiomorphies in the early whorls and advanced evolutionary features in the body chamber. If the age assignment is correct, it is the oldest *Kheraiceras* known to date. Hence, in all probability, Kutch is a rare allopatric site (cf. Gould and Eldredge, 1977) where an immigrant ancestor, *Bullatimorphites*, gave rise to *Kheraiceras*. The newly emerged Kutch basin subsequently prompted speciation and migrational events when sea - routes became well established.

### Acknowledgements

A. Kayal, D. Mukherjee and S. Das (J. U.) helped at various stages both in the field and laboratory works, T. Chakraborty, Geological Survey of India, Calcutta, helped in computer study. The Director of the Geological Survey of India granted permission for studying the holotype and other materials kept at the Repository while P. H. Bhatti (Bhuj) provided the logistical and administrative support in Kutch. One of the authors (S. B. ) received financial aid from Department of Science and Technology, India (ESS/23/VES/022/98).

### References

- Ager, D. V., 1984: *The nature of the stratigraphical record*, 122 p. Macmillan Publishers Ltd., Hong Kong.
- Arkel, W. J., 1952-54: Monograph of the English Bathonian ammonites. *Palaeontographical Society London*, vol. 106-107 (3, 4), p. 73-128.
- Arkel, W. J. 1956: *Jurassic Geology of the World*, 806 p. Oliver and Boyd, Edinburgh and London.
- Bardhan, S. and Datta, K., 1987: Description and stratigraphic distribution of *Kheraiceras* Spath, 1924 in Kutch, India. *Mesozoic Research*, vol. 1, p. 147-150.
- Bardhan, S., Datta, K., Jana, S. K., and Praminik, D., 1994: Dimorphism in *Kheraiceras* Spath from the Callovian Chari Formation, Kutch, India. *Journal of Paleontology*, vol. 68, p. 287-293.
- Bardhan, S., Datta, K., Khan, D., and Bhaumik, D., 1988: Tullitidae genus *Bullatimorphites* from Upper Bathonian Patcham Formation, Kutch, India. *Newsletters on Stratigraphy*, vol. 20, p. 21-27.
- Bardhan, S., Sardar, S. and Jana, S. K., 1999: The Middle Jurassic *Kheraiceras* Spath from the Indian Subcontinent. *Proceedings of V International Symposium on Cephalopods*, Vienna. (in press).
- Bayle, E., 1878: Atlas I, Fossiles principaux des terrains. *Mémoires pour servir à l'explication de la Carte Géologique détaillée de la France*, vol. 4, pl. 158.
- Biswas, S. K., 1977: Mesozoic rock-stratigraphy of Kutch, Gujarat. *Quarterly Journal of the Geological, Mineralogical and Metallurgical Society of India*, vol. 49, p. 1-51.
- Biswas, S. K., 1991: Stratigraphy and sedimentary evolution of the Mesozoic basin of Kutch, Western India. In, Tandon, S. K., Pant, C. C. and Casshay, S. M. eds., *Sedimentary Basins of India: tectonic context*, p. 74-103. Gyanodya Prakashan, Nainital.
- Buckman, S. S., 1909-30: *Type Ammonites*, 790p. Wheldon and Wesley, London.
- Callomon, J. H., 1993: On *Perisphinctes congener* Waagen, 1875, and the age of the Patcham Limestone in the Middle Jurassic of Jumara, Kutch, India, *Geologische Blätter für Nordost-Bayern*, vol. 43, p. 227-246.
- Callomon, J. H., Dietl, G. and Page, K. N., 1988: On the ammonite faunal horizons and standard zonations of the Lower Callovian Stage in Europe. In, Rocha, R. B. and Zeiss, A. eds., *2nd International Symposium on Jurassic Stratigraphy*, vol. 1, p. 359-376. Lisboa, 1987.
- Cariou, E., 1984: Biostratigraphic Subdivisions of the Callovian Stage in the Subtethyan province of ammonites, correlations with the Subboreal zonal scale. In, Michelsen, O. and Zeiss, A. eds., *International Symposium on Jurassic Stratigraphy*, (I. U. G. S.), vol. 1, p. 315-326, Erlangen.
- Das, S. S., Bardhan, S., and Lahiri, T. C., 1999: The Late Bathonian gastropod fauna of Kutch, Western India-a new assemblage. *Paleontological Research*, vol. 3, p. 268-286.
- Datta, K. 1992: *Facies, fauna and sequence: an integrated approach in the Jurassic Patcham and Chari Formation, Kutch, India*, 167 p. Unpublished Ph. D. dissertation, Jadavpur University, Calcutta.
- Datta, K., Bhaumik, D., Jana, S. K. and Bardhan, S., 1996: Age, ontogeny and dimorphism of *Macrocephalites triangularis* Spath — the oldest macrocephalid ammonite from Kutch, India. *Journal of the Geological Society of India*, vol. 47, p. 447-458.
- Dietl, G., 1994: Der hochstetteri-Horizont-ein Ammonitenfaunen-Horizont (Discus-Zone, Ober-Bathonium, Dogger) aus dem Schwabischen Jura. *Stuttgarter Beiträge zur Naturkunde, Series B*, vol. 202, p. 1-39.
- Donovan, D. T., Callomon, J. H. and Howarth, M. K., 1981: Classification of the Jurassic Ammonoidea. In, House, M. R. and Senior, J. R. eds., *The Ammonoidea*, Systematics Association Special Vol. 18, p. 101-155. Academic Press, London.
- Eldredge, N. and Cracraft, J., 1980: *Phylogenetic Patterns and the Evolutionary Process*, 349 p. Columbia University Press, New York.
- Fürsich, F. T., Oschmann, W., Singh, I. B. and Jaitly, A. K., 1992: Hardgrounds, reworked concretion levels and condensed horizons in the Jurassic of Western India: Their significance for basin analysis. *Journal of the Geological Society of London*, vol. 149, p. 313-331.
- Fürsich, F. T. and Oschmann, W., 1993: Shell beds as tools in basin analysis: the Jurassic of Kachchh, Western India. *Journal of the Geological Society of London*, vol. 150, p. 169-185.
- Géczy, B. and Galacz, A., 1998: Bathonian ammonites from

