Paleontological Research
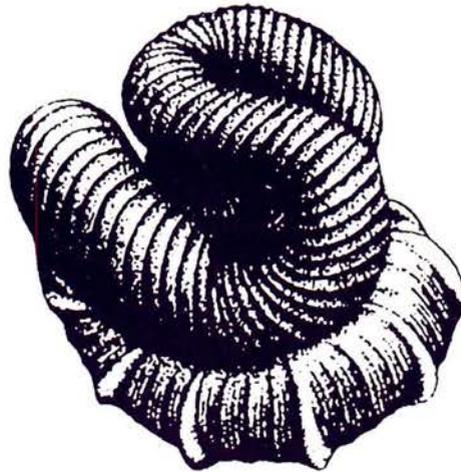
Formerly
Transactions and Proceedings
of the
Palaeontological Society of Japan

Vol. 5 No.3
September 2001

The Palaeontological Society of Japan

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

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

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

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

All communication relating to this journal should be addressed to the

PALAEONTOLOGICAL SOCIETY OF JAPAN

c/o Business Center for Academic Societies,

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

Visit our society website at

http://ammo.kueps.kyoto-u.ac.jp/palaeont/

Ostracode biostratigraphy of the Lower Cretaceous Wakino Subgroup in northern Kyushu, Japan

KEIICHI HAYASHI

Faculty of Science and Engineering, Konan University, Kobe, 658-8501, Japan
(*e-mail: Kihayasi@center.konan-u.ac.jp*)

Abstract. Nonmarine ostracodes from the Lower Cretaceous Wakino Subgroup in northern Kyushu were studied biostratigraphically. Analysis of abundant fossil ostracodes has led to recognition of 11 assemblages and subassemblages. Vertical changes of these assemblages have made possible biostratigraphical zonation by ostracodes as follows: the *Darwinula* a. z. (assemblage zone), the transitional a. z. and the large Cypridacean a. z. in ascending order. Using this zonation, the formations of the Wakino Subgroup in the eastern area are correlated with those in the western type area.

Key words: Biostratigraphy, Lower Cretaceous, Northern Kyushu, ostracodes, southwest Japan, Wakino Subgroup

Introduction

The correlation of Lower Cretaceous nonmarine sediments is controversial in Eastern Asia, because their relations with marine sediments are known only in restricted regions (Matsukawa and Obata, 1992, 1994). The same is true in Japan. Molluscan fossils have been traditionally used in the correlation of Cretaceous strata of Japan by many investigators (Kobayashi and Suzuki, 1936; Ota, 1960; Hase, 1960; etc.). This approach is not reliable due to the fact that the same molluscan assemblages and characteristic species occur in several different horizons showing similar depositional environments (Matsukawa and Ito, 1995). Thus, other methods have recently been introduced for the correlation of Cretaceous nonmarine sediments; for examples by using other fossil groups such as fish (Yabumoto, 1994) and sedimentary facies suites (Sakai *et al.*, 1992; Seo *et al.*, 1992, 1994). One potential approach is to use the ostracode fossils that are abundantly found in Early Cretaceous nonmarine sediments. Cao (1996) described fossil ostracodes from the Cretaceous in Japan and compared them with those in China. However, her correlation is still insufficient because she discussed faunal assemblages based on the samples from restricted localities. For estimating the stratigraphical significance of each species and genus, a more detailed study of ostracode biostratigraphy is necessary. Recently, Hayashi (1998) reported 74 ostracode species belonging to 17 or more genera from Cretaceous nonmarine sediments. This study aims to establish a biozonation by using fossil ostracodes from the Lower Cretaceous Wakino Subgroup in North Kyushu and to propose a correlation scheme.

Geologic settings

Geologic settings of the study area were already reported in Hayashi (1998). Only the outlines of the geology are described here to the extent necessary for later description and discussion in this paper. Early Cretaceous nonmarine sediments are scattered in the Inner Zone of Southwest Japan. Especially in northern Kyushu and western Chugoku situated in the western areas of the Zone, they are assigned as the Kanmon Group (Matsumoto, 1951). The group is composed of the Wakino Subgroup in the lower part and the Shimonoseki Subgroup in the upper part. The Shimonoseki Subgroup overlies disconformably the Wakino Subgroup and oversteps the older basement in places.

In northern Kyushu, the group is distributed in two major areas (Figure 1). To the west of Nakama and Nogata cities, the upper part is generally observed sequecially from south to north, though it is discontinuously crop out into several isolated areas by some folding and faulting; to the east of Nakama and Nogata cities, obscure upper sequences are seen from south to north, but it is divided into many isolated blocks by much folding and faulting; hence the stratigraphic positioning of these delimited exposures is difficult.

Among many areas occupied by the Wakino Subgroup in Figure 1, three areas, i. e. Wakino, Yurino and southern Kokura areas, were selected for this study, because ostracode fossils have been known to occur only in these areas. As the Wakino and Yurino areas are relatively close to each other, those two are described together.

Figure 1. Geological map showing the distribution of the Kanmon Group in northern Kyushu (modified from Seo et al., 1992). A: Wakino area, B: Yurino area, C: southern Kokura area.

Area	Wakino area			Yurino area	Southern Kokura area		
Reference	Kobayashi & I. Ota (1936)	Ota (1953)	Hase (1958, 1960)	Ota (1960)	Hase (1958, 1960)	Ota (1955, 1957, 1960)	Ota et al (1979)
Subgroup / Wakino — Miyata shale	Upper Wakamiya Fm.	Upper Wakamiya Fm.			Equivalent of the Upper Wakamiya Fm.	Uppermost Fm. =W4	The Fourth Fm.
Kinsho sandstone	Lower Wakamiya Fm.	Lower Wakamiya Fm.	W3		Equivalent of the Lower Wakamiya Fm.	Upper Fm. =W3	The Third Fm.
Sengoku conglomerate	Nyoraida Fm.	Nyoraida Fm.	W2		Equivalent of the Nyoraida Fm.	Middle Fm. =W2	The Second Fm.
Wakino Fm.	Sengoku Fm.	Sengoku Fm.	W1		Equivalent of the Sengoku Fm.	Lower Fm. =W1	The First Fm.

Figure 2. Comparison of stratigraphy of the Wakino Subgroup by previous studies.

Wakino-Yurino area

In North Kyushu, the stratigraphical study of Mesozoic nonmarine strata was started by Kobayashi and Ota (1936) (Figure 2). They divided nonmarine strata of the Wakino area into the Wakino Formation and the unconformably overlying Sengoku conglomerate, Kinsho sandstone and Miyata shale in ascending order. Ota (1953), later, proposed the present stratigraphy consisting of the Sengoku, Nyoraida, Lower Wakamiya and Upper Wakamiya Formations in ascending order. This division in the Wakino area was supported by Hase (1958, 1960), and has been the standard stratigraphy of the Wakino Subgroup in northern Kyushu and western Chugoku.

The Wakino area, the type area of the Wakino Subgroup, is situated in the southernmost part of the areas occupied by the Kanmon Group (Figure 1). Successions ranging from the Sengoku to Nyoraida Formations are observed from south to north (Figure 3). The Sengoku Formation begins with the basal conglomerate that clinounconformably overlies the Sangun Metamorphic rocks (Figure 1). The basal facies are interpreted as a deposit dominated by debris flows by Okada et al. (1991). The middle and upper parts of the formation are made up of laminated or massive black mudstone, massive sandstone and pebble conglomerate, with intercalations of acidic tuff. They are considered to be a mixture of shallow-water, deltaic and lacustrine deposits. The Nyoraida Formation consists of rhythmic argillite intercalated with sandstone and granule to pebble conglomerate. These sediments are tuffaceous, and many of them show graded bedding. The argillite sediments are considered to have been deposited in deep-water lacustrine environments. The coarse-grained sediments are referred to as turbidite or

debris flow deposits (Seo et al.,1992).

The Yurino area is situated 7 km northeast of the Wakino area. The geology of the area was mainly studied by Hase (1958, 1960). He considered that the equivalents of the Sengoku, Nyoraida and Lower Wakamiya Formations are distributed northeastward. These formations were assigned to W1, W2 and W3 formations respectively by Ota (1960). The lowermost strata in the Yurino area are, however, regarded as the Nyoraida Formation by Hayashi (1998). An upper sequence which is not found in the Wakino area is distributed in the Yurino area (Figure 4). The Lower Wakamiya Formation is composed of laminated or massive black mudstone intercalated with poorly sorted reddish sandstone and conglomerate. The Lower and Upper Wakamiya Formations are lithologically somewhat similar to each other. The former is, however, more frequently intercalated with discontinuous layers of pebble conglomerate. The Lower Wakamiya Formation shows various sedimentary structures and yields fossils indicative of very shallow water and desicated terrestrial environments at some horizons. The occurrence of estherids indicates that the formation was deposited in very shallow water (Kusumi, 1979). The Upper Wakamiya Formation is composed of laminated or massive black mudstone intercalated with acidic tuff, sandstone and conglomerate. The formation shows various sedimentary structures and contains fossils indicative of shallow-water environments. The abundance of ostracodes indicates that the formation was deposited in a shallow-water environment.

Southern Kokura area

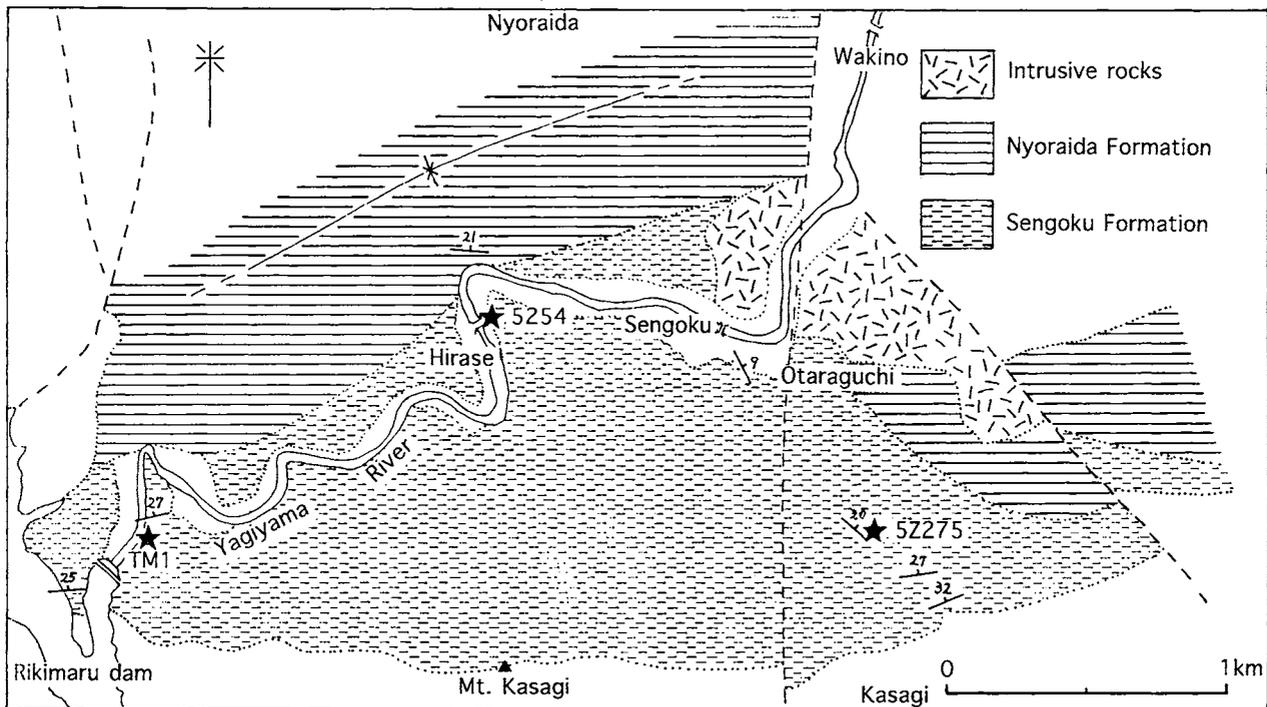Previous stratigraphical studies in this area were reviewed

Figure 3. Geological sketch map and sampling localities of the Wakino Subgroup in the Wakino area (after Hayashi, 1998).
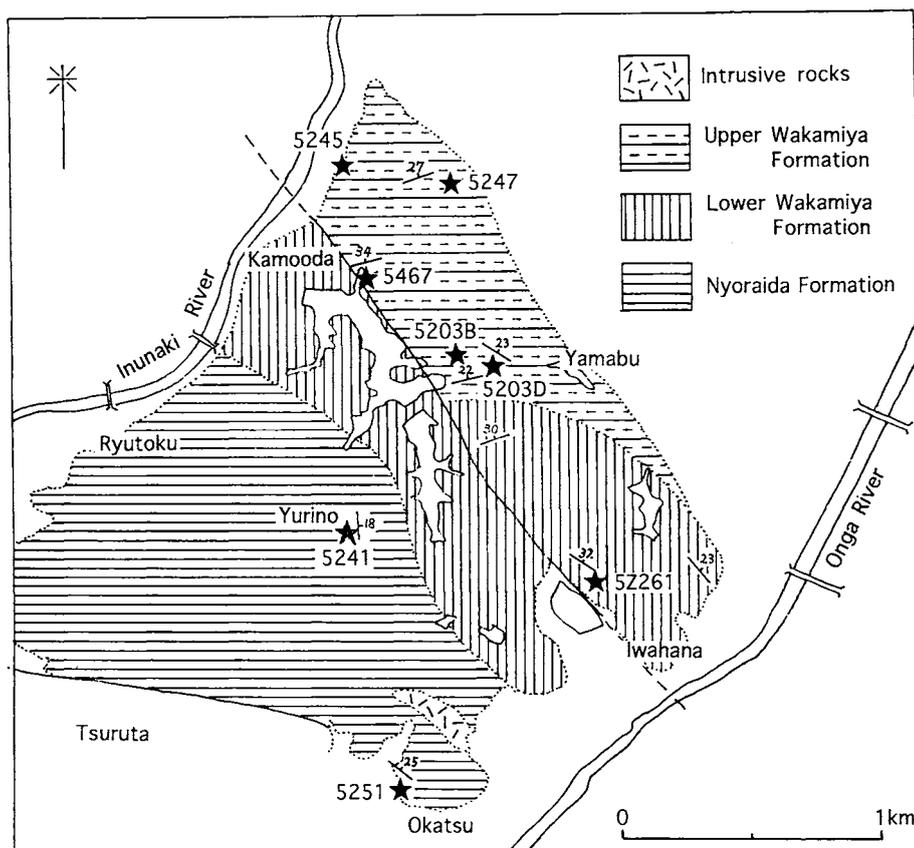
Figure 4. Geological sketch map and sampling localities of the Wakino Subgroup in the Yurino area (after Hayashi, 1998).

by Hayashi (1998). Ota (1955) revealed that the Wakino Subgroup of the southernmost area (Dobaru district) is composed of Lower, Middle and Upper formations in ascending order (Figure 2). Ota (1957) later added the Uppermost Formation to these three formations based on studies in the northern areas. Ota (1960) correlated these formations with the formations of other areas in the northern Kyushu and western Chugoku regions, and named them W1, W2, W3 and W4 formations. This division in the southern Kokura area was supported by Hase (1958, 1960), though he called them the equivalents of the Sengoku, Nyoraida, Lower Wakamiya and Upper Wakamiya formations, respectively. On the other hand, Ota et al. (1979) adopted the First, Second, Third and Fourth formations as the names of these formations, according to Matsushita (1968). This idiosyncratic nomenclature is presumably due to difficulties in lithological correlation over a wide area. The main reason for such variability of the stratigraphical units is that the lithology of the Wakino Subgroup is changeable laterally except for that of the Nyoraida Formation. In this paper, following Matsumoto (1962), the W1, W2, W3 and W4 formations of Ota (1960) are adopted for the subdivisions in the southern Kokura area.

The southern Kokura area is subdivided into several districts. In the southernmost part of the southern Kokura area, Dobaru district, W1 and W2 formations are distributed with a northward dip of the strata (Figures 5, 8). In other

districts, however, the strata of the Wakino Subgroup are there in many faulted blocks and have suffered deformation by folding on various scales. Hence, the stratigraphical position of many blocks remains undetermined, though all of them are assigned to formations by previous studies (Ota, 1955, 1957, 1960; Hase,1958; Ota et al., 1979). In this study, the stratigraphical positions of five blocks, the Dobaru, Gamo, Washimine, East Kumagai and West Kumagai blocks, are reexamined and determined by using the ostracode zonation. With respect to the geological structure, this paper follows Hayashi (1998), who adopted the interpretations of Ota (1957) and Sakai et al. (1992) (Figure 5).

Method of study

All the forms of ostracode fossils in this paper were already described briefly by Hayashi (1998). Systematic descriptions and discussions on each species should be looked for there.

In this paper, first, ostracodes from each locality are referred to as assemblages based on dominant, subdominant, common and characteristic species and genus and on species association. However, the exact recognition of assemblages is difficult due to the small numbers of specimens, and some assemblages are gathered to establish one "assemblage zone" based on the similarity of their general
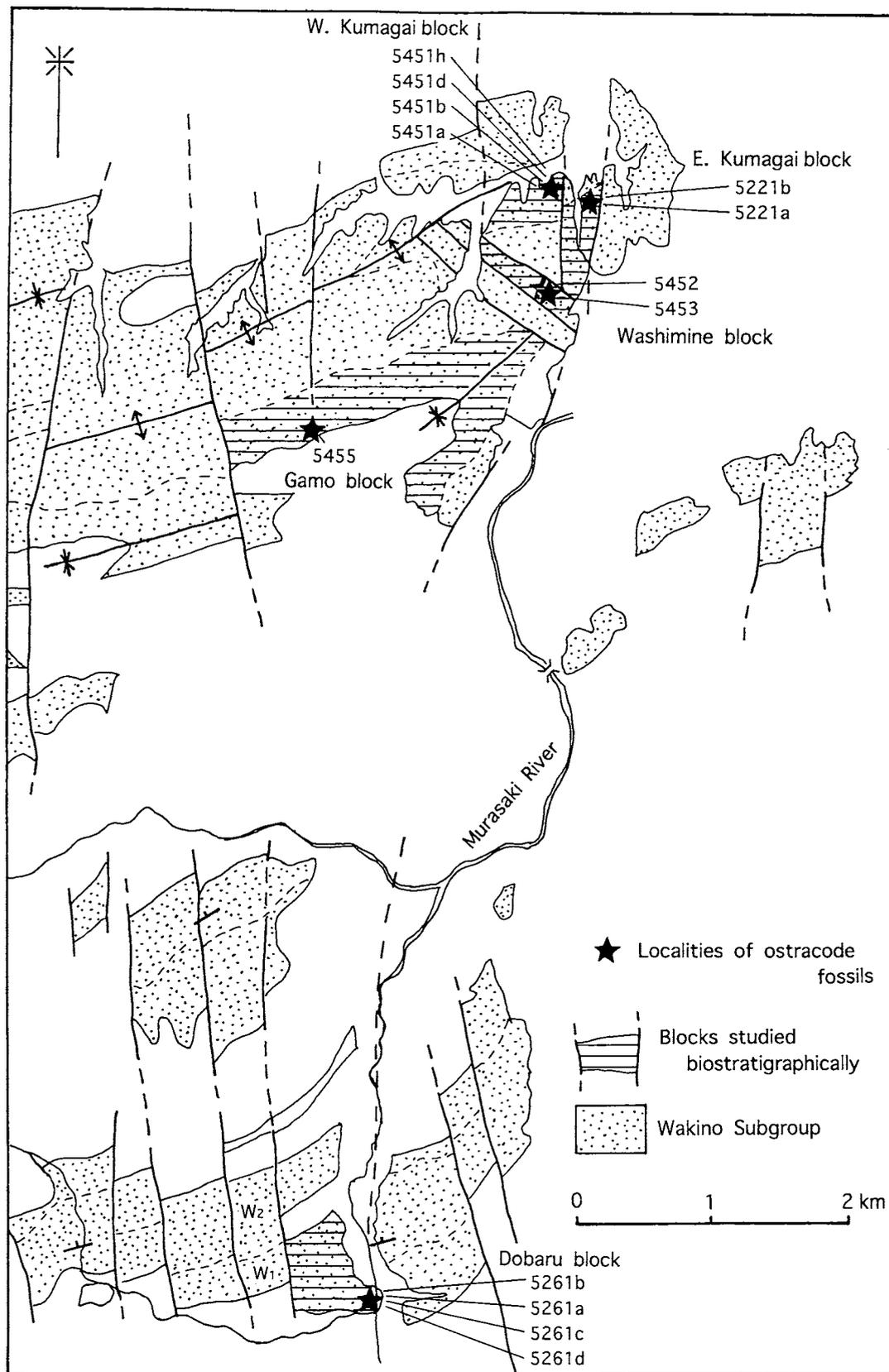
Figure 5. Geological sketch map and sampling localities of the Wakino Subgroup in the southern Kokura area (modified from Hayashi, 1998).

features. The reasoning of this method is that the fairly large variation in the ostracode faunas was presumably caused by a transportation mechanism of ostracode eggs in the Early Cretaceous which was different from that in the Recent. Krömmelbein (1962) pointed out that living non-marine ostracodes are occasionally transported a long distance by birds in mud sticking to feet and feathers.

With this method, an ostracode zonation has been successfully established in the Wakino Subgroup of the Wakino-Yurino area, northern Kyushu. Paleoenvironments of the ostracode assemblages are also discussed on the basis of other fossils and sedimentary structures.

Based on the ostracode zonation, the Wakino Subgroup in several blocks of the southern Kokura area is correlated to the level of formation with the Wakino Subgroup in the Wakino-Yurino area.

Analysis of fossil ostracode assemblages

Occurrence

Ostracodes occur in the Sengoku, Nyoraida, Lower Wakamiya and Upper Wakamiya Formations in the Wakino-Yurino area, where 11 localities lie. In the southern Kokura area, ostracodes are found at 13 localities in five blocks, each of which consists of one or two units of those W1 to W4 formations distinguished by Ota (1960). These localities are shown in Figures 3-5, and their stratigraphic positions are shown in Figure 8.

Ostracode fossils occur almost always in mudstone or sandy mudstone. The mudstone of the Sengoku (W1) Formation, which is variable in lithology, contains poorly preserved fossil ostracodes at many horizons. The mudstone of the Nyoraida (W2) Formation, however, scarcely yields fossil ostracodes. The scarcity is explained by the fact that the mudstone is interbedded with graded sandstone of turbidite origin. The mudstone of the Lower Wakamiya (W3) Formation, which is intercalated with poorly sorted discontinuous sandstone layers, also yields few ostracodes in the Wakino-Yurino area, but does so abundantly in the southern Kokura area. Such a regional scarcity is presumably due to the dominance of terrestrial fluvial plain environments. In contrast, the mudstone of the Upper Wakamiya (W4) Formation, which is thinly well-stratified and intercalated with sorted sandstone layers from horizon to horizon, contains abundant and varied fossil ostracodes. This may be related to widespread shallow-water environments during deposition of the formation.

Ostracode assemblages

Twelve ostracode assemblages have been identified in the Wakino Subgroup in the study area: five in the Wakino-Yurino area and seven in the southern Kokura area. Each of the ostracode assemblages is described below.

Wakino-Yurino area

One ostracode assemblage has been identified from the Sengoku Formation in the Wakino area, and five assemblages from the Nyoraida, Lower Wakamiya and Upper Wakamiya Formations in the Yurino area (Figures 6, 8).

1. *Darwinula* assemblage

In the Sengoku Formation of the Wakino area and the Nyoraida Formation of the Yurino area, the ostracode assemblages at all the localities are commonly characterized by the abundant occurrence of species belonging to the genus *Darwinula*. This assemblage, named the *Darwinula* assemblage, is variable in generic composition. In the lower Sengoku and upper Nyoraida Formations, it contains the genus *Damonella* which is here represented by a single species, *D.* cf. *obata*. The species is especially abundant in the lower Sengoku Formation. The genus *Clinocypris*, comprising one or two species, is present in the assemblage at some localities. *Damonella* and *Clinocypris* are characteristic genera of the *Darwinula* assemblage, but they are not always common at all the localities. The genus *Cypricercus*, represented by a single species, seems to be another characteristic genus, but it is obtained from only one locality. It is noticeable that the assemblage is characterized by the entire absence of the genus *Cypridea*, which is a dominant or common genus in all the other assemblages.

The dominant genus *Darwinula* comprises different species at different localities. For example, this component is composed exclusively of *D. incruva* at Locs. TM1 and 5251, and *D. submuricata* in Loc. 5254, and *D.* cf. *giganimpudica*, *D. postitruncata* and *D.* sp.1 at Loc. 5Z275, and consists of *D.* cf. *oblonga* and other new species at Loc. 5241. The subordinate genus *Clinocypris* also comprises different species at different localities. Namely, it is represented by *C. obliquetruncata* at Loc. TM1, and *C.*? sp. 2 and *C.*? sp. 4 at Loc. 5251. *Damonella* cf. *obatai* occurs closely together in abundance, especially forming "ostracode layers" in the black mudstone at Loc. 5Z275.

2. *Cypridea*? cf. *renalata* subassemblage

At Loc. 5Z261, where is exposed the middle part of the Lower Wakamiya Formation, only one assemblage from that formation is defined. In this paper, an assemblage which is found at only one locality is dealt with as a subassemblage (written as S.A.), because it may represent only one part of the indicated assemblage. The subassemblage is taxonomically monotonous with a small number of individuals. The dominant species is small-sized *Cypridea*? cf. *renalata*, which is also characteristic of the subassemblage. It makes up about 70% or more of the total ostracode speciemens of the subassemblage, in spite of sporadical occurrence. The subordinate species are *Cypridea* sp. 4, *Mongolianella* cf. *zerussata longiuscula*, *M.* aff. *zerussata longiuscula* and *Rhinocypris*? cf. *jurassica*, all of which are small in size and rare.

3. *Mongolianella-Cypridea* assemblage

This assemblage is recognized in the lower and upper parts of the Upper Wakamiya Formation.

At Locs. 5203D and 5203B of the Yurino area in the lower part of the Upper Wakamiya Formation, the ostracode assemblage is characterized by many species of *Mongolianella* and *Cypridea*. Among them, *Mongolianella zerussata longiuscula*, *M.* cf. *palmosa*, *M.* sp. 1, *Cypridea tera*, *C.* (*C.*) cf. *delnovi* and *C.* (*Cyamocypris*) sp.1 possess a large-sized carapace, and are not found in the underlying formations (Figure 9). Medium-sized *Cypridea* such as *C. kyushuensis* and *C.* (*Pseudocypridina*) aff. *jianchangensis*

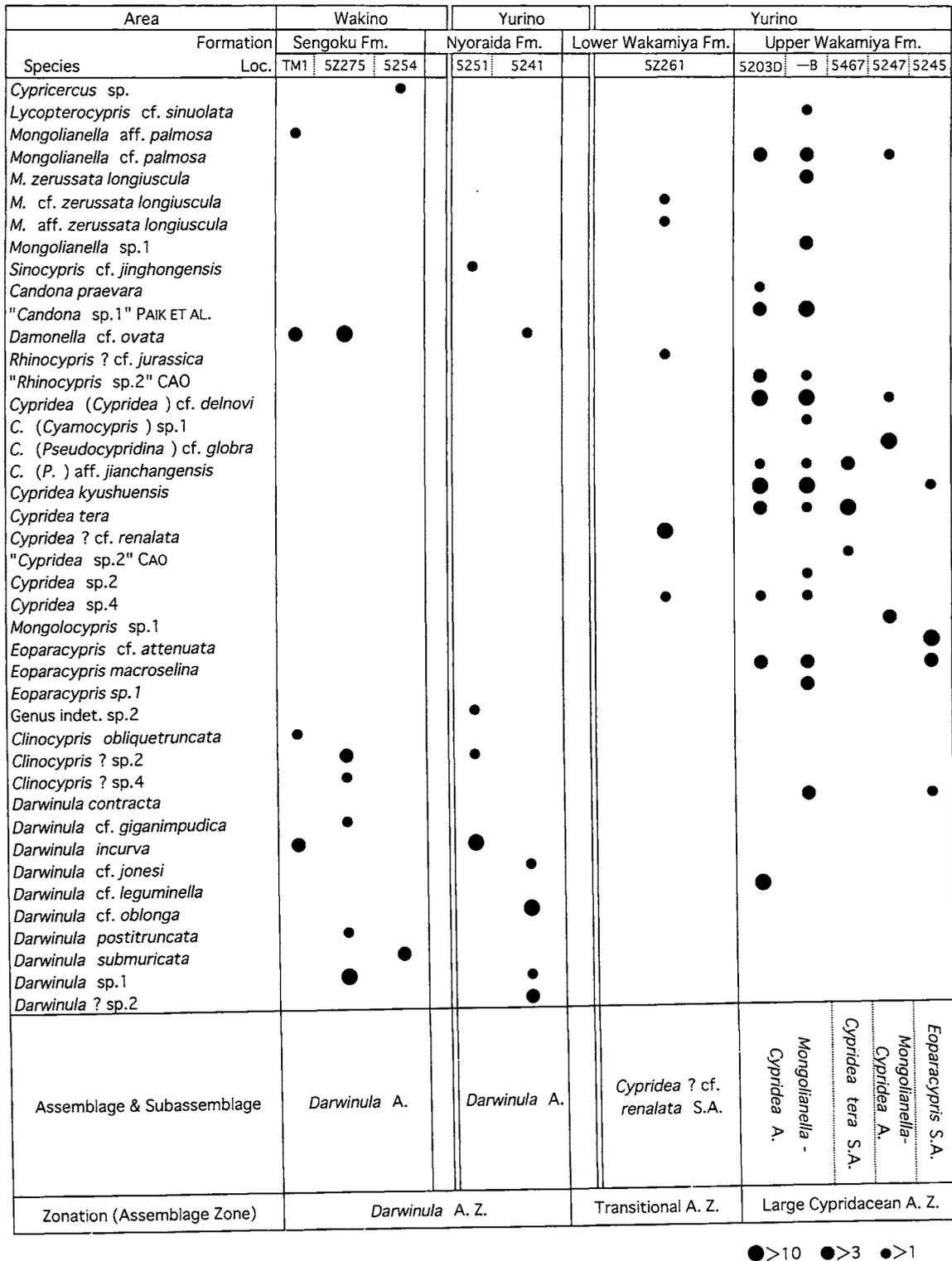| Area	Wakino			Yurino			Yurino					
Formation	Sengoku Fm.			Nyoraida Fm.			Lower Wakamiya Fm.	Upper Wakamiya Fm.				
Species Loc.	TM1	5Z275	5254	5251	5241		5Z261	5203D	—B	5467	5247	5245
Cypricercus sp.			●									
Lycopterocypris cf. *sinuolata*									●			
Mongolianella aff. *palmosa*	●											
Mongolianella cf. *palmosa*								●	●		●	
M. zerussata longiuscula									●			
M. cf. *zerussata longiuscula*							●					
M. aff. *zerussata longiuscula*							●					
Mongolianella sp.1									●			
Sinocypris cf. *jinghongensis*				●								
Candona praevara								●				
"Candona sp.1" PAIK ET AL.								●	●			
Damonella cf. *ovata*	●	●			●							
Rhinocypris ? cf. *jurassica*							●					
"Rhinocypris sp.2" CAO								●	●			
Cypridea (*Cypridea*) cf. *delnovi*								●	●		●	
C. (*Cyamocypris*) sp.1									●			
C. (*Pseudocypridina*) cf. *globra*											●	
C. (*P.*) aff. *jianchangensis*								●	●	●		●
Cypridea kyushuensis								●	●	●		●
Cypridea tera								●	●	●		
Cypridea ? cf. *renalata*							●					
"Cypridea sp.2" CAO										●		
Cypridea sp.2							●		●	●		
Cypridea sp.4											●	
Mongolocypris sp.1												●
Eoparacypris cf. *attenuata*								●	●			●
Eoparacypris macroselina									●			
Eoparacypris sp.1												
Genus indet. sp.2				●								
Clinocypris obliquetruncata	●											
Clinocypris ? sp.2		●		●								
Clinocypris ? sp.4		●								●		●
Darwinula contracta												
Darwinula cf. *giganimpudica*		●										
Darwinula incurva	●			●								
Darwinula cf. *jonesi*					●							
Darwinula cf. *leguminella*					●			●				
Darwinula cf. *oblonga*					●							
Darwinula postitruncata		●										
Darwinula submuricata			●									
Darwinula sp.1		●			●							
Darwinula ? sp.2					●							
Assemblage & Subassemblage	*Darwinula* A.			*Darwinula* A.			*Cypridea* ? cf. *renalata* S.A.	*Mongolianella - Cypridea* A.		*Cypridea tera* S.A.	*Mongolianella- Cypridea* A.	*Eoparacypris* S.A.
Zonation (Assemblage Zone)	*Darwinula* A. Z.						Transitional A. Z.	Large Cypridacean A. Z.				

●>10 ●>3 ●>1

Figure 6. Ostracode species, assemblages and biostratigraphical zonation in the Wakino-Yurino area.

are also common or abundant in the assemblage. *Eoparacypris* and *Candona* appear for the first time in this assemblage. Almost all the species of this assemblage have not been found in the underlying assemblages. Among them are "*Rhinocypris* sp. 2" of Cao (1996) with three very large laterally located nodules and *Eoparacypris macroselina* with a characteristic elongate-triangular carapace in lateral view. Consequently, this assemblage is quite different from the *Darwinula* assemblage and the *Cypridea*? *renalata* subassemblage.

In the upper part of the Upper Wakamiya Formation at Loc. 5247 of the Yurino area, the ostracode assemblage is dominated by *Cypridea* (*Pseudocypridina*) *globra* and subdominated by *Mongolocypris* sp. 1. Other species, *Cypridea* (*C.*) cf. *delnovi* and *Mongolianella* cf. *palmosa*, are rare in occurrence; their number of specimens are less than 20% of the total number of individuals. It is almost the same as the above-mentioned assemblage in the lower part of the same formation, with little differences in species composition. This assemblage shows a lower species diversity ($\lambda = \Sigma Xi (Xi-1)/N(N-1) = 0.44$) than the assemblage at Locs. 5203D ($\lambda = 0.15$) and 5203B ($\lambda = 0.18$).

4. *Cypridea tera* subassemblage

In the middle part of the Upper Wakamiya Formation at Loc. 5467 of the Yurino area, a small number of fossil ostracodes occurs sporadically in mudstone. The ostracode assemblage is dominated by *Cypridea tera* and subdominated by *Cypridea* (*Pseudocypridina*) aff. *jianchangensis*. "*Cypridea* sp. 2" of Cao (1996) is also rarely associated in it. This species association is referred to as a subassemblage, because they come from a single locality. This subassemblage is here named after the most dominant *C. tera*.

The subassemblage is thought to be closely related to the *Mongolianella-Cypridea* assemblage, because of the dominance of the characteristic species of the *Mongolianella-Cypridea* assemblage.

5. *Eoparacypris* subassemblage

In the uppermost part of the Upper Wakamiya Formation at Loc. 5245 of the Yurino area, the ostracode assemblage is dominated by the genus *Eoparacypris*. This is also assigned to a subassemblage, owing to the occurrence at a single locality. The genus *Eoparacypris* in this subassemblage consists of *E.* cf. *attenuata* and *E. macroselina*. Other genera such as *Cypridea* and *Darwinula* are included in the assemblage, but they are less than 20% of the total number. Therefore, this assemblage is characterized by low species diversity ($\lambda = 0.41$).

The genus *Eoparacypris* is found only in the *Mongolianella-Cypridea* assemblage other than in this subassemblage. The subordinate species are *Cypridea kyushuensis* and *Darwinula contracta*, the former is also included in the *Mongolianella-Cypridea* assemblage at both Locs. 5203D and 5203B, and the latter in the same assemblage at Loc. 5203B. Therefore, the *Eoparacypris* subassemblage shows a close affinity to the *Mongolianella-Cypridea* assemblage.

Southern Kokura area

Seven ostracode assemblages have been identified in the Wakino Subgroup in five blocks of the southern Kokura area (Figures 7, 8). One assemblage was identified in each of the Dobaru and Gamo blocks, and the Washimine and East Kumagai blocks together. Four other assemblages were identified from the West Kumagai block. They are described as follows.

6. *Cypridea-Darwinula* assemblage

Dark gray sandy mudstone overlying unconformably the Sangun Metamorphic Rocks at Locs. 5261d, 5261c, 5261a and 5261b in the Dobaru block of the southern Kokura area is undoubtedly assigned to the W1 formation. These localities are situated closely together within a stratigraphical interval of only 5.3 m. As shown in Figure 7, the ostracode assemblages from this mudstone appear to be different in species composition at different horizons. This, however, is due to differences in individual numbers at respective localities; relatively large numbers of individuals and species were collected from Locs. 5261c and 5261b, relatively small numbers from Locs. 5261d and 5261a. Consequently, the ostracode assemblage is better represented at Locs. 5261c and 5261b. In spite of these differences, *Cypridea*? sp. 3 is common among samples from the four localitlies. Therefore, the species from these four localities are considered to form together a single assemblage.

This assemblage is characterized by species of the genera *Cypridea* and *Darwinula* with six and three species, respectively. *Clinocypris* is a common genus in the assemblage, with one certain and three uncertain species. The genus *Mongolianella* is also common in the assemblage.

All the six species of *Cypridea*, except for *C.* (*C.*) cf. *tuberculorostrata*, are confined to this assemblage. These are interpreted to be older forms of *Cypridea* than those in the Wakino-Yurino area. Thus, they are probably contemporary with the *Darwinula* assemblage. The occurrence of the subgenus *Cypridea* (*Cyamocypris*) should be noted, because according to Cao (1996), the species of the subgenus lived in very limited environments in China. A few individuals of *C.* (*C.*) cf. *oblonga*, however, were obtained here. This scarcity may imply that this locality was in relatively open environments.

As to the genus *Darwinula*, relatively large forms such as *D.* cf. *leguminella* are dominant, but any species is not stratigraphically significant. They are significant, however, as indices of paleoclimate (Ye, 1994).

Damonella cf. *ovata*, one of the characteristic species of the *Darwinula* assemblage in the Wakino-Yurino area, is included in this assemblage.

7. *Cypridea tera* subassemblage

The ostracode assemblage from Loc. 5455 in the Gamo block is characterized by the abundance of *Cypridea tera*, accompanied by *Cypridea* (*Pseudocypridina*) aff. *jianchangensis* and *C.* cf. *anhuaensis*. It is almost the same as that from the Upper Wakamiya Formation at Loc. 5467 of the Wakino-Yurino area.

The subassemblage has a relation to the *Mongolianella-Cypridea* assemblage, because two of the three dominant and subordinate species are also found commonly in the *Mongolianella-Cypridea* assemblage.

Block of Southern Kokura area	Dobaru					Gamo	Washimine		E. Kumagai		W. Kumagai			
Formation	W1				W2	W4	W3		W3		W4			
Species / Loc.	5261d	—c	—a	—b		5455	5453	5452	5221a	—b	5451a	—b	—d	—h
Cyprinotus toutaiensis									●	●				
Eucypris ? sp.1										●				
Lycopterocypris cf. sinuolata				●					●					
Mongolianella zerussata longiuscula													●	
M. cf. zerussata longiuscula	●		●											
M. aff. zerussata longiuscula									●					
Mongolianella aff. palmosa									●					
Mongolianella cf. palmosa											●			
Mongolianella ? sp.2						●								
Mongolianella ? sp.3							●		●					●
Mantelliana jingguensis		●												
Mantelliana ? sp.1										●				
Sinocypris cf. jinghongensis									●					
Candona praevara						●				●				
"Candona sp. 4" PAIK ET AL.										●				
Cyclocypris ? cf. valida										●				
Cyclocypris ? sp. 1			●											
Damonella cf. ovata			●											
Rhinocypris cf. tuberculata														●
"Rhinocypris cf. jurassica j. " CAO														●
Rhinocypris ? cf. jurassica									●	●				●
Rhinocypris ? aff. jurassica	●								●	●	●			●
"Rhinocypris sp.1" CAO														●
"Rhinocypris sp.2" CAO														●
Cypridea (C.) cf. actuosa	●	●		●										
Cypridea (C.) cf. tuberculorostrata	●	●							●					
Cypridea (C.) aff. delnovi									●					●
"Cypridea (C.) sp.4" PAIK ET AL.											●			
Cypridea (Cyamocypris) cf. oblonga		●												
C. (Pseudocypridena) jinjuria							●							
C. (P.) jianchangensis	●	●		●										
C. (P.) aff. jianchangensis						●								
Cypridea cf. anhuaensis						●								
Cypridea kyushuensis							●		●					
Cypridea tera						●								
Cypridea ? sp.1		●		●										
Cypridea ? sp.3	●	●	●	●										
Cypridea sp.5											●			
Clinocypris sp.1				●										
Clinocypris ? sp.2				●										
Clinocypris ? sp.3			●											
Clinocypris ? sp.4			●											
Darwinula contracta														●
Darwinula incurva						●								
Darwinula cf. jonesi				●										
Darwinula cf. leguminella	●	●	●	●			●		●	●				
Darwinula cf. submuricata				●										
Darwinula cf. sarytirmensis									●					
Darwinula aff. subparallela						●			●	●				
Assemblage & Subassemblage	Cypridea - Darwinula A.					Cypridea tera S.A.	Darwinula - Mongolianella - Rhinocypris ?- Candona A.				Large Cypridea S.A.	Nodular Cypridea S.A.	Mongolianella S.A.	Rhinocypris S.A.

Figure 7.   Ostracode species and assemblages in five blocks in the southern Kokura area.   The formations in Gamo, Washimine, East Kumagai and West Kumagai blocks are respectively inferred from their ostracode assemblages.
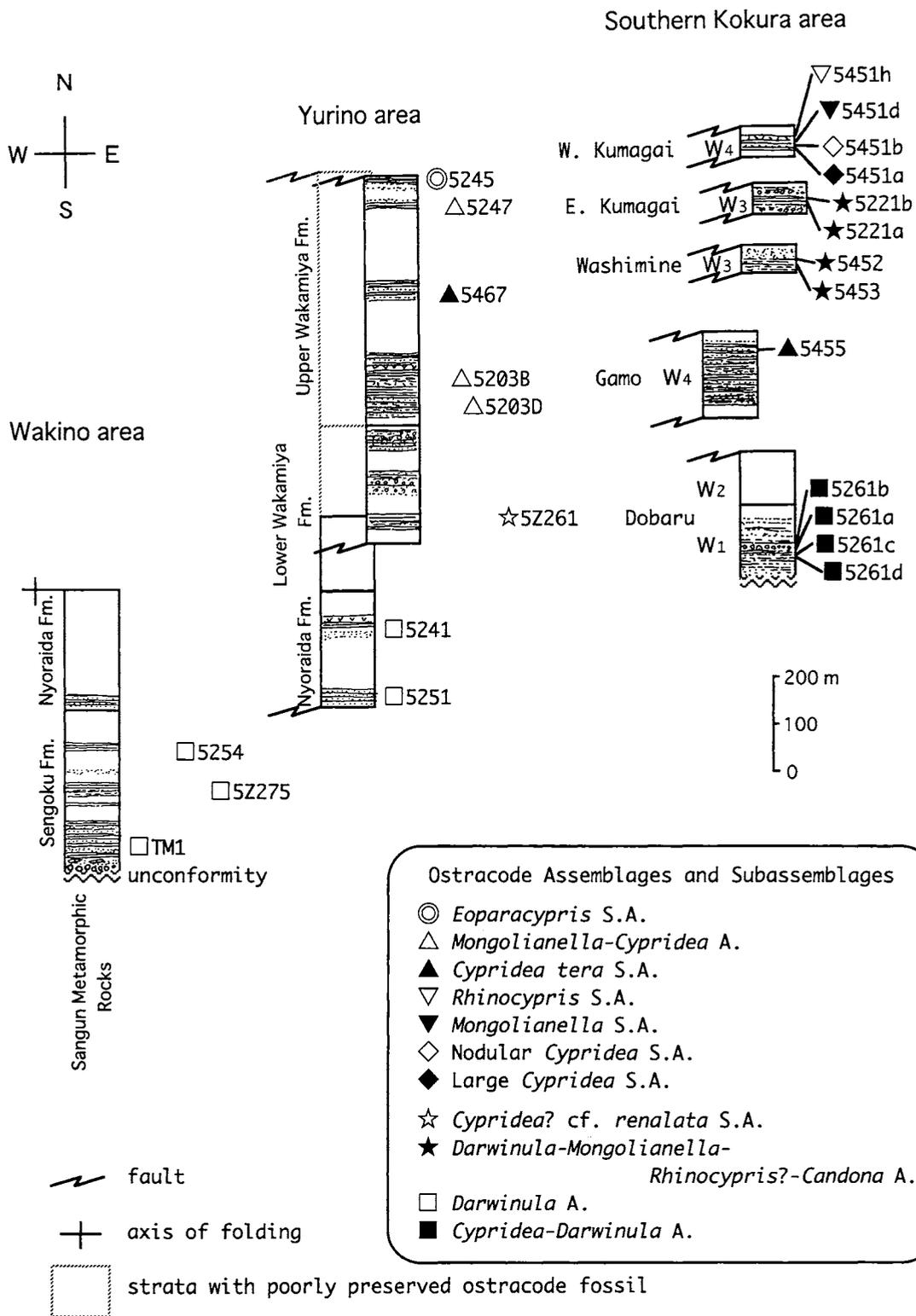
Southern Kokura area

N

W ─┼─ E

S

Yurino area

∇5451h
▼5451d
W. Kumagai W4   ◇5451b
              ◆5451a
E. Kumagai W3   ★5221b
              ★5221a
Washimine W3   ★5452
              ★5453

©5245
△5247

▲5467   Gamo W4   ▲5455

△5203B
△5203D

Wakino area

Upper Wakamiya Fm.

Lower Wakamiya Fm.

☆5Z261   Dobaru   W2   ■5261b
                  W1   ■5261a
                      ■5261c
                      ■5261d

Nyoraida Fm.

□5241

□5251

Nyoraida Fm.

□5254

□5Z275

Sengoku Fm.

□TM1
unconformity

200 m
100
0

Sangun Metamorphic Rocks

Ostracode Assemblages and Subassemblages

© Eoparacypris S.A.
△ Mongolianella-Cypridea A.
▲ Cypridea tera S.A.
∇ Rhinocypris S.A.
▼ Mongolianella S.A.
◇ Nodular Cypridea S.A.
◆ Large Cypridea S.A.

☆ Cypridea? cf. renalata S.A.
★ Darwinula-Mongolianella-
                    Rhinocypris?-Candona A.
□ Darwinula A.
■ Cypridea-Darwinula A.

fault

axis of folding

strata with poorly preserved ostracode fossil

Figure 8. Stratigraphical distribution of ostracode assemblages. The relationships between assemblages and biostratigraphical zones are shown in Figure 6.

8. *Darwinula-Mongolianella-Rhinocypris?-Candona* assemblage

From Locs. 5221a and 5221b in the East Kumagai block, the former located 7m below the latter, a high-diversity (λ = 0.11–0.24) ostracode assemblage was obtained. The assemblage involves 19 species belonging to 11 genera. The faunal composition is the most complex among all the assemblages described in this paper. The sample size for the two dominant species, *Darwinula* aff. *subparallela* and *Rhinocypris?* cf. *jurassica*, are only slightly larger than those for several subordinate species. Therefore, it is inadequate to name the assemblage after the leading generic or species names. Among the subordinate species, four species belong to the genus *Mongolianella* and two species to the genus *Candona*. Thus, the high-diversity assemblage is named the *Darwinula-Mongolianella-Rhinocypris?-Candona* assemblage.

The assemblage is somewhat similar to the *Cypridea-Darwinula* assemblage and *Darwinula* assemblage in the abundance of *Darwinula*, and also resembles the *Mongolianella-Cypridea* assemblage in the abundance of *Mongolianella*. This may mean that the assemblage is transitional from early *Darwinula*-dominant assemblages to later large Cypridacean-abundant assemblages.

At species level, however, the components of the genus *Darwinula* in this assemblage are different from those of the *Darwinula* assemblage of the Sengoku and Nyoraida Formations and the *Cypridea-Darwinula* assemblage of the Dobaru block, except for *D.* cf. *leguminella* with a long stratigraphical range extending throughout the Wakino Subgroup. Two of the three species of the genus *Cypridea* are held in common the *Cypridea-Darwinula* assemblage in the Upper Wakamiya Formation in the Yurino area, and the remaining one is common with the assemblage of the Dobaru block.

