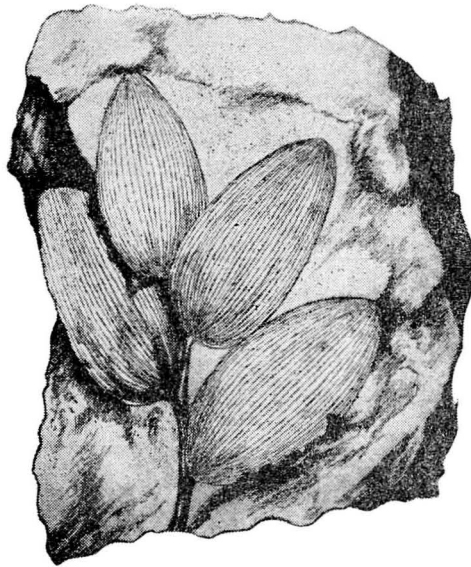


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The fossil on the cover: Original figure of *Podozamites Reinii* GEYLER, 1877, from the Tetori group. GEYLER's description marked the onset of modern palaeontology in Japan.

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680. AN OCCURRENCE OF *ORDOSOCERAS* IN JEHOLO, NORTHEAST CHINA, AND A NOTE ON THE POLYDESMIIDAE\*

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熱河産の *Ordosoceras* と Polydesmiidae について: Actinoceroid の最古の属とされていた *Polydesmia* について私はかって詳論したことがあるが、爾来 35 年間に多くの新事実が報告されている。熱河産の *Ordosoceras jeholense*, nov. を記載するに当たって、その観察の記載のみならず、Polydesmiidae の分類と分布を再検討した。その結果旧称の Chazyian 前期、今日の Whiterock にはほぼ相当する丸山期に、東アジアでは先づ *Wulinoceras* が、次いで *Polydesmia*, *Ordosoceras* が出現した。これら 2 属は黄河盆地特産である。華中の *Meitanoceras* は恐らくヒマラヤのいわゆる *Ordosoceras* 数種と共に新科をなしている。小林貞一

*Polydesmia* is an interesting example in taxonomy that a gastropod genus turned out a senior synonym of a cephalopod genus. In 1931 I described *Maruyamaceras*, nov. as an Ordovician cephalopod genus (KOBAYASHI, 1931a), but later when I happened to see LORENZ's paper from the reverse side, I was struck to find that his *Polydesmia* of which he quoted that "Die Schnecken-natur dieser Versteinerung ist unzweifelhaft (1906, S. 103)", essentially coincided with the siphuncle of *Maruyamaceras*. Merit to TEICHERT (1937) their synonymy was subsequently warranted through LORENZ's type revision.

In 1940 I have studied available specimens of *Polydesmia* including a phragmocone of the type-species. As the result I proposed a new family, Polydesmiidae for *Polydesmia* (*Polydesmia* and *Maruyamacerina*). Because of its archaeism special attention was paid on it for the evolution of the Actinoceratida

(TEICHERT, 1933; FLOWER, 1957, 1968).

During these thirty-seven years many informations were added to our knowledge on this family including *Ordosoceras* CHANG, 1959 and other new allied species. It was long ago that TOKUDA has submitted me a small collection of Ordovician fossils from Jehol in the extreme southwestern part of Northeast China (Manchuria). At that time I simply noted an inclusion of *Polydesmia* by preliminary identification (KOBAYASHI and CHOH, 1942), but recently I found the Jehol *Polydesmia* to be a new species of *Ordosoceras* CHANG, 1959 by reexamination. Therefore *Ordosoceras jeholense* is proposed for it and its detailed description is presented in this paper.

On this occasion I reconsidered the speciality of the Polydesmiidae with additional facts gathered since its proposal. The siphuncular segment whose lateral wall is composed of a median annulation and a constriction on each side is quite distinctive of this family as well as the Meitanoceratidae, nov.

\* Received May 10, 1977; read June 18, 1977, at Shizuoka.

Compared to the former the segment is narrower and taller, radial canals are extending from the central canal laterally and lamellar structure is undeveloped in siphuncular deposits in the latter family. The Polydesmiidae comprise *Polydesmia*, *Maruyamacerina* and *Ordosoceras* among which the posterior constriction is more and less developed respectively in *Ordosoceras* and *Maruyamacerina*. The horn-shaped siphuncular deposits and oblique radial canals are best shown in *Polydesmia* and some species of *Ordosoceras*. The septum is elliphoanoidal in *Ordosoceras*, but apparently holochanoidal in the two others.

These three genera are typical of the Maruyaman or early Tofangian fauna of the Hwangho basin. In the Alashan-Chaotzushan section in western Ordos the *Wutinoceras*, *Polydesmia*, *Ordosoceras* and *Chisiloceras* horizons are in ascending order (CHANG, 1959, 1960). They are younger than the Wolungian *Manchuroceras*-*Archaeoscyphia* fauna whose age is late or middle-late Canadian. Therefore the Maruyaman fauna is approximate to the early Chazyan or Whiterock age in North America and Llanvirnian of Europe.

