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Cover: Typical Pleistocene fossils from the Japanese Islands. Front cover: *Sinomegaceros yabei* (Shikama). Back cover: *Paliurus nipponicum* Miki, *Mizuhopecten tokyoensis* (Tokunaga), *Neodenticula seminae* (Simonsen and Kanaya) Akiba and Yanagisawa and *Emiliana huxleyi* (Lohmann) Hay and Mohler.

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Lithology and foraminiferal fauna of allochthonous limestones (Changhsingian) in the upper part of the Toyoma Formation in the South Kitakami Belt, Northeast Japan

FUMIO KOBAYASHI

*Institute of Natural and Environmental Sciences, Himeji Institute of Technology,
Sanda, Hyogo, 669-1546, Japan (E-mail: kobayasi@nat-museum.sanda.hyogo.jp)*

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Abstract. Allochthonous limestones less than 3 m thick are intercalated lenticularly within sandstones and mudstones of the upper part of the Upper Permian Toyoma Formation in the South Kitakami Belt. They are bedded and laminated, and have many thin interbeds of sandstone and mudstone. These limestones are narrowly distributed exclusively in the Kesenuma area, and largely differ from platform limestones of the Lower Permian Sakamotozawa and Middle Permian Kanokura formations, both widely distributed in the South Kitakami Belt, in their occurrence and extent. Thirty-two species of foraminifers, some of which are restricted to the Changhsingian, are discriminated in limestones, limestone conglomerates, and calcareous sandstones of the upper part of the Toyoma Formation. This foraminiferal fauna evidently belongs to the Tethyan province paleobiogeographically, and is characterized by dominant *Colaniella parva*, subordinate *Nanlingella cf. meridionalis*, and accessory *Palaeofusulina* sp. These three species are described herein.

Key words: allochthonous limestones, Changhsingian foraminifers, South Kitakami-Kurosegawa Old Land, upper part of Toyoma Formation

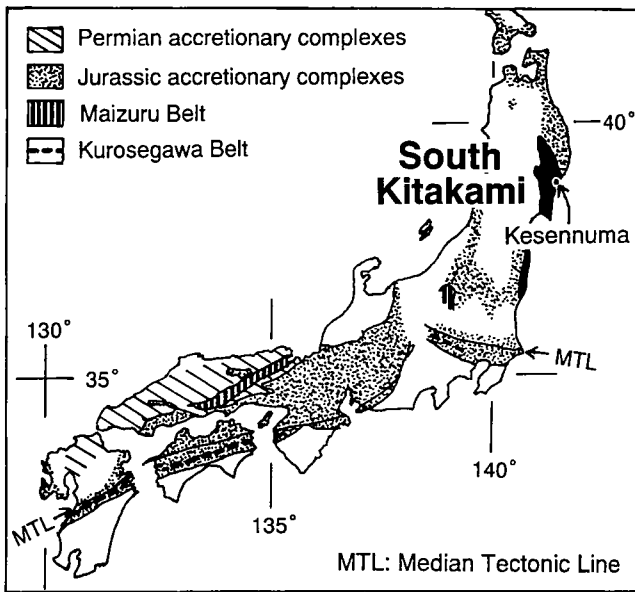
Introduction

The South Kitakami Belt in Northeast Japan along with the Kurosegawa Belt in Southwest Japan is a distinct tectonic unit bounded by strike slip faults associated with serpentinite (Figure 1). Middle Silurian to Lower Cretaceous deposits rest on pre-Silurian granitic and metamorphic rocks in the South Kitakami Belt (Kawamura *et al.*, 1990) and in the Kurosegawa Belt (Yoshikura *et al.*, 1990). Paleozoic formations in these two belts are marked by shelf limestones containing terrigenous deposits and terrestrial plant fossils, which are absent in the pre-Cretaceous accretionary complexes of Japan.

The Permian of the South Kitakami Belt is subdivided into three units: Lower Permian Sakamotozawa Formation, Middle Permian Kanokura Formation, and Upper Permian Toyoma Formation (Figure 2). The Sakamotozawa Formation is dominated by platform limestones and overlies unconformably the Upper Carboniferous (Bashkirian) Nagaiwa Formation. The Kanokura Formation is marked by Murgabian to Midian reef complexes and thick granitic conglomerate. Based on faunas, floras, and limestone

lithologies of the Sakamotozawa and Kanokura formations, the South Kitakami Belt is thought to have been deposited in the equatorial Tethys in proximity to South China (Kawamura and Machiyama, 1995; Ehiro, 1997; Kobayashi, 1999). On the other hand, Middle Permian brachiopod faunas of the South Kitakami Belt are thought to be allied to those of Northeast China, Inner Mongolia, and South Primorye, and are different from the typical Tethyan faunas (Tazawa, 1991, 1998). The Toyoma Formation is represented by dominant argillaceous rocks. Limestones are less than 3 m thick, restricted to the upper part of this formation in the Kesenuma area, and present a striking contrast to widespread Lower and Middle Permian limestones in the South Kitakami Belt.

Fusulinaceans and their biostratigraphic zonation in the Sakamotozawa and Kanokura formations (Figure 2) were studied by Kanmera and Mikami (1965), Choi (1970), and others. Details on foraminiferal faunas of the Toyoma Formation have remained uncertain except for the occurrence of *Colaniella* and *Lantschichites* described by Tazawa (1975) and some late Permian foraminifers listed by Ishii *et al.* (1975).



This paper describes and discusses the limestone lithology and Changhsingian foraminiferal fauna of the upper part of the Toyoma Formation in the Kesennuma area. The allochthonous origin of the limestones of this formation is demonstrated. Three species of foraminifers, *Colaniella parva*, *Nanligella cf. meridionalis*, and *Palaeofusulina* sp., are described among the 32 taxa distinguished. All the described and illustrated specimens are stored in the Museum of Nature and Human Activities, Sanda, Hyogo, Japan.

Lithostratigraphy

The Toyoma Formation consists mostly of mudstone (Figure 2), and yields Late Permian ammonoids (Ehiro and

Figure 1. Index geotectonic map of the Japanese pre-Cretaceous showing the South Kitakami Belt (black) and the Kesennuma area.

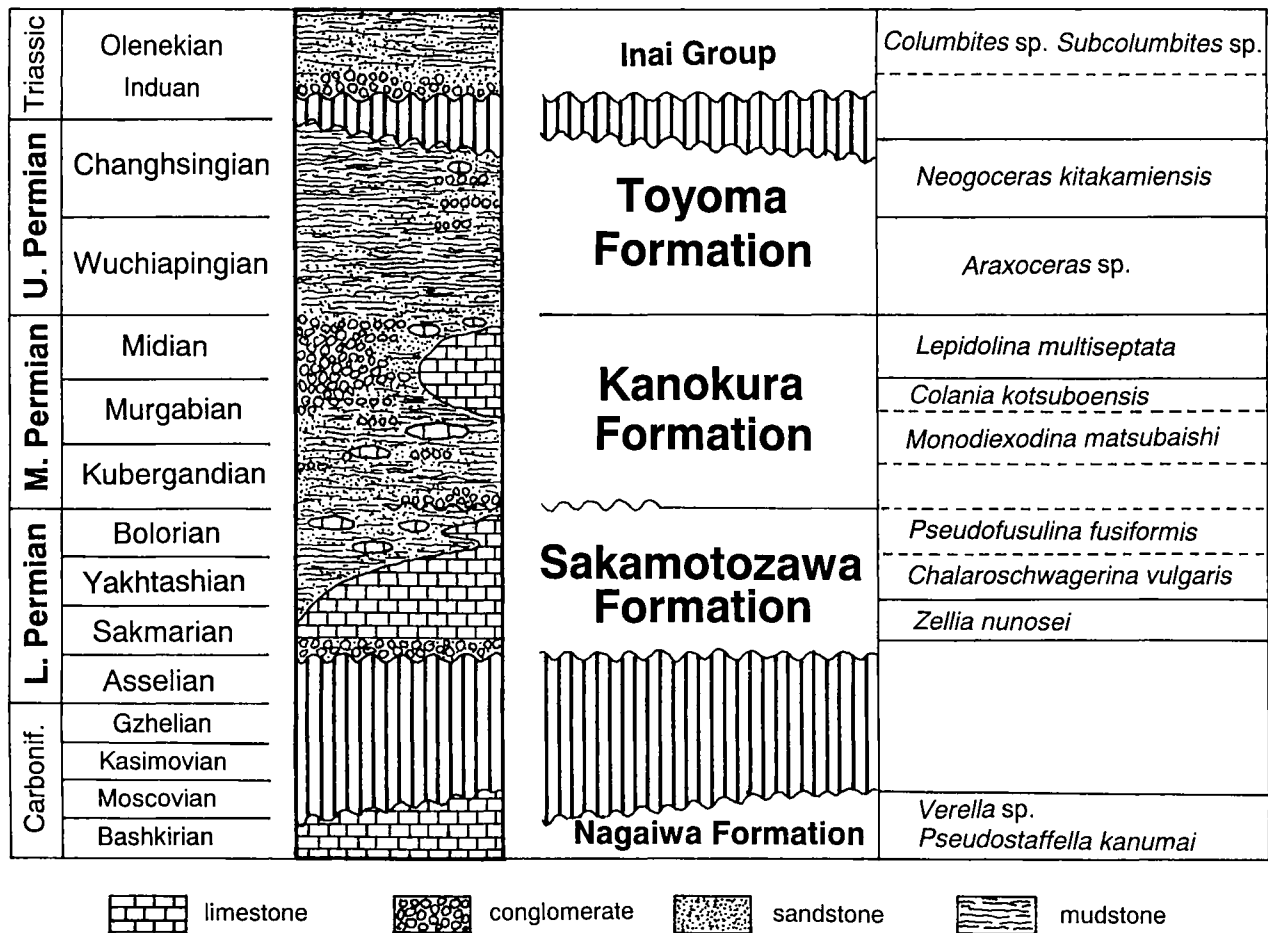
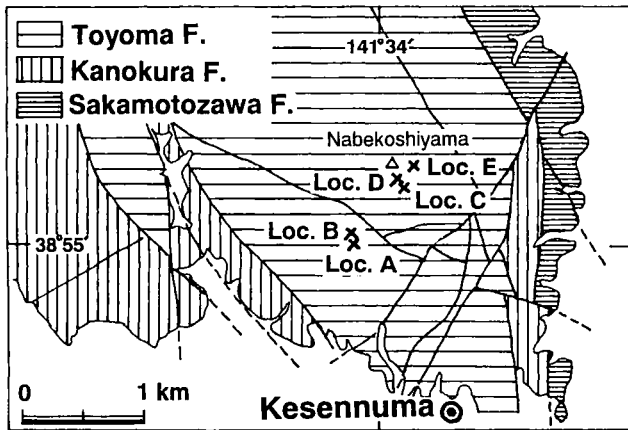


Figure 2. Schematic profile of the Permian of the South Kitakami Belt. Permian fusulinacean biostratigraphic subdivision is simplified based on Kanmera and Mikami (1965) and Choi (1970), and Permian ammonoids based on Ehiro (1987). Lower Permian Sakamotozawa Formation rests unconformably on the Upper Carboniferous Nagaiwa Formation.



Bando, 1985; Ehiro, 1987), brachiopods (Tazawa, 1975, 1987), and others. In the Kesennuma area, the Toyoma Formation is divisible into lower and upper parts, and is partly intruded by dike rocks (Tazawa, 1976). The lower part consists of mudstone more than 600 m thick. The upper part is composed of a more than 500 m thickness of sandstone and mudstone interbedded with small amounts of thin conglomerate and limestone (Tazawa, 1975, 1976). Limestones and limestone conglomerates are lenticular, well-bedded, and have thin interbeds of sandstone and

Figure 3. Index geologic map showing locations of stratigraphic columns in Locs. A to E (shown in Figure 4) in the Kesennuma area, simplified based on Tazawa (1976).

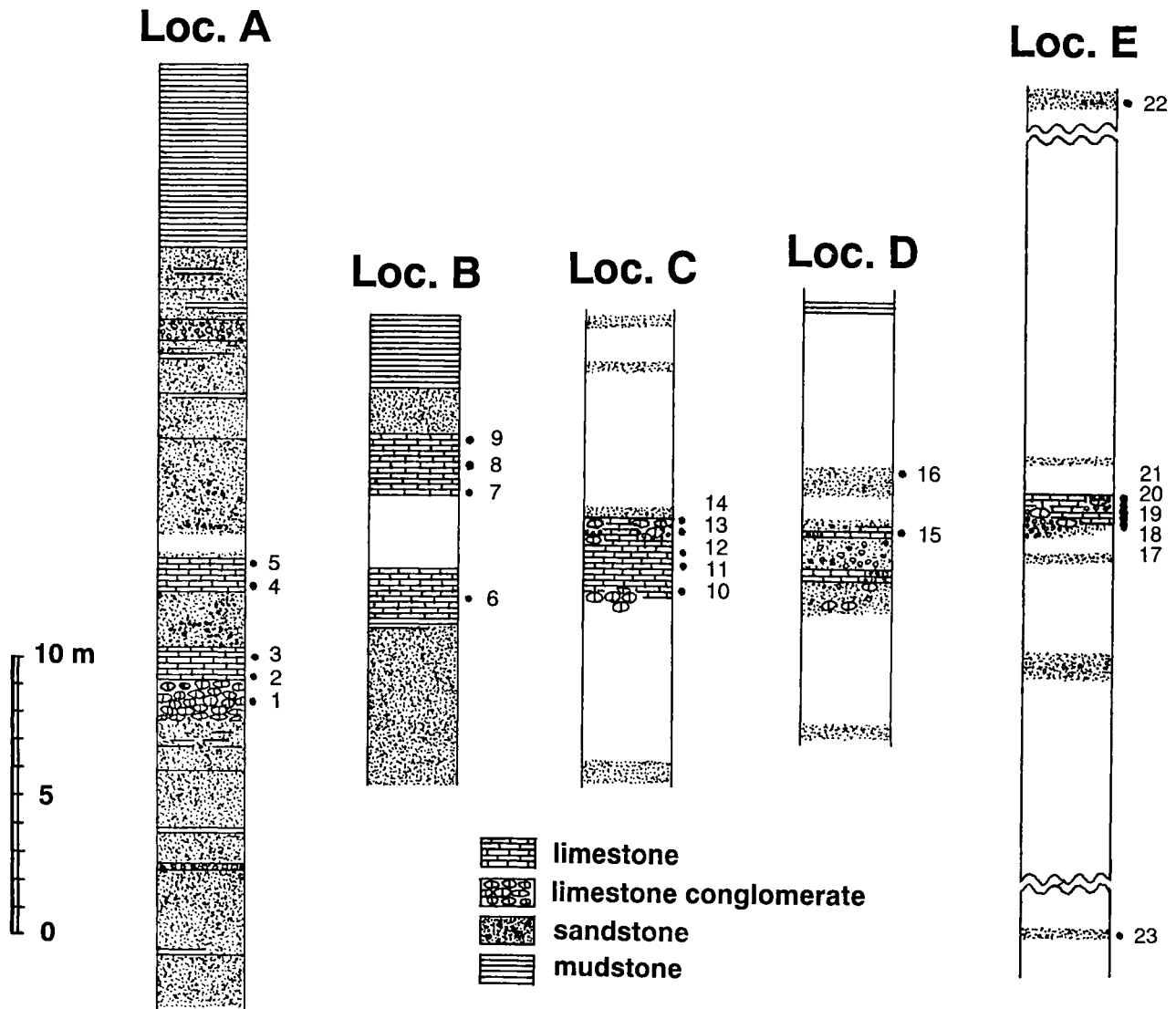


Figure 4. Columnar sections of the upper part of the Toyoma Formation in Locs. A to E. Dots with number shows stratigraphic level of samples. Stratigraphically, sample 22 is about 40 m higher than sample 21, and sample 23 is about 65 m lower than sample 17.

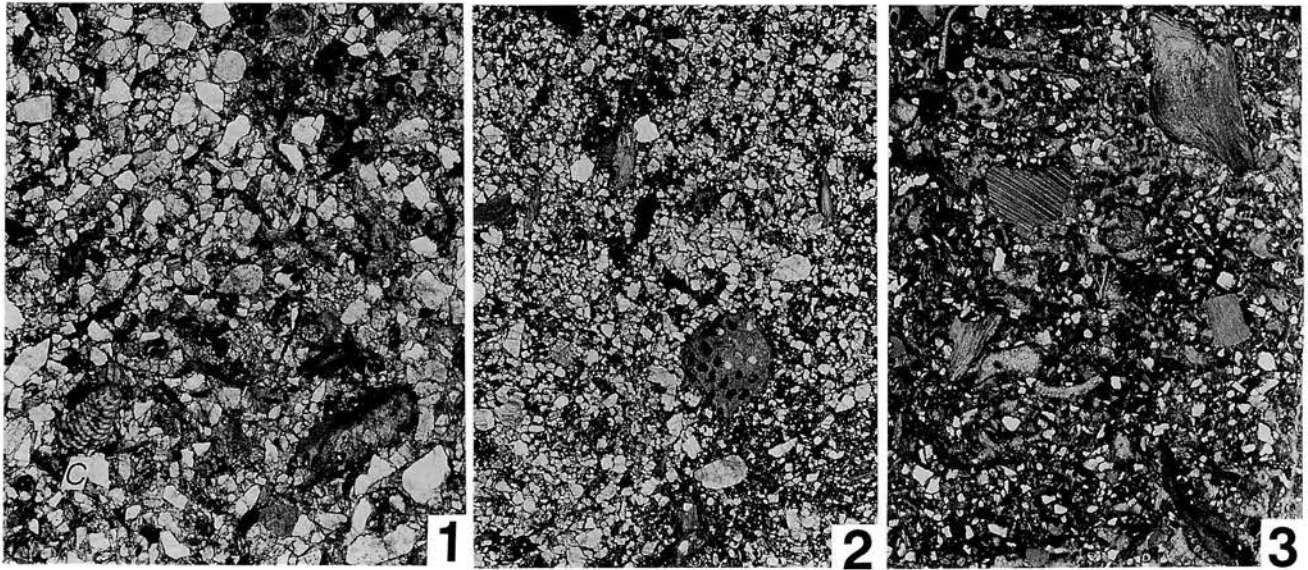


Figure 5. Photomicrographs of sandstone and arenaceous limestone. **1, 2.** Sandstone containing many lithic clasts and bioclasts. *Colaniella parva* (C) is found at the lower left corner in **1**. **1.** Loc. D-16, $\times 10.8$. **2.** Loc. E-23, $\times 6.6$. **3.** Arenaceous limestone containing many fossil fragments, and many detrital quartz and calcite grains within calcareous argillaceous matrix, Loc. E-19, $\times 6.6$.

mudstone. They are less traceable laterally, and sporadically distributed in five localities (Locs. A to E) north of Kesennuma (Figures 3, 4).

At Loc. A, a lenticular block surrounded by sandstone is exposed. It is 5.7 m thick, and consists of limestone conglomerate, lower limestone, sandstone, and upper limestone. The limestone conglomerate is 1.2 m thick, fossiliferous, and contains many subrounded pebbles to cobbles of limestone. This limestone conglomerate is overlain by the lower limestone, which has more than ten interbeds of mudstone and sandstone less than 5 mm thick. The lower limestone is 1.3 m thick, laminated, thinly bedded, and contains well-sorted abundant fossils. Many fragments of brachiopods and crinoids are arranged parallel to the bedding plane of the lower limestone. The overlying coarse-to medium-grained sandstone is 2 m thick, highly calcareous, and partly porous due to the solution of calcareous materials and limestone clasts. Graded bedding is well developed in its basal part. The upper limestone overlying the sandstone is 1.2 m thick, well-bedded, and highly fossiliferous. It is lithologically similar to that of the lower limestone. The upper part of the upper limestone contains a few interbeds of mudstone 0.5 to 1 cm thick. The upper limestone is in contact with medium-to coarse-grained calcareous sandstone with many granules of limestone.

At Loc. B, limestones are developed in two horizons (Figure 4). The stratigraphic relationship between them is unknown. The lower limestone rests on the mudstone

without limestone conglomerate as found at Loc. A. The upper limestone is overlain by medium-to coarse-grained calcareous sandstone. Lower and upper limestones at Loc. B appear to be stratigraphically about 50 m higher than those at Loc. A. They are well-bedded, and contain abundant fossils and many thin interbeds of sandstone and mudstone like at Loc. A. These limestones at Locs. A and B have very similar lithologic characters and thicknesses.

Around Locs. C, D, and E, limestone and limestone conglomerate are more widely distributed than at Locs. A and B. They have in common thicknesses less than 3 m, are well-bedded, and have thin interbeds of calcareous sandstone and mudstone. Limestone conglomerate contains abundant fossil fragments, and ill-sorted granules to boulders of limestone, sandstone, and mudstone, all of which are packed within calcareous mudstone and sandstone. Many limestone granules and pebbles and fossil fragments are also found in sandstone (Figure 5.2). Bioclasts of foraminifers are contained in some of the sandstones (Figure 5.1).

The stratigraphic relationship of limestone and limestone conglomerate between Locs. A and B and Locs. C, D, and E is not confirmed exactly because of the sporadic occurrences of the limestone and a thick cover of soil and vegetation in this area. Besides these limestone conglomerates, a thin conglomerate with pebbles of granitic and porphyritic rocks without limestones is also found around Locs. C, D, and E.

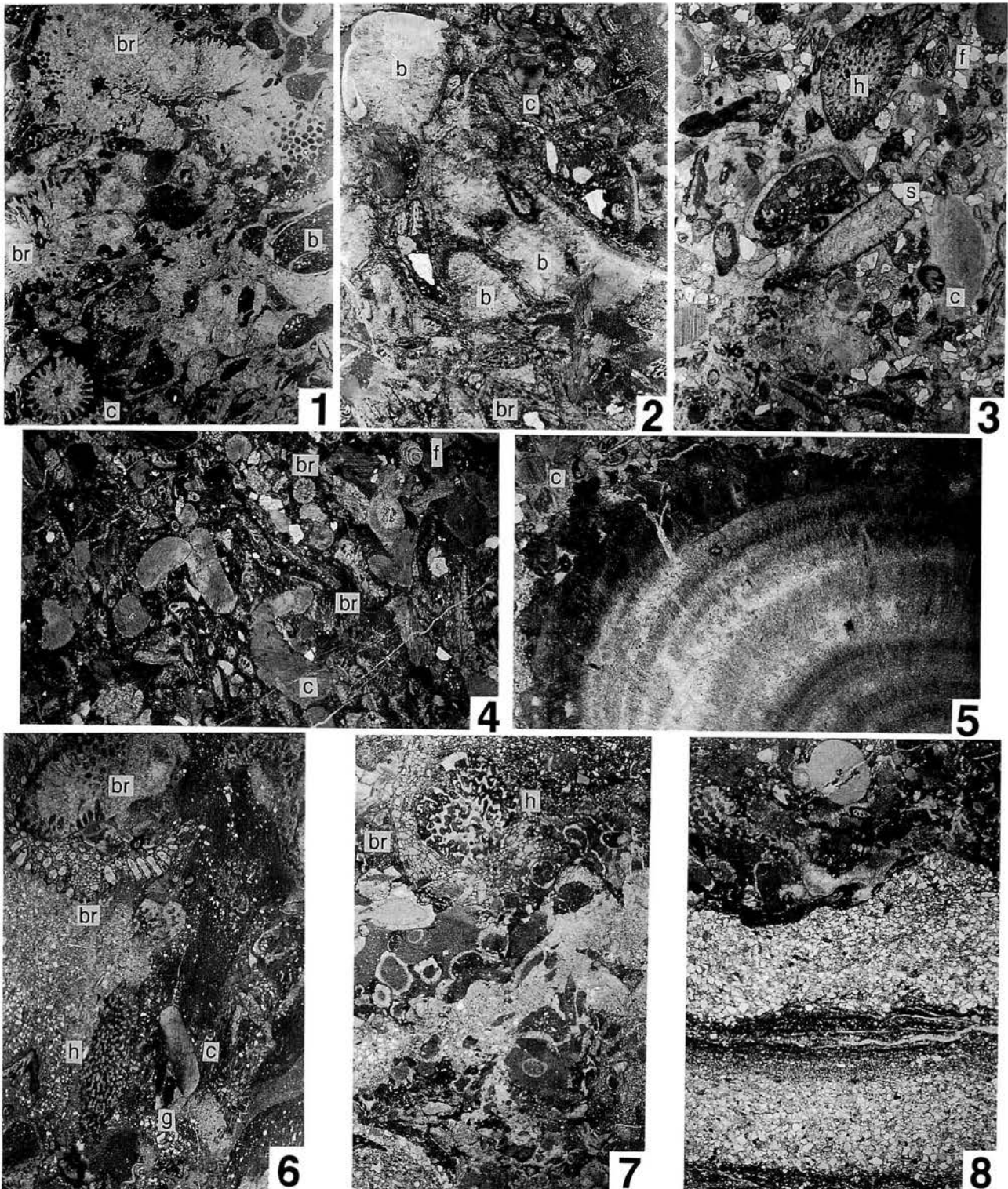


Figure 6. Photomicrographs of limestone and limestone conglomerate. **1.** Rudstone, Loc. A-1, $\times 4$. **2.** Skeletal packstone/rudstone, Loc. A-3, $\times 4$. **3.** Skeletal grainstone, Loc. E-18, $\times 4$. **4.** Skeletal packstone, Loc. B-8, $\times 4.5$. **5.** Stomatolite contained in limestone conglomerate, Loc. E-18, $\times 5.1$. **6, 7.** Limestone conglomerate consisting of skeletal grains surrounded by highly calcareous argillaceous and arenaceous matrix, **6.** Loc. E-21, **7.** Loc. E-17, both $\times 5.1$. **8.** Cobble of limestone (skeletal packstone) in contact with alternating beds of calcareous sandstone and mudstone showing lamination and graded bedding, Loc. E-17, $\times 5.1$. Skeletal grains contained show: bryozoans (br), crinoids (c), brachiopods (b), sponges (s), hydrozoa ? (h), green algae (g), and foraminifer (f).

Lithologic characters and allochthonous origin of limestone

Limestones of the upper part of the Toyoma Formation are characterized by containing many detrital quartz grains and numerous and varied fossils, which in addition are small in size, intercalation of sandstone and mudstone, and well-developed stratification. Many fossils and detrital quartz grains are also contained in limestone granules to boulders of limestone conglomerates.

Limestones are composed of dominant skeletal packstone (Figure 6.2, 6.4). Rudstone (Figure 6.1) and skeletal grainstone (Figure 6.3) are also found. Some of these limestones contain discontinuous intercalations of sandstone and mudstone, and partly show a conglomeratic appearance. The limestone cobbles and pebbles in the conglomeratic part of the limestone at Loc. E are in contact with alternating beds of sandstone and mudstone with an undulated sharp boundary (Figure 6.8). Commonly found arenaceous limestone consists of fossils and lithic fragments packed with impure lime-mud (Figure 5.3). It is somewhat similar to calcareous sandstone containing many fossil fragments (Figure 5.1, 5.2). Fossils contained in these limestones are predominantly crinoids and bryozoans, with subordinate to accessory brachiopods, green algae, cyanobacteria, sponges (?), hydrozoans (?), foraminifers, and others.

Limestone conglomerate is composed of granules to boulders of fossiliferous limestone surrounded by highly calcareous mudstone and sandstone. Grain size, outline, and proportion of lithic fragments and skeletal grains against the surrounding mudstone and sandstone are variable in places (Figure 6.6, 6.7). Limestone granules to boulders also contain many detrital quartz grains, and are lithologically more diverse than the bedded limestone mentioned above. They consist of rudstone, skeletal packstone, skeletal grainstone, lime-wackestone, and lime-mudstone. The boundary between the limestone pebbles and surrounding calcareous mudstone is imprecise in some of the limestone conglomerate. Cyanobacteria, green algae, sponges, and hydrozoans (?) are commonly found in limestone conglomerates along with abundant crinoids and bryozoans. Stromatolites are sometimes included (Figure 6.5).

Occurrences and lithologies of lenticular limestone and conglomeratic limestone closely resemble those in the Upper Permian of the Kurosegawa Belt (Kobayashi, 2001b; unpublished data by the author) and the Maizuru Belt (unpublished data by the author). They are easily distinguishable from contemporaneous seamount limestones by having many detrital quartz grains and thin interbeds of sandstone and mudstone. Within the Japanese Upper Permian, limestone and limestone conglomerate of the upper part of the

Toyoma Formation are most similar to those of the Kuma Formation in the Kurosegawa Belt of west Kyushu. Fossil fragments contained in sandstones (Figure 5.1, 5.2), granules to boulders of limestones, and lenticular limestones are nearly the same age in the former. On the other hand, those of Yakhtashian to Bolorian, Midian, and Lopingian ages are confirmed in the latter (Kobayashi, 2001b). Although pre-Late Permian pebbles have not been found and the ages of the sandstone and mudstone are not exactly known, the lithology and occurrence of limestones and limestone conglomerates in the upper part of the Toyoma Formation suggest that they are allochthonous to the surrounding sandstone and mudstone, as well as the Kuma Formation. Kobayashi (2001b) concluded that limestones of the Kuma Formation had been redeposited in the setting of an active continental margin of the Kurosegawa Old Land in Late Permian time.

Abundant detrital quartz grains and fossils strongly evidence original limestone deposition on the shallow continental shelf in the upper part of the Toyoma Formation along with the Kuma Formation. The pre-Cretaceous formations in the South Kitakami and Kurosegawa belts are closely related stratigraphically and lithologically to each other, and the two belts are thought to have been isolated paleogeographically from the ancient Asian continent by the early Cretaceous amalgamation (Saito and Hashimoto, 1982; Kobayashi, 1999). Accordingly, all limestones of the upper part of the Toyoma Formation are considered to have been originally deposited on the shallow shelf referable to the South Kitakami-Kurosegawa Old Land as well as the Kuma Formation. Collapse and redeposition of limestone probably resulted from upheaval of the South Kitakami-Kurosegawa Old Land preceding the deposition of the Lower Triassic Inai Group resting unconformably on the Toyoma Formation. Remarkable differences in thickness, occurrence, and development of limestones between the Toyoma Formation and the underlying Sakamotozawa and Kanokura formations (Figure 2) are thought to be due to the allochthonous origin of these limestones in addition to the narrowing of the sedimentary basin of the Toyoma Formation.