- the classic Middle Jurassic locality of Villany, South Hungary. *Révue de Paléobiologie*, vol. 17, p. 479-511.
- Gemmellaro, G. G., 1872-82: *Sopra Alcune Faune Giuresi e Liasiche di Sicilia: Studi Palaeontologici*, 434 p. Palermo.
- Gould, S. J. and Eldredge, N., 1977: Punctuated equilibria: tempo and mode of evolution reconsidered. *Paleobiology*, vol. 3, p. 115-151.
- Gregory, J. W., 1900: The corals. *Palaeontologia Indica, Geological Survey of India, Series 9, Memoir 2*, p. 12-196.
- Grossouvre, A. de, 1891: Sur le Callovien de l'Ouest de la France et sur sa Faune. *Bulletin de la Société géologique de France*, vol. 19, p. 247-262.
- Hahn, W., 1969: Die Perisphinctidae Steinmann (Ammonoidea) des Bathonium (Brauner Jura  $\in$ ) in Südwestdeutschen Jura. *Jahrbuch des Geologischen Landesamtes in Baden-Württemberg*, vol. 11, p. 29-86.
- Hahn, W., 1971: Die Tullitidae S. Buckman, Sphaeroceratidae S. Buckman und Clydoniceratidae S. Buckman (Ammonoidea) des Bathoniums (Brauner Jura  $\in$ ) in Südwestdeutschen Jura. *Jahrbuch des Geologischen Landesamtes in Baden-Württemberg*, vol. 13, p. 55-122.
- Halder, K., *in press*: Diversity and biogeographic distribution of Jurassic nautiloids of Kutch, India vis-a vis fragmentation of Gondwanaland. *Journal of African Earth Sciences*.
- Halder, K., and Bardhan, S., 1996: The Oxfordian (Upper Jurassic) nautiloid fauna of Kutch, Western India.—*Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, vol. 201, p. 17-32.
- Jain, S., Callomon, J. H. and Pandey, D. K., 1996: On the earliest known occurrence of the Middle Jurassic ammonite genus *Reineckeia* in the Upper Bathonian of Jumara, Kachchh, Western India. *Paläontologische Zeitschrift*, vol. 70, p. 129-143.
- Kanzilal, S., 1978: A new species of *Kheraia* Spath (Ammonoidea) from the Lower Callovian of Habo Hill, Kutch. *Journal of Paleontology*, vol. 52, p. 495-496.
- Kayal, A. and Bardhan, S., 1998: *Epistrenoceras* Bentz (Ammonoidea) from Middle Jurassic of Kutch: a new record and its chronostratigraphic implication. *Canadian Journal of Earth Sciences*, vol. 35, p. 931-935.
- Krishna, J., 1984: Current status of the Jurassic stratigraphy of Kachchh, Western India. In, Michelsen, O. and Zeiss, A. eds., *International Symposium on Jurassic Stratigraphy*, vol. 3, p. 731-742. Erlangen.
- Krishna, J., and Cariou, E., 1990: Ammonoid faunal exchanges during Lower Callovian between the Indo-East African and Submediterranean Provinces: Implications for the long distance East-West Correlations. *Newsletters on Stratigraphy*, vol. 23, p. 109-122.
- Krishna, J., Cariou, E. and Enay, R., 1987: Succession of Macrocephalitininae assemblages as revealed at Keera dome in Kachchh, Western India, In, *2nd International Symposium on Jurassic Stratigraphy*, p. 68-67. Lisboa.
- Lissajous, M., 1923: Élude Sur la Faune du Bathonien des environs de Macon. *Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon*, Mémoire 3, p. 1-112.
- Lóczy, L., 1915: Monographie der Villanyer Callovien Ammoniten. *Geologica Hungarica*, vol. 1, p. 255-502.
- Mangold, C., 1970: Stratigraphie des étages bathonien et callovien du Jura méridional. *Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon*, vol. 41, p. 1-376.
- Mangold, C., 1984: Report of the Bathonian Working Group. In, Michelsen, O. and Zeiss, A. eds., *International Symposium on Jurassic Stratigraphy, Erlangen* (I. U. G. S.), vol. 1, p. 67-76.
- Mangold, C. and Rioult, M., 1997: Bathonien. In Cariou, E. and Hantzpergue, P. eds., *Biostratigraphie du Jurassique ou est-européen et méditerranéen: zonations parallèles et distribution des invertébrés et microfossiles. Bulletin des Centres de Recherches Elf-Aquitaine-Production*, Mmoire 17, p. 55-62.
- Mitra, K. C., Bardhan, S. and Bhattacharya, D., 1979: A study of Mesozoic stratigraphy of Kutch, Gujarat with a special reference to rock-stratigraphy and bio-stratigraphy of Keera dome, *Bulletin of Indian Geologists' Association*, vol. 12, p. 129-143.
- Mukherjee, D., Bardhan, S., and Ghosh, D. N., *in press*: Two new species to *Cryptorhynchia* Buckman, (Brachiopoda) from the Middle Jurassic of Kutch, India and their evolutionary significance. *Journal of Paleontology*.
- Noetling, F., 1896: Fauna of the Kellaways of Mazar Drik. *Palaeontologia Indica, Geological Survey of India, Series 16, Memoir 1*, p. 1-22.
- Orbigny, A. de 1842-51: *Paléontologie française, Terrains Jurassique, I, Céphalopodes*, 642p. Masson, Paris.
- Pandey, D. K. and Fürsich, F. T. 1993: Contributions to the Jurassic of Kachchh. I. The coral fauna. *Beringeria*, vol. 8, p. 3-69.
- Pandey, D. K. and Westermann, G. E. G., 1988: First record of Bathonian *Bullatimorphites* (Jurassic Ammonitina) from Kachchh, India. *Journal of Paleontology*, vol. 62, p. 148-150.
- Parona, C. F. and Bonarelli, G., 1895: Sur la fauna du Callovian inferieur (Chanasian) de Savoie, *Mémoire, Académie des Sciences, Chambéry*, vol. 6, p. 183.
- Popovici-Hatzeg, V., 1905: Les Céphalopodes du Jurassique moyen du Mont Strunga. *Mémoires de la Société Géologique de France*, no. 35, p. 1-27.
- Riccardi, A. G., Westermann, G. E. G. and Elmi, S., 1989: The Middle Jurassic Bathonian-Callovian Ammonite Zones of the Argentine-Chilean Andes. *Geobios*. vol. 22, p. 593-597.
- Roemer, J., 1911: *Die Fauna der Aspidoides-Schichten von Lechstedt bei Hildesheim*, 64p. Inaugural-Dissertation, Göttingen.
- Sandoval, J., 1983: *Bioestratigrafía y Paleontología del Bajocense y Bathonense en las Cordilleras Béticas*, 613p. Tesis doctoral, Universidad de Granada, Granada, Spain.
- Sandoval, J., Westermann, G. E. G. and Marshall, M. C., 1990: Ammonite fauna, stratigraphy and ecology of the Bathonian-Callovian (Jurassic) Tecocunca Group, South Mexico. *Palaeontographica*, vol. 210, p. 93-149.
- Sowerby, J. de C., 1840: Memoir to illustrate a Geological Map of Kutch. *Transaction Geological Society*, London, vol. 5, p. 327-329.
- Spath, L. F., 1924: On the Blake Collection of ammonites from Kachh, India. *Palaeontologia Indica, Geological Survey of India, New Series 9, Memoir 1*, p. 1-129.
- Spath, L. F., 1925: Jurassic Cephalopoda from Madagascar. *Bulletins of American Paleontology*, vol. 11, p. 6-29.
- Spath, L. F., 1927-33: Revision of Jurassic Cephalopod fauna of Kachh (Cutch). *Palaeontologia Indica, Geological Survey of India, New Series 9, Memoir 2*, p. 1-945.
- Waagen, W., 1875: Jurassic Fauna of Kutch, the Cephalo-