While *Manchuroceras* was widely distributed in the western Pacific area (KOBAYASHI, 1977), the family Polydesmiidae were endemic to the Hwangho basin. *Meitanoceras subglobosum* CHEN, 1975 occurs in central China in the early Llandeilian Kuniutan Formation, but the Himalayan *Ordosoceras* species may be a little older. They reveal another group of endemic cephalopods in the Himalayan-Yangtze area.

Before going further, I record my sincere thanks to Dr. N. KAMBE of the Geological Survey of Japan and Prof. I. HAYAMI of the University Museum,

University of Tokyo for their kind assistances in preparation of this article.

Family Polydesmiidae KOBAYASHI, 1940

*Diagnosis*.—Shell medium sized, mostly longiconic, straight, but sometimes a little curved or breviconic, subcircular in cross section. Septum holochanoidal or elliphoanoidal, cyrtochanitic; septal neck hook-shaped, but varying from semicircular to abruptly recurved; siphuncle subcentral to submarginal, broad; siphuncular segments short; wall of the segment composed of a median annulation and constrictions on its two sides; radial canals highly oblique to subrectangular to central canal; siphuncular deposits lamellar; stereoplasmic deposit not well developed in camerae.

*Remarks*.—*Polydesmia* and *Ordosoceras* are two typical genera of this family which are well characterized by the annulated and somewhat shouldered lateral projection and constrictions on its two sides, highly oblique radial canals and lamellar siphuncular deposits. Because the constrictions are reduced in *Maruyamaceras peshanense*, I have proposed *Maruyamacerina* for it as a subgenus of *Maruyamaceras* i. e. *Polydesmia* in 1936. Yet the septal neck is hook-shaped, though the hook is depressed and the lamellar deposits and oblique radial canals show its being a terminal form of the family in parallel to the *Actinoceras*-*Armenoceras* trend of specialization. Because no intermediate link has as yet been found between *Maruyamacerina* and *Polydesmia* s. str., the former would be better accepted for the time being as a distinct genus of the same family.

CHAO et al. (1965) placed *Discoactinoceras* in this family, but judging from the septal form and siphuncular segment

the genus was considered more allied to the Huroniidae by SHIMANSKY (1962), TEICHERT (1964) and others. In my opinion it represents a new family, as will be discussed in detail in near future.

*Distribution*.—This is a small but very distinct family in the early and (?) middle Toufangian age in the Hwangho basin.

Genus *Polydesmia* LORENZ, 1906

Synonym: *Maruyamaceras* KOBAYASHI, 1931

*Diagnosis*.—Conch straight or slightly curved longicone or brevicone, sub-circular in cross section; surface annulated in type-species; siphuncle large, subcentral; septum apparently holochoanoidal; stereoplasmic deposit not well developed in camerae. Siphuncular wall composed of a large annulation, medium sized anterior hook or constriction and small posterior constriction triangle in section; radial canals strongly or moderately oblique; siphuncular deposit composed of radially disposed lamellae, which grow typically from the pro-*Actinoceras* stage to the *Polydesmia* stage through the *Actinoceras* stage.

*Type-species*.—*Polydesmia canaliculata* LORENZ, 1906.

*Remarks*.—Shell is abruptly expanding in *P. shimamurai* and slightly curved in *P. watanabei*. In 1940 I have described and discussed this genus in detail. Since then several new species were added and new localities reported. Beside the type-species the genus comprises now the followings including one of provisional reference:

*Armenoceras elegans* ENDO, 1932

Liaoning

*Maruyamaceras shimamurai* KOBAYASHI, 1931 North Korea

*Maruyamaceras watanabei* KOBAYASHI, 1931 North Korea

*Maruyamaceras* sp. KOBAYASHI, 1931 North Korea

*Polydesmia canaliculata magna* KOBAYASHI, 1940 Liaoning

*Polydesmia* sp. KOBAYASHI, 1940 i. e.

*Armenoceras elegans* ENDO, (pars) Liaoning

*Polydesmia zuezhanshanensis* CHANG, 1959 Ordos, Shantung (CHEN, 1976)

*Polydesmia yilehetoensis* CHANG, 1959 Ordos

*Polydesmia* 3 spp. A, B, C CHANG, 1959 Ordos

*Polydesmia changkiuensis* CHANG, 1960 Ordos

*Polydesmia* ? sp. CHEN, 1975

Qilianshan

*Armenoceras elegans* ENDO, 1932 (pars) in pl. 15, fig. 2 was identified with *Polydesmia canaliculata* by KOBAYASHI (1940). A specimen of this species from Minshankou, near Penhsihu, Liaoning, Northeast China is a well preserved phragmocone with camerate portion. While they constitute a solid species, *P. canaliculata manga* is so isolated that it is better recognized an independent species. SHIMIZU and OBATA (1937) reported *Polydesmia* from Hopei, but it remained undescribed. *Polydesmia* listed from Jehol (KOBAYASHI and CHOH, 1942) is known now to be an *Ordosoceras*. *Polydesmia* ? sp. from a little known locality in South Korea (KOBAYASHI, 1966, p. 41) is here eliminated from this genus.