Foraminiferal fauna

Thirty-two species of foraminifers are distinguished in limestone, limestone conglomerate, and calcareous sandstone in the upper part of the Toyoma Formation in the Kesenuma area (Figures 7-9). Among them, *Colaniella parva* is the most representative in the Kesenuma fauna, and recognizable in almost all samples containing foraminifers. It is one of the most widespread species in the Upper Permian (Lopingian) of the Tethyan regions, ranging from the Mediterranean Sea regions to Japan and

	Loc. A					Loc. B				Loc. C					Loc. D		Loc. E							
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	
<i>Ammodiscus</i> sp.												x												
<i>Glomospira</i> ? sp.							x					?												
<i>Eolasiiodiscus</i> spp.						x	x														x			
<i>Lunucammia</i> cf. <i>palmata</i> (Wang)		x																			x	x		
<i>Colaniella parva</i> (Colani)	x	x	x	x	?	x	x	x	?	x	x	x	x	?	x	x	x	x	x	x	x	x	x	x
Palaeotextulariidae gen. and sp. indet.		x																			x			
<i>Dagmarita</i> ? sp.		x																						
<i>Tetrataxis</i> sp.								x																
<i>Abadehella</i> sp.		x					x	x										x			x			
<i>Reichelina changhsingensis</i> Sheng and Chang		x	x	x				x				x	x							x				
<i>Nanlingella</i> cf. <i>meridionalis</i> Rui and Sheng	x	x					x			x	?										x			
<i>Palaeofusulina</i> sp.			x																			x		
<i>Nankinella</i> sp.		x																						
<i>Pseudovidalina</i> spp.																					x	x		
<i>Raphconilia</i> ? sp.																						x		
<i>Calcivertella</i> ? sp.																						x		
<i>Agathammina</i> cf. <i>pusilla</i> (Geinitz)	x						x					x												
<i>Agathammina</i> sp.	x							?				x												
<i>Agathammina</i> ? sp. A		x																				x		
<i>Agathammina</i> ? sp. B		x	x																					
<i>Hemigordius</i> sp. A							x					?												
<i>Hemigordius</i> sp. B							x																	
<i>Neodiscus</i> sp.																						x		
<i>Nikitinella</i> sp. A			x				x															x		
<i>Nikitinella</i> ? sp.			x			x	x						x									x		
<i>Kamurana</i> ? sp. A	x	x	x										x								x	x	x	
<i>Kamurana</i> ? sp. B		x	x																			x	x	
<i>Cryptoseptida</i> sp.							x															?	x	
<i>Geinitzina</i> spp.			x									x												
<i>Nodosinelloides</i> sp.										x												x		
<i>Pachyphloia</i> sp.	x						x																	
<i>Vervilleina</i> sp.		x		x			x															x		

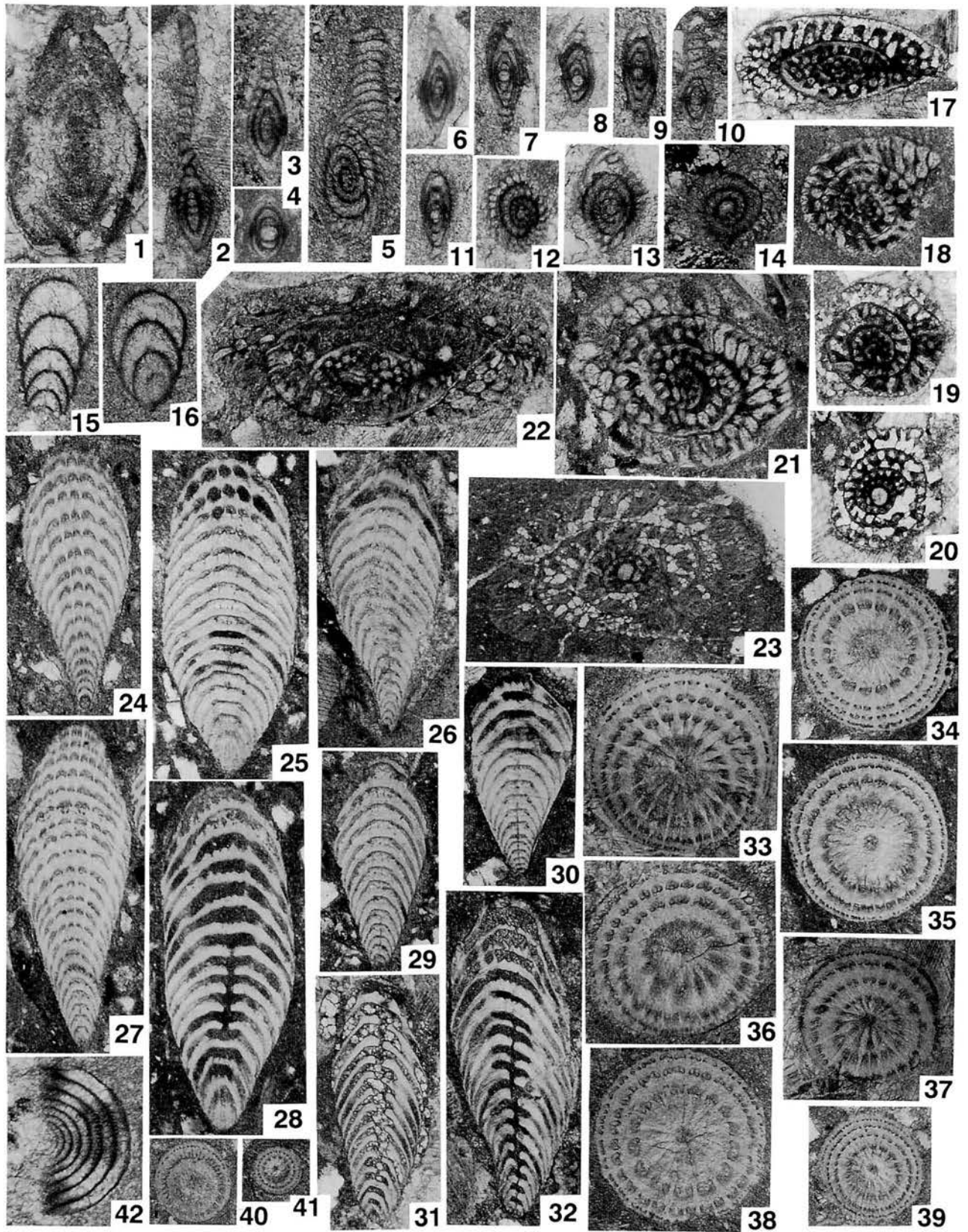
Figure 7. Foraminifers distinguished in Locs. A to E.

South Primorye (Jenny-Deshusses and Baud, 1989; Kobayashi, 1999). In Japan, *Colaniella parva* and allied species occur in the Changhsingian limestones of the Maizuru Group (Ishii *et al.*, 1975) and the Iwai-Kanyo area, southeastern part of the Kanto Mountains (Kobayashi, 1997), exclusive of the upper Toyoma Formation of the Kesenuma area, South Kitakami Belt. However, they have neither been reported from seamount limestones of Japan nor from any limestones of the Circum-Pacific regions.

Nanlingella cf. *meridionalis* is possibly identical with the original specimens of *N. meridionalis* described from the lower part of the Changhsingian of Guangdong and Hunan (Rui and Sheng, 1981). *Nanlingella simplex* and *Nanlingella* spp. are known from the Wuchiapingian limestone of Shaanxi (Rui *et al.*, 1984). According to Rui and Sheng (1981), *Nanlingella* probably appeared in the upper part of the *Codonofusiella* Zone (Wuchiapingian) and flourished in the lower and middle part of the *Palaeofusulina* Zone (Changhsingian). In Japan, *Nanlingella* cf. *meridionalis* in association with *Codonofusiella kwang-*

siana, *C. kueichowensis*, and others is known from the Wuchiapingian limestones of the Southern Chichibu Belt (Ota *et al.*, 2000; Kobayashi, 2001a). An incomplete specimen referred to as *Lantschichites* sp. by Tazawa (1975) from the upper Toyoma Formation of the Kesenuma area is probably referable to *Nanlingella*. Other schubertellids are very rare in the Kesenuma fauna. *Palaeofusulina* occurs exclusively in the Changhsingian, and is the most reliable foraminiferal genus for age determination of the uppermost Permian throughout the Tethyan regions (Rui and Sheng, 1981; Kobayashi, 1999).

Although a detailed age assignment is impossible, *Reichelina changhsingensis* and some genera such as *Abadehella* and *Dagmarita* found in the Kesenuma fauna are also common in the Upper Permian. Two forms possibly assignable to *Kamurana* and unidentified species referable to *Nikitinella* and *Pseudovidalina* are characteristic in some limestone samples. These milioliporid, baisalinid, and involutinid foraminifers have not been reported from Japanese Permian limestones. Although they were not reported in Kobayashi (1997), they have been distinguished



in the Iwai-Kanyo fauna according to my reexamination of the fauna. They also occur in the Upper Permian limestones of the Maizuru Belt (unpublished data by the author). Staffellid fusulinaceans and *Tetrataxis* common in the Upper Permian are very rare, and endothyrids along with such genera as *Paraglobivalvulina*, *Robuloides*, and *Globivalvulina*, also common in the Changhsingian, are entirely lacking in the Kesennuma fauna.

A Changhsingian age for the present fauna is strongly suggested by the occurrences of *Colaniella parva*, *Nanlingella* cf. *meridionalis*, and *Palaeofusulina* sp. Paleobiogeographically, the Kesennuma fauna evidently belongs to the Tethyan province, and is allied to the Late Permian faunas known from the Kurosegawa and Maizuru Belts of Japan, South China, and Southeast Asia (Kobayashi, 1999). On the other hand, a Boreal-Tethyan mixed faunal component within South Kitakami, Maizuru, and Kurosegawa is suggested on the basis of geographical distribution of Permian brachiopods, especially of Middle Permian ones (Tazawa, 1987, 1998, 2000).

Description of species

Family Colaniellidae Fursenko in Rauser-Chernousova and Fursenko, 1959

Genus *Colaniella* Likharev, 1939

Colaniella parva (Colani, 1924)

Figure 8.24-8.41

Pyramis parva Colani, 1924, p. 181, pl. 29, figs. 2, 4-14, 15a-15f, 16, 17, 19, 21, 24; Reichel, 1946, p. 544-547, Figs. 32-34, pl. 19, figs. 13, 14.

Colaniella parva (Colani). Tazawa, 1975, p. 632, 633, pl. 1, figs. 5-11; Kobayashi, 1997, pl. 2, figs. 1-27.

Paracolaniella leei Wang. Tazawa, 1975, p. 633, pl. 1, figs. 1-4.

Material.—More than 30 axial, slightly oblique axial, and transverse sections have been examined, of which 18 are illustrated.

Description.—Subfusiform test deviating to the terminal

part, about 0.8 mm in maximum width and more than 2 mm in maximum length. Initial chamber about 0.03 mm, followed by more than 20 chambers, dish-shaped in outline, strongly overlapping, gradually increasing in height and width. Chambers divided into chamberlets by 15 or more primary platy partitions extending along test axis. Each chamberlet subdivided by two or three secondary platy partitions. Secondary ones well developed even in early ontogenetic stage. Tertiary ones present partly at test margins. Wall finely perforate with fibrous structure.

Discussion.—Many specimens based on definitely oriented thin sections show variable appearances in biocharacters such as size and outline of test, apical angle, degree of tapering of test and overlapping of chambers, mode of incision of three kinds of platy partitions, and their ontogenetic development. The present materials are identical with the original specimens from Vietnam (Colani, 1924) based on variously oriented thin sections. They are also closely similar to the Iwai-Kanyo (Kobayashi, 1997) and other specimens. Collaniellids named *Colaniella parva* (Colani) and *Paracolaniella leei* Wang by Tazawa (1975) from the Kesennuma area are thought to be conspecific.

Occurrence.—Common to rare in Locs. A to E.

Family Schubertellidae Skinner, 1931

Genus *Nanlingella* Rui and Sheng, 1981

Nanlingella cf. *meridionalis* Rui and Sheng, 1981

Figure 8.17-8.21

Lantschichites sp., Tazawa, 1975, pl. 1, fig. 12.

Nanlingella cf. *meridionalis* Rui and Sheng. Ota *et al.*, 2000, fig. 6. 2-4; Kobayashi, 2001a, fig. 3. 14-18.

Material.—Tangential, sagittal, and three oblique sections illustrated herein, and others.

Discussion.—Although axial sections have not been obtained, the present materials are probably assignable to *Nanlingella*, and are compared with type species of this genus from South China. One sagittal section shown in

← **Figure 8.** 1. *Nankinella* sp., D2-022307a, Loc. A-2, ×45. 2-14. *Reichelina changhsingensis* Sheng and Chang. 2. D2-022286a, Loc. A-2. 3. D2-022320, Loc. A-3. 4. D2-022364, Loc. B-7. 5. D2-022361a, Loc. B-7. 6. D2-022361a, Loc. B-7. 7. 022359a, Loc. B-7. 8. D2-022242a, Loc. C-12. 9. D2-022361b, Loc. B-7. 10. D2-022189, Loc. E-19. 11. D2-022324, Loc. A-3. 12. D2-022362, Loc. B-7. 13. D2-022359b, Loc. B-7. 14. D2-022349, Loc. B-8. All ×60. 15, 16. *Lunucamina* cf. *palmata* (Wang). 15. D2-022198. 16. D2-022194a. Both Loc. E-20, ×60. 17-21. *Nanlingella* cf. *meridionalis* Rui and Sheng. 17. D2-022296, Loc. A-2. 18. D2-022197a, Loc. E-20. 19. D2-022292, Loc. A-2. 20. D2-022286b, Loc. A-2. 21. D2-022205a, Loc. E-20. All ×30. 22, 23. *Palaeofusulina* sp. 22. D2-022322a, Loc. A. 23. D2-022207a, Loc. E-20. Both ×30. 24-41. *Colaniella parva* (Colani). 24. D2-022197b, Loc. E-20. 25. D2-022201a, Loc. E-20. 26. D2-022195A, Loc. E-20. 27. D2-022203a, Loc. E-20. 28. D2-022205b, Loc. E-20. 29. D2-022197, Loc. E-20. 30. D2-022389, Loc. B-6. 31. D2-022309, Loc. A-2. 32. D2-022390, Loc. B-6. 33. D2-022307b, Loc. A-2. 34. D2-022195b, Loc. E-20. 35. D2-022206, Loc. E-20. 36. D2-022211a, Loc. E-20. 37. D2-022280, Loc. A-2. 38. D2-022205c, Loc. E-20. 39. D2-022208a, Loc. E-20. 40. D2-022196, Loc. E-20. 41. D2-022200a, Loc. E-20. 24-32. ×30, 33-41. ×45. 42. *Eolasiolus* sp. D2-022372b, Loc. B-7, ×60.

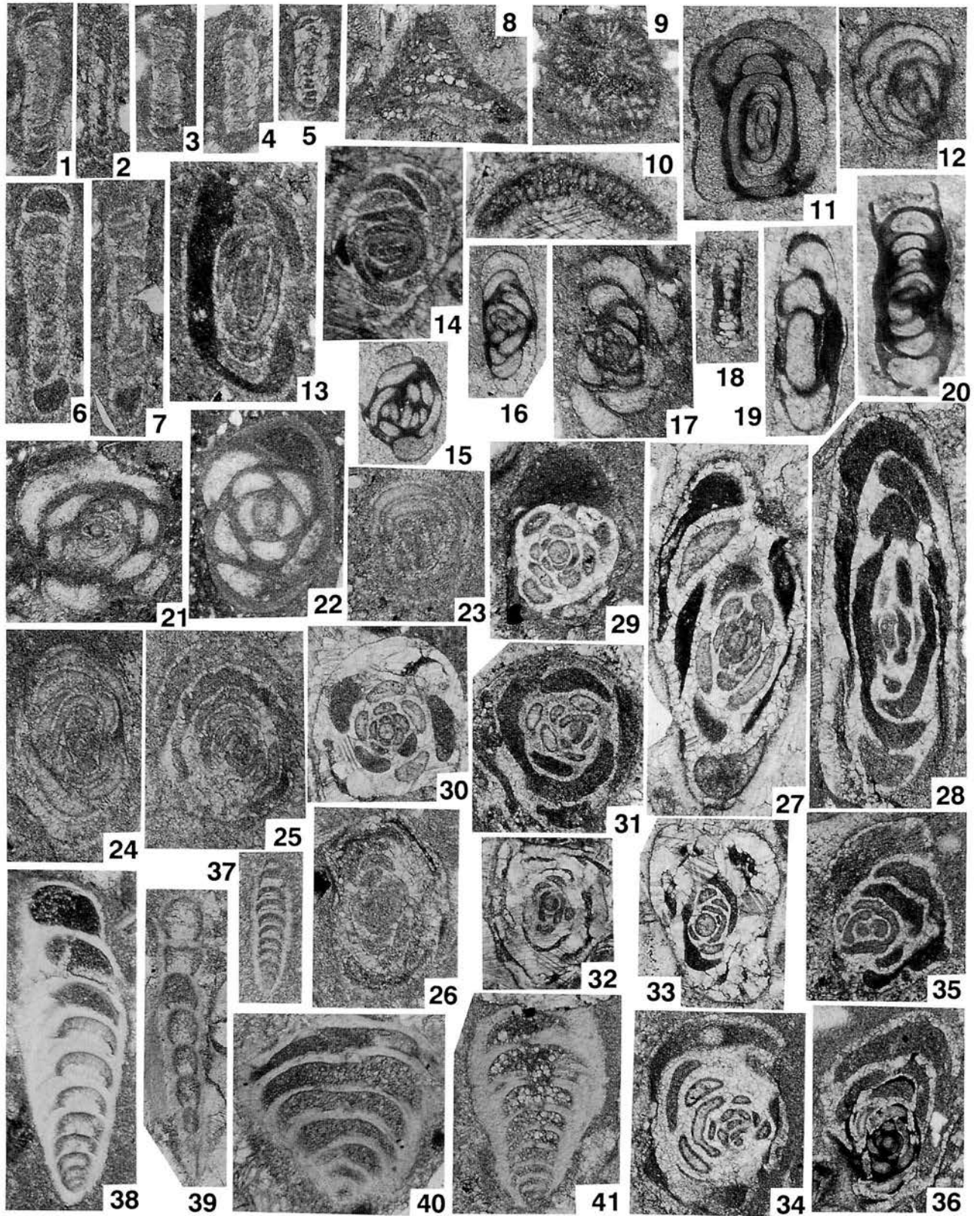


Figure 8.20 may be distinct from this species. An illustrated incomplete specimen, named *Lantschichites* sp. by Tazawa (1975) from the Kesenuma area possibly agrees with the present forms. *Nanlingella* cf. *meridionalis* of Ota *et al.* (2000) and Kobayashi (2001a) resembles the present materials in size of shell, septal fluting, and expansion of shell.

Occurrence.—Rare in Locs. A, B, C, and E, associated with *Palaeofusulina* sp. in Locs. A and E.

Genus *Palaeofusulina* Deprat, 1912

Palaeofusulina sp.

Figure 8.22, 8.23

Material.—Tangential section and oblique section here illustrated, and others.

Discussion.—An oblique section illustrated in Figure 8.23 is thought to be more reasonably assignable to *Palaeofusulina* than to *Nanlingella* or other schubertellid genera based on lack of inner endothyroid volutions and proloculus size. A tangential section shown in Figure 8.22 is ascribed to the genus with reservation. Specific identification and further discussion are postponed until better oriented specimens are recovered. It is difficult to conclude that one incomplete specimen illustrated by Ota *et al.* (2000, fig. 6–5) is undoubtedly assignable to *Palaeofusulina*.

Occurrence.—Very rare in Locs. A and E.

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← **Figure 9.** 1–5. *Pseudovidalina* spp. 1. D2–022191, Loc. E–20. 2. D2–022202a, Loc. E–20. 3. D2–022203b, Loc. E–20. 4. D2–022200b, Loc. E–20. 5. D2–022201b, Loc. E–20. All $\times 60$. 6, 7. *Raphconilia* ? sp. 6. D2–022208b, Loc. E–20. 7. D2–022202b, Loc. E–20. Both $\times 60$. 8–10. *Abadehella* sp. 8. D2–022353, Loc. B–8, $\times 45$. 9. D2–022201c, Loc. E–20, $\times 30$. 10. D2–022181, Loc. E–18, $\times 30$. 11, 12. *Agathammina* cf. *pusilla* (Geinitz). 11. D2–022208b, Loc. E–20. 12. D2–022242b, Loc. C–12. Both $\times 60$. 13, 14. *Agathammina* ? sp. A. 13. D2–022195c, Loc. E–20. 14. D2–022299, Loc. A–2. Both $\times 50$. 15–17. *Agathammina* sp. 15. D2–022277a. 16. D2–022277b. 17. D2–02227901c. All Loc. A–1, $\times 60$. 18. *Hemigordius* sp. A. D2–022359, Loc. B–7, $\times 80$. 19, 20. *Hemigordius* sp. B. 19. D2–022361c. 20. D2–022373. Both Loc. B–7, $\times 60$. 21, 22. *Neodiscus* sp. 21. D2–022200c. 22. D2–022207b. Both Loc. E–20, $\times 30$. 23–26. *Nikitinella* spp. 23. D2–022194b, Loc. E–20. 24. D2–022203c, Loc. E–20. 25. D2–022328b, Loc. A–3. 26. D2–022358a, Loc. B–7. All $\times 60$. 27, 28. *Agathammina* ? sp. B. 27. D2–022184, Loc. E–18. 28. D2–022312, Loc. A–3. Both $\times 30$. 29–34. *Kamurana* ? sp. A. 29. D2–022313a, Loc. A–3. 30. D2–022297, Loc. A–2. 31. D2–022325, Loc. A–3. 32. D2–022316, Loc. A–3. 33. D2–022295, Loc. A–2. 34. D2–022313b, Loc. A–3. 35, 36. *Kamurana* ? sp. B. 35. D2–022317, Loc. A–3. 36. D2–022216, Loc. E–21. Both $\times 30$. 37. *Nodosinelloides* sp. D2–022211b, Loc. E–20. $\times 60$. 38. *Pachyphloia* sp. D2–022366b, Loc. B–7. $\times 60$. 39. *Vervilleina* sp. D2–022293, Loc. A–2. $\times 60$. 40, 41. *Cryptoseptida* sp. 40. D2–022366c. 41. D2–022358b. Both Loc. B–7, $\times 60$.

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A new coelacanth from the Early Cretaceous of Brazil (Sarcopterygii, Actinistia)

YOSHITAKA YABUMOTO

Kitakyushu Museum of Natural History and Human History, 2-4-1, Higashida, Yahatahigashiku, Kitakyushu, Fukuoka, 805-0071, Japan (e-mail:yabumoto@kmnh.jp)

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Abstract. A new coelacanth fish of the genus *Mawsonia*, *M. brasiliensis* sp. nov. is described on the basis of a specimen from the Early Cretaceous Romualdo Member of the Santana Formation in the Araripe Plateau, Brazil. This is the third species of coelacanth from the Cretaceous of Brazil and the holotype is the first complete, articulated specimen of the genus. This new species differs from its congeners in the proportion of the cranium, gular plates and angular, and the position of the otic canal fossa. *M. brasiliensis* has thin cycloid scales without ornament (no tubercles or ridges). This new addition to the genus *Mawsonia* is significant in increasing understanding of the diversity of the suborder Latimeroidei in the early Cretaceous, which lineage continues to the Recent coelacanths of the genus *Latimeria*.

Key words: Araripe, Brazil, coelacanth, Early Cretaceous, *Mawsonia*, new species, Santana Formation

Introduction

The Araripe Plateau, northeastern Brazil, is well known for its excellently preserved Early Cretaceous shallow marine and freshwater fossil assemblages (Maisey, 1991; Martill, 1993; Evans and Yabumoto, 1998). Two coelacanth species have been described from Cretaceous deposits in Brazil: *Mawsonia gigas* Woodward, 1907 from the Neocomian of Bahia, and *Axelrodichthys araripensis* Maisey, 1986 from the Romualdo Member of the Santana Formation. On the basis of an almost complete articulated specimen recovered from the Romualdo Member of the Santana Formation, Araripe Plateau, Brazil, a new species of the genus *Mawsonia* is proposed. An almost complete neurocranium and some other disarticulated head bones from the Romualdo Member that Maisey (1986) described as *M. cf. gigas* are referable to this new species. This new addition to the genus *Mawsonia* is significant in increasing understanding of the diversity of the suborder Latimeroidei in the early Cretaceous, which lineage continues to the Recent forms of coelacanths of the genus *Latimeria*. Figures were made using a camera lucida. Terminology of coelacanth bones follows Forey (1998) and of median fins follows Uyeno (1991).

Systematic description

Order Coelacanthiformes Huxley, 1861
Suborder Latimeroidei Schultz, 1993
Family Mawsoniidae Schultz, 1993
Genus *Mawsonia* Woodward, 1907

Mawsonia brasiliensis sp. nov.

Figures 1–4

Mawsonia cf. *gigas* Maisey, 1986, p. 3–13, figs. 1–11; Maisey, 1991, p. 317–323.

Material.—KMNH (Kitakyushu Museum of Natural History and Human History) VP 100,247, holotype, an almost complete, articulated specimen preserved in a calcareous concretion.

Type locality.—Exact locality not recorded, Araripe Plateau, Brazil. The type horizon is probably the Romualdo Member of the Santana Formation, which has yielded many fish fossils preserved in the same type of calcareous concretions as was the holotype. Although the age of this formation is considered to be Cretaceous, there are different opinions as to its exact age—Aptian (Santos and Valenca, 1968), Albian (Lima, 1979), Aptian-Albian (Schobbenhaus and Campos, 1986), older Neocomian (Maisey, 1986), Aptian-Albian (Maisey, 1991) and early Cenomanian (Martill, 1990).

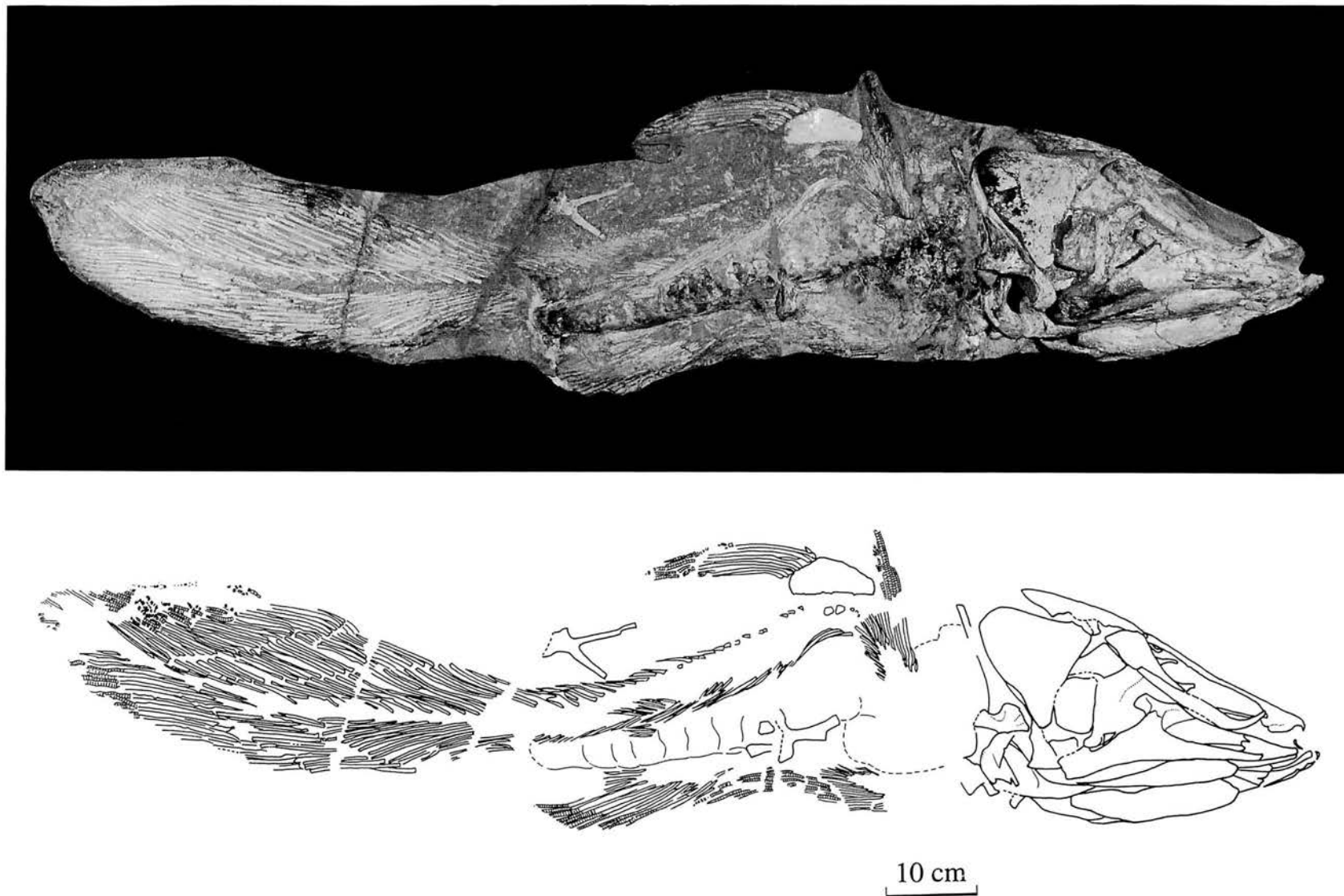


Figure 1. *Mawsonia brasiliensis* sp. nov., holotype (KMNH VP 100,247, 1277 mm SL) from the Romualdo Member of the Santana Formation in the Araripe Plateau, Brazil.