- poda. *Palaeontologia Indica, Geological Survey of India, Series 9, Memoir 1*, p. 1-247.
- Westermann, G. E. G., 1958: Ammoniten-Fauna und Stratigraphie des Bathonien NW-Deutschlands. *Beihefte zum Geologischen Jahrbuch*, vol. 32, p. 1-103.
- Westermann, G. E. G., 1993: Global bio-events in mid-Jurassic ammonites controlled by seaways. In House, M. R. eds., *The Ammonidea: Environment, Ecology and Evolutionary Change*, Systematics Association Special Vol. 47, p. 187-226. Clarendon Press, Oxford.
- Westermann, G. E. G. and Callomon, J. H., 1988: The Macrocephalitinae and associated Bathonian and Early Callovian (Jurassic ) ammonoids of the Sula Islands and New Guinea. *Palaeontographica*, vol. 203, p. 1-90.
- Westermann, G. E. G., Corona, R. and Carrasco, R., 1984: The Andean Mid-Jurassic *Neuquenicer* Ammonite Assemblage of Caulac. *Geological Association of Canada, Special Paper*, no. 27, p. 99-112. Ottawa.
- Westermann, G. E. G. and Riccardi, A. G., 1979: Middle Jurassic ammonoid fauna and biochronology of the Argentine-Chilean Andes, Part II: Bajocian Stephano-cerataceae. *Palaeontographica*, vol. 164, p. 85-188.
- Zittel, K. A., 1884: Cephalopoden. *Handbuch der Palaeontologie*, vol. 1, p. 329-522.