The assemblages at Locs. 5453 and 5452, the former 10 m below the latter are also identified with the *Darwinula-Mongolianella-Rhinocypris?-Candona* assemblage. This identification is based on the abundance of *Darwinula* and *Mongolianella*, and on the fact that four of the seven species comprising the assemblage also occur in the high-diversity assemblage of the East Kumagai block. In particular, three of the four species characteristically occur in the East Kumagai block.

9. Large *Cypridea* subassemblage

At Loc. 5451a of the West Kumagai block, a very large *Cypridea*, *C.* sp.5, occurs exclusively. This species is the biggest in all the ostracodes of the Wakino Subgroup. Other species are few and cannot be identified to species because of poor preservation. This unique assemblage seems to have settled in a limited environment on ash-field bottoms. This ostracode association is assigned to a subassemblage owing to its restriction to the limited occurrence at a single locality.

10. Nodular *Cypridea* subassemblage

The characteristic *Cypridea* with nodulated surface, "*C.* sp. 4" of Paik *et al.* (1988), occurs dominantly at Loc. 5451b, which is about 3.8 m above Loc. 5451a within the same West Kumagai block. Such a nodulate species is very rare in the Wakino Subgroup, though another nodulate species is present in the *Rhinocypris* subassemblage from the same West Kumagai block and the *Mongolianella-Cypridea* assemblage from the Upper Wakamiya Formation in the Yurino area. A subordinate species is large-sized *Mongolianella* cf. *palmosa*, which is characteristic of the Upper Wakamiya Formation in the Wakino-Yurino area. This association of ostracodes is also assigned to a subassemblage owing to its occurrence at a single locality.

11. *Mongolianella* subassemblage

A quite different assemblage from that of Locs. 5451a and 5451b is found at 5451d about 1.5 m above Loc. 5451b. Because of small numbers of individuals, only one species was so far found at this locality. This exclusive species is *Mongolianella zerussata longiuscula*, which is, in contrast, coexistent with many other species at Loc. 5203B. This ostracode association is also assigned to a subassemblage owing to its appearing at a single locality.

12. *Rhinocypris* subassemblage

This assemblage is found at Loc. 5451h, which is located 3.4 m above Loc. 5451d, and shows the highest diversity (λ = 0.21) among the four localities within the West Kumagai block. It is named because of the abundance of *Rhinocypris*.

The genus *Rhinocypris* of this subassemblage consists of five species, *R.* cf. *tuberculata*, *R.?* cf. *jurassica*, "*R.* cf. *jurassica jurassica*", "*R.* sp.1" and "*R.* sp.2", among which the last three were described by Cao (1996). Of the three species, "*Rhinocypris* sp. 2" of Cao (1996) is common to the *Mongolianella-Cypridea* assemblage from the Upper Wakamiya Formation in the Yurino area. *Cypridea* (*C.*) aff. *delnovi* is also abundant in the subassemblage.

Ostracode assemblages and sedimentary environments

Characteristics of Early Cretaceous ostracode assemblages.—Generally, the diversity of nonmarine ostracode assemblages from the Wakino Subgroup is extremely high as compared to those of Recent or Cenozoic ones. This high diversity is most remarkable in the Lower Cretaceous ostracode assemblages all over the world. However, the reasons behind this high diversity have not been sufficiently discussed until now, in spite of the importance for assessments of ostracode assemblages.

Some living ostracode assemblages from isolated lakes around the world are remarkably similar to one another. This owes much to transport by migratory water birds, either in mud sticking to their feet and trapped in feathers or in the intestinal tract (Krömmelbein, 1962, Brasier, 1980). Since most nonmarine ostracode eggs are very resistant against desiccation, their dispersion could be largely accomplished by water birds. However, such Early Cretaceous migratory water birds are unknown (Figure 10). The oldest evidence of water birds in East Asia is the footprints of webbed feet from the Upper Cretaceous Uhangri Formation of Korea (Yang *et al.*, 1995; Figure 10). The age of the formation is younger than 85-92 Ma (radiometric age of the Hwangsan Tuff in the underlying formation) and older than 63-67 Ma (radiometric age of the Haennam basin intrusives in the overlying formation).
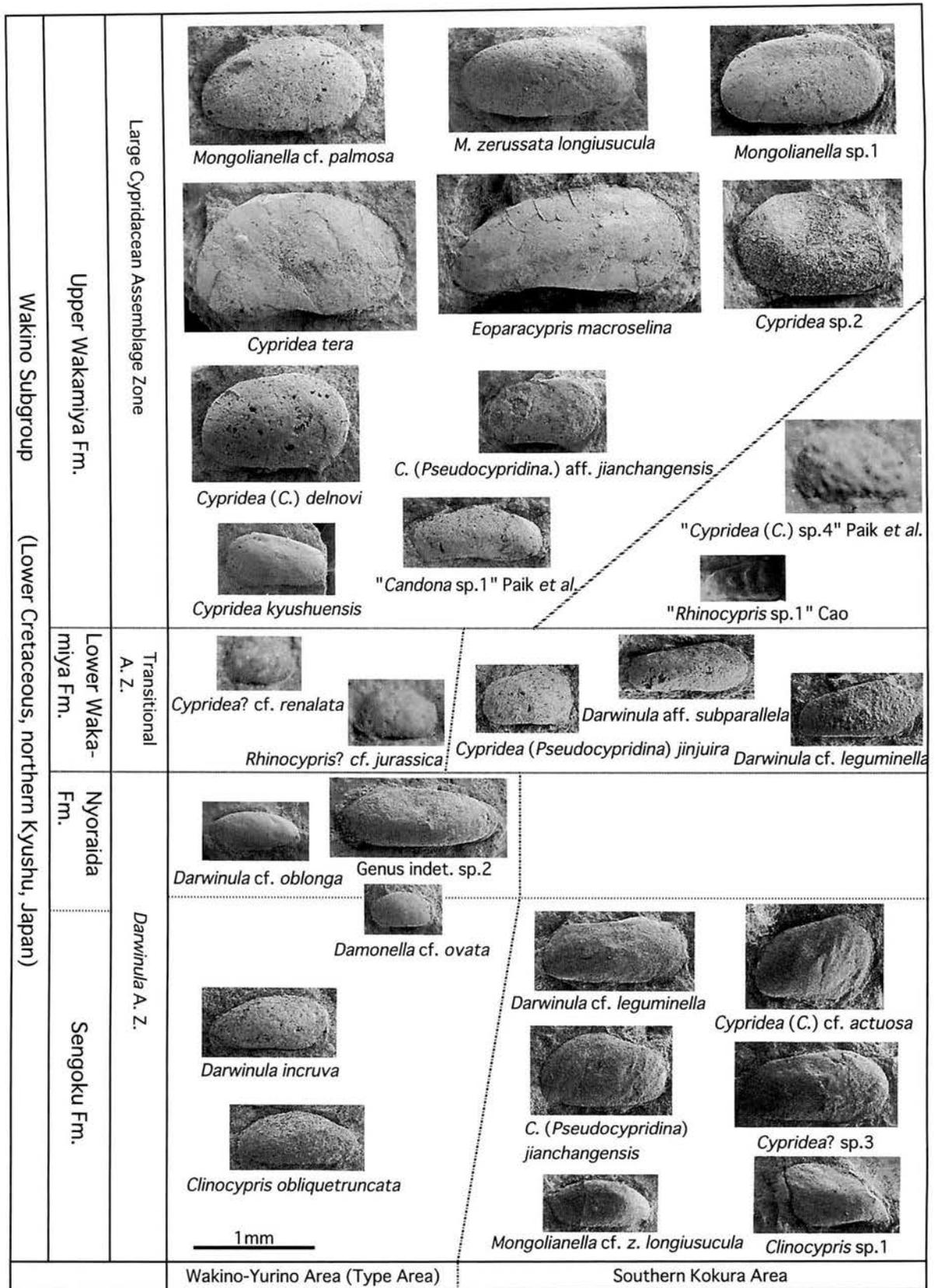
On the other hand, shore birds had already become habi-

Figure 9. Some of the representative ostracodes from the Wakino Subgroup are arranged at their stratigraphical and geographical positions.

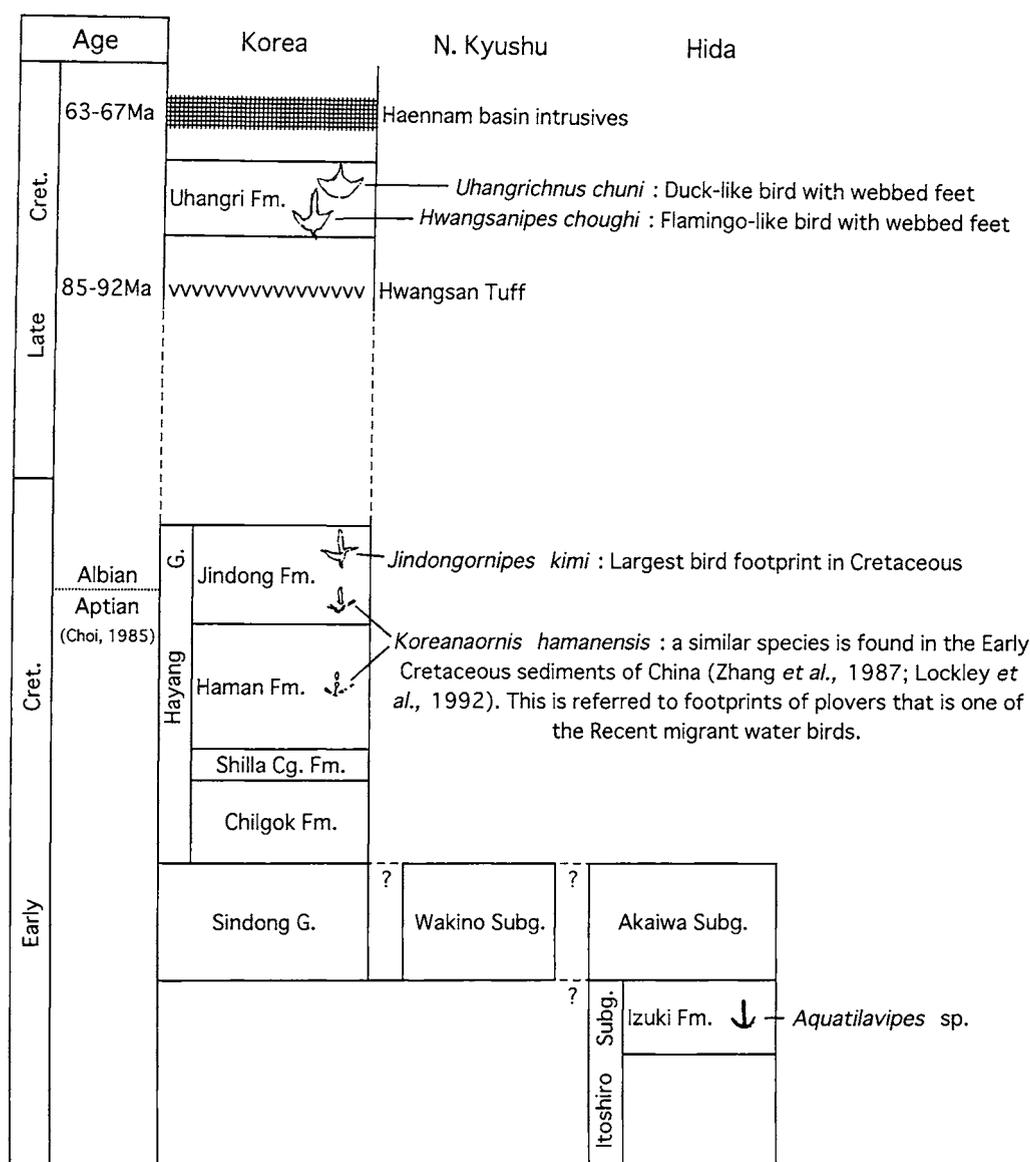| Age		Korea	N. Kyushu	Hida

Figure 10. Occurrence of Cretaceous water and shore birds in Korea and Japan.

tants of lacustrine shorelines in East Asia by Early Cretaceous. For example, Kim (1969) reported avian tracks associated with many invertebrate trace fossils from the Haman Formation of the Lower Cretaceous Hayang Group of the Kyeongsang Supergroup in Korea. More rencently Choi (1985) has suggested that these deposits are probably Aptian to early Albian in age. Yang et al. (1990) and Lockley et al. (1991) discovered many avian tracks at 31 localities in the Jindong Formation that overlies the Haman Formation. They concluded that there appear to be at least two quite distinct footprint types, *Jindongornipes kimi* and *Koreanaornis hamanensis* in the Jindong Formation. *Koreanaornis hamanensis* resembles the footprint of various modern species of plovers. Recent plovers are migratory shore birds, one of which is known to migrate several thousand kilometers. Matsukawa (1991) reported bird tracks

from the Valanginian-Hauterivian? Izuki Formation (upper part of the Itoshiro Subgroup of the Tetori Group) in central Japan, which is slightly older than or almost contemporaneous with the Wakino Subgroup.

Considering that aviform tracks are widespread and a significant component of Early Jurasssic ichnological assemblages, birds presumably evolved rapidly in the Late Jurassic and Early Cretaceous (Lockley et al.,1992). The shore bird radiation may have occurred in Early Cretaceous, but this apparently did not yet produce fully aquatic birds. Given this, it may be surmised that only shore birds were active on the shore of the sedimentary basin of the Early Cretaceous Wakino Subgroup. Consequently, the ostracodes whose eggs could then be transported by birds were restricted to shoreline-inhabiting species. It is considered that species living in water deeper than 10 cm or so

were seldom transported by birds. Therefore, many species presumably evolved in situ in each lake, giving rise to high-diversity assemblages. The similarity of contemporaneous ostracode assemblages within the same lakes may have been maintained. The similarity, however, was not warranted in assemblages of isolated lakes long distances aprt in the Early Cretaceous. Namely, it is suspected that the ostracode assemblages were different from lake to lake.

As Lower Cretaceous ostracode assemblages were changeable from place to place, ostracode biostratigraphical zonation and correlation should not be based directly on ostracode assemblages of a certain kind, but on more general features common among closely related assemblages.

Sedimentary environments indicated by fossil charophytes and estherids.—At some horizons of the Wakino Subgroup, fossil charophytes are found abundantly together with ostracode fossils. Fossil estherids occur accompanying ostracode fossils at many horizons. These charophyte and estherid fossils are useful to assess sedimentary environments. Ecological discussions of these taxa have been little done, in spite of their importance 'for indications of paleoenvironments. Then, it should be discussed what kind

of environments these taxa indicate.

Sedimentary environments indicated by fossil charophytes: Fossil charophytes occur abundantly in the Sengoku Formation at Loc. TM1 of the Wakino area and the Upper Wakamiya Formation at Loc. 5247 of the Yurino area.

According to the classification generally accepted, charophytes consist of 3 orders and 6 families including fossil species. But of the three only one order (*Charales*) with four families survives today, of which only one family (Characeae) has living species. About 250 living species are known from all over the world, of which about 70 species are living in Japan.

This group appeared in the Silurian, and became highly diversified by the Cretaceous but declined to the Recent. The ecology of recent charophytes is very significant, because it forms "*Chara* zone" in the lowermost part of the depth distribution of aquatic plants in lakes (Kazaki, 1967; Figure 11). The depth of the lower limit of the "*Chara* zone" is inferred to be about twice the average depth of transparency in summer, based on the data shown in Figure 11. The upper limit of the "*Chara* zone" is determined by the depth of the overlying "zone of Submerged Plants", which ranges from one to

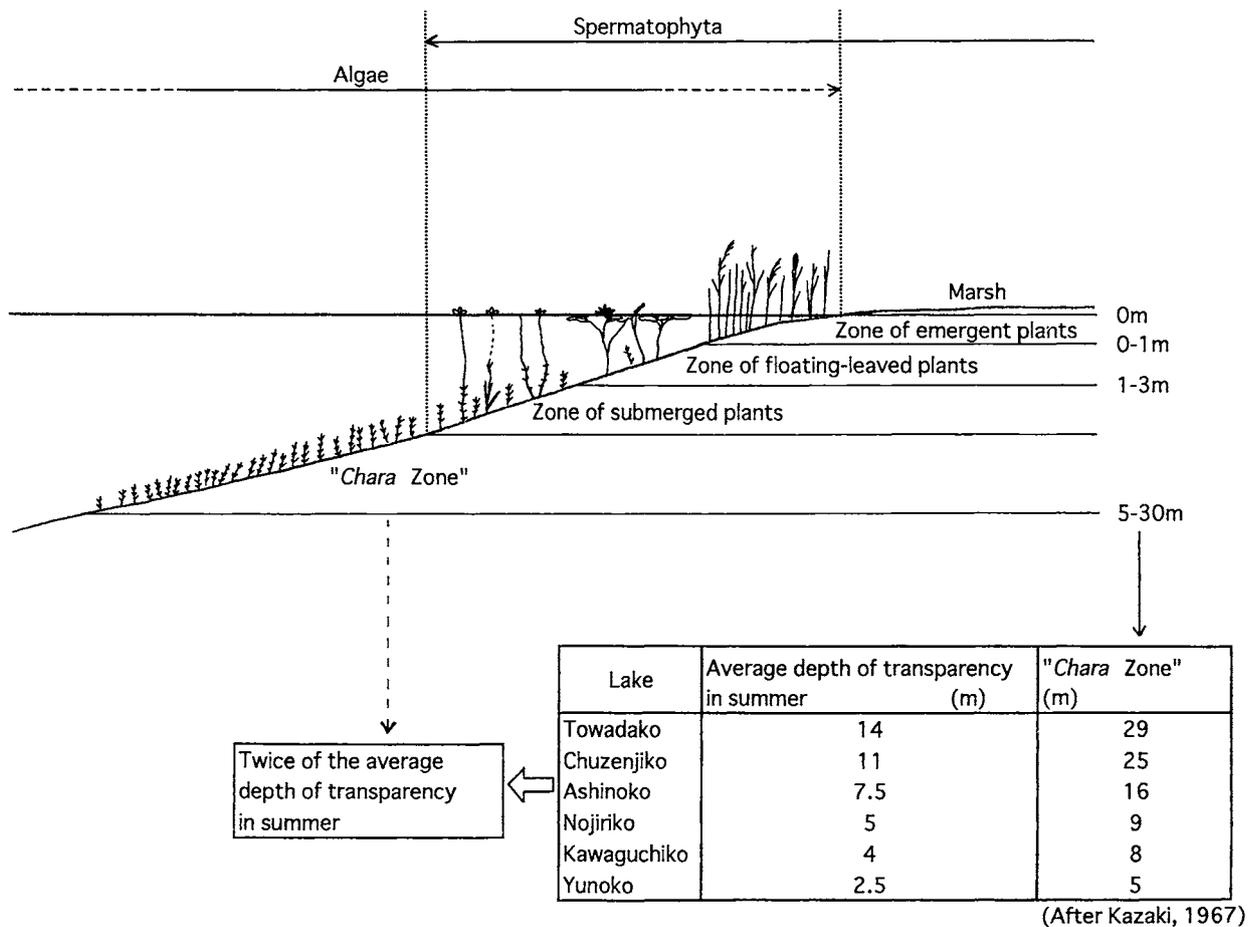| Lake	Average depth of transparency in summer (m)	"*Chara* Zone" (m)
Towadako	14	29
Chuzenjiko	11	25
Ashinoko	7.5	16
Nojiriko	5	9
Kawaguchiko	4	8
Yunoko	2.5	5

(After Kazaki, 1967)

Figure 11. Schematic diagram showing vertical zonation of aquatic large plants in lake shore environments (partly adopted from Kazaki, 1967). Compiled from many ecological studies of recent freshwater botany. Vertical zonation is generally formed in the aquiherbosa, that is, a shallow bottom covered by aquatic plants. The lowermost part is exclusively abundant in charophytes, which form the "*Chara* zone".

several meters. Consequently, the Recent "*Chara* zone" is usually formed on the shallow bottom that is deeper than several meters and shallower than 30 m. In the Cretaceous, however, the upper limit of the zone is inferred to have been shallower than that in the Recent, because plants forming zones over the "*Chara* zone", most of which belong originally to terrestrial spermatophyta, invaded submerged environments from terrestrial environments during or after the Cretaceous. Therefore, the "*Chara* zone" is considered to have been a little wider, namely, a few to 30 m. If this is true, charophytes accompanied by many other aquatic plants indicate the "zone of the submerged plants", which is shallower than a few meters.

In such shallow water, a calm environment in which plants can grow is considered to have been restricted to enclosed margins of lakes or marshes on the fluvial plain, because waves and currents usually prevent plants from growing. Large aquatic plants tend to grow in bays rather than in open-shore environments (Ikushima, 1969). Among many kinds of aquaplants, charophytes especially prefer lentic environments to litic environments, as lentic environments favor the swimming of sperm during fertilization.

As discussed above, the abundant occurrence of fossil charophytes surely indicates shallow and calm water environments. Such environments can be seen in enclosed bottom parts of marginal lakes, shallow swamps or marshes on the fluvial plain.

Sedimentary environments indicated by fossil estherids: In the southern Kokura area, estherids were collected by Ota (1957) from W3 and W4 formations exposed near Yamada Park and were described as *Euestheria imamurai, E. kokuraensis* and *Cyclestheroides* sp. by Kusumi (1960). Additional estherids were collected by Ota *et al.* (1979) from W3 and W4 formations in the same place. Among them, those from the basal part of W4 formation were identified as *Euestheria imamurai, E. kokurensis* and *Cyclestheroides* sp. by Kusumi (1979). In the Wakino-Yurino area, estherid fossils have been newly found in the Lower Wakamiya Formation at Loc. 5Z261 of the Yurino area. They were identified as *Orthestheria kokurensis* (the genus *Orthestheria* has replaced *Euestheria*) by Chen (1996).

According to a recent classification, estherids are formally called Conchostraca, an order of Branchiopoda (Crustacea). Six Recent species are known in Japan, and at least four of them are unique to Japan. All the species of Recent Conchostraca live in very limited environments with very shallow (about 5 to 10 cm, in maximum 20 cm) muddy bottoms which dry up occasionally. Desiccation is indispensable for eggs of Conchostraca to mature. In East Asia, at present, the drying up of lakes takes place in winter. If this was true for Cretaceous time, the Conchostraca could be useful as a indicator of paleoenvironments.

Sedimentary environments of the ostracode assemblages. —The sedimentary environments of the ostracode assemblages described above are discussed below.

1. *Darwinula* assemblage
This assemblage generally suggests such depositional environments as marginal lacustrine bottoms or terrestrial shallow ponds on the fluvial plain. Charophytes, gastropods and plant fragments co-occur abundantly with

ostracodes in poorly sorted sandy siltstone at Loc. TM1. As discussed above, the siltstone containing these kinds of fossils is considered to have been deposited in water shallower than several meters. The bottom was covered with many kinds of aquatic plants, as is easily inferred from numerous plant fossil remains. The water must have been stagnant except for episodic events of storms and floods. Such stagnant and shallow-water environments are supposed to have been in the enclosed part of lacustrine shores shallower than a few meters, or marshes on the fluvial plain.

The assemblage at Loc. 5Z275 must have been in environments somewhat different from those of Loc. TM1, because the sediments at the former locality are made up exclusively of black sandy siltstone with ostracode-crowded layers. The lack of plant fossils suggests that the siltstone was deposited on a bottom deeper than the base of the vertical distribution of aquatic plants (cf. Figure 11), or in open shallow-water environments. The former is considered more probable because of the scarcity of fossils. Moreover, if the latter was the case for Loc. 5Z275, many kinds and large numbers of animals should have lived there. However, the depositional environment is not thought to have been so deep, because it was also inhabited by many individuals of the gastropod *Brotiopsis wakinoensis*. The genus *Brotiopsis* belongs to the Pleuroceridae, almost all the Recent species of which live on lake or river bottoms shallower than several meters.

Far deeper environments are thought to have existed in the surroundings of Loc. 5254 of the Wakino area and Loc. 5251 of the Yurino area, based on analysis of sedimentary facies. Mudstone with thin silty laminae at Loc. 5254 is compared to a deposit resulting from seasonal suspension clouds, and mudstone intercalated by graded sandstone at Loc. 5251 is inferred to be of turbidite origin by Seo *et al.* (1992). These facies are relatively poor in ostracode and other fossils.

In contrast, the depositional environments of the Nyoraida Formation at Loc. 5241 are considered to have been shallow-water ones because of the relative abundance of ostracodes in massive mudstone, presumably bioturbated. This assemblage indicates a subtropical-tropical climate, the work of Ye (1994) having shown that the genus *Darwinula* was widely distributed and able to diversify in southern China, but declined to the north.

2. *Cypridea*? cf. *renalata* subassemblage
This subassemblage is inferred to suggest a fluvial plain, judging from estherid fossils and sedimentary facies. Estherids live only in shallower water than 20 cm, where the bottom is occasionally emerged and dried up. Laterally changeable lithologies from clay to pebbly conglomerate and sedimentary structures such as channel structures and cross-laminations support flood plain environments.

This kind of severe environments for aquatic animals allows ostracode life for only a short term, and so, almost all of the individuals are of small size. The scarcity of ostracodes in the Lower Wakamiya Formation is explained by such a severe environment.

3. *Mongolianella-Cypridea* assemblage
This assemblage at Locs. 5203D and 5203B is presumed to have been on a variable widespread shallow-water bot-

tom, because many kinds of niches seem to have existed in the same water mass, as suggested by the variety of ostracodes and sediments (Matsukawa et al., 1996).

This assemblage at Loc. 5247 shows a lower species diversity ($\lambda = 0.44$) than the ones at Locs. 5203D ($\lambda = 0.15$) and 5203B ($\lambda = 0.18$). It is explained by a relatively deeper environment, which is shown by exclusively abundant charophyte fossils. Such an environment corresponds to the so-called "Chara zone", which is the lowermost zone in the vertical distribution of aquatic plants at water depths from a few to 30 m as already discussed.

4. Cypridea tera subassemblage

This subassemblage is known both in the Wakino-Yurino and the southern Kokura area.

With thin parallel laminations of dark gray mudstone intercalated with sandstone, the depositional environment for the Cypridea tera subassemblage in the Wakino-Yurino area (Loc. 5467) is inferred to have been similar to that of Locs. 5203D and 5203B: a variable widespread shallow-water bottom. On closer view, the environment at Loc. 5467 seems to have been somewhat antagonistic to ostracodes, as the ostracode-bearing layer is overlain by sandstone as thick as 7 m.

The same subassemblage is in thinly parallel-laminated mudstone intercalated with sandstone at Loc. 5455 in the Gamo block in the southern Kokura area. From the lithological similarity, the depositional environment is inferred to have been similar to that of Locs. 5203D , 5203B and 5467. The environment may have been of widespread shallow-water bottom, though the environment of Loc. 5455 may have been slightly hostile to ostracode life, as sandstone intercalations are relatively frequent.

5. Eoparacypris subassemblage

The low diversity of species ($\lambda = 0.41$) in this subassemblage suggests that species of the genus Eoparacypris lived in restricted environments. Judging from the lithology without intercalations of sandstone, it is certain that a quiet environment persisted for a long time. According to Anderson (1985), this genus is relatively abundant in marly beds. This may suggest shallow lake environments, where the rate of evaporation was high. However, carbonate is not preserved in any of the studied materials.

6. Cypridea-Darwinula assemblage

This assemblage lived in a shallow and enclosed part of the marginal lacustrine environment, because massive sandy mudstone shows repeated bioturbations and sporadically contains granules of secondarily formed iron sulfate. Many kinds of animal fossils other than ostracodes, such as fish, turtles and gastropods occur in this sandy mudstone. The turtle fossils are especially indicative of near-shoreline environments. This sandy mudstone, however, contains few plant fossils, which are generally rich in enclosed parts of the marginal lacustrine environments and terrestrial marshes on the fluvial plain.

According to Ye (1994), the genus Darwinula was widely distributed and evolved diversely in southern China while declining to the north in the Late Cretaceous. This means that the genus Darwinula preferred a subtropical-tropical climate to temperate-cold one. The occurrence of the genus Darwinula indicates that the Cypridea-Darwinula assem-

blage existed in subtropical-tropical climates, as did the Darwinula assemblage in the Wakino-Yurino area.

7. Darwinula-Mongolianella-Rhinocypris?-Candona assemblage

This highly diversified assemblage ($\lambda = 0.11-0.24$) at Locs. 5221a, 5221b, 5452 and 5453 was on shallow-water bottoms, which were dried up temporally. Sedimentary structures such as channels and mudcracks and the lithology of reddish sandstone indicate fluvial depositional environments. The topset of deltas may have spread here.

8. Large Cypridea subassemblage

This subassemblage must have been under the influence of intense volcanic activity, because the lithology consists mostly of white tuff. Intercalations of poorly sorted reddish sandstone exhibit shallow-water bottoms which saw occasional emergence. It is to be expected that only the extremely large-sized species survived drastic environmental changes caused by ash fall that killed other species which lived there.

9. Nodular Cypridea subassemblage

The environment for this subassemblage is inferred to resemble that of the underlying large Cypridea subassemblage from the lithology of tuffaceous mudstone at Loc. 5451a. No difference between them has been found.

10. Mongolianella Subassemblage

The bottom environment of this subassemblage is similar to that of the large Cypridea subassemblage and the nodular Cypridea subassemblage, as far as the lithology is concerned.

11. Rhinocypris subassemblage

The bottom environment for this subassemblage is presumed to have been almost the same as that for the large Cypridea (Loc. 5451a), nodular Cypridea (Loc. 5451b), and Mongolianella (Loc. 5451d) assemblages in view of the similar lithologies among them.

Zonation and correlation

Biostratigraphical zonation based on the ostracode assemblages has been established in the Wakino-Yurino area. By using this zonation, the Wakino Subgroup in several blocks of the southern Kokura area is correlated with the formations in the Wakino-Yurino area.

Zonation by ostracode assemblages.—Remarkable shifts in the ostracode assemblages were clearly recognized in the Wakino Subgroup in the Wakino-Yurino area (Figure 9); hence the subgroup can be divided into the following three assemblage zones toward the top of the sequence.

1. Darwinula assemblage zone

All the ostracode assemblages from the Sengoku and Nyoraida formations are assigned to the Darwinula assemblage (Figure 6). The range of the Darwinula assemblage provides a basis for a single biostratigraphical zone. This zone is called here the "Darwinula assemblage zone (in brief, a. z.)".

2. Transitional assemblage zone

The Cypridea? cf. renalata subassemblage was obtained from only one locality, as the Lower Wakamiya Formation is only sparsely fossiliferous (Figure 6). But the subassemblage shows clearly different characteristics from both the

Stratigraphy	Molluscan zone (Ota, 1960)	Molluscan fauna (Hase, 1960)	Fish fauna (Yabumoto, 1994)	Ostracode assemblage zone (this paper)
Upper Wakamiya Fm.	*Viviparus onogoensis-Nakamuranaia* ? cf. *chingshanensis* ZONE	Upper Wakino or Wakamiya faunule	*Diplomystus-Wakinoichthys* fauna	Large Cypridacean Assemblage Zone
Lower Wakamiya Fm.			*Paraleptolepis-Wakinoichthys* fauna	Transitional Assemblage Zone
Nyoraida Fm.		barren	barren	*Darwinula* Assemblage Zone
Sengoku Fm.	*Brotiopsis wakinoensis* ZONE	Lower Wakino or Sengoku faunule	*Nipponamia-Aokiichthys* fauna	

Figure 12. Comparison among biostratigraphical zonations by various kinds of faunas.

underlying and overlying assemblages. This poorly designated subassemblage is regarded as a "transitional" assemblage from the underlying *Darwinula* assemblage to the overlying cypridacean-dominant assemblages, and defines the "transitional assemblage zone (a. z.)".

3. Large Cypridacean assemblage zone

Three different ostracode assemblages were recognized in the Upper Wakamiya Formation, though other formations of the Wakino Subgroup each contain a single assemblage (Figure 6). One of the three assemblages, the *Mongolianella-Cypridea* assemblage, represents a recurrence within the formation. Two of the three assemblages, the *Cypridea tera* subassemblage and the *Eoparacypris* subassemblage are observed at a single locality. The differences among these three subassemblages seem to be determined by environmental differences. Consequently, it is practical to adopt the general characteristics and names of higher taxa. Hence, the Upper Wakamiya Formation is biostratigraphically named the "Large Cypridacean assemblage zone" after large forms of *Cypridea, Mongolianella* and *Candona*, all of which belong to the superfamily Cypridacoidea.

This ostracode biostratigraphical zonation is compared with the other biostratigraphical zonations previously proposed on the basis of defferent kinds of fossils (Figure 12). The Nyoraida Formation, which has been biostratigraphically considered to be barren by Hase (1960) and Yabumoto (1994) and assigned to the lower part of the molluscan *Viviparus onogoensis-Nakamuranaia*? cf. *chingshanensis* zone by Ota (1960) (originally, he described it as the *Viviparus onogoensis-Nakamuranaia*? sp. cf. *N. chingshanensis* zone), was assigned to the upper part of the *Darwinula* assemblage zone in the ostracode zonation. The Lower Wakamiya and Upper Wakamiya Formations can be distinguished from each other by the ostracode zonation in the same ways as the fish zonation by Yabumoto (1994), though they cannot be discriminated by the molluscan zonation (Ota, 1960; Hase, 1960).

Correlation of formations in the southern Kokura area.—In the southern Kokura area, the Wakino Subgroup is divided into many blocks by faults. Owing to such complicated geological structures, it is difficult to determine the exact stratigraphical positions of the exposure at each block.

Therefore, the same block has been regarded as different formations by previous studies.

1. Dobaru block

The strata which have been assigned to the W1 formation (Ota, 1955, 1960; Hase, 1958) and contain the *Cypridea-Darwinula* assemblage in the Dobaru block were correlated with the Sengoku or Nyoraida Formation of the Wakino-Yurino area by ostracode biostratigraphy, because the *Cypridea-Darwinula* assemblage from the lower stratigraphical part in the Dobaru block is similar to the *Darwinula* assemblage from the Sengoku and Nyoraida Formations in the Wakino-Yurino area in the abundance of *Darwinula*. However, there is a great difference in the abundance of the genus *Cypridea*. This is probably owing to the rareness of plants covering the bottom, as described above in this section. No species of *Cypridea* in the *Cypridea-Darwinula* assemblage is in common with those of the five assemblages and subassemblages in the Lower Wakamiya and Upper Wakamiya Formations of the Wakino-Yurino area. This fact also supports the above correlation. During the early depositional stage of the Wakino Subgroup, in which *Darwinula* was dominant, the deeper and stagnant nearshore water environments probably allowed ancestral species of *Cypridea* to live. *Damonella* cf. *ovata*, known only from the *Darwinula* a. z. and occurring in both the *Cypridea-Darwinula* assemblage and the *Darwinula* assemblage, also strengthens the correlation.

2. Gamo blocks

The sediments in the Gamo block were correlated with the Upper Wakamiya Formation in the Wakino-Yurino area, because they contain the same *Cypridea tera* subassemblage belonging to the Large Cypridacean assemblage zone in the Wakino-Yurino area.

The block has been assigned to the W4 formation in the previous studies (Ota, 1957, 1960; Hase, 1958; Ota *et al.*, 1979). The ostracode zonation leads to the same conclusion.

3. East Kumagai and Washimine blocks

The East Kumagai block has been regarded as distributing the W3 formation by Ota (1957, 1960) and Hase (1958). Recently, however, Sakai *et al.* (1992) considered it to be "Unit B" of their subdivisions of the Wakino Subgroup in Yamada Park of Kokura. On the other hand, the strata in

the Washimine block have been assigned to different forma-tions by different authors; for example, to the W3 formation by Ota (1957, 1960), equivalent of the Nyoraida (W2) Formation by Hase (1958), and "Unit A" by Sakai et al. (1992).

Both the Lower Cretaceous strata in the East Kumagai and Washimine blocks yield the same high-diversity (5453: λ = 0.12, 5221a, 5221b: λ = 0.11, 0.12) ostracode assem-blage. The Darwinula-Mongolianella-Rhinocypris?-Candona a. z. shows some relations to the Mongolianella-Cypridea assemblage that belongs to the large Cypridacean a. z. in the Wakino-Yurino area, because it contains Cypridea kyūshuensis, which is one of the characteristic species of the Mongolianella-Cypridea assemblage. Such relations are also shown by the abundance of Mongolianella.

On the other hand, the abundance of Darwinula suggests subtropical-tropical climates. Lycopterocypris cf. sinuolata from the East Kumagai block is common with the Cypridea-Darwinula assemblage of W1 formation in the Dobaru block.

Rhinocypris? cf. jurassica from the East Kumagai block is found only in the transitional a. z. in the Wakino-Yurino area. In the southern Kokura area, however, this species survived until the depositional time of the West Kumagai block, which may be assigned to the large Cypridacean a. z. as dis-cussed below.

In summary, the strata bearing the Darwinula-Mongolianella-Rhinocypris?-Candona a. z. in the East Kumagai and Washimine blocks are correlated with the tran-sitional a. z. in the Wakino-Yurino area, namely, with the Lower Wakamiya Formation.

4. West Kumagai block

The West Kumagai block has been considered to be occu-pied by the W3 formation (equivalent to the Lower Wakamiya Formation) by Ota (1957, 1960) and Hase (1958), though Ota et al. (1979) regarded the strata in the block as the W4 formation (the Fourth Formation). Recently, Sakai et al. (1992) assigned it to "Unit B", which overlies "Unit A".

The block contains four ostracode subassemblages: the large Cypridea, nodular Cypridea, Mongolianella and Rhinocypris ones in ascending order. These four assem-blages have common characteristics with one another; all of them contain large-sized species or nodulate species of the superfamily Cypridoidea. They are Cypridea sp. 5, Mongolianella cf. palmosa, M. zerussata longiuscula, "Cypridea (C.) sp. 4" of Paik et al. (1988), Rhinocypris cf. tuberculata and "Rinocypris sp. 1" and "R. sp. 2" of Cao (1996). These characteristics lend themselves to the corre-lation with the large Cypridacean assemblage zone in the Wakino-Yurino area. Therefore, the strata in the West Kumagai block were correlated with the Upper Wakamiya Formation.

5. Stratigraphy and geological structure of the Wakino Subgroup

In conclusion, the ostracode biostratigraphy revealed that the staratigraphy and geological structures in the southeren Kokura area are as follows.

The formations previously called the W1, W2, W3 and W4 formations are formally called here the Sengoku, Nyoraida, Lower Wakamiya and Upper Wakamiya Formations, respec-tively, because the ostracode biostratigraphical zonation that

has been established in the type areas is well discernible in the southern Kokura area.

The Sengoku Formation in this area consists of more fine-grained sediments, and secondarily formed iron in them shows a more reducing environment than in the Wakino area. The Lower Wakamiya Formation in this area was de-posited in widespread shallow water and rarely dried-up en-vironments, because it yields much abundant in the way of ostracode fossils than in the Yurino area. In contrast to the Sengoku and Lower Wakamiya Formations, the Nyoraida and Upper Wakamiya Formations in this area do not seem to be different from the Wakino-Yurino area.

In the Dobaru district, the Wakino Subgroup begins with the Sengoku Formation, which clino-unconformably overlies the Paleozoic strata. The Sengoku and the overlying Nyoraida Formations are distributed with a northward dip-ping structure, and are faulted to bound on the basement rocks or intrusive rocks.

In the northern part of the area, the Lower Wakamiya and Upper Wakamiya Formations are distributed in a principal anticline. Specifically, the Upper Wakamiya Formation is distributed in the southern Gamo block and the northern West Kumagai block, and the Lower Wakamiya Formation is in the Washimine and East Kumagai blocks, both of which are situated in an axial part of the anticline. In detail, how-ever, many small faults and foldings are involved in places in this area.

Conclusions

As the first biostratigraphical study on Mesozoic nonmarine ostracodes in Japan, 11 assemblages have been established, and the zonation based on these assemblages has been proposed. Major results of these investigations are summarized as follows:

1) From the Wakino Subgroup in the Wakino-Yurino area, five assemblages and subassemblages were recognized: the Darwinula assemblage from the Sengoku and Nyoraida Formations, the Cypridea? cf. renalata subassemblage from the Lower Wakamiya Formation, and the Mongolianella-Cypridea assemblage, the Cypridea tera subassemblage and the Eoparacypris subassemblage from the Upper Wakamiya Formation.

2) Based on stratigraphical changes in general features of these assemblages, stratigraphical zonation by ostracodes was proposed as the Darwinula a. z. (assemblage zone), transitional a. z. and large Cypridacean a. z. in ascending order. This method of zonation is reasoned by vertical changes of the ostracode assemblages. These assem-blages were easily recognized because of their characteris-tic species composition. This probably is due to the absence of water birds as main transporters of ostracode eggs, though ostracode eggs of shoreline-inhabiting species could have been transported by shore birds.

3) In the southern Kokura area, seven ostracode assem-blages and subassemblages were recognized in the Wakino Subgroup in five blocks: the Cypridea-Darwinula assem-blage from the W1 formation in the Dobaru block, the Cypridea tera s. a. in the Gamo block that has been as-signed to the W4 formation, the Darwinula-Mongolianella-

Rhinocypris?-Candona assemblage in the Washimine and East Kumagai blocks, the large *Cypridea*, nodular *Cypridea*, *Mongolianella* and *Rhinocypris* subassemblages from the West Kumagai block. With regard to the stratigraphical zonation proposed in the Wakino-Yurino area, each of the blocks was correlated as follows: the strata in the Gamo block certainly belong to the large Cypridacean a. z., those in the Washimine and East Kumagai blocks are probably assigned to the transitional a. z., and the West Kumagai block is surely attributed to the large Cypridacean a. z.

Acknowledgements

References

Anderson, F. W., 1985: Ostracod faunas in the Purbeck and Wealden of England. *Journal of Micropalaeontology*, vol. 4, p. 1-68.

Brasier, M. D., 1980: *Microfossils*, 193 p. George Allen and Unwin, London.

Cao, M. Z., 1996: Nonmarine Cretaceous ostracods from Inner Zone of SW Japan. *Bulletin of the Kitakyushu Museum of Natural History*, no. 15, p. 13-30.

Chen, P. J., 1996: Lower Cretaceous conchostracans of SW Japan. *Bulletin of the Kitakyushu Museum of Natural History*, no. 15, p. 1-12.

Choi, D. C., 1985: Spores and pollen from the Gyeongsang Supergroup, southeastern Korea and their chronologic and paleoecologic implications. *Journal of the Paleontological Society of Korea*, vol. 1, p. 33-50.

Hase, A., 1958: The stratigraphy and geologic structure of the Late Mesozoic formations in western Chugoku and northern Kyushu. *Geological Report of the Hiroshima University*, no. 6, p. 280-342. (*in Japanese*)

Hase, A., 1960: The Late Mesozoic formations and their molluscan fossils in the West Chugoku and North Kyushu, Japan. *Journal of Science of the Hiroshima University, series C*, vol. 3, p. 1-50.

Hayashi, K., 1998: Nonmarine Ostracoda from the Lower Cretaceous Wakino Subgroup in northern Kyushu, Japan. *Bulletin of Tokyo Gakugei University, Section IV*, vol. 50,

p. 77-113.

Ikushima, I., 1969: Fig. III. 63 Vertical distribution of living weight of large aquatic plants in Lake Biwa. *In*, Numata, M. *ed. Ecology of plants*, p.100. Asakura-shoten, Tokyo. (*in Japanese*)

Kazaki, H., 1967: Concept of aquatic plant. Genetics, vol. 21, p. 4-9. (*in Japanese*)

Kim, B. K., 1969: A study of several sole marks in the Haman Formation. *Journal of the Geological Society of Korea*, vol. 5, p. 243-258.

Kobayashi, T. and Ota, I., 1936: Wakino beds in North Kyushu. *Journal of Geography, Tokyo Geographical Society*, vol. 48, p. 298-302. (*in Japanese*)

Kobayashi, T. and Suzuki, K., 1936: Non-marine shells of the Naktong-Wakino series. *Japanese Journal of Geology and Geography*, vol. 13, p. 243-257.

Krömmelbein, K., 1962: Zur Taxionomie und Biochronologie stratigraphische wichtiger Ostracoden-Arten aus der Oberjurassisch?-unterkretazischen Bahia-Serie (Wealden-Fazies) NE-Brasiliens. *Senckenbergiana Lethtaea*, vol. 43, p. 437-527.

Kusumi, H., 1960: On the occurrence of Cretaceous estherids in North Kyushu. *Journal of Science of the Hiroshima University, Series C*, vol. 3, p. 15-24.

Kusumi, H., 1979: On the Estherids from the Kanmon Group in the Kitakyushu City. *Bulletin of the Kitakyushu Museum of Natural History*, no. 1, p. 31-39.

Lockley, M. G., Fleming, R. F., Yang, S. Y. and Lim, S. K.,1991: The distribution of dinosaur and bird tracks in the Jindon Formation of South Korea: implications for paleoecology. Fukuoka International Symposium and IGCP Workshop No. 245, Kyushu University, (*Abstract*), p. 62.

Lockley, M. G., Yang, S. Y., Matsukawa, M., Fleming, F. and Lim, S. K., 1992: The track record of Mesozoic birds: evidence and implications. *Philosophical Transactions of the Royal Society of London, Series B*, vol. 336, p. 113-134.

Matsukawa, M. *ed.*, 1991: *Lower Cretaceous nonmarine and marine deposits in Tetori and Sanchu, Honshu*, 116 p. IGCP-245 Field Trip Guide Book, Fukuoka International Symposium, Kyushu University.

Matsukawa, M. and Ito, M., 1995: Evaluation of nonmarine bivalves as index fossils based on those from the Japanese Lower Cretaceous. *Journal of the Geological Society of Japan*, vol. 101, p. 42-53.

Matsukawa, M. and Obata, I., 1992: Correlation of nonmarine and marine formations in the Lower Cretaceous of Japan: A contribution to nonmarine formations in Asia. *In*, Mateer, N. J. and Chen, P. J.*eds.*, *Aspect of Nonmarine Cretaceous Geology*, p. 78-93. China Ocean Press, Beijing.

Matsukawa, M. and Obata, I., 1994: Dinosaurs and sedimentary environments in the Japanese Cretaceous: A contribution to dinosaur facies in Asia based on the molluscan paleontology and stratigraphy. *Cretaceous Research*, vol. 15, p. 101-125.

Matsukawa, M., Takahashi, O., Hayashi, K. and Ito, M., 1996: Early Cretaceous paleogeography of Mollusca (ammonites etc.) and dinosaurs in East Asia. *Monthly Earth*, vol. 18, p. 742-747. (*in Japanese*)

Matsumoto, T., 1951: The Yezo Group and the Kwanmon Group. *Journal of the Geological Society of Japan*, vol.

57, p. 95-98. (in Japanese)

Matsumoto, T., 1962: Mesozoic erathem. In, Matsumoto T. ed., Regional Geology of Japan, Kyushu, p. 19-41. Asakura-shoten, Tokyo. (in Japanese)

Matsushita, H., 1968: Report of Geological Research in Kitakyushu City, 43 p. Kitakyushu City.

Okada, H., Sakai, T. and Seo, S. G., 1991: Symposium field trip guide book, 92 p. 1991 Fukuoka International Symposium, Kyushu University.

Ota, M., Toriyama, R., Hojo, Y., Sotsuka, T., Nishida T., Fujii, A., Sugimura, A., Haikawa, T., Nagai, K. and Sugiyama, T., 1979: Geology of the Kanmon Group in the southern district of Kokura, Kitakyushu City. Bulletin of the Kitakyushu Museum of Natural History, no. 1, p. 1-10.

Ota, Y., 1953: On the Mesozoic System in Mt. Kasagi District (so-Called Wakino District), Kurategun, Fukuoka Prefecture. Bulletin of Fukuoka Gakugei University, no. 2, p. 206-213. (in Japanese)

Ota, Y., 1955: Stratigraphy and Geologic Structure of the Mesozoic formations of the Dobaru Area, Kokura City. Bulletin of Fukuoka Gakugei University, no. 5, p. 29-39. (in Japanese)

Ota, Y., 1957: On the Mesozoic formations of the Southern Kokura and Yahata Cities. Bulletin of Fukuoka Gakugei University, no. 7, p. 63-73. (in Japanese)

Ota, Y., 1960: The zonal distribution of the non-marine fauna in the Upper Mesozoic Wakino Subgroup. Memoirs of the Faculty of Science, Kyushu University, Series D, vol. 9, p. 187-209.

Paik, K. H., Kim, Y. K. and Huh, M., 1988: Ostracoda from the Chinju Formation (Cretaceous, nonmarine) in Kyeongsang basin, Korea. Journal of the Paleontological Society of Korea, vol. 4, p. 94-109.