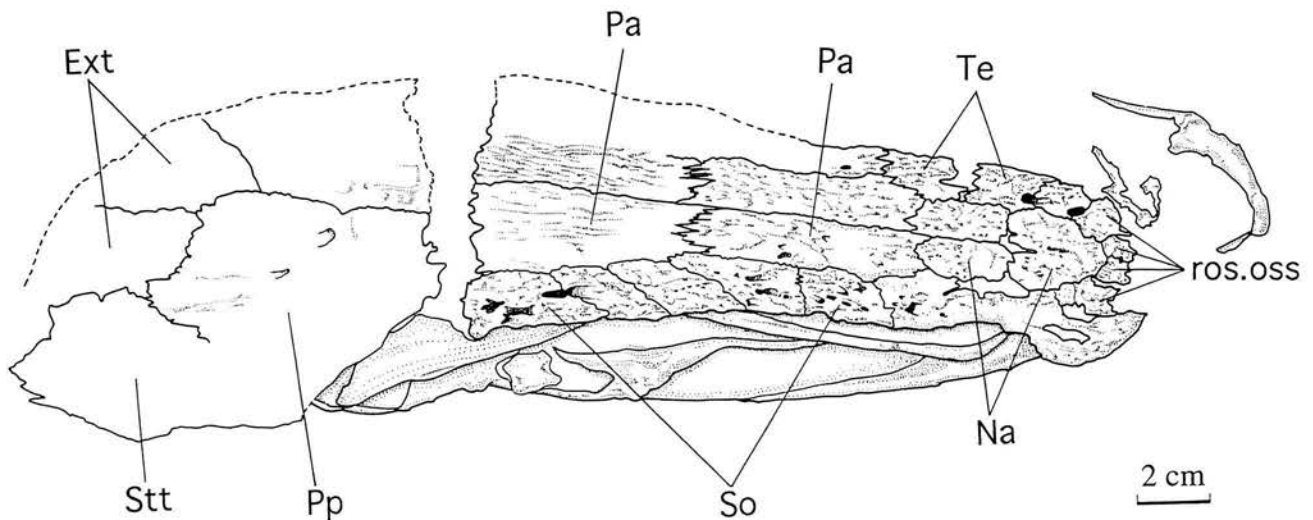
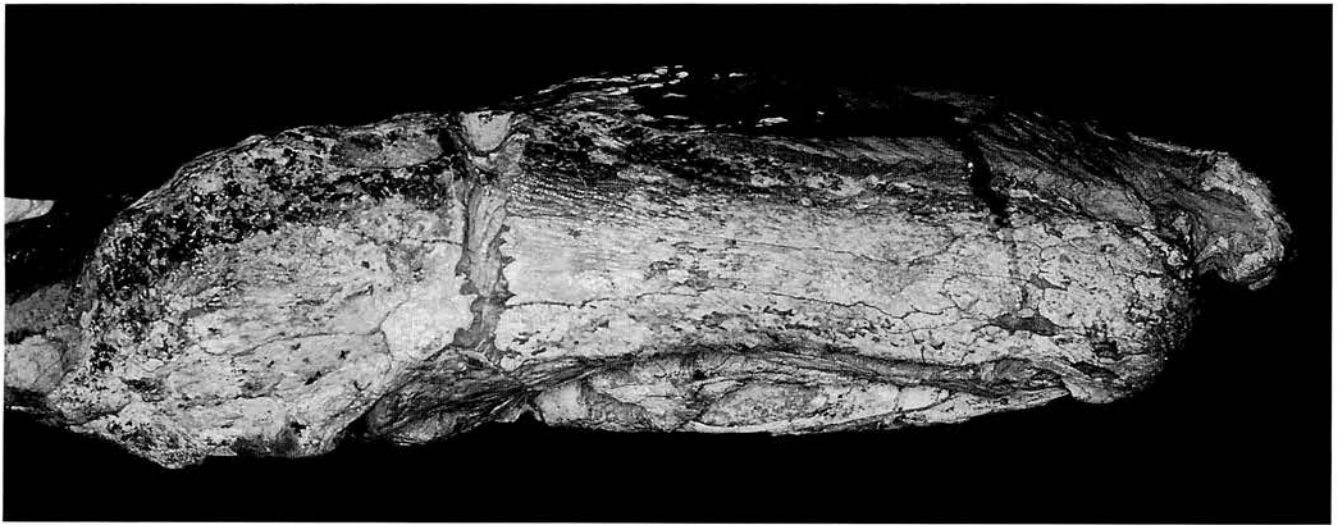


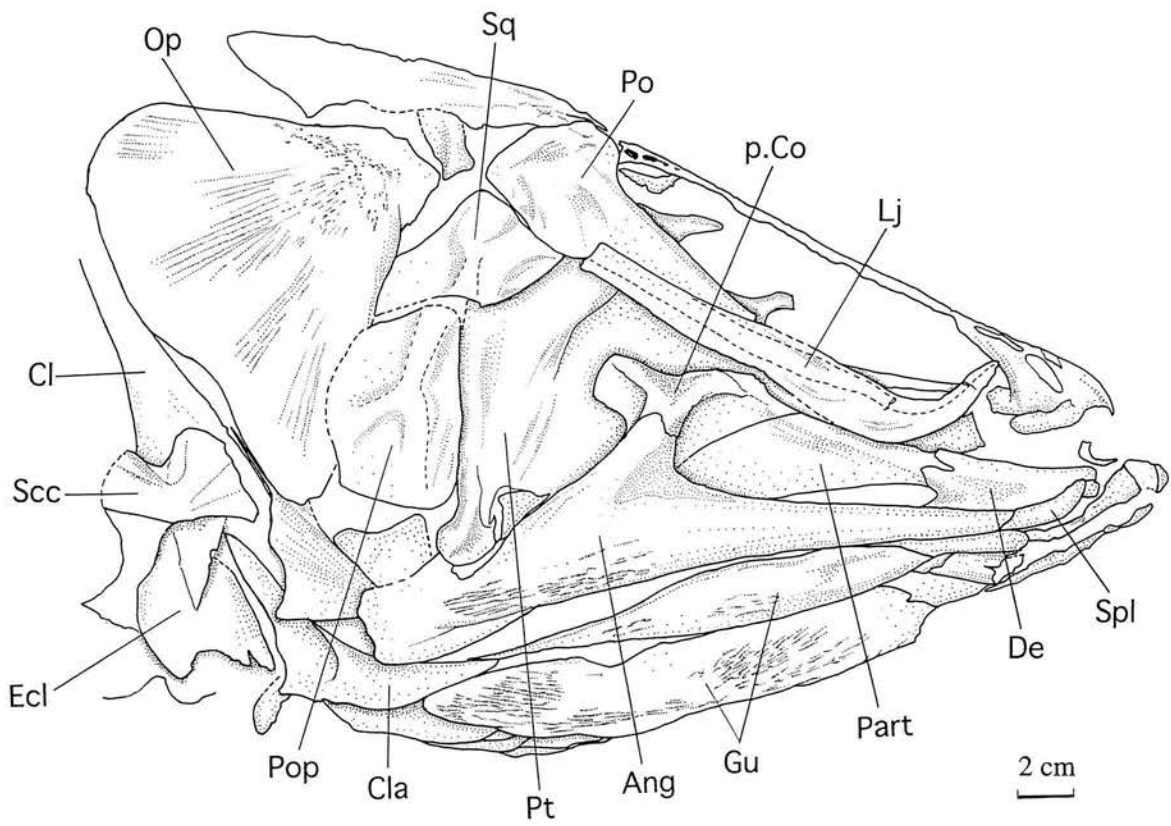
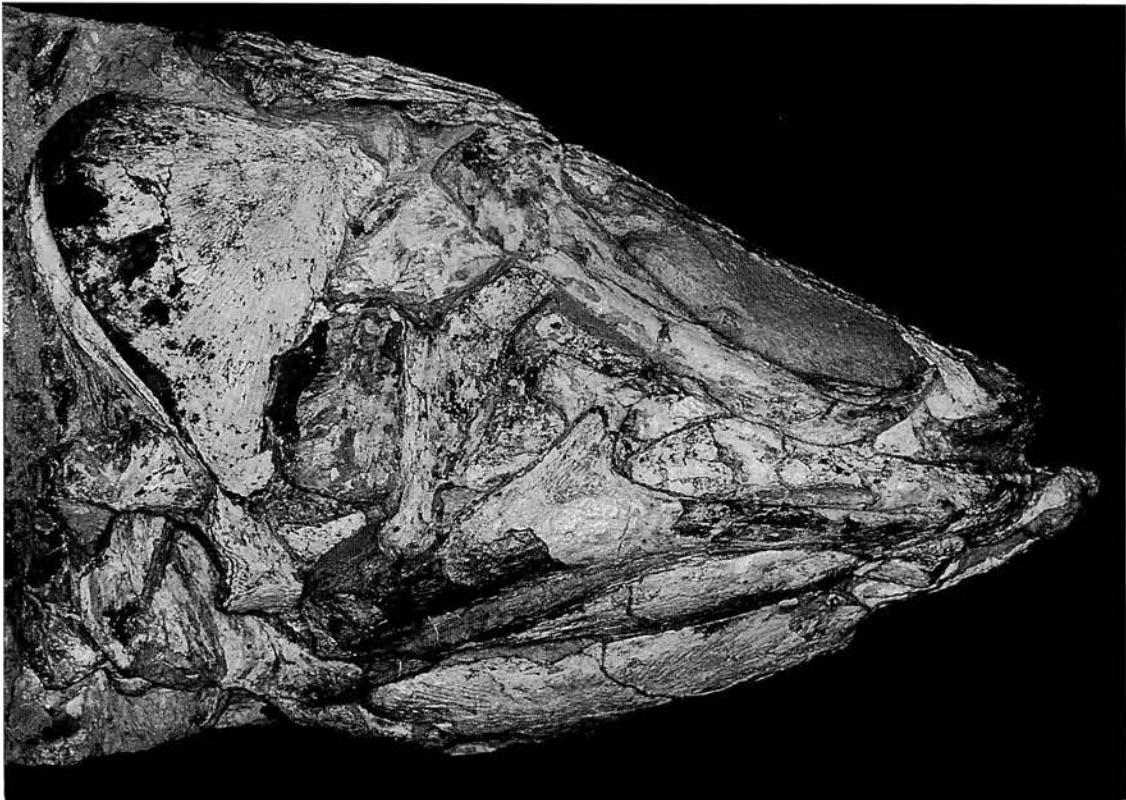
Figure 2. *Mawsonia brasiliensis* sp. nov., skull in dorsal view, holotype (KMNH VP 100,247, 1277 mm SL) from the Romualdo Member of the Santana Formation in the Araripe Plateau, Brazil. Abbreviations: Ext = extrascapular; Na = nasal; Pa = parietal; Pp = postparietal; ros.oss = rostral ossicles; So = supraorbital; Stt = supratemporal; Te = tectal.

Etymology.—The species is named for the country in which the specimen was found.

Diagnosis.—Length of the parietonasal shield is about twice its width. Its size is about 1.5 times that of the postparietal shield. Width of the postparietal shield is about 1.2 times its length. The fossa for the otic canal (foc) is present on the lateral surface of the postparietal and close to the small anterior apophysis (apa). The oval gular plate has no ridge running from the anterior to posterior ends. The ridges on the operculum are radial and weak. The angular is deep at its posterior, steep at the posterior dorsal edge, narrow at its anterior, and its anterior dorsal margin (where it articulates with the principal coronoid and

prearticular) is deeply concave. The scales are thin and have fine bony ridges (circuli) on the exposed portion, but have no ornamental tubercles or ridges typical of coelacanths.

Description of holotype.—The body is slender; body depth at the origin of the first dorsal about 300 mm; total length 1435 mm; standard length 1277 mm; head length 375 mm. Length of the parietonasal shield is 185.6 mm, the posterior end being broader, width of the right half 43.1 mm. Both parietals are narrow, the posterior one is wider, but the anterior one is just a bit longer. There is one anterior nasal, possibly fused, which is almost the same width as the width of the posterior nasals. The paired posterior



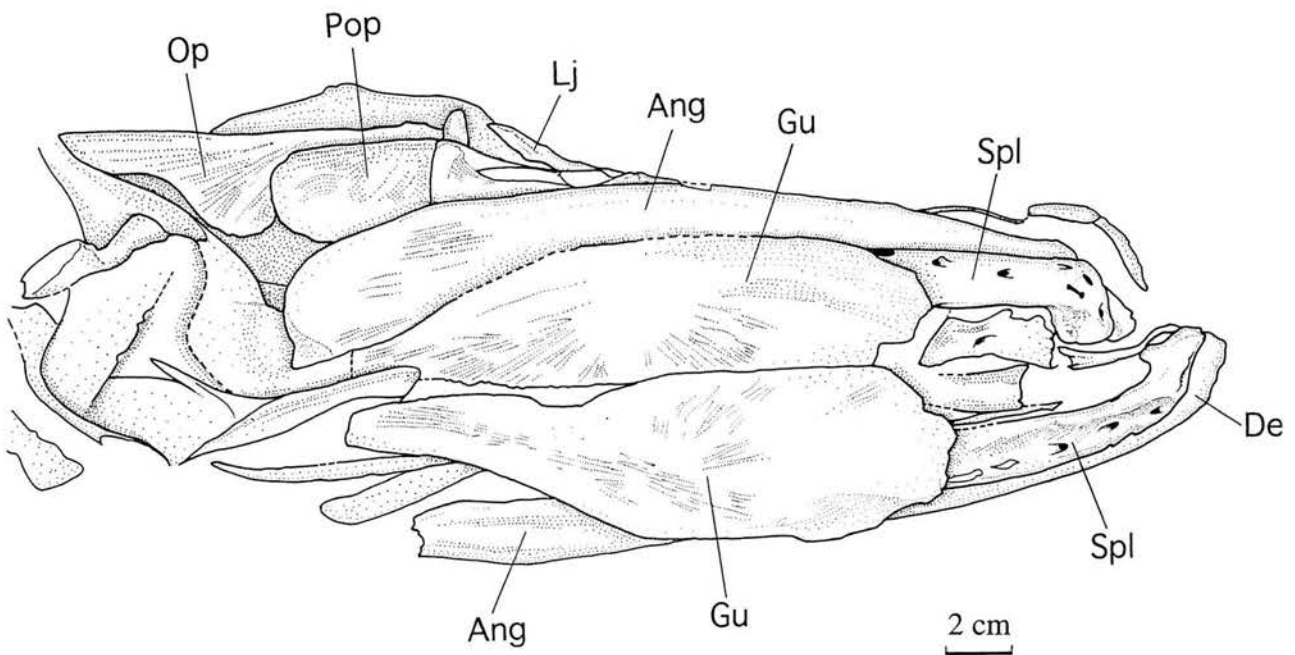


Figure 4. *Mawsonia brasiliensis* sp. nov., skull in ventral view, holotype (KMNH VP 100,247) from the Romualdo Member of the Santana Formation in the Araripe Plateau, Brazil. Abbreviations: Ang = angular; De = dentary; Gu = gular plate; Lj = lachrymojugal; Op = operculum; Pop = preoperculum; Spl = splenial.

← **Figure 3.** *Mawsonia brasiliensis* sp. nov., skull in lateral view, holotype (KMNH VP 100,247) from the Romualdo Member of the Santana Formation in the Araripe Plateau, Brazil. Abbreviations: Ang = angular; Cl = cleithrum; Cla = clavicle; De = dentary; Ecl = extracleithrum; Gu = gular plate; Lj = lachrymojugal; Op = operculum; Part = prearticular; p.Co = principal coronoid; Po = postorbital; Pop = preoperculum; Pt = pterygoid; Scc = scapulocoracoid; Spl = splenial; Sq = squamosal.

nasals are short, about 40% the length of the anterior parietals, and about 2.5 times their own width.

The paired posterior and anterior tectals are separated by a small space and are almost the same size, 22.5 mm in length and 16 mm in width. While the left tectals are well preserved, the right pair are slightly broken. The anterior tectal suture has posterior and anterior nasals and posterior rostral ossicles, while the posterior tectal suture has anterior parietals and posterior nasals. Each anterior tectal has a foramen which opens forward.

There are three pairs of rostral ossicles, all attached to the anterior nostril. While the anterior ossicles are small, 10.1 mm in length, 5.9 mm in width, the posterior and middle rostral ossicles are almost the same size: posterior pair 17.8 mm in length, 12.5 mm in width; middle pair 18.2 mm in length, 14.5 mm in width. There is a relatively large foramen, 5.2 mm long, between the posterior and middle rostral ossicles. The middle rostral ossicles also possess a foramen. There is a groove between the middle and anterior rostral ossicles.

Four supraorbitals are present, all about the same width. While the outline of the left supraorbitals is not distinct because the surface is broken, the right ones are well preserved. The length of the most anterior supraorbital is longest, 67.0 mm, about 1.5 times that of the others. Each supraorbital possesses a small foramen. Most of the first supraorbital attaches to the anterior parietal, but the posterior end attaches to the posterior parietal. The other supraorbitals attach to the posterior parietal.

The postparietal shield consists of a pair of postparietals, supratemporals and extrascapulars, the middle extrascapular being absent. Although most of the postparietals are broken, the suture between each bone can be recognized, except for the portion between the postparietal and supratemporal. About half of the left side and half of the right surface of the postparietal shield are missing. Of this shield, the postparietal, with two short processes on the anterior ventral surface, is the largest bone with a length of 76.7 mm. The width of the right extrascapular is 30.1 mm.

All cheekbones are well preserved. The postorbital, with a length of 119.2 mm and a height of 54.1 mm, has a long anterior process ventrally, extending 71.7 mm to the middle of the lachrymojugal. The depth at the base of the process is 21.1 mm. While the upper edge of the squamosal at 36.7 mm width is almost twice that of the lower edge, the depth is 53.8 mm. The preoperculum is deep, with a depth of 62.2 mm, about 1.5 times the width (44.5 mm). It is also narrow and round at the upper margin and along the lower margin of the squamosal. A sensory canal forks into two at the center of the preoperculum. The lachrymojugal is 149.1 mm long. Its anterior end curves upward, and a sensory canal runs along the upper

margin of this curved part.

The mentomeckelian is short, 42.2 mm in length, thick (13.7 mm) at the anterior end, and thin (2.8 mm) at its posterior.

The dentary lies outside the mentomeckelian and the lateral swelling is absent. It is long (left dentary 140.6 mm), almost half that of the mandible, curves medially at the anterior part, and the surface overlapping the angular is long. The upper limb of the dentary (81.7 mm in length) is short and contacts the prearticular, while the lower limb is long and occupies almost half of the mandible. There are two tooth plates on the dentary, but even though all the teeth are missing, many alveoli are visible, a few are 1 mm deep, and the rest of them minute.

The angular is long (from the anterior end of the inside to the posterior end of the outside, 149.2 mm), its deepest part is slightly behind the middle of the mandible, and at this point, the suture has a principal coronoid, forming a dorso-anterior process. Anterior to this point, it abruptly narrows, while posteriorly it gradually narrows, its depth posteriorly being almost twice that at the anterior.

The 72.2 mm long principal coronoid consists of anterior and posterior portions separated by a narrow section (24.3 mm deep) at the middle where the suture has the angular. The anterior portion has an almost triangular shape, and its antero-ventral margin contacts the prearticular. The posterior portion is rectangular with a depth of 16.9 mm and a length of 26.0 mm from the narrow section. The dorsal part of the posterior portion also forms a ridge that continues to the angular.

The anterior portion of the prearticular joins with the dentary and angular on the distal surface of the jaw to form a large foramen, while its posterior portion contacts the angular ventrally and the principal coronoid dorsally. Its deepest part, at 26.2 mm, is just behind the lateral midpoint.

The articular is small, 16.8 mm in depth, 24.4 mm long, and separated from the retroarticular. It joins with the retroarticular ossification to form glenoid articulation with a quadrate.

The right splenial is well preserved, its length about 5 times the width, and has five sensory canal openings. It contacts the ventro-mesial face of the dentary, and its anterior end curves mesially. While the width of the anterior end is 20.6 mm and the length 93.6 mm, the posterior portion gradually broadens to 18.8 mm.

The pterygoid, quadrate, and metapterygoid (including the anterior portion of the articular surface for the antotic surface) are exposed, but the pterygoid is covered for the most part by the lachrymojugal and lower jaw. Also, the border between the pterygoid and metapterygoid is covered by the postorbital and lachrymojugal. The quadrate has a slightly twisted upper portion, and articulates with the lower jaw by condyles the distal one of which is exposed.

There is a short dorso-anterior process on the upper end of the metapterygoid.

The cleithrum, extracleithrum and clavicle are well preserved. While the cleithrum is long and reaches up to about the level of the upper edges of the operculum, its upper portion has a cylindrical shape while its lower portion is broad and complicated in structure. Also a flange extends outward and backward at the antero-ventral portion of the cleithrum. Its triangular postero-ventral portion joins with the extracleithrum to form a postero-ventral section of the shoulder girdle. The extracleithrum is a broad bony plate and slightly curves anteriorly. The clavicle contacts the ventral edge of the cleithrum and the anterior edge of the extracleithrum. It consists of anterior and posterior flanges, the latter being narrow along the dorsal edge. The anocleithrum is not preserved in this specimen.

The scapulocoracoid, shaped like a twisted bowtie, is preserved on the cleithrum slightly below the middle of the cleithrum, and is slightly apart from extracleithrum.

The triangular operculum extends slightly antero-ventrally, while its postero-ventral margin becomes slightly concave below the middle of the margin. Its anterior margin is thick, being thickest at the dorsal end. Most of the opercular surface is missing, but weak radiating ridges are visible.

The first dorsal fin with 10 fin rays is well preserved. Its basal plate, 92.5 mm long and 40.8 mm deep, is kidney-shaped with the anterior portion slightly extended, deepest at slightly behind the midpoint, while the posterior dorsal edge supports the dorsal fin rays. The depth of the anterior end of the plate is 16.7 mm. The first five fin rays articulate with the thick edge which fans out from the portion slightly behind the center of the plate. From this portion a weak ridge runs forward.

The second dorsal fin rays are not preserved. Its basal plate has two anterior branches, the upper branch at 72.5 mm being longer and more slender than the lower (54.0 mm). The length of the preserved part is 112.9 mm. Even with the very end missing, it can be seen that the posterior portion of the basal plate is broad.

Both pectoral fins are preserved. The right pectoral fin with thirty-two countable fin rays is preserved behind the head and covers the anterior part of the basal plate of the dorsal fin. Twenty-five rays can be counted on the portion of the left pectoral fin preserved below the right pelvic girdle.

Three bones of the pelvic girdle are preserved above the middle of the left pectoral, the most anterior one being the largest and T-shaped, and consisting of three processes. The posterior end of the bone is missing. Its anterior process abruptly becomes narrow anteriorly, while the dorsal process is shorter than the ventral process, and slightly curves backward. Two small bones behind the large pel-

vic bone are considered to be axial mesomeres of the pelvic girdle. The anterior portions of the mesomeres are missing; however what remains of the ventral cylindrical one gradually thickens posteriorly. It is larger than the dorsal one. Twenty-two fin rays can be counted in the left pelvic fin. A part of the right pelvic fin is preserved on the ribs. The first anal fin is missing.

The centra are unossified. Their anterior neural spines are short and pebble-like, but the posterior ones are longer. Neural spines that articulate with pterygiophores of the third dorsal fin are long and stout at the dorsal end. The base of the neural spines is divided and forms the neural arches. There are 20 neural spines for the third dorsal pterygiophores and 33 anterior to them. Twenty-three relatively long, slender ribs are found along the dorsal margin of the swim bladder.

There are 23 third dorsal fin rays. Four haemal spines can be identified anterior to the first pterygiophore of the second anal fin. Fifteen haemal spines reach to the 21 pterygiophores of the second anal fin. The number of second anal fin rays is 25.

Only part of the caudal fin is preserved. The posterior end is missing. Four rays of the upper lobe and 7 rays of the lower lobe are preserved.

Scales are thin and well preserved, but no typical coelacanth tubercle or ridge ornamentation is visible, except for fine bony ridges (circuli) on the exposed portion.

Remarks.—Cloutier and Forey (1991) recognized the following five species in the genus *Mawsonia*: *M. gigas* Woodward, 1907, *M. tegamensis* Wenz, 1975, *M. ubangiana* Casier, 1961, *M. lavocati* Tabaste, 1963, and *M. libyca* Weiler, 1935. *M. gigas* was described from South America, the others from Africa. Maisey (1986) described the specimen AMNH 11758, acid-prepared bones: parietonasal and postparietal shields, right postorbital, squamosal, lachrymojugal, incomplete operculum, pterygoid, metapterygoid, quadrate, autopalatine, and coronoid from a single specimen as *M. cf. gigas*. The author compared the present specimen with specimen AMNH 11758 and now regards it as *M. brasiliensis*, because the proportions of these bones are the same. The specimen AMNH 11758 has the fossa for the otic canal of the postparietal on the lateral surface of the postparietal close to the anterior apophysis.

On the basis of the following characters, this new species belongs to the genus *Mawsonia*: length of the parietonasal shield is about 1.5 times the length of the postparietal shield, postorbital (dermosphenotic in Maisey, 1986) has a splint-like anterior projection, posterior two-thirds of the elongated lachrymojugal is almost straight.

This new species differs from *M. tegamensis* from the Aptian of Niger in having the length of the parietonasal shield twice (versus 1.7 times) its width and 1.5 times (ver-

1.4 times) the length of the postparietal shield; width of the postparietal shield 1.2 times (versus 1.6 times) its length; long, oval gular plates versus gular plates with a wide, rather than slender, anterior portion; radial ornamentation on the anterior portion of the operculum versus a mesh-like pattern.

This new species differs from *M. ubangiana* from the Neocomian of Zaire in having the fossa for the otic canal of the postparietal (parietal in Maisey, 1986) on the lateral surface of the postparietal close to the anterior apophysis. In *M. ubangiana*, the fossa is present on the ventral surface of the postparietal distant from the anterior apophysis of the postparietal.

In *M. lavocati* from the Albian of Morocco, the anterior end of the angular is higher than that of the new species, and the angle between the postero-dorsal edge and the ventral edge of the angular is larger. Also, the ornamentation in *M. lavocati* is more pronounced.

This new species differs from *M. libyca* from the Albian of Egypt in having the dorsal edge of the angular deeply concave at the midpoint versus slightly concave.

Although this new species is close to *M. gigas* from the Neocomian of Bahia, Brazil in appearance, it differs in having the small anterior apophysis of the postparietal and the fossa for the otic canal close to the anterior apophysis versus a large anterior apophysis of the postparietal and the fossa for the otic canal distant from the anterior apophysis of the postparietal; the antero-lateral surface of the postparietal forming a steep (versus gentle) slope; the angular being deeper; and no ridge running from the anterior to posterior ends on the gular plates.

This new addition to the genus *Mawsonia* is significant in increasing understanding of the diversity of the suborder Latimeroidae in the early Cretaceous, which lineage continues to the Recent coelacanths of the genus *Latimeria*.

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Echigoceras sasakii, a new Middle Carboniferous nautilid from the Omi Limestone Group, Central Japan

SHUJI NIKO

Department of Environmental Studies, Faculty of Integrated Arts and Sciences, Hiroshima University,
Higashihiroshima, 739–8521, Japan (e-mail: niko@hiroshima-u.ac.jp)

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Abstract. A new genus and species of the trigonoceratid nautilid, *Echigoceras sasakii*, is described. Specimens of this cephalopod occur in the Middle Carboniferous (probable late Bashkirian) bioclastic rudstone/grainstone of the Omi Limestone Group, Central Japan. *Echigoceras* is most closely related to the Early Carboniferous genus *Stroboceras*, but differs in its strongly curved cyrtoconic shell and siphuncular position near the ventral margin. It is possible that *Echigoceras* is the descendant of *Stroboceras*.

Key words: *Echigoceras* gen. nov., Middle Carboniferous, Nautiloidea, Omi Limestone Group, Trigonoceratidae

Introduction

Following Niko (2001), the present report on a new trigonoceratid nautilid genus and species is the second installment in a series describing the Carboniferous cephalopod fauna of the Omi Limestone Group in Niigata Prefecture, Central Japan. All of the material documented herein is from the light gray, massive limestone belonging to bioclastic rudstone/grainstone of Middle Carboniferous (probable late Bashkirian) age at the southern corner of Higashiyama Quarry, the identical locality to that for the previously described orthoconic forms (Niko, 2001). The material is deposited in the University Museum of the University of Tokyo (UMUT).

Systematic paleontology

Order Nautilida Agassiz, 1847
Superfamily Trigonoceratoidea Hyatt, 1884
Family Trigonoceratidae Hyatt, 1884
Genus *Echigoceras* gen. nov.

Type species.—*Echigoceras sasakii* sp. nov., by monotypy.

Diagnosis.—Trigonoceratid with strongly curved cyrtoconic shell whose surface is indented by longitudinal ridges and grooves; gross profiles of whorl are mostly subtrapezoidal, with inflated dorsal side; lobed peristome preserved as distinct growth lines characterized by V-shaped ventral sinus; siphuncular position near ventral margin;

septal necks orthochoanitic, with very narrow septal foramina.

Etymology.—The generic name is derived from Echigo, which is a historic provincial name for the type locality.

Echigoceras sasakii sp. nov.

Figures 1–4

Stroboceras sp., Oyagi, 2000, p. 108.

Diagnosis.—Same as for the genus.

Description.—Strongly curved, horseshoe-like cyrtocones consisting of less than one full circle, comprising approximately 0.91 of a full circle; shell size moderate for the family, maximum whorl diameter of holotype 45.0 mm; gross profiles of whorl are mostly subtrapezoidal with broadly inflated dorsal side and width/height ratio (form ratio) of approximately 0.94, then changing to laterally compressed suboval cross section near aperture, where whorl dimensions of 11.7 mm in width and 15.0+ mm in height give a form ratio of 0.78–; body chamber represented adorally by approximately one-third of whorl. Shell surface is indented by strongly prominent bilaterally symmetrical longitudinal ridges, as follows: 1 ventral (vr), 2 ventrolateral (v-lr1, v-lr2), 2 lateral (lr1, lr2), and 1 dorsolateral (d-lr); except for dorsal side of the shell, interspaces between longitudinal ridges are depressed and form longitudinal grooves; among these, there is a groove sandwiched between the ventrolateral and lateral longitudinal ridges (= between v-lr2 and lr1) that is deeply concave.