## SHORT NOTES

# Replacement names for Permian stauraxon radiolarians

Kazuhiro Sugiyama

Marine Geology Department, Geological Survey of Japan, 1-1-3 Higashi, Tsukuba, Ibaraki 305-8567, Japan

Received 6 April 2000; Revised manuscript accepted 21 July, 2000

**Abstract.** New names are proposed for two genera of Permian stauraxon radiolarians to correct existing homonymy; the replacement names are *Raciditor* Sugiyama for *Nazarovella* De Wever and Caridroit and *Kimagior* Sugiyama for *Deflandrella* De Wever and Caridroit. This action makes the family Deflandrellidae De Wever and Caridroit invalid according to Art. 39 of ICZN (1999), therefore the family Kimagioridae is established to replace Deflandrellidae.

**Key words:** *Deflandrella*, *Nazarovella*, replacement name, Permian, stauraxon radiolarians

## Introduction

Radiolarians are diverse marine zooplankton having a long evolutionary history beginning, to our knowledge, with the Cambrian period (e.g., Won and Below, 1999). When discussing the evolution, phylogenetic classification and systematics of the Radiolaria of a particular period or era (e.g. Permian, Mesozoic), it is essential to establish a geological-historical context by examining materials of the preceding and subsequent geologic ages. This approach to research will ensure correct knowledge of the characteristics of each period or era.

However, most radiolarian researchers tend to specialize throughout their careers in the radiolarians of a particular geologic age. For example, those working on Paleozoic radiolarians generally do not have a basic knowledge of Cenozoic radiolarians. At the least, when we establish new taxa, it is necessary to consult a variety of monographic studies on radiolarians of other geologic time periods to avoid taxonomic confusion created by the creation of homonyms and synonyms.

In this short paper, I introduce new names for two genera of Permian stauraxon radiolarians which are junior homonyms. The invalid names were originally in honor of famous radiolarian researchers. When creating such names, particular attention should be paid to the likely possibility of the names already having been employed by other researchers.

## Systematic paleontology

Superfamily Ruzencevispongacea Kozur, 1980

**Remarks.**—Some researchers have used the name Latentifistulidea Nazarov and Ormiston, 1983, for this superfamily (e.g. Nazarov and Ormiston, 1983; Sashida and Tonishi, 1986). However, this is obviously an invalid name

according to Art. 36 of ICZN (1999), as mentioned in detail by Kozur and Mostler (1989).