Sakai, T., Seo, S. G. and Okada, H., 1992: Lithostratigraphy and sedimentological features of the Lower Cretaceous Wakino Subgroup in and around Yamada Park, south of Kokura, Kitakyushu City. Science Reports, Department of Earth and Planetary Sciences, Kyushu University, vol. 17, no. 3, p. 55-66. (in Japanese)

Seo, S. G., Sakai, T. and Okada, H., 1992: Occurrence and origin of rhythmites, in Lower Cretaceous lacustrine sediments in the Wakino Subgroup, Kyushu. Science Reports, Department of Earth and Planetary Science, Kyushu University, vol. 17, p. 45-54. (in Japanese)

Seo, S. G., Sakai, T. and Okada, H., 1994: Depositional environments of the Wakino Subgroup of the lower Cretaceous Kanmon Group in the Kitakyushu area, Japan. Memoirs of the Faculty of Science, Kyushu University, series D, vol. 18, p. 41-60.

Yabumoto, Y., 1994: Early Cretaceous freshwater fish fauna in Kyushu, Japan. Bulletin of the Kitakyushu Museum of Natural History, no. 13, p. 107-254.

Yang, S. Y., Lockley, M. G., Greben, R., Erickson B. R. and Lim, S. K.,1995: Flamingo and duck-like bird tracks from the Late Cretaceous and Early Tertiary: evidence and implications. Ichnos, vol. 4, p. 21-34.

Yang, S. Y., Lim, S. K., Lockley, M. G., and Fleming, R. F.,1990: On Cretaceous bird tracks from the Jindong Formation, Gyeongsong Group, Korea. Journal of the Geological Society of Korea, vol. 20, p. 580.

Ye, C. H.,1994: Succession of Cypridacea (Ostracoda) and nonmarine Cretaceous stratigraphy of China. Cretaceous Research, vol. 15, p. 285-303.

Further notes on the turrilitid ammonoids from Hokkaido– Part 2 (Studies of the Cretaceous ammonites from Hokkaido and Sakhalin-XC)

TATSURO MATSUMOTO[1] and TAKEMI TAKAHASHI[2]

[1]c/o Kyushu University Museum, Fukuoka, 812-8581, Japan

[2]28-109 Hanazono-cho, Mikasa, 068-2124, Japan

Abstract. Six species of *Turrilites*, two species of *Mesoturrilites* and two species of *Mariella* are described on the basis of material from the lower and middle parts of the Cenomanian (mid-Cretaceous) in the central and northwestern Hokkaido. Several of them are well known for their worldwide distribution and occur in Hokkaido at correlatable stratigraphic levels. Three new species, *Turrilites complexus*, *T. miroku* and *Mesoturrilites pombetsensis*, are established, showing interesting but still questionable relationships with some previously known ones. Two species in open nomenclature require further study.

Key words: Cenomanian, Hokkaido, *Mariella*, *Mesoturrilites*, *Turrilites*

Introduction

The material from the Cretaceous Yezo Group of Hokkaido provides not only examples of well known, widespread species but also of other, little known or new ones. Selected examples of both categories are studied to improve systematic, biostratigraphic and biogeographic knowledge. The studied specimens came primarily from the Cenomanian of the Ikushunbetsu Valley of the Mikasa district, central Hokkaido, and the Abeshinai-Saku area of the Nakagawa district, northwestern Hokkaido. For the stratigraphy of the two areas, readers may refer to the two papers: Matsumoto (compiled, 1991, p. 3-5, 21-24) for the former and Matsumoto (1942, p. 180-214) for the latter. The material depends primarily on the collections of T. T. and T. M. In addition to them several specimens from these and also adjacent areas treated in the two papers written in Japanese, i. e., Nishida *et al.* (1997) and Hayakawa and Nishino (1999) are cited with brief remarks. An additional specimen from Abeshinai has been provided by M. Okamura.

Repositories.—The specimens treated in this paper are officially registered in the following institutions, with prefixes:

GK: Geological Collections, Kyushu University Museum, Fukuoka, 812-8581, Japan

GS: Geological Collections in Saga University, Saga, 840-8502, Japan

IGPS: Museum of Natural History, Tohoku University, Sendai, 980-8578, Japan

NMA: Nakagawa Museum of Natural History, Nakagawa, 098-2802, Hokkaido, Japan

UMUT: University Museum, University of Tokyo, Hongo, Tokyo, 113-0033, Japan

The specimen collected by T. T. is indicated with the previous number in brackets. Likewise, the specimen collected by T. M. and once stored in UMUT under the heading of GT is indicated in brackets, for it is now officially transferred to GK.

Systematic descriptions

(continued from Part 1)

Genus *Turrilites* Lamarck, 1801

Type species.—*Turrilites costatus* Lamarck, 1801 (p. 101) by original designation.

Diagnosis. — Tightly coiled turrilitids with small apical angle. Ribs with no or two to four rows of tubercles; ribs and tubercles equal in number in all rows (modified from Wright and Kennedy, 1996, p. 349).

Remarks.—Besides well known *T. scheuchzerianus* Bosc, 1801, *T. costatus* Lamarck, 1801 and *T. acutus* Passy, 1832, two new species established below occur in the Cenomanian of Hokkaido.

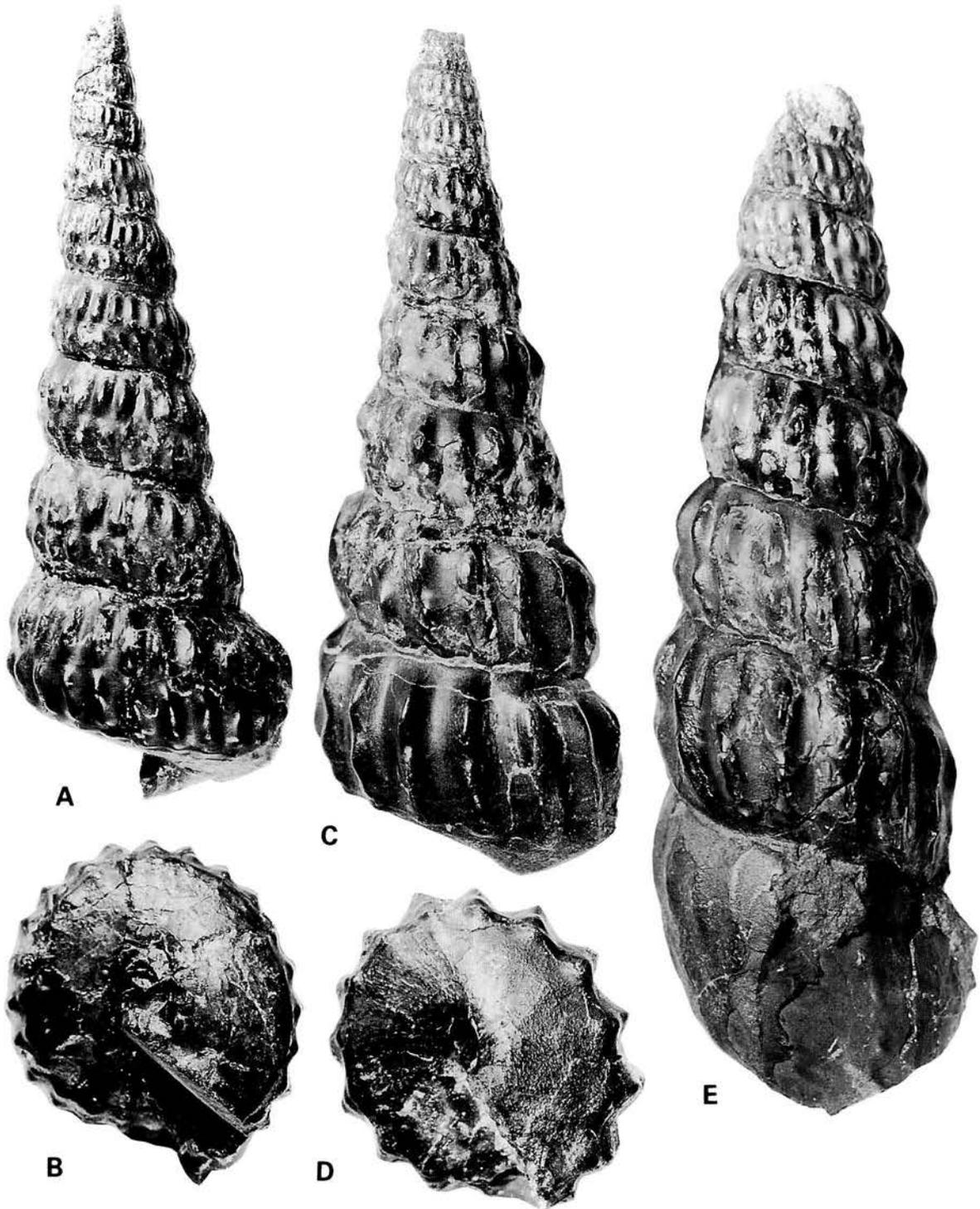### *Turrilites complexus* sp. nov.
Figures 1, 2, 3A-D

Figure 1. *Turrilites complexus* sp. nov. **A, B.** GK.H8552 (holotype). **C, D.** GK.H8553. **E.** GK.H8554. **A, C, E:** lateral views. **B, D:** basal views. Figures are all ×1.5. Photos courtesy of M. Noda.

Table 1. Measurements of *Turrilites complexus* sp. nov.

Specimen	NW	Hp	Ht	D	ap	h	d	h/d	R(T)
GK.H8552	9.0	84.0	102.0	30.0	20°	12.0	23.5	0.51	26–22
GK.H8553	8.5	87.0	105.3	33.5	19°	14.5	28.2	0.51	22–16
GK.H8554	7.0	103.5	133.0	31.0	20°	15.5	31.0	0.50	24–17
GK.H8550	7.5	40.7	55.0	16.8	22°	7.2	15.0	0.48	31–22
NMA–151	7.5	33.8	–	13.6	19°	5.3	11.0	0.48	27–23 (?)

NW = number of preserved whorls, Hp = total height of the preserved shell, Ht = total height of shell from the preserved last whorl to the estimated apex, D = diameter of the preserved last whorl, ap = estimated apical angle. h = height of an exposed flank of a late whorl, diameter of the same whorl, R or T = number of ribs or tubercles in a given row per whorl, showing change with growth, if any.   Linear dimension is in mm.

Material and occurrence.—Holotype is GK.H8552 [= previous S.40·5·16] (Figure 1A, B; Figure 3A, B) collected by T. T. in 1965 at Loc. Ik1100, on the right side of the River Ikushunbetsu, from the lower part of the Member IIb of the Mikasa Formation (see Matsumoto, 1991, p. 22, fig. 1). Paratypes from the type locality are GK.H8550 [= S.39·4·27] (Figure 3C, D), GK.H8553 [= S.40·8·7] (Figure 1C, D) and GK.H8554 [= S.50·4·13] (Figure 1E), collected by T. T. in 1964, 1965 and 1975 respectively.   Another paratype is a large but incomplete specimen, GK.H8558 [= previous GT. I–3150] (Figure 2A, B), collected by T. M. in 1938 at Loc. T591b on the left side of the River Abeshinai of the Nakagawa district.   Also NMA–151, collected by T. Nishino at "Loc. Y" [Yasukawa] and illustrated by Hayakawa and Nishino (1999, pl. 10, fig. f) as *T. costatus*, should now be transferred to this species.   There are more examples from both Mikasa and Nakagawa districts, but at present they belong to private possessions.

Diagnosis.—Turreted shell with a low apical angle, showing the ontogenetic change of ornamentation from numerous, crowded ribs with scarcely discernible tubercles to the diagnostic ribs with tubercles of moderate intensity like *Turrilites costatus*.   In addition to the three rows of ribs or tubercles like those of *T. costatus*, there are clavate small tubercles of the fourth row, from which radial ribs run on the lower (or basal) surface to the narrow umbilicus.   The concave zone between the upper and lower ribs is faint in youth, moderately distinct in the middle or main stages, and may become indistinct at the last stage.

Description.—The available specimens are scarcely affected by secondary deformation.   They are, however, incomplete in that the very apex is lacking and their last whorl is more or less deficient.   The holotype (Figure 1A, B; Figure 3A, B) and a paratype, GK.H8553 (Figure 1C, D) are slightly over 100 mm in the original height.   In both specimens the preserved last whorl is still septate.   GK.H8554 (Figure 1E) is the largest of the four specimens from the type locality, showing 133 mm in the total height of the shell. The body chamber is preserved in this specimen, but its apertural part is destroyed.   GK.H8550 (Figure 3C, D) shows the characters of the young shell, although the initial part is lacking.

Despite some deficiencies mentioned above, they show as a whole the above-described diagnostic characters. This is also supplemented by the measurements (Table 1).
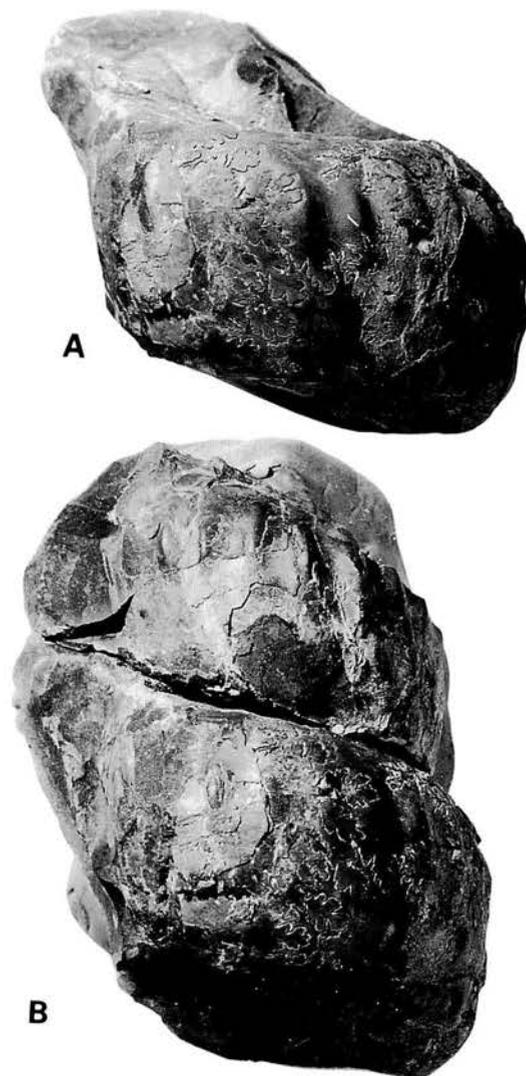

Figure 2.   *Turrilites complexus* sp. nov.   **A, B.** GK.H8558. **A** is the detached lower whorl of **B** and slightly turned clockwise to show clearly the saddle between E and L.   Figures are ×1. Photos by C. Ueki.

Minor differences between specimens can be regarded as infraspecific variation. For instance, the decrease in the rib density with growth varies from individual to individual (see Figure 4). The tubercles on the last whorl of GK.H8554 (Figure 1E) become weaker than those of the preceding whorls, but a similar feature often occurs in the last whorl of the turrilitid ammonoids.

The septal suture at a young stage is exposed partly on GK.H8550. L is situated on the concave zone between the upper and lower ribs. The suture of a late growth stage is much incised (see Figure 2). The E-L saddle is so broad that L is shifted toward the lower whorl seam and U is in the middle part of the lower whorl face (Figure 2A). The incised branches of an element (probably I) are extended from the concealed side (Figure 2B).

Comparison and discussion.—With respect to the characters of the middle to late growth stages this species resembles *Turrilites costatus* Lamarck, but it is distinguished by the

Figure 3. **A–D.** *Turrilites complexus* sp. nov. **A, B.** GK.H8552 (holotype). Fig. **3A** is 180° turned from Fig. **1A**; **Fig. 3B** is another basal view in a different light from Fig. **1B**. Figures slightly over natural size. **C, D.** GK.H8550, lateral and basal views, ×2. **E, F.** *Turrilites* aff. *costatus* Lamarck. GK.H8549, lateral and basal views, ×2. **G.** *Turrilites scheuchzerianus* Bosc, 1801. Gk.H8563, half exposed from the rock matrix, ×1.5. **H, I.** *Turrilites costatus* Lamarck, 1801. **H.** GK.H1373, ×2. **I.** GK.H8560, ×1. **J–M.** *Turrilites acutus* Passy, 1832. **J.** GS.G114, ×2. **K.** GS.G113, ×2. **L.** GS.G127, ×1.7. **M.** GK.H8559, ×1. **N.** *Mesoturrilites* cf. *aumalensis* (Coquand). GK.H8562, ×2. Photos courtesy of M. Noda (A–D), N. Egashira (G, H, J–L) and C. Ueki (I, M, N).
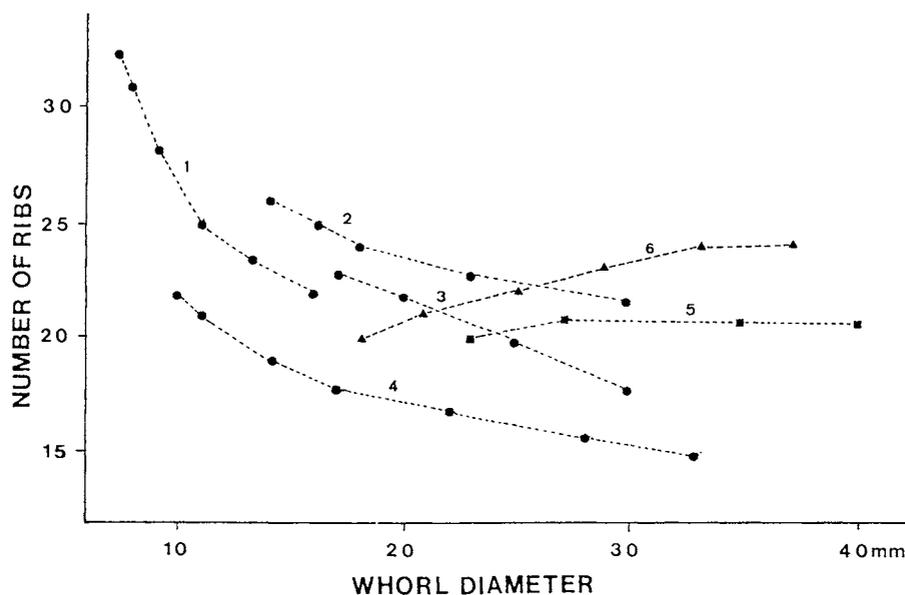
Figure 4. Diagram showing the ontogenetic change of rib density in some representative specimens of *Turrilites complexus* sp. nov. (small solid circle), *Turrilites costatus* Lamarck (solid square), and *Turrilites scheuchzerianus* Bosc (solid triangle). **1:** GK.H8550, **2:** GK.H8552 (holotype), **3:** GK.H8554, **4:** GK.H8553, **5:** GK.H8560, **6:** BG5 GSM 7772 (Sharpe, 1857, pl. 26, fig. 1).

presence of spirally elongated tubercles of the fourth row. In younger growth stages the two species are undoubtedly different in ornamentation. Also, as is shown in Figure 4, in contrast to the ontogenetic decrease of rib density in *T. complexus*, *T. costatus* maintains uniform density with growth.

With respect to the morphological characters of young shells this species resembles *Turrilites scheuchzerianus* Bosc in showing interrupted ribs on rather flat or only gently convex flank, without or with very faintly appeared swellings. The number of ribs seem to vary between individuals in *T. scheuchzerianus*, but the decrease of the number with growth is not so remarkable as in *T. complexus*. Again, the presence of the clavate tubercles of the fourth row in *T. complexus* is a distinction. As to the characters of the middle to late stages *T. complexus* is clearly different from *T. scheuchzerianus*.

Stratigraphically *T. complexus* first appears from a lower level than *T. scheuchzerianus* and *T. costatus*. Hence, it can be presumed that the latter two species may have branched from the former almost simultaneously or successively at slightly different times.

The middle-aged shell of this species resembles *Mariella (Mariella) oehlerti* (Pervinquière, 1910) (see also Matsumoto *et al.*, 1999, p. 109, figs. 2-4; Matsumoto *et al.*, 2000, p. 8, fig. 3) in the whorl shape and ornamentation. The latter shows a wide extent of variation in the density of tubercles, as Klinger and Kennedy (1978, p. 32, fig. 9) have demonstrated. But the ontogenetic change of ornament in the latter species is not so great as in *T. complexus*. On the average tubercles are predominant over ribs in *M. (M.) oehlerti*, but ribs in the upper row characterize the middle-aged whorls of *T. complexus* as in the main part of the *T. costatus* shell. The spirally elongated tubercles of the

fourth row are common in *M. oehlerti* and *T. complexus*.

There is, however, to some extent infraspecific variation. For instance, Klinger and Kennedy (1978, p. 33) pointed out the presence of "variety A" in *M. (M.) oehlerti* "which differs from the "typical form" in possessing moderately to well-developed ribs". Numerous specimens of *M. (M.) oehlerti* from Zululand and Natal in South Africa seem to be more or less fragmentary, as are shown by the illustrations by Klinger and Kennedy (1978, pl. 6, figs. H-N, P; pl. 7, fig. G). If fragmentary pieces of a middle-aged shell of *T. complexus* were mixed with them, they might be regarded as the ribbed variety of *M. (M.) oehlerti*.

Discussion.—This species occurs in the lower part of the Member IIb of the Mikasa Formation. This unit is biostratigraphically defined as the Zone of *Mantelliceras japonicum* - *Sharpeiceras kongo*, that is, the second unit in the three subdivisions of the lower Cenomanian in the Ikushunbetsu Valley. It was erroneously listed as *Turrilites costatus* in the stratigraphic notes by Matsumoto *et al.* (1969, p. 287) and also Matsumoto (*in*, Matsumoto, 1991, p. 22). It occurs also in the Abeshinai Valley of the Nakagawa district. A specimen from Loc. T591b is referable to the middle or upper part of the lower Cenomanian, because Loc. T591b is above Loc. T591a, where *Mesoturrilites* cf. *aumalensis* (Coquand, 1862) (see description in later pages) was obtained, and well below Loc. T591d, where *Turrilites acutus* Passy, 1832 (see below) occurred. The "Locality Y" of Yasukawa, where a specimen of *T. complexus* (NMA–151) was collected, is a fairly extensive exposure of strata, about 70 m in thickness, but the stratigraphic level of NMA – 151 is not precisely recorded by Hayakawa and Nishino (1999). Although they ascribed the entire thickness of the exposed strata of "Loc. Y" to the middle Cenomanian, the assignment is questionable, because *Cunningtoniceras*

Table 2. Measurements of *Turrilites costatus* Lamarck.

Specimen	NW	Hp	Ht	D	ap	h	d	h/d	R(T)
GK.H8560	6	105.0	150.0	41.0	20°	20.0	37.0	0.54	22
NMA-145	5	115.0	165.0	45.0	23°	24.0	42.5	0.56	ca.21

Legend as for Table 1. In NMA-145 about 120° of each whorl is embedded in the rock matrix.

Table 3. Measurements of *Turrilites* aff. *costatus* Lamarck.

Specimen	NW	Hp	Ht	D	ap	h	d	h/d	R(T)
GK.H8549	8.0	19.6	20.8	10.2	3°	3.7	8.0	0.46	15-24

Legend as for Table 1.

sp., an index of middle Cenomanian, was obtained, according to the collector (Yutaka Koike), from the uppermost part of the sequence.

At present this species is known to occur only in Japan. In view of the worldwide distribution of *T. scheuchzerianus* and *T. costatus*, whether *T. complexus* has a more extensive distribution should be clarified.

Turrilites scheuchzerianus Bosc, 1801

Figure 3G

Turrilites scheuchzerianus Bosc, 1801, p. 190; Wright and Kennedy, 1996, p. 349 (with full synonymy)

Type.—"The status and whereabouts of the type material (Bosc, 1801, p. 190) have not been well established" (Wright and Kennedy, 1996, p. 349).

Material.—GK.H8563 [= previous GT.I-3154] (Figure 3G) collected by T. M. from a floated nodule at Loc. T32-33p, Saku-gakko-no-sawa, Nakagawa district. NMA - 144, NMA-143 and NMA-142, collected by T. Nishino from "Loc. T" of Nakagawa district and described in Japanese by Hayakawa and Nishino (1999, p. 11, pl. 10, figs. a, b-c, e).

Descriptive remarks.—This species has been amply described and discussed by Wright and Kennedy (1996, p. 349, pl. 106, figs. 7, 8, 11, 12; pl. 107, figs. 1-7; text-figs. 137G, J; 138C, D, F-I, N; 139D-I; 140A, D-I; 143H; 147A, B) on the basis of numerous specimens from South England and extensive regions in the world. In addition to the specimens reported by Hayakawa and Nishino (*vide supra*), we know that a well preserved specimen occurred in the Zone of *Cunningtoniceras takahashii* at Loc. Ik1051b of the Ikushunbetsu Valley. It is quite similar to a British specimen (BMNH 30210, Wright and Kennedy, 1996, pl. 107, fig. 7), but it is not officially registered.

Distribution.—Middle part of the Cenomanian in Hokkaido. For the range in South England and the worldwide distribution see Wright and Kennedy, 1996, p. 353.

Turrilites costatus Lamarck, 1801

Figure 3 H, I

Turrilites costatus Lamarck, 1801, p. 102 (pars); Wright and Kennedy 1996, p. 354, pl. 103, figs. 1, 2, 5; pl. 104, figs. 1-4, 6, 8-10; pl. 105, figs. 1, 5, 6, 10, 12, 13, 16, 17, 19; pl. 106, figs.

1-6, 9, 10; text-figs. 137C; 139A-C; 142A, F, G; 143A-G, L-P (with full synonymy).

Type.—The specimen from Rouen figured by Douvillé (1904, p. 54a, fig. 1) in the Lamarck Collection is the lectotype designated by Kennedy (1971, p. 30). It is kept in the Muséum National d'Histoire Naturelle, Paris and was reillustrated by Wright and Kennedy (1996, text-fig. 142F).

Material and occurrence. — GK.H8560 [= GT.I-3157a] (Figure 3I) and GK.H8561 (not figured) collected by T. M. in 1938 on the left side of the River Shakotan [= Sakugawa]; NMA-176 and NMA-145 collected by T. Nishino from "Loc. T" on the right bank of the River Teshio, all in the Nakagawa district. GK.H1373 (Figure 3H) collected by T. M. in 1939 from Loc. Y524, Tengu-zawa of the Shuparo area (for the location see Matsumoto, 1942, pl. 25).

Descriptive remarks.—This specimen is well defined by previous authors, especially by Wright and Kennedy, 1996 (*vide supra*). GK.H8560 is a good example from Hokkaido, for it resembles the lectotype. NMA-145 could be regarded as a passage form to *T. acutus* Passy in its pointed tubercles. It is, however, quite similar to GK.H8560 (see ap, h/d and R(T) in Table 2).

Distribution. — The described specimens from Hokkaido are of middle Cenomanian age. For the range in England and also worldwide distribution of this species see Wright and Kennedy, 1996, p. 358.

Turrilites aff. costatus Lamarck, 1801

Figure 3 E, F

Material.—A single specimen, GK.H8549 [= previous S.4 3·5·7] (Figure 3E, F) collected by T. T. in 1968 at Loc. Ik1100 from the lower part of the Member IIb of the Mikasa Formation.

Descriptive remarks.—This is a small, probably immature specimen. It looks like *T. costatus*, but it shows a larger apical angle and lower whorls in comparison with the latter (compare Table 3 with Table 2). Its younger whorls show rather prominent tubercles in the upper row at moderate intervals (15-17 per whorl) and corresponding number of small tubercles in the lower row. Hence, the young shell is rather similar to *T. acutus* (*vide post*). The later whorls have tuberculated ribs like those of *T. costatus*, but they are rather

Table 4. Measurements of *Turrilites acutus* Passy.

Specimen	NW	Hp	Ht	D	ap	h	d	h/d	T
GK.H8559	3	40.0	77.0	32.5	27°	12.0	25.0	0.48	20
NMA–131	6	50.0	60.0	25.0	30°	9.0	19.0	0.47	18
GK.H8551	9	175.0	—	ca.77	—	ca.32	ca.67	ca.0.48	20

Legend as for Table 1. GK.H8551 is so much deformed that D and d are roughly estimated on the basis of the measured maximum and minimum dimensions.

crowded and numerous (24 in the preserved last whorl). There are closely set two rows of spirally elongated tubercles along the lower whorl seam. Thus, the shell of this stage is similar to the middle-aged shell of *T. complexus*. The morphological characters of the still later stage of this specimen are not known.

Despite the incomplete preservation, the specimen is so peculiar that it is tentatively described under the above heading. Its relation with *Mariella* (*M.*) *oehlerti* (Pervinqière, 1910) (see Matsumoto *et al.*, 1999) should be examined on the basis of further material.

Turrilites acutus Passy, 1832

Figures 3 J-M, 5, 6

Turrilites acutus Passy, 1832, p. 9, pl. 16, figs. 3, 4; Wright and Kennedy, 1996, p. 358, pl. 103, fig. 3; pl. 104, figs. 5, 7, 11; pl. 105, fig. 21; pl. 108; figs. 1–4, 8, 11, 12; text-figs. 138M; 141A; 146N-O (with full synonymy).

Lectotype.—The original of Passy, 1832, pl. 16, fig. 3 by the subsequent designation of Juignet and Kennedy, 1977, p. 65. For its photographic illustration see Wright and Kennedy, 1996, pl. 108, fig. 8a-c.

Material and occurrence.—GK.H8559 [= previous GT.I-3155] (Figure 3M) collected by T. M. in 1938 at Loc. T591d, a cliff on the left side of the River Abeshinai and NMA–131 collected by Nishino from "Loc. T" on the right bank of the River Teshio (Hayakawa and Nishio, 1999, p. 11, pl. 10, fig. h), both in the Nakagawa district. GS.G113, GS.G114 and GS.G127 (Figure 3K, J, L; reproduced here from Nishida *et al.*, 1997, pl. 7, figs. 10, 11 and pl. 12, fig. 5) collected by Kawashita and Egashira from a floated nodule in the Fuku-no-sawa, a branch of the River Shumarinai in the Soeushinai area (for the location see Nishida *et al.*, 1997, text-fig. 8). GK.H8551 [= previous S.43·4·30] (Figure 5) collected by T. T. in 1968 at Loc. Ik1102, north side of the River Ikushunbetsu, from the bed with *Cunningtoniceras takahashii* (Matsumoto). The above records of occurrence all indicate a middle Cenomanian age.

Diagnosis.—On the basis of the previous works the diagnosis may be written as follows. A species of *Turrilites* characterized by pointed tubercles of two rows on the flank, with a concave zone between them, and also clavate smaller tubercles of the third row along the lower whorl seam; the upper tubercles are bullate upward; weak radial ribs may run on the lower surface at least partly. Whorls are rather low, showing h/d below 0.5; hence the apical angle is normally 25°-30°.

Description.—GK.H8559 is similar to the lectotype and some other specimens of the corresponding growth stage, e. g., those illustrated by Wright and Kennedy (1996, pl. 106, figs. 1, 2, 8, 17) or by Atabekian (1985, pl. 29, figs. 1, 2, 4).
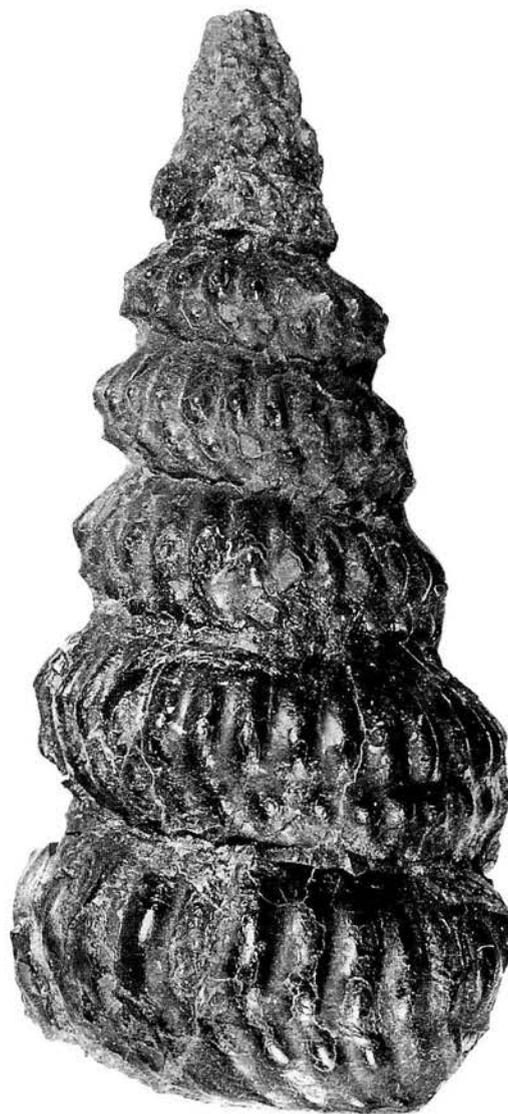

Figure 5. *Turrilites acutus* Passy, 1832. GK.H8551. Lateral view of a deformed specimen, ×0.8. Photo courtesy of M. Noda.

On the basal surface of GK.H8559 weak radial ribs run from the clavate tubercles of the third row, showing a gentle curvature. The suture is well shown on this specimen (Figure 6). It is essentially similar to the suture illustrated by Atabekian (1985, pl. 29, figs. 1a, 1b).

GK.H8551 is a large specimen, although it is deformed. The diagnostic characters are clearly manifested by its main part, but in its later whorls the tubercles are rather blunt and transitional to longer ribs (see Figure 5).

Distribution.—Middle Cenomanian in Hokkaido. For the worldwide distribution see Wright and Kennedy (1996, p. 361).

Turrilites miroku sp. nov.

Figure 7

Material.—Holotype, here designated, is GK.H5916 from Loc. Ik1067p, Shimo-ichino-sawa of the Ikushunbetsu

Figure 6. *Turrilites acutus* Passy, 1832. Septal suture of GK.H8559 at h = 12.5 mm. Broken line = whorl seam, dotted line = approximate outline of a tubercle or rib, E = external lobe, L = lateral lobe, U = umbilical lobe. A branch of an internal element (probably I) is extended from the unexposed side. Figure is about ×4. Drawing by T. M.

Figure 7. *Turrilites miroku* sp. nov. GK.H5916 (holotype). Two lateral (**A** and **B** turned 180°) and basal (**C**) views; also another lateral view (**D**) which is turned 120° anticlockwise from A. A–C are ×1; D is ×1.5. Photos courtesy of M. Noda.

Table 5. Measurements of *Turrilites miroku* sp. nov.

Specimen	NW	Hp	Ht	D	ap	h	d	h/d	R(T)
GH.H5716	4	68.0	107.0	31.0	21°	13.0	23.0	0.57	22

Legend as for Table 1.

Valley.

Specific name.—Miroku [= Maitraya in Sanskrit], a deity in Buddhism, who will help people in the remote future.

Diagnosis.—A species of *Turrilites* with small apical angle. Each whorl is characterized by downward steeply inclined flat flank, with its maximum diameter at the level of lower tubercles. The upper, longer ribs rather weak and faintly tuberculated at their lower end. Lower ribs short, prorsiradiate, and sharply tuberculated in their upper part, terminating at the smaller tubercles of the third row aligned along the lower whorl seam. The lower (or basal) whorl face gently convex and nearly smooth.

Description.—The holotype consists of four whorls of 68 mm in total height. It lacks the whorls of the early and also the last stages. Assuming that one more whorl is the lost body chamber, the restored shell would be at least 105 mm in total height and 40 mm in diameter of the basal surface. The estimated apical angle is 21°

Each whorl of this specimen shows a peculiar shape, for its main part of the flank is flat, without convexity, and steeply inclines downward to the level of the prominent tubercles in the lower part, where the maximum diameter is located. Downward from this level, the lower portion of the flank inclines inward for a short distance to the lower whorl seam. Whorls are tightly in contact. The ratio of height (h) to diameter (d) in each whorl, excluding the unexposed lower surface, distinctly exceeds 0.5 (see Table 5).

The ornament is also peculiar to this species. The ribs on the upper flank are weak but moderately numerous, 22 per whorl. Each of them terminates at a small and blunt tubercle. Below this first row of tubercles there is a narrow and shallow, spiral groove; then comes the second row of moderately prominent tubercles, where the flank is somewhat angular at the tubercle or shouldered along the interspace. A short but sharp rib runs from each tubercle of the second row downward to a less prominent small tubercle of the third row, which runs along the lower whorl seam. The upper ribs run transversally with slight curvature, whereas the lower ribs are clearly prorsiradiate together with the bullate tubercles. Lower or basal surface of the whorl is almost smooth and gently inflated around a narrow umbilicus.

Septal sutures are partly exposed but not clearly traced.

Comparison.—At present only one specimen (holotype) is available for this species. Its approximate size described above is somewhat larger than the lectotype of *Turrilites acutus* Passy, 1832 (pl. 16, fig. 3; reillustrated by Wright and Kennedy, 1996, pl. 105, fig. 5) and probably smaller than the lectotype of *Turrilites wiestii* Sharpe, 1857 (pl. 27, fig. 8; reillustrated by Wright and Kennedy, 1996, pl. 105, fig. 18).

Some young shells of *Turrilites scheuchzerianus* Bosc, 1801, exemplified by such specimens as illustrated by Wright and Kennedy (1996, text-fig. 138C-D, F-G, N; pl. 107, fig. 1), are somewhat similar to the present species in

showing a downward broadening whorl, nodelike swelling, if not tuberculation, of the lower ribs, and the smooth basal surface. However, in typical examples of *T. scheuchzerianus* the apical angle is smaller, the whorl flank is gently convex, and the tubercles are not developed.

With respect to the characteristic whorl shape, the present species is similar to a certain form of *T. wiestii* represented by a group of specimens illustrated by Wright and Kennedy, 1996, pl. 105, figs. 7, 8, 11 and pl. 108, figs. 9, 13. It is, however, different from the above form as well as the lectotype of *T. wiestii* (Sharpe, 1857, pl. 27, fig. 8; reillustrated by Wright and Kennedy, 1996, pl. 105, fig. 18) in its more numerous and less distant ribs with weaker tubercles. The lectotype shows a dissimilar whorl shape.

This species could be referred to the subgenus *Ostlingoceras* (*Ostlingoceras*) Hyatt, 1900, but in the latter the transversal ribs are more numerous and crowded, the tubercles of the second row are smaller and weaker, and the lower (or basal) surface of the whorl has radial ribs, with third and/or fourth rows of small tubercles on its marginal zone. The ribs on the holotype of *T. miroku* are 22 per whorl, showing nearly the same density as that of *T. costatus* (see Tables 2 and 5).

Discussion.—This species is somewhat peculiar in its morphological characters. In this paper it is assigned at least tentatively to *Turrilites* on the grounds of the above comparison.

The holotype of this species was in a transported nodule, which can be inferred to have been derived from somewhere in the lower Cenomanian on account of its having been recovered close to Loc. Ik1065b, where a lower Cenomanian species, *Ostlingoceras* (*O.*) *bechei* (Sharpe) was obtained (see Matsumoto and Takahashi, 2000, p. 262). It should be noted that *T. wiestii* is recorded from the lower Cenomanian of England near the boundary of the *Mantelliceras dixoni* Zone and the *Acanthoceras rhotomagense* Zone (Wright and Kennedy, 1996, p. 354).

At any rate, we have to get more material to clear up questionable points about the systematic and biostratigraphic allocation of the present species.

Genus *Mesoturrilites* Breistroffer, 1953

Type species.—*Turrilites aumalensis* Coquand, 1862.

Diagnosis.—Turrilitid ammonoids with four rows of tubercles or ribs; the first row on the main part of flank made up of ribs and/or tubercles, the second and the third rows of small tubercles on spirally elongated, narrow ridges separated by a groove; the fourth row of small tubercles on the marginal zone of the lower whorl surface where radial ribs run to a narrow umbilicus (modified from Matsumoto and Inoma, 1999, p. 37).

Mesoturrilites cf. *aumalensis* (Coquand, 1862)

Figure 3 N

Compared.—
Turrilites aumalensis Coquand, 1862, p. 323, pl. 35, fig. 3.
Mesoturiilites aumalensis (Coquand, 1862).   Wright and Kennedy, 1996, p. 346, pl. 98, fig. 5; pl. 105, figs. 2, 3, 14; text-figs. 134J, K; 138S-U, W; 146A-G (with full synonymy).

*Material.—*GK.H8562 [= previous GT.I-3310] (Figure 3N), collected by T. M. in 1938 at Loc. T591a, the lowest part of a sequence of strata exposed on the right side of the River Abeshinai in the Nakagawa district.

*Descriptive remarks.—*This specimen is small and incompletely preserved.   It shows a pyramidal shape, conical tubercles of moderate intensity and density at about the midflank, and corresponding number of spirally elongated tubercles in two rows, with a narrow groove in between, along the lower whorl seam.   The clavate tubercles of the fourth

row and radial ribs arising from them are faintly discernible on the lower face.   Although the preservation is insufficient, this specimen can be called *Mesoturrilites* cf. *aumalensis*. It occurs at the level immediately below that of *Turrilites complexus* (*vide ante*).

Mesoturrilites pombetsensis sp. nov.

Figures 8, 9

*Material and occurence.—*Holotype, here designated, is GK.H8532 [= previous S. 37·7·17] (Figure 8A-D) collected by T. T. in 1963 from a transported nodule on the Onkonosawa, a branch of the River Ponbetsu in the Mikasa district.   Paratype is GK.H8548 (Figure 8E, F), collected by T. T. at Loc. Ik1101 on the right side of the R. Ikushunbetsu. The fossiliferous sandy rocks which contain the above specimens are referred to the lower part of the Member IIb of the Mikasa Formation.

*Diagnosis.—*Pyramid-shaped species of *Mesoturrilites*

Figure 8.   A-F. *Mesoturrilites pombetsensis* sp. nov.   Three lateral (**A**, **B** and **C** turned about 120° anticlockwise) and basal (**D**) views of GK.H8532 (holotype), slightly, over natural size.   Lateral (**E**) and basal (**F**) views of GK.H8548, ×1.67.   Photos courtesy of M. Noda.

Table 6. Measurements of *Mesoturrilites pombetsensis* sp. nov.

Specimen	NW	Hp	Ht	D	ap	h	d	h/d	R(T)
GK.H8532	5.5	55.0	60.0	46.0	47°	14.7	33.7	0.44	18
GK.H8548	3.0	29.0	42.0	28.0	45°	8.3	19.3	0.43	22

Legend as for Table 1.

with moderate apical angle, ornamented by fairly coarse ribs on the upper flank, each of which is provided with a node at about the midflank immediately above a shallow concave zone; also two closely set rows of spirally elongate tubercles in the lower part with a groove in between. In more or less later stages the prorsiradiate ribs run across the concave zone and the groove. The ribs further extend radically on the gently convex lower (or basal) surface, with tubercles of the fourth row on the margin of the circular base.

Description.—The holotype consists of nearly six septate whorls, with a fraction of crushed body chamber at the preserved end (Figure 8A, D). It is moderately large (Table 6). A single paratype is small and corresponds to the young part of the holotype. The entire shell shape is pyramidal; the exposed outer face of the whorl consists of a nearly flat or gently inclined upper portion, steeply inclined main part, and incurved lower portion. The interwhorl junction is deep.

The ornament somewhat changes with growth. In the early growth stage the upper ribs are very coarse and tuberculated at their lower end. This is well manifested at the early stage (with d < 15 mm) of the paratype, but is less clear in the holotype. Below the zone of upper ribs a shallowly concave, spiral zone runs at about the midflank. In the middle to late growth stages, the ribs are elongated and the spiral groove is reduced. The prorsiradiate ribs run across the shallowing groove and connect themselves with the spirally elongated tubercles of the second and third rows. They extend to the radial ribs on the lower surface. The ribs are curved at about the rounded, small tubercles of the fourth row. On the well preserved lower face, delicate spiral lines or lirae may be observed and tiny dots may be discernible at the crossing points with the radial ribs (Figure 8 D, F).

Septal suture is deeply and finely indented. Moreover, the extra branches of a lobe (l?) are extended from the other side (Figure 9).

Comparison and discussion.—The holotype of this species is the largest among hitherto reported specimens of *Mesoturrilites*. If its body chamber is preserved, it would be about 80 mm in height and 75 mm in basal diameter. However, it is actually difficult to estimate the real size of the adult shell in the previously described species, because their types are incompletely preserved.

The present species is somewhat allied to *Mesoturrilites aumalensis* (Coquand, 1862) (p. 323, pl. 35, fig. 3), redefined by Wright and Kennedy (1996, *vide ante*) in the general shell shape and the ornamentation of the young stage. In later growth stages ribs become predominant in the former, whereas tubercles characterize the latter. In this respect this species may be somewhat allied to *M. corrugatus* Wright and Kennedy (1996, p. 348, pl. 98, figs. 4, 17), but the ribs in the latter are narrower and sharper, without such
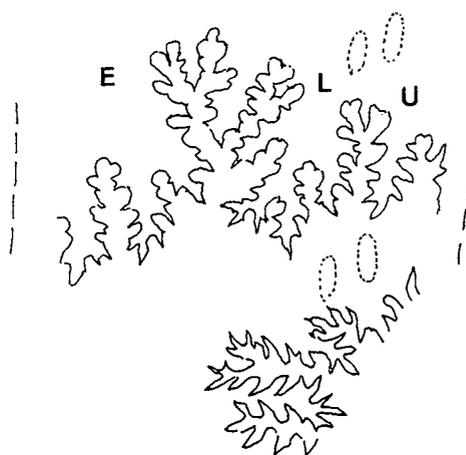

Figure 9. *Mesoturrilites pombetsensis* sp. nov. External suture of GK.H8532 (holotype) at h = 15 mm. Figure is about ×4. Symbols as for Figure 6. Drawing by T. M.

nodes as seen on the ribs of *M. pombetsensis*.

Distribution.—At present this species is represented by only two specimens from the lower part of the Cenomanian in Hokkaido. Although they are fairly well preserved, more material should be searched for to ascertain the vertical range and geographical distribution.

Genus *Mariella* Nowak, 1916

Subgenus *Mariella* (*Mariella*) Nowak, 1916

Remarks.—Altogether 10 species of *M.* (*Mariella*) from Hokkaido have been recently described (Matsumoto *et al.*, 1999; Matsumoto and Kawashita, 1999; Matsumoto and Kijima, 2000; Matsumoto *et al.*, 2000). Two more species are described below.

Mariella (*Mariella*) *cenomaniensis* (Schlüter, 1876)

Figure 10

Type.—Lectotype, by the subsequent designation of Kennedy, 1971 (p. 29), is the original of Schlüter, 1876, pl. 37, fig. 6. The specimen illustrated by Wright and Kennedy (1996, text-fig. 141B) is supposed to be this specimen.

Material and occurrence.—Gk.H8557 [= previous S.55·9·14] (Figure 10A, B), collected by T. T. in 1960 at the point of the Hachigatsu-zawa, near the confluence with the branch rivulet called the Okufutamata-zawa. It is in a calcareous nodule of fine sandstone derived probably from the lower

Figure 10. *Mariella (Mariella) cenomanensis* (Schlüter, 1876). Lateral (**A**) and basal (**B**) views of GK.H8557, ×1.5. Photos courtesy of M. Noda.

Cenomanian part exposed upstream from this locality (see the Geological Map of Kamiashibetsu by Shimizu *et al.*, 1953).

Description.—This single specimen is small but it shows 9 whorls. Its estimated apical angle is low (about 20°), although it is somewhat deformed. The outer exposed whorl face is convex and the whorl junction is deeply impressed. The exposed part of each whorl in lateral view is comparatively high, showing h/d = 0.62 in a measured part.

The tubercles in two rows on the main part of the flank are coarse, numbering 18 per whorl in each row. There is a smooth sloping zone above the upper row of subrounded tubercles. The tubercles of the second row are somewhat clavate. There are spirally elongated tubercles of the closely set third and fourth rows at about the edge between the lateral and lower (or basal) faces.

Remarks.—This specimen resembles smaller examples of *M. (M.) cenomanensis*, e. g., those described by Kennedy (1971, p. 28, pl. 8, fig. 10) and Atabekian (1985, p. 41, pl. 10, figs. 1–6). It is certainly identified with this species on the grounds of the described characters. The apical angle 23° by Wright and Kennedy (1996, p. 342) is somewhat larger than that in ours or in Atabekian's small specimens. This may depend on estimations made from the whorls of different growth stages.

Distribution.—*M. (M.) cenomanensis* has been reported to occur in the lower Cenomanian of various regions in the world (see Wright and Kennedy, 1996, p. 344).