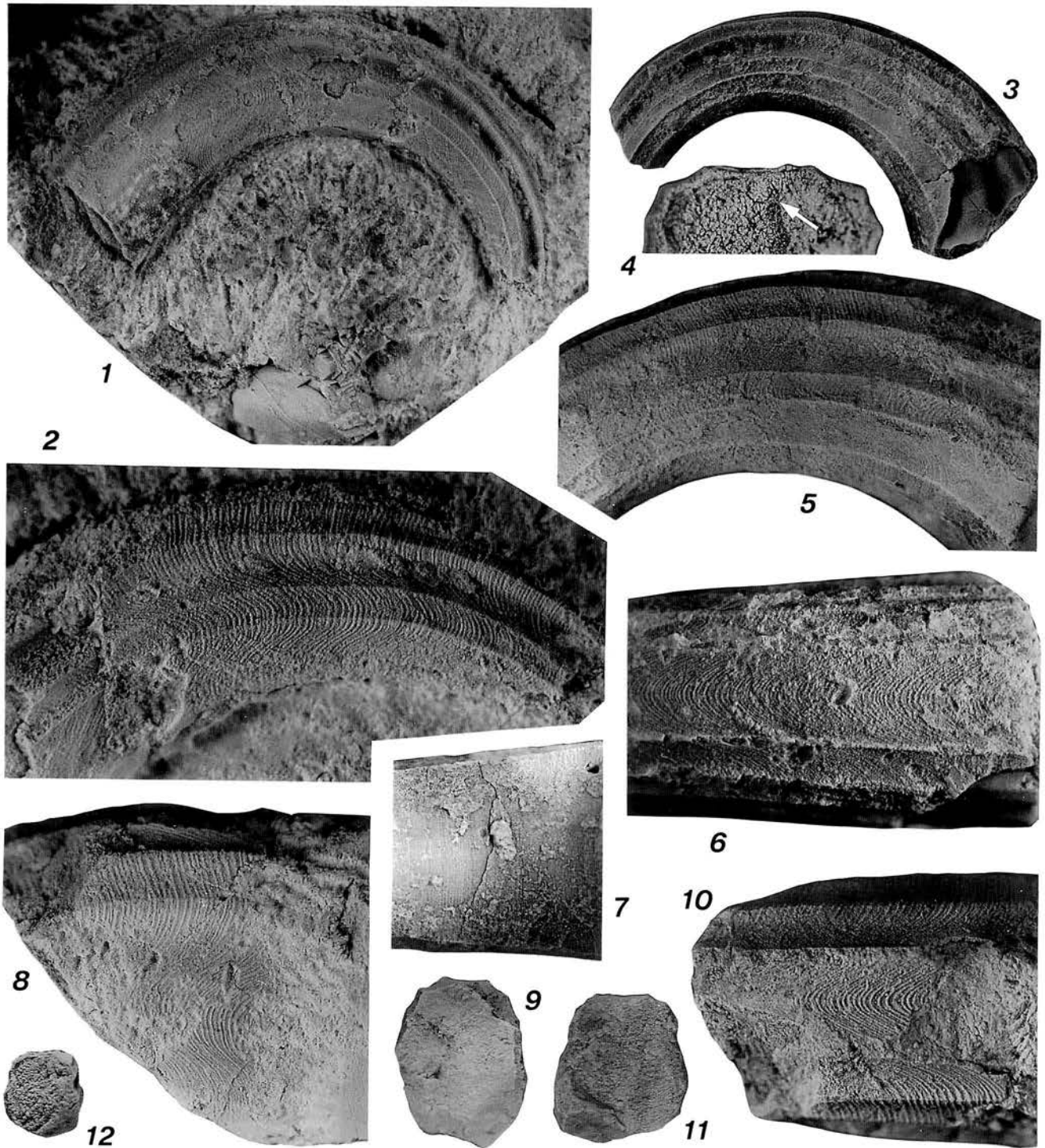


Figure 1. *Echigoceras sasakii* gen. et sp. nov. **1, 2.** Holotype, UMUT PM 27920; **1**, lateral view, aperture on left, apical shell embedded in matrix, and apertural shell partly removed, $\times 2$; **2**, details of surface ornamentation, $\times 4$. **3–7, 11, 12.** Paratype, UMUT PM 27919; **3**, lateral view, aperture on right, $\times 2$; **4**, enlargement of ventral margin of Figure 1.12, showing siphuncular position (arrow), $\times 6$; **5**, details of surface ornamentation, $\times 4$; **6**, ventral view showing details of surface ornamentation, aperture on right, $\times 4$; **7**, dorsal view showing details of surface ornamentation, aperture on right, $\times 4$; **11**, cross-sectional view of adoral end, venter up, $\times 2$; **12**, cross-sectional view of apical end, venter up, $\times 2$. **8–10.** Paratype, UMUT PM 27921; **8**, lateral view, aperture on right, showing details of surface ornamentation and partial peristome, $\times 4$; **9**, apertural view, venter up, dorsal shell partly lacking, $\times 2$; **10**, ventral view, aperture on right, showing details of surface ornamentation, $\times 4$.

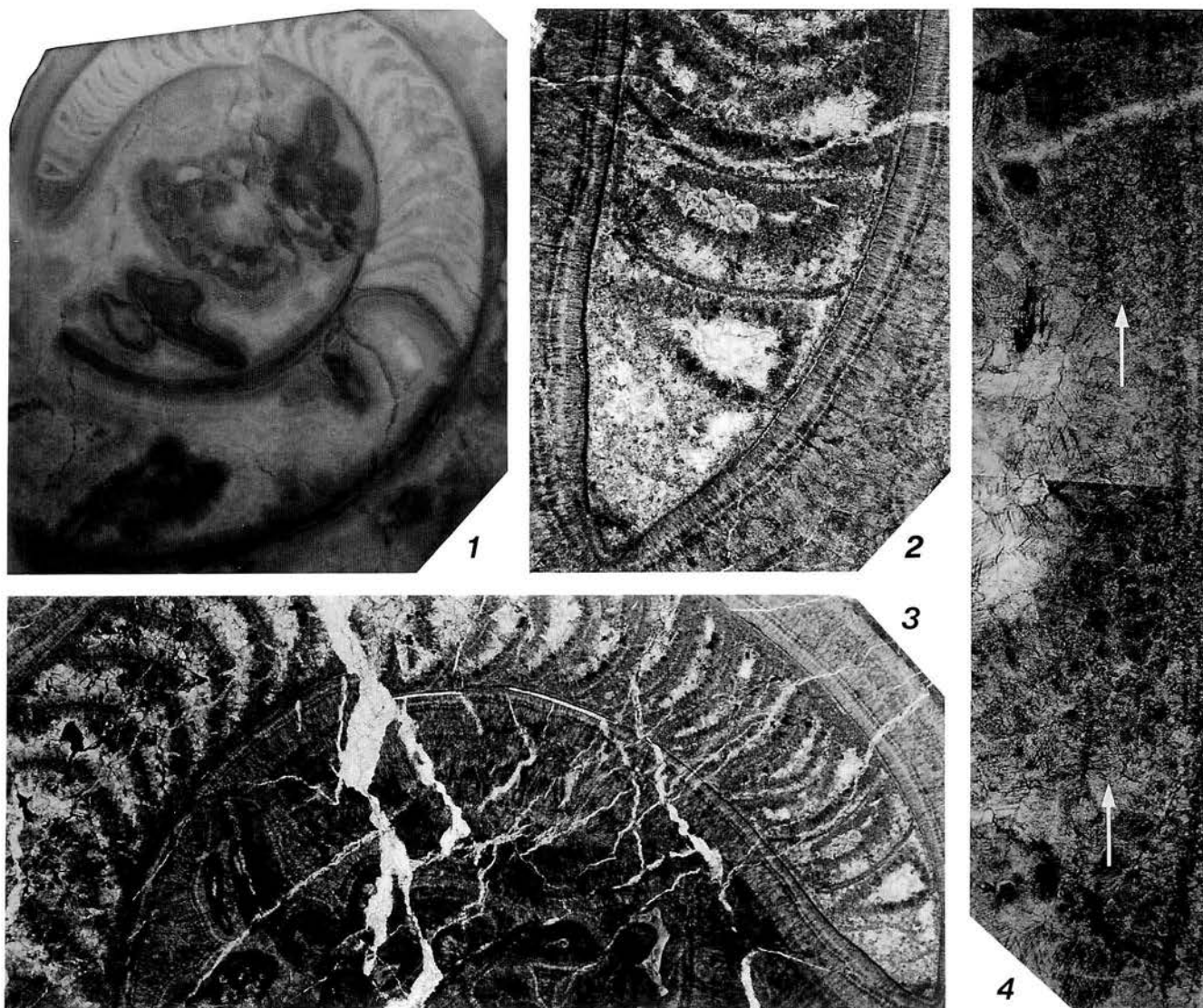


Figure 2. *Echigoceras sasakii* gen. et sp. nov. 1-4. Holotype, UMUT PM 27920, longitudinal sections; 1, polished section, $\times 2$; 2, thin section showing embryonic shell, not through siphuncle, $\times 10$; 3, thin section of apical shell, $\times 5$; 4, thin section with arrows indicate the septal foramina, $\times 25$.

Peristome lobed, with deep, V-shaped ventral (hyponomic) sinus, broadly rounded ventrolateral saddle, moderately deep lateral (ocular) sinus and nearly transverse dorsal apertural rim; peristome preserved as distinct growth lines throughout shell; lateral and dorsolateral longitudinal ridges become subdued, and grooves between these ridges disappear near aperture. Judging from longitudinal section, embryonic shell probably is cone-shaped. Sutures not observable in all examined specimens, but serial longitudinal sections do not indicate distinguished obliquity and sutural elements. Cameral length moderate for family; there are 3 to 4 camerae in corresponding whorl height.

Septa moderately concave for family, and form retrochoanitic siphuncle near ventral margin; ratio of minimum distance of central axis of septal foramen from whorl surface per corresponding whorl height (siphuncular position ratio) is approximately 0.08; septal necks orthochoanitic and relatively short with 0.71 mm in well-preserved dorsal septal neck at whorl height of approximately 9.5 mm, where diameters of septal foramina are very narrow for family at approximately 0.32 mm; connecting rings probably tube-like. Cameral and endosiphuncular deposits absent.

Discussion.—An Early Carboniferous genus *Stroboceras*

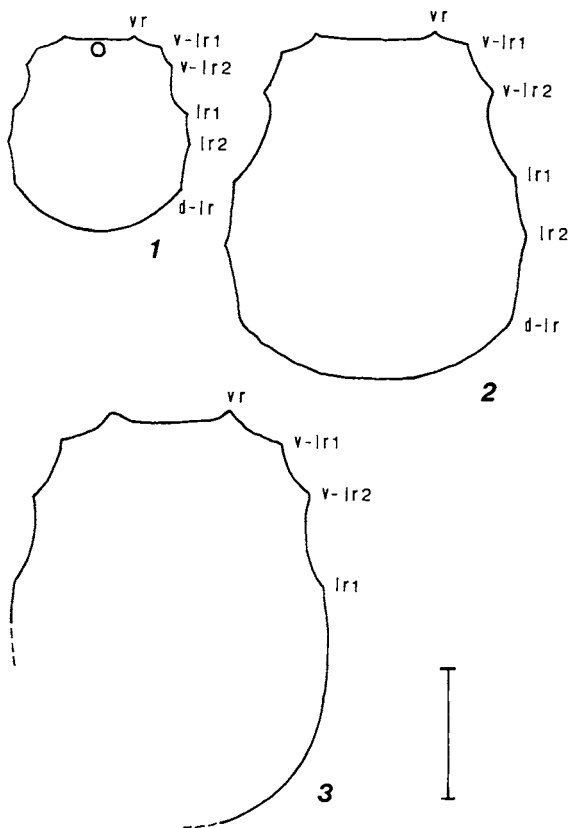


Figure 3. *Echigoceras sasakii* gen. et sp. nov., diagrams from cross sections of whorls, venter up. 1, 2. Paratype, UMUT PM 27919; 1, phragmocone, note siphuncular position; 2, body chamber. 3. Paratype, UMUT PM 27921, body chamber near aperture. Abbreviations: vr = ventral ridge; v-lr1, v-lr2 = ventrolateral ridges; lr1, lr2 = lateral ridges; d-lr = dorsolateral ridge. Scale bar equals 5 mm.

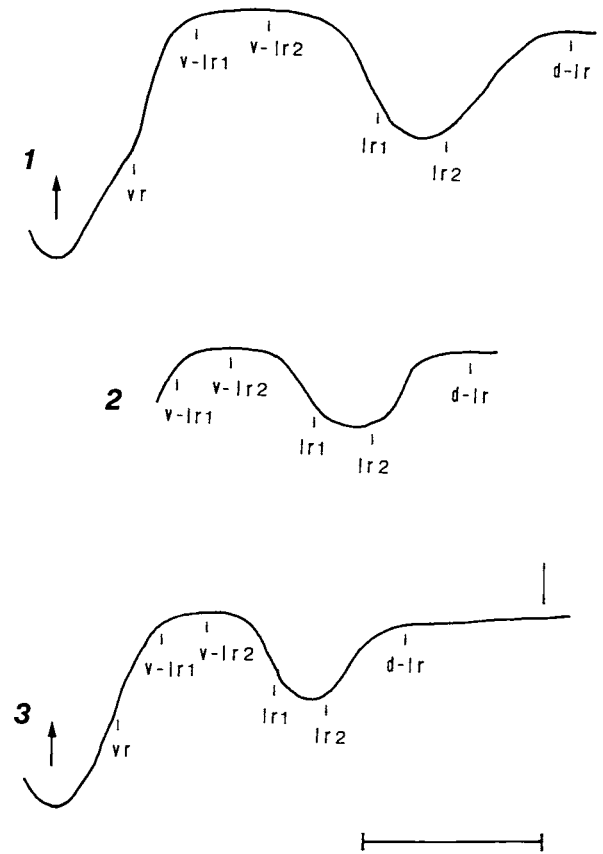


Figure 4. *Echigoceras sasakii* gen. et sp. nov., diagrams of growth lines to show peristome shapes in relation to the positions of the longitudinal ridges. 1. Paratype, UMUT PM 27921. 2. Holotype, UMUT PM 27920. 3. Paratype, UMUT PM 27919. Positions of longitudinal ridges are indicated by symbols (see explanation of Figure 3). Scale bar equals 5 mm.

(Hyatt, 1884; type species, *Gyroceras harttii* [sic] Dawson, 1868) has the longitudinal ridges of, and a peristome outline similar to, *Echigoceras sasakii* gen. et sp. nov., and moreover all the outer whorls of *Stroboceras* are partly divergent each from the preceding one. Therefore, from fragmentary shells such as the present two paratypes (UMUT PM 27919, 27921), a distinction between *Echigoceras* and *Stroboceras* would be difficult to make based only on external morphology. In this case, the siphuncular position is the most diagnostic feature separating these genera; i.e., the position of the siphuncle near the ventral margin of the new genus contrasts with the siphuncular position of *Stroboceras*, which is subcentral to nearly midway between the center and the ventral margin. All trigonoceratids have cyrtoconic stages in their early ontogeny. In particular, the early juvenile shell of *Stroboceras hartii* illustrated by Bell (1929) most closely resembles that of *Echigoceras sasakii*, and the cyrtoconic

parts of *Catastrobocheras* (Turner, 1965; type species, *Nautilus quadratus* Fleming, 1828) and *Pseudocatastrobocheras* (Turner, 1965; type species, *Coelonautilus trapezoidalis* Jackson, 1919) also possess longitudinal ridges, but they are less than 20 mm in shell diameter.

Among the known nautilids *Echigoceras* has the most similar shell morphology to *Stroboceras* as alluded to in the above comparisons. In addition, the range of *Stroboceras*, Viséan to early Namurian of the Early Carboniferous (e.g., Gordon, 1964), was replaced by that of *Echigoceras*, for which a Middle Carboniferous (probable late Bashkirian) age is suggested. *Echigoceras* is the probable descendant of *Stroboceras*.

A figured specimen from the Omi Limestone Group cited as *Stroboceras* sp. by Oyagi (2000) is probably conspecific with *Echigoceras sasakii*. In addition, it should seem that *Stroboceras* sp. listed by Nishida and Kyuma (1986) from the Bashkirian to Moscovian of the

Akiyoshi Limestone Group, Southwest Japan, needs re-evaluation based on present knowledge. However, the specimens from these two localities are not presently available for re-examination.

Etymology.—The specific name honors the late Dr. Madoka Sasaki, in recognition of his contributions to the taxonomic study of living cephalopods.

Material examined.—The holotype, UMUT PM 27920, is a complete specimen. Unfortunately, attempts to separate the embryonic shell and apertural rim of the holotype from the well-indurated matrix were not successful. The following two paratypes of the fragmentary shells are assigned to the species: UMUT PM 27919, incomplete phragmocone with apical body chamber, 35.3 mm in length, and UMUT PM 27921, adoral body chamber including apertural rim, 15.9 mm in length.

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Turrilitid ammonoid *Carthaginites* from Hokkaido (Studies of the Cretaceous ammonites from Hokkaido and Sakhalin—XCIV)

TATSURO MATSUMOTO

c/o The Kyushu University Museum, Fukuoka, 812-8581, Japan

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Abstract. This paper gives a revised definition of the genus *Carthaginites* Pervinquière, 1907 on the basis of material from Hokkaido, Japan, that enhances previously available material. Two species from the middle Cenomanian rocks of Hokkaido are described: *C. asiaticum* (Matsumoto and Takahashi, 2000) and *C. yamashitai* sp. nov. Brief comments are also made on some species which were previously described from the upper Cenomanian rocks of North America and Europe. Morphologically and stratigraphically *Carthaginites* is intimately related to *Neostlingoceras* Klingler and Kennedy, 1978, of early Cenomanian age.

Key words: *Carthaginites*, Cenomanian, Cretaceous, Hokkaido, *Neostlingoceras*, *Raynaudia*

Introduction

A well preserved specimen of a turreted ammonite was collected by Minoru Yamashita and was provided to me for study in 1981, but it was left undescribed, because I failed to understand adequately its peculiar characters. Meanwhile my work on the turrilitid ammonoids proceeded step by step, mostly with coworkers, and in this connection I noticed that the species described as *Neostlingoceras asiaticum* Matsumoto and Takahashi, 2000 is peculiar in its very small size and much weaker ornamentation. I also noticed that its suture is so peculiar that my previous drawing should be revised. Thus, the genus *Carthaginites* Pervinquière, 1907 came to my mind. At the same time I became aware that the specimen provided by Yamashita is an excellent example of *Carthaginites*. These two species came from the middle, instead of the lower, part of the Cenomanian. In this paper the results of my study are presented in the customary style of systematic description.

Conventions.—The specimens from Hokkaido described in this paper are kept at the Kyushu University Museum under the heading GK. Other specimens mentioned are cited according to the usual form used for the given institutions.

Sutural elements are designated E, L, U, and I for the external, lateral, umbilical and internal lobes, following normal usage for the group.

Systematic descriptions

Order Ammonoidea Zittel, 1884
Suborder Ancyloceratina Wiedmann, 1966
Superfamily Turrilitoidea Gill, 1871
Family Turrilitidae Gill, 1871
Genus *Carthaginites* Pervinquière, 1907

Type species.—*Turrilites* (*Carthaginites*) *kerimensis* Pervinquière, 1907 (p. 101, pl. 4, figs. 18, 19; text fig. 29) by original designation (Pervinquière, 1907, p. 96).

Diagnosis.—Small turreted shell, with low apical angle; surface in early growth stage nearly smooth, with a shallow median spiral depression; later row of faint nodes discernible above the median depression and another row of numerous, tiny tubercles along the lower whorl seam. Suture abnormal in showing L and in part E/L and L/U saddles on the exposed whorl face, without full half of E. In other words, the siphuncle does not run along the upper edge of the whorl but deviates at some distance toward the umbilical margin of the preceding whorl.

Discussion.—*Carthaginites* was proposed by Pervinquière (1907, p. 96) as a subgenus of *Turrilites* Lamarck, 1801. It was raised to the rank of a full genus by Dubourdieu (1953, p. 44), who erected another species *Carthaginites krorzaensis* Dubourdieu (1953, p. 66, pl. 4, figs. 49–52, text-fig. 20) on the basis of a single isolated whorl, which is about 3 mm in height and 5 mm in diameter. There is a very shallow spiral depression at midflank

and a row of narrow clavi along the lower whorl seam. Owing to the isolated condition of the whorl, the suture was fully illustrated from the umbilicus of the lower surface, via the whorl flank, to the upper surface, and the position of the siphuncle is shown much apart from the angle of the upper whorl seam to the vicinity of the umbilicus of the upper surface (see Dubourdieu, 1953, text-fig. 20).

The features described above are the most important characters of the genus *Carthaginites*. It should be also noted that the suture is not necessarily simple but moderately incised like that of immature *Ostlingoceras* (see fig. 2 in Matsumoto and Takahashi, 2000). Generally the degree of sutural incision depends on species, growth stage and mode of preservation or effect of weathering. In any event, in regard to the above points Wright and Kennedy (1996, p. 361) seem to have inadequately presented the generic diagnosis. However, I agree with them in their allotment of their British specimen (BMNH C76469) (Wright and Kennedy, 1996, p. 361, pl. 98, fig. 11) to the genus *Carthaginites*.

Dubourdieu (1953, p. 67) and also Wright and (Kennedy 1996, p. 361) described the distinction between *Carthaginites* and *Raynaudia* Dubourdieu, 1953 (type species *Turrilites (Carthaginites) raynaudiensis* Collignon (1932, p. 19, pl. 1, figs. 22–25; text-figs. 24–26). Dubourdieu (1953, fig. 13) presumed that *Carthaginites* evolved from *Raynaudia*, but no substantial evidence was given. Judging from the shell form and ornamentation, *Carthaginites* is related more closely to *Neostlingoceras* Klinger and Kennedy, 1978 (type species *Turrilites carcitanensis* Matheron, 1842). Generally the former is smaller and more faintly ornamented than the latter. The unusual position of the siphuncle and the consequent abnormal disposition of the sutural elements are particular to *Carthaginites*.

Distribution.—The type species (*C. kerimensis*) was recorded by Pervinquier (1907, p. 101) from the “Vraconian” of Tunisia, but it is regarded as a late Cenomanian species by Wright and Kennedy (1996, p. 361). *C. krorzaensis* is from the upper Cenomanian rocks in the neighbourhood of Djebel Quenza, SE of Djebel Krorza in Algeria (Dubourdieu, 1953, p. 68). The British specimen (*vide supra*) is from the upper Cenomanian *Calycoceras guerangeri* Zone of Devon, southern England (Wright and Kennedy, 1996, p. 363). The two species from Hokkaido (northern Japan), described below, came from the middle Cenomanian *Calycoceras (Newboldiceras) asiaticum* Zone. Some of the species described under *Neostlingoceras* from the upper Cenomanian rocks of the North American Western Interior region are to be transferred to *Carthaginites* (see discussion below).

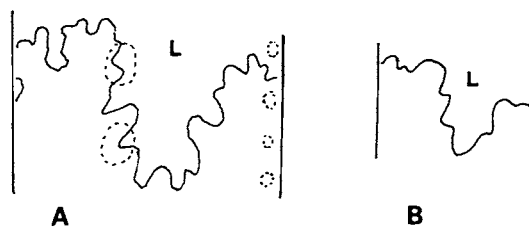


Figure 1. *Carthaginites asiaticus* (Matsumoto and Takahashi), Sutures on the whorl flank. A. GK H8536 (holotype), $\times 10$. B. GK. H8537 (younger paratype), $\times 12$.

Carthaginites asiaticus (Matsumoto and Takahashi, 2000)

Figure 1

Neostlingoceras asiaticum Matsumoto and Takahashi, 2000, p. 266, figs. 5A–C, D–F, G; 6.

Material.—GK. H8536 (holotype), GK. H8537 and GK. 8538, collected by T. Takahashi (for more details see Matsumoto and Takahashi, 2000, p. 266).

Revised diagnosis.—Shell slender with a low apical angle; whorl at early growth stage rather smooth, with rounded upper shoulder, shallow spiral groove at midflank, and sharply demarcated lower edge. Later, a row of blunt nodes developed on the upper part, with shallow spiral groove below it, and numerous, minutely pointed clavate tubercles along the lower whorl seam. Sutural element L exposed at about the middle of the flank, whereas E and U are unexposed on the flank; siphuncle situated at some distance from the upper edge of the whorl flank, running below the unexposed roof of the whorl.

Measurements.—See Matsumoto and Takahashi 2000, table 3.

Remarks.—The suture of the newly prepared part of the holotype (GK. H8536) is shown in Figure 1A; that of the paratype (GK H8537) in Figure 1B. The latter was incorrectly drawn in Matsumoto and Takahashi (2000, fig. 6) on account of the incomplete cleaning of the shelly material in the zones along the upper and the lower seams of the whorl.

Based on the above revision, *Neostlingoceras asiaticum* Matsumoto and Takahashi should now be called *Carthaginites asiaticus* (Matsumoto and Takahashi).

Discussion.—As in the case of Hokkaido, some of the species described under *Neostlingoceras* from the upper Cenomanian rocks in the Western Interior of North America described by Cobban *et al.* (1989) should be reexamined. As I have had no opportunity to examine the original specimens, I merely give suggestions. *N. procerum* Cobban, Hook and Kennedy (1989, p. 60, figs 62, 95 O–Q, S) from the upper Cenomanian *Metoicoceras mosbyense* Zone is probably an example of *Carthaginites*,

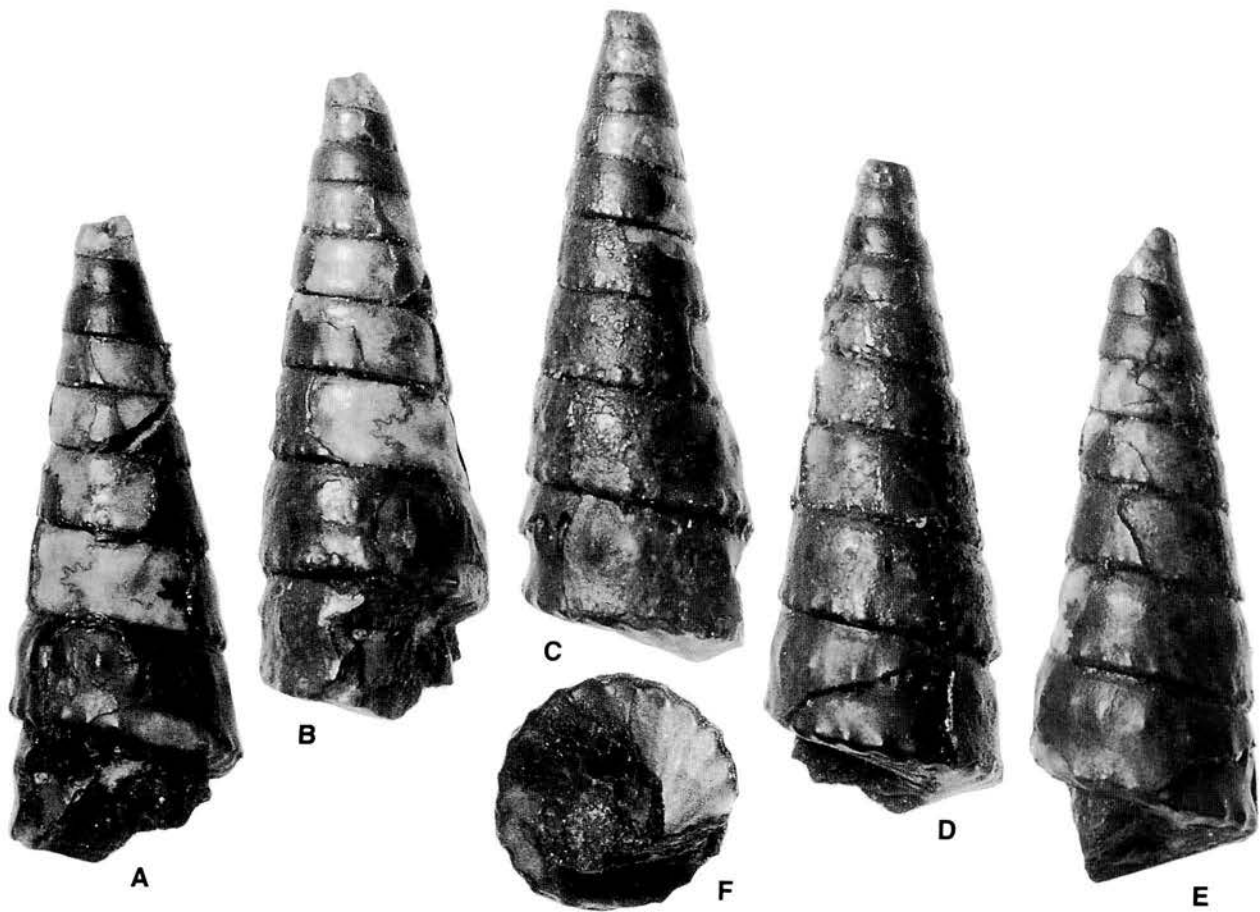


Figure 2. *Carthaginites yamashitai* sp. nov. Lateral views (A–E anticlockwise turned) and basal view (F) of GK. H8539 (holotype), $\times 3$. Photos courtesy of T. Nishida.

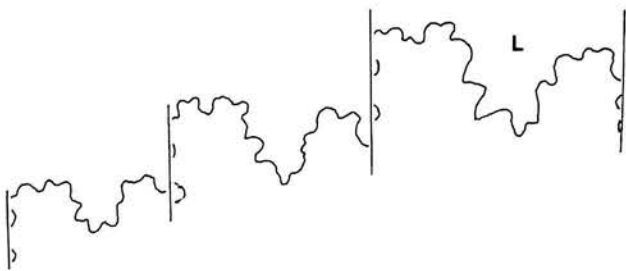


Figure 3. *Carthaginites yamashitai* sp. nov. Sutures on the flank of three successive whorls of GK. H8539 (holotype), $\times 8$.

because it has a small and feebly ornamented shell and abnormal configuration of the suture. *N. bayardense* Cobban, Hook and Kennedy (1989, p. 60, figs. 95R, 96R) from the same zone may be another species of *Carthaginites*, although its suture was not illustrated.

Occurrence.—The holotype and the two paratypes of this species came from Loc. Ik 1103 (for the location see

Matsumoto and Takahashi, 2001, fig. 4), where the middle Cenomanian Zone of *Calycoceras* (*Newboldiceras*) *asiaticum* Zone is exposed.

***Carthaginites yamashitai* sp. nov.**

Figures 2 and 3

Material.—Holotype is GK. H8539 (Figure 2) collected by Minoru Yamashita from a cutting, SE of Poronai, Mikasa district and later donated to the Kyushu University Museum. This is well preserved, but no other specimens are available.