Family Ormistonellidae De Wever and Caridroit, 1984  
Genus *Raciditor* Sugiyama, new name

Not *Nazarovella* Kozur and Mostler, 1979, p. 68 (type species: *N. tetrafurcata* Kozur and Mostler, 1979).

*Nazarovella* De Wever and Caridroit, 1984, p. 101 (type species: *N. gracilis* De Wever and Caridroit, 1984).

**Type species.**—*Raciditor gracilis* (De Wever and Caridroit) = *Nazarovella gracilis* De Wever and Caridroit, 1984.

**Remarks.**—The generic name *Nazarovella* was first used by Kozur and Mostler (1979) for Triassic spherical radiolarians (spumellarian or entactinarian) possessing isometrically arranged spines with a quadrifurcated tip. Based on Arts. 23 and 60 of ICZN (1999), therefore, the replacement name *Raciditor* is given herein for *Nazarovella* proposed by De Wever and Caridroit (1984), who studied Permian stauraxon spumellarians from the Ultra-Tamba terrane of SW Japan, and named those stauraxon spumellarians having one short horn and three, long and grooved arms forming a flattened-tetrahedral structure as *Nazarovella*.

**Etymology.**—Named by use of an anagram of the family name of Dr. M. Caridroit, who first made excellent studies on the Ultra-Tamba terrane, SW Japan, using radiolarians. This name is of masculine gender.

Family Kimagioridae Sugiyama, new name

Deflandrellidae De Wever and Caridroit, 1984.

**Type genus.**—*Kimagior* Sugiyama, described below as a new name for *Deflandrella* De Wever and Caridroit, 1984.

**Remarks.**—Since the type genus of the family Deflandrellidae De Wever and Caridroit, 1984, is a junior homonym as discussed below, a replacement name for the

family is called for based on Art. 39 of ICZN (1999).

Genus *Kimagior* Sugiyama, new name

Not *Deflandrella* Loeblich and Tappan, 1961, p. 227 (type species: *Campylacantha cladophora* Jørgensen, 1905).

*Deflandrella* De Wever and Caridroit, 1984, p. 99 (type species: *D. manica* De Wever and Caridroit, 1984).

*Type species.* — *Kimagior manicus* (Deweever and Caridroit) = *Deflandrella manica* De Wever and Caridroit, 1984.

*Remarks.*—Since the generic name *Campylacantha* had already been used, Loeblich and Tappan (1961) introduced a replacement name *Deflandrella* for a homonymous name, *Campylacantha* Jørgensen, 1905, which was established for a plagiacanthid nassellarian from Norwegian plankton materials. Some radiolarian researchers have regarded *Deflandrella* Loeblich and Tappan as a junior subjective synonym of *Neosemantis* Popofsky, 1913 (e.g. Goll, 1979), whereas others have treated *Deflandrella* and *Neosemantis* as independent genera (e.g. Petrushevskaya, 1981). In any event, *Deflandrella* proposed by Loeblich and Tappan (1961) still remains valid taxonomically, which means that the identical name *Deflandrella* used by De Wever and Caridroit (1984) for Permian stauraxon spumellarian with three coplanar tubes is invalid.

*Etymology.*—Named by creating an anagram of a local place name, Kamigori, Hyogo Prefecture, SW Japan, near the type locality of the type species. This name is of masculine gender.