Mariella (Mariella) aff. *circumtaeniata* (Kossmat, 1895)

Figure 11

Compared. —
Turrilites circumtaeniatus Kossmat, 1895, p. 141, pl. 18, figs. 4, 5.
Mariella (Mariella) circumtaeniata (Kossmat, 1895). Klinger and Kennedy, 1978, p. 26, pl. 5, figs. A–C; text figs. 3G, 6D (with full synonymy)

Material.—IGPS 108380 (Figure 11A, B), collected by Makoto Okamura in 1972, at his Loc. AB14 [= Loc. T590c of Matsumoto (1942)] on the left side of the River Abeshinai in the Nakagawa district.

Descriptive remarks.—This specimen is a highly distorted body chamber, measured as 106 × 50 mm in the basal outline. The flank on the figured part (Figure 11A) is well rounded, but the other side is flattened. The ornament consists of three rows of tubercles and the looped ribs. The looping or intercalation of the ribs is frequent in the space between the upper row of tubercles and the upper whorl seam. The interval between the upper and middle rows of tubercles is slightly wider than that between the middle and lower rows. The coiling is sinistral and the ribs are prorsiradiate, extending to the radial ones on the basal surface.

The tubercles of the first row and the ribs of the upper part are very weak. Whether this is the original character or a secondary feature created by weathering is not clear. As the body chamber alone is available, we have to leave the present material in open nomenclature. More material should be searched for to clear up the classification.

M. (Mariella) circumtaeniata has been reported to occur in the upper Albian of southern India, Madagascar, South Africa (Zululand) and (?) New Zealand (see Klinger and Kennedy, 1978, p. 26). The locality of the present specimen is referred to the Unit IIa (lower part of the Cenomanian) in the Abeshinai Valley.
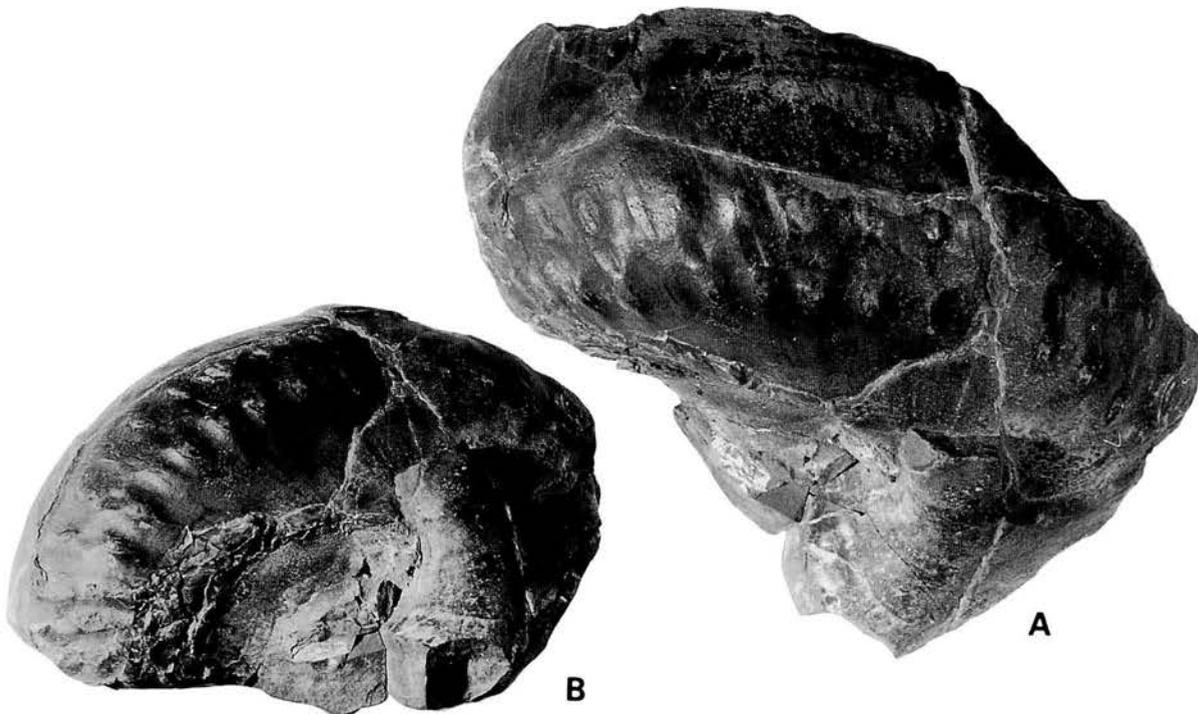
Figure 11. *Mariella* (*Mariella*) aff. *circumtaeniata* (Kossmat, 1895). Lateral (**A**) and basal (**B**) views of IGPS 108380 (a crushed body chamber). A is ×1 and B is ×0.8. Photos courtesy of M. Noda.

Conclusions

To conclude this paper the following results are summarized.

(1) Three well known species of worldwide distribution, *Turrilites scheuchzerianus* Bosc, *T. costatus* Lamarck and *T. acutus* Passy, occur in the middle Cenomanian of Japan.

(2) *Turrilites complexus* sp. nov. is established on several specimens from the Mikasa and Nakagawa districts of Hokkaido, which were previously misidentified with *T. costatus*. This new species shows in youth some features of *T. scheuchzerianus* and later those of *T. costatus*. It retains also some characters of *Mariella* (*Mariella*) *oehlerti* (Pervinquière).

(3) Another new species, *T. miroku*, based on a single specimen from Mikasa, is similar in some respects to a certain form of *T. wiestii* Sharpe, but distinct from the lectotype of the latter. Further study of more material is required.

(4) *Mesoturrilites* cf. *aumalensis* (Coquand) is found in the lower Cenomanian of Nakagawa. Furthermore, *M. pombetsensis* sp. nov. is erected on the specimens from the lower Cenomanian of Mikasa. It has distinct ribs and weaker tubercles.

(5) *Mariella* (*Mariella*) *cenomanensis* (Schlüter), another cosmopolitan, is first recorded from Hokkaido.

(6) *M.* (*M.*) aff. *circumtaeniata* (Kossmat) is reported from Nakagawa, but more material is required for adequate taxonomy and age correlation.

Acknowledgments

References cited

Atabekian, A. A., 1985: Turrilitids of the late Albian and Cenomanian of the southern part of the USSR. *Academy of Sciences of the USSR, Ministry of Geology of the USSR, Transactions*, vol. 14, p. 1–112, pls. 1–34. (*in Russian*)

Bosc, J. A., 1801: *In*, Buffon, G. L. Leclerc, Comte de, *Histoire Naturelle des Coquilles*, 5, Paris, 395p.

Breistroffer, M., 1953: L'evolution des Turrilitidés albiens et cénomaniens. *Compte Rendus Hebdomadaires des Sciences de l'Académie des Sciences*, vol. 237, p.

1349-1351.

Coquand, H., 1862: Géologie et paléontologie de la region sud de la Province de Constantine. *Mémoires de la Sociéte d'Emulation de la Province, Marseille*, vol. 2, p. 1-320, 321-341 (supplement), pls. 1-35.

Douvillé, H., 1904: *Turrilites costatus* Lamarck. *Paléontologie Universalis*, no. 54, p. 54-54b.

Hayakawa, H. and Nishino, T., 1999: Cenomanian ammonite fauna from Nakagawa, Hokkaido, Japan. *Bulletin of Nakagawa Museum of Natural History*, vol. 2, p. 1-40. (*in Japanese with English abstract*)

Hyatt, A., 1900: Cephalopoda. *In*, Zittel, K. A.: *Textbook of Palaeontology*, 1st English edition translated by C. R. Eastman, p. 502-592. Macmillan, London and New York.

Juignet, P. and Kennedy, W. J., 1977: Faunes d'Ammonites et biostratigraphie comparée du Cénomanien du nordouest de la France (Normandie) et du sud de l'Angleterre. *Bulletin trimestriel, Société Géologique de Normandie et des Amis de Muséum du Havre*, vol. 63, p. 1-192.

Kennedy, W. J., 1971: Cenomanian ammonites from southern England. *Special Papers in Palaeontology*, vol. 8, p. 1-133, pls. 1-64.

Klinger, H. C. and Kennedy, W. J., 1978: Turrilitidae (Cretaceous Ammonoidea) from South Africa, with a discussion of the evolution and limits of the family. *Journal of Molluscan Studies*, vol. 44, p. 1-48, pls. 1-9.

Kossmat, F., 1895: Untersuchungen über die Südindische Kreide-Formation. *Beiträge zur Paläontologie und Geologie Oesterreich-Ungarns und des Orients*, vol. 9, p. 97-203, pls. 15-25.

Lamarck, J. B. P. A. de Monet de, 1801: *Système des animaux sans vertèbres*, Paris, 432p.

Matsumoto [Matumoto], T., 1942: Fundamentals in the Cretaceous stratigraphy of Japan, Part 1. *Memoirs of the Faculty of Science, Kyushu Imperial University*, Ser. D, vol. 1, no. 3, p. 129-280, pls. 1-20.

Matsumoto, T. (compiled), 1991: The mid-Cretaceous ammonites of the family Kossmaticeratidae from Japan. *Palaeontological Society of Japan, Special Papers*, no. 33, p. i-vi, 1-143, pls. 1-31.

Matsumoto, T. and Inoma, A., 1999: The first record of *Mesoturrilites* (Ammonoidea) from Hokkaido, *Paleontological Research*, vol. 3, no. 1, p. 36-40.

Matsumoto, T., Inoma, A. and Kawashita, Y., 1999: The turrilitid ammonoid *Mariella* from Hokkaido - Part 1. *Paleontological Research*, vol. 3, no. 2, p. 106-120.

Matsumoto, T. and Kawashita, Y., 1999: The turrilitid

ammonoid *Mariella* from Hokkaido-Part 2. *Paleontological Research*, vol. 3, no. 3, p. 162-172.

Matsumoto, T. and Kijima, T., 2000: The turrilitid ammonoid *Mariella* from Hokkaido-Part 3. *Paleontological Research*, vol. 4, no. 1, p. 33-36.

Matsumoto, T., Muramoto, T. and Takahashi, T., 1969: Selected acanthoceratids from Hokkaido. *Memoirs of the Faculty of Science, Kyushu University*, Ser. D, vol. 19, no. 2, p. 251-296, pls. 25-38.

Matsumoto, T. and Takahashi, T., 2000: Further notes on the turrilitid ammonoids from Hokkaido-Part 1. Paleontological Research, vol. 4, no.4, p. 261-273.

Matsumoto, T., Takashima, R. and Hasegawa, K., 2000: Some turrilitid ammonoids from the mid-Cretaceous of the Shuparo Valley, central Hokkaido. *Bulletin of the Mikasa City Museum, Natural Science*, no. 4, p. 1-13.

Nishida, T., Matsumoto, T., Kawashita, Y., Egashira, N., Aizawa, J. and Ikuji, Y., 1997: Biostratigraphy of the middle part of the Cretaceous Yezo Group in the Soeushinai area of Hokkaido - with special reference to the transitional part from Lower to Upper Cretaceous: supplement. *Journal of the Faculty of Culture and Education, Saga University*, vol. 1, no. 1, p. 237-279. (*in Japanese with English abstract*)

Nowak, J., 1916: Über die bifiden Loben der oberkretazischen Ammoniten und ihre Bedeutung für die Systematik. *Bulletin International de l'Académie des Sciences de Cracovie, serie B*, 1915, p. 1-13.

Passy, A., 1832: *Description géologique du département de la Seine inférieure, Rouen*, 371 p:, 20 pls.

Pervinquière, L., 1910: Sur quelques ammonites du Cretacé algerien. *Mémoires de la Sociéte Géologique de France, Paléontologie*, vol. 17, mémoir 42, p. 1-86, pls. 1-7.

Schlüter, C., 1876: Cephalopoden der oberen deutschen Kreide. *Palaeontographica*, vol. 24, p. 121-264, pls. 36-55.

Sharpe, D., 1857: Description of the fossil remains of Mollusca found in the Chalk of England. Cephalopoda, part 3. *Monograph of the Palaeontographical Society*, London, no. 36, p. 37-68, pls. 17-27.

Shimizu, S., Tanaka, K. and Imai, I., 1953: Kamiashibetsu. Explanatory Text of the Geological Map of Japan, 1: 50000, 78p. (in Japanese) + 21 p. (résume in English). Geological Survey of Japan.

Wright, C. W. and Kennedy, W. J., 1996: The Ammonoidea of the Lower Chalk, part 5. *Monograph of the Palaeontographical Society*, London, no. 601, p. 320-403, pls. 95-124.

Small Permian dicynodonts from India

SANGHAMITRA RAY

Geological Studies Unit, Indian Statistical Institute, 203 B. T. Road, Calcutta 700 035, India
(*email: sray@samuseum.ac.za*)

Abstract. The Lower Gondwana Kundaram Formation of the Pranhita-Godavari valley records the sole occurrence of Permian amniotes in India. The horizon has yielded various dicynodonts, mainly represented by medium-sized *Endothiodon*. This assemblage also contains several small dicynodonts belonging to the family Pristerodontidae and Emydopidae. *Pristerodon* (*P. mackayi* Huxley, 1868), *Emydops* (*E. platyceps* Broom and Haughton, 1917) and *Cistecephalus* (*C. microrhinus* Owen, 1876) are described here. This is the first detailed description of these genera from outside Africa. The older name *Emydops* in place of *Emydoses* is retained and the Indian specimens of *Pristerodon*, *Emydops* and *Cistecephalus* are compared with those from the Beaufort Group, Karoo Supergroup of South Africa. Based on its vertebrate fauna, the Kundaram Formation is broadly correlated with the *Tropidostoma* and *Cistecephalus* Assemblage Zones of the Beaufort Group, Karoo Supergroup, South Africa, the basal beds of the Madumabisa Mudstones of Zambia, the Ruhuhu and the lower part of the Kawinga Formation of Tanzania and the Morro Pelado Member of the Rio do Rasto Formation of Brazil. It suggests a Late Permian Tatarian age for the Kundaram Formation. The distribution of the Kundaram dicynodonts in the other Gondwanan countries indicates the close proximity of the continents during that period and a lack of endemism or provinciality.

Key words: Dicynodont, Gondwana, Kundaram, Pranhita-Godavari valley

Introduction

Permian dicynodonts have been reported from the Kundaram Formation, a Lower Gondwana horizon of the Pranhita-Godavari valley, one of the several Gondwana basins in India (Kutty, 1972; Ray, 1997). The formation is underlain by the coal-bearing Barakar Formation and overlain by the sand-dominant Kamthi Formation (Table 1). The fluvial sediments of the Kundaram Formation comprise red mudstone, sandstone, sandstone-mudstone alternations and ferruginous shale (Ray, 1997).

The extensive red mudstone ground of the Kundaram Formation contains abundant fossils of Permian dicynodonts, which have been collected from the two localities near Golet (Figure 1) in the northwestern part of the Pranhita-Godavari valley (Kutty, 1972). Most of the specimens were encrusted with a hard iron matrix, resulting in the masking of the original shapes and forming oblate and spherical nodules. These were collected *in situ* as isolated skulls with and without lower jaws and other cranial fragments. The separated skulls and lower jaws are mainly preserved with their dorsal sides up. Those skulls with associated lower jaws are found lying on their sides with their lateral sides up. Postcranial elements are relatively rare though a few in the form of rolled vertebrae and broken limb

ends are present and show signs of rolling, abrasion and rounding.

Fossil material prepared mechanically with a dental vibrotool reveals the preponderance of medium-sized *Endothiodon* (superfamily Endothiodontoidea). There are at present two species of *Endothiodon*, *E. uniseries* and *E. mahalanobisi* (Ray, 2000). The former has a skull length (SL) around 300 mm while in the latter it is around 160 mm. In addition, the assemblage contains some very small dicynodonts (SL 50 mm approx.) characterised by a broad intertemporal bar relative to the interorbital region. The aim of this paper is to describe the small and varied dicynodonts of the Kundaram Formation. These dicynodonts are known mainly from Africa and those mentioned here are the first forms from outside Africa to be described in detail. The paper also discusses the biostratigraphic and palaeobiogeographic implications of this unique fauna.

Systematic palaeontology

Infraorder Dicynodontia Owen, 1859
Superfamily Pristerodontoidea Cluver and King, 1983
Family Pristerodontidae King, 1988
Genus *Pristerodon* Huxley, 1868

Table 1. Lower Gondwana succession of the Pranhita-Godavari valley, India.

Formations	Main lithologies	Fossils	Age
Kamthi	Sandstone and siltstone	?dicynodont	Permo-Triassic
Kundaram	Mudstone, sandstone and ferruginous shale	dicynodonts, captorhinid	Late Permian
Barakar	Sandstone, carbonaceous shale and coal	Glossopteris flora	Early to Late Permian
Talchir	Tillite, greenish shale, sandstone		Early Permian

Type species.—*Pristerodon mackayi* Huxley, 1868 (subsequent designation by Keyser, 1993).

Pristerodon mackayi Huxley, 1868

Figures 2A–E, 3–4

Pristerodon mackayi Huxley, 1868, p. 204–205, pl. 12; King, 1988, p. 113; Keyser, 1993, p. 47 (see for prior synonymies).

Holotype.—BMNH R1810, skull and lower jaw from East London, Cape Province, South Africa; *Cistecephalus* Assemblage Zone, Late Permian.

Diagnosis.—Small dicynodonts with or without maxillary tusks; broad intertemporal region; wide parietal exposure; palatine large, leaf-like; postcanine teeth in an oblique, anteriorly converging row; long interpterygoidal vacuity extending to the rear of the vomer; median interpterygoid ridge continues anteriorly on the ventral surface of the anterior pterygoid process; deep dentary sulcus, prominent lateral dentary shelf (Cluver and King, 1983; King, 1988; Keyser, 1993).

Material.—ISIR 209, anterior part of a laterally compressed skull and lower jaw; ISIR 369, anterior part of skull; ISIR 370, distorted skull with lower jaw, ISIR 372, occiput.

Repository.—The specimens are housed in the Geology Museum, Indian Statistical Institute, Calcutta.

Locality and horizon.—Near Golet, Pranhita-Godavari valley, India; Kundaram Formation, Late Permian.

Description.—The Indian material includes a well preserved but laterally compressed, small, anterior half of a skull with associated lower jaw (ISIR 209). Its total length measured along the dorsal midline is inferred to be about 50.6 mm. The morphology of the skull and lower jaw follows the typical dicynodont pattern and the description of individual bones is not repeated here.
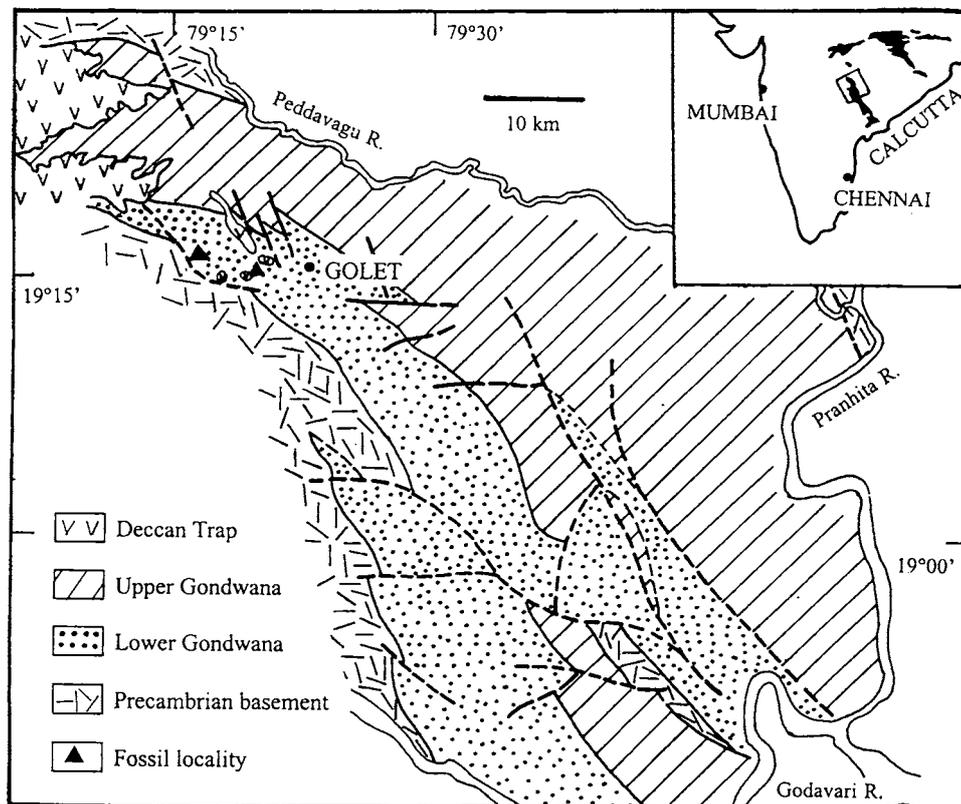

Figure 1. Geological map of the Pranhita-Godavari valley, India (after Kutty *et al.*, 1987) showing the fossil localities. Inset: Major Gondwana basins of India.
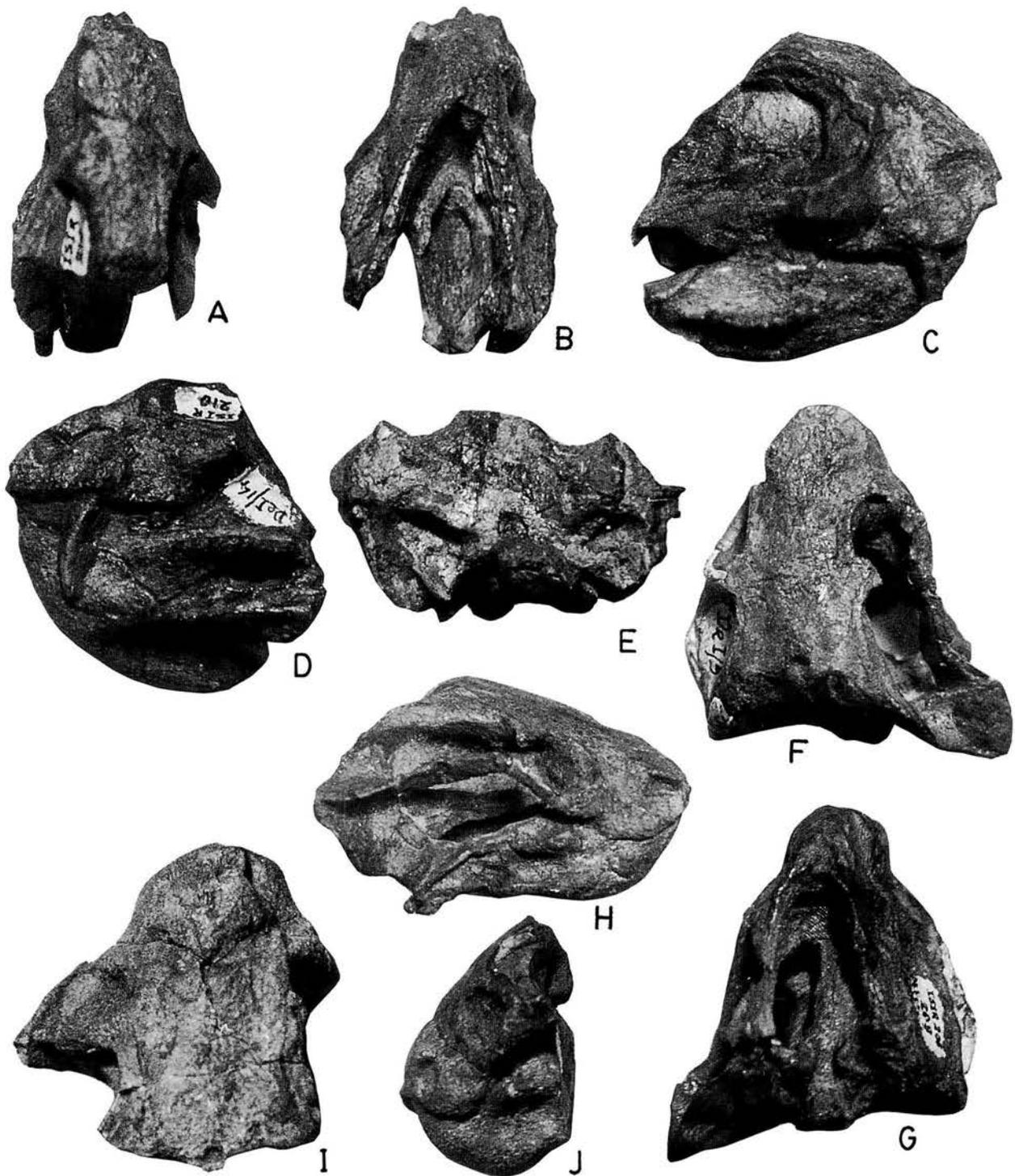
Figure 2. **A–E.** *Pristerodon mackayi* Huxley, 1868. **A–D.** ISIR 209. Partial skull with attached lower jaw in **A**, dorsal, **B**, ventral, **C**, right lateral, **D**, left lateral views. ×1.1. **E**. ISIR 372. Partial occiput in posterior view. ×1.3. **F–H.** *Emydops platyceps* Broom and Haughton, 1917. ISIR 208. Skull and lower jaw in **F**, dorsal, **G**, ventral, **H**, right lateral views. ×1. **I–J.** *Cistecephalus microrhinus* Owen 1876. ISIR 210. Partial skull and lower jaw in **I**, dorsal view. ×1.3. **J**, left lateral view. ×0.8.

Figure 3. *Pristerodon mackayi* Huxley, 1868. ISIR 209. Restored partial skull and lower jaw in **A**, dorsal, **B**, ventral and **C**, lateral views. Hatched lines indicate broken surfaces. Scale bar represents 10 mm.

Figure 4. *Pristerodon mackayi* Huxley, 1868. ISIR 369. Anterior part of skull in ventral view. Scale bar represents 10 mm.

Skull

Snout and skull roof. The narrow and tapering snout is composed of the completely fused premaxillae, which continue posteriorly to form a wedge between the external nares. The nares open near the extremity of the snout. Small, subrounded septomaxilla, recessed within the naris, forms its posteroventral margin. The maxilla occupies the anterolateral sides of the skull and bears large caniniform tusks and about 3-4 postcanine teeth. The preorbital length (measured from the tip of the snout to the anterior end of orbit) is 16.6 mm. It is covered by the elongated, paired nasals mostly, followed by the frontals posteriorly. Only the anterior part of the orbit is preserved, well defined by a narrow rim. The preserved part of the interorbital region is broad (9 mm), flat and formed by the relatively extensive frontal. Anterolaterally the orbital rim consists of the subtriangular prefrontal, which is rather large in comparison to the more ventrally placed subrounded lacrimal and slender jugal. The lacrimal bears a prominent foramen just

flush with the orbital rim.

Palate. Palatal features are studied from ISIR 369 and ISIR 372 along with ISIR 209 as in the latter the lower jaw is in position. The anteriormost premaxilla forms a sharp peripheral rim and posteriorly is in sutural contact with the vomer medially and palatine and maxilla laterally. Posteromedial to the caniniform tusk in ISIR 209 or to the subcircular alveolus in ISIR 369, the maxilla bears a uniserial, short tooth row, tending to converge anteriorly. Though teeth are not preserved in ISIR 369, the apertures of the alveoli are confluent and form a short, shallow groove. The margin of this groove is raised above the surface of the maxilla. The palatines in ISIR 369 are broad, leaf-shaped, bearing undulations and forming the lateral margin of the choanal slits. The anterior pterygoid rami have sharp ventral edges (ISIR 209). In ISIR 372, the parasphenoid-basisphenoid complex as in other dicynodonts is fused to the posterior end of the pterygoidal plate. The basiphenoid tubera are separated by a deep median cleft. Two distinct ridges run along the anterior surface of the tubera while their faces are laterally oriented, concave and consist of the foramen ovalis. In ISIR 209, the cultriform process of the parasphenoid extends as a slender rostrum between the interpterygoid vacuity. Anteriorly the sphenethmoid complex stands in a groove on the dorsal surface of the cultriform process.

The epipterygoid is L-shaped with a short anterior and longer posterior quadrate ramus. The quadrate-quadratojugal complex is typical of dicynodonts.

Occipital and otic regions. In ISIR 372, the occiput is subrectangular in shape and is flanked on either side by the squamosal. The occipital condyle is situated medially almost near its ventral margin. Above the condyle is situated an elongate foramen magnum. A major portion of the occiput is formed by the large, medially placed supraoccipital ventrally and interparietal dorsally. Laterally the supraoccipital is in sutural contact with the tabulars and ventrolaterally with the rodlike opisthotic. This latter suture is interrupted by a distinct post-temporal fenestra. The opisthotic forms the ventral margin of the occiput. Laterally on either side of the condyle is a pair of jugular foramen, piercing the exoccipitals.

Lower jaw

The portion of the lower jaw anterior to the Meckelian fenestra is preserved in ISIR 209. The relationships of the various elements of the lower jaw follow the normal dicynodont pattern. The anterior dentary symphyseal end is narrow, slender and forms a cutting edge. Though the dorsal surface is hardly visible as the lower jaw is attached to the skull, a deep but short, longitudinal dentary sulcus is discerned, which is for occlusion with the upper jaw teeth. Laterally the jaw ramus bears a distinct and high dentary shelf just above and anterodorsal to the Meckelian fenestra, which is quite long and elliptical. The dentary extends up to the posterodorsal end of the fenestra while the angular forms its ventral margin. The subrounded reflected lamina of the angular extends well below the ventral margin of the lower jaw. A small, elongated splenial medially forms the anteroventral margin of the lower jaw. The anterior end of

the rodlike prearticular is preserved and in sutural contact with the splenial.

Discussion. — An imperfect 'lacertilian' skull collected by G. Mackay from East London, South Africa was originally described by Huxley (1868) as *Pristerodon mackayi.* It was a nearly complete skull with a posteriorly widening intertemporal bar. The skull was considered by Seeley (1895) to be an endothiodont because of its postcanine teeth. Many diverse dicynodonts bearing little or no resemblance to each other except for the postcanine teeth were traditionally placed under Endothiodontidae. Later works by Van Hoepen (1934) and Cluver and King (1983) led to the placement of *Pristerodon* and its related forms within the family Pristerodontidae. King and Rubidge (1993) considered *Pristerodon* to be characterised by a broad intertemporal bar with exposed parietals, large, leaflike palatine, postcanine teeth in a short oblique row, long interpertygoid vacuity, deep dentary sulcus and a prominent lateral dentary shelf. All the *Pristerodon* species (*P. mackayi, P. agilis, P. boonstrai, P. buffaloensis, P. vanhoepeni and P. whaitsi*) were differentiated on the bases of the presence or absence of the maxillary tusk, nasal bosses and position of the alveolus (King, 1988).

However, investigation of a large number of toothed dicynodonts earlier considered as endothiodont by Keyser (1993) revealed that the vast majority of the described species belonging to *Pristerodon* and various other genera are junior synonyms of *Pristerodon mackayi,* the only valid species of *Pristerodon.* He further suggested that the crista oesophagea forming ridges on the anterior pterygoid rami is a diagnostic feature of *Pristerodon.* On the other hand, King and Rubidge (1993) emphasised the sigmoidal curve of the anterior pterygoid ramus of *Pristerodon.*

All the Indian specimens (ISIR 209, ISIR 369, ISIR 370, ISIR 372) are skulls of small dicynodonts with an average skull length of about 50 mm. These are characterised by caniniform tusks, wide intertemporal regions, short, oblique postcanine tooth row, large, leaflike palatines, high and distinct lateral dentary shelf and deep dentary sulcus. All these features definitely show that these pertain to *Pristerodon mackayi.*

Superfamily Diictodontoidea Cluver and King, 1983
Family Emydopidae Cluver and King, 1983
Subfamily Emydopinae Cluver and King, 1983
Genus **Emydops** Broom, 1912

Type species. — *Emydops minor* Broom, 1912 (subsequent designation by Keyser, 1993).

Emydops platyceps Broom and Haughton, 1917

Figures 2F-H, 5-6, 7E-F

Emydops platyceps Broom and Haughton, 1917, p. 125: King, 1988, p. 116.
Emydops tener Keyser, 1993, p. 49, fig. 5.1.

Holotype. — SAM-PK-2667, skull from Dunedin, Beaufort West, South Africa; *Cistecephalus* Assemblage Zone, Late Permian.
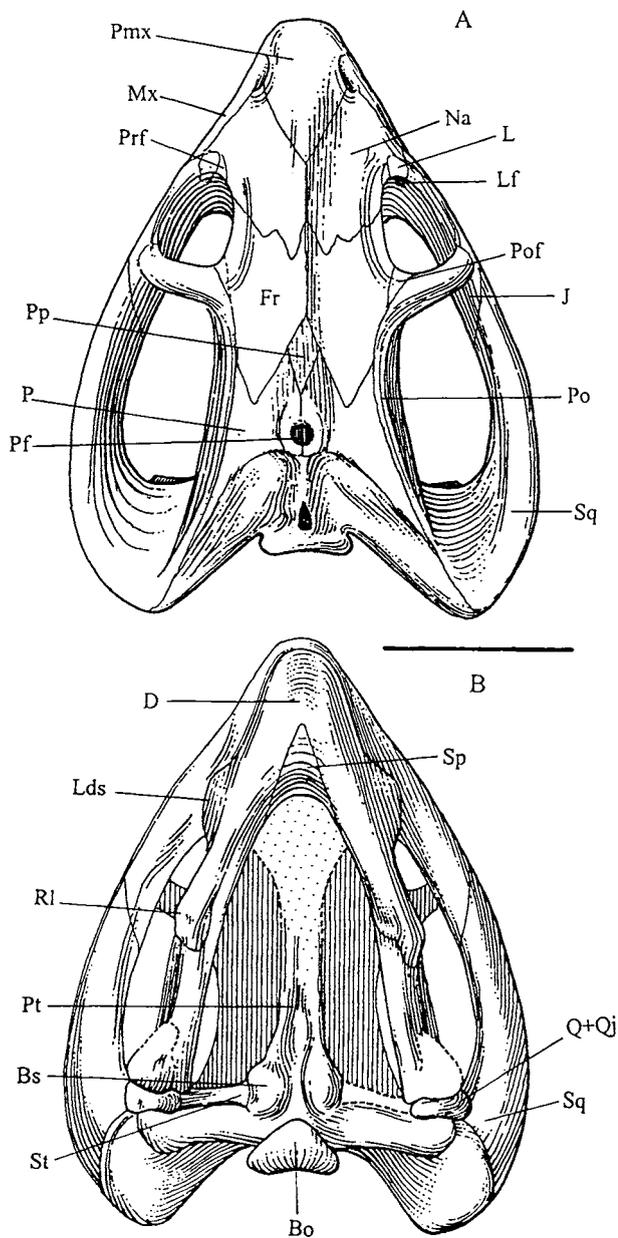
Figure 5. *Emydops platyceps* Broom and Haughton, 1917. ISIR 208. Restored skull and lower jaw in **A**, dorsal and **B**, ventral views. The stippled area indicates matrix covering. Scale bar represents 20 mm.

Revised diagnosis.—Small dicynodonts with or without caniniform tusks; prominent lacrimal foramen; wide intertemporal region with parietal exposure; median premaxillary ridge on palate bordered by grooves on either side, irregularly placed maxillary and dentary teeth; small palatal embayment just anterior to caniniform process; flat, squarish palatine with notched medial and concave posterior margins; straight anterior pterygoid process, prominent lateral dentary shelf; dentary symphysis drawn up into a sharp cutting edge.

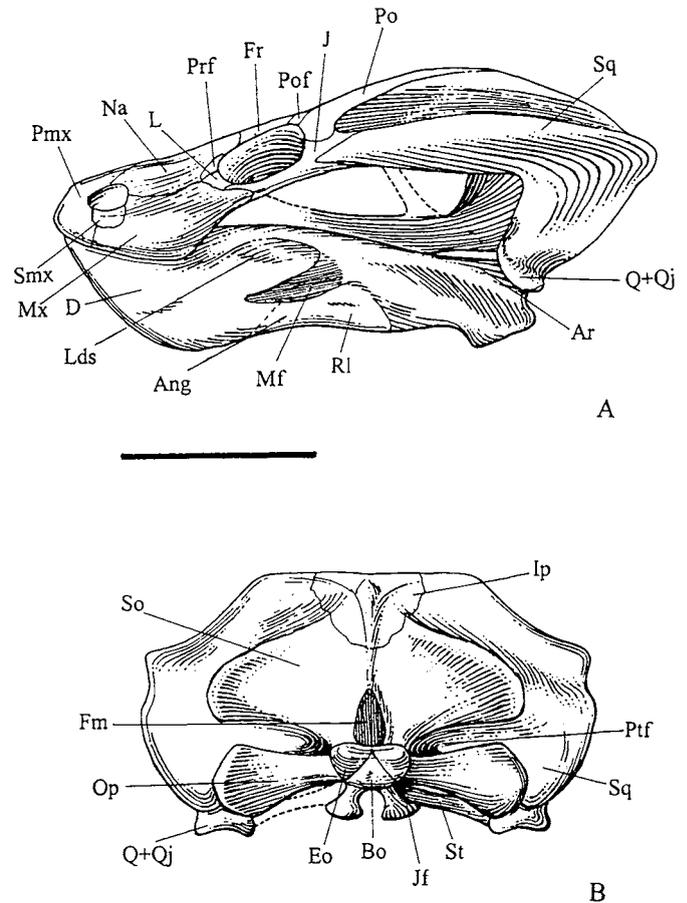*Material.*—ISIR 208, a complete, slightly distorted skull

Figure 6. *Emydops platyceps* Broom and Haughton, 1917. ISIR 208. Restored skull and lower jaw in **A**, lateral and **B**, occipital views. Scale bar represents 20 mm.

with attached lower jaw.

Repository.—The specimen is housed in the Geology Museum, Indian Statistical Institute, Calcutta.

Locality and horizon.—The specimens were collected near Golet (Figure 1), Adilabad district, Andhra Pradesh, India from the Late Permian Kundaram Formation, Gondwana Supergroup.

Description.—

Skull

General features. The small and triangular skull measures 47.8 mm along the dorsal midline. The snout is narrow, tapering anteriorly and quite short (preorbital length is 10 mm). Measurements of the skull are given in Table 2. The elliptical nostril is situated close to the midline at the extremity of the snout. It is bordered by the premaxilla anterodorsally, nasals posterodorsally and the maxilla posteriorly and ventrally. The orbit is relatively small, subrounded (diameter 10 mm approx.) and anterodorsally positioned. The interorbital region is flat, quite broad and about 15.5 mm. Beyond the orbit, the zygomatic arch flares out and meets the occipital plane at a high angle. The temporal fenestra is large, elongated and extended beyond the level of the occipital condyle. The intertemporal region is much wider than the

Table 2. Measurements of the skull (ISIR 208) of *Emydops platyceps*. All measured in mm.

Parameters	*Emydops platyceps* (ISIR 208)
Skull length	
a. Measured along the dorsal midline	47.8
b. Over squamosal wings	58.4
c. At palatal midline	—
Preorbital snout length	10
Postorbital snout length	25
Length from anterior edge of premaxilla to anterior edge of pineal foramen	37
Skull width across squamosal	44.5
Diameter of pineal foramen	2.8
Interorbital width	15.5
Intertemporal width	28
Snout width	16.7
Length of temporal fenestra	31.6
Width of temporal fenestra	14.3
Greatest width of occiput	41.3
Width of occipital condyle	13.8
Least squamosal width of the occiput	28
Occipital height	25.5

interorbital bar (Table 2) and gradually widens posteriorly. A small, circular pineal foramen is situated medially on a slightly raised area at the posterior end of the skull. The skull roof is relatively flat but gently sloping anteriorly. The occiput is trapezoid in shape with a large, elliptical occipital condyle situated medially near its ventral margin.

Snout and skull roof. The anteriormost premaxilla separates the nostrils dorsally and forms a wedge-shaped contact with the paired nasals posteriorly. Posterolaterally it is in contact with the maxilla, a major element on the anterolateral sides of the skull. The maxilla borders the nasal openings ventrally and posteriorly. The septomaxilla is slightly exposed along the posteroventral border of the nasal cavity. In dorsal view, posterior to the premaxilla is a pair of large nasals. This is followed posteriorly by the frontal occupying most of the skull roof anterior to the temporal fenestra. Posterolaterally the nasal is bordered by a small elongated prefrontal. The latter, along with the relatively large, subrounded lacrimal, form the anterior margin of the orbit. There is a distinct lacrimal foramen. Dorsally and posterodorsally the circumorbital rim is formed by the frontal and a small, triangular postfrontal respectively. Ventrally the orbit is bordered by the jugal. The slender, rodlike postorbital forms the narrow anteromedial border of the temporal fenestra. Characteristically the intertemporal region comprises mostly the widely exposed parietals. Medially at the frontoparietal junction is a large, rhomboidal preparietal, which lies entirely in front of the pineal foramen. The circular pineal foramen is situated on a slightly raised area, at the posterior end of the skull roof and is bounded by the parie-

tals. Posterior to the pineal foramen is a single, large interparietal, which occupies a dorsomedial position on the occiput. The squamosal is the posteriormost element in dorsal view and divisible into three parts as is typical of dicynodonts. Attached to the anterior face of the squamosal is a small quadratojugal.

Palate. The anterior part of the palate cannot be partly seen because of matrix covering and as the lower jaw is in position. Posteriorly the pterygoid bone is narrow with a poorly developed pterygoidal crest.

The parasphenoid-basisphenoid complex is fused to the posterior end of the pterygoidal plate. The basisphenoid consists of two anteriorly converging tubera separated by a narrow and deep median cleft. The faces of the tubera are laterally oriented, concave and house the foramen ovalis.

The quadrate is strongly fused with the more laterally placed quadratojugal, though there is deep groove between them. The palatal face of the quadrate, as in other dicynodonts, is composed of a broad, medial and a lateral condyle separated by a shallow groove. Lying between the medial face of the quadrate and the fenestra ovalis is a thin, long, rodlike, imperforate stapes with slightly expanded ends.

Occipital and otic regions. In posterior view, the occiput is trapezoid in outline. It bears a prominent, elliptical occipital condyle medially, which is composed of the paired exoccipitals and the basioccipital. Above the condyle is an elongated, triangular foramen magnum. The dorsal margin of the foramen magnum is formed by the supraoccipital, which also forms the roof of the braincase. The interparietal, situated on the dorsal side of the supraoccipital, is characterised by a median ridge tapering ventrally. Ventrolateral to the condyle is a jugular foramen, piercing the exoccipital and the rodlike opisthotic, which expand laterally overlapping the squamosal. A large posttemporal fenestra is present near the occipital condyle at the sutural contact between the opisthotic and the dorsally placed supraoccipital. Laterally the occiput is margined by the winglike flanges of the squamosal. The anterior face of the occiput bears a pair of small, flat prootics, which along with the opisthotics form the anterior and posterior walls, respectively of the otic capsule.

Lower jaw
The lower jaw is attached to the skull. The anterior end is relatively slender and is drawn up into a sharp cutting edge. The dentary symphysis is strongly fused. Laterally the jaw ramus bears a distinct, high dentary shelf and a large Meckelian fenestra. The anteriormost element of the lower jaw, the dentary, extends posteriorly as far as the posterior end of the Meckelian fenestra. It is bounded posteriorly by the surangular and posteroventrally by the angular. Presence or absence of teeth cannot be determined as the lower jaw is in position. The reflected lamina of the angular is quite small and is in line with the ventral margin of the lower jaw. The transversely widened posterodorsal surface of the articular forms lateral and medial condyles separated by a low ridge as found in the dicynodonts. It slopes downward posteriorly to form the retroarticular process.

Discussion.—

On the genus *Emydops*

A small dicynodont skull, about 45 mm in length, was first described by Broom (1912) from Kuilspoort, Beaufort West, South Africa as a new genus and species *Emydops minor.* It is tuskless with a wide intertemporal region, a large median preparietal forming the anterior margin of the pineal foramen, a slender postorbital arch and a feeble beak. Broom (1913) redefined *Emydops* as a small tuskless form with a few unserrated postcanine teeth. Subsequently, a number of *Emydops* species, collected from the Permian part of the Beaufort Group of South Africa, were described by Broom (1913, 1921). These species were distinguished based on the shapes and arrangements of the bones of the frontal and parietal regions. Broom and Haughton (1917) described another new species of *Emydops, E. platyceps* based on a tusked skull from Dunedin, Beaufort West, South Africa.

Broom (1921) created a new genus *Emydopsis* (the type species is *Emydopsis trigoniceps*), characterised by the presence of only three or four posteriorly serrated teeth. Toerien (1953) stated that the number and size of the teeth alone cannot be used to differentiate between *Emydops, Emydopsis* and *Pristerodon*, then considered to be closely related to the former two genera. He further concluded that *Emydops* may be differentiated from *Pristerodon* on the basis of the size of the palatine and the absence of the palato-premaxillary contact in *Pristerodon*.

The holotypes of the type species of *Emydops, E. minor* (AMNH 5525; Figure 7A) and *Pristerodon, P. mackayi* (BMNHR 1810; Figure 7B) were again examined by Cluver and King (1983). They stated that in both specimens, few characters of taxonomic importance are visible. They supplemented the generic diagnoses of *Emydops* and *Pristerodon* from the information accumulated from other species of the two genera. According to them, the characteristic features of *Emydops* include: small dicynodonts with wide intertemporal region and exposed parietals (Figure 7C), platelike palatine with concave posterior border, quite short interpterygoidal vacuity, presence of embayment in the palatal rim and weak interpterygoidal crest, prominent lateral dentary shelf, dentary symphysis drawn up into sharp cutting edge and shallow groove on the dorsal edge of the dentary.

Keyser (1993) while reviewing the small dicynodonts of South Africa transferred most of the holotypes of *Emydops* species to *Pristerodon mackayi.* According to him, *Emydops minor*, the type species of *Emydops*, displays no distinctive features—a view also shared by Cluver and King (1983). Keyser (1993) found *E. minor* to be similar to *Pristerodon mackayi* and considered *Emydops minor* as *nomen dubium.* He suggested that *E. platyceps* is the only valid species, characterised by large and square palatines which are perforated by foramina. He renamed *Emydops* in part as *Emydoses* (Keyser, 1993, p. 48) and assigned two species to the genus, namely *Emydoses tener* (Figure 7D) and *Emydoses platyceps* (*Emydops platyceps* of Broom and Haughton, 1917; holotype SAM-PK-2667; Figure 7E).

However, King and Rubidge (1993) considered *Emydops* to be well characterised. *Emydops* is differentiated from the other toothed dicynodonts (*Eodicynodon, Pristerodon* and *Robertia*), based on such features of the palate and lower
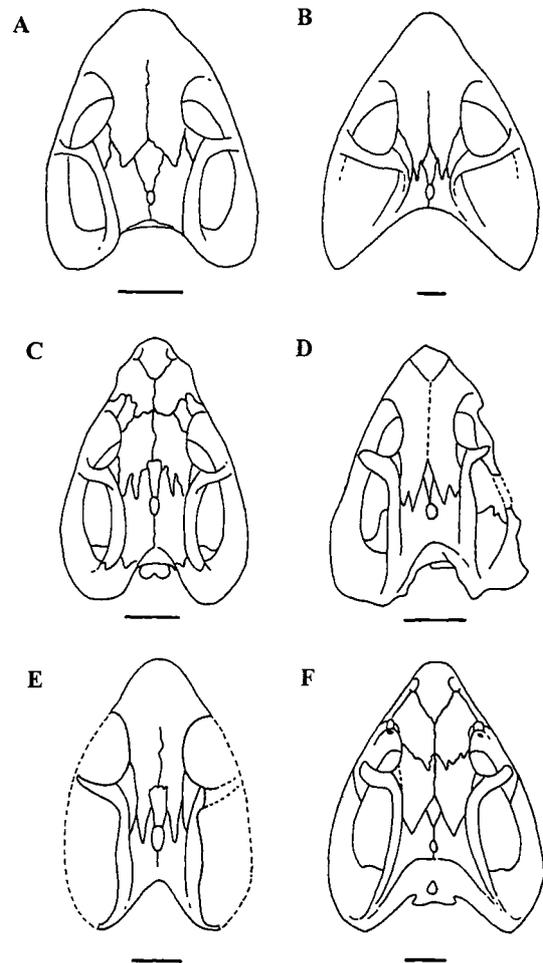

Figure 7. Skulls in dorsal view. **A.** *Emydops minor,* holotype AMNH 5525 (after Cluver & King, 1983). **B.** *Pristerodon mackayi,* holotype BMNHR 1810 (after Cluver and King, 1983). **C-F.** *Emydops platyceps,* **C,** SAM-PK-11060 (after Cluver & King 1983); **D,** SAM-PK-K10170 (syntype, *Emydoses tener* of Keyser, 1993); **E,** holotype SAM-PK-2667, **F,** ISIR 208. Scale bars represent 10 mm.

jaw as the size and shape of the palatine, arrangement of the postcanine teeth, lateral dentary shelf and dorsal surface of the lower jaw (King and Rubidge, 1993; p. 141, table 2).