Diagnosis.—Small flat-sided turricon, with estimated apical angle of 18° . Young whorls look almost smooth, but for faint spiral depression at midflank and numerous minute tubercles aligned immediately above the lower whorl seam. In later growth stages blunt major tubercles developed above the spiral depression and minor ones along the lower whorl seam. The latter are pointed at their top immediately above the lower whorl seam but

clavate at their base, forming a wavy spiral line. Thus, a kind of double feature is shown. Configuration of the sutural elements abnormal in showing the entire L and parts of the saddles E/L and L/U on the exposed whorl face; E almost entirely unexposed on the flank (Figure 3).

Description.—This single available specimen consists of 9 whorls, without the youngest part and the destroyed last portion of the body chamber. It is 27 mm in total height, and the diameter of the last whorl is 10 mm. Each whorl is trapezoidal in lateral view, with the larger dimension along the lower row of small tubercles. For instance, the ratio of height to lower diameter is 0.45 and of height to upper diameter 0.50.

The shallow spiral depression is better discernible on the internal mould. It is at about the midflank in young whorls and gradually shifted downward with growth. I notice a questionable feature that several minutely pointed upper tubercles are discernible in a part of the preserved first whorl (see Figure 2C, D). Whether this is a constant character or merely accidental cannot be decided without examining more specimens.

In later growth stages major tubercles of the upper row may be somewhat bullate upward. The tubercles of the lower row are small but fairly distinctly pointed and slightly bullate upward. They are twice as numerous as the nodes of the upper row; for instance 30 against 15 in the whorl of the middle growth stage. They rest on a wavy spiral ridge which forms an edge between the flank and the lower face of the whorl. On the basal face of the preserved last whorl a radial rib runs from each wave of the ridge toward the umbilicus with gentle curvature (Figure 2F).

The suture on the flank of the successive three whorls is illustrated in Figure 3.

Comparison.—This species is undoubtedly referred to *Carthaginites* on account of its small size, faint ornamentation with a shallow spiral groove at about the midflank and the deviation of the siphuncle from the upper edge of the whorl flank inward below the upper whorl face as shown by the particular configuration of the sutural elements.

The estimated apical angle of *C. yamashitai* is larger than that in *C. kerimensis* and *C. asiaticus*. As to the degree of minor sutural incisions, there is no significant difference between *C. yamashitai* and *C. krorzaensis* or *C. asiaticus*, if the gradual change with growth is taken into consideration. The gradual change of ornamentation with growth in this species is analogous to that of *C. asiaticus*. The two species are distinguished by the difference in the whorl shape and the style of ornamentation.

Occurrence.—The holotype was collected from the middle Cenomanian *Calycoceras* (*Newboldiceras*) *asiaticum* Zone exposed at a cutting of a forestry road, about 3500 m S60° E from the Poronai colliery, Mikasa district. This

fossil locality is marked in the official geological map "Iwamizawa" (Matsuno *et al.*, 1964). I went there later but failed to obtain additional material. The fossiliferous bed is referred to the Mikasa Formation which consists mainly of sandy sediments of shallow sea facies.

Concluding remarks

(1) The genus *Carthaginites* Pervinquier, 1907 was previously represented by small and more or less incompletely preserved specimens of rare occurrence from Tunisia and Algeria. In addition to the original works of Pervinquier (1907) and Dubourdiou (1953) the better preserved specimens from Hokkaido are taken into consideration, and thus the diagnosis of the genus *Carthaginites* is given clearly in this paper.

(2) The species previously called *Neostlingoceras asiaticum* Matsumoto and Takahashi, 2000 is revised in this paper to *Carthaginites asiaticus* (Matsumoto and Takahashi, 2000) and redescribed with necessary amendment. Furthermore, *Carthaginites yamashitai* sp. nov. is established on a fine specimen collected by M. Yamashita. The above two species occurred in the middle Cenomanian *Calycoceras* (*Newboldiceras*) *asiaticum* Zone in the Mikasa district of central Hokkaido.

(3) Morphologically and stratigraphically *Carthaginites* is intimately related to *Neostlingoceras* but differs in its smaller size, weaker ornamentation and especially by the deviated position of the siphuncle to the inner part of the whorl.

(4) In view of the peculiar characters as mentioned above, *Carthaginites* is presumed to have had a peculiar mode of life, but this ecological problem is not treated in this paper and left for further investigation.

Acknowledgements

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The Anthracotheriidae (Mammalia; Artiodactyla) from the Eocene Pondaung Formation (Myanmar) and comments on some other anthracotheres from the Eocene of Asia

TAKEHISA TSUBAMOTO¹, MASANARU TAKAI¹, NAOKO EGI¹, NOBUO SHIGEHARA¹,
SOE THURA TUN², AYE KO AUNG³, AUNG NAING SOE² AND TIN THEIN⁴

¹Primate Research Institute, Kyoto University, Inuyama, Aichi, 484–8506, Japan (e-mail: tsuba@pri.kyoto-u.ac.jp)

²Department of Geology, University of Patheingyi, Patheingyi, Myanmar

³Department of Geology, Dagon University, Yangon, Myanmar

⁴Department of Geology, University of Yangon, Yangon, Myanmar

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Abstract. We reevaluate the classifications of the anthracotheres (Mammalia; Artiodactyla) from the latest middle Eocene Pondaung Formation (central Myanmar), mentioning other anthracotheres from the Eocene of Asia. The three anthracotheriid genera previously known from the Pondaung Formation, *Anthracothema*, *Anthracokeryx*, and *Anthracohyus*, are synonymized into *Anthracotherium*. As many as 13 species had been recognized in the Pondaung anthracotheres, but they are summarized into four species (*Anthracotherium pangani*, *Anthracotherium crassum*, *Anthracotherium birmanicum*, and *Anthracotherium tenuis*), based on the difference of M₁ size (~ body size). Dental morphology in each species indicates high variation, and the four species are not separable based on their dental morphology. The dental morphology of the Pondaung *Anthracotherium* species is distinct from that of other species and is the most primitive. In addition, the Pondaung *Anthracotherium* species are the oldest of the genus. The genus *Anthracotherium* might have originated and rapidly radiated around the Pondaung area during the latest middle Eocene. *Siamotherium pondaungensis* described from the Pondaung Formation as an anthracotheriid is synonymized to *Pakkokuhyus lahiri* (Artiodactyla; Helohyidae).

Key words: Anthracotheriidae, *Anthracotherium*, Eocene, Myanmar, Pondaung Formation, systematics

Introduction

The Anthracotheriidae is an extinct group of browsing suiform artiodactyls that achieved wide distribution across Eurasia, parts of Africa, and North America from the Eocene to Plio-Pleistocene periods (Black, 1978; Ducrocq, 1997; Kron and Manning, 1998). Their body size ranges from small, terrier-sized animals to beasts approaching the size of a hippopotamus (Black, 1978). Typical early anthracotheres have complete dentition and bunodont or bunoselenodont molars, five cusped upper molars without hypocone and four cusped lower molars without paraconid (Ducrocq *et al.*, 1996). Their low-crowned teeth and frequent occurrence in paleochannel deposits suggest habits and habitat similar to those of modern hippos (Kron and Manning, 1998).

The fossil record of anthracotheres is abundant and diverse throughout the world. In East Asia, they appeared from the middle Eocene and survived until the Plio-Pleistocene (Colbert, 1938; Ducrocq, 1997). In Europe, they appeared during the late Eocene and became extinct in the Miocene. In Africa, they evolved from the late Eocene to the Plio-Pleistocene (Black, 1978; Ducrocq, 1994a, 1997). In North America, they are recorded from the late middle Eocene to the early Miocene, but the fossil record of North American anthracotheres is neither particularly abundant nor very diverse (Kron and Manning, 1998).

In regard to the anthracotheres' phyletic relationships, traditionally, most researchers have considered that anthracotheres might have originated from a helohyid stock (Pilgrim, 1928, 1940, Coombs and Coombs, 1977; Ducrocq *et al.*, 1997) or from diacodexoid forms (Ducrocq, 1994b),

and that they might have been the ancestors of extant hippos because some types of anthracotheres are considered to have had a hippopotamid mode of life and a body structure similar to hippos (Black, 1978; Colbert, 1935; Gentry and Hooker, 1988; Thewissen *et al.*, 2001). According to molecular data (e.g., Nikaido *et al.*, 1999), hippopotamids comprise a monophyletic clade with cetaceans, so that anthracotheres might have originated from a stock of the [Cetacea + Hippopotamidae] clade (Rose, 2001). On the other hand, a few researchers (Pickford, 1983; but see Ducrocq, 1994b for discussion) suggested that hippopotamids could have originated not from an anthracothere stock but from a peccary one (Ducrocq, 1997).

In regard to regional origin, many researchers have considered that anthracotheres might have originated in East Asia during the Eocene (e.g., Pilgrim, 1928; Suteethorn *et al.*, 1988; Ducrocq, 1994a, 1999), because Eocene anthracotheres of East Asia are abundant and well diversified and because they show a primitive bunodont condition (Ducrocq, 1999).

The anthracotheres from the Eocene Pondaung Formation (Myanmar) are the first mammalian taxa in this formation to have been described (Pilgrim and Cotter, 1916). They are among the oldest anthracotheres in East Asia and consist of three genera and as many as 13 species (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938). Therefore, many studies have viewed the Pondaung anthracotheres in relation to the origin and early radiation of this group (e.g., Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938; Coombs and Coombs, 1977; Ducrocq, 1999).

Despite the richness of the fossil collections, the classification of the Pondaung anthracotheres has been problematic (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938; Holroyd and Ciochon, 1991). The taxonomic confusion on the Pondaung anthracotheres is likely to be due to their highly varied and primitive dental morphology.

In this paper, we reevaluate the classification of the Pondaung anthracotheres based on previously described fossil materials (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938) and new collections. We then also discuss classifications of some other Eocene anthracotheres of East Asia in relation to the revision of the classification of the Pondaung anthracotheres.

Institutional abbreviations

AMNH = American Museum of Natural History, New York, USA; **CM** = Carnegie Museum of Natural History, Pittsburgh, USA; **BMNH** = The Natural History Museum (formerly British Museum of Natural History), London, United Kingdom; **DMR** = Department of Mineral Resources, Bangkok, Thailand; **GSI** = Geological Survey of

India, Kolkata, India; **IVPP** = Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **NSM** = National Science Museum, Tokyo, Japan; **UCMP** = Museum of Paleontology, University of California, Berkeley, USA.

Materials

The new collections of Pondaung anthracotheres used here were discovered in 1997 by Myanmar researchers (Pondaung Fossil Expedition Team, 1997; Takai *et al.*, 1999), and in 1998 (November) and 1999 (November) by Myanmar-Japan joint team (Takai *et al.*, 2000, 2001; Egi and Tsubamoto, 2000; Tsubamoto *et al.*, 2000a, b, 2001, 2002; Shigehara *et al.*, 2002; Gebo *et al.*, in press). These new fossil materials are stored in the National Museum of the Union of Myanmar (Yangon, Myanmar). They are serially catalogued under **NMMP-KU** specimen numbers. **NMMP** stands for National Museum, Myanmar, Paleontology; and **KU** for Kyoto University (Japan). The dental measurements used here are listed in the Appendix.

Geologic setting

The Pondaung Formation is distributed in the western part of central Myanmar (Figure 1). The Pondaung Formation overlies and partially interfingers with the middle Eocene Tabyin Formation, and is conformably overlain by the late Eocene Yaw Formation (Stamp, 1922; Bender, 1983; Aye Ko Aung, 1999). The Pondaung Formation consists of alternating mudstone, sandstone, and conglomerate, and is subdivided into the "Lower" and "Upper" Members (Aye Ko Aung, 1999). The "Lower Member" is dominated by greenish pebbly sandstone and mudstone and contains only a few fossil leaf fragments in its upper part (Aye Ko Aung, 1999). The "Upper Member" is dominated by fine- to medium-grained sandstone and variegated mudstone and contains many terrestrial mammalian and other vertebrate fossils that indicate a freshwater environment (Colbert, 1938; Bender, 1983; Aye Ko Aung, 1999; Aung Naing Soe, 1999; Aung Naing Soe *et al.*, 2002). Its mammalian fauna and the fission-track age of the "Upper Member" (37.2 ± 1.3 Ma) indicate a latest middle Eocene age (Tsubamoto *et al.*, 2002).

Previous studies on Pondaung anthracotheres

Pilgrim and Cotter (1916) first described three genera (*Anthracohyus*, *Anthracotherium*, and *Anthracokeryx*) and seven species of anthracotheres from the Pondaung Formation. Pilgrim (1928) revised the Pondaung anthracotheres into three genera (*Anthracohyus*, *Anthracothema*, and *Anthracokeryx*) and 13 species, describing new

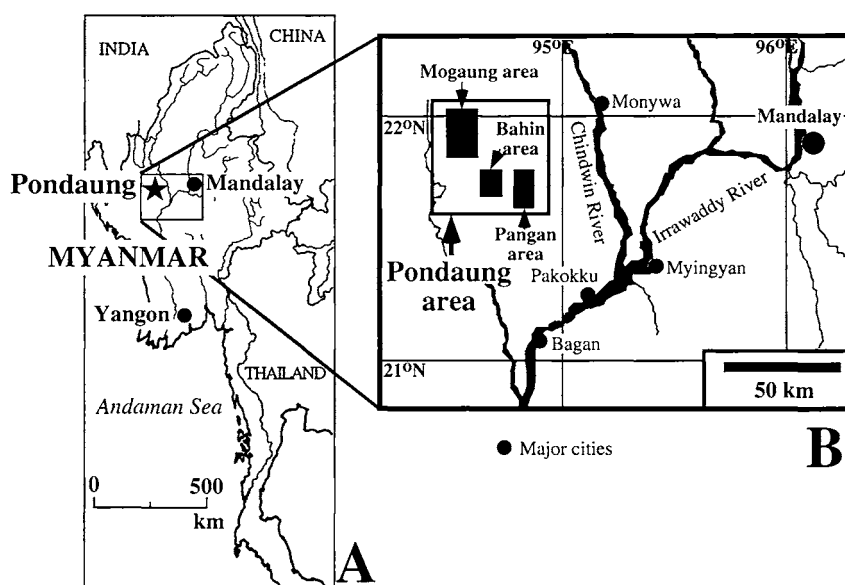


Figure 1. A. Map of Myanmar showing the location of the Pondaung area. B. Map of the Pondaung area showing the location of the three main regions of fossil localities.

materials. Colbert (1938) reviewed the Pondaung anthracotheres, and recognized the same three genera as Pilgrim (1928) and seven to nine species, also describing new materials. Thus, in the Pondaung Formation, the three anthracothere genera *Anthracohyus*, *Anthracothema*, and *Anthracokeryx* have been traditionally recognized. All these three genera were established based on the material from the Pondaung Formation. Most of the anthracothere materials collected from the Pondaung Formation have been assigned to *Anthracothema* or *Anthracokeryx*, whereas remains of *Anthracohyus* have been very rare.

Anthracohyus was established by Pilgrim and Cotter (1916) and was characterized particularly by the absence or very feeble development of the styles on the upper molars. Originally, this genus included three species, that is, *Anthracohyus choeroides*, *Anthracohyus rubricae*, and *Anthracohyus palustris*. Subsequently, the latter two species were moved to a new genus *Anthracothema* as determined by Pilgrim (1928). This classification is followed by Colbert (1938). The only remaining species in the genus *Anthracohyus*, *A. choeroides*, was characterized by the conical cusps on its molars, by the absence or very feeble development of the molar styles, and by the mesiodistal diameter of the upper molar being shorter on the buccal side than on the lingual side (Colbert, 1938).

Anthracothema was established by Pilgrim (1928). Four species of the Pondaung anthracotheres described by Pilgrim and Cotter (1916) were referred to this genus: *Anthracohyus rubricae*, *Anthracohyus palustris*, *Anthracotherium pangan*, and *Anthracotherium crassum*. All

these species were renamed by Pilgrim (1928) as *Anthracothema rubricae*, *Anthracothema palustre*, *Anthracothema pangan*, and *Anthracothema crassum*, respectively. Afterwards, *A. palustre* and (questionably) *A. crassum* were synonymized to *A. pangan* by Colbert (1938). Therefore, two (or three) species of the Pondaung *Anthracothema* were still recognized by him. The genus *Anthracothema* was characterized by its larger size, weaker molar styles, and its more conical molar cusps than those of *Anthracokeryx* from the Pondaung Formation (Pilgrim, 1928; Colbert, 1938). Recently, *Anthracothema* was synonymized to *Anthracotherium* by Ducrocq (1999).

Anthracokeryx was erected by Pilgrim and Cotter (1916). They described two species of *Anthracokeryx*, *Anthracokeryx birmanicus* and *Anthracokeryx tenuis*. Pilgrim (1928) then described six more species of this genus, namely *Anthracokeryx hospes*, *Anthracokeryx bambusae*, *Anthracokeryx myaingensis*, *Anthracokeryx ulnifer*, *Anthracokeryx moriturus*, and *Anthracokeryx? lahirii*. Colbert (1938) later on recognized four to six species of the Pondaung *Anthracokeryx*. The genus *Anthracokeryx* was characterized by its smaller size, better marked molar styles, and its more crescentic (selenodont) molar cusps than *Anthracothema* and *Anthracohyus* from the Pondaung Formation (Pilgrim, 1928; Colbert, 1938). On the other hand, the taxonomic validity of keeping *Anthracokeryx? lahirii* in the Anthracotheriidae was discussed by both Pilgrim (1928) and Colbert (1938). Recently, this species was referred to the Helohyidae (Artiodactyla) and renamed *Pakkokuhyus lahirii* by Holroyd and Ciochon (1995).

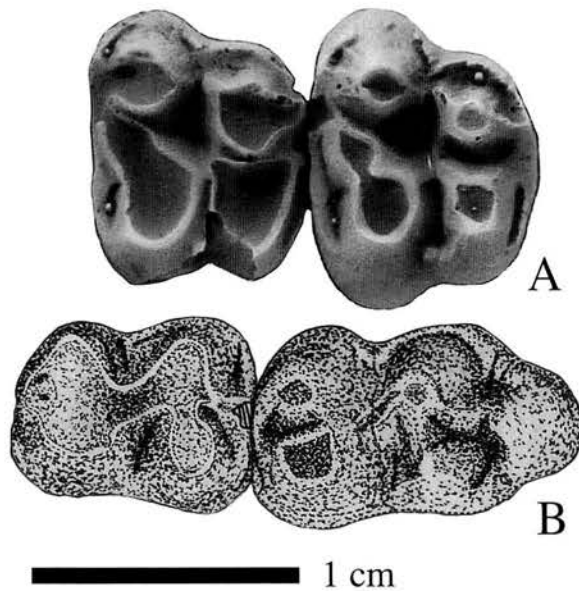


Figure 2. Comparison of *Siamotherium pondaungensis* and *Pakkokuhyus lahirii*. **A.** M^{2-3} of the type of *Siamotherium pondaungensis* [NMMP-KU 0039 (Kdw 6): a right maxillary fragment with M^{2-3}] in occlusal view (reversed). **B.** M_{1-3} of the type of *Pakkokuhyus lahirii* (GSI B-766: a right mandibular fragment with M_{1-3}) in occlusal view.

On *Siamotherium pondaungensis*

Based on a right maxillary fragment with M^{2-3} (Kdw 6 = NMMP-KU 0039; Figure 2A) from the Pondaung Formation, *Siamotherium pondaungensis* was described by Ducrocq *et al.* (2000) as a new species of *Siamotherium* (Anthracotheriidae). *Siamotherium* was known only from the Krabi basin, the late Eocene of Thailand (Suteethorn *et al.*, 1988; Ducrocq, 1999). However, the dentition displayed by the unique material of *S. pondaungensis* matches that of *Pakkokuhyus lahirii* (Helohyidae) (Figure 2B) described from the Pondaung Formation by Pilgrim (1928) and Holroyd and Ciochon (1995) based on a right mandibular fragment with M_{1-3} . Ducrocq *et al.* (2000) did not compare *S. pondaungensis* with *P. lahirii*. Although the upper dentition of *P. lahirii* has never been described, we believe that this upper dental material described as *S. pondaungensis* should be referred to *P. lahirii* rather than to another taxon because (1) the upper molars of *S. pondaungensis* are conical, bunodont, and brachyodont mo-

lars, like the lower molars of *P. lahirii*; (2) the sizes and cusp configurations of M^2 and M^3 of *S. pondaungensis* well match those of M_2 and M_3 of the type of *P. lahirii* (GSI B-766), respectively (e.g., M^2 protocone, M^3 protocone, and M^3 metaconule match M_2 talonid basin, M_3 talonid basin, and M_3 hypoconulid basin, respectively) (Figure 2); (3) the upper dental morphology of *S. pondaungensis* is similar to that of helohyids, such as *Helohyus*, in having similar dental size, bunodont and conical cusps with enlarged metaconule, and no or vestigial styles; and additionally, (4) both *S. pondaungensis* and *P. lahirii* have been found only in the Pondaung Formation. Further discoveries of better materials are necessary to settle the classification, but following our observations on the dental materials, we treat *Siamotherium pondaungensis* as a junior synonym of *Pakkokuhyus lahirii* (Helohyidae) in this paper.

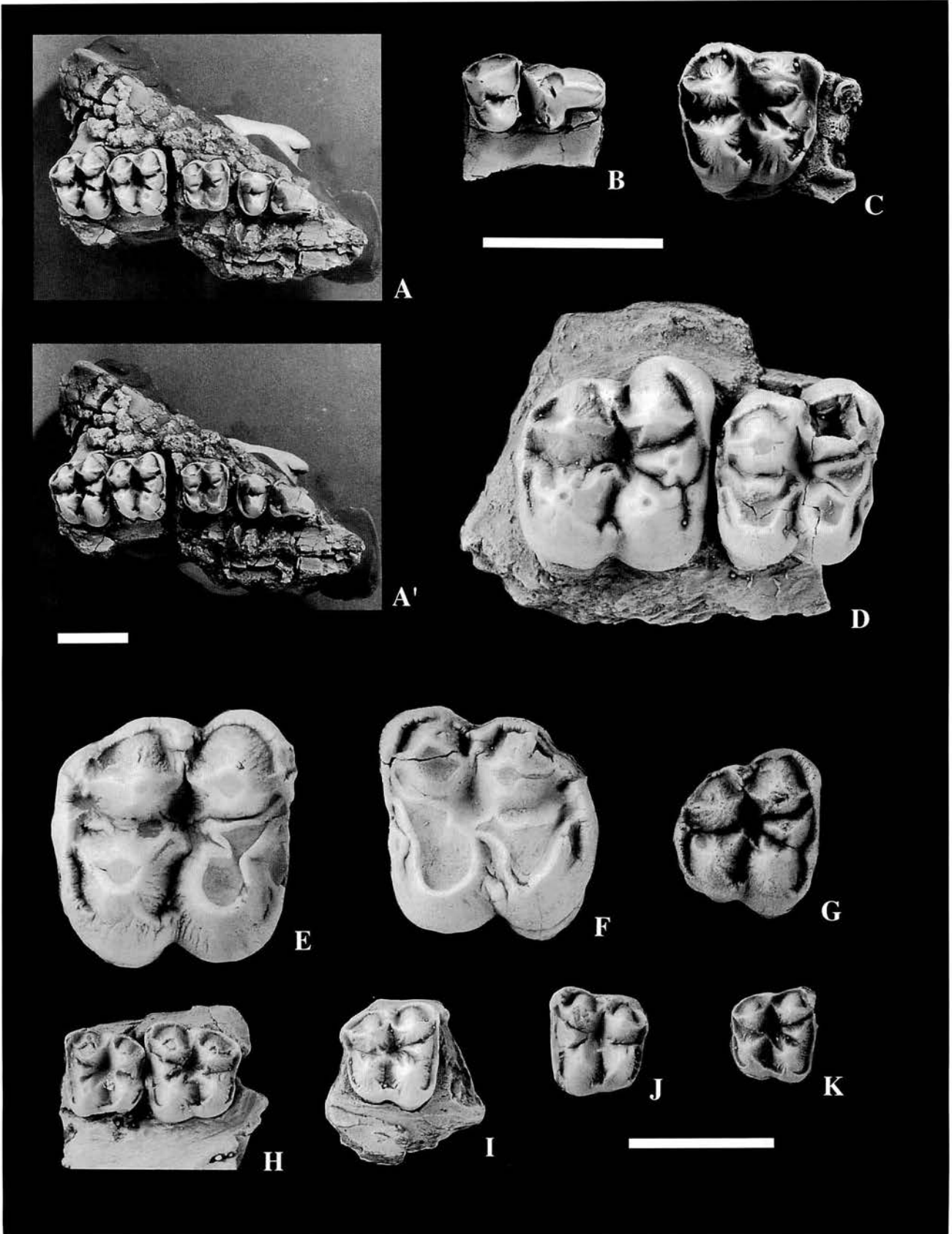
Dental morphology and size variation of Pondaung anthracotheres and their classification

Generic status of *Anthracothema* and *Anthracokeryx*

As mentioned above, after the review of Colbert (1938), the Pondaung anthracotheres have been classified into three genera, *Anthracohyus*, *Anthracothema*, and *Anthracokeryx*, and into as many as 13 species. This is because Colbert (1938) and earlier researchers (Pilgrim and Cotter, 1916; Pilgrim, 1928) recognized various dental morphologies among the Pondaung anthracotheres.

However, the differences in dental morphologies between two of the genera, *Anthracothema* and *Anthracokeryx*, in the Pondaung Formation are very subtle compared to other anthracotheriid taxa. In addition, these two genera have variations in selenodonty (crista development) and style development on the upper molars, which were the diagnostic characters for distinguishing them (Figures 3–5; Pilgrim and Cotter, 1916, plates 2–5; Pilgrim, 1928, plates 1–4; Colbert, 1938, figs. 41–52). Although *Anthracokeryx*, the smaller anthracothere group, generally has rather selenodont molars with better developed molar styles compared to *Anthracothema*, and although *Anthracothema*, the larger anthracothere group, generally has rather bunodont molars with less-developed styles compared to *Anthracokeryx*, the development of selenodonty and styles is variable. We examined all previously described materials of the Pondaung anthracotheres stored in AMNH and GSI, and recently collected materials in the National

➔ **Figure 3.** New upper dental materials of the Pondaung anthracotheres (*Anthracotherium*) in occlusal view (1). **A, A'**. NMMP-KU 0053, an right upper jaw with P^3-M^3 (stereo pair). **B.** NMMP-KU 0455, a right maxillary fragment with P^{3-4} . **C.** NMMP-KU 0327, a right mandibular fragment with dP^4 . **D.** NMMP-KU 0056, a right maxillary fragment with M^{2-3} . **E.** NMMP-KU 0404, a right M^3 . **F.** NMMP-KU 0411, a left maxillary fragment with M^3 . **G.** NMMP-KU 0070, a right M^3 . **H.** NMMP-KU 0382, a left maxillary fragment with M^{2-3} (or M^{1-2}). **I.** NMMP-KU 0326, a right maxillary fragment with $M^{3(ox2)}$. **J.** NMMP-KU 0379, a left M^3 . **K.** NMMP-KU 0384, a right $M^{1(ox2)}$. Scale bars = 2 cm (left middle scale corresponds to A, A', central upper scale corresponds to B–C, and right lower scale corresponds to D–K).