### References

- De Wever, P. and Caridroit, M., 1984: Description de quelques nouveaux Latentifistulidea (Radiolaires Polycystines) Paléozoïques du Japon. *Revue de Micropaleontologie*, vol. 27, no. 2, p. 98–106.
- Goll, R. M., 1979: The Neogene evolution of *Zygocircus*, *Neosemantis* and *Calimitra*: their bearing on nassellarian classification. *Micropaleontology*, vol. 25, no. 4, p. 365–396, pls. 1–5.
- ICZN (International Commission on Zoological Nomenclature), 1999: *International Code of Zoological Nomenclature*, Fourth edition, 306 p. The International Trust for Zoological Nomenclature, London.
- Jørgensen, E., 1905: The protist plankton and the diatoms in bottom samples. *Bergens Museum Skrift*, 1905, ser. 1 (7), p. 49–151, 195–225, pls. 6–18.
- Kozur, H., 1980: Ruzhencevispongidae, eine neue Spumellaria-Familie aus dem Oberen Kungurian (Leonardian) und Sakmarian des Vorurals. *Geologisch-Paläontologische Mitteilungen Innsbruck*, vol. 10, p. 235–242.
- Kozur, H. and Mostler, H., 1979: Beiträge zur Erforschung der mesozoischen Radiolarien. Teil III: Die Oberfamilien Actinommacea HAECKEL 1862 emend., Artiscacea HAECKEL 1882, Multiarcusellacea nov. der Spumellaria und triassische Nassellaria. *Geologisch-Paläontologische Mitteilungen Innsbruck*, vol. 9, p. 1–132.
- Kozur, H. and Mostler, H., 1989: Radiolarien und Schwammskleren aus dem Unterperm des Vorurals. *Geologisch-Paläontologische Mitteilungen Innsbruck*, Sonderband 2, p. 147–275.
- Loeblich, A. R., Jr. and Tappan, H., 1961: Remarks on the systematics of the Sarkodina (Protozoa), renamed homonyms and new and validated genera. *Proceedings of the Biological Society of Washington*, vol. 74, p. 21–234.
- Nazarov, B. B. and Ormiston, A. R., 1983: A new superfamily of stauraxon polycystine Radiolaria from the Late Paleozoic of the Soviet Union and North America. *Senckenbergiana Lethaea*, vol. 64 (2/4), p. 363–379.
- Petrushevskaya, M. G., 1981: Radiolyarii otryada Nassellaria Mirovogo Okeana. *Opredeliteli po Faune SSSR. Izdavaemye Zoologicheskim Institutom Akademii Nauk SSSR*, no. 128, p. 1–406.
- Popofsky, A., 1913: Die Nassellarien des Warmwassergebietes. *Wissenschaftliche Ergebnisse der Deutschen Sydpolar-Expedition 1901–1903 auf dem Schiff "Gauss,"* vol. 14 (Zool. 6), no. 1, p. 217–416, pls. 28–38.
- Sashida, K. and Tonishi, K., 1986: Upper Permian stauraxon polycystine Radiolaria from Itsukaichi, western part of Tokyo Prefecture. *Science Reports of the Institute of Geoscience, University of Tsukuba, Section B*, vol. 7, p. 7–13, pls. 1–4.
- Won, M.-Z. and Below, R., 1999: Cambrian Radiolaria from the Georgina Basin, Queensland, Australia. *Micropaleontology*, vol. 45, no. 4, p. 325–363.



## A GUIDE FOR PREPARING MANUSCRIPTS

PALEONTOLOGICAL RESEARCH is dedicated to serving the international community through the dissemination of knowledge in all areas of paleontological research. The journal publishes original and unpublished articles, normally not exceeding 24 pages, and short notes, normally less than 4 pages, without abstract. Manuscripts submitted are subject to review and editing by reviewers and a language editor. Manuscripts accepted for publication will generally be published in order of submission. Authors submit three copies of their manuscript for editorial review. After review, two copies of the revised manuscript are to be returned for copy editing.

Text: Paleontological Research is intended to be read by an international audience, therefore it is particularly critical that language be clear and concise. Manuscripts should be written in English. Either British or American usage style is acceptable. The editors strongly recommend the author(s) whose mother language is not English to ask critical reading and stylistic corrections of the manuscript before submission by specialist(s) who are familiar with English. Use SI (Système International d'Unités) units wherever possible.

Text should be typed always in double space on one side of white paper of not less than either 210 × 280 mm (A4 size) or 8 1/2 × 11 inches in the following order.

Cover sheet. Cover sheet should contain (1) full name, address, phone and fax numbers, and e-mail address of the author taking responsibility for the galley proofs, (2) running title composed of less than 40 characters, and (3) the numbers of tables and figures.

Title page. Title of the paper, names of authors and their professional affiliations with postal and e-mail addresses (or residential address, if an author is unaffiliated). Titles are to be brief and simple. Spell out one or more of the authors' first names.

Abstract. Abstract should be a condensation and concentration of the essential qualities of the paper. All the papers, excluding Short Notes, are to be accompanied by an abstract not exceeding 500 words. New taxonomic or stratigraphic names should be mentioned in the abstract.

Key words. Select keywords (not more than six words or phrases) which identify the most important subjects covered by the paper and arrange them in alphabetical order.

Main text. Use three or fewer levels of heading. No footnotes are to be used. Bibliographical references are to be identified by citing the authors' names, followed, in parentheses, by the date of publication, with a page number if desired. All citations must have a corresponding entry in the reference list. Acknowledgments should be placed at the end of the text, before References. Do not use honorifics such as Dr., Prof., Mrs., etc. Footnotes should be avoided. Stratigraphic nomenclature must follow the International Stratigraphic Guide.