From the above review, it is evident that a disagreement persists regarding the nomenclature of the genus *Emydops.* Though Keyser (1993) in effect renamed *Emydops* as *Emydoses* because most of the earlier described species, including the type species of the formers, had in his view become junior synonyms of *Pristerodon mackayi*, the generic diagnosis remains nearly the same for *Emydops* and *Emydoses.* Moreover, *Emydops* is a long-accepted name in its accustomed meaning. Thus in the present study priority is given to the older name of the genus and the name *Emydops* is retained, to provide stability and avoid confusion in the nomenclature by introducing a new name.

On the species of *Emydops*

As mentioned earlier Keyser (1993) considered *E.*

Table 3. Comparative measurements of several specimens of *Emydops*. All measured in mm. Abbreviations used: SL, skull length along dorsal midline; SLsq, skull length over the squamosals, PSL, preorbital snout length; SnW, snout width, IO, interorbital width, IT, intertemporal width; TF, length of temporal fenestra; SW, skull width; OcH, occipital height; OcW, occipital width.

Specimens	Parameters										
	SL	SL sq	PSL	SnW	IO	IT	IT/IO	TF	SW	OcH	OcW
ISIR 208	47.8	58.4	10	16.7	15.5	28	1.81	31.6	44.5	25.5	41.3
SAM-PK-2667	40.58	51.9	9.75	15.68	10.69	15.69	1.48	-	34.54	-	-
SAM-PK-10170	49.33	61.36	7.97	17	10.52	19.88	1.89	32.9	47.46	18.35	39.58
SAM-PK-10148	51.06	58.72	16.26	16.28	10.96	18.38	1.68	30.2	42.88	23.66	35.34
SAM-PK-K1671	30.38	39.37	7.58	12.34	4.9	9.8	2	20.55	29.1	15.74	21.95
SAM-PK-3721	44	54.1	-	12.15	11.2	15.85	1.42	29.44	-	18.89	30.4
SAM-PK-10172	40.16	46.03	11.34	10.33	8.11	14.8	1.82	-	33.3	-	-
SAM-PK-11060	41.23	47.32	11.13	-	12	15.86	1.32	21	28.96	20.38	27.78
SAM-PK-K1517	46.69	56.64	11.58	-	15.38	19.77	1.3	17.5	30.4	22.03	30.6
SAM-PK-K5974	56.2	65.5	-	-	14.95	22.63	1.51	35.94	43.83	27	48.8
SAM-PK-K6693	47.94	59.56	12.33	16.37	12.08	18.54	1.53	25.7	44.4	18.85	33.22
SAM-PK-K6623	46.03	54.85	12.21	16.98	13.52	16.55	1.22	30.46	53.88	24.5	33.31

platyceps Broom and Haughton, 1917 and *E. tener* Keyser, 1993 as the only valid species. The former was characterised by large, squarish palatines, which are perforated by foramina and the latter by its "slender" build (Keyser 1993). The use of features like slender or delicate skull to define species is subjective (King, 1993) and avoided in the present study. A close examination of *Emydops* specimens housed at the South African Museum, Cape Town, including the holotype SAM - PK - 2667 of *E. platyceps* and the syntypes (SAM-PK-10148 and SAM-PK-10170) of *E. tener* reveal that the shape of the palatines are similar in all the specimens. The palatal portion of the palatine is flat, squarish and bears a notch or palatine foramen in its medial margin. Its posterior margin is concave. Although the area between the medial margin of the palatine and the vomer along the ventral midline is covered with matrix in most of the specimens, the presence of the notch can be clearly discerned, especially in SAM - PK - 10148, SAM - PK - 3721, SAM - PK - K1671, SAM - PK - 11060 and SAM - PK - K6623. Moreover, it appears that the syntypes of *E. tener* do not have any feature different from *E. platyceps* Broom and Haughton, 1917. It is considered here as the junior synonym of *E. platyceps* Broom, 1912. Thus, from the specimens available for study, it appears that the genus *Emydops* has only one valid species, *E. platyceps* and is now distinguished by the generic features of *Emydops*: small dicynodonts which may be tusked or tuskless, prominent lacrimal foramen flush with the orbit, wide intertemporal region with broad parietal exposure, irregularly placed maxillary and dentary teeth, small embayment on the palatal rim anterior to the caniniform process, premaxillary ridge bordered by grooves on either side, flat, squarish palatine with notched medial and concave posterior margins, straight anterior pterygoid process, dentary symphysis drawn up into a sharp cutting edge and a prominent lateral dentary shelf.

Comparison between the Indian and South African forms

ISIR 208 (Figure 7F) is a small skull (47.8 mm) with broad intertemporal region and widely exposed parietal. The pterygoid bridge posterior to the choanae, though not well preserved, is quite narrow (Figure 5B). The lateral dentary shelf is very distinct and high and the dentary symphysis is drawn up into a sharp cutting edge. Thus, it is assigned to the genus *Emydops*. The anterior palatal features are not visible because of the position of the lower jaw. Table 3 gives a detailed comparison of ISIR 208 with a number of South African forms, including the holotype of *E. platyceps* (SAM-PK-2667), based on different cranial parameters. It shows that the overall skull proportions of ISIR 208 such as length, width, occipital height, occipital width and length of the temporal fenestra fall within the range of the South African forms. On the other hand, the snout length is much shorter while the interorbital and intertemporal width with respect to the skull length is much greater than that of the SAM specimens. IT/IO ratio (1.8) though again within the range, which varies from 1.22 (SAM-PK-K6623) and 2 (SAM-PK-3721), is at the higher end of the range. The interorbital (IO) and intertemporal (IT) width relative to the skull length and IT/IO ratio are found to be not reliable specific characters (Keyser, 1975; King, 1993) and are not considered here. However, in ISIR 208 the pineal foramen is situated near the end of the intertemporal bar. The preparietal lies entirely in front of the pineal foramen and does not form its anterior margin (Figure 7F). Though this feature is not found in any other *Emydops* specimens and is unique to ISIR 208, more specimens with this feature need to be discovered before it can be considered as a reliable specific character. Apart from this, ISIR 208 bears overall similarity with *E. platyceps* and is placed within *Emydops platyceps*.

Subfamily Cistecephalinae Broom, 1903
Genus *Cistecephalus* Owen, 1859

Type species.—*Cistecephalus microrhinus* Owen, 1876
(subsequent designation by King, 1988).

Cistecephalus microrhinus Owen, 1876

Figures 2I-J, 8-10, 11A-B

Cistecephalus microrhinus Owen, 1876, p. 63, pl. 64, fig. 4-7: King, 1988, p.118, fig. 33 (see for prior synonymies).

Holotype.—BMNH R 47066, an imperfect skull from Stylkraans, Graaff-Reinet, Cape Province, South Africa; *Cistecephalus* Assemblage Zone, Late Permian.

Diagnosis.—Small, toothless emydopids with broad or narrow intertemporal region; lacrimal foramen, postfrontal and preparietal absent; pterygoid meeting below parabasisphenoid complex; interpterygoidal vacuity absent; stapes perforated or deeply incised; prominent lateral

Figure 9. *Cistecephalus microrhinus* Owen, 1876. ISIR 366. Anterior part of skull in ventral view. Scale bar represents 10 mm.
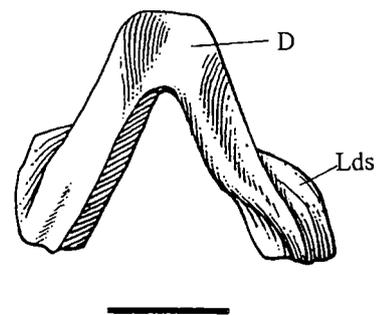

Figure 10. *Cistecephalus microrhinus* Owen, 1876. ISIR 367. Anterior part of lower jaw in dorsal view. Scale bar represents 10 mm.

Figure 8. *Cistecephalus microrhinus* Owen, 1876. ISIR 210. Partial skull with lower jaw in **A**, dorsal and **B**, lateral views. Scale bar represents 20 mm.

dentary shelf (Keyser, 1973; King, 1988).

Material.—ISIR 210, anterior portion of a skull with attached lower jaw, lacking the posterior part of the zygomatic arch, squamosals, occiput and postdentary bones, ISIR 365, a laterally compressed skull with attached lower jaw, ISIR 366, left portion of skull, ISIR 367, snout region, ISIR 368, anterior part of a lower jaw.

Repository.—The specimens are housed in the Geology Museum, Indian Statistical Institute, Calcutta.

Locality and horizon.—The specimens were collected near Golet (Figure 1), Adilabad district, Andhra Pradesh, India from the Late Permian Kundaram Formation, Gondwana Supergroup.

Description.—

Skull

ISIR 210 is a small, triangular skull with a slight lateral and anteroposterior distortion. Its length along the dorsal midline from the anterior end of the premaxilla to the posterior end of the pineal foramen is 41 mm while the total length is inferred to be about 52 mm. Different measurements of ISIR 210 are given in Table 4. Its snout is short, broad and tapers anteriorly with the nostrils situated close to the midline and separated by a large, swollen and wedge-shaped premaxilla. The maxilla occupies the anterolateral sides of the skull. The septomaxilla is completely recessed within the nostril. The orbits are circular, relatively small, anterodorsally placed and separated by a wide interorbital
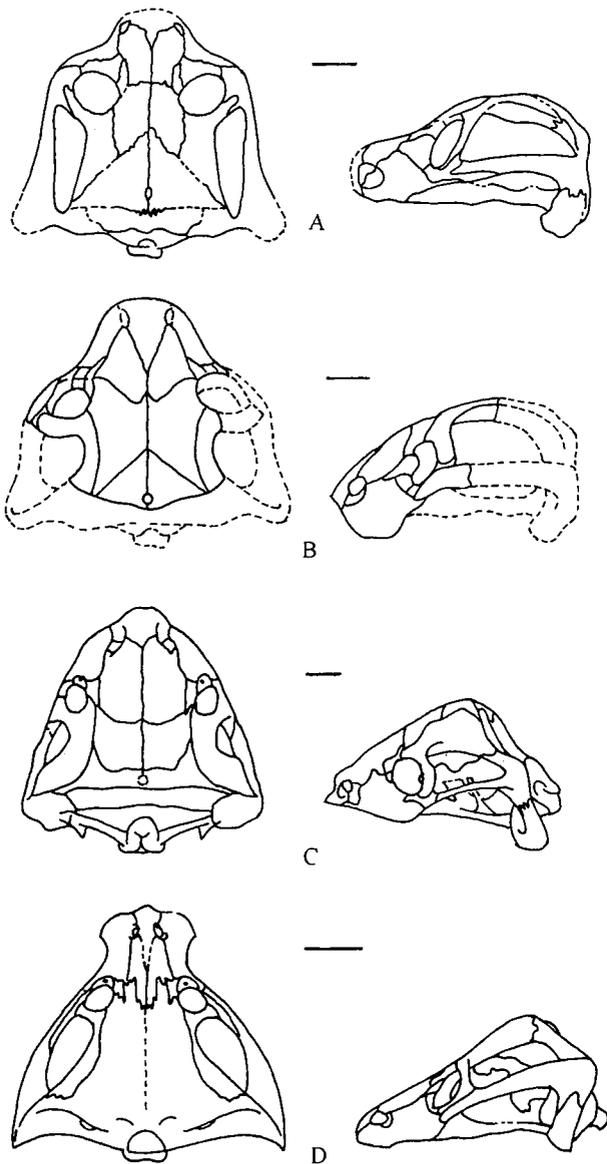
Figure 11. Skulls in dorsal and lateral views; **A - B**, *Cistecephalus microrhinus*. **A**, after Broili and Schroder, 1935; **B**, ISIR 210; **C**, *Cistecephaloides boonstrai* (after Cluver, 1974a); **D**, *Kawingasaurus fossilis* (after Cox, 1972). Scale bars represent 10 mm.

region. This region consists of large, paired nasals anteriorly and frontals posteriorly. The anterior part of the circumorbital rim is formed by the large, elongated prefrontal and rectangular lacrimal. The postfrontal is absent. The intertemporal region widens considerably (31 mm approx.) especially at the posterior end of the skull. A small, circular pineal foramen is situated at the far end of the skull roof. The paired parietals constituting the intertemporal bar are broad, widely exposed and laterally bordered by the slightly raised but narrow postorbital. The postorbital is separated from the prefrontal by the frontal. The preparietal is absent.

Table 4. Measurements of the skull (ISIR 210) of *Cistecephalus microrhinus*. Asterix (*) indicates inferred measurements. All measured in mm.

Parameters	*Cistecephalus microrhinus* (ISIR 210)
Skull length	52*
Preorbital snout length	17.5
Postorbital snout length	23
Length from anterior edge of premaxilla to posterior edge of pineal foramen.	41
Diameter of the pineal foramen	2
Interorbital width	28.5
Intertemporal width	31
Snout width	27.5

Beyond the pineal foramen, the posterior part of the skull and the zygomatic arches are broken.

In ISIR 210, the slender jugal is completely overlapped by the squamosal; the latter reaches the maxilla because of antero-posterior compression. The usual *Cistecephalus* feature of maxilla and squamosal separated by the jugal is preserved in ISIR 365. The palate of the specimen ISIR 210 cannot be studied as the lower jaw is in position and attached to the skull. The anterior part of the palate is studied from the specimens ISIR 365 and ISIR 367. It is edentulous and consists of a sharp palatal rim formed anteriorly by the premaxilla and posterolaterally by the maxilla. The palatines are very small and curved posteriorly. A narrow vomerine septum separates the very small internal nostrils.

Lower jaw

The lower jaw is described from the specimens ISIR 210, ISIR 365 and ISIR 368. It is short, robust and deep. The dentaries are completely fused at the symphysis and form sharp, transverse cutting edge anteriorly. Posterior to the cutting edge, the dorsal surface of the dentary is slightly raised and further posteriorly it bears a pair of ridges. Posteriorly the lower jaw is flared out laterally. Above the Meckelian fenestra is present a distinct lateral dentary shelf. The posterior ends of the specimens and the postdentary bones are not preserved in the specimens ISIR 210 and ISIR 367. In ISIR 210, the lower jaw is attached to the palate showing that the latter is much wider than the symphyseal region of the lower jaw.

Discussion. — The subfamily Cistecephalinae contains small, toothless emydopids with very broad intertemporal region lacking the postfrontal and preparietal (King, 1988). Other characteristic features of this subfamily include perforated or deeply incised stapes, vestigial or no interpterygoid vacuity, reduced palatine, premaxilla extended far back posteriorly, anterior edge of the dentary symphysis forming a sharp cutting edge and a prominent lateral dentary shelf.

This subfamily is composed of three genera, *Cistecephalus* Owen, 1876 (Figures 11A-B), *Cistecephaloides* Cluver, 1974a (Figure 11C) and *Kawingasaurus* Cox, 1972 (Figure 11D). The cranial and postcranial morphology

Table 5. Distinguishing features of *Cistecephalus*, *Cistecephaloides* and *Kawingasaurus* (sources: Broili and Schroder, 1935; Cox, 1972; Cluver, 1974a; King, 1988).

Parameters	*Cistecephalus*	*Cistecephaloides*	*Kawingasaurus*
Snout	Short and broad	Short and broad	Flattened, laterally expanded
Orbits	Large, anterolaterally placed orbits	Small	Small
Interorbital region	May be broad or narrow	Broad	Broad
Lacrimal foramen	Absent or present low down within the orbit	Large	Large
Relation between prefrontal, frontal and postorbital	Prefrontal separated from postorbital by frontal	Prefrontal meeting postorbital	Prefrontal separated from post-orbital by frontal
Postorbital	Relatively slender	Very robust	Relatively slender
Pineal foramen	Circular, situated at the far end of the intertemporal bar	Very small, insignificant	Absent
Squamosal	May be separated from maxilla by jugal	Separated from maxilla by jugal	Reaches maxilla
Otic region	Normal	Normal	Highly inflated

of these taxa have been studied in detail (Seeley, 1894; Broom, 1932, 1948; Broili and Schroder, 1935; Keyser, 1973 and Cluver, 1974a, b, 1978) and show that the features like the broad, triangular skull with wide interorbital and intertemporal regions, rounded occiput and absence of the interpterygoidal vacuity are of a highly specialised animal with fossorial habits. However, *Cistecephaloides* differ from *Cistecephalus* in having a very high skull roof, sloping anteriorly and with the prefrontal in sutural contact with a robust postorbital, while *Kawingasaurus* is distinguished by the absence of the pineal foramen and an inflated otic region. The other distinctive features of *Cistecephalus* are given in Table 5.

The Indian specimens exhibit a short snout, circular orbit, absence of the postfrontal, preparietal and the lacrimal foramen, frontal separating the postorbital and prefrontal, wide intertemporal region, circular pineal foramen, transverse cutting edge of the dentary and prominent lateral dentary shelf (Figure 11B). These features clearly indicate that the specimens belong to the genus *Cistecephalus*.

A large number of *Cistecephalus* species were originally erected, distinguished by parameters such as their size differences, broad or narrow skull, and variations in the arrangement of the skull roof bones (Owen, 1876; Broom, 1932, 1948). All the fossils were collected from the Permian part of the Beaufort Group of South Africa. Keyser (1973) suggested that *Cistecephalus* species are members of a growth series and synonymised all the species with *C. microrhinus*, the latter being the only valid species of the genus. The Indian *Cistecephalus* is compared with the South African forms (SAM-PK-K6814, SAM-PK-K7667, SAM-PK-K7852, SAM-PK-K8304 and SAM-PK-10665) collected from the Late Permian part of the Beaufort Group of the Karoo Supergroup and housed in the South African Museum, Cape Town (Table 6). The total skull lengths of the African specimens studied vary between 42 mm and 63 mm. The skull length of ISIR 210 and ISIR 365 (Table 6) falls well within that range. The intertorbital width of the African specimens varies between 10 and 18 mm and that of

Table 6. Comparative measurements of several specimens of *Cistecephalus*. All measured in mm. Index to the abbreviations is given in Table 3.

Specimen	Parameters				
	SL	SW	IO	IT	IT/IO
SAM-PK-K6814	54.38	59.06	16.88	39.38	2.33
SAM-PK-K7667	63	70	17	25	1.47
SAM-PK-K7852	42	37	10	25	2.5
SAM-PK-10665	48.46	42.69	11.54	32.31	2.8
SAM-PK-K8304	55	62	18	45	2.5
ISIR 210	52*	—	28.5	31	1.1
ISIR 365	46.4	—	18.2	23	1.2

*inferred

ISIR 365 is 18.2 mm. The specimen ISIR 210 shows a marked increase in interorbital width (about 28 mm) because of antero-posterior compression. However, in all other aspects, the Indian specimens bear an overall similarity with the African forms.

Concluding remarks

The Permian in India is very poorly represented by vertebrate fossils. Apart from some palaeoniscoid fishes and temnospondyl amphibians from other Gondwana basins (Werneburg and Schneider, 1996), the Kundaram vertebrates record the sole occurrence of the Permian amniotes in India. Studies have shown that the fauna is largely represented by the two species of *Endothiodon* (Ray, 2000). The present work further strengthens this fauna with the addition of three more genera, *Pristerodon* (*P. mackayi*), *Emydops* (*E. platyceps*) and *Cistecephalus* (*C. microrhinus*). King (1992) reported the presence of *Oudenodon*. The only non-dicynodont member is a captorhinid (Kutty, 1972). Although the study of the Kundaram fauna is far from completion, it is worthwhile to mention some important aspects

of the fauna.

1. The most complete vertebrate record of the Late Permian period is found in the lower part of the highly fossiliferous Beaufort Group of the Karoo Supergroup, South Africa and is subdivided into six biozones. The Kundaram fauna bears a remarkably close similarity to that of the Beaufort Group of South Africa. *Pristerodon* has a wide range covering all the five Permian biozones of the Beaufort Group except for the *Eodicynodon* Assemblage Zone (Rubidge, 1995), and hence is not useful for precise correlation. *Endothiodon* first appears in the *Pristerognathus* Assemblage Zone but predominates in the *Tropidostoma* Assemblage Zone. In this latter zone, *Cistecephalus* occurs very infrequently and *Emydops* makes its first appearance (Figure 12). In contrast, *Endothiodon* persists as a rare fossil while *Cistecephalus* becomes abundant in the succeeding *Cistecephalus* Assemblage Zone. This zone also records the first appearance of *Oudenodon*.

However, the Kundaram fauna shows a preponderance of *Endothiodon* amounting to about thirty individuals with four or five partial skulls of *Cistecephalus* and *Emydops*. The dominance of *Endothiodon* followed by *Emydops* and *Cistecephalus* in the Kundaram fauna indicates a broad correlation with the *Tropidostoma* and *Cistecephalus* Assemblage Zones of the Beaufort Group of South Africa. The Kundaram Formation is also correlated with the basal beds of the Madumabisa Mudstones of Zambia, the Ruhuhu and lower part of the Kawinga Formation of Tanzania and the Morro Pelado Member of the Rio do Rasto Formation of Brazil. It suggests a Late Permian Tatarian age for the Kundaram Formation.

2. Another distinctive feature of the Kundaram vertebrate fauna is the small size of its individual members. *Endothiodon* shows two distinct clusters of skull size. *E. mahalanobisi* has an average SL of about 160 mm and is much smaller than the other known *Endothiodon* species, while that of *E. uniseries* is about 350 mm. Other dicynodonts of the Kundaram Formation like *Pristerodon*

mackayi (SL ca. 50.6 mm), *Emydops* sp. (SL ca. 47.8) and *Cistecephalus microrhinus* (SL ca. 50 mm) are also small. This smallness of size is also reflected in the captorhinid (SL ca. 50 mm).

The dominance of the small forms in the Kundaram fauna is comparable with that of the *Cistecephalus* Assemblage Zone. In this zone, more than 70% of the total faunal assemblage is composed of small forms, in marked contrast to that of the underlying *Tropidostoma* Assemblage Zone. The latter zone is characterised mainly by medium to large dicynodonts such as *Rhachiocephalus* (Rubidge, 1995). There are too many unknown parameters, to say with confidence what might have caused this size differentiation. It may be due to preservational bias, transportational sorting or palaeoclimatic and palaeogeographic influences and necessitates further study of the Permian Kundaram fauna.

3. The distribution of Kundaram dicynodonts, *Endothiodon*, *Oudenodon*, *Pristerodon*, *Emydops* and *Cistecephalus*, in the now widely separated geographic areas (Table 7) suggests that there was no apparent physical barrier between these regions. Moreover, the Pangean distribution of these dicynodont-bearing regions shows a broad and regular zone, extending from Brazil in the west to India in the east (Ray, 1999). It indicates the close proximity of the continents during that time and a lack of endemism or provinciality among these genera.

Table 7. Distribution of the five dicynodont genera (after Anderson and Cruikshank, 1978; King, 1992; Ray, 1999).

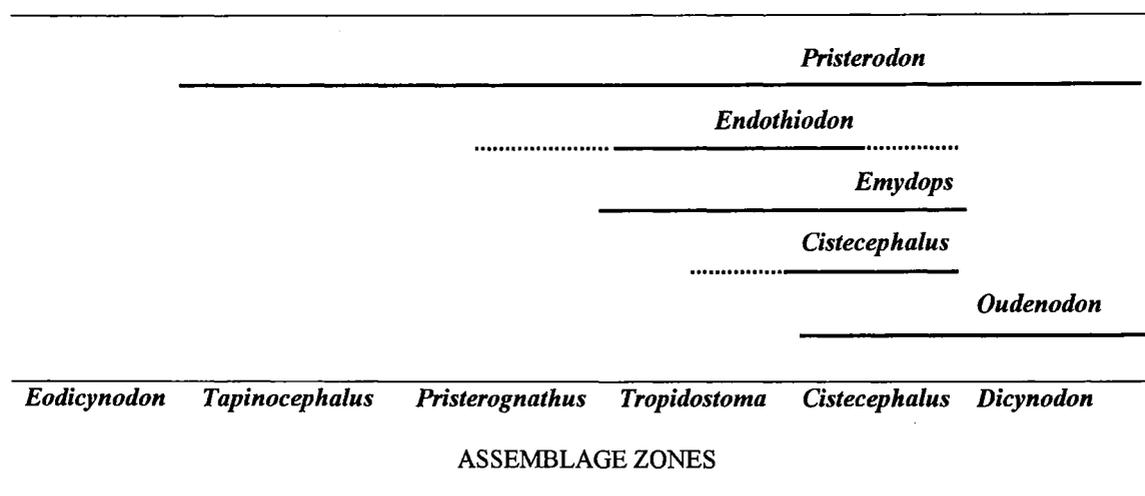| South Africa	India	Mala-gasy	Tan-zania	Zambia	Mozam-bique	Brazil
Pristerodon	+		+	+		
Endothiodon	+		+	+	+	+
Emydops	+			+		
Cistecephalus	+					
Oudenodon	+	+		+		

Figure 12. Ranges of the Kundaram dicynodont genera present in the Beaufort Group, Karoo Supergroup, South Africa (after Rubidge, 1995).

Acknowledgements

References

Anderson, J. M. and Cruickshank, A. R. I., 1978: The biostratigraphy of the Permian and Triassic. Part 5: A review of the classification and distribution of Permo-Triassic tetrapods. *Palaeontologia Africana*, vol. 21, p. 15–44.

Broili, F. and Schroder, J., 1935: Beobachtungen an Wirbeltieren der Karooformation. VI. Über den Schädel von *Cistecephalus* Owen. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften*, vol. 1935, p. 1–20.

Broom, R., 1903: On the classification of the theriodonts and their allies. *Report of the South African Association for the Advancement of Science*, vol. 1, p. 286–295.

Broom, R., 1912: On some new fossil reptiles from the Permian and Triassic beds of South Africa. *Proceedings of Zoological Society of London*, vol. 1912, p. 859–876.

Broom, R., 1913: On some new genera and species of dicynodont reptiles with notes on a few others. *Bulletin of American Museum of Natural History*, vol. 32, p. 441–457.

Broom, R., 1921: On some new genera and species of anomodont reptiles from the Karoo beds of South Africa. *Proceedings of Zoological Society of London*, vol. 1921, p. 647–674.

Broom, R., 1932: *The Mammal-like Reptiles of South Africa and the Origin of Mammals.* 376 p. H. F. and G. Witherby, London.

Broom, R., 1948: A contribution to our knowledge of the vertebrates of the Karoo beds of South Africa. *Transactions of the Royal Society of Edinburgh*, vol. 61, p. 577–629.

Broom, R. and Haughton, S. H., 1917: Some new species of Anomodontia (Reptilia). *Annals of the South African Museum*, vol. 12, no. 5, p. 119–125.

Cluver, M. A., 1974a: The skull and mandible of a new cistecephalid dicynodont. *Annals of the South African Museum*, vol. 64, p. 137–155.

Cluver, M. A., 1974b: The cranial morphology of the Lower Triassic dicynodont *Myosaurus gracilis*. *Annals of the South African Museum*, vol. 66, p. 35–54.

Cluver, M. A., 1978: The skeleton of the mammal-like reptile *Cistecephalus* with evidence of a fossorial mode of life. *Annals of the South African Museum*, vol. 76, no. 5, p. 213–246.

Cluver, M. A. and King, G. M., 1983: A reassessment of the relationships of Permian Dicynodontia (Reptilia, Therapsida) and a new classification of dicynodonts. *Annals of the South African Museum*, vol. 91, no. 3, p. 195–273.

Cox, C. B., 1972: A new digging dicynodont from the Upper Permian of Tanzania. *In*, Joysey, K. A. and Kemp, T. S. eds., *Studies in Vertebrate Evolution*. p. 173–189. Oliver and Boyd, Edinburgh.

Huxley, T. H., 1868: On *Saurosternon bainii* and *Pristerodon mackayi*, two new fossil lacertilian reptiles from South Africa. *Geological Magazine*, vol. 5, p. 201–205.

Keyser, A. W., 1973: A preliminary study of the type area of the *Cistecephalus* zone and the revision of the family Cistecephalidae. *Memoir of the Geological Survey of Republic of South Africa*, vol. 62, p. 1–71.

Keyser, A. W., 1975: A re-evaluation of the cranial morphology and systematics of some tuskless Anomodontia. *Memoir of the Geological Survey of South Africa*, vol. 67, p. 1–110.

Keyser, A. W., 1993: A re-evaluation of the smaller Endothiodontidae. *Memoir of Geological Survey of South Africa*, vol. 82, p. 1–53.

King, G. M., 1988: Anomodontia. *In*, Wellnhofer P., ed., *Encyclopedia of Paleoherpetology*, vol. 17C, p. 1–174. Gustav Fischer Verlag, Stuttgart.

King, G. M., 1992: The palaeobiogeography of Permian anomodonts. *Terra Nova*, vol. 4, p. 633–640.

King, G. M., 1993: How many species of *Diictodon* were there? *Annals of the South African Museum*, vol. 102, no. 9, p. 303–325.

King, G. M. and Rubidge, B. S., 1993: A taxonomic revision of small dicynodonts with postcanine teeth. *Zoological Journal of the Linnean Society*, vol. 107, p. 131–154.

Kutty, T. S., 1972: Permian reptilian fauna from India. *Nature*, vol. 237, p. 462–463.

Kutty, T. S., Jain, S. L. and RoyChowdhury, T. 1987: Gondwana sequence of the Northern Pranhita-Godavari valley: its stratigraphy and vertebrate faunas. *Palaeobotanist*, vol. 36, p. 214–229.

Owen, R., 1859: On the orders of fossil and recent Reptilia and their distribution in time. *Report of the British Association for the Advancement of Science*, vol. 1859, p.153–166.

Owen, R., 1876: *Descriptive and Illustrative Catalogue of the Fossil Reptilia of South Africa in the Collection of British Museum (Natural History)*. 88 p. Taylor and Francis, London.

Ray, S., 1997: Some contributions to the Lower Gondwana stratigraphy of the Pranhita-Godavari valley, Deccan India. *Journal of the Geological Society of India*, vol. 50, no. 5, p. 633–640.

Ray, S., 1999: Permian reptilian fauna from the Kundaram Formation, Pranhita-godavari Valley, India. *Journal of African Earth Sciences*, vol. 29, no. 1, p. 211–218.

Ray, S., 2000: Endothiodont dicynodonts from the Late Permian Kundaram Formation, India. *Palaeontology*, vol. 43, no. 2, p. 375–404.

Rubidge, B. S., 1995: Biostratigraphy of the Beaufort Group. *South African Commission for Stratigraphy, Biostratigraphic Series* 1, p. 1–45.

Seeley, H. G., 1894: Researches on the structure, organisation and classification of the fossil Reptilia. Part IX, section 1. On the Therosuchia. *Philosophical Transactions of the Royal Society, Series B*, vol. 185, p. 987–1018.

Seeley, H. G., 1895: Researches on the structure, organisation and classification of the fossil Reptilia. Part IX, section 6. Associated remains of two small skeletons

from Klipfontein, Fraserburg. *Philosophical Transactions of the Royal Society, Series B*, vol.186, p. 149-162.

Toerien, M. J., 1953: Evolution of the palate in some anomodonts and its classificatory significance. *Palaeontologia Africana*, vol. 1, p. 49-117.

Van Hoepen, E. C. N., 1934: Oor die indeling van die Dicynodontidae na aanleiding van nuwe vorme. *Palaeontologiese Navorsing van die Nasionale Museum, Bloemfontein*, vol. 2, p. 67-101.

Werneburg, R. and Schneider, J. S., 1996: The Permian temnospondyle amphibians of India. *Special Papers in Palaeontology*, vol. 52, p. 105-128.

Appendix

Institutional abbreviations

AMNH, American Museum of Natural History, New York; BMNH, British Museum (Natural History), London; ISI, Indian Statistical Institute, Calcutta; SAM, South African Museum, Cape Town.

Anatomical abbreviations

Alv	Alveolus	Pal	Palatine
Ang	Angular	Pf	Pineal foramen
Ar	Articular	Pmx	Premaxilla
Bo	Basioccipital	Po	Postorbital
Bs	Basisphenoid	Pof	Postfrontal
D	Dentary	Pp	Preparietal
Eo	Exoccipital	Pr	Prootic
Fr	Frontal	Prf	Prefrontal
Fm	Foramen magnum	Pt	Pterygoid
Ip	Interparietal	Ptf	Post-temporal fenestra
Ipt.v	Interpterygoidal vacuity	Q	Quadrate
J	Jugal	Qj	Quadratojugal
Jf	Jugular foramen	Rl	Reflected lamina
L	Lacrimal	Sph	Sphenethmoid complex
Lds	Lateral dentary shelf	St	Stapes
Lf	Lacrimal foramen	Smx	Septomaxilla
Mx	Maxilla	So	Supraoccipital
Mf	Meckelian fenestra	Sp	Splenial
Na	Nasal	Sq	Squamosal
Op	Opisthotic	V	Vomer
P	Parietal		

Quantification of optically granular texture of benthic foraminiferal walls

RITSUO NOMURA

Foraminiferal Laboratory, Faculty of Education, Shimane University,

Matsue, 690-8504, Japan (e-mail: nomura@edu.shimane-u.ac.jp)

Abstract. Three main textures may occur in optically granular walls of hyaline calcareous foraminifera: mosaic granular, jagged granular, and minute granular. The size and shape of the optical granules within them indicates that these wall textures are intimately related to the crystalline arrangement of the units and their elements, and also to the wall thicknesses of the foraminiferal tests. Highly complex minute-granular textures are observed if the foraminiferal tests are large and walls are thick. In general, crystallographically compound and intermediate wall structures correspond to the minute-granular texture. Both formsize (ratio of perimeter to area) and Shannon-Wiener index for polarized crystal units explain these different wall textures well. This study suggests a method for quantification of wall textures based on image processing.

Key words: benthic foraminifera, crystal unit, ecology, optical textures, test walls

Introduction

Hyaline calcareous walls of benthic foraminiferal tests consist of small crystallites and their assembled crystal units. Hansen (1968, 1970) clarified these crystalline structures by scanning electron microscope studies, and in the 1970s several authors examined these foraminiferal test structures in diverse foraminiferal taxa (e.g., Banner and Williams, 1973; Stapleton, 1973; Bellemo, 1974a, b; Conger et al., 1977). Features of the crystalline structures in test walls are revealed by high interference colors under polarizing microscopy. Wood (1949) introduced the terms radial and granular structures for these optical features of foraminiferal walls. Nomura (1983, 1988) further recognized variations in each optical texture, and subdivided granular structure into mosaic, jagged, and minute (Figure 1.1-1.3), and radial textures into distinct and indistinct. These subdivisions of the granular walls are based on the optical grain size and the structure. Although a clear-cut distinction between them is sometimes difficult, the mosaic granular has larger and less jagged appearances than the jagged one. Optical grains of the minute granular are conspicuously small and complicated in comparison with the mosaic and jagged ones. These optical textures clearly reflect the complexity of crystalline structures consisting of various optical axes of the crystal units and their elements (Nomura, 1983).

The optical textures of foraminiferal walls have mainly been utilized for systematic purposes. Loeblich and Tappan (1964, 1974, 1987) used optical features of foraminiferal walls for their hierarchical classification. This classification now needs to be reexamined in view of increased knowledge. Apart from its application to foraminiferal systematics, wall texture can be used to assist in interpretation of foraminiferal ecology and paleoecology (Nomura, 1988, 1997). In a preliminary report (Nomura, 1997), I suggested that granular textures show variations corresponding to the preferred ecology of individual species. The best example is found in the ecological difference between epifaunal and infaunal species. Mosaic granular texture is mainly found in infaunal taxa, and minute granular texture is seen in epifaunal taxa (Nomura, 1997). It is empirically understood that the crystal units of foraminiferal tests show variations in their perimeter and area in polarized light. As there are gradual changes among the mosaic, jagged, and minute granular textures, however, application of these optical textures to ecology and paleoecology is not definitive. Information on the ecological and ontogenetic characters of the wall textures is still limited.

In order to clarify the optical grains of these textures by quantitative analyses, I examined live and dead specimens having different textures and different growth stages. Observations of the wall texture using a polarizing microscope are particularly useful on account of the simple methodology employed. Definition of analytical methods is needed however to perform reliable comparisons of foraminiferal wall textures.
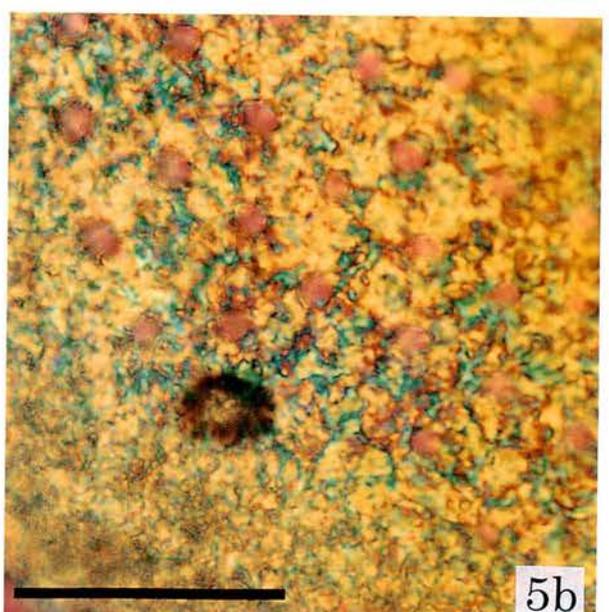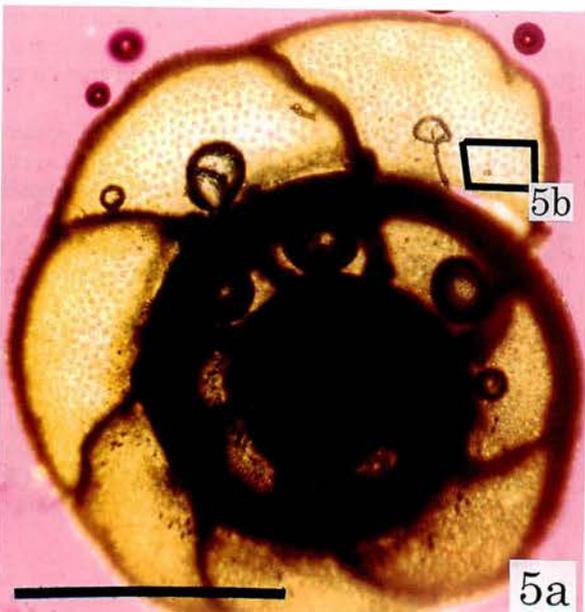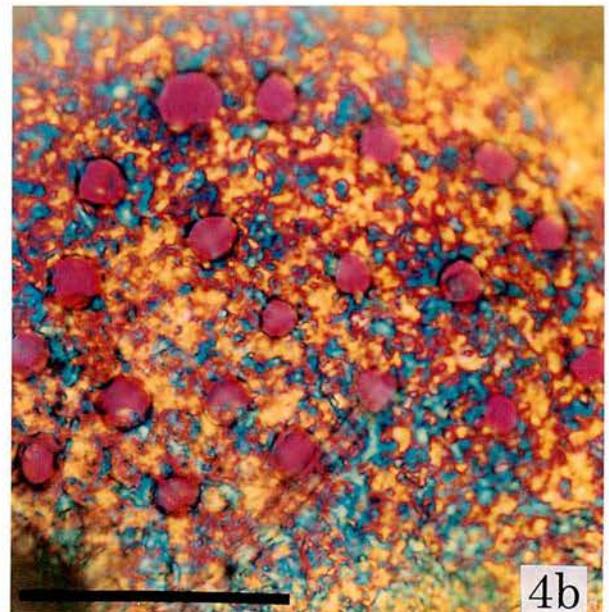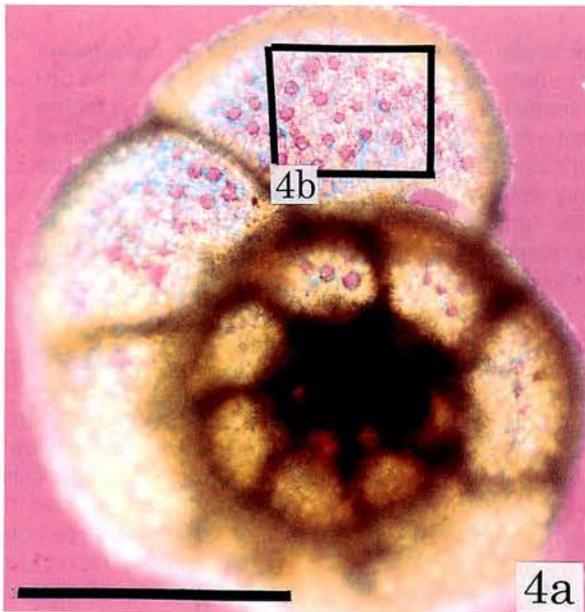
Table 1. Species examined in this study.

taxa	test size (mm)	wall thickness (μm)	depth in m (sample)	condition
Anomalinoides glabratus (Cushman)	0.24–0.56	2.5–15.0	54(HK–1*)	dead
Cassidulina reniforme (Norvang)	0.14–0.20	1.0–2.5	194(HN3–9*)	dead
Chilostomella oolina Schwager	0.38–0.49	1.0–3.8	Pliocene Iioka Formation, Choshi **	fossil
Cibicides lobatulus (Walker and Jacob)	0.38–0.78	6.8–18.2	54(HK–1*)	dead
Cibicides refulgens Montfort	0.22–0.71	4.5–12.5	54(HK–1*)	dead
Cibicidoides pseudoungerianus (Cushman)	0.56–0.83	8.0–11.3	99(HK–4*)	dead
Cibicidoides wuellerstorfi (Schwager)	0.23–0.72	1.5–20.0	99(HK–4*)	dead
Elphidium advenum (Cushman)	0.20–0.62	2.0–12.5	54(HK–1*)	live, dead
Fursenkoina pauciloculata (Brady)	0.29–0.83	1.3–6.2	54(HK–1*)	live, dead
Globocassidulina oriangulata Belford	0.17–0.33	2.0–5.0	99(HK–4*)	dead
Gyroidina orbicularis d'Orbigny	0.20–0.49	2.5–14.0	99(HK–4*)	dead
Gyroidinoides nipponicus (Ishizaki)	0.22–0.37	3.8–4.0	54(HK–1*)	dead
Heterolepa subhaidingeri (Parr)	0.40–0.86	6.3–19.5	99(HK–4*)	live
Nonionellina labradorica (Dawson)	0.22–0.39	1.0–4.7	150(CB4–1*)	live
Nonion manpukuziensis Otuka	0.27–0.66	2.5–7.5	54(HK–1*)	dead
Oridorsalis umbonatus (Reuss)	0.18–0.46	1.0–4.3	150(CB4–1*)	dead
Pullenia bulloides d'Orbigny	0.16–0.32	2.8–5.0	150(CB4–1*)	dead
Paracassidulina neocarinata (Thalmann)	0.206–0.32	2.2–5.5	99(HK–4*)	dead

* KT–90–15, Tansei-maru Cruise, off Shimane and Yamaguchi Prefectures, Sea of Japan (Ocean Research Institute, Univ. of Tokyo)
**Well preserved

Methods

The last chambers of live and well preserved dead specimens of 18 foraminiferal species were analyzed (Table 1). Foraminiferal tests were first embedded in glycerin jelly and covered with a thin glass cover slip as in standard preparation for microscope observation. Tests were crushed and fragments of the final chamber walls were arranged carefully by pressing the glass under a binocular microscope while the jelly was liquid enough to allow the wall pieces to move.

Observations and measurements of the crystal units were carried out under a polarizing microscope at a magnification of ×400. Measurements of the wall thickness were made on final wall fragments set vertically on the glass at the magnification of ×1000, after wall texture photography. Crystal units were observed most effectively using the first-order interference colors arising from insertion of a gypsum plate. The image analysis was carried out using Winroof (version 3.5.2; Mitani Corporation, 2000), which runs on Windows computers. The observations were made at an angle of 45° to the optically positive or negative orientations of the crystal units. Two methods were used to quantify the texture image. Firstly the perimeters and areas of manually selected crystal units were measured to calculate the ratio of perimeter to area (A/P ratio or formsize) (Nomura, 1997). Ten to twenty crystal units were measured for each wall

piece. Because this method is subjective, sometimes selection errors can be made, especially when the unit is not clearly differentiated from neighboring units. To avoid such selection errors, I applied a second method that detects crystal units after color processing which disintegrates the original color image into RGB (red, green, and blue).

Crystal units are more effectively distinguished in the G (green) image at specific threshold values (Figure 2). Thresholding is a brightness discrimination, which selects pixels belonging to features of interest (Russ, 1990). Possible values range from 0 to 255. A block model of the green image, in which the peaks correspond to the brightness intensities, is shown in Figure 2.2. Selection of the crystal unit areas is thus critically controlled by the threshold values. Various threshold values were examined to find the best texture images. Statistically, pixel brightness has a characteristic frequency distribution for each texture, and usually shows a normal distribution (Figure 2.4). The following formula was used to determine the threshold value for each specimen examined: Threshold value = Average threshold value + Standard deviation. Between 100 and 500 areas of selected crystal units were counted for each specimen.

The selected unit images were subsequently converted to binary images (Figure 2.3) and their areas, perimeters, and formsizes then calculated. These measurements were

← Figure 1. Variations of optically granular wall texture. **1.** Mosaic-granular texture of *Chilostomella ovoidea*. Scale bar = 50 μm. **2.** Jagged-granular texture of *Elphidium advenum*. Scale bar = 50 μm. **3.** Minute-granular texture of *Cibicidoides pseudoungerianus*. Scale bar = 50 μm. **4a, 4b.** Horizontal section of a small *Heterolepa subhaidingeri* and close-up of the final chamber wall showing the minute-granular texture. Scale bar: 4a, 200 μm, 4b, 100 μm. **5a, b.** Horizontal section of a larger *H. subhaidingeri* and close-up of the final chamber wall showing indistinct crystal unit boundaries. Scale bar: 5a, 500 μm, 5b, 100 μm.
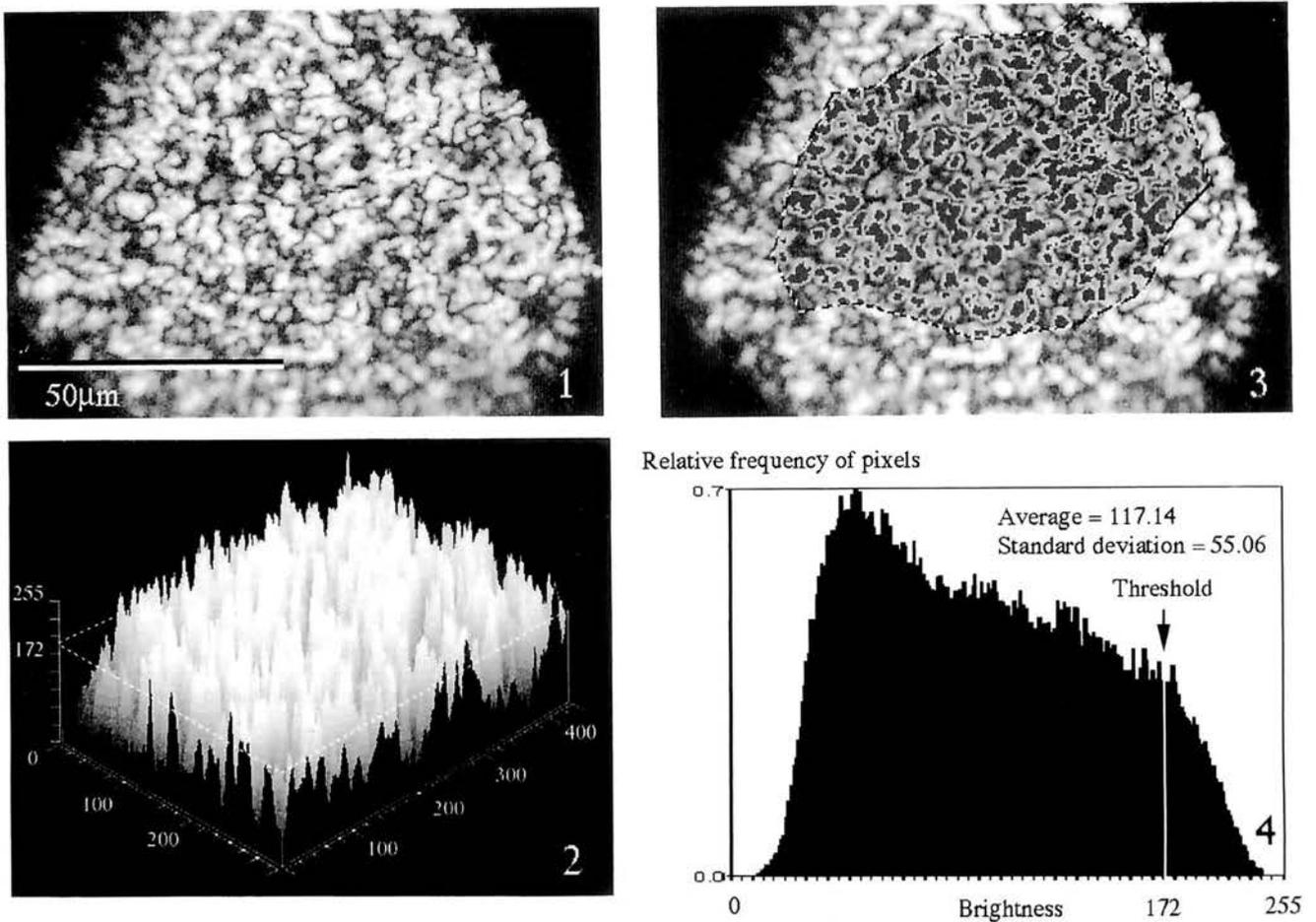
Figure 2. Explanations for the image processing of *Fursenkoina pauciloculata*. **1.** Green image of the texture separated from the blue and red images. **2.** Block diagram of the green image. Thresholding is the brightness value used to distinguish particular images from others, ranging from 0 to 255. Dotted horizontal lines indicate the threshold value (172) in this analysis. **3.** Binary image of the crystal unit areas at threshold value 172. **4.** Histogram showing the relative frequency of pixel brightness (0–255). The averaged brightness is 117.14 and the standard deviation is 55.06. Thresholding at 172 (sum of the average and the standard deviation) accounts for 20.35% of the selected texture.

based on the binary images at threshold values of 130–240. The formsize of each crystal unit is calculated by the formula: Formsize = 2·(Area)/(Perimeter). Values are ≥ 1. If the formsize is 1, the crystal unit is perfectly circular and its radius is 1. The A/P ratio (Nomura, 1997) is a simple expression of this formsize.