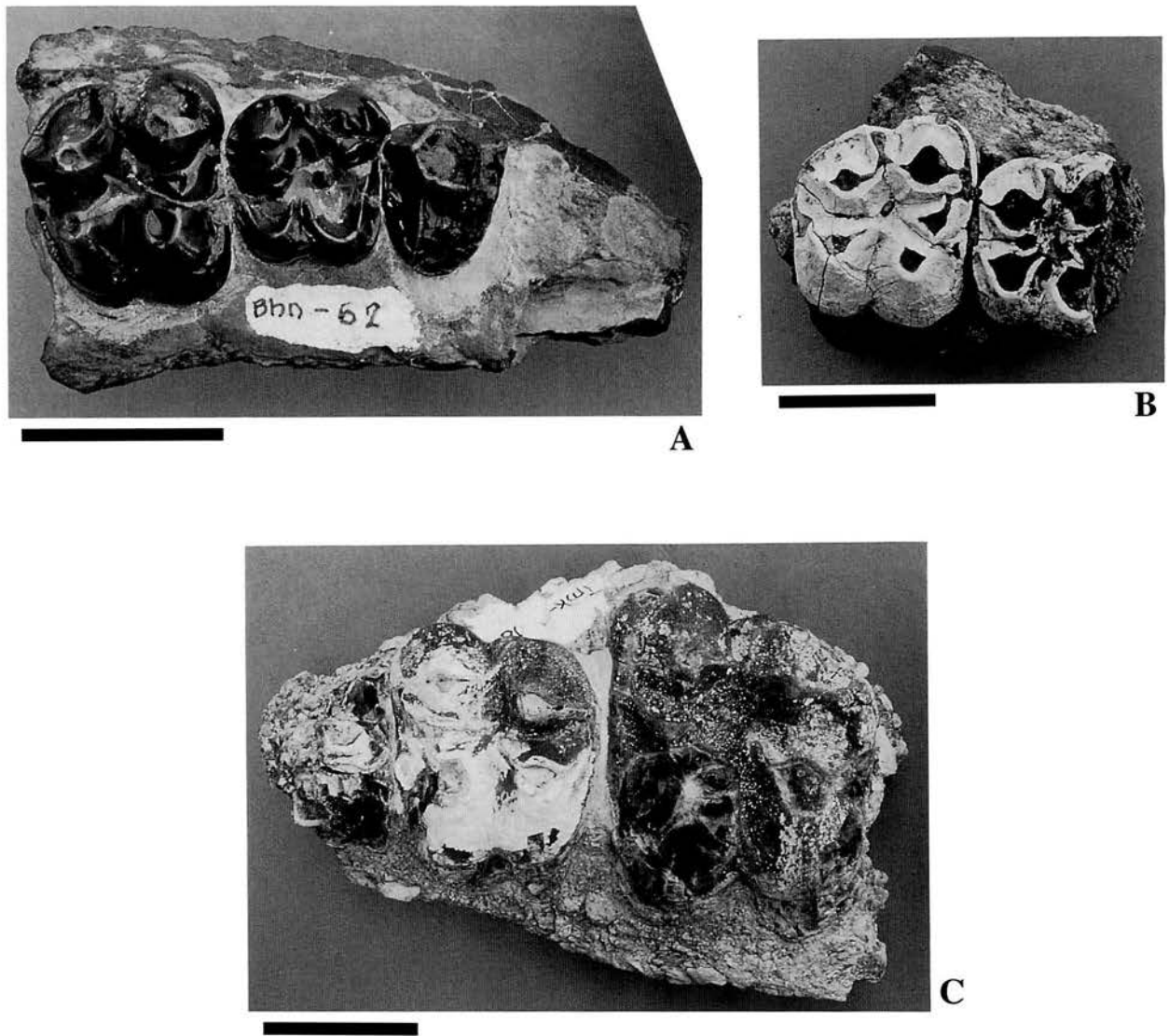
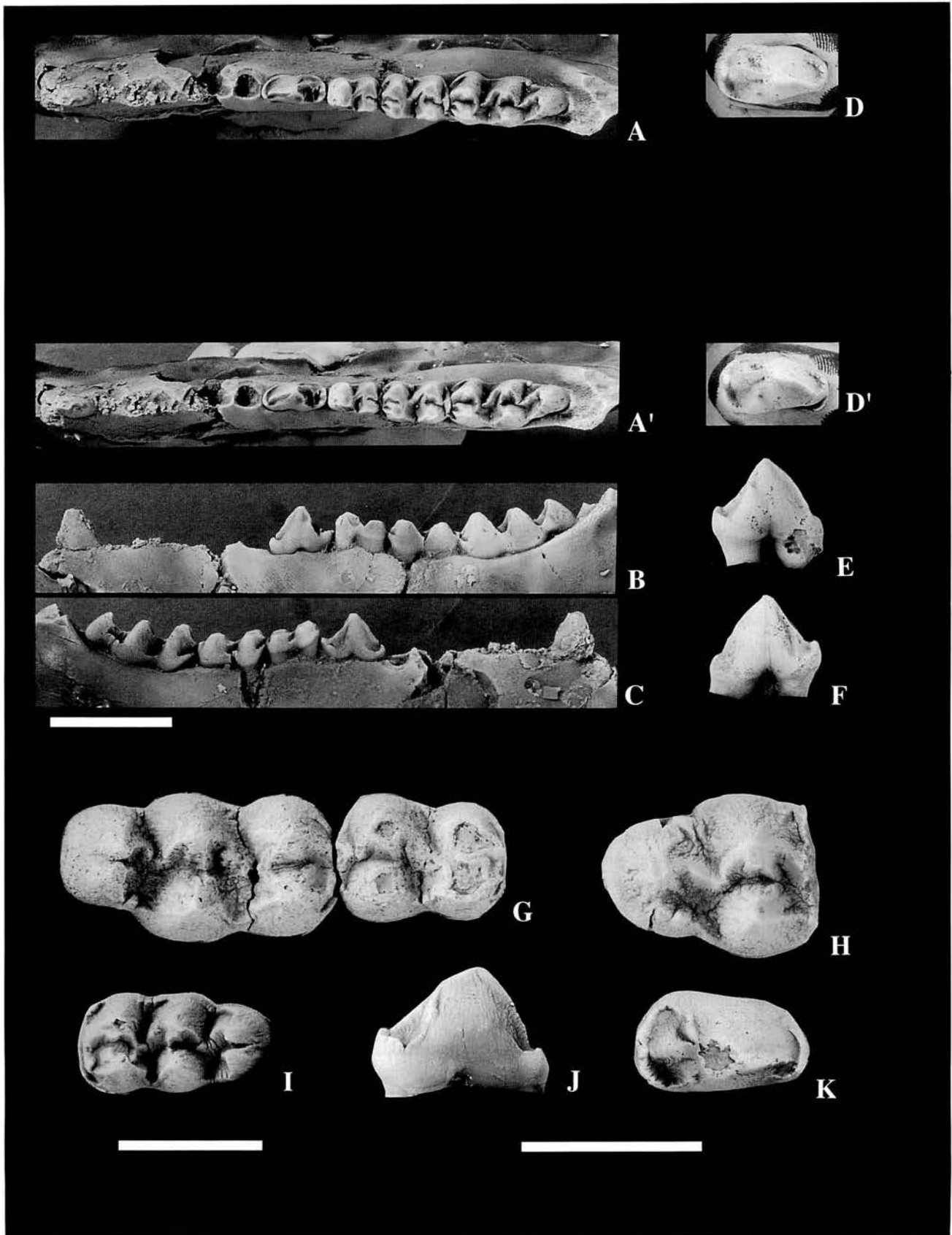


Figure 4. New upper dental materials of the Pondaung anthracotheres (*Anthracotherium*) in occlusal view (2). **A**, NMMP-KU 0413, a right maxillary fragment with P¹M¹⁻². **B**, NMMP-KU 0216, a right maxillary fragment with M²⁻³. **C**, NMMP-KU 0329, a left maxillary fragment with M¹⁻³. Scale bars = 2 cm.

Museum of Myanmar. We did not find any critical differences in selenodonty and style development between the Pondaung *Anthracothema* and *Anthracokeryx*. Furthermore, we did not recognize any dental characteristics separating these two Pondaung anthracotheriid genera. For example, NMMP-KU 0056, a right maxillary fragment

with M²⁻³ (Figure 3D), has large dental size suggesting that it is referable to *Anthracothema*. However, the molar styles of this material are developed as well as or more than the small molar materials in Figure 3G–K, which may be referable to *Anthracokeryx*. Therefore, we conclude that the two genera are identical to each other.

→ **Figure 5.** New lower dental materials of the Pondaung anthracotheres (*Anthracotherium*). **A, A', B–C**, NMMP-KU 0052, a right mandibular fragment with P₁P₂–M₃: **A, A'**, occlusal view (stereo pair); **B**, lingual view; **C**, buccal view. **D, D', E–F**, NMMP-KU 0086, a left P₄: **E, E'**, occlusal view (stereo pair); **F**, lingual view; **G**, buccal view. **G**, NMMP-KU 0330, a left mandibular fragment with M₂₋₃, in occlusal view. **H**, NMMP-KU 0419, a talonid part of left M₃, in occlusal view. **I**, NMMP-KU 0332, a right mandibular fragment with M₃, in occlusal view. **J, K**, NMMP-KU 0433, a right P₄: **J**, lingual view; **K**, occlusal view. Scale bars = 2 cm (left middle scale corresponds to A–C, A', and left lower scale corresponds to D–K, D', and right lower scale corresponds to J–K).



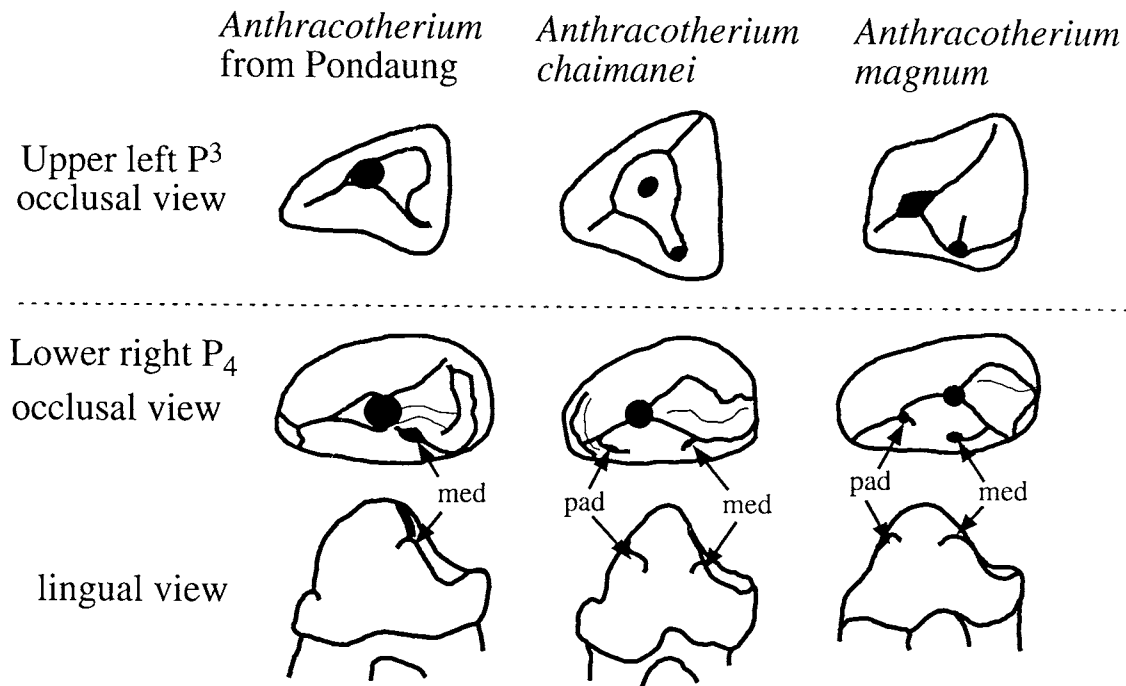


Figure 6. Schematic drawings of left P^3 and right P_4 of the Pondaung *Anthracotherium*, *Anthracotherium chaimanei*, and *Anthracotherium magnum*. Abbreviations: pad, paraconid; med, metaconid.

Furthermore, these two genera, *Anthracothema* and *Anthracokeryx*, are also similar to the genus *Anthracotherium* in regard to dental morphology (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938). Describing a new species of *Anthracotherium* from the late Eocene Krabi basin of Thailand, Ducrocq (1999) synonymized *Anthracothema* to *Anthracotherium*. He mentioned that the graduation observed in the style development of P^4 – M^3 , in the robustness and orientation of P^3 , and in the development of the lingual crests on the lower premolars among *Anthracothema pangan* from Pondaung, *Anthracotherium chaimanei* from Krabi, and *Anthracotherium monsvialense* from Europe probably indicates a direct relationship among these three taxa. We concur with Ducrocq's (1999) conclusion. In addition, we also synonymize *Anthracokeryx* to *Anthracotherium* in this paper because *Anthracokeryx* and *Anthracothema* are not separable from each other, as mentioned above. All these three genera have bunodont dentition, quite similar upper and lower molar morphologies to one another, and mesiodistally elongated simple P_4 . No distinct characteristics of dental morphology distinguish the three genera.

Specific identification

Among the species of the genus *Anthracotherium*, definitive characteristics in upper and lower posterior premolars distinguish the Pondaung *Anthracotherium* species from

more progressive *Anthracotherium* species, such as *Anthracotherium chaimanei* from the late Eocene Krabi basin of Thailand and European *Anthracotherium* (e.g., *Anthracotherium magnum* from the Oligocene). These premolar characteristics indicate that the Pondaung *Anthracotherium* species resemble each other in their dental morphology more than they do any other species of this genus (Figures 3, 5, 6). The P^3 in all materials of the Pondaung *Anthracotherium* has a mesiodistally elongated triangular outline in occlusal view with pre- and postprotocrista extending mesiodistally; whereas the P^3 of *A. chaimanei* has a more mesiodistally compressed triangular outline with the pre- and postprotocrista running more diagonally, and that of *A. magnum* has a trapezoidal outline in occlusal view with pre- and postprotocrista running more diagonally (Figure 6; Ducrocq, 1999). The P_4 in all materials of the Pondaung *Anthracotherium* has a vestigial metaconid but does not have any trace of paraconid, whereas *A. chaimanei* and *A. magnum* have both tiny paraconid and metaconid (Figure 6). The P^4 in all materials of the Pondaung *Anthracotherium* is less selenodont and has much weaker styles than those in the P^4 of *A. magnum* and *A. chaimanei*, as mentioned by Ducrocq (1999). Also, the development of the lingual crests on the lower premolars of the Pondaung *Anthracotherium* is weaker (Ducrocq, 1999). In such premolar morphologies, there are no critical characteristics that distinguish any group

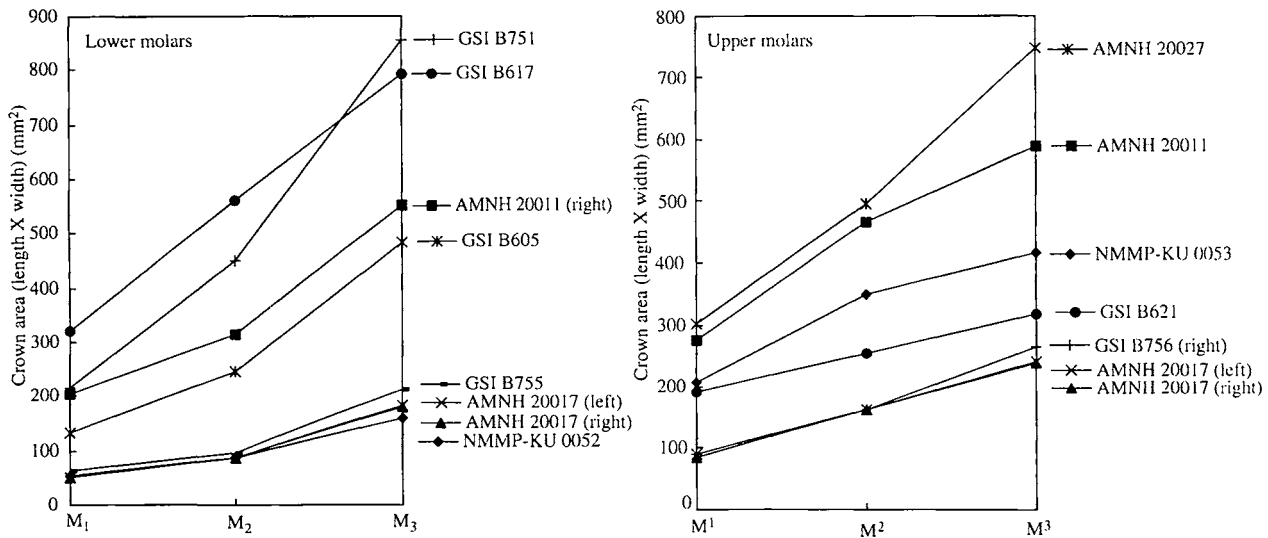


Figure 7. Size change (line chart) of upper and lower molars of the Pondaung anthracotheres in each individual.

among the Pondaung *Anthracotherium*. In addition, although there are individual variations, the Pondaung *Anthracotherium* species are distinct from other *Anthracotherium* species in having such molar morphologies as weaker selenodonty and weaker development of styles (Figures 3–5). These characteristics indicate that the Pondaung *Anthracotherium* species possess the most primitive dentition within the genus (Ducrocq, 1999).

Similar to the case of the dental morphology, the dental sizes of the Pondaung anthracotheres are highly variable. Figure 7 shows the line chart of the molar areas (width X length) in individuals of the Pondaung anthracotheres. The size of M^1_1 relative to M^2_2 and M^2_2 relative to M^3_3 in a single individual is not constant among the Pondaung anthracotheres. For example, M_1 in GSI B751 is much smaller than in GSI B617, while M_3 in the former is rather larger than in the latter. This kind of variation shown in Figures 7 can be explained by individual variation and cannot be attributed to specific differences, as mentioned below.

The dental sizes of each tooth class of all the Pondaung anthracothere materials are also highly variable (Figures 8, 9). For example, the size of smallest M^3 is about 15 mm in width and 14 mm in length, while that of largest M^3 is about 45 mm in width and 39 mm in length (Figure 8). Such size differences do not support the idea that the Pondaung anthracotheres consist of one species. However, this distributional pattern of the dental size supports the argument that these animals belong to the same taxonomic category (that is, genus) because the scatter plots of the mesiodistal length and buccolingual width of $P^{3/3}$ – $M^{3/3}$ are easily fitted to a straight-line by simple regression

(Figures 8, 9).

Among the dental size distributions (Figures 8, 9), it is noteworthy that the M_1 size can be more readily divided into four groups than the other tooth classes. In general, the first molars are the first of the adult dentition to erupt and express less size variation among the adult dentition. A number of extant herbivores, including both browsing and grazing forms and certain species of hippos and suids, compensate for tooth wear by sequential or delayed tooth eruption (Kron and Manning, 1998). As the anterior teeth (and/or teeth erupting earlier) wear out, the emerging last molars (typically enlarged) take a progressively greater role in food comminution, resulting in no net loss of feeding efficiency (Kron and Manning, 1998). Thus, the teeth erupting later (posterior molars and premolars) are considered to express much wider dental size variations than do first molars in each species. In particular, lower first molars (M_1) have been considered to express less size variation compared to upper first molars (M^1), and to correlate very closely to the body size of mammals compared to other tooth classes (Gingerich, 1974; Gingerich and Schoeninger, 1979; Legendre, 1986, 1989; Conroy, 1987; Legendre and Roth, 1988; Dagosto and Terranova, 1992; Bown *et al.*, 1994).

Therefore, the distributional pattern of M_1 size (\sim body size) in the Pondaung anthracotheres (Figure 9) suggests that the Pondaung anthracotheres can be divided into four subgroups within a single taxonomic group, that is, four species within a single genus, although a very high degree of size variation exists particularly in the posterior molars.

In relation to the specific classification of the Pondaung anthracotheres, we should mention here one dental charac-

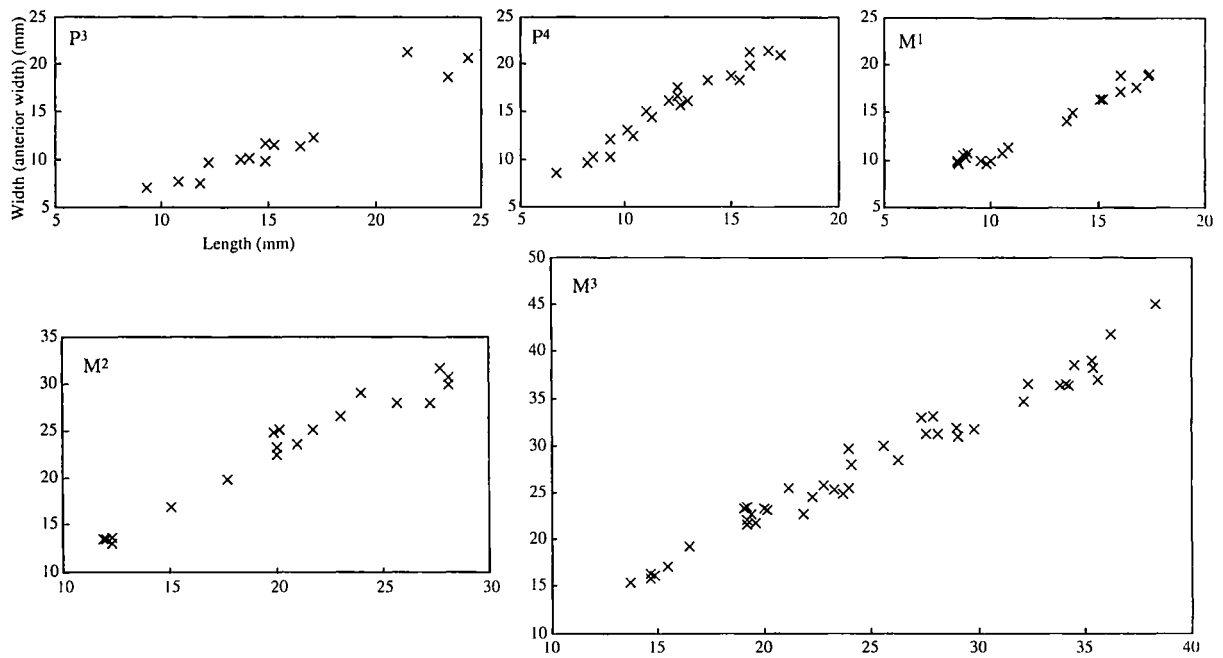


Figure 8. Size distribution of P³⁻⁴ and upper molars of the Pondaung anthracotheres.

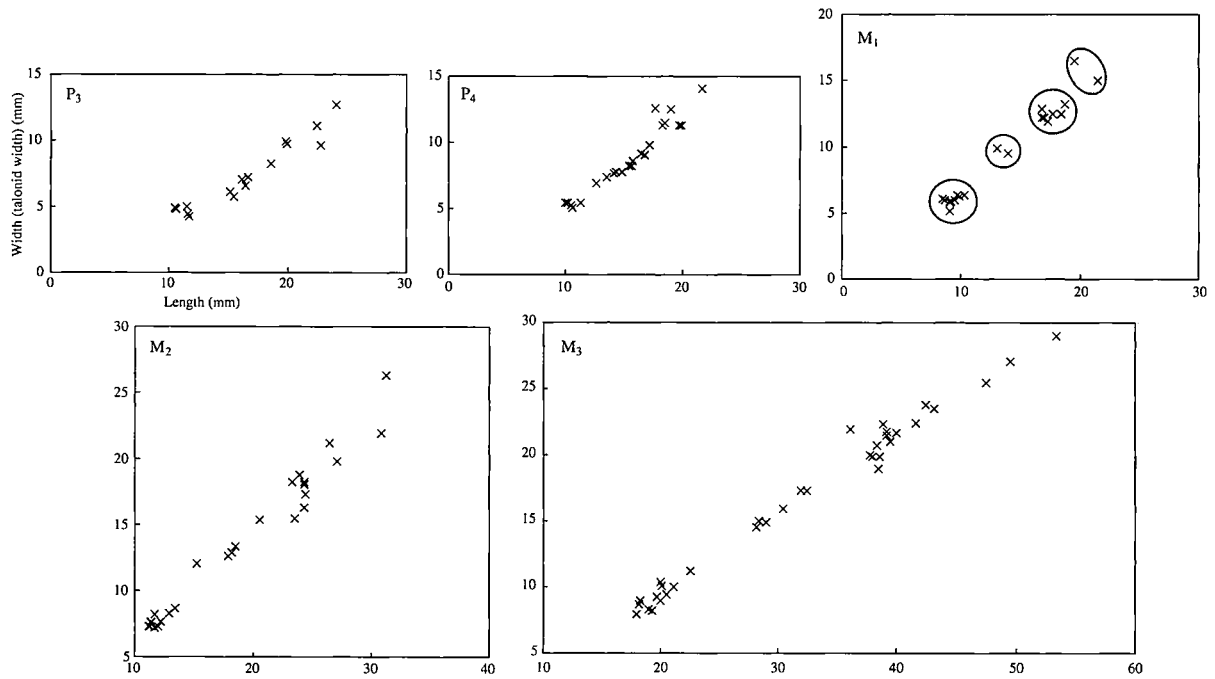


Figure 9. Size distribution of P₃₋₄ and lower molars of the Pondaung anthracotheres.

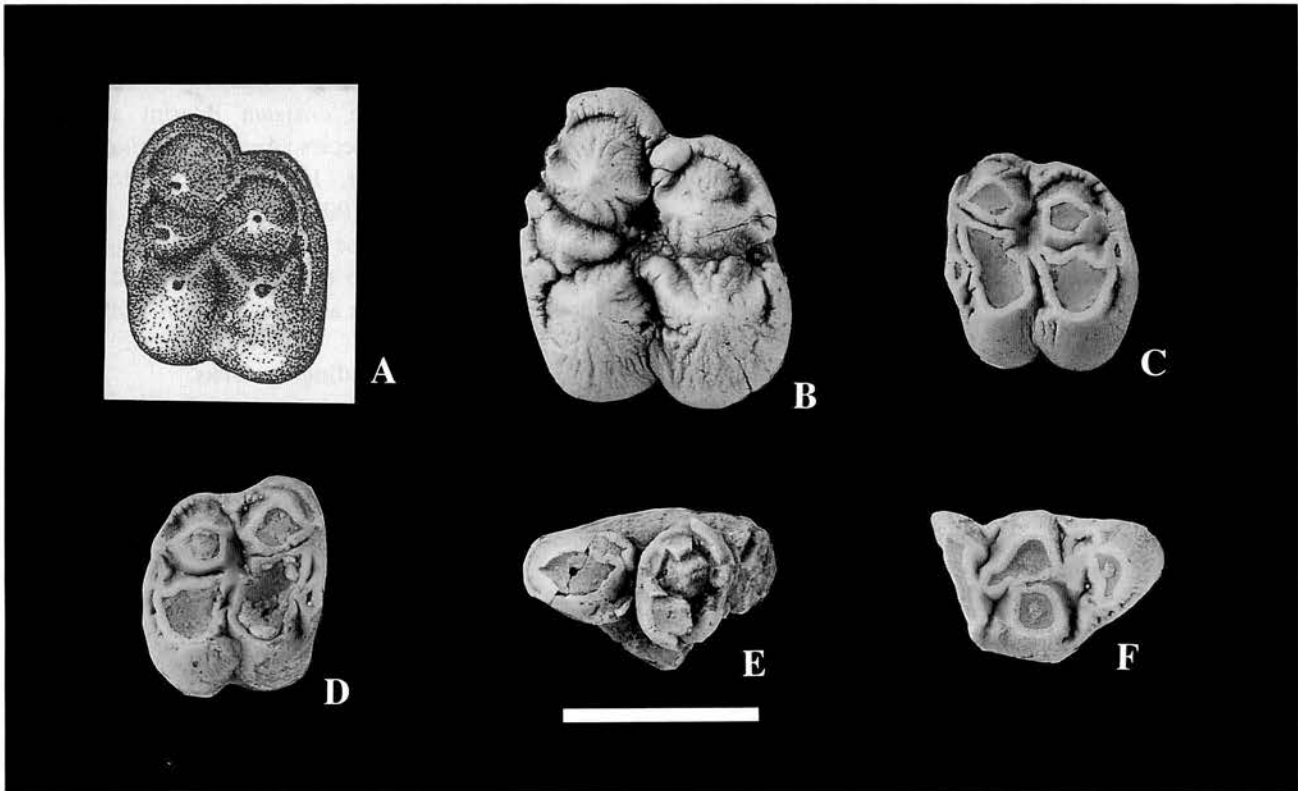


Figure 10. The Pondaung anthracothere materials of *Anthracohyus*-type in occlusal view. A. GSI B603 (holotype of *Anthracohyus choeroides*), a left M^1 . B. NMMP-KU 0452, a left M^1 . C. NMMP-KU 0454, a left M^1 . D. NMMP-KU 0453, a right M^1 . E. NMMP-KU 0500, a left maxillary fragment with P^{3-4} . F. NMMP-KU 0475, a right M_3 . Scale bar = 2 cm.

teristic of M_3 . Pilgrim (1928) distinguished the two small Pondaung anthracotheres, *Anthracokeryx ulnifer* and *Anthracokeryx myaingensis*, from one another on the basis of the morphology of the hypoconulid on M_3 ; the former has a single cusp at the hypoconulid region on M_3 , whereas the latter has a double cusp. Although most of the Pondaung anthracotheres have a double cusp at the hypoconulid region on M_3 , the buccal of which is always larger and more distinct than the lingual one, the development of the lingual one is highly variable among all the examples of M_3 in the Pondaung anthracotheres. For example, the lingual cusp in the hypoconulid on M_3 is almost as large as the buccal one in NMMP-KU 0330 (Figure 5G), whereas it is very small and faint in NMMP-KU 0419 (Figure 5H). We consider this difference to be individual variation, not a specific characteristic.

Status of *Anthracohyus*

We also synonymize the remaining genus among the Pondaung anthracotheres, *Anthracohyus*, to *Anthracotherium*. Although *Anthracohyus* has unique dental structures in the upper molars (GSI B603, Figure 10A) (Pilgrim and Cotter, 1916; Pilgrim, 1938; Colbert, 1938),

the basic structures of its upper molars are referable to those of the Pondaung *Anthracotherium* (Figures 3, 4). Furthermore, the lower dental material of *Anthracohyus choeroides*, GSI B605 (a right mandibular fragment with complete dentition) (Pilgrim and Cotter, 1916, pl. 2, figs. 3, 3a-e, 4, 4a-e), is identical to that of *Anthracokeryx birmanicus* from the Pondaung Formation (Pilgrim, 1928, pl. 4, fig. 5; Colbert, 1938, fig. 45); there is no morphological or size distinction among the lower dental materials of the two species.

On the other hand, there are a few new specimens whose dental morphologies seem to be identical to that of *Anthracohyus* (Figure 10B-F): NMMP-KU 0452 (a left M^1), 0453 (a right M^1), 0454 (a left M^1), 0475 (a right M_3), and 0500 (a left maxillary fragment with P^{3-4}) [the latter four specimens (NMMP-KU 0453, 0454, 0475, and 0500) probably belong to the same individual]. The upper molars among these (NMMP-KU 0452, 0453, 0454) have characteristics of *Anthracohyus*: very conical cusps, no or very vestigial styles on the upper dentition, and mesiodistally shorter buccal margins than the lingual one on the upper molars. The three examples of M^1 , GSI B603 (type of *Anthracohyus choeroides*) (length: 21.2 mm;

width: 25.4 mm), NMMP-KU 0452 (length: 27.9 mm; width: 33.0 mm), and NMMP-KU 0453 (length: 19.6 mm; width: 21.8 mm), are separately scattered in the same linear size-distributional pattern prevalent among the Pondaung anthracotheres (Figure 6). Although these three specimens are not M_1 and are considered to have relatively great size variation, they may be referred to the second largest, largest, and second smallest groups among the four groups of the Pondaung anthracotheres mentioned above, respectively, according to their sizes. Therefore, this size-distributional pattern also suggests that these *Anthracohyus*-type materials express one of the variations among the Pondaung anthracotheres, that is, species of *Anthracotherium*.

In conclusion, taking the variations of molar morphology (particularly development of upper molar styles) and size of the Pondaung anthracotheres into consideration (Figures 3–5), we interpret the dental morphology of *Anthracohyus* as one of the unusual individual variations of the Pondaung *Anthracotherium*. Otherwise, a multiplicity of species (of *Anthracothema*, *Anthracokeryx*, and *Anthracohyus*) which are morphologically and phyletically very close to one another, have to be maintained in a single fossil fauna (the Pondaung fauna). Such a situation seems unreasonable.

Classification

To review, we synonymize all the genera of the Pondaung anthracotheres (*Anthracothema* Pilgrim, 1928, *Anthracokeryx* Pilgrim and Cotter, 1916, and *Anthracohyus* Pilgrim and Cotter, 1916) to *Anthracotherium* Cuvier, 1822. We group the Pondaung *Anthracotherium* materials into four species on the basis of M_1 size (\sim body size). Materials lacking M_1 are tentatively assigned to one of the four species based on the sizes of available teeth (Appendix).