The typical format for arrangement of systematic paleontology can be learned from current issues of the Journal. All descriptions of new taxa must include a diagnosis, and, as appropriate, stratigraphic and geographic indications, designation of a type or types, depository information, and specification of illustrations. In synonyms use an abbreviated form of the reference, consisting only of authors of reference, date of publication, and number of pages, plates, figures and text-figures referring to the organism or organisms in question.

References. Heading for the bibliography can be "References." Entries are to be listed alphabetically. No abbreviations will be used in article and book titles. Journal titles are written out, not abbreviated. Series, volume, and number or part are to be given, with the appropriate word abbreviated in each case ("ser.", "vol.", etc.; see the examples).

Illustrations. All illustrations, including maps, geologic sections, and half-tone illustrations (including "plates") are to be called figures and must be numbered in the same sequence as they are first cited in the text. Citations of illustrations in the text are to be spelled out in full (e. g., Figure 2 or Figure 2.1). Figure captions are to be typed separately. Plan the illustrations so that they take up either the entire width of the printed page (170 mm) or the width of one column (80 mm). Originals should not be smaller than the final intended size for printing. No foldouts will be accepted. Mark all originals clearly with authors' names and figure number. Photographs of all specimens except sections must be illuminated from the upper left side, as is conventional.

Manuscripts on disk. Authors are encouraged to deliver final, revised manuscript copy on disk, but disks should be sent only after the paper has been accepted. 3.5 inch disk with the RTF file (not the text file) write by a recent version of Word Perfect or Microsoft Word (ver. 5.1 or higher) for Windows 3.1 or higher, or Mac OS is acceptable. Be sure to specify, in a covering note, the hardware and the word-processing package used.

Galley proofs and offprints. Galley proofs will be sent to authors about one month before the expected publication date and should be returned to the Editors within 3 days of receipt. The authors are responsible for reading the first galley proof. Minor changes submitted by the author will be permitted while a paper is in galleys, but a charge will be made for substantial alterations.

The authors receive 50 free of charge offprints without covers. Additional copies and covers can be purchased and should be ordered when the proofs are returned.

Charges. If a paper exceeds 24 printed pages, payment of page charges for the extra pages is a prerequisite for acceptance. Illustrations in color can also be published at the authors' expense. For either case, the Editors will provide information about current page charges.

Return of published figures. The manuscripts of the papers published will not be returned to the authors. However, figures will be returned upon request by the authors after the paper has been published.

- Ager, D. V., 1963: *Principles of Paleoecology*, 371p. McGraw-Hill Co., New York.
- Barron, J. A., 1983: Latest Oligocene through early Middle Miocene diatom biostratigraphy of the eastern tropical Pacific. *Marine Micropaleontology*, vol. 7, p. 487-515.
- Barron, J. A., 1989: Lower Miocene to Quaternary diatom biostratigraphy of Leg 57, off northeastern Japan, Deep Sea Drilling Project. In, Scientific Party, *Initial Reports of the Deep Sea Drilling Project*, vols. 56 and 57, p. 641-685. U. S. Govt. Printing Office, Washington, D. C.
- Burckle, L. H., 1978: Marine diatoms. In, Haq, B. U. and Boersma, A. eds., *Introduction to Marine Micropaleontology*, p. 245-266. Elsevier, New York.
- Fenner, J. and Mikkelsen, N., 1990: Eocene-Oligocene diatoms in the western Indian Ocean: Taxonomy, stratigraphy, and paleoecology. In, Duncan, R. A., Backman, J., Peterson, L. C., et al., *Proceedings of the Ocean Drilling Program, Scientific Results*, vol. 115, p. 433-463. College Station, TX (Ocean Drilling Program).
- Kuramoto, S., 1996: Geophysical investigation for methane hydrates and the significance of BSR. *The Journal of the Geological Society of Japan*, vol. 11, p. 951-958. (in Japanese with English abstract)
- Zakharov, Yu. D., 1974: Novaya nakhodka chelyustnogo apparata ammonoidey (A new find of an ammonoid jaw apparatus). *Paleontologicheskii Zhurnal* 1974, p. 127-129. (in Russian)