The areas of the selected crystal units show a wide variation between 1 to 2000s pixels. Statistical values with high standard deviation make the comparison of the formsize unreliable. However, both the number of the selected areas and the number of pixels they contain represent the difference between the textures, so that they conform to the concept of ecological heterogeneity that accounts for the amount of order or disorder in any given part of the wall. The Shannon-Wiener information function (H') is herein applied to evaluate the diversity of the textures:

$$H' = -\sum_{i=1}^{N}(Pi)(\log_2 Pi)$$

where N is the total number of the crystal units selected and Pi is the proportion in the i th-selected area to the total areas selected. Higher values of H' indicate the textures are characterized by a more complex crystalline arrangement, whereas lower values represent textures consisting of more simple arrangements.

It is difficult to measure the thicknesses of fixed parts of the walls, because breakage occurs randomly during crushing. Analysis was limited to flat pieces of final chamber walls. Sutural areas consist of complicated crystalline structures showing interwoven crystal units and elements. Such areas are not suitable for this analysis. Wall thickness is proportional to test size, and so increases in individuals with growth, even though it varies between foraminiferal species. Thus, careful selection of wall fragments is necessary if reliable results are to be obtained.

Results

The smaller specimens examined here (maximum diameter 0.15–0.25 mm) usually have final chamber walls between 1.0–5.0 μm thick. However, mature specimens of species such as *Chilostomella ovoidea*, *Nonionellina labradorica*, and *Cassidulina reniforme* may also have thin walls (< 5.0 μm). Large specimens (0.4–0.9 mm diameter) of species such as *Heterolepa subhaidingeri* show a wide range of wall thickness (6.3–19.5 μm; Table 1). Wall thickness differs between taxa, and appears to be reflected in wall texture. Thin-walled specimens show well defined boundaries between crystal units displaying distinct blue, red, and yellow areas, but thicker specimens have indistinct boundaries, and blue and red areas are much reduced. These color changes are caused by the interference order of polarizing light, because internal refraction of incident light occurs in every crystal element in the unit and at the unit boundary. Thin-walled crystal units present first-order interference color, but thicker walls containing assembled crystal units produce multiple interference. Brightness of pale yellow images thus increases with increasing wall thickness.

Change of optical texture in relation to the wall thickness can also be seen within individuals as they grow. As observed in *Cibicidoides pseudoungerianus* tests of differing
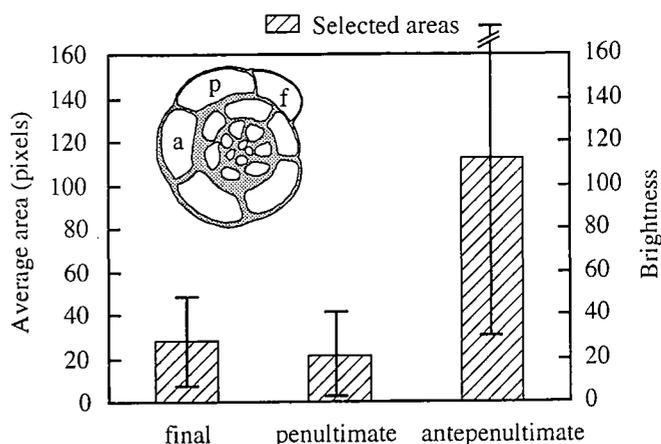
Figure 3. Results of averaged areas with standard deviations for the last three chambers of a sectioned *Oridorsalis umbonatus*. Threshold value is 130. Increased areas in the antepenultimate chamber are caused by indistinct boundaries between the crystal units. f: final chamber. p: penultimate. a: antepenultimate.
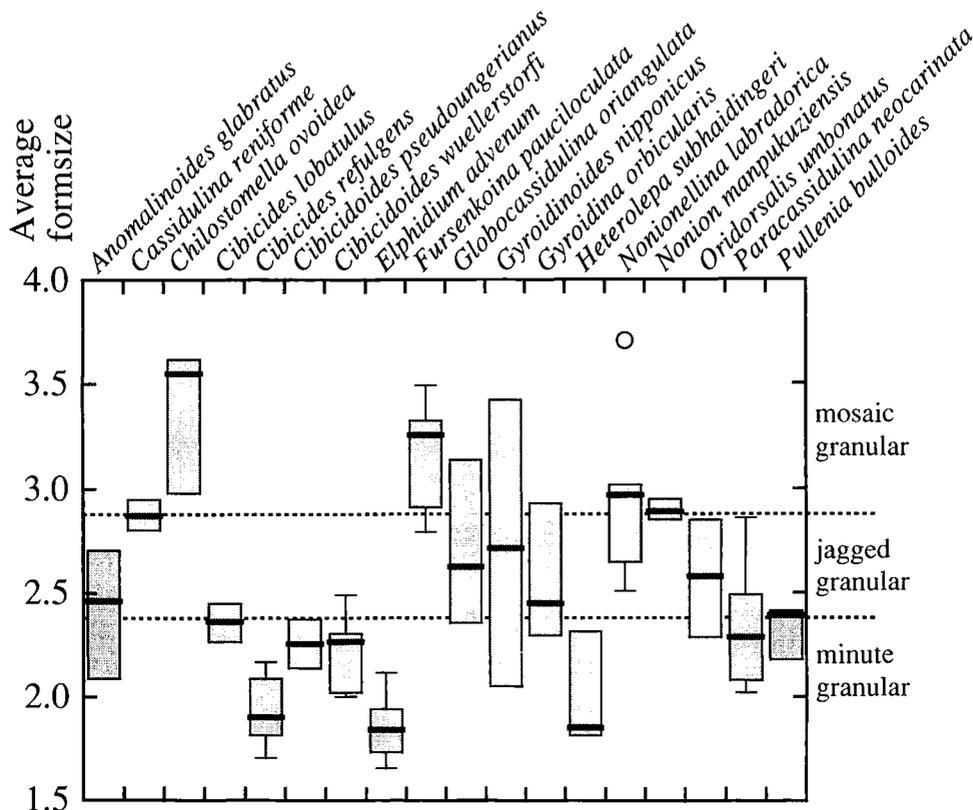
Figure 4. Average formsize in each species. Many species have a wide variation in formsize, which is related to the different textures. Mosaic-granular texture is typified by formsize of > 2.8; formsize of minute-granular textures are < 2.4; and values for jagged-granular texture lie between 2.4 and 2.8. Hatched boxes enclose 50% of the formsizes and the tops and bottoms of the box mark ±25%. Thick horizontal line indicates the median. Small circle is an exceptional value.

size (Figure 1.4, 1.5), unit boundaries of crystal units in the final chamber wall can be easily distinguished. In thicker walls, higher interference makes the boundaries less clear (Figure 1.5b). As noted above, the yellowish color in the antepenultimate chamber is caused by higher-order interference colors. The variations in average areas of the selected crystal units and the brightness in the walls of the last three chambers of *Oridorsalis umbonatus* are shown in Figure 3. The average area of the crystal units in the antepenultimate chamber walls is four to five times larger than that in the walls of the final and the penultimate chambers. Areal increase in the antepenultimate chamber walls is clearly related to the brightness, which makes the unit boundary indistinct. Clear discrimination of the crystal units is possible in the final chamber, where wall thickness is usually < 3-4 µm.

Based on the formsize, mosaic-granular texture occurs in *Chilostomella ovoidea* and many immature specimens (i.e., small specimens) of *Cassidulina reniforme*, *Fursenkoina pauciloculata*, *Globocassidulina oriangulata* , *Gyroidinoides nipponicus*, *Gyroidina orbicularis*, *Nonion manpukuziensis* and *Nonionellina labradorica*. This texture is recognized by formsizes of over 2.8 (Figure 4). The walls of *Nonionellina labradorica* show atypical mosaic-granular texture, where either the optically positive or negative conditions are dominant in the apertural face. Optical axes of the crystal elements are equally arranged over large areas, but are oblique to the test surface. This texture can also be seen in taxa having larger apertural faces, such as *Nonion* and *Nonionella*. Typical minute-granular texture is shown by most species of the genera *Cibicidoides*, *Cibicides*, and *Heterolepa*. This texture reflects the original complexity of their crystalline arrangement. In the Cibicidinae (Bellemo, 1974b, 1976), this is termed compound and the intermediate structure. Similar formsize is also seen in other mature specimens of *Anomalinoides glabratus*, *E. advenum*, *G. oriangulata*, *G. nipponicus*, *G. orbicularis*, *O. umbonatus*, *Paracassidulina neocarinata* and *P. bulloides*, except for *Chilostomella ovoidea* and *Cassidulina reniforme*. However, their crystalline structures differ slightly from those of the Cibicidinae in having larger crystal units and herringbone structure (e.g., Nomura, 1983). Thus, the minute-granular texture is formed by the original complex crystalline structure and by an apparent feature of thick walls consisting of mosaic and jagged-granular textures. The boundary between minute-granular and jagged-granular may be around a formsize of 2.4 (Figure 4). Jagged-granular texture is usually recognized between 2.4 and 2.8.

These three wall textures show wide variations in the measured formsize values. In particular, thinner walls (< 5 mm) are characterized by high standard deviation values (Figure 5). Gradual changes between the different textures also occur. Excepting the Cibicidinae, most species show three differing textures according to the growth stages of the individual: mosaic-granular texture corresponds to the stage of new chamber formation or the younger growth stage of individual foraminifera; jagged- and minute-granular textures correspond to the full-grown stages of individuals.

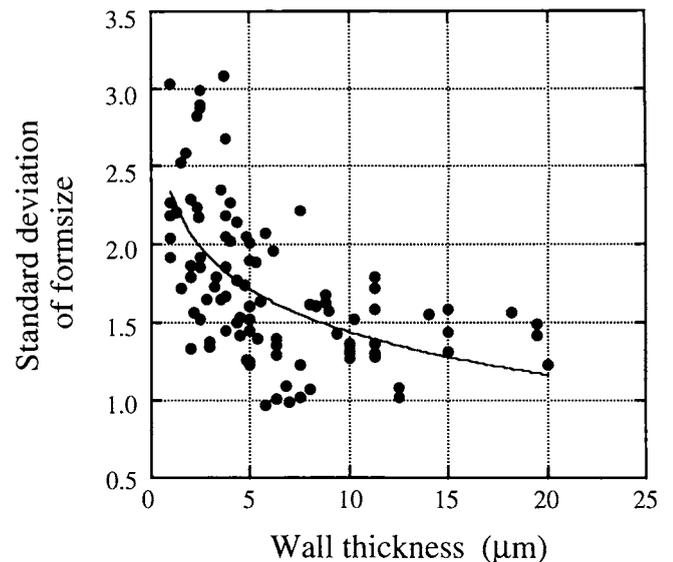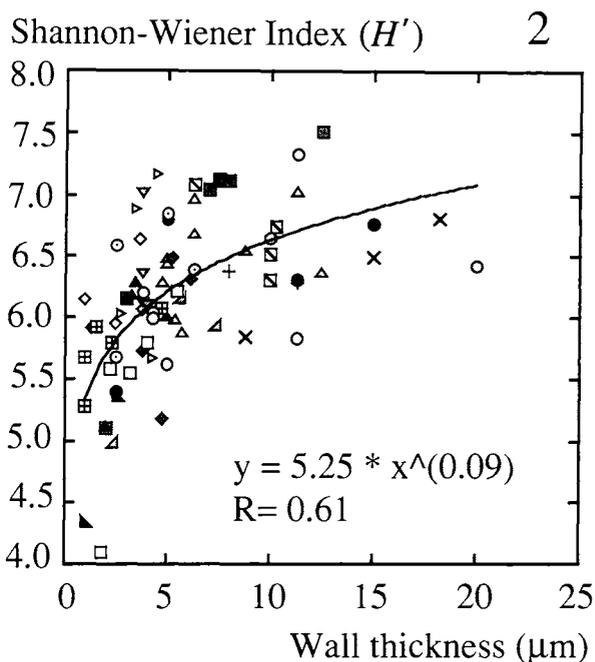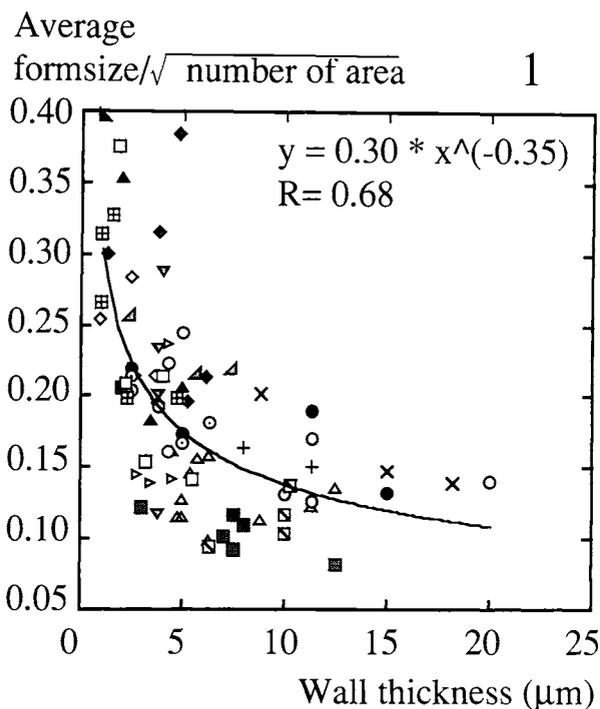A significant relationship is indicated between modified formsize (formsize divided by the square root of the number

Figure 5. Plots of standard deviation of formsize and wall thickness showing large variations in thinner test walls.

of selected crystal units) and wall thickness (Figure 6.1). This relationship can be expressed as an exponential, with $r = 0.68$. The formsize is divided by the square root of the number of crystal units because formsize is dependent on the number of selected areas. Mosaic granular textures are characterized by low numbers of selected crystal units and higher formsizes, whereas minute-granular textures have larger numbers of crystal units and lower formsize values. The results clearly indicate that larger formsizes have thinner walls, whereas specimens with smaller formsize values have thicker walls and/or originally smaller and complex crystal units. Shannon-Wiener information theory is the other quantitative expression to account for the heterogeneity of selected units that consist of large and small areas. The result of this information function is opposite to the relationship between formsize and wall thickness (Figure 6.2). It is thus negatively correlated with modified formsize at a statistically significant level ($p < 0.001$) (Figure 7). If the Shannon-Wiener information index is higher, then the modified formsize is smaller, and textures are complex. Conversely, if the information index is lower, then modified formsize is higher and textures are simpler.

As a result, distribution of respective wall textures on the formsize overlaps among different species, due to changes in the wall texture through growth. Little change in the wall texture is observed between the final and the preceding walls, as well as among different-sized specimens of thinly walled species such as *Chilostomella ovoidea* and *Cassidulina reniforme*. These species are characterized by having larger original crystal units and additional thin laminae in walls formed subsequently.
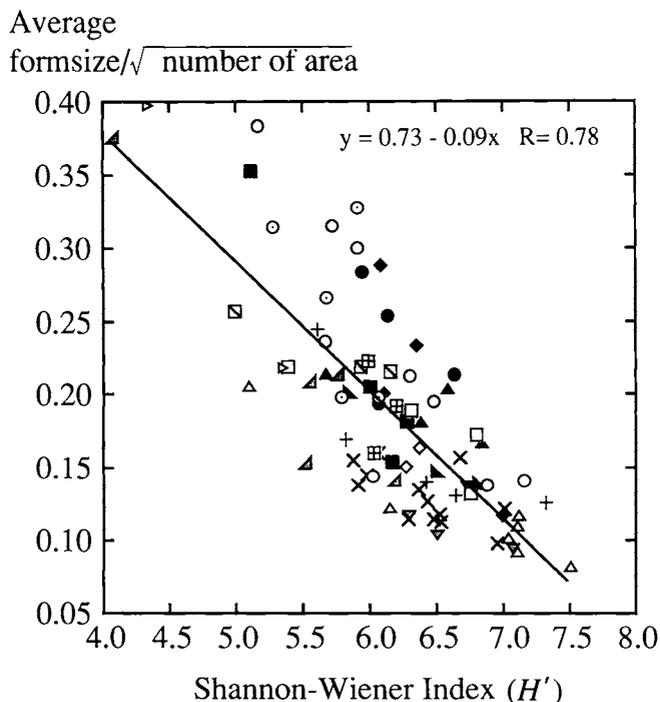
Discussion and Conclusions

Mosaic, jagged and minute granular optical wall textures result from the arrangement of crystal units and the ele-

Average formsize/√ number of area   **1**

$$y = 0.30 * x^{(-0.35)}$$
$$R = 0.68$$

Wall thickness (μm)

Shannon-Wiener Index (H') **2**

$$y = 5.25 * x^{(0.09)}$$
$$R = 0.61$$

Wall thickness (μm)

- ● *A. glabratus*
- ▲ *C. reniforme*
- ◇ *C. ovoidea*

- ○ *C. wuellerstorfi*
- ■ *E. advenum*
- ◆ *F. pauciloculata*

- ▲ *G. oriangulata*
- ▽ *G. nipponicus*
- ○ *G. orbicularis*

- ○ *O. umbonatus*
- □ *P. neocarinata*
- ▷ *P. bulloides*

- × *C. lobatulus*
- + *C. pseudoungerianus*
- ▵ *C. refulgens*

- ⓝ *H. subhaidingeri*
- ⊞ *N. labradorica*
- ◿ *N. manpukuziensis*

Figure 6. **1.** Plots of average formsize and wall thickness of the species, showing a negative exponential relationship. Formsize is here divided by the square root of the number of the area. **2.** Plots of the Shannon-Wiener index (H') and the wall thickness of the species examined show a positive exponential relationship.

Average formsize/√ number of area

$$y = 0.73 - 0.09x \quad R = 0.78$$

Shannon-Wiener Index (H')

ments within any wall thickness. Mosaic-granular texture is formed by larger crystal units and thinner walls, and was once named "clumpy crystalline structure" (Nomura, 1983). Jagged-granular texture is correlated with "intricate crystalline structure" (Nomura, 1983). Minute-granular texture is formed by two types of crystalline structures: 1) intricate crystalline structures within thicker walls, and 2) complex arrangement of crystal elements such as the compound and intermediate structures of Bellemo (1974b, 1976). Ratios of the perimeter to the area of the selected crystal unit have been introduced as a method of quantitatively discriminating these wall textures (Nomura, 1997). However, initially this method used manual selection of crystal units and thereby sometimes produced errors. Criteria for the selection of crystal units are needed. The present study confirms that the intimate relationships between optical texture and crys-

◀ Figure 7. Plot of average formsize and Shannon-Wiener index (H') showing a negative relationship with a statistically significant correlation coefficient (r=0.78). Formsize is here divided by the square root of the number of the area. Symbols as in Figure 5.

talline structure can be recognized in walls showing first-order interference colors. Even in this case, image processing is required to overcome individual variations. Several adjoining crystal units may apparently form large single units in polarizing light. Such units must be eliminated to make realistic measurements and comparisons. The thresholding proposed is a simple method of discriminating various texture images.

Classification of optically granular texture in hyaline calcareous foraminifera (Nomura, 1988, 1997) is not only a species character, but is also related to the wall thickness of the foraminiferal test and the complexity of crystalline structures. In general, thinner walls show mosaic-granular texture, whereas thicker walls and complex crystalline structures (compound and intermediate) exhibit minute-granular texture. Jagged-granular texture is present in walls of intermediate and moderate thickness. To evaluate these optical textures, the relationships between formsizes of the crystal units were examined for differing growth stages of foraminiferal individuals of selected species. The results suggest that the formsize of the crystal units shows a gradual change in accordance with the crystalline complexity of the test walls in different foraminiferal growth stages. The relationship between formsize and the wall thickness is statistically significant and exponential. Shannon-Wiener information theory is applicable for quantification of the textures, and the Shannon-Wiener index is negatively correlated with the modified formsize parameter.

Acknowledgments

References

Banner, F. T. and Williams, E., 1973: Test structure, organic skeleton and extrathalamous cytoplasm of *Ammonia Brünnich*. *Journal of Foraminiferal Research*, vol. 3, p. 49-69, pls. 1-10.

Bellemo, S., 1974a: Ultrastructures in Recent radial and granular calcareous foraminifera. *Bulletin of the Geological Institute of the University of Uppsala, N. S.*, vol. 6, p. 117-122, pls. 1-6.

Bellemo, S., 1974b: The compound and intermediate wall structures in Cibicidinae (Foraminifera) with remarks on the radial and granular wall structures. *Bulletin of the Geological Institute of the University of Uppsala, N. S.*, vol. 6, p. 1-11, pls. 1-9.

Bellemo, S., 1976: Wall ultrastructure in the foraminifer *Cibicides floridanus* (Cushman). *Micropaleontology*, vol. 22, p. 352-362

Conger, S. D., Green II, H. W. and Lipps, J. H., 1977: Test ultrastructure of some calcareous foraminifera. *Journal of Foraminiferal Research*, vol. 7, p. 278-296, pls. 1-9.

Hansen, H. J., 1968: X-ray diffractometer investigations of a radiate and a granulate foraminifera. *Bulletin of the Geological Society of Denmark*, vol. 18, p. 345-348

Hansen, H. J., 1970: Electron-microscopical studies on the ultrastructures of some perforate calcitic radiate and granulate foraminifera. *Det Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter*, vol. 17, no. 2, p. 1-16, pls. 1-26.

Loeblich, A. R., Jr. and Tappan, H., 1964: Sarcodina chiefly "thecamoebians" and Foraminiferida, vol. 1 and 2. *In*, Moore, R. C. ed., *Treatise on Invertebrate Paleontology, Protista 2 Part C*. The Geological Society of America and the University of Kansas Press, p. 1c-900c.

Loeblich, A. R., Jr. and Tappan, H., 1974: Recent advances in the classification of the Foraminiferida. *In*, Hedley, R. H. and Adams, C. G. eds., *Foraminifera*, no. 1, p. 1-53, Academic Press, New York.

Loeblich, A. R., Jr. and Tappan, H., 1987: *Foraminiferal Genera and Their Classification*, 970 p., 847 pls. Van Nostrand Reinhold Company, New York.

Mitani Corporation, 2000: WinRoof, version 3.5.2.

Nomura, R., 1983: Cassidulinidae (Foraminiferida) from the uppermost Cenozoic of Japan (Part 1). *Science Report of Tohoku University, 2nd Series (Geology)*, vol. 53, p. 1-101.

Nomura, R., 1988: Ecological significance of wall microstructure of benthic foraminifera in the southwestern Sea of Japan. *Revue de Paléobiologie, Special Volume 2*, p. 859-871.

Nomura, R., 1997: Application of optical structure of foraminiferal test walls to analyze the ecology and paleoecology. *Kaseki (Fossils)*, no. 62, p. 1-14. (*in Japanese with English abstract*)

Russ, J. C., 1990: *Computer-Assisted Microscopy: The Measurement and Analysis of Image*, 453 p. Plenum Press, London.

Stapleton, R. P., 1973: Ultrastructure of tests of some Recent benthic hyaline foraminifera. *Palaeontographica, Abt. A*, vol. 142, p. 16-49, pls. 1-25.

Wood, A., 1949: The structure of the wall of the test in the foraminifera: Its value in classification. *Quarterly Journal of the Geological Society of London*, vol. 104, p. 229-255.

Origin of the Ceratitida (Ammonoidea) inferred from the early internal shell features

YASUNARI SHIGETA[1], YURI D. ZAKHAROV[2] and ROYAL H. MAPES[3]

[1]Department of Geology and Paleontology, National Science Museum, 3-23-1 Hyakunincho,

Shinjuku-ku, Tokyo, 169-0073 Japan (e-mail: shigeta@kahaku.go.jp)

[2]Federal Far Eastern Geological Institute, Far Eastern Branch, Russian Academy of Sciences,

Prospect Stoletiya Vladivostoka 159, 690022 Vladivostok, Russia (e-mail: yurizakh@mail.ru)

[3]Department of Geological Sciences, Ohio University, Athens, Ohio 45701, U.S.A.

(e-mail: mapes@oak.cats.ohiou.edu)

Abstract. The early internal shell features in 40 species of the Goniatitida, Prolecanitida and Ceratitida are described on the basis of well-preserved specimens from the Carboniferous and the Permian of North America, England, Siberia and Urals. Seven morphotypes were recognized in the species examined by differences of the caecum shape (bottle-shaped, gourd-shaped, subelliptical, or elliptical), the proseptum length on the dorsal side (long or short), position of the second septum (close to proseptum or not) and initial position of the siphuncle (ventral, subcentral, or central). *Paraceltites elegans*, the oldest known representative of the Ceratitida, has a long proseptum on the dorsal side, a relatively small ammonitella angle, the second septum does not appear in close vicinity to proseptum, and the siphuncle is ventral. These features are essentially the same as those of the prolecanitid *Daraelites elegans*. This fact supports the hypothesis that the Ceratitida evolved from the Prolecanitida, probably *Daraelites*.

Key words: Ceratitida, early internal shell features, Goniatitida, phylogeny, Prolecanitida

Introduction

The Ceratitida, which is the dominant ammonoid order of the early Mesozoic and one of the major orders of Ammonoidea, ranged from early Permian to the end of Triassic times, and has an almost worldwide distribution (Hewitt et al., 1993; Page, 1996). The origin of this order has been thought to be from a member of the Prolecantitida, because previous authors believed that both taxa shared a common lobe development (i.e., VU type of Ruzhencev, 1960, 1962 or U type of Schindewolf, 1934, 1953; see Smith, 1932; Spath, 1934; Spinosa et al., 1975; Shevyrev and Ermakova, 1979; Saunders and Work, 1997). Zakharov (1983, 1984, 1988), however, showed that the Prolecanitida (Medlicottida in Zakharov, 1983) and the Permian Ceratitida (Paraceltitina in Zakharov, 1984) do indeed share the same lobe developmental type, (i.e., VLU type of Ruzhencev, 1960, 1962 or A type of Schindewolf, 1934, 1953), but one identical to that of the Goniatitida. He also pointed out the difficulty in determining the ancestor of the Ceratitida based on the lobe development patterns, because all early to middle Permian ammonoids have the

same lobe development pattern (Zakharov, 1984). After his works, no detailed observations of various shell characters have been done as a basis for discussion of the ancestor of the Ceratitida.

Since Branco (1879, 1880), the ammonoid early internal shell features have been studied by many authors, and it has been determined that there are a number of common characters in the early shells of all ammonoids. States of these characters appear to be stable at suborder or superfamily levels (Druschits and Khiami, 1970; Druschits and Doguzhaeva, 1974, 1981; Tanabe et al., 1979; Tanabe and Ohtsuka, 1985; Ohtsuka, 1986; Landman et al., 1996). This fact suggests that the early internal shell features are strongly constrained phylogenetically, and therefore, it is possible to investigate the higher phylogenetic relationships within the Ammonoidea by analyzing these character state changes (Shigeta, 1989).

As compared with Jurassic and Cretaceous ammonoids, Carboniferous and Permian ammonoids have been little studied for their early internal shell features. Most previous studies (Shul'ga-Nesterenko, 1926; Böhmers, 1936; Miller and Unklesbay, 1943; Bogoslovskaya, 1959; Zakharov,
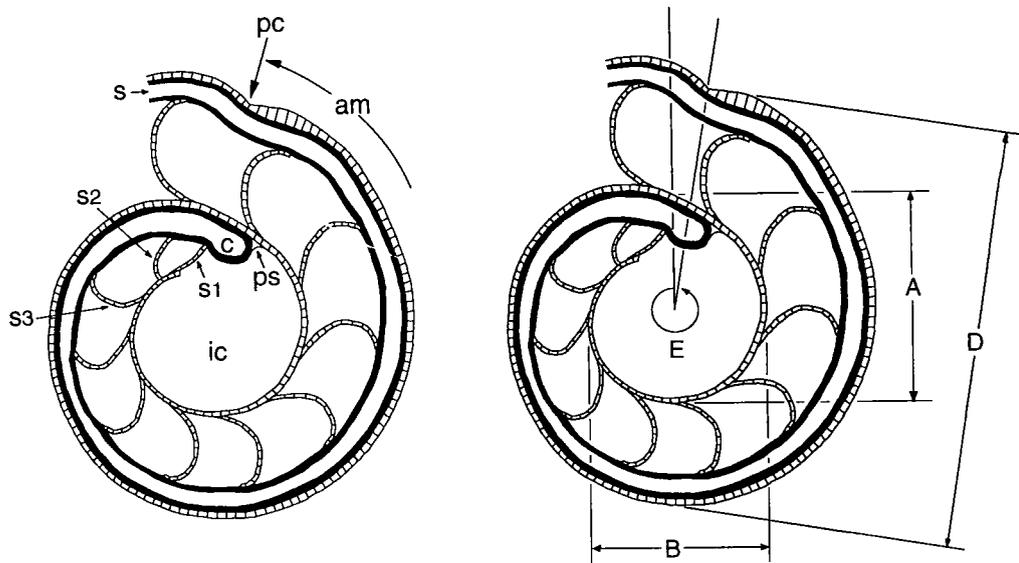
Figure 1. Diagrams of the internal shell structure (left) and measurements (right) of the early ammonoid shell in median section. The terminology is from Branco (1879, 1880), Grandjean (1910), and Drushchits and Khiami (1970). Abbreviations: am: ammonitella; c: caecum; ic: initial chamber; pc: primary constriction; ps: prosiphon; s: siphunclar tube; s1: proseptum (first septum); s2: primary septum (second septum); s3: third septum; A: maximum initial chamber size; B: minimum initial chamber size; D: ammonitella size; E: ammonitella angle.

1978) excluding Tanabe *et al.* (1994) and Landman *et al.* (1999) are based on optical microscopic observations. Detailed microstructural relationships of the morphologic features have received little examination.

We have studied the early internal shell features of some Carboniferous and Permian ammonoids belonging to the Goniatitida, Prolecanitida and Ceratitida, by means of scanning electron microscopy. In this paper, we describe some of our observations and discuss the results of our analysis with special reference to the origin of the Ceratitida.

Material and methods

Five species of the Prolecanitida, 34 species of the Goniatitida and one species of the Ceratitida have been examined (Appendix 1). Specimens of these ammonoids were collected from the Carboniferous and Permian strata of South Urals (Kazakhstan), Siberia (Russia), England and the U.S. mid-continent (Nevada and Texas). They include genera and species studied and figured by Tanabe *et al.* (1994). Higher categories of these genera and species were determined following the classification of Bogoslovskaya *et al.* (1999).

Every specimen was cut and polished along the median plane. The polished surface was etched with 5% acetic acid for a few minutes; the etched surface was washed with distilled water, dried in air, and then coated with gold or platinum using an ioncoater. The early internal features of each specimen were observed by means of a JEOL model JSM-5310 scanning electron microscope. Four characters: maximum initial chamber size, minimum initial chamber size, ammonitella size and ammonitella angle (= spiral length of ammonitella in degrees), were measured on the etched sur-

face using a digital micrometer (accuracy ±0.001 mm) attached to a Nikon model V16D profile projector.

Figure 1 illustrates the terms used to describe the morphologic features of the early shell in median section. The terminology is based on Branco (1879, 1880), Grandjean (1910), and Drushchits and Khiami (1970) (see Landman *et al.*, 1996, figure 1). The specimens observed are reposited at the University Museum, University of Tokyo (UMUT) for those described by Tanabe *et al.* (1994) and at the National Science Museum, Tokyo (NSM) for the remaining specimens.

Observations

Prolecanitida and Goniatitida

The early whorls of the Carboniferous and Permian Prolecanitida and Goniatitida consist of initial chamber (protoconch), caecum, prosiphon, proseptum (first septum), septa, siphuncle, septal neck and outer shell wall, as in other Paleozoic and Mesozoic Ammonoidea. The maximum initial chamber size in median section (A in Figure 1) ranges from 0.356 mm to 0.645 mm in the Prolecanitida and from 0.356 mm to 0.590 mm in the Goniatitida (Appendix 2). The ammonitella diameter (D in Figure 1) ranges from 0.702 mm to 1.250 mm in the Prolecanitida and from 0.660 mm to 1.048 mm in the Goniatitida (Appendix 1). The ammonitella angle (E in Figure 1) is generally small (328–355°) in the Prolecanitida and relatively large (352 – 385°) in the Goniatitida. The early internal shell features of the species examined can be classified into seven morphotypes; here named for the genera that best show each variation: *Epicanites*, *Neopronorites*, *Daraelites*, *Goniatites*, *Marathonites*, *Agathiceras* and *Thalassoceras* morphotypes (Figure
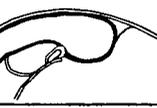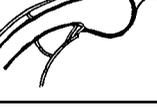
Morphotype	Shape of caecum in median section	Length of proseptum (dorsal side)	Proseptum & 2nd septum (dorsal side)	Initial position of siphuncle
Epicanites	Bottle-shaped	Long	Separate (fairly)	Ventral
Neopronorites	Gourd-shaped	Long	Separate (a little)	Ventral
Daraelites	Bottle-shaped	Long	Separate (a little)	Ventral
Goniatites	Subelliptical	Long	Close	Ventral
Marathonites	Elliptical	Short	Close	Ventral
Agathiceras	Elliptical	Short	Close	Central
Thalassoceras	Elliptical	Short	Close	Subcentral

Figure 2. Comparison of the early internal shell features in seven morphotypes of the Carboniferous and Permian ammonoids. Each morphotype is named for the genera that best show each variation.

2). There is no intermediate form between a pair of these internal shell feature morphotypes in our data base. All of the morphotypes have a circular initial chamber in median section and a short prosiphon.

Epicanites morphotype.—In median section, caecum is elongate and subelliptical (bottle-shaped), without a conspicuous constricted base at proseptum and second septum; prosiphon is short and gently curved ventrally, and proseptum resting on dorsal side of initial chamber wall is long and strongly convex adapically. Second septum is convex adorally in median section, with a retrochoanitic septal neck, and is located far from proseptum. Siphuncle keeps ventral position throughout ontogeny.

Akmilleria electaensis, Artioceras rhipaeum (Figure 3.5, 6) and *Epicanites loeblichi* (Figure 4.1, 2) possess the early internal shell morphology of this morphotype. Early internal shell features of this morphotype have been reported in other Medlicottioidea (Shul'ga-Nesterenko, 1926; Böhmers, 1936; Miller and Unklesbay, 1943; Bogoslovskaya, 1959).

Neopronorites morphotype.—Caecum is gourd-shaped,

with a slightly constricted base at the proseptum, bulging part between proseptum and second septum, and gradual contracting part after second septum. Prosiphon is short, tube-like and straight. Proseptum resting on dorsal side of initial chamber wall is relatively long and slightly convex adorally in median section. Second septum is slightly concave adorally in median section, with a retrochoanitic septal neck, and is located relatively far from proseptum. Siphuncle is ventral throughout ontogeny.

Neopronorites skvorzovi (Figure 3.3, 4) possesses the early internal shell morphology of this morphotype, as described by Zakharov (1986). A similar shaped caecum was described in *Parapronorites* cf. *biformis* by Shul'ga-Nestere nko (1926), hence she named it as a double caecum. Böhmers (1936), Miller and Unklesbay (1943) and Bogoslovskaya (1959) reported similar early internal shell features in other Pronoritoidea.

Daraelites morphotype.—Caecum is elongate and subelliptical (bottle-shaped), without a conspicuous constricted base at proseptum and second septum. Proseptum resting on

Figure 3.   Median sections through the early whorls of the Permian prolecanitids. Over views of the early whorls showing the primary constriction (pc) (1, 3, 5) and close-up of the prosiphon (ps), the caecum (c), the proseptum (s1), the second septum (s2) and third septum (s3) (2, 4, 6).   Scale bars in 1, 3 and 5: 0.5 mm.   Scale bars in 2, 4 and 6: 0.1 mm. **1, 2**.   *Daraelites elegans* Tchernow (Prolecanitoidea), Artinskian, South Urals (NSM PM16189). **3, 4**.   *Neopronorites skvorzovi* (Tchernow) (Pronoritoidea), Artinskian, South Urals (NSM PM16190).   **5, 6**. *Artioceras rhipaeum* (Ruzhencev) (Medlicottioidea), Artinskian, South Urals (NSM PM16192).

Figure 4. Median sections through the early whorls of the Carboniferous ammonoids. Overviews of the early whorls showing the primary constriction (pc) (1, 3, 5) and close-up of the prosiphon (ps), the caecum (c), the proseptum (s1), the second septum (s2) and third septum (s3) (2, 4, 6). Scale bars in 1, 3 and 5: 0.5 mm. Scale bars in 2, 4 and 6: 0.1 mm. **1, 2.** *Epicanites loeblichi* Miller & Furnish (Prolecanitida: Prolecanitoidea), Chesterian, Oklahoma (NSM PM16188). **3, 4.** *Girtyoceras meslerianum* (Girty) (Goniatitida: Dimorphoceratoidea), Chesterian, Oklahoma (NSM PM16193). **5, 6.** *Cravenoceras incisum* (Hyatt) (Goniatitida, Neoglyphioceratoidea), Chesterian, Texas (NSM PM16198).