There is a possibility that the larger two and smaller two of the four species might in fact be sexual dimorphic pairs as implied by Holroyd and Ciochon (1991). Most anthracotheres show a moderate amount of sexual dimorphism, but it is expressed by the canines: the individuals adjudged to have been male have larger canines than do the females (Kron and Manning, 1998). However, the fossil materials of the Pondaung anthracotheres are too poor to evaluate distribution of canine size, so there is no evidence to confirm that the larger two and smaller two represent male-and-female of sexually dimorphic species. Also, no critical difference in canine size relative to M_1 is observed among the currently available materials. Therefore, we treat these four groups of the Pondaung *Anthracotherium* as four species in this paper.

Although the specific nomenclature of the Pondaung anthracotheres has been very complicated as mentioned above (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert,

1938), the following four species names can be retained based on the rule of priority: largest species, *Anthracotherium pangan* Pilgrim and Cotter, 1916; second largest species, *Anthracotherium crassum* Pilgrim and Cotter, 1916; second smallest species, *Anthracotherium birmanicum* (Pilgrim and Cotter, 1916); and smallest species, *Anthracotherium tenuis* (Pilgrim and Cotter, 1916). The possibility remains that the larger two (*A. pangan* and *A. crassum*) and smaller two (*A. birmanicum* and *A. tenuis*) might each be combinable as a sexually dimorphic species.

Concluding remarks

The dental morphological comparisons in this study indicate that the Pondaung anthracotheres consist of four species of one genus (*Anthracotherium*). Their dental morphology, such as selenodonty, development of styles, and premolar shapes, suggest that the four species are much more similar to one another than to any other species of *Anthracotherium* from other deposits, although the dental morphology trend seems to be highly variable within the Pondaung *Anthracotherium*. In addition, the group of Pondaung *Anthracotherium* species has the other following features: (1) it is the oldest among the genus; (2) in basic dental morphology, the Pondaung *Anthracotherium* are likely to be the most primitive among the genus; and (3) their fossil materials predominate in collections of the Pondaung mammal fauna, suggesting a dominant population size (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938; Tsubamoto, 2001). Therefore, it is suggested that: (1) the genus *Anthracotherium* originated and rapidly radiated around the Pondaung area during the latest middle Eocene, and (2) *Anthracotherium* migrated from southern East Asia to Europe during the latest middle to late Eocene (Ducrocq, 1995).

Systematic paleontology

Order Artiodactyla Owen

Family Anthracotheriidae Leidy

Genus *Anthracotherium* Cuvier, 1822

Synonyms.—*Anthracohyus* Pilgrim and Cotter, 1916; *Anthracokeryx* Pilgrim and Cotter, 1916; *Anthracothema* Pilgrim, 1928.

Type species.—*Anthracotherium magnum* Cuvier, 1822.

Included species from Europe.—*Anthracotherium monsvialense* De Zigno, 1888; *Anthracotherium alsaticum* Cuvier, 1822; *Anthracotherium seckbachense* Kinkelin, 1884; *Anthracotherium illyricum* Teller, 1886; *Anthracotherium bumbachense* Stehlin, 1910; *Anthracotherium cuvieri* Gaudry, 1873; *Anthracotherium hippoideum* Rüttimeyer, 1857; *Anthracotherium valdense*

Kowalevski, 1876; *Anthracotherium dalmatinum* von Meyer, 1854. (after Ducrocq, 1999)

Included species from Asia.—*Anthracotherium bugtiense* Pilgrim, 1907 (*sensu* Pickford, 1987); *Anthracotherium silistrense* Pentland, 1828 (*sensu* Pickford, 1987); *Anthracotherium changlingensis* Zhao, 1993; *Anthracotherium chaimanei* Ducrocq, 1999; *Anthracotherium thailandicus* (Ducrocq, 1999) new combination; *Anthracotherium gungkangensis* (Qiu, 1977) new combination; *Anthracotherium verhoeveni* (von Koenigswald, 1967); *Anthracotherium pangan* Pilgrim and Cotter, 1916; *Anthracotherium crassum* Pilgrim and Cotter, 1916; *Anthracotherium birmanicum* (Pilgrim and Cotter, 1916) new combination; *Anthracotherium tenuis* (Pilgrim and Cotter, 1916) new combination.

Revised diagnosis.—Large- to small-sized bunodont and primitive anthracothere. Differs from selenodont and bunoselenodont anthracotheres, such as *Elomeryx* and *Bothriogenys*, in having much simpler premolars and less developed selenodontology. Differs from *Siamotherium* in having double premetacristid on the lower molars (there is no distinct outer metacristid on those of *Siamotherium*), much better developed molar styles, less lingually located molar metacone in relation to paracone, much less mesiodistally compressed M^3 , and much better developed protocone compared to paracone on P^{3-4} . Differs from *Anthracosenex* in having mesially or mesiobuccally oriented outer premetacristid rather than buccally oriented in *Anthracosenex*. Differs from *Heptacodon* in having less developed P_4 cristids, and in lacking such strongly developed and prominent styles on the upper molars as in *Heptacodon*, and molar postentocristid that runs distobuccally and links to posthypocristid making a V-shaped notch. Differs from *Microbunodon* in having more bunodont cusps, less developed cingulum, rather straight (not V-shaped) ectoloph on P^{3-4} , and mesiodistally longer P^3 .

Anthracotherium pangan Pilgrim and Cotter, 1916

Anthracotherium pangan Pilgrim and Cotter, 1916, p. 59–60, pl. 4, figs. 1–3.

Anthracothema pangan (Pilgrim and Cotter, 1916). Pilgrim, 1928, p. 10–13, pl. 1, figs. 1–7; Colbert, 1938, p. 353–355, figs. 41–42.

Anthracohyus rubricae Pilgrim and Cotter, 1916 (in part), p. 55–57, pl. 2, fig. 5–6, pl. 3, fig. 1–2.

Anthracothema rubricae (Pilgrim and Cotter, 1916) (in part). Pilgrim, 1928, p. 14; Colbert, 1983, p. 356–358.

Anthracotherium crassum Pilgrim and Cotter, 1916 (in part), p. 60–61, pl. 4, fig. 4–5, 5a.

Anthracothema crassum (Pilgrim and Cotter, 1916) (in part). Pilgrim, 1928, p. 16–18; Colbert, 1938, p. 355–356.

Anthracohyus palustris Pilgrim and Cotter, 1916, p. 58, pl. 3, figs. 7–9.

Anthracothema palustre (Pilgrim and Cotter, 1916). Pilgrim, 1928, p. 14–16, pl. 2, figs. 8–10; Colbert, 1938, p. 355.

Lectotype.—GSI B619, a left maxillary fragment with M^{2-3} (Colbert, 1938).

Revised diagnosis.—Large-sized and one of the most primitive *Anthracotherium* species. The dental morphology is almost identical to other Pondaung *Anthracotherium* species (i.e., *A. crassum*, *A. birmanicum*, and *A. tenuis*). Differs from the other Pondaung *Anthracotherium* species in having larger M_1 . Differs from more progressive *Anthracotherium*, such as *A. magnum*, *A. monsvialense*, *A. bugtiense*, and *A. chaimanei*, in having slightly less selenodont cusps, less developed styles, mesiodistally elongated triangular outline of P^3 in occlusal view having mesiodistally (not diagonal to the tooth row) extending paracrista, less developed lower premolar cristids, and less molariform P_4 lacking a trace of paraconid. Differs from *A. thailandicus* in having slightly lower tooth crown in the lower dentition, less selenodontology, and metaconid on P_4 , and lacking paraconid on P_4 . Differs from *A. silistrense* in having larger size and slightly lower P_{3-4} . Differs from *A. gungkangensis* in having larger size, slightly less developed selenodontology and styles, more rounded outline of upper molars in occlusal view, and slightly wider and shorter upper molars. Differs from *A. verhoeveni* in lacking hypertrophied metastyle on the distal face of M^3 . Differs from *A. changlingensis* in being smaller.

Anthracotherium crassum Pilgrim and Cotter, 1916

Anthracotherium crassum Pilgrim and Cotter, 1916 (in part), p. 60–61, pl. 5, fig. 1.

Anthracothema crassum (Pilgrim and Cotter, 1916) (in part). Pilgrim, 1928, p. 16–18; Colbert, 1938, p. 355–356.

Anthracohyus rubricae Pilgrim and Cotter, 1916 (in part), p. 55–57, pl. 2, fig. 7, pl. 3, figs. 3–6, 5a.

Anthracothema rubricae (Pilgrim and Cotter, 1916) (in part). Pilgrim, 1928, p. 14, pl. 2, figs. 1–7; Colbert, 1983, p. 356–358, figs. 43–44.

Anthracohyus choeroides Pilgrim and Cotter, 1916 (in part), p. 52–55, pl. 2, figs. 1–2.

Anthracokeryx moriturus Pilgrim, 1928, p. 32, pl. 4, figs. 1–3; Colbert, 1938, p. 376–379, figs. 51–52.

Holotype.—GSI B615, a left maxillary fragment with M^{2-3} .

Revised diagnosis.—Second largest (medium-sized) Pondaung *Anthracotherium*. Differs from *A. pangan* in having smaller M_1 . Differs from *A. birmanicum* and *A. tenuis* in having larger M_1 .

Anthracotherium birmanicum (Pilgrim and Cotter, 1916)

Anthracokeryx birmanicus Pilgrim and Cotter, 1916 (in part), p. 61–62, pl. 5, figs. 2, 4; Pilgrim, 1928, p. 18–19, pl. 4, figs. 5, 5a; Colbert, 1938, p. 360–362, fig. 45.

Anthracokeryx hospes Pilgrim, 1928, p. 29–30; Colbert, 1938, p. 362–363.

Anthracohyus choeroides Pilgrim and Cotter, 1916 (in part), p. 52–55, pl. 2, figs. 3–4, 3a–3e, 4a–4e.

Holotype.—GSI B621, a right maxillary fragment with P³–M³.

Revised diagnosis.—Second smallest (medium-sized) Pondaung *Anthracotherium*. Differs from *A. pangan* and *A. crassum* in having smaller M₁. Differs from *A. tenuis* in having larger M₁.

Anthracotherium tenuis (Pilgrim and Cotter, 1916)

Anthracokeryx tenuis Pilgrim and Cotter, 1916, p. 62–63, pl. 5, figs. 6–8; Colbert, 1938, p. 364.

Anthracokeryx birmanicus Pilgrim and Cotter, 1916 (in part), p. 61–62, pl. 5, figs. 3, 5.

Anthracokeryx bambusae Pilgrim, 1928, p. 29; Colbert, 1938, p. 363.

Anthracokeryx myaingensis Pilgrim, 1928, p. 30–31, pl. 3, figs. 4–7; Colbert, 1938, p. 364–365.

Anthracokeryx ulnifer Pilgrim, 1928, p. 19–29, pl. 3, figs. 1–3, pl. 4, fig. 6; Colbert, 1938, p. 365–375, figs. 46–50.

Holotype.—GSI B625 (a left maxillary fragment with M¹⁻²) and GSI B626 (a left mandibular fragment with M₁ and posterior part of dP₄).

Revised diagnosis.—Smallest (small-sized) Pondaung *Anthracotherium*. Differs from other Pondaung *Anthracotherium* species in having smaller M₁. Further differs from *A. thailandicus* in lacking the high and ventrally salient mandibular symphysis under P₁, and in having longer diastema between P₂ and P₃. Further differs from *A. silistrense* in having longer diastema in the anterior premolar dentition.

Family Helohyidae Marsh

Genus ***Pakkokuhyus*** Holroyd and Ciochon, 1995***Pakkokuhyus lahirii*** (Pilgrim, 1928)

Anthracokeryx? lahirii Pilgrim, 1928, p. 32–33, pl. 4, figs. 4, 4a; Colbert, 1938, p. 379.

Pakkokuhyus lahirii (Pilgrim, 1928). Holroyd and Ciochon, 1995, p. 178–180, fig. 1A, B.

Siamotherium pondaungensis Ducrocq *et al.*, 2000, p. 756, fig. 2.

Holotype.—GSI B766, right mandibular fragment with M₁₋₃.

Revised diagnosis.—A helohyid having bunodont and conical cusps, lacking hypocone at least on M²⁻³ and paraconid at least on M₂₋₃. Differs from *Gobiohyus* and *Helohyus* in having more bunodont and conical cusps, a basally inflated crown, larger metaconule on M³, entoconid slightly posterior to hypoconid and less pronounced ectoflexid on the lower molars, a continuous labial cingulid on M₃, shorter and less distinct hypoconulid loop on M₃, stronger labial cingulids on M₁₋₂, and absolutely and relatively greater mandibular depth, and in lacking trace of molar hypocone, lingual cingulum and styler cusps on the upper molars, and molar paraconid. Further differs from *Gobiohyus* in having relatively higher crowns and from *Helohyus* in having a stronger hypoconulid on the distal cingulid and in lacking accessory cusplids on the hypoconulid loop. Differs from *Progeniohyus* in having smaller dental size, larger hypoconulid on M₃, and labial cingulid on M₃, and in lacking paraconid on M₂. Differs from the possible raoellid *Haqueina* in having entoconid slightly posterior to hypoconid, a stronger hypoconulid on the distal cingulid, and weaker hypolophid and cristid obliqua, a weaker and less constricted hypoconulid loop and a single hypoconulid on M₃. Differs from anthracotheriids in having smaller dental size, more conical (less selenodont) cusps, straight hypolophid on the lower molars, and shorter hypoconulid loop on M₃, and in lacking a double premetacristid on the lower molars.

Comments on some other Eocene anthracotheres from Asia

We reappraise several Eocene anthracotheres from Asia in relation to the revision of the Pondaung anthracotheres. *Anthracothema* and *Anthracokeryx* have been also reported from other deposits in the Eocene of Asia. Because the Pondaung *Anthracothema* and *Anthracokeryx* are the types of the two genera and the two were referred to *Anthracotherium*, all species of *Anthracothema* and *Anthracokeryx* are referred to *Anthracotherium*, except for *Anthracokeryx sinensis* (including *Anthracokeryx dawsoni* and *Anthracothema minima*), *Anthracokeryx litangensis*, and *Anthracothema lijiangensis*.

Anthracokeryx birmanicus, *Anthracokeryx moriturus*, *Anthracokeryx* sp. (= *Anthracokeryx* sp. cf. *bambusae*), and *Anthracothema rubricae*, which are conspecific with one or another of the Pondaung anthracotheres, are recorded from the late Eocene Nado Formation, Bose and Yongle basins, Guangxi, southern China (Chow, 1957; Tang *et al.*, 1974; Qiu, 1977; Russell and Zhai, 1987). The materials of these species are poor, so that for the time being we tentatively refer these materials to the same species as

Anthracotherium from the Pondaung Formation. We refer *Anthracothema rubricae* and *Anthracokeryx moriturus* to *Anthracotherium crassum*, *Anthracokeryx birmanicus* to *Anthracotherium birmanicum*, and *Anthracokeryx* sp. to *Anthracotherium* sp.

Anthracokeryx gungkangensis and *Anthracokeryx kwangsiensis* are recorded from the late Eocene Gongkang Formation, which overlies the Naduo Formation (Qiu, 1977). *Anthracokeryx kwangsiensis* is also recorded from the Naduo Formation (Zhao, 1993). Ducrocq (1999) mentioned that these two species likely correspond to only one form in terms of their very similar morphology and dimensions. Following his suggestion, we treat *Anthracokeryx kwangsiensis* as a junior synonym of *Anthracokeryx gungkangensis*. Therefore, both of these species are referred to *Anthracotherium gungkangensis*.

Anthracokeryx sinensis is recorded from the Heti (Yuanchu basin), Xiangshan (Lijiang basin, Yunnan), and Huangzhuang (Qufu, Shandong) formations of the middle Eocene of China (Zdansky, 1930; Xu, 1962; Shi, 1989; Zhong *et al.*, 1996). We think that *Anthracokeryx sinensis* is not a bunodont but a primitive bunoselenodont anthracothere, so that this species is not referable to *Anthracotherium* (bunodont anthracothere). The P_4 of *Anthracokeryx sinensis* (Zdansky, 1930, pl. 1, fig. 18; Xu, 1962, p. 241, fig. 1-3a) is much more molarized than that of progressive *Anthracotherium* species, such as *Anthracotherium magnum*. It has a somewhat triangle-shaped trigonid in occlusal view and resembles that of bunoselenodont or selenodont anthracotheres. Also, the upper molars of *Anthracokeryx sinensis* reveal stronger selenodontology than those of *Anthracotherium*. In particular, the paraconule of the upper molars of *A. sinensis* is much more selenodont than that of *Anthracotherium*. The selenodontology of the upper molars of *A. sinensis* also appears similar to that of bunoselenodont anthracotheres, such as *Bothriogenys*. Therefore, we consider that it is better to establish a new genus for *Anthracokeryx sinensis*.

We suspect that it is better to synonymize both *Anthracokeryx dawsoni* and *Anthracothema minima* to *Anthracokeryx sinensis*. First, *Anthracokeryx dawsoni* was described by Wang (1985) from the late middle Eocene Zhaili Member of the Heti Formation (Yuanchu basin, central China), which also yields *Anthracokeryx sinensis*. The material of *Anthracokeryx dawsoni* consists of a skull with upper dentition. This material (IVPP V7915) has very similar dental morphology and size to *Anthracokeryx sinensis* except for a few dental differences (Xu, 1962, pl. 1, fig. 2-3, 8, 2A-3A, pl. 2, fig. 2, 2A; Wang, 1985, p. 58, pl., 1); such subtle differences seem to be within the range of intraspecific variation. Second, *Anthracothema minima* was described by Xu (1962, p. 233, 244, pl. 1, fig. 1, 1A) from the late middle Eocene Rencun Member of the Heti

Formation, which also yields *Anthracokeryx sinensis*. *Anthracothema minima* consists of only one upper molar (IVPP V2661), which has conical cusps like that of the Pondaung *Anthracothema* and *Anthracohyus*. However, its overall dental morphology and size are similar to that of *Anthracokeryx sinensis*. Taking the case of the Pondaung anthracotheres mentioned above into consideration, it may be better to consider that *Anthracothema minima* is also not a distinct species but one of the variations of *Anthracokeryx sinensis*.

Anthracokeryx litangensis was described from the late Eocene to early Oligocene Gemusi basin of Litang County (Sichuan, China), based on a right mandibular fragment with P_4M_1 and an astragalus by Zhong *et al.* (1996). Although its only preserved lower molar (M_1) is heavily worn (Zhong *et al.*, 1996, p. 265, pl. 21, fig. 3), the lower molar is rather selenodont than bunodont, having more lingually oriented preparacristid and cristid obliqua than *Anthracotherium* and *Anthracokeryx sinensis*. Its P_4 is mesiodistally elongated and with well-developed cristids, suggesting it is referable neither to *Anthracotherium* nor to *Anthracokeryx sinensis*. The dental morphology of *Anthracokeryx litangensis* is rather similar to that of selenodont anthracotheres, such as *Bothriodon*.

Anthracokeryx thailandicus was described from the late Eocene Krabi basin of Thailand by Ducrocq (1999). We refer this species to the genus *Anthracotherium* and introduce for it the new combination *Anthracotherium thailandicus*.

Ducrocq (1999, p. 125, pl. 14G) described an anthracotheriid left M^3 (DMR TF2662) from the Krabi basin as Anthracotheriinae gen. *et* sp. indet. This material is morphologically similar to that of *Anthracohyus* from the Pondaung Formation (Ducrocq, 1999) and is similar to *Anthracotherium thailandicus* in size. Thus, DMR TF2662 might be one of the individual variations of *A. thailandicus*.

Anthracokeryx sp. from the middle Eocene Lizhuang Formation (Henan, central China) was described by Wang and Zhou (1982) based on a broken right upper molar. Although this material was not illustrated, Wang and Zhou (1982) mentioned its morphological similarity to upper molars of *Anthracokeryx sinensis*. Here, we tentatively refer this material to cf. *Anthracokeryx sinensis*.

Cf. *Anthracokeryx* sp. was cited in the early to early middle Eocene Kuldana Formation (Indo-Pakistan) by Gingerich *et al.* (1979) and Russell and Zhai (1987). It is only represented by BMNH 32168, a left M_3 , which was referred to *Lammidhania wardi* (Anthracobunidae) by Gingerich (1977). However, the dental morphology of BMNH 32168 is identical M_3 of bunoselenodont anthracotheres, such as *Bothriogenys*, and is definitely not referable to *Anthracokeryx* (= *Anthracotherium*). Besides,

BMNH 32168 may be from the overlying Murree Formation (Russell and Zhai, 1987). Therefore, the existence of an *Anthracokeryx* (*Anthracotherium*)-like anthracothere in the Kuldana Formation is highly doubtful.

Cf. *Anthracokeryx* sp. was cited also in the late middle Eocene Shara Murun Formation (Inner Mongolia, northern China) by Russell and Zhai (1987). The sole specimen of this form, AMNH 22090 (a right mandibular fragment with M_3), was originally described as *Gobiohyus robustus* (Helohyidae) by Matthew and Granger (1925). The M_3 of the specimen has three large and distinct cusps at the hypoconulid region and reveals a bilophodont structure, which have never been seen in anthracotheres. Therefore, the existence of an *Anthracokeryx* (*Anthracotherium*)-like anthracothere in the Shara Murun Formation is also highly doubtful.

Anthracothema lijiangensis was described from the middle Eocene Xiangshan Formation (Lijiang basin, Yunnan, southern China) by Zong *et al.* (1996). This species differs from *Anthracotherium* in having straight (not V-shaped) hypolophid, mesiodistally rather than mesiolingually oriented cristid obliqua, and no buccal premetacristid directed mesiobuccally on the lower molars (Zong *et al.*, 1996, p.279, pl. 35, fig. 2). These characteristics demand rejection of a reference of *Anthracothema lijiangensis* to *Anthracotherium*. It may be better to establish a new genus for this species (*Anthracothema lijiangensis* is distinguished from *Anthracokeryx sinensis*). On the other hand, although the material of *Anthracothema lijiangensis* was referred to the Anthracotheriidae by Zong *et al.* (1996) and Huang (1999), this familial position of *A. lijiangensis* is also doubtful because the species have straight hypolophid and no trace of mesiobuccally-directed premetacristid on the lower molars, both which are not appropriate to the anthracotheriid diagnosis (Holroyd and Ciochon, 1995).

Anthracotherium chaimanei was originally reported as *Anthracothema* sp. cf. *A. pangan* from the Krabi basin of Thailand by Ducrocq *et al.* (1992). It was formally described by Ducrocq (1999).

Anthracotherium verhoeveni was originally described from Timor (Indonesia) (but see Ducrocq, 1996, p.765) as *Anthracothema verhoeveni* by von Koenigswald (1967). It was referred to the genus *Anthracotherium* by Ducrocq (1999).

Anthracotherium? spp. were cited in the middle middle Eocene Lushi Formation (Henan, central China) by Chow *et al.* (1973). However, this report contained no illustration of their material. In addition, the mammalian fauna of the Lushi Formation, which was referred to the middle middle Eocene (Irdinmanhan East Asian Land Mammal Age) (Russell and Zhai, 1987), is much older than the latest middle Eocene Pondaung Formation including the oldest posi-

tive *Anthracotherium* species. Therefore, the presence of the genus *Anthracotherium* in the Lushi Formation is doubtful (Russell and Zhai, 1987).

Heothema is recorded from the late Eocene Naduo and Gongkang Formations (Bose and Yongle basins, Guangxi) and lower part of Yongning Formation (late Eocene or early Oligocene; Nanning basin, Guangxi) of southern China (Tang, 1978; Zhao, 1981, 1983, 1993). Although the genus *Heothema* was synonymized to *Anthracotherium* by Ducrocq (1999), this genus may be valid because: (1) the molars and P^4 of *Heothema* are more selenodont than those of *Anthracotherium*; (2) crests on the lingual face of lower premolars in *Heothema* (Tang, 1978, pl. 3, fig. 1, 1A) are stronger than those in *Anthracotherium*; and (3) P_4 of *Heothema* seems to be more molariform than that of *Anthracotherium*, having a somewhat triangularly-shaped trigonid outline in occlusal view (Tang, 1978, pl. 3, fig. 1). Judging from these morphological points, *Heothema* might be one of the primitive bunoselenodont anthracotheres. For specific division of *Heothema*, we follow the grouping by Ducrocq (1999, p. 121), who recognized two species, *Heothema bellia* and *Heothema chengbiensis*.

Huananothema imparilica was described as a new genus and species of the Anthracotheriidae by Tang (1978) based on an upper molariform tooth from the late Eocene Naduo Formation, which also yields *Heothema*. According to Tang (1978), the type and unique material of *Huananothema imparilica* (IVPP V4964) is an upper molar, and therefore this species is identified by its upper molar having an anterior buccolingual width less than its posterior buccolingual width, in contrast to other anthracotheres (in the upper molars of all other anthracotheres, the anterior buccolingual width is greater than the posterior buccolingual width). However, this feature in IVPP V4964 is a typical dP^4 morphology of large anthracotheres as seen in DMR TF 2901, a right dP^4 of *Anthracotherium chaimanei* from the Krabi basin of Thailand (Ducrocq, 1999, pl. 5, fig. B), and also in NMMP-KU 0327, an upper dental specimen of the Pondaung *Anthracotherium* (Figure 3C). Therefore, IVPP V4964 is dP^4 , so that the diagnosis of *Huananothema imparilica* by Tang (1978) is invalid. By comparing its size and morphology with those of anthracotheres from the Naduo Formation, we consider that IVPP V4964 is a dP^4 of *Heothema chengbiensis*. Therefore, we synonymize both the genus *Huananothema* and species *Huananothema imparilica* to genus *Heothema* and species *Heothema chengbiensis*, respectively.

The materials of *Probrachyodus* are poor. Russell and Zhai (1987, p. 130) mentioned that this genus may be inseparable from *Anthracokeryx* (that is, *Anthracotherium* or the same genus as *Anthracokeryx sinensis*). However, the upper molars of *Probrachyodus* show bunoselenodonty, so

that this species differs from *Anthracotherium*, which comprises bunodont anthracotheres. *Probrachyodus* is distinct from *Anthracokeryx sinensis* and also further from *Anthracotherium* in having more lingually procumbent molar paracone and metacone. Therefore, we consider this genus a valid one. *Probrachyodus panchiaoensis* was described from the middle Eocene Lumeiyi Formation (Yunnan, Lunan basin, southern China) by Xu (1962). *Probrachyodus?* sp. nov. was cited in the middle Eocene Dongjun Formation (Guangxi, southern China) by Ding *et al.* (1977).

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Appendix. Dental measurements (in mm) of the Pondaung *Anthracotherium* used in this paper (Figures 7–9). Abbreviations: L, anteroposterior length; W, buccolingual width; *, estimate; [] (square bracket), the data are from the literature (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938).