## 行事予定

- ◎第150回例会は、2001年1月27日(土)と28日(日)に「茨城県自然博物館」で開催されます。27日にシンポジウム「新生代軟体動物古生物学の最近の動向(世話人:野田浩司・天野和孝・島本昌憲・間嶋隆一)」が行われます。個人講演の申し込み締切日は2000年12月1日(金)です。
- ◎2001年年会・総会は、2001年6月29日(金)、6月30日(土)、7月1日(日)に「国立オリンピック記念青少年総合センター」で開催されます。21世紀最初の年会ですので、「21世紀の古生物学」を統一テーマとし、29日に統一シンポジウム、30日と1日に17件の課題別シンポジウムが行われる予定です。現在、学会の「将来計画委員会」によってプログラムの詳細を立案中です。一般講演はポスター講演だけに限って受け付けます。口答発表形式による一般講演はありませんのでご注意ください。ポスター講演の申し込み締切日は2001年5月9日(水)です。
- ◎第151回例会(2002年1月下旬開催予定)の開催申し込みは、今のところありません。
- ◎2002年年会・総会(2002年6月下旬開催予定)には福井県立博物館から開催申し込みがありました。
- ◎古生物学会では、小人数で実施されるワークショップやショートコースを主催しております。学会から金銭を含む援助を行なうことができますので、企画をお持ちの方は行事係までお問い合わせ下さい。

### 個人講演・シンポジウム案の申し込み先

個人講演の申し込みは予稿集原稿を直接お送り下さい。e-mailやファックスでの申し込みは、原則として受け付けておりません。

〒240-0067 横浜市保土ヶ谷区常盤台79-2  
横浜国立大学教育人間科学部自然環境講座  
TEL 045-339-3349(直通) FAX 045-339-3264(学部事務室)  
E-mail majima@edhs.ynu.ac.jp  
間嶋隆一(行事係)

お問い合わせは、行事係か下記の行事幹事までお寄せ下さい。

〒250-0031 小田原市入生田499  
神奈川県立生命の星・地球博物館  
TEL 0465-21-1515 FAX 0465-23-8846  
E-mail taru@pat-net.ne.jp  
樽 創(行事幹事)

本誌の発行に要する費用は、会員の会費以外に、文部省科学研究費補助金ならびに賛助会員からの会費が当てられています。現在の賛助会員は下記の通りです。

インドネシア石油株式会社 神奈川県立生命の星・地球博物館 北九州市立自然史博物館  
石油資源開発株式会社 帝国石油株式会社 兵庫県立人と自然の博物館  
ミュージアムパーク茨城県自然博物館 (アイウエオ順)

○文部省科学研究費補助金(研究成果公開促進費)による。

2000年9月22日 印刷  
2000年9月29日 発行

ISSN 1342-8144  
Paleontological Research

第4巻, 第3号

2,500円

発行者 日本古生物学会  
〒113-8622 東京都文京区本駒込5-16-9  
日本学会事務センター内  
電話 03-5814-5801  
編集者 棚部一成・加瀬友喜  
編集幹事 遠藤一佳・重田康成・佐々木猛智  
印刷者 学術図書印刷株式会社 富田 潔  
〒176-0012 東京都練馬区豊玉北2の13の1  
電話 03-3991-3754



# Paleontological Research

Vol. 4, No. 3

September 29, 2000

## CONTENTS

<b>Naoki Ikegami, Alexander W. A. Kellner and Yukimitsu Tomida:</b> The presence of an azhdarchid pterosaur in the Cretaceous of Japan .....	165
<b>Ritsuo Nomura and Yokichi Takayanagi:</b> The suprageneric classification of the foraminiferal genus <i>Murrayinella</i> and a new species from Japan .....	171
<b>Takehisa Tsubamoto, Patricia A. Holroyd, Masanaru Takai, Nobuo Shigehara, Aye Ko Aung, Tin Thein, Aung Naing Soe and Soe Thura Tun:</b> Upper premolar dentitions of <i>Deperetella birmanica</i> (Mammalia: Perissodactyla: Deperetellidae) from the Eocene Pondaung Formation, Myanmar .....	183
<b>Mia Mohammad Mohiuddin, Yujiro Ogawa and Kunitaru Matsumaru:</b> Late Oligocene larger foraminifera from the Komahashi-Daini Seamount, Kyushu-Palau Ridge and their tectonic significance .....	191
<b>Sudipta K. Jana, Subhendu Bardhan and Subrata K. Sardar:</b> <i>Kheraicerias</i> Spath (Ammonoidea) -new forms and records from the Middle Jurassic sequence of the Indian subcontinent .....	205
<b>SHORT NOTES</b>	
<b>Kazuhiro Sugiyama:</b> Replacement names for Permian stauraxon radiolarians .....	227
<b>PROCEEDINGS</b> .....	229