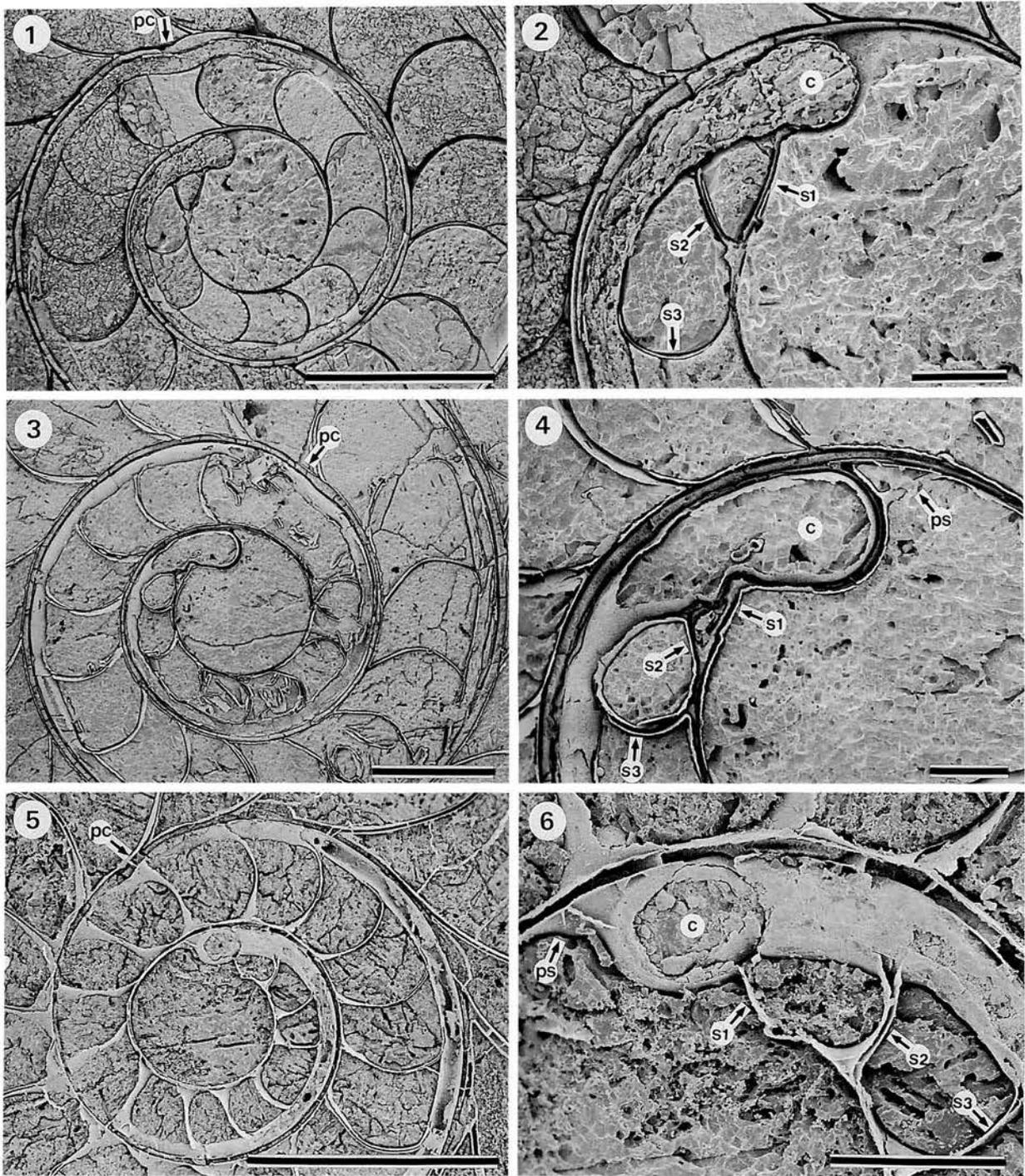**Figure 5.** Median sections through the early whorls of the Permian goniatitids. Overviews of the early whorls showing the primary constriction (pc) (1, 3, 5) and close-up of the prosiphon (ps), the caecum (c), the proseptum (s1), the second septum (s2) and third septum (s3) (2, 4, 6). Scale bars in 1, 3 and 5: 0.5 mm. Scale bars in 2, 4 and 6: 0.1 mm. **1, 2.** *Popanoceras annae* Ruzhencev (Popanoceratoidea), Artinskian, South Urals (NSM PM16214). **3, 4.** *Marathonites invariabilis* (Ruzhencev) (Marathonitoidea), Artinskian, South Urals (NSM PM16207). **5, 6.** *Uraloceras* sp. (Neoicoceratoidea), Wolfcampian, Nevada (NSM PM16213).
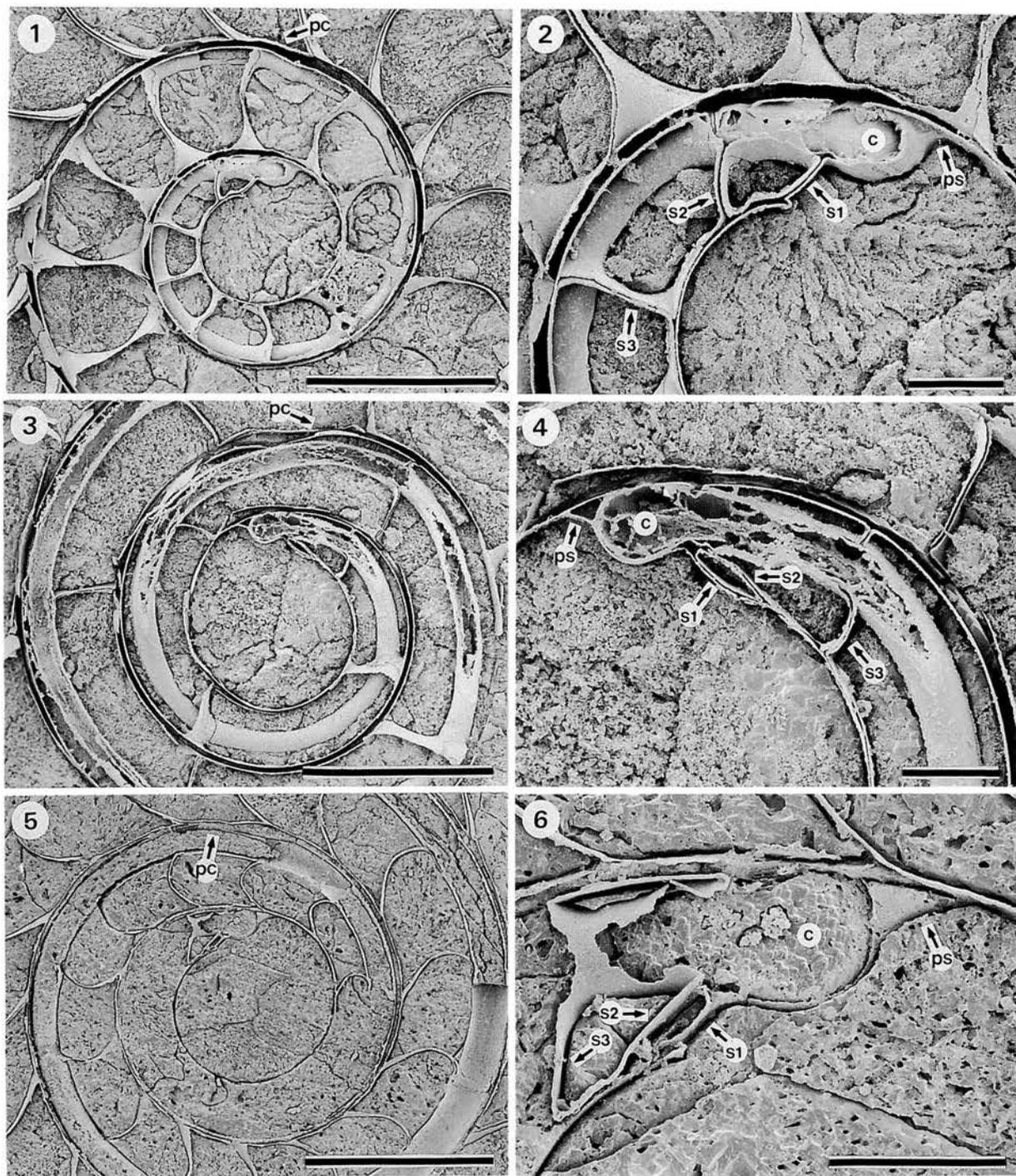
Figure 6. Median sections through the early whorls of the Permian goniatitids. Overviews of the early whorls showing the primary constriction (pc) (1, 3, 5) and close-up of the prosiphon (ps), the caecum (c), the proseptum (s1), the second septum (s2) and third septum (s3) (2, 4, 6). Scale bars in 1, 3 and 5: 0.5 mm. Scale bars in 2, 4 and 6: 0.1 mm. **1, 2.** *Agathiceras uralicum* (Karpinsky) (Goniatitoidea), Artinskian, South Urals (NSM PM16195). **3, 4.** *Thalassoceras gemmellaroi* Karpinsky (Thalassoceratoidea), Artinskian, South Urals (NSM PM16203). **5, 6.** *Crimites subkrotowi* Ruzhencev (Adrianitoidea), Artinskian, South Urals (NSM PM16204).
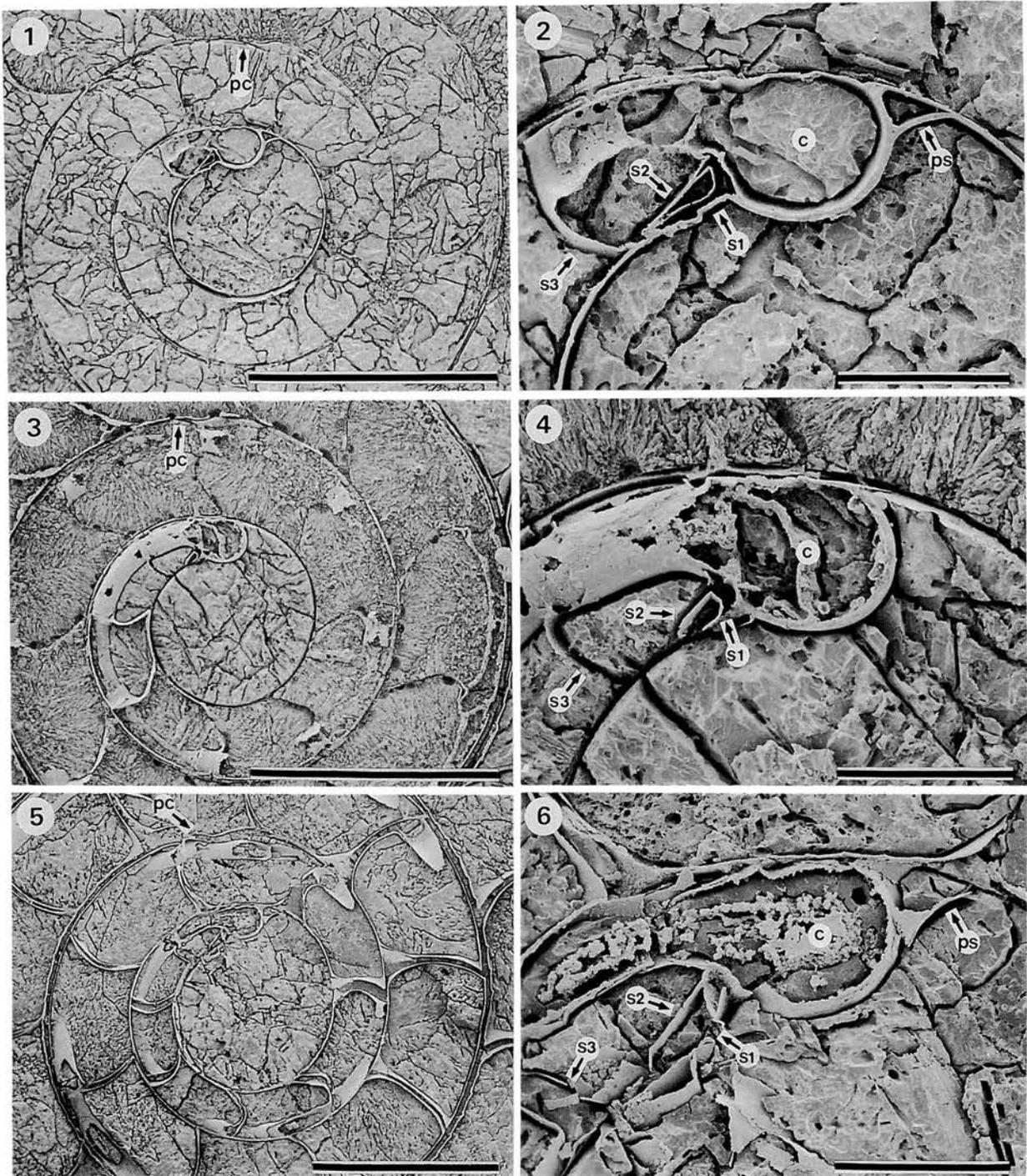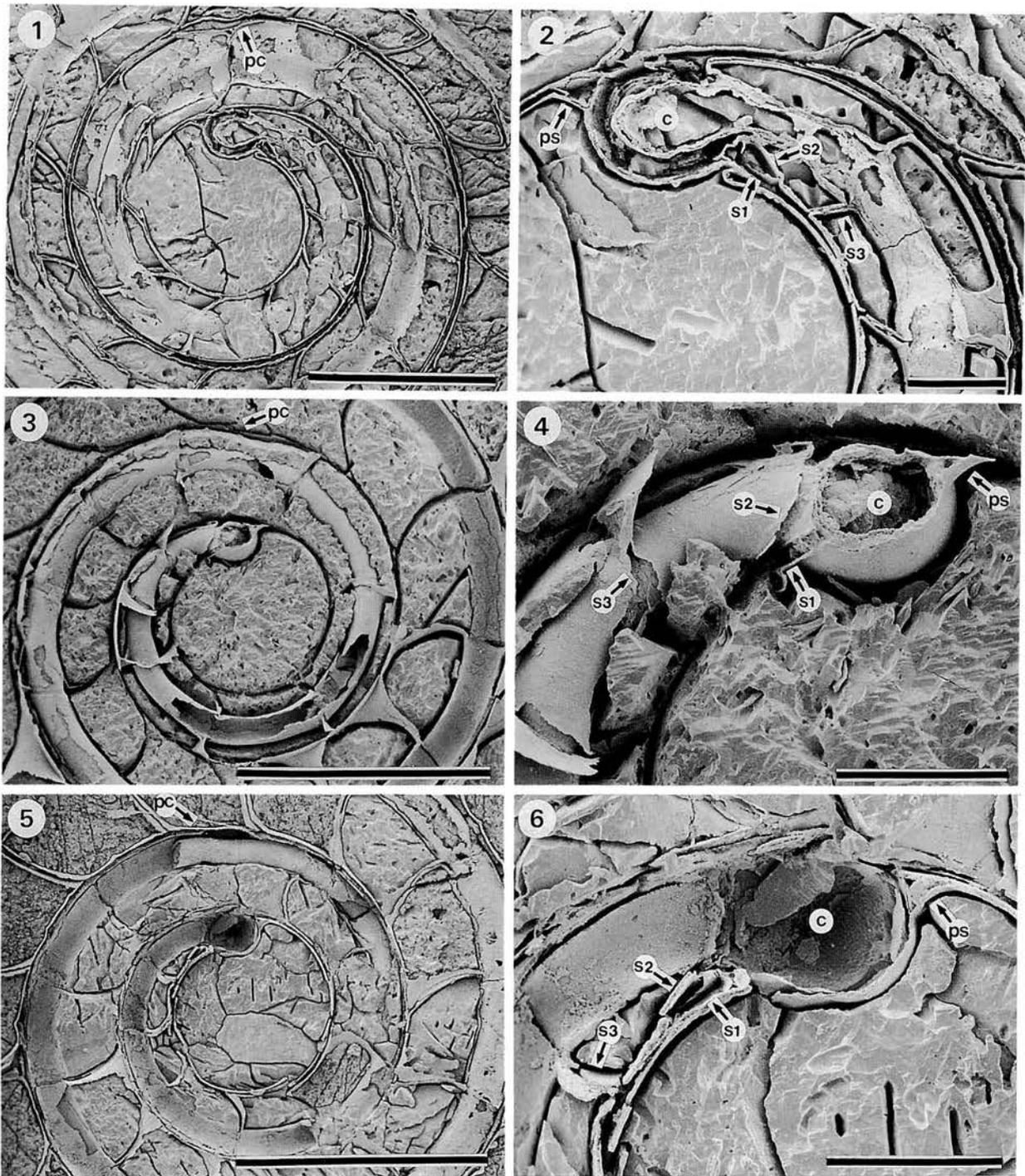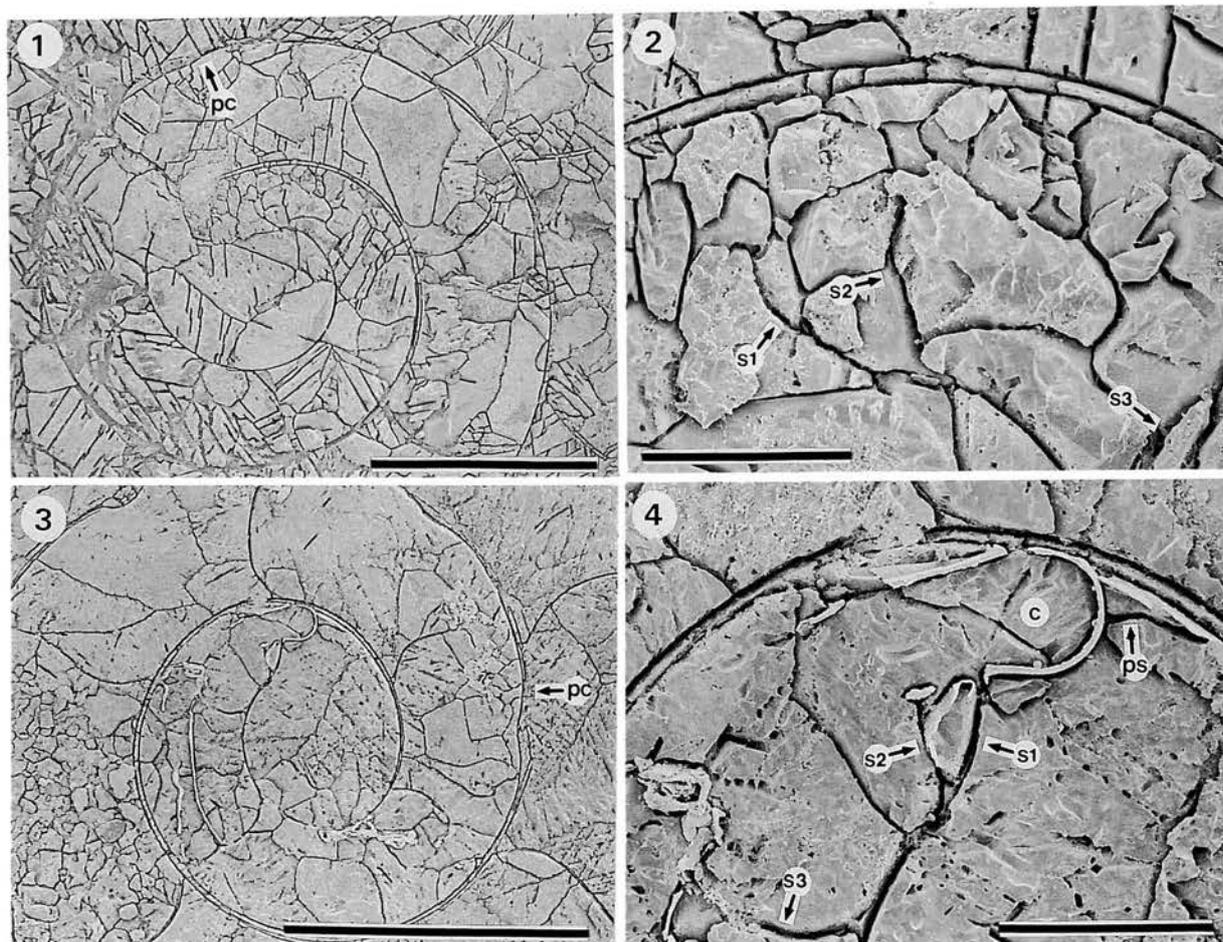
Figure 7. Median sections through the early whorls of the Permian and Triassic ceratitids. Overviews of the early whorls showing the primary constriction (pc) (1, 3) and close-up of the prosiphon (ps), the caecum (c), the proseptum (s1), the second septum (s2) and third septum (s3) (2, 4). Scale bars in 1 and 3: 0.5 mm. Scale bars in 2 and 4: 0.1 mm. **1, 2.** *Paraceltites elegans* Girty (Xenodiscoidea), Roadian, Texas (NSM PM16215). **3, 4.** *Nordophiceras jacksoni* (Hyatt & Smith) (Noritoidea), Spathian, Bear Lake area, Idaho (NSM PM16216).

dorsal side of initial chamber wall is long and slightly convex adapically in median section. Second septum is convex adorally in median section, with a retrochoanitic septal neck, and does not appear to be in close vicinity to proseptum. Siphuncle keeps a ventral position throughout ontogeny.

Daraelites elegans possesses the early internal shell morphology of this morphotype (Figure 3.1, 2). Early internal shell features of this morphotype have been found in other species of *Daraelites* (Böhmers, 1936; Miller and Unklesbay, 1943).

Goniatites morphotype.— In median section, caecum is subelliptical, without a conspicuous constricted base at proseptum and second septum; prosiphon is short and gently curved ventrally, and proseptum on dorsal side is long and slightly convex adapically. Second septum is attached to proseptum on the dorsal side, forming a necklike structure in median section. Siphuncle keeps a ventral position throughout ontogeny.

Genera in the major superfamilies of the Carboniferous Goniatitida, including those in the Dimorphoceratoidea, Goniatitoidea, Neoglyphioceratoidea, Somoholitoidea and Gastrioceratoidea listed in Appendix 1, possess the early internal shell morphology of this morphotype (Figure 4.3–6; Appendix 1). Our observations are consistent with the descriptions by previous authors (Böhmers, 1936; Miller and Unklesbay, 1943; Tanabe *et al.*, 1994).

Marathonites morphotype.—In median section, caecum is ellipsoid with a strongly constricted base at proseptum and second septum; prosiphon is short and gently curved ventrally, and proseptum on dorsal side is short and convex adapically. Second septum is attached to proseptum on dorsal side, forming a necklike structure in median section. Siphuncle keeps a ventral position throughout ontogeny.

Many superfamilies of the Permian Goniatitida, including the Adrianitoidea, Marathonitoidea, Neoicoceratoidea and Popanoceratoidea, possess the early internal shell morphol-

ogy of this morphotype (Figures 5; 6.5, 6; Appendix 1). Additionally, our observations are consistent with the data of other authors (Shul'ga-Nesterenko, 1926; Böhmers, 1936; Miller and Unklesbay, 1943; Bogoslovskaya, 1959; Tanabe et al., 1994).

Agathiceras morphotype.—In median section, caecum is ellipsoid with a strongly constricted base at proseptum and second septum; prosiphon is short and gently curved ventrally, and proseptum on dorsal side is short and slightly convex adapically. Second septum is convex adorally, with a retrochoanitic septal neck, and is close to proseptum on dorsal side, forming a necklike structure in median section. Siphuncle keeps a central position in first three whorls, and subsequently gradually shifts its position toward the venter. Migration of siphuncle to ventral marginal side is completed at end of fifth whorl.

Two species of *Agathiceras* examined possess the early internal shell morphology of this morphotype (Figure 6.1, 2; Appendix 1). Schindewolf (1934) and Böhmers (1936) reported similar early internal shell features in other Permian *Agathiceras*.

Thalassoceras morphotype.—In median section, caecum, which is preceded by short and curved prosiphon, is ellipsoid with a strongly constricted base at proseptum and second septum; proseptum on dorsal side is short, and second septum is close to proseptum on dorsal side. Siphuncle occupies a central to subcentral position in first whorl, and subsequently shifts its position gradually to the venter in the early part of second whorl.

Three taxa assigned to the Thalassoceratoidea, *Bisatoceras* sp., *Eothalassoceras inexpectans* and *Thalassoceras gemmellaroi*, possess the early internal shell morphology of this morphotype (Figure 6.3, 4; Appendix 1).

Ceratitida

The initial chamber of *Paraceltites elegans* is circular in median section (Figure 7.1, 2). Although the caecum, prosiphon and siphuncular tube are not preserved in specimen NSM PM16215, Spinosa et al. (1975, text-fig. 11) described an elongate and subelliptical caecum without a conspicuous constricted base at proseptum and one short prosiphon. The proseptum resting on the dorsal side of the initial chamber wall is long and slightly convex adapically in median section. The second septum does not appear in close vicinity to the proseptum, and the siphuncle maintains a ventral position throughout ontogeny. The maximum initial chamber size, ammonitella size and ammonitella angle in NSM PM16215 are 0.463 mm, 0.921 mm and 342° respectively (Appendix 1).

The early internal shell morphology of the early Triassic ceratitid *Nordophiceras jacksoni* (Figure 7.3, 4) is similar to those observed in *Paraceltites elegans* and *Daraelites elegans* except for the much smaller ammonitella angle (264°).

Discussion

Since the lobe development in the Prolecanitida has been thought to be identical with that in the Ceratitida, many authors have attributed the ancestor of the Ceratitida to the Prolecanitida (Spath, 1934; Schindewolf, 1953; Ruzhencev, 1960). The oldest representative of the Ceratitida is known from the lower Middle Permian (Roadian) and is referable to *Paraceltites*, which is characterized by a thinly discoidal, widely evolute conch, round venter, a prominent ventral salient in the growth lines, and unserrated lobes (Spinosa et al., 1975). Compared to the other prolecanitid ammonoid genera, the genus shares more similar features of conch and suture morphology with *Daraelites*, so that previous authors considered that *Paraceltites* evolved from a daraelitid stock in the Prolecanitida, probably *Daraelites* (Ruzhencev, 1960, 1962).

Zakharov (1984, 1988), however, showed that the lobe development of the Prolecanitida is identical with that of the Goniatitida. He noted that the ammonoid family occurring in the Lower Permian, which shares common features of conch morphology, ornamentation and suture with *Paraceltites*, is the Eothinitidae in the Goniatitida. *Paraceltites* and Eothinitidae both display a widely evolute conch with marginal ribs rather than nodes, round venter, and simple adult suture line. Based on these facts Zakharov (1984, 1988) suggested that *Paraceltites* evolved from the Eothinitidae, probably *Epiglyphioceras* (Zakharov, 1984, 1988). However, except for the simple adult suture line, *Daraelites* also possesses these characters. Inference of a possible ancestor of *Paraceltites* on the basis of only conch morphology and ornamentation should be avoided if other features can be utilized to resolve this ancestor-descendant problem.

The Prolecanitida and Goniatitida each exhibit certain distinct features in their early internal shell features that can be brought to bear on this problem. Available data show that the Prolecanitida share a short and curved prosiphon, a bottle-shaped or gourd-shaped caecum without a conspicuous constricted base at proseptum in median section, long prosepta on dorsal side, a ventral siphuncle, and a relatively small ammonitella angle (328–350°). The second septum does not appear in close vicinity to the proseptum. Meanwhile, species of the Goniatitida share a short and curved prosiphon, a subelliptical or elliptical caecum with a strongly constricted base at proseptum, short prosepta on dorsal side, a ventral siphuncle, and a relatively large ammonitella angle (352–385°). The second septum is close to proseptum on the dorsal side, forming a necklike structure in median section.

Paraceltites elegans has a long proseptum on the dorsal side, and the second septum does not appear in close vicinity to proseptum. The ammonitella angle is 342° in the specimen examined. These features are characteristic of early internal shell features of the prolecanitid *Daraelites elegans* rather than the Goniatitida. These similarites of early ontogenetic shell features as well as the conch morphology of shell shape, ornamentation and sutural development strongly suggest a close phylogenetic relationship between *Daraelites* and *Paraceltites*. These observations strongly support the hypothesis of the daraelitid origin for the Ceratitida as proposed by Ruzhencev (1960, 1962).

Acknowledgments

References

Bogoslovskaya, M. F., 1959: Vnutrennee stroenie rakovin nekotorykh artinskikh ammonoidej. *Paleontologicheskij Zhurnal*, 1959, no. 1, p. 49–57, pl. 2. [Internal structure of the shells of some Artinskian ammonoids.] (*in Russian*)

Bogoslovskaya, M. F., Kuzina, L. F. and Leonova, T. B., 1999: Klassifikatsiya i rasprostranenie pozdnepaleozojskikh ammonoidej. *In*, Rozanov, A. Yu. and Shevyrev, A. A. eds., *Fossil Cephalopods: Recent advances in their study*, p. 89–124. Paleontological Institute, Moscow. [classification and distribution of Late Paleozoic ammonoids] (*in Russian with English abstract*)

Böhmers, J. C. A., 1936: *Bau und Struktur von Schale und Sipho bei permischen Ammonoidea*, 125 p. Drukkerij University, Amsterdam.

Branco, W., 1879: Beiträge zur Entwickelungsgeschichte der fossilen Cephalopoden. *Palaeontographica*, vol. 26, p. 15–50, pls. 4–13.

Branco, W., 1880: Beiträge zur Entwickelungsgeschichte der fossilen Cephalopoden. *Palaeontographica*, vol. 27, p. 17–81, pls. 3–11.

Druschits, V. V. and Doguzhaeva, L. A., 1974: O nekotorykh osobennostyakh morfogeneza fillotseratid i litotseratid (Ammonoidea). *Paleontologicheskij Zhurnal*, 1974, no. 1, p. 42–53, pls. 3, 4. [Some morphogenetic characteristics of phylloceratids and lytoceratids (Ammonoidea).] (*in Russian*)

Druschits, V. V. and Doguzhaeva, L. A., 1981: *Ammonity pod elektronnym mikroskopom*, 238 p., 43 pls. Moscow University Press, Moscow. [Ammonites under the Electron Microscope.] (*in Russian*)

Druschits, V. V. and Khiami, N., 1970: Stroyeniye sept, stenki protokonkha i nachal'nykh oborotov rakoviny nekotorykh rannemelovykh ammonitov. *Paleontologicheskij Zhurnal*, 1970, no. 1, p. 35–47, pls. 1, 2. [Structure of the septa, protoconch walls and initial whorls in early Cretaceous ammonites.] (*in Russian*)

Grandjean, F., 1910: Le siphone des ammonites et des belémnites. *Bulletin de la Société Géologique de France, Série 4*, vol. 10, p. 496–519.

Hewitt, R., Kullmann, J., House, M. R., Glenister, B. F. and Wang Yi-Gang, 1993: Mollusca: Cephalopoda (Pre-Jurassic Ammpnoidea). *In*, Benton, M. J., ed., *Fossil Record 2*, p. 189–212. Chapman and Hall, London.

Landman, N. H., Tanabe, K. and Shigeta, Y., 1996: Ammonoid embryonic development. *In*, Landman, N. H., Tanabe, K. and Davis, R., eds., *Ammonoid Paleobiology*, p. 343–405. Plenum Press, New York.

Landman, N. H., Mapes, R. H., and Tanabe, K., 1999: Internal features of the internal shells of Late Carboniferous Goniatitina. *In*, Olóriz, F. and Rodriguez-Tovar, F. J., eds., *Advancing Research on Living Cephalopods*, p. 243–254. Plenum Press, New York.

Miller, A. K. and Unklesbay, A. G., 1943: The siphuncle of Late Paleozoic ammonoids. *Journal of Paleontology*, vol. 17, no. 1, p. 1–25, pls. 1–5.

Ohtsuka, Y., 1986: Early internal shell microstructure of some Mesozoic Ammonoidea: implications for higher taxonomy. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 141, p. 275–288, pls. 45–50.

Page, K. N., 1996: Mesozoic ammonoids in space and time. *In*, Landman, N. H., Tanabe, K. and Davis, R., eds., *Ammonoid Paleobiology*, p. 755–794. Plenum Press, New York.

Ruzhencev, V. E., 1960: Printsipy sistematiki sistema i filogeniya paleozojskikh ammonoidej. *Akademiia Nauk SSSR, Trudy Paleontologicheskogo Instituta*, vol. 83, p. 1–331. [Principles of systematics, system and phylogeny of Paleozoic ammonoids.] (*in Russian*)

Ruzhencev, V. E., 1962: Nadotryad Ammonoidea. Ammonoiden. Obshchaya chast. *In*, Ruzhencev, V. E. ed., *Osnovy paleontologii, Mollyuski-Golovonogie*. 1, p. 243–334. Izdatel'stvo Akademii Nauk SSSR, Moscow. [Superorder Ammonoidea. General part.] (*in Russian*)

Saunders, W. B. and Work, D. M., 1997: Evolution of shell morphology and suture complexity in Paleozoic prolecanitids, the rootstock of Mesozoic ammonoids. *Paleobiology*, vol. 23, no. 3, p. 301–283.

Schindewolf, O. H., 1934: Zur Stammesgeschichte der Cephalopoden. *Jahrbuch der Preußischen Geologischen Landesanstalt zu Berlin*, 1934, vol. 55, p. 258–283, pls. 19–22.

Schindewolf, O. H., 1953: On development, evolution, and terminology of ammonoid suture line. *Bulletin of the Museum of Comparative Zoology*, vol. 112, no. 3, p. 217–237.

Shigeta, Y., 1989: Systematics of the ammonite genus *Tetragonites* from the Upper Cretaceous of Hokkaido. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 156, p. 319–342.

Shul'ga-Nesterenko, M., 1926: Vnutrennee stroenie rakoviniy artinskikh ammonitov. *Bulletin de la Société impériale des naturalistes de Moscou. Nouvelle série*, vol. 34, p. 81–100, pl. 2. [Nouvelles données sur l'organisation intérieure des conques des ammonites de l'étage d'Artinsk.] (*in Russian*)

Smith, J. P., 1934: Lower Triassic ammonoids of North America. *U. S. Geological Survey, Professional Paper*, 167, p. 1–199.

Spath, L. F., 1934: *Catalogue of the fossil Cephalopoda in the British Museum (Natural History), Part 4, The Ammonoidea of the Trias*, 521 p., 18 pls. London.

Spinosa, C., Furnish, W. M. and Glenister, B. F., 1975: The Xenodiscidae, Permian ceratitoid ammonoids. *Journal of Paleontology*, vol. 49, no. 2, p. 239–283.

Shevyrev, A. A. and Ermakova, S. P., 1979: K sistematike tseratitov. *Paleontologicheskij Zhurnal*, 1979, no. 1, p. 52–58. [On ceratitid systematics.] (*in Russian*)

Tanabe, K., Obata, I., Fukuda, Y. and Futakami, M., 1979: Early shell growth in some Upper Cretaceous ammonites and its implications to major taxonomy. *Bulletin of the National Science Museum, Tokyo, Series C (Geology and*

Paleontology), vol. 5, no. 4, p. 157-176, pls. 1-6.

Tanabe, K., Landman, N. H. and Mapes, R. H., 1994: Early shell features of some Late Paleozoic ammonoids and their systematic implications. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 173, p. 384-400.

Tanabe, K. and Ohtsuka, Y., 1985: Ammonoid early internal shell structure: its bearing on early life history. *Paleobiology*, vol. 11, no. 3, p. 310-322.

Zakharov, Y. D., 1978: *Rannetriasovye ammonoidei Vostoka SSSR*. 224 p., Nauka, Moscow. [Lower Triassic ammonoids of East USSR.] (*in Russian*)

Zakharov, Y. D., 1983: Rost i razvitie ammonoidej i nekotorye problemy ekologii i evolutsii. *In*, Starobogatov, Ya. I. and Nesis K. N. eds., *Sistematika i ekologiya golovonogikh molluskov*, p. 26 - 31. Akademiia Nauk SSSR,

Zoologicheskij Institut, Leningrad. [Growth and development of the ammonoids and some problems of ecology and evolution.] (*in Russian*)

Zakharov, Y. D., 1984: Ontogenez permskikh Pronoritidae i Medlicottiidae i problema proiskhozhdeniya tseratitov. *In*, Gramm, M. N. and Zakharov, Y. D. eds., *Sistematika i evolutsiya bezpozonitchnykh Dalnego Vostoka*, p. 23-40. Dalnevostotchnyi Nautchnyi Tsentr Akademii Nauk SSSR, Vladivostok. [Ontogeny of the Permian Pronoritidae and Medlicottidae and the problem of ceratitid origin.] (*in Russian*)

Zakharov, Y. D., 1988. Parallelism and ontogenetic acceleration in ammonoid evolution. *In*. Wiedmann, J. and Kullmann, J. eds., *Cephalopods-Present and Past*, p. 191 - 206. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Appendix 1.   List of material, and measurement data and character states of the species exam-
morphotype, G: *Goniatites* morphotype, E: *Epicanites* morphotype, M: *Marathonites* morphotype, N:
Bogoslovskaya *et al.* (1999).

Species	Horizon	Locality	Sample
Order Prolecanitida			
Prolecanitoidea			
Epicanites loeblichi Miller & Furnish	Chesterian	Jack Fork Creek, Oklahoma	NSM PM16188
Daraelites elegans Tchernow	Artinskian	Aktasty R., South Urals	NSM PM16189
Pronoritoidea			
Neopronorites skvorzovi (Tchernow)	Artinskian	Aktasty R., South Urals	NSM PM16190
Medlicottioidea			
Akmilleria electraensis (Plummer & Scott)	Wolfcampian	Buck Mountain, Nevada	NSM PM16191
Artioceras rhipaeum (Ruzhencev)	Artinskian	Aktasty R., South Urals	NSM PM16192
Order Goniatitida			
Dimorphoceratoidea			
Girtyoceras meslerianum (Girty)	Chesterian	Jack Fork Creek, Oklahoma	NSM PM16193
Eumorphoceras plummeri Miller & Youngquist	Chesterian	San Saba, Texas	UMUT PM19030
Gatherites morrowensis (Miller & Moore)	Morrowan	Gather Mt., Arkansas	UMUT PM19032
Goniatitoidea			
Goniatites multiliratus Gordon	Chesterian	Jack Fork Creek, Oklahoma	NSM PM16194
Goniatites aff. *crenistria* Phillip	Chesterian	Ahloso, Oklahoma	UMUT PM19019-2
Goniatites choctawensis Shumard	Meramecian	Clarita, Oklahoma	UMUT PM19020-2
Agathiceras uralicum (Karpinsky)	Artinskian	Aktasty R., South Urals	NSM PM16195
Agathiceras applini Plummer & Scott	L. Permian	Coleman, Texas	NSM PM16196
Neoglyphioceratoidea			
Neoglyphioceras abramovi Popow	Namurian	Menkyule R., Verkhoyansk	NSM PM16197
Cravenoceras incisum (Hyatt)	Chesterian	San Saba, Texas	NSM PM16198
Cravenoceras lineolatum Gordon	Chesterian	Lick Mountain, Arkansas	NSM PM16199
Cravenoceras richardsonianum (Girty)	Chesterian	Wapanucka, Oklahoma	UMUT PM19021
Somoholitoidea			
Glaphyrites hyattianus (Girty)	Desmoinesian	Okmulgee, Oklahoma	NSM PM16200
Glaphyrites warei (Miller & Owen)	Desmoinesian	Collinsville, Oklahoma	NSM PM16201
Glaphyrites jonesi (Miller & Owen)	Desmoinesian	Collinsville, Oklahoma	UMUT PM19027
Glaphyrites clinei (Miller & Owen)	Desmoinesian	Collinsville, Oklahoma	UMUT PM19028
Gastrioceratoidea			
Homoceras subglobosum (Bisat)	L. Namurian	Stonehead Beck, Yorkshire	NSM PM16202
Arkanites relictus (Quinn, McCaleb & Webb)	Morrowan	Bradshaw Mt., Arkansas	UMUT PM19029
Thalassoceratoidea			
Bisatoceras sp.	Desmoinesian	Okmulgee, Oklahoma	UMUT PM19033-1
Eothalassoceras inexpectans (Miller & Owen)	Desmoinesian	Okmulgee, Oklahoma	UMUT PM19036-1
Thalassoceras gemmellaroi Karpinsky	Artinskian	Aktasty R., South Urals	NSM PM16203
Adrianitoidea			
Crimites subkrotowi Ruzhencev	Artinskian	Aktasty R., South Urals	NSM PM16204
Crimites elkuensis Miller, Furnish & Clark	Wolfcampian	Buck Mountain, Nevada	NSM PM16205
Texoceras sp.	Roadian	El Capitan, Texas	UMUT PM19037-1
Marathonitoidea			
Kargalites typicus (Ruzhencev)	Artinskian	Aktasty R., South Urals	NSM PM16206
Marathonites invariabilis (Ruzhencev)	Artinskian	Aktasty R., South Urals	NSM PM16207
Neoicoceratoidea			
Metalegoceras sp.	Wolfcampian	Buck Mountain, Nevada	NSM PM16208
Metalegoceras baylorense White	Wolfcampian	Buck Mountain, Nevada	UMUT PM19035
Eothinites kargalensis Ruzhencev	Artinskian	Aktasty R., South Urals	NSM PM16209
Paragastrioceras kirghizorum Voinova	Artinskian	Aktasty R., South Urals	NSM PM16210
Paragastrioceras artolobatum Ruzhencev	Artinskian	Aktasty R., South Urals	NSM PM16211
Uraloceras complanatum (Voinova)	Artinskian	Aktasty R., South Urals	NSM PM16212
Uraloceras sp.	Wolfcampian	Buck Mountain, Nevada	NSM PM16213
Popanoceratoidea			
Popanoceras annae Ruzhencev	Artinskian	Aktasty R., South Urals	NSM PM16214
Order Ceratitida			
Xenodiscoidea			
Paraceltites elegans Girty	Roadian	Guadalupe Mts., Texas	NSM PM16215

ined.   Data source: 1. Spinosa *et al.* (1975).   Abbreviations: A: *Agathiceras* morphotype, D: *Daraelites*
Neopronorites morphotype, T: *Thalassoceras* morphotype.   Major taxonomic positions from

Initial chamber size (mm)		Ammonitella		Length of pro-siphon	Shape of caecum in median section	Length of prpseptum (dorsal side)	Proseptum & 2nd septum (dorsal side)	Initial position of sipuncle	Morpho-type
Max.	Min.	size (mm)	angle (deg.)						
0.426	0.393	0.870	355	Short	Bottle-shaped	Long	Separate (fairly)	Ventral	E
0.466	0.405	0.913	350	?	Bottle-shaped	Long	Separate (a little)	Ventral	D
0.645	0.578	1.147	328	Short	Gourd-shaped	Long	Separate (a little)	Ventral	N
0.633	0.550	1.250	338	Short	Bottle-shaped	Long	Separate (fairly)	Ventral	E
0.356	0.311	0.702	334	Short	Bottle-shaped	Long	Separate (fairly)	Ventral	E
0.543	0.462	0.906	368	Short	Subelliptical	Long	Close	Ventral	G
—	—	1.032	—	?	?	?	?	Ventral	?
0.416	0.370	0.833	385	?	?	Long	Close	Ventral	G
0.545	0.470	0.978	360	Short	Subelliptical	Long	Close	Ventral	G
0.566	0.533	0.995	380	?	Subelliptical	Long	Close	Ventral	G
0.541	0.483	0.996	383	Short	Subelliptical	Long	Close	Ventral	G
0.513	0.451	0.949	369	Short	Elliptical	Short	Close	Central	A
0.520	0.466	1.010	365	?	Elliptical	Short	Close	Central	A
0.522	0.476	0.927	370	Short	Subelliptical	Long	Close	Ventral	G
0.490	0.446	0.910	360	Short	Subelliptical	Long	Close	Ventral	G
0.484	0.403	0.815	368	Short	Subelliptical	Long	Close	Ventral	G
0.486	0.446	0.813	367	?	?	Long	Close	Ventral	G
0.590	0.498	1.048	370	Short	Subelliptical	Long	Close	Ventral	G
0.527	0.458	0.916	369	Short	Subelliptical	Long	Close	Ventral	G
0.535	0.470	0.920	372	?	?	Long	Close	Ventral	G
0.413	0.373	0.720	379	?	?	Long	Close	Ventral	G
0.496	0.458	0.933	367	Short	Subelliptical	Long	Close	Ventral	G
—	—	0.800?	—	?	?	?	?	?	?
0.360	0.335	0.620	358	Short	Elliptical	Short	Close	Subcentral	T
0.386	0.360	0.680	365	Short	?	Short	Close	Subcentral	T
0.365	0.338	0.694	356	Short	Elliptical	Short	Close	Subcentral	T
0.376	0.332	0.681	365	Short	Elliptical	Short	Close	Ventral	M
0.384	0.350	0.725	365	Short	Elliptical	Short	Close	Ventral	M
—	—	0.958	—	?	?	?	?	?	?
0.468	0.419	0.909	360	Short	Elliptical	Short	Close	Ventral	M
0.382	0.356	0.767	366	Short	Elliptical	Short	Close	Ventral	M
0.472	0.411	0.833	365	?	?	Short	Close	Ventral	M
0.480	0.410	0.866	365	Short	Elliptical	Short	Close	Ventral	M
0.381	0.349	0.672	372	?	?	Short	Close	Ventral	M
0.396	0.366	0.689	365	?	?	Short	Close	Ventral	M
0.413	0.377	0.736	365	?	?	Short	Close	Ventral	M
0.408	0.370	0.735	362	.?	Elliptical	Short	Close	Ventral	M
0.517	0.463	0.850	371	Short	Elliptical	Short	Close	Ventral	M
0.356	0.321	0.660	352	Short	Elliptical	Short	Close	Ventral	M
0.463	0.400	0.921	342	Short[1]	Bottle-shaped[1]	Long	Separate (a little)	Ventral	D

Taxonomy and distribution of Plio-Pleistocene *Buccinum* (Gastropoda: Buccinidae) in northeast Japan

KAZUTAKA AMANO[1] and MIKIKO WATANABE[2]

[1]Department of Geoscience, Joetsu University of Education, Joetsu City, Niigata Prefecture
943-8512, Japan (E-mail: amano@juen.ac.jp)

[2]Yatashinmachi 174-2, Nanao City, Ishikawa Prefecture 926-0015, Japan

Abstract. Twelve species of *Buccinum* are recorded from the Plio-Pleistocene of northeast Japan. Two new species, *Buccinum shibatense* and *B. saitoi*, are proposed, and a total of six distributional types (Types A-FJ) are recognized among the 12 species. Three extinct species comprise the type FJ, which is endemic to the Japan Sea borderland. Type A is for species that are extinct in the Japan Sea, but are still living in the Sea of Okhotsk and Bering Sea. Type B species are known as fossils only along the Japan Sea margin, and now live in the northern Japan Sea as well as in the Northwest Pacific and the Sea of Okhotsk. Type C species have been recorded as fossils from the Pacific and the Japan Sea coasts and still live in both coasts. Type D species live only on the Pacific side, and are recorded as fossils only from there. Type E species occur as fossil and living specimens only in the Japan Sea. Species in both types A and FJ species underwent extinction owing to anoxic conditions during Pleistocene glacial episodes along the Japan Sea borderland. The type E species survived in the lower sublittoral to upper bathyal waters of the Japan Sea which had normal salinity and were oxic.

Key words: *Buccinum*, distribution, Pliocene, Pleistocene, taxonomy

Introduction

Buccinum is a common group of gastropods which lives in cold and rather deep water around the North Pacific Ocean. Some species of *Buccinum* invaded the Arctic and North Atlantic Oceans after the opening of the Bering Strait in the late Miocene or Pliocene at 4.8-5.5 Ma (Marincovich and Gladenkov, 1999) in the same manner as did the gastropod *Neptunea* (Durham and MacNeil, 1967; Vermeij, 1991).

The modern species of *Buccinum* have been taxonomically summarized by Golikov (1980) and Tiba and Kosuge (1984). Golikov (1980) described 86 species and 6 subspecies from the world ocean while Tiba and Kosuge (1984) recorded 107 species and 9 subspecies from just the North Pacific. In another study, 68 species and 13 subspecies have been reported in and around Japan (Higo *et al.*, 1999). These differences in number of species and subspecies result mainly from the wide range of morphological variation that obscures the limits of species and subspecies in this genus. Mitochondrial DNA sequences show that the genus can be subdivided into five clades (probably equivalent to subgenera) that are nearly concordant with the characteristics of shell morphology: the *B. felis*, *B. inclytum*, *B. aniwanum*, *B. middendorffi* and *B. tsubai* groups (Endo and Ozawa, 2001).

Recently, Amano *et al.* (1996) and Amano (1997) summarized the taxonomy and distribution of Plio-Pleistocene buccinids, Ancistrolepidinae and *Neptunea*, from the Japan Sea borderland. These studies demonstrated for both Ancistrolepidinae and *Neptunea* that many species which no longer live in the Japan Sea continue to dwell in the Sea of Okhotsk and Bering Sea. These authors noted that such species suffered extinction in the Japan Sea owing to paleoenvironmental changes during the Quaternary ice ages. In order to gain further insights into this phenomenon, it is necessary to examine the distributional pattern of additional taxa. *Buccinum* is well suited to this purpose, because of its ecological similarity to Ancistrolepidinae and *Neptunea*.

Before discussing the distributional pattern of *Buccinum*, it is necessary to clarify the relationships between the species. However, since most species generally have a thin and fragile shell, it is difficult to obtain well preserved specimens. This unsettled classification of the modern species and the poor preservation of fossils preclude a taxonomic summary of this genus in northeastern Japan. In this paper, we will reexamine some well preserved Plio-Pleistocene specimens of *Buccinum* and will add two new species to the genus.

Based on our taxonomical reexamination, we also will discuss the distributional pattern of the genus.

Materials

Fossils identified as *Buccinum* were recently collected from the following ten localities (Figure 1).

Loc. 1. Large cliff 2.2 km upstream from the mouth of Sakashi-no-sawa, Teshio Town, Hokkaido; gray siltstone; late Pliocene Yuchi Formation.

Loc. 2. Outcrop along Shichirinagahama beach about 1.5 km north to Kawajiri, Ajigasawa Town, Aomori Prefecture; greenish gray sandy siltstone; late Pliocene Narusawa Formation.

Figure 1. Collecting localities of *Buccinum* (using the topographical maps of "Onoppunai," "Matsunoyama-Onsen," "Iiyama," scale 1:50,000; "Morita," "Echigo-Shimoseki," "Sugatani," "Ojiya" and "Kanazawa," scale 1:25,000 published by Geographycal Survey Institute of Japan).

Loc. 3. Riverside cliff along a side creek of the Onnagawa River, about 600 m south of Housaka Bridge, Sekikawa Village, Niigata Prefecture (Loc. 4 of Amano *et al.*, 1996); siltstone; late Pliocene Kuwae Formation.

Loc. 4. Small outcrop on the Koide River about 1.1km upstream of its mouth, Shibata City, Niigata Prefecture (Fossil locality of Amano, 1998); muddy fine-grained sandstone; late Pliocene Kuwae Formation.

Loc. 5. River bank along the Shinano River, 250 m northeast of Unoki, Ojiya City, Niigata Prefecture (Loc. 7 of Amano, 1997); conglomerate; early Pliocene Kawaguchi Formation

Loc. 6. Riverside cliff of the Sabaishi River about 300 m east to Azamihira, Matsudai Town, Niigata Prefecture; pebble-bearing sandstone; late Pliocene Higashigawa Formation.

Loc. 7. Outcrop at Taihei, Matsudai Town, Niigata Prefecture; black mudstone; early Pliocene Kurokura Foramtion (upper part).

Loc. 8. Riverside cliff of the Shibumi River 400 m east of Taihei, Matsudai Town, Niigata Prefecture; black mudstone; early Pliocene Kurokura Formation (upper part).

Loc. 9. Outcrop at Kutta, Iiyama City, Nagano Prefecture; siltstone; early Pliocene Nagasawa Formation.

Loc. 10. River bank of the Saikawa River, 1.1 km upstream from the Okuwa Bridge, Kanazawa City, Ishikawa Prefecture (Loc. 12 of Amano *et al.*, 1996); fine-grained sandstone; early Pleistocene Omma Formation

We examined all specimens stored at the Joetsu University of Education (JUE), including the above-cited specimens as well as those obtained in the following studies: Amano and Kanno (1991), Nakata and Amano (1991), Amano and Karasawa (1993), Amano (1994) and Amano and Sato (1995). In addition, specimens including types were reexamined at the following institutions and museums: Tohoku University (IGPS), Saito Ho-on Kai Museum of Natural History (SHM), University of Tsukuba (IGUT), National Science Museum(NSM), and Kyoto University (JC). Moreover, private collections of Mr. Masayuki Shimizu (Tateyama Mus.) were also examined.

In addition to our collections and those mentioned above, geographical distributions were compiled from a critical survey of the literature (Iwai, 1965; Noda and Masuda, 1968; Baba, 1990).

Systematic description of new species

Family Buccinidae Rafinesque, 1815
Genus ***Buccinum*** Linnaeus, 1758
Buccinum shibatense sp. nov.

Figure 2. 3, 2. 6

Type specimen.—Holotype, JUE no. 15699, 39.7 mm high, 23.3 mm wide; Paratype, JUE no. 15700, 25.6 mm high, 24.6 mm wide.
Type locality. —Loc. 4.
Diagnosis. —Small species of *Buccinum* characterized by numerous spiral cords (36 to 40 on body whorl), two fine columellar plaits at base of inner lip, and thick outer lip weakly crenulated on inner side.

Description.—Shell rather small for genus, conico-ovoidal shape; protoconch one and a half smooth whorls; teleoconch of seven whorls. Height of body whorl occupying about five-eighths of shell height. Suture shallow and slightly undulating on body whorl. Axial sculpture of many fine growth lines; spiral cords low, separated by shallow grooves, 16 (holotype) and 20 (paratype) on penultimate whorl, 36 (holotype) to 40 (paratype) on body whorl. Spiral cords on body whorl with one shallow groove. Aperture ovate; inner lip covered by thin calcareous callus, two fine and distinct columellar plaits at its base; outer lip thick, with 19 weak striae along inner side, excavated behind. Siphonal canal shallow and slightly twisted; posterior sinus narrow and short.

Remarks.—At a glance, this species resembles *Pseudoliomesus ooides* (Middendorff, 1849) in its shell outline and slightly twisted basal part of the inner lip. It differs from *P. ooides* by lacking a deep suture or a subsutural area.

Comparison. —The present species is closely allied to *Buccinum habui* Tiba, 1984, now living at 400–500 m depth off southern Hokkaido (Higo *et al.*, 1999). *B. habui* is also characterized by numerous spiral cords (26 on penultimate; 44 on body whorl), one or two fine columellar plaits at the base of the inner lip, and weak crenulations in the inner side of the thick outer lip. However, *B. shibatense* can be easily distinguished from *B. habui* by its larger shell size, less slender shell outline, existence of a posterior sinus, and slightly twisted siphonal canal.

Buccinum saitoi sp. nov.
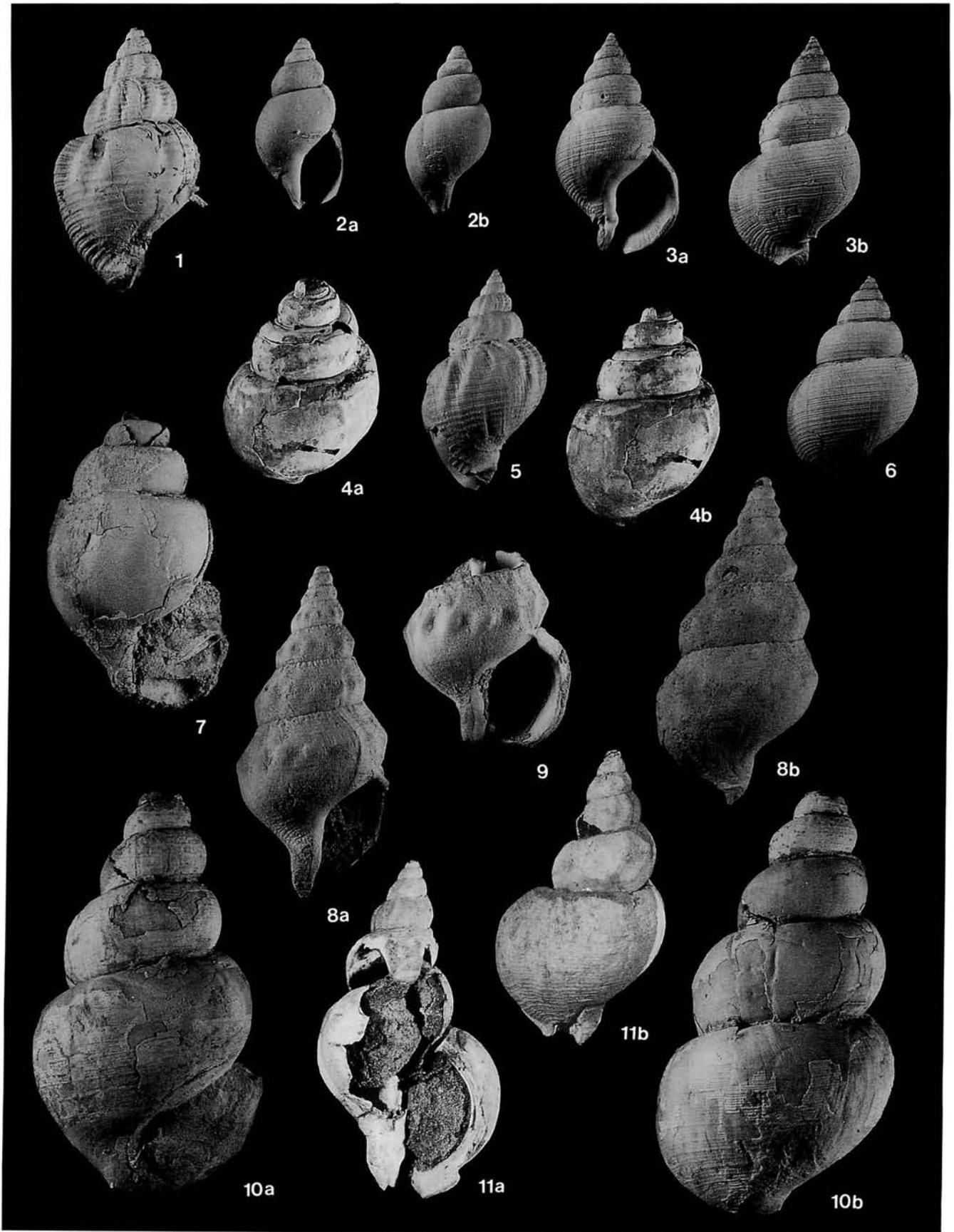
Figure 2. 8, 2. 9

Type specimen.—Holotype, JUE no. 15701, 58.8+ mm high, 29.1 mm wide; Paratype, JUE no. 15702, 31.8 mm wide.
Type locality.—Loc. 4.
Diagnosis. — Medium-size *Buccinum* characterized by thick and high spire, numerous and fine subsutural granulations, distinct nodes on shoulder (13 on body whorl).