Upper dentition

Specimen number	Taxa	P3/ L	P3/ W	P4/ L	P4/ W	M1/ L	M1/ W	M2/ L	M2/ W	M3/ L	M3/ W
NMMP-KU 0053	<i>A. birmanicum</i>	14.1	10.1	10.4	12.5	13.8	15.0	17.7	19.8	19.2	21.6
NMMP-KU 0056	<i>A. sp. cf. A. crassum</i>							23.0	26.6	28.1	31.2
NMMP-KU 0066	<i>A. tenuis</i>					10.8	11.4				
NMMP-KU 0067	<i>A. sp. cf. A. crassum</i>			12.1	16.1						
NMMP-KU 0070	<i>A. birmanicum</i>									20.2	23.2
NMMP-KU 0071	<i>A. sp. cf. A. crassum</i>					15.1	16.4				
NMMP-KU 0074	<i>A. sp. cf. A. pangan</i>			13.9	18.3						
NMMP-KU 0081	<i>A. birmanicum</i>									19.2	23.4
NMMP-KU 0082	<i>A. birmanicum</i>									19.4	22.6
NMMP-KU 0083	<i>A. birmanicum</i>									19.1	23.3
NMMP-KU 0103	<i>A. pangan</i>			15.9	21.2						
NMMP-KU 0105	<i>A. sp. cf. A. crassum</i>			11.0	15.0						
NMMP-KU 0106	<i>A. sp. cf. A. birmanicum</i>	13.7	9.9								
NMMP-KU 0122	<i>A. sp. cf. A. birmanicum</i>	17.1*	12.2	12.5	16.6	15.2	16.5				
NMMP-KU 0128	<i>A. sp. cf. A. birmanicum</i>									21.9	22.7*
NMMP-KU 0215	<i>A. sp. cf. A. birmanicum</i>	14.9	11.6								
NMMP-KU 0216	<i>A. sp. cf. A. crassum</i>									24.1	28.0
NMMP-KU 0275	<i>A. pangan</i>									38.3	45.0
NMMP-KU 0284	<i>A. sp. cf. A. birmanicum</i>									23.3	25.3
NMMP-KU 0325	<i>A. tenuis</i>					10.5	10.7				
NMMP-KU 0328	<i>A. pangan</i>									35.6	37.0
NMMP-KU 0329	<i>A. pangan</i>							27.7	31.6	36.2	41.8
NMMP-KU 0379	<i>A. tenuis</i>									13.7	15.3
NMMP-KU 0380	<i>A. tenuis</i>					8.5	9.7				
NMMP-KU 0385	<i>A. tenuis</i>					8.4	9.8				
NMMP-KU 0387	<i>A. tenuis</i>					9.5	10.0				
NMMP-KU 0388	<i>A. tenuis</i>					10.0	10.0				
NMMP-KU 0389	<i>A. tenuis</i>					10.5	10.7				
NMMP-KU 0401	<i>A. sp. cf. A. birmanicum</i>									22.8	25.8
NMMP-KU 0403	<i>A. sp. cf. A. crassum</i>									29.1	30.9
NMMP-KU 0404	<i>A. sp. cf. A. pangan</i>									34.2	36.4
NMMP-KU 0407	<i>A. sp. cf. A. pangan</i>									34.1	36.5
NMMP-KU 0408	<i>A. pangan</i>							28.1	30.0		
NMMP-KU 0409	<i>A. sp. cf. A. crassum</i>									27.4	32.9
NMMP-KU 0410	<i>A. sp. cf. A. crassum</i>							20.2	25.1*	24.0	29.6
NMMP-KU 0411	<i>A. sp. cf. A. crassum</i>									29.8	31.7
NMMP-KU 0412	<i>A. pangan</i>									35.3	38.9
NMMP-KU 0413	<i>A. crassum</i>			12.6	15.7	16.8	17.7	21.0	23.6		
NMMP-KU 0414	<i>A. sp. cf. A. crassum</i>					17.4	19.1	25.7	28.0		
NMMP-KU 0452	<i>A. sp. cf. A. crassum</i>									27.9	33.0
NMMP-KU 0453	<i>A. birmanicum</i>									19.2	22.1
NMMP-KU 0454	<i>A. birmanicum</i>									19.6	21.8
NMMP-KU 0455	<i>A. tenuis</i>	9.3	7.0	6.7	8.5						
NMMP-KU 0459	<i>A. sp. cf. A. crassum</i>									25.6	29.9
NMMP-KU 0463	<i>A. sp. cf. A. birmanicum</i>									22.3	24.5*
NMMP-KU 0476	<i>A. sp. cf. A. pangan</i>			15.4	18.4						
NMMP-KU 0480	<i>A. pangan</i>			17.3	21*						
NMMP-KU 0500	<i>A. birmanicum</i>	12.2	9.7	10.1	13.1						
AMNH 20011	<i>A. crassum</i>	16.5*	11.3	11.3	14.5	16.0	17.3	20.0	23.3	23.7	24.8
AMNH 20015	<i>A. birmanicum</i>									20.0	23.3
AMNH 20017 (right)	<i>A. tenuis</i>					8.4	10.0	12.0	13.5	14.7	16.3
AMNH 20017 (left)	<i>A. tenuis</i>	10.8	7.6	8.2*	9.6	8.8	10.2	11.9	13.5	14.9	16.1
AMNH 20024	<i>A. crassum</i>							20.0*	22.5*	24.0*	25.5
AMNH 20027	<i>A. crassum</i>			12.5*	17.6	16.0	18.9	19.9	24.9	26.3	28.4
AMNH 32525	<i>A. crassum</i>			13.0	16.2	17.3*	18.9				
AMNH 32526	<i>A. pangan</i>							[24]	[29]	32.3	36.5

Specimen number	Taxa	P3/ L	P3/ W	P4/ L	P4/ W	M1/ L	M1/ W	M2/ L	M2/ W	M3/ L	M3/ W
GSI B603	<i>A. crassum</i>									21.2	25.4
GSI B604	<i>A. crassum</i>	15.6	11.2								
GSI B608	<i>A. pangan</i>	24.6	20.4								
GSI B609	<i>A. pangan</i>									32.8	34.8
GSI B610	<i>A. pangan</i>							26.3	30.3		
GSI B611	<i>A. crassum</i>			14.4	18.8						
GSI B615	<i>A. crassum</i> (type)							21.7	25.1	27.6	31.2
GSI B616	<i>A. pangan</i>			15.9	19.9						
GSI B618	<i>A. pangan</i>	24.2	19.3								
GSI B619	<i>A. pangan</i> (type)							27.1	30.0*	34.0	36.4
GSI B621	<i>A. birmanicum</i> (type)	14.6	9.6	9.3*	11.8	13.0*	14.0*	15.0	16.8	16.7	19.0
GSI B622	<i>A. tenuis</i>							12.1	12.9	14.6	15.6
GSI B625	<i>A. tenuis</i> (type)					9.7	9.5				
GSI B748	<i>A. pangan</i>	21.5*	21.2*	16.2	22.3						
GSI B750	<i>A. pangan</i>							[28.1]	[30.8]	36.4	38.4
GSI B752	<i>A. pangan</i>									33.4	39.8
GSI B756 (right)	<i>A. tenuis</i>	11.6	7.2	8.9	10.4	8.5	10.7	11.9	13.5	15.6	17.0
GSI B756 (left)	<i>A. tenuis</i>			9.2	10.4	8.9	10.7	12.3	13.5		
GSI B763	<i>A. crassum</i>									27.6*	30.0*

Lower dentition

Specimen number	Taxa	P/3 L	P/3 W	P/4 L	P/4 W	M/1 L	M/1 W	M/2 L	M/2 W	M/3 L	M/3 W
NMMP-KU 0052	<i>A. tenuis</i>			10.6	5.1	9.1	5.8	12.0	7.3	19.0	8.3
NMMP-KU 0062	<i>A. sp. cf. A. crassum</i>							27.1	19.8		
NMMP-KU 0063	<i>A. tenuis</i>					9.1	5.9				
NMMP-KU 0077	<i>A. sp. cf. A. crassum</i>									43.1	23.5
NMMP-KU 0079	<i>A. sp. cf. A. birmanicum</i>	16.2	7.0								
NMMP-KU 0086	<i>A. sp. cf. A. crassum</i>			15.5	8.2						
NMMP-KU 0087	<i>A. sp. cf. A. crassum</i>									38.8*	22.3
NMMP-KU 0093	<i>A. tenuis</i>									18.2	8.7
NMMP-KU 0107	<i>A. tenuis</i>	11.5	5.0								
NMMP-KU 0113	<i>A. tenuis</i>			10.5	5.3						
NMMP-KU 0116	<i>A. sp. cf. A. birmanicum</i>			14.8	7.8			18.2*	12.9		
NMMP-KU 0125	<i>A. birmanicum</i>	15.5	5.7	13.5	7.4			17.9	12.6		
NMMP-KU 0263	<i>A. tenuis</i>									20.1	10.1
NMMP-KU 0267	<i>A. tenuis</i>					9.2	5.9	11.2	7.3		
NMMP-KU 0274	<i>A. crassum</i>	19.9	9.7	18.5	11.5	17.7*	12.5*				
NMMP-KU 0306	<i>A. sp. cf. A. pangan</i>	22.8	9.6								
NMMP-KU 0307	<i>A. sp. cf. A. pangan</i>			18.3	11.3						
NMMP-KU 0330	<i>A. crassum</i>							24.3	18.2	39.2	21.5
NMMP-KU 0331	<i>A. crassum</i>							24.4	17.3		
NMMP-KU 0332	<i>A. birmanicum</i>									28.2	14.5
NMMP-KU 0399	<i>A. tenuis</i>									19.3	8.2
NMMP-KU 0415	<i>A. sp. cf. A. crassum</i>									42.4	23.8
NMMP-KU 0417	<i>A. sp. cf. A. crassum</i>									40*	21.7
NMMP-KU 0418	<i>A. pangan</i>							31.2	26.3		
NMMP-KU 0421	<i>A. crassum</i>					17.3	11.9				
NMMP-KU 0422	<i>A. tenuis</i>							11.7	8.2	20.0*	10.4
NMMP-KU 0423	<i>A. tenuis</i>									18.3	9.0
NMMP-KU 0424	<i>A. crassum</i>									38.5	19.9
NMMP-KU 0426	<i>A. crassum</i>							23.3*	18.2*	39.5*	21.0*
NMMP-KU 0427	<i>A. sp. cf. A. crassum</i>									41.6	22.4
NMMP-KU 0429	<i>A. crassum</i>							24.3	16.3	37.7	20.0
NMMP-KU 0430	<i>A. birmanicum</i>	16.5	6.6	14.3	7.8						
NMMP-KU 0432	<i>A. sp. cf. A. crassum</i>			15.7	8.2						
NMMP-KU 0433	<i>A. pangan</i>			19.9	11.3						

Specimen number	Taxa	P/3	P/3	P/4	P/4	M/1	M/1	M/2	M/2	M/3	M/3
		L	W	L	W	L	W	L	W	L	W
NMMP-KU 0434	<i>A. pangan</i>			17.7	12.6						
NMMP-KU 0435	<i>A. crassum</i>			16.8	9.1						
NMMP-KU 0457	<i>A. crassum</i>									38.4	19.0
NMMP-KU 0458	<i>A. tenuis</i>					9.9*	6.3	13.4	8.7		
NMMP-KU 0465	<i>A. tenuis</i>									22.6	11.2
NMMP-KU 0466	<i>A. tenuis</i>							12.2	7.7		
NMMP-KU 0468	<i>A. crassum</i>					18.4	12.5				
NMMP-KU 0470	<i>A. tenuis</i>							11.3	7.3	20.5	9.4
NMMP-KU 0478	<i>A. birmanicum</i>					10.3	6.4	12.9	8.3		
NMMP-KU 0505	<i>A. sp. cf. A. crassum</i>			15.8	8.6						
AMNH 20006	<i>A. pangan</i>									49.5*	27.0
AMNH 20011 (right)	<i>A. crassum</i>	16.7	7.2	16.5	9.2	16.8*	12.2	20.5	15.4	31.9	17.3
AMNH 20011 (left)	<i>A. crassum</i>									32.4	17.3
AMNH 20015 (right)	<i>A. birmanicum</i>									29.0*	14.9
AMNH 20015 (left)	<i>A. birmanicum</i>									28.4	15.0
AMNH 20017 (right)	<i>A. tenuis</i>	10.5*	4.9	10.2*	5.5	8.4	6.1	11.4*	7.7	20.0	9.0
AMNH 20017 (left)	<i>A. tenuis</i>	10.6	4.8	10.0	5.5	8.6	6.0	11.4	7.6	19.7	9.3
AMNH 20028	<i>A. crassum</i>	18.6	8.2	17.2	9.8						
AMNH 20029	<i>A. crassum</i>									37.9	19.9
AMNH 32522	<i>A. crassum</i>					18.7	13.2	23.5*	15.5*		
GSI B605	<i>A. birmanicum</i>	[14.9]	[5.8]	14.3	7.7	14.0	9.5	18.0	13.4	29.7	16.0
GSI B607	<i>A. pangan</i>									52.7	29.7
GSI B612	<i>A. crassum</i>					[10.8]	[16.7]	[11.8]	[23.7]	[17.4]	
GSI B613	<i>A. crassum</i>									38.2	20.5
GSI B614	<i>A. crassum</i>	21.3	9.8								
GSI B617	<i>A. pangan</i>			19.3	12.4	19.5*	16.5*	26.1	21.9	36.7	22.2
GSI B620	<i>A. pangan</i>									47.7	24.5
GSI B626	<i>A. tenuis</i>					9.2	6.0				
GSI B627	<i>A. tenuis</i>							11.7	7.4	18.0	8.7
GSI B745	<i>A. pangan</i>	24.1	12.7	21.7	14.1	21.5*	15.0*	30.8	21.9		
GSI B751	<i>A. crassum</i>	19.8	9.9	19.7	11.3	16.8	12.9	23.9	18.8	39.2	21.8
GSI B755	<i>A. tenuis</i>	[11.7]	[4.3]	11.3	5.6	9.3	6.4	11.6	8.1	21.0	9.4
GSI B760	<i>A. tenuis</i>					[9.1]	[5.2]				
GSI B761	<i>A. tenuis</i>	11.9	3.9								
GSI B767	<i>A. birmanicum</i>			12.9	7.0	12.9	9.9	15.5	11.8		

SHORT NOTES

Permian orthoconic cephalopods of the Ochiai Formation in the Southern Kitakami Mountains, Northeast Japan

SHUJI NIKO¹ AND MASAYUKI EHIRO²

¹Department of Environmental Studies, Faculty of Integrated Arts and Sciences, Hiroshima University, Higashihiroshima, 739–8521, Japan (e-mail: niko@hiroshima-u.ac.jp)

²The Tohoku University Museum, Tohoku University, Sendai, 980–8578, Japan (e-mail: ehiro@mail.cc.tohoku.ac.jp)

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Introduction and geologic setting

Middle to Upper Permian strata in the Southern Kitakami Mountains, Northeast Japan, contain a relatively diverse orthoconic cephalopod assemblage. Although they were the subject of investigations by Hayasaka (1924), Shimizu and Obata (1936), Ouchi (1971) and Koizumi (1975), information from the Southern Kitakami Mountains has been ignored in modern cephalopod taxonomy owing to a lack of adequate illustrations and descriptions. Knowledge of Middle to Late Permian orthoconic cephalopods is very limited and comes mainly from the Peri-Gondwana region that includes Iran (e.g., Teichert and Kummel, 1973), Oman (Niko *et al.*, 1996), the Salt Range (Waagen, 1879), Timor (Haniel, 1915), and the South China region (e.g., Zhao *et al.*, 1978). Revision of the Kitakami fauna, therefore, may be of phylogenetic and paleobiogeographic importance. In view of this, the present study focuses on orthocerid species from the Kamiyasse area, Miyagi Prefecture, and an adjoining area to the north in Iwate Prefecture (Figure 1). The repository for these specimens is the University Museum of the University of Tokyo (UMUT).

In an earlier geologic study, Tazawa (1973) investigated the Kamiyasse area, and elucidated the detailed lithostratigraphy of the Permian deposits as the Sakamotozawa, Kanokura and Toyoma series. With the exception of the lowest, carbonate-rich strata assigned to the Nakadaira Formation, most of these series were synthesized and assigned in the subsequent works of Ehiro (1974, 1977) to the Ochiai Formation (Onuki, 1969), from which the present cephalopod specimens were collected. The Ochiai Formation is divisible into three members: the Toyazawa

Member (Ehiro, 1977), consisting of sandstone interbedded with calcareous shale and impure limestone layers, represents the middle part of the formation, whereas the unnamed lower and upper members are mainly massive shale with minor amounts of conglomerate, sandstone and limestone.

Systematic paleontology

Order Orthocerida Kuhn, 1940
Superfamily Orthoceratoidea M'Coy, 1844
Family Brachycycloceratidae Furnish, Glenister
and Hansman, 1962
Genus *Brachycycloceras* Miller,
Dunbar and Condra, 1933

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

Brachycycloceras sp.

Figure 2.1, 2.2

Description.—Single, deformed orthocone, 56 mm in length, consisting of annulated, apical phragmocone with gently curved (exogastric?) apical shell; shell expansion rapid for orthoceratids. Prominent annulations form rounded to bluntly pointed crests and deep interspaces that appear as rounded concavities in longitudinal profile; annulations quite oblique, slope toward dorsal (?) side. Except for weak dorsal (?) sinus, sutures run roughly parallel to annulations.

Discussion.—No siphuncular structure is preserved in this specimen. However, its rapidly expanded shell with

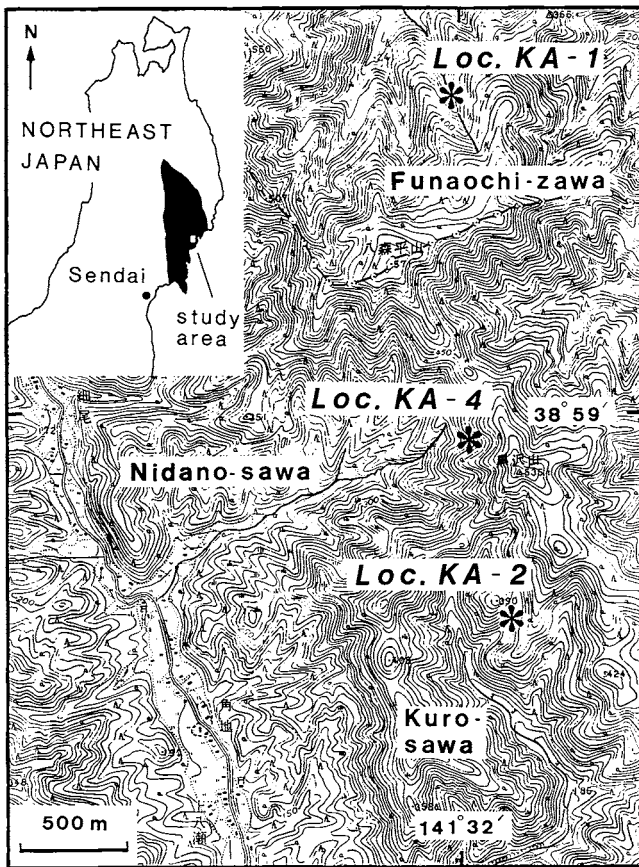


Figure 1. Index map of fossil localities in the Southern Kitakami Mountains (inset), using the 1:25,000 map of "Shishiori" published by the Geographical Survey Institution.

gently curved apical part and strongly prominent annulations warrant generic assignment to *Brachycycloceras*. In addition to *Brachycycloceras* sp. from the Early Permian of western Australia (Teichert, 1951) and *B. rustaqense* Niko, Pillecuit and Nishida, 1996, from the Wordian (Middle Permian in a three-fold division) of the central Oman Mountains, this discovery represents the third Permian occurrence of the genus.

Material examined and occurrence.—UMUT PM 28065. This specimen was recovered as float from shale in the Funaochi-zawa Valley at locality KA-1 (Figure 1). Judging from the lithofacies of the matrix, the geology around this locality, and the associated ammonoid fauna, it was probably derived from the middle-upper portion (Roadian-Wordian; Middle Permian) of the lower member of the Ochiai Formation.

Family Geisonoceratidae Zhuravleva, 1959
cf. Geisonoceratid, genus and species uncertain

Figure 2.4, 2.7

Discussion.—A deformed body chamber of an orthoconic shell, 115 mm in length, is available for this study. This specimen is tentatively considered to be a geisonoceratid, because of the characteristic ornamentation of its transverse ridges that indicates asymmetrical (steep side towards aperture) longitudinal profiles, and because of the absence of a shell constriction. Similar ornamentation is also known to occur in some Carboniferous bactritoids, such as *Ctenobactrites isogramma* (Meek, 1871; Sturgeon *et al.*, 1997, pl. 1-1, figs. 8-11, pl. 1-42, fig. 3) and *Bactrites peytonensis* Mapes (1979, pl. 8, figs. 7, 11), although characteristic dorsal carina and/or well-developed wrinkle-layer of ornamented bactritoids are not recognized in this specimen.

Material examined and occurrence.—UMUT PM 28066. This specimen was recovered as float in talus deposits of shale located on a tributary of the Kuro-sawa Valley (locality KA-2), where the upper member is exclusively distributed. Based on ammonoids collected near this locality, Ehro and Araki (1997) inferred a late Capitanian (Middle Permian) age for the cephalopod-bearing shale of the lower part of the upper member of the Ochiai Formation.

Superfamily Pseudorthoceratoidea Flower
and Caster, 1935

Family Pseudorthoceratidae Flower and Caster, 1935
Subfamily Spyroceratinae Shimizu and Obata, 1935
Genus *Lopingoceras* Shimanskiy in Ruzhentsev, 1962

Type species.—*Orthoceras lopingense* Stoyanow, 1909.

Other included species.—*Lopingoceras acutanolatum* Zhao, Liang and Zheng, 1978; *L. cf. acutanolatum* (this report); *L. bicinctum* (Abich, 1878); *L. cyclophorum* (Waagen, 1879); *L. guangdeense* Zhao, Liang and Zheng, 1978; *L. hayasakai* Niko and Ozawa, 1997; *L. margaritatum* (Abich, 1878); *L. maubesiense* (Haniel, 1915); *L. ? obliqueannulatum* (Waagen, 1879); *L. sp.* (Teichert *et al.*, 1973), and *L. sp.* (Zheng, 1984).

Range.—Known from the late Gzhelian (Late Carboniferous)-early Asselian (Early Permian) boundary through the Changhsingian (Late Permian).

Diagnosis.—Early juvenile shell gently curved, nonannulated with transverse surface lirae. See Shimanskiy in Ruzhentsev (1962, p. 90) for diagnosis of adult shell, which we accept.

Discussion.—The distinction between *Lopingoceras* and the Early Carboniferous genus *Cycloceras* (M'Coy, 1844; type and only reliably included species, *Orthoceras laevigatum* M'Coy, 1844, see Histon, 1991, and BZN 50, 1993, opinion 1720) has long been plagued by an inadequate description of the latter's type species. Except for differences in age range, the former differs from the latter only in the shape of annulations, i.e., *Cycloceras* having

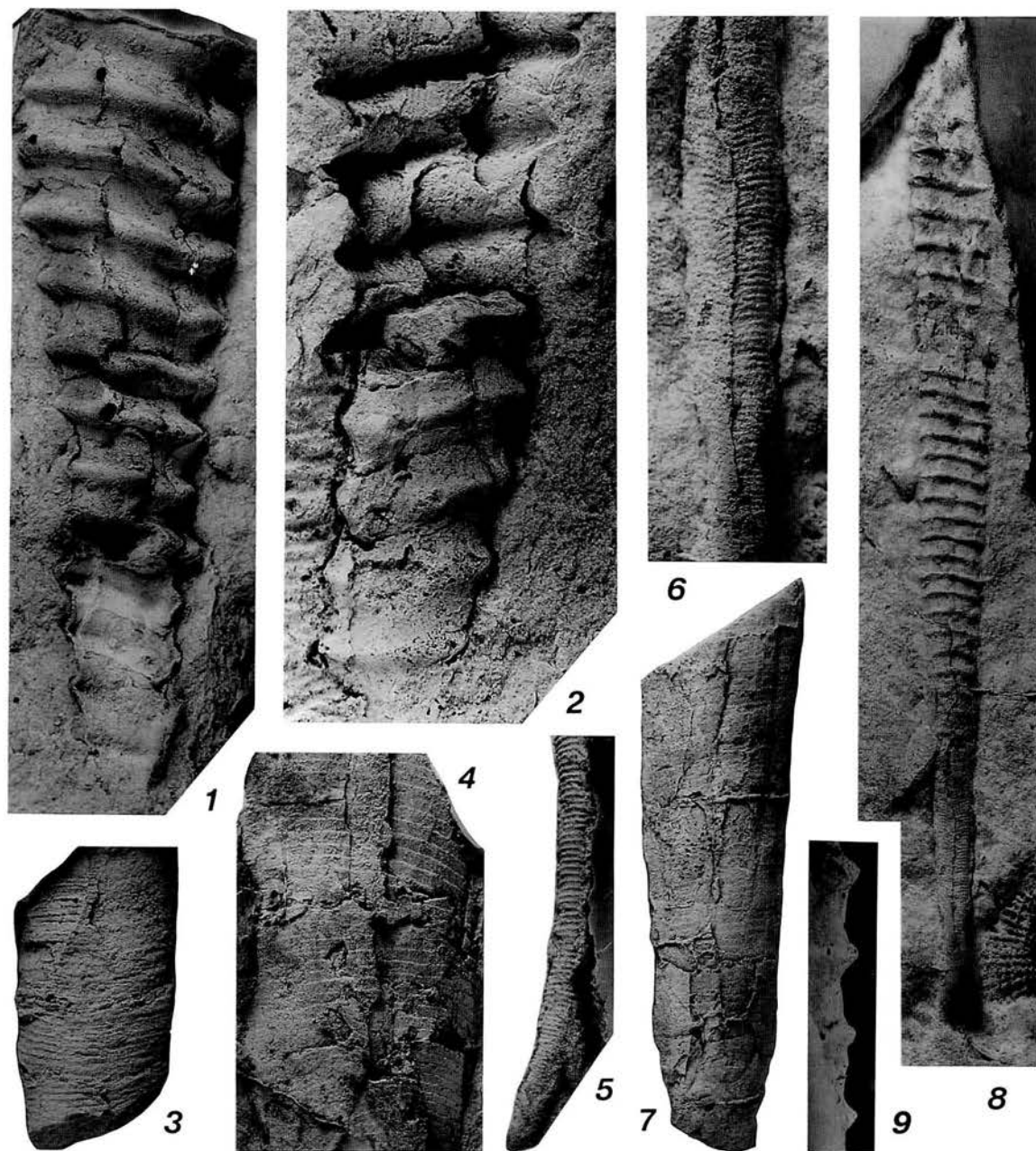


Figure 2. 1, 2. *Brachycycloceras* sp., UMUT PM 23065. 1, lateral view of silicone rubber cast, venter on left (?), $\times 2$; 2, external mold with steinkern of apical shell, note gently curved shell and sutures, venter on right (?), $\times 3$. 3. Orthocerid, superfamily, family, genus and species uncertain, UMUT PM 28068, side view, $\times 2$. 4, 7. Cf. geisonoceratid, genus and species uncertain, UMUT PM 28066. 4, details of surface ornamentation, silicone rubber cast, $\times 2$; 7, steinkern, side view, $\times 1$. 5, 6, 8, 9. *Lopingoceras* cf. *acutanolatum* Zhao, Liang and Zheng, 1978, UMUT PM 28067, silicone rubber cast. 5, details of early juvenile shell, $\times 4$; 6, details of ornamentation of nonannulated part, $\times 5$; 8, side view, $\times 2$; 9, details of annulations, note triangular longitudinal profiles, $\times 5$.

contiguous annulations with equally rounded crests and interspaces, whereas in *Lopingoceras* the annulations are more or less distant in spacing and have triangular profiles. Whether these external differences are of supraspecific

rank seems questionable in modern taxonomy. The Kitakami material described herein includes the first known example of an early juvenile shell of *Lopingoceras*, whose characters add to the generic concept. The taxonomic

problem will be solved when the apical shell morphology and internal structure of *Cycloceras laevigatum* are known well enough for comparison with the newly refined diagnosis of *Lopingoceras*.

Lopingoceras cf. *acutanolatum* Zhao,
Liang and Zheng, 1978

Figure 2.5, 2.6, 2.8, 2.9

Compare with.—

Lopingoceras acutanolatum Zhao, Liang and Zheng, 1978, p. 63, 64, pl. 31, figs. 11, 12, pl. 33, figs. 3, 4.

Description.—This species represented by a single external mold of gradually expanded shell, 65 mm in length, whose adoral part is strongly deformed, with no internal structure preserved; adoral end attains approximately 4 mm (reconstructed as circular cross section) in shell diameter. Nonannulated early juvenile shell gently curved, with circular cross section and transverse lirae; this nonannulated part, approximately 21.5 mm in length, followed by monotonously annulated shell where lirae disappear; embryonic shell may be cone-shaped; annulations may be roughly transverse with wide spacing for genus, with triangular longitudinal profiles and pointed crests; there are 1–2 annulations in corresponding reconstructed shell diameter; interspaces probably weakly depressed.

Discussion.—The annulation shape and spacing of the present specimen strongly resemble *Lopingoceras acutanolatum* from the Wuchiapingian (Late Permian) Laoshan Shale in South China. Nevertheless, since *L. acutanolatum* is described from fragmentary specimens and its apical shell morphology is unknown, the Kitakami specimen is only provisionally assigned to this species. Comparison between *Lopingoceras* cf. *acutanolatum* and figured specimens from the Ochiai Formation cited as *Lopingoceras* ? sp. by Koizumi (1975) is impossible. Judging from his illustrations (Koizumi, 1975, pl. 4, figs. 4, 5), the specimens are inadequate for systematic treatment because of poor preservation.

Material examined and occurrence.—UMUT PM 28067. This specimen was collected from a float block of shale in the riverbed of the Nidano-sawa Valley at locality KA-4. The exact stratigraphic horizon from which this block was derived is unknown, but it is highly likely that this block came from the middle part of the Toyazawa Member of the Ochiai Formation, based on its lithofacies and collected locality. Thus, this specimen is considered to be of Wordian (or Capitanian) age.

Superfamily, family, genus and species uncertain

Figure 2.3

Discussion.—A fragmentary specimen of a deformed orthoconic shell, 22 mm in length, shows transverse lirae that consist of alternating strongly prominent and less prominent ridges. Similar ornamentation occurs in several post-Carboniferous orthocerid genera; such as the orthoceratid *Trematoceras* (Eichwald, 1851), the geisonoceratid *Pseudotemperoceras* (Stschastlivtseva, 1986), and the pseudorthooceratid *Dolorthoceras* (Miller, 1931). No internal structures are preserved in the present specimen, so it cannot be identified even to the superfamily level.

Material examined and occurrence.—UMUT PM 28068. Same as the specimen above assigned to cf. geisonoceratid, genus and species uncertain.

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行事予定

◎第152回例会は、2003年1月24日（金）～26日（日）に横浜国立大学教育人間科学部にて開催します。1月24日（金）にシンポジウムとして「白亜紀海洋無酸素事件の解明：世話人 平野弘道・北里 洋・西 弘嗣」が、また1月25日（土）にシンポジウム「中・古生代微化石研究の現状と将来－テレーン解析後の使命－：世話人 指田勝男」が開催されます。なお、講演の申し込み締め切りは、2002年11月29日（金）です。講演申し込みの予稿集原稿送付の際には発表で使用する機器（液晶プロジェクター、OHP、スライドなど）の希望について明記して下さい。

◎2003年年会総会は、2003年6月27日（金）～29日（日）に静岡大学理学部で開催の予定です。シンポジウム「生物多様性を古生物学から考える：世話人 塚越 哲・北村晃寿・生形貴男」を開催予定です。講演の申し込み締め切りは2003年5月2日（金）の予定です。このほか、夜間小集会などの希望予定がありましたら、2002年12月初旬までに行事係までお知らせ下さい。

個人講演・シンポジウム案の申し込み方法

個人講演の申し込みは予稿原稿を下記まで直接お送り下さい。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。また行事全般に関するお問い合わせも行事係か行事係幹事までお寄せください。

〒305-8571 つくば市天王台 1-1-1
筑波大学地球科学系（古生物学会行事係）
小笠原 憲四郎
Tel: 0298-53-4302（直通） Fax: 0298-51-9764
E-mail: ogasawar@arsia.geo.tsukuba.ac.jp

本山 功（行事係幹事）
〒305-8571 つくば市天王台 1-1-1
筑波大学地球科学系
Tel: 0298-53-4212（居室） or 53-4465（実験室） Fax: 0298-51-9764
E-mail: isaomoto@sakura.cc.tsukuba.ac.jp

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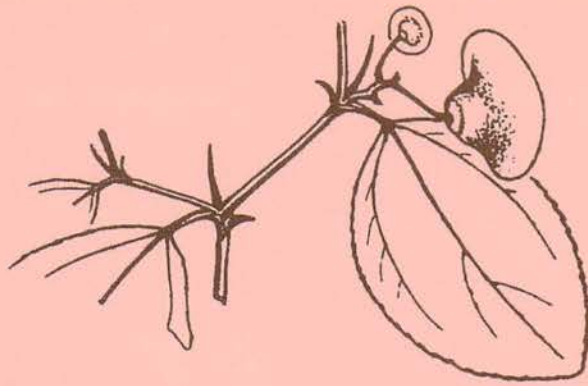
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電話 03-5814-5801
編集者 棚部一成・加瀬友喜
編集幹事 遠藤一佳・重田康成・佐々木猛智
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