Description.—Shell size medium for genus, slender and thick; protoconch poorly preserved and of more than one whorl; teleoconch of six whorls. Spire rather high, occupying about half of shell height. Suture shallow and slightly undulating on body whorl, with many fine subsutural granulations. Above shoulder, 13 oblique low axial ribs; 13 distinct nodes at shouldered edge; spiral cords low, fine, separated by narrow grooves, 13 on penultimate and 15 on body whorl. Below shoulder including base, surface sculpture consisting only of spiral cords; 8 on penultimate and 25 on body whorl. Aperture ovate; inner lip covered by thin calcareous callus, nearly straight at its base; outer lip thick, smooth on inner side, excavated behind. Siphonal canal shallow; posterior sinus narrow and very short.

Comparison.—The present new species is closely allied to *Buccinum verrucosum* Tiba, 1980 now living in the Sea of Okhotsk. *B.verrucosum* shares the following characteristics with the present new species: similar shell outline, thick shell, many fine subsutural plications, axial ribs above the shoulder and some granulations on the shoulder. However, *B. verrucosum* differs from *B. saitoi* by having three strong

spiral cords and two obscure columellar plaits.

Buccinum opisoplectum Dall, 1907 can be easily distinguished from *B. saitoi* in having a smaller shell, lacking granulation on the shoulder and having three strong spiral cords.

Etymology.—This species is named after Mr. Atsushi Saito of Niigata Higashi High School, who collected the type specimens.

Revision of some fossil species

Buccinum sinanoense was originally established by Makiyama (1927) based on the specimen (Figure 3. 4) from the early Pliocene Joshita Formation in Nagano Prefecture. Nomura (1937) illustrated a specimen as *B. sinanoense* Kuroda (?) [sic] from the Pliocene Kannonji Formation in Yamagata Prefecture. Based on an examination of his specimen, it is not referable to *B. sinanoense* because of its low and large body whorl. However, the poor preservation of its shell surface prevents us from definitely assigning this specimen to a species.

Buccinum aomoriensis Hatai, Masuda and Suzuki,1961 is represented by a single specimen (Figure 3. 9) from the early Pleistocene Hamada Formation in Aomori Prefecture. This species is characterized by a large shell (shell height = 95.0 mm), many fine subsutural plications, 17 axial folds on the penultimate whorl, two strong spiral cords with two to seven intercalating cords on each whorl, and an inner lip with two columellar plaits. When they established this species, Hatai *et al.* (1961) did not compare their species with the closely related species, *B. inclytum* Pilsbry, 1904. The two species cannot be consistently distinguished, so we consider *B. aomoriensis* to be a junior synonym of *B. inclytum.*

Akamatsu and Suzuki (1992) illustrated a fragmentary specimen from the early Pleistocene Shimonopporo Formation as *Buccinum opisthoplectum* Dall [sic]. However, judging from their figure, this specimen is referable to *B. inclytum* because of its large shell (more than 50 mm without body whorl) and three rather strong spiral cords.

Hatai and Nisiyama (1952) proposed the new species *Buccinum wakimotoense* based on a specimen from the middle Pleistocene Shibikawa Formation in Akita Prefecture, which Kanehara (1942) referred to as "*B. schantaricum* Middendorff." However, they did not give a description or definition at that time. Judging from Kanehara's (1942) figure and a specimen from the Shibikawa Formation (Figure 2. 5), there is no difference between *B. wakimotoense* and the modern *B. middendorffi* Verkrüzen, 1882 as pointed out by Masuda and Noda (1976). Therefore, *B. wakimotoense* is a junior synonym of *B. middendorffi.*

Buccinum rhodium Dall, 1919 lives in the Sea of Okhotsk and Bering Sea (Tiba and Kosuge, 1984). It has 22 strong sigmoid axial ribs. The specimen figured by Fujii and Shimizu (1988; Figure 3. 7) as *Plicifuscus* [this should be "*Plicifusus*"] cf. *plicatus* [sic] from the Pliocene Mita Formation in Toyama Prefecture has a rather large body whorl, 18 sigmoid axial ribs and 40 spiral cords. Judging from the outline and shell sculpture, their specimen is referable to *B. rhodium.* The spiral cords of modern specimens are generally weaker than on fossils.

Nomura (1937) recorded one specimen as *Ancistrolepis fragilis* Dall var. (Figure 3. 5) from the Pliocene Kannonnji Formation in Yamagata Prefecture. However, it lacks a deeply channeled suture which is characteristic of Ancistrolepidinae. This specimen should be referred to *Buccinum unuscarinatum* Tiba, 1981, which lives in the Sea of Okhotsk, because of the one keel at its shoulder and many fine weak spiral cords.

Buccinum cf. *striatissimum* Sowerby was described by Ozaki (1958) from the Plio-Pleistocene Iioka Formation in Chiba Prefecture. His specimen has a constricted body whorl, a large protoconch, and a deeply channeled subsutural area, all of which are characters of Ancistrolepidinae. Therefore, the Iioka specimen is not a *Buccinum.*

Buccinum suruganum kasimensis was established by Ozaki (1958) as a new subspecies, based on one imperfect specimen (NSM P1 4402) from the Pliocene Naarai Formation. Based on our reexamination of this specimen, it is clear that the number of spiral cords (four cords on the penultimate whorl) and the condition of interspaces of the ribs are included in the variation of *B. leucostoma* Lischke, 1872.

When he established *Buccinum yoroianum* as a new species, Ozaki (1958) designated a small specimen (Figure 2. 2) as the paratype. However, this paratype specimen differs from the holotype in having very weak spiral cords and well inflated whorls. Based on the shell outline, size and sculpture of the paratype specimen, it is assigned to *B. bulimiloideum* Dall, 1907.

Distributional patterns

The twelve Plio-Pleistocene species of *Buccinum* and their geological distributions in northeastern Japan are shown in Table 1. There are six types of distribution (Types A-FJ; Figures 4, 5).

Type A (*B. rhodium* and *B. unuscarinatum*) is for species that are extinct in the Japan Sea, but are still living at lower sublittoral to upper bathyal depths in the Sea of Okhotsk and Bering Sea. Some Ancistrolepidinae and *Neptunea* show a similar distribution (Amano *et al.*, 1996; Amano, 1997).

Buccinum middendorffi and *B. inclytum* belong to Type B. Fossils of these species are known only from the Japan Sea

---

← **Figure 2.** **1, 5.** *Buccinum middendorffi* Verkrüzen. 1, x1, JUE no. 15706, Loc. 1, Yuchi Formation. 5, x1, JUE no. 15707, Loc. Anden, Akita Pref., Shibikawa Formation. **2a, b.** *Buccinum bulimiloideum* Dall, x1.5, NSM no. 4464, "Paratype" of *B. yoroianum* Ozaki, Iioka Formation. **3a, b, 6.** *Buccinum shibatense* sp. nov. 3a, b, x1, JUE no. 15699, Holotype; 6, x1, JUE no. 15700, Paratype; Loc. 4, Kuwae Formation. **4a, b, 7.** *Buccinum tsubai* Kuroda. 4a, b, IGUT no.15602, Loc. Kitaubushi, Hokkaido, Yuchi Formation. 7, x1, JUE no. 15708, Loc. 6, Higashigawa Formation. **8a, b, 9.** *Buccinum saitoi* sp. nov. 8a, b, x1, JUE no.15701, Holotype; 9, x1, JUE no. 15702, Paratype; Loc. 4, Kuwae Formation. **10a, b.** *Buccinum striatissimum* Sowerby, x0.8, JUE no. 15709, Loc. 8, Kurokura Formation. **11a, b.** *Buccinum ochotense* (Middendorff), x0.9, IGPS no. 90462, Loc. 6 of Hatai *et al.* (1961), Hamada Formation.
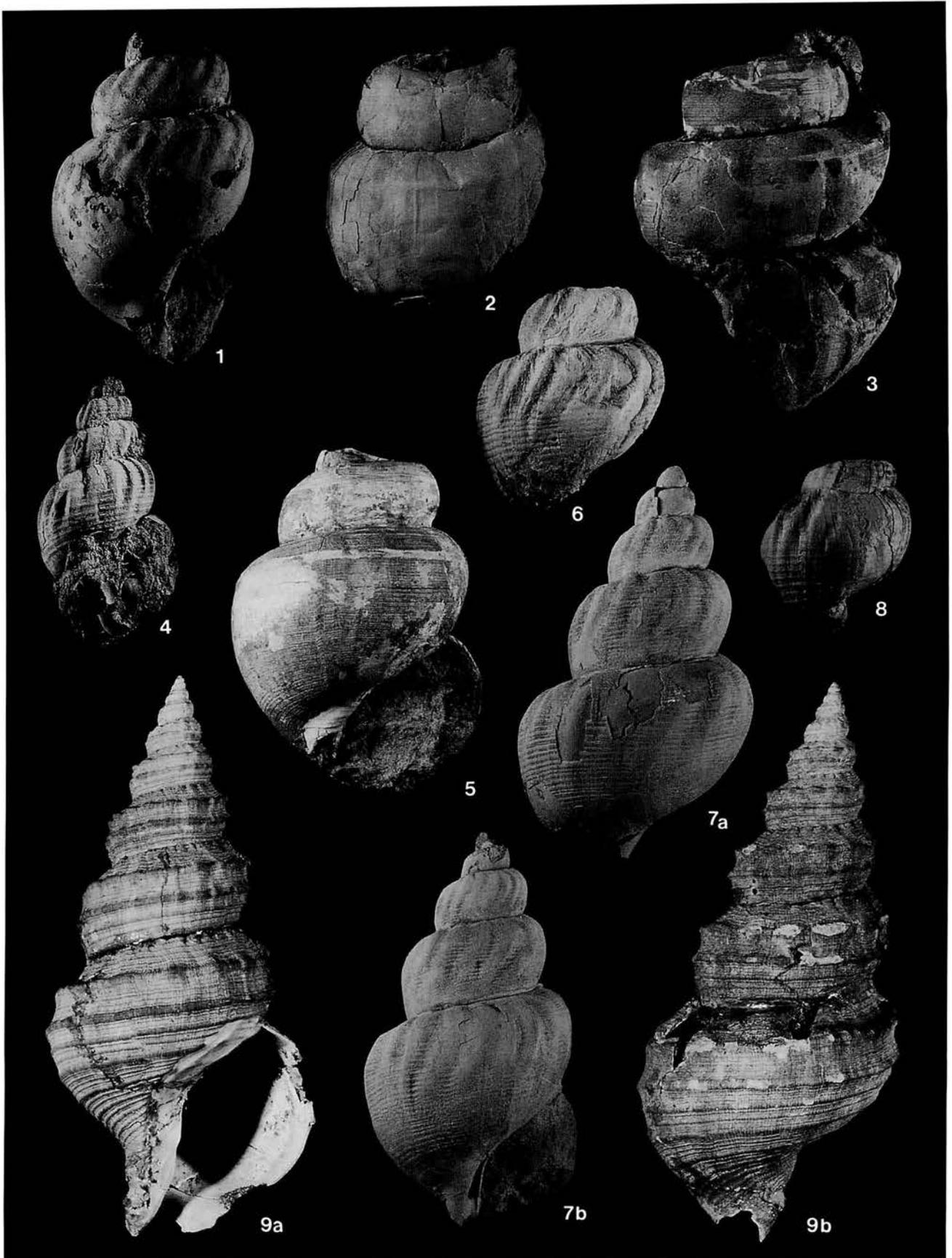
Table 1. Distribution of the Plio-Pleistocene *Buccinum*. * living depth after Higo *et al.* (1999).

Species	Age and formation	Depth range*
Type A		
Buccinum rhodium Dall	Pliocene Nakawatari F., Nagasawa F., Mita F.	100–300m
B. unuscarinatum Tiba	Pliocene Kannonji F., Kuwae F., Kurokura F. Nagasawa F., Nadachi F.	—
Type B		
B. middendorffi Verkrüzen	Pliocene Yuchi F.; Early Pleistocene Omma F.; Middle Pleistocene Shibikawa F.	0–10m
B. inclytum Pilsbry	Early Pleistocene Shimonopporo F., Hamada F.	0–50m
Type C		
B. ochotense (Middendorff)	Pliocene Gobanshoyama F.; Early Pleistocene Shimonopporo F., Hamada F., Daishaka F.	0–50m
Type D		
B. leucostoma Lischke	Pliocene to early Pleistocene Kazusa G.	50–600m
B. bulimiloideum Dall	Early Pleistocene Iioka Formation	300–900m 0–50m
Type E		
B. striatissimum Sowerby	Pliocene Narusawa F., Kurokura F., Nagasawa F., Nadachi F.	200–500m
B. tsubai Kuroda	Pliocene Yuchi F., Kawaguchi F., Higashigawa F., Mita F.	100–700m
Type FJ		
B. sinanoense Makiyama	Pliocene Joshita F., Ogikubo F.	—
B. shibatense sp. nov.	Pliocene Kuwae F.	—
B. saitoi sp. nov.	Pliocene Kuwae F.	—

borderland. Type B species now live in the upper sublittoral zone of the northern Japan Sea as well as the Northwest Pacific and the Sea of Okhotsk.

Type C includes only one species, *B. ochotense*. This type of species is the same as the C type of *Neptunea* which has been recorded as fossils from the Pacific and the Japan Sea coasts and also lives in the upper sublittoral zone of both coasts.

Two species (type D) live only from the lower sublittoral to the upper bathyal zone on the Pacific side, and their fossils are also recorded only from the Pacific side. These are *B. leucostoma* and *B. bulimiloideum*. Such a distribution has also been observed in the buccinids *Clinopegma unicum, Neptunea kuroshio, N. fukueae* and *N. kanagawaensis* (Amano et al., 1996; Baba, 1990; Kato, 1993).

Type E species (*B. striatissimum* and *B. tsubai*) are known as fossil and living specimens only from the Japan Sea. No species of *Neptunea* or Ancistrolepidinae shows this type of distribution.
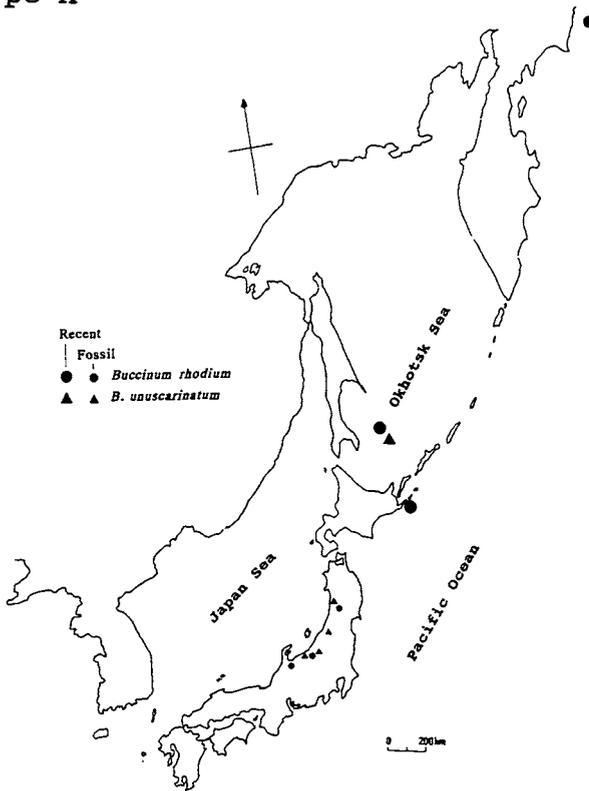
Three extinct species (*B. sinanoense, B. shibatense* and *B. saitoi*) comprise type FJ, endemic to the Japan Sea borderland. It is noteworthy that no extinct species of *Buccinum* is confined to the Plio-Pleistocene of the Pacific Ocean side. This type of distribution does occur in Ancistrolepidinae (Amano et al., 1996) and *Neptunea* (E type; Amano, 1997).

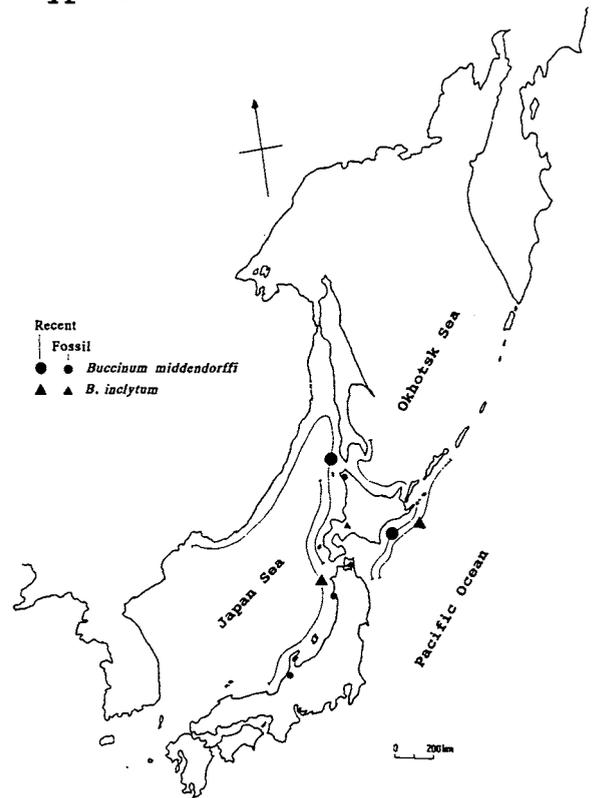**Discussion of distribution**

Species of types A and FJ underwent extinction during the Pleistocene in the Japan Sea borderland. Tada (1994) noted that bottom sediments alternated between oxic and anoxic conditions with the glacio-eustatic sea level changes many times after the late Pliocene. He also pointed out that remarkable sea level oscillations are recognized during the last 0.8 m.y. During the low glacial sea level stands, freshwater input reduced salinity and created euxinic conditions in the enclosed Japan Sea. The type A species occurred

◂ **Figure 3.** 1, 6, 7a, b. *Buccinum rhodium* Dall. 1, ×1, JUE no. 15360, Loc. N5 of Nakata and Amano (1991); 6, ×1, JUE no. 15703, Loc. 9; Nagasawa Formation. 7a,b, ×1, Loc. Rengeji, Toyama Pref., illustrated by Fujii and Shimizu (1988) as *Plicifuscus* cf. *plicatus*, Mita Formation. 2, 3, 5. *Buccinum unuscarinatum* Tiba. 2, ×1, JUE no. 15704, Loc. 7, Kurokura Formation. 3, ×0.8, JUE no. 15613, Loc. 32 of Amano and Kanno (1991), Nadachi Formation. 5, ×1, SHM no. 8407, Loc. Futago, Yamagata Prefecture, illustrated by Nomura (1937) as *Ancistrolepis fragilis* var., Kannonji Formation. 4. *Buccinum sinanoense* Makiyama, ×1, JC no. 610024, Holotype, Joshita Formation. 8. *Buccinum middendorffi* Verkrüzen, ×1, JUE no. 15705, Loc. 10, Omma Formation. 9 a,b. *Buccinum inclytum* Pilsbry, IGPS no. 90509, Hamada Formation, "Holotype" of *B. aomoriensis* Hatai, Masuda and Suzuki.

Type A

Type B

Recent
| Fossil
● ● *Buccinum rhodium*
▲ ▲ *B. unuscarinatum*

Recent
| Fossil
● ● *Buccinum middendorffi*
▲ ▲ *B. inclytum*

Type C

Type D

Recent
| Fossil
▲ ▲ *Buccinum ochotense*

Recent
| Fossil
● ● *Buccinum leucostoma*
▲ ▲ *B. bulimiloideum*

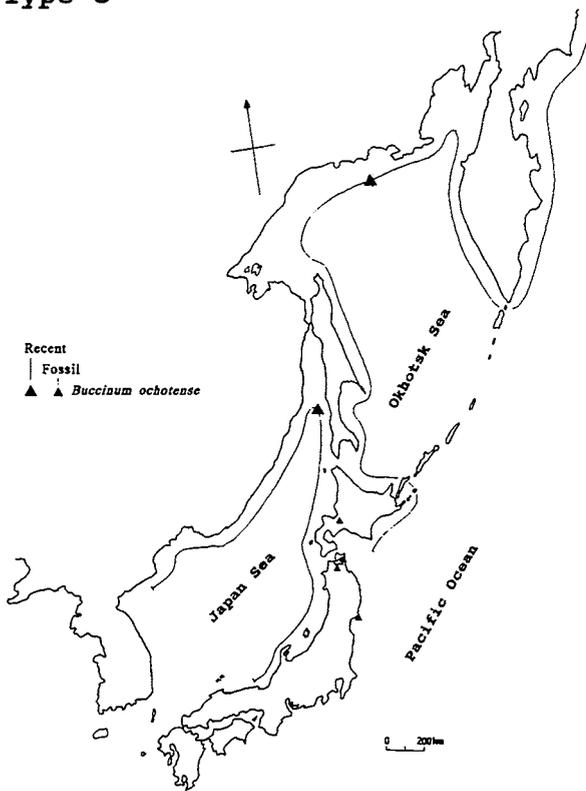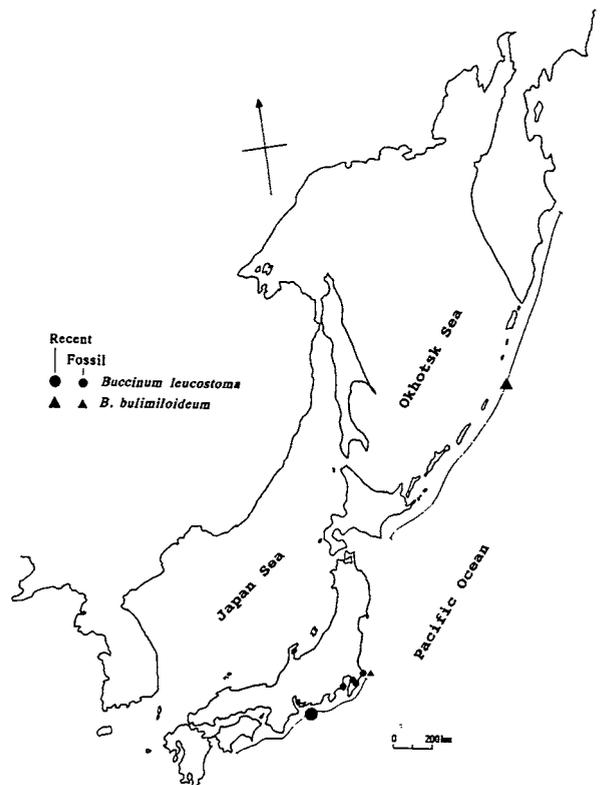**Figure 4.**   Distributional pattern (types A-D) of *Buccinum*.

from the lower to upper Pliocene while the type Fᴊ species ranged from the lower to middle Pliocene. Thus, it is reasonable to infer that type A species became extinct in the Japan Sea whereas the Sea of Okhotsk and Bering Sea populations survived. The narrowly distributed endemic Fᴊ type species became extinct after the late Pliocene.

Two explanations are available to explain the distribution pattern of the types B and C. First, the species of these types survived the deteriorated environment in the Japan Sea during the Quaternary ice ages. Second, the populations of species in types B and C became extinct in the Japan Sea, but survived on the Pacific side. Species of both types live in upper sublittoral depths while those of other types dwell in lower sublittoral to upper bathyal waters. Based on the presence of type A and Fᴊ species and the low-salinity surface water of the glacial age, it is reasonable to accept the second hypothesis. Thus, the modern populations of types B and C species in the Japan Sea may represent recent invasions through its shallow northern entrance.

The fossil records of the type D species are concentrated in the Pacific side of central Japan (Kanto Region). These species are also deep-water dwellers and survived the glacial episodes only in the Pacific Ocean.
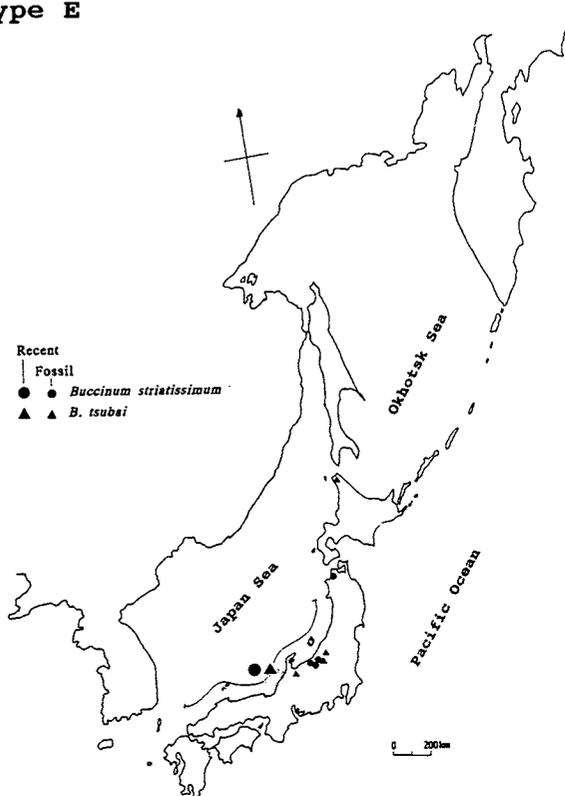
Type E species that survive as endemics in the Japan Sea live in intermediate waters. As already noted by Amano (1996), *Portlandia toyamaensis* (Kuroda, 1929) also shows this type of distribution. The same pattern occurs in the buccinids *Mohnia yanamii* (Yokoyama, 1926) and *Lussivolutopsius furukawai* (Oyama, 1951). *Mohnia yanamii* is a

Table 2. Bathymetric distribution of the Japan Sea endemic species with fossil records. * living depth after Higo *et al.* (1999).

Species	Depth (m)*
Alvania sitta (Yokoyama)	200–204
Lussivolutopsius furukawai (Oyama)	200–350
Mohnia yanamii (Yokoyama)	50–400
Buccinum striatissimum Sowerby	200–500
B. tsubai Kuroda	100–700
Curtitoma exquisita (Yokoyama)	300–400
Propebela komakahida (Otuka)	200–350
P. tayensis (Nomura and Hatai)	150
Yoldia kikuchii Kuroda	100–150
Portlandia toyamaensis (Kuroda)	100–600

characteristic species of the Omma-Manganji fauna (Otuka, 1939) and now lives in 50–400 m depth in the Japan Sea (Higo *et al.*, 1999). *Lussivolutopsius furukawai* is also known as an endemic species in the Japan Sea (200–350 m depth; Higo *et al.*, 1999) and there is one fossil specimen from the lower Pleistocene Sawane Formation at Tohoku University (IGPS no. 73410). Summarizing the Japan Sea endemic species that have fossil records (Table 2), all live in depths from 100 m–400 m. Horikoshi (1986) suspected that some species at an intermediate depth could survive during the Quaternary glacial ages. Based on radiolarian fossils from a core at GH–95 St 1208, off Shakotan Peninsula,
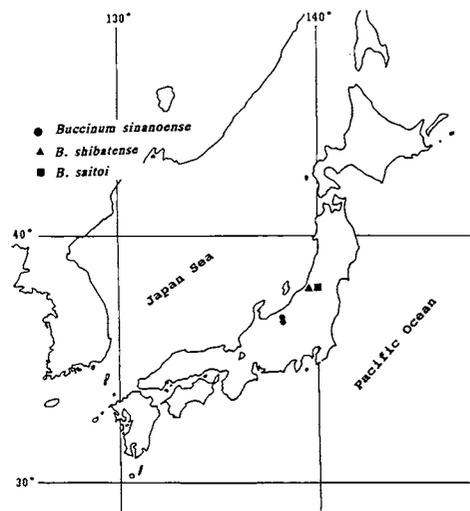
Type E

Type Fᴊ

Figure 5. Distributional pattern (types E, Fᴊ) of *Buccinum*.

Table 3. Distributional types of *Buccinum, Neptunea* and Ancistrolepidinae.
*Amano (1997) ** Amano *et al.* (1996)

Types	Buccinum	Neptunea*	Ancistrolepidinae**
FJ	*B. sinanoense*	*N. eos*	*Ancistrolepis masudaensis*
	B. shibatense	*N. hataii*	*A. koyamai*
	B. saitoi	*N. nikkoensis*	*A. peulepis*
			A. aff. hikidai
			Clinopegma fragilis
A	*B. rhodium*	*N. lamellosa*	*Ancistrolepis grammatus*
	B. unuscarinatum	*N. satura*	*Clinopegma borealis*
		N. insularis	*Bathyancistrolepis trochoideus*
		N. vinosa	
B	*B. middendorffi*	*N. lyrata*	—
	B. inclytum	*N. bulbacea*	
		N. rugosa	
C	*B. ochotense*	*N. intersculpta*	—
		N. arthritica	
D	*B. leucostoma*	*N. kuroshio*	*Clinopegma unicum*
	B. bulimiloideum	*N. fukueae*	
		N. kanagawaensis	
E	*B. striatissimum*	—	—
	B. tsubai		

Hokkaido, Itaki *et al.* (1996) inferred normally saline and oxic water at depths of 200–300 m during the last glacial age (18–15 kyr BP). The inferred survival depth (200–300 m) of radiolarians is similar to that for the molluscs (100–400 m). Therefore, the endemic molluscs noted above, including type E of *Buccinum*, might have been able to survive the Quaternary glacial ages in the normal saline and oxic water lying between the brackish surface and the euxinic bottom waters.

Based on the discussion above, we synthesize the distributional pattern of *Buccinum, Neptunea* and Ancistrolepidinae in Table 3. It is noteworthy that 20 species (56%) belong to the type FJ or A, and there are no extinct species whose fossil records are confined to the Pacific side. Many authors have cited temperature change as one of the important causes of extinction (ex. Stanley, 1984). However, from the above lines of evidence, we postulate that the extinction of species was induced by environmental change in the Japan Sea accompanying the glacio-eustatic sea level changes during the Quaternary ice ages, not by sea surface temperature.

Valentine and Jablonski (1991) noted that marine invertebrate faunas that are not perched are unlikely to suffer extinction by eustatic sea-level changes alone. They also pointed out that the trapped fauna in enclosed areas are vulnerable to any local environmental deterioration. The present study reveals the mechanism of extinction associated with glacio-eustatic sea level changes in a marginal sea.

Tada (1994) illustrated the two-layer model of the Japan Sea during the glacial period with a surface brackish layer and deep anoxic water. However, the existence of type E

species in *Buccinum* suggests the possibilities of normal oceanic water between these two layers.

References

Akamatsu, M. and Suzuki, A., 1992: Stratigraphy and paleoenvironment of the lower Pleistocene on the hills around Ishikari Lowland, Hokkaido. *Annual Report of the Historical Museum of Hokakido*, no. 20, p.1-30. (*in Japanese with English abstract*)

Amano, K., 1994: Pliocene molluscan fauna and its paleoenvironment in Matsunoyama-machi, Niigata Prefecture. *Journal of Geography*, vol. 103, no. 6, p. 653-673. (*in Japanese with English abstract*)

Amano, K., 1996: *Portlandia toyamaensis* (Kuroda) as an endemic bivalve of Japan Sea. *In*, Noda, H. and Sashida, K. *eds., Prof. H. Igo Commemorial Volume on Geology and Paleontology of Japan and Southeast Asia*, p. 141-146. Gakujutsu Tosho Insatsu Co., Tokyo.

Amano, K., 1997: Biogeography of the genus *Neptunea* (Gastropoda: Buccinidae) from the Pliocene and the lower Pleistocene of the Japan Sea borderland. *Paleontological*

Research, vol. 1, no. 4, p. 274–284.

Amano, K., 1998: First discovery of fossil *Humilaria* (Bivalvia: Veneridae) from Japan. *Venus*, vol. 57, no. 4, p. 271–280.

Amano, K. and Kanno, S., 1991: Composition and structure of Pliocene molluscan associations in the western part of Joetsu City, Niigata Prefecture. *Fossils*, no. 51, p. 1–14. (*in Japanese with English abstract*)

Amano, K. and Karasawa, S., 1993: Molluscan fauna and paleoenvironment of the Pliocene Ogikubo Formation in the northern part of Nagano Prefecture. *Journal of Geography*, vol. 102, no. 5, p. 572–582. (*in Japanese with English abstract*)

Amano, K. and Sato, H., 1995: Relationship between embaymental associations and relict species-Molluscan fauna from the Pliocene Joshita Formation in the northern part of Nagano Prefecture. *Fossils*, no. 59, p. 1–13. (*in Japanese with English abstract*)

Amano, K., Ukita, M. and Sato, S., 1996: Taxonomy and distribution of the subfamily Ancistrolepidinae (Gastropoda: Buccinidae) from the Plio-Pleistocene of Japan. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 182, p. 467–477.

Baba, K., 1990: *Molluscan Fossil Assemblages of the Kazusa Group, South Kwanto, Central Japan*, 445 p., Keio Yochisha, Tokyo. (*in Japanese*)

Dall, W. H., 1907: Description of new species of shells, chiefly Buccinidae, from the dredgings of the U.S.S. "Albatross" during 1906, in the northwestern Pacific, Bering, Okhotsk and Japanese Seas. *Smithsonian Miscellaneous Collections*, vol. 50, no. 2, p. 139–173.

Dall, W. H., 1919: Description of new species of Mollusca from the north Pacific Ocean in the collection of the United States National Museum. *Proceedings of the United States National Museum*, vol. 56, no. 2295, p. 293–371.

Durham, J. W. and MacNeil, F. S., 1967: Cenozoic migrations of marine invertebrates through the Bering Strait region. *In*, Hopkins, D. M. *ed.*, *The Bering Land Bridge*, p. 326–349. Stanford University Press, Stanford, California.

Endo, M. and Ozawa, T., 2001: Phylogenetic analysis of *Buccinum* and *Neptunea* inferred from mtDNA sequences. *Abstract with Programs of the 150th Regular Meeting of the Palaeontological Society of Japan*, p. 45. (*in Japanese*)

Fujii, S. and Shimizu, M., 1988: On the molluscan fossils occurred from Rengeji, Fuchu-machi, Neigun, Toyama Prefecture, central part of Japan. *Journal of the College of Liberal Arts, Toyama University, Natural Science*, vol. 21, no. 2, p. 75–89. (*in Japanese with English abstract*)

Golikov, A. N., 1980: The molluscs Buccininae of the world Ocean. *Fauna of the USSR, Mollusca*, vol. 5, Sect. 2, p. 1–465, pls.1–42. (*in Russian*)

Hatai, K., Masuda, K. and Suzuki, Y., 1961: A note on the Pliocene megafossil fauna from the Shimokita Peninsula, Aomori Prefecture, Northeast Honshu, Japan. *Saito Ho-on Kai Museum, Research Bulletin*, no. 30, p. 18–38, pls. 1–4.

Hatai, K. and Nisiyama, S. 1952: Check list of Japanese Tertiary marine Mollusca. *Science Reports of the Tohoku University, 2nd Series, Special Volume*, no. 3, p. 1–464.

Higo, S., Callomon, P. and Goto, Y. 1999: *Catalogue and Bibliography of the Marine Shell-bearing Mollusca of Japan*, 749 p. Elle Scientific Publications, Yao.

Horikoshi, M., 1986: Biofacies and communities of Japan Sea. *In*, Horikoshi,M., Nagata, Y. and Sato, T *eds.*, *Seas around Japanese Islands*, p.257–271, Iwanami Shoten, Tokyo. (*in Japanese*)

Itaki, T., Funakawa, T. and Motoyama, I., 1996: Change in the radiolarian communities in the northeast part of Japan Sea, off Shakotan, Hokkaido, since the last glacial age. *Preliminary Reports on Researches in the 1995 Fiscal Year, Comprehensive Study on Environmental Changes in the Western Hokkaido Coastal Area*, p. 171–185, Geological Survey of Japan, Tsukuba. (*in Japanese*)

Iwai, T., 1965: The geological and paleontological studies in the marginal area of the Tsugaru basin, Aomori Prefecture, Japan. *Bulletin of Educational Faculty of Hirosaki University*, no. 15, p. 1–68, pls. 12–20.

Kanehara, K., 1942: Fossil Mollusca from Tayazawa, Wakimoto-mura, Katanishi oil field. *Journal of the Geological Society of Japan*, vol. 49, no. 581, p. 130–133, pl. 3. (*in Japanese*)

Kato, S., 1993: Studies on the genus *Neptunea*, principally from Japan and the surrounding seas. *Hitachiobi*, nos. 61/62, p. 6–74, pls. 1–40. (*in Japanese*)

Kuroda, T., 1929: Catalogue of Japanese Mollusca. *Venus*, vol. 1, appendix, p. 1–26.

Kuroda, T., 1931: Mollusca. *In*, Homma F. *ed.*, *Shinano Chubu Chishitsu-shi* (*Geology of Central Shinano*), pt. 4, p. 1–90, pls. 1–13. Kokin-shoin, Tokyo. (*in Japanese*)

Linnaeus, C., 1758: *Systema Naturae Editio decima*. 823 p., Stockholm.

Lischke, C. E., 1872: Diagnosen neuer Meeres-Conchylien von Japan. *Malakozoologische Blätter*, vol. 19, p. 100–109.

Makiyama, J., 1927: Preliminary report on the Tertiary fossils from Kami-Minochi-gun, Shinano. *Chikyu* (*Globe*), vol. 8, no. 2, p. 181–188, pl. 3. (*in Japanese*)

Marincovich, L., Jr., and Gladenkov, A. Y., 1999: Evidence for an early opening of the Bering Strait. *Nature*, vol. 397, p. 149–151.

Masuda, K and Noda, H., 1976: Check list and bibliography of the Tertiary and Quaternary Mollusca of Japan, 1950–1974. *Saito Ho-on Kai, Special Publication*, no. 1, p. 1–494.

Middendorff, A. T. v., 1849: *Beiträge zu einer Malacologia Russica, Abt. 3. Aufzahlung und Beschreibung der zur Meeresfauna Russlands gehörigen Zweischaler.* 94 p., 21 pls., St. Petersburg.

Nakata, Y. and Amano, K., 1991: Pliocene molluscan associations in the Tomikura District, extended over Niigata and Nagano Prefectures, Japan. *Bulletin of the Mizunami Fossil Museum*, no. 18, p. 77–91, pls. 5–7. (*in Japanese with English abstract*)

Noda, H. and Masuda, K., 1968: On the early Miyagian marine fauna from the Ojika Peninsula, Miyagi Prefecture, Japan. *Saito Ho-on Kai Museum, Research Bulletin*, no. 37, p. 1–9, pl. 1.

Nomura, S., 1937: On some Neogene fossils from along the upper course of the Nikko-gawa, Akumi-gun, Yamagata-ken, Northeast Honshu, Japan. *Saito Ho-on Kai Museum, Research Bulletin*, no. 13, p. 173–178, pl. 24.

Otuka, Y. 1939: Mollusca from the Cainozoic System of eastern Aomori Prefecture, Japan. *Journal of the Geological*

Society of Japan, vol. 44, no. 544, p. 23-31, pl. 2.

Oyama, K., 1951: Molluscan assemblages at intermediate depths on the Pacific and Japan Sea sides of the main islands of Japan. *Bulletin of the Biogeographical Society of Japan*, vol. 15, no. 2, p. 1-4. (*in Japanese*)

Ozaki, H., 1958: Stratigraphical and paleontological studies on the Neogene and Pleistocene formations of the Tyosi district. *Bulletin of the National Science Museum*, vol. 4, no. 1, p. 1-182, pls. 1-24.

Pilsbry, H. A., 1904: New species of *Buccinum* from the Kuril Islands. *Nautilus*, vol. 18, no. 3, p.87-89.

Rafinesque, C. S., 1815: *Analyse de la nature, ou tableau de l'univers et des corps organisés*, 224 p. Barravechia, Palermo.

Sowerby, G. B. III, 1899: Descriptions of two new species of shells from Japan. *Annals and Magazine of Natural History, Series* 7, vol. 4, p. 370-372.

Stanley, S. M., 1984: Marine mass extinction: a dominant role for temperature. *In*, Nitecki, M., *ed.*, *Extinctions*, p.69-117, University of Chicago Press, Chicago.

Stimpson, W., 1865: Review of the northern buccinums, and remarks on some other northern marine mollusks. Part 1. *The Canadian Naturalist and Geologist, New Series*, vol. 2, p. 364-389.

Tada, R., 1994: Paleoceanographic evolution of the Japan Sea. *Palaeogeography, Palaeoclimatology, Palaeoeco-logy*, vol. 108, nos. 3/4, p. 487-508.

Tiba, R., 1980: Description of four new species of the genus *Buccinum* (Buccinidae, Gastropoda). *Bulletin of the Institute of Malacology, Tokyo*, vol. 1, no. 5, p. 77-80, pls. 24-27.

Tiba, R., 1981: Description of two new species of the genus *Buccinum*. *Bulletin of the Institute of Malacology, Tokyo*, vol. 1, no. 7, p. 110-112, pls. 37-38.

Tiba, R., 1984: Description of a new species of the genus *Buccinum*. *Bulletin of the Institute of Malacology, Tokyo*, vol. 1, no. 10, p. 141-142, pl. 48.

Tiba, R. and Kosuge, S., 1984: North Pacific shells (14) Genus *Buccinum* Linnaeus. *Occasional Publication of the Institute of Malacology of Tokyo*, p. 1-124. (*in Japanese*)

Valentine, J.W. and Jablonski, D., 1991: Biotic effects of sea level change; the Pleistocene test. *Journal of Geophysical Research*, vol. 96, no. B4, p. 6873-6878.

Verkrüzen, T.A., 1882: *Buccinum*, L. (Fortsetzung). *Jahrbuch der Deutschen Malakozoologischen Gesellschaft*, vol. 3, p. 205-221, 279-301, 356-365.

Vermeij, G.J., 1991: Anatomy of an invasion: the trans-Arctic interchange. *Paleobiology*, vol. 17, no. 3, p. 281-307.

Yokoyama, M., 1926: Fossil shells from Sado. *Journal of the Faculty of Science, Imperial University of Tokyo, sec.* 2, vol. 1, pt. 8, p. 249-312, pls. 32-37.

The Palaeontological Society of Japan has revitalized its journal. Now entitled **Paleontological Research,** and published in English, its scope and aims have entirely been redefined. The journal now accepts and publishes any international manuscript meeting the Society's scientific and editorial standards. In keeping with the journal's new target audience the Society has established a new category of membership **(Subscribing Membership)** which, hopefully, will be especially attractive to new and existing overseas members. The Society looks forward to receiving your applications. Thank you.

APPLICATION FOR OVERSEAS MEMBERSHIP TO THE PALAEONTOLOGICAL SOCIETY OF JAPAN

1. NAME: _____
                  Last (Surname)   First (Given name)   Middle Initial

2. POSTAL ADDRESS: _____

   _____

   _____

3. TELEPHONE AND FAX (please include country code if known):
   TEL _____
   FAX _____
           country code   area code   number

4. E-MAIL: _____

5. MEMBERSHIP CATEGORY (please check one):
   ☐**Full Member** receives four issues of **Paleontological Research** ················**8,500 JP Yen**
      and two issues of **Kaseki** (a Japanese language journal of paleontology)
      in a year and all privileges of the Society including voting rights and
      conference programs
   ☐**Subscribing Member of PR** receives four issues of ························**6,000 JP Yen**
      Paleontological Reasearch in a year   (Current JP Yen is 0.0083 U.S. $)

6. METHOD OF PAYMENT (Please check one box):
   ☐I enclose a bank draft made payable to the PSJ.
   ☐I will remit/have remitted the above amount on_____ JP Yen through my bank to the
     account of JPS, a/c #062-0211501, The Bank of Tokyo-Mitsubishi, Kasuga-cho Branch, Tokyo.
   ☐I agree to pay the amount of_____ JP Yen by my credit card.
      ☐Master   ☐VISA   ☐American Express
      ☐Diners Club   ☐Access   ☐Euro
      Card Account Number ☐☐☐☐ ☐☐☐☐ ☐☐☐☐ ☐☐☐☐
      Signature (required) _____ Card Expiration _____

7. SIGNATURE _____ DATE _____

8. MAIL TO: Palaeontological Society of Japan
           c/o Business Center for Academic Societies, Japan
           5-16-9 Honkomagome, Bunkyo-ku, Tokyo, 113-8622 Japan

A GUIDE FOR PREPARING MANUSCRIPTS

PALEONTOLOGICAL RESEARCH is dedicated to serving the international community through the dissemination of knowledge in all areas of paleontological research. The journal publishes original and unpublished articles, normally not exceeding 24 pages, and short notes, normally less than 4 pages, without abstract. Manuscripts submitted are subject to review and editing by reviewers and a language editor. Manuscripts accepted for publication will generally be published in order of submission. Authors submit three copies of their manuscript to: Dr. Kazushige Tanabe, Editor of Paleontological Research, Department of Earth and Planetary Science, University of Tokyo, Hongo 7-3-1, Tokyo 113-0033, Japan. After review, two copies of the revised manuscript are to be returned for copy editing.

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

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

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

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

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

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

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

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

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

see the examples).

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

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

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

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

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

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

Ager, D. V., 1963: *Principles of Paleoecology*, 371p. McGraw-Hill Co., New York.

Barron, J. A., 1983: Latest Oligocene through early Middle Miocene diatom biostratigraphy of the eastern tropical Pacific. *Marine Micropaleontology*, vol. 7, p. 487-515.

Barron, J. A., 1989: Lower Miocene to Quatemary diatom biostratigraphy of Leg 57, off northeastern Japan, Deep Sea Drilling Project. *In*, Scientific Party, *Initial Reports of the Deep Sea Drilling Project*, vols, 56 and 57, p. 641-685. U. S. Govt. Printing Office, Washington, D. C.

Burckle, L. H., 1978: Marine diatoms. *In*, Haq, B. U. and Boersma, A. eds., *Introduction to Marine Micropaleontology*, p. 245-266. Elsevier, New York.

Fenner, J. and Mikkelsen, N., 1990: Eccene-Oligocene diatoms in the westem Indian Ocean: Taxonomy, stratigraphy, and paleoecology. *In*, Duncan, R. A., Backman, J., Peterson, L. C., *et al.*, eds.*Proceedings of the Ocean Drilling Program, Scientific Results*, vol. 115, p. 433-463. College Station, TX (Ocean Drilling Program).

Kuramoto, S., 1996: Geophysical investigation for methane hydrates and the significance of BSR. *The Journal of the Geological Society of Japan*, vol. 11, p. 951-958. (*in Japanese with English abstract*)

Zakharov, Yu. D., 1974: Novaya nakhodka chelyustnogo apparata ammonoidey (A new find of an ammonoid jaw apparatus). *Paleontologicheskii Zhurnal* 1974, p. 127-129. (*in Russian*)

・・・・・・・・・・・行 事 予 定・・・・・・・・・・・

◎第151回例会は，2002年1月26日（土），1月27日（日）の両日にわたりに鹿児島大学理学部で開催され
ます．1月27日（日）午後に公開講演として「21世紀は自然史の時代 ―古生物学・フィールド科学か
らの提言―：世話人，森 啓・矢島道子；平成13年度科研費研究成果公開発表（B）」を実施致します．
また1月26日（土）には，昨年と今年度の学術賞受賞者の特別講演6件を予定しております．一般講演
の申し込み締切は2001年11月30日（金）です．

◎2002年年会・総会は福井県立恐竜博物館（福井県勝山市）で開催します．開催日程は6月下旬から7月
はじめで現在調整中です．なお講演の申し込み締切は2002年5月7日（火）です．

◎古生物学会では，小人数で実施されるワークショップやショートコースを主催しております．これには
学会から補助金を得ることができます．企画をお持ちの方は行事係りまでお問い合せ下さい．

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先は，
　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

　　　行事係幹事　本山 功
　　　〒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

Paleontological Research

Vol. 5, No. 3   September 28, 2001

CONTENTS