*Distribution*.—In summarizing the above occurrences, it can be said that the genus was widely distributed in Eastern Asia in North Korea, Liaoning, Shantung, Hopei?, Ordos and ? Kilianshan, all in the so-called Hwangho basin in the Ordovician palaeogeography. *Armenoceras elegans* from the Middle

Ordovician of east Siberia which apparently lacks constrictions on the siphuncular segments and whose siphuncular deposits are not horn-shaped (BALASHOV, 1964), looks like an armenoceroid rather than a *Polydesmia*.

Genus *Ordosoceras* CHANG, 1959

*Diagnosis*:—Similar to *Polydesmia*, but different principally in the siphuncular wall in longitudinal section which is composed of a large annulation completely separated from septa by two constrictions the anterior and posterior one of which are hook-shaped and linear or subtriangular respectively. Septa apparently ellipsochanooidal; camerae with stereoplasmic deposits.

*Type-species*:—*Ordosoceras sphaeriforme* CHANG, 1959.

*Remarks*:—CHANG described beside the above species the followings from Ordos:

*Ordosoceras quasilineatum* CHANG, 1959

*Ordosoceras* sp. CHANG, 1959

*Ordosoceras honguezense* CHANG, 1960

*Ordosoceras ordosense* CHANG, 1960

*Ordosoceras* aff. *sphaeriforme* CHANG, 1960

*Ordosoceras sphaeriforme okotiense* CHANG, 1960

Recently CHEN (1976) described *O. quasilineatum* from Shantung, while *Ordosoceras jeholense*, nov. is added to them in this paper from Jehol.

CHEN (1975) described additional four species from the Himalaya as follows:

*Ordosoceras nyalamense* CHEN, 1975

*Ordosoceras chiantsunense* TSOU (MS) in CHEN, 1975

*Ordosoceras contractum* CHEN, 1975

*Ordosoceras yaliense* CHEN, 1975

These Himalayan species are similar to the North Chinese species in the aspect of the siphuncular wall, but quite different in the siphuncular structure.

Namely, the radial canals look nearly straight and rectangular to the central canal in the Himalayan ones. Their siphuncle is narrower and their siphuncular segments are taller in comparison with the breadth of the segment at the constriction. In these aspects the Himalayan species are certainly closer to *Meitanoceras subglobosum* from Central China (CHEN and LIU, 1974). Whether or not they are congeneric with *M. subglobosum* is a question. I think, however, that they are proper to be included in the Meitanoceratidae rather than the Polydesmiidae. None of them has the horn-shaped siphuncular deposits and oblique radial canals typical of the Polydesmiidae.

*Distribution*:—Ordos, Shantung and Jehol, western Liaoning, all in the Hwangho basin of Eastern Asia, if the Himalayan forms are excluded.

*Ordosoceras jeholense* KOBAYASHI  
sp. nov.

Plate 17, Figures 1, 2; Plate 18,  
Figures 2-4

*Description*:—Orthoconic phragmocone, about 9 mm in length, in tan-coloured limestone with scattered earthy patches. Septal sutures on the weathered surface of the limestone are transversal, but gently sinuated adapically in the median part of the ventral side, forming a broad ventral sinus like hyponomic sinus; six sutures and five intervals in the length of 20-22 mm. This camera wall is broadly convex, but the convexity is strengthened on lateral sides. Judging from this curvature the conch seems to be not elliptical, but suboval in cross section having a fairly flattened venter. The siphuncle is large, submarginal and apparently suboval in cross section.

The phragmocone was cut longitudinally, but slightly oblique to the central canal so that the canal disappears out of the section in the adoral half. In the longitudinal section the conch appears to expand somewhat more rapidly than the siphuncle. The central canal is located at about one-third the diameter of the siphuncular from the dorsal margin. The stereoplasmic deposit is well developed in the camerae on the ventral side, although the outer shell is gone. The camerate portion is not preserved on the other side, because the septa are thin and the camerae were vacant. There the siphuncle was exposed under erosion before the deposition of the limestone. The original internal structure of the phragmocone is, however, well preserved on the ventral side.

The siphuncle, about 85 mm long, is composed of 19-20 siphuncular segments. Three septa and two intervals are countable in the length of 8 mm and 10 mm respectively in the adapical and adoral part. A siphuncular segment consists of a median annulation and two constrictions on its both sides.

In the longitudinal section the septal neck is hook-shaped. The connecting ring describes therefrom almost three-quarters of a circle and then straight down obliquely, outlining a triangular cavity. The diameter of the circle is half as long as a septal interval. The median annulation is protruded anterolaterally and isolated from the septa on its two sides, but its distance from the septum is shorter on the adoral side than the other, because the constriction on the former side is smaller than on the latter side.

The siphuncular deposit is quite different from the usual annulus. It encrusts largely the inside of the con-

necting ring as far as the preceding septal neck. The stereoplasmic deposition in this stage, however, cannot be analyzed in detail with this specimen, for growth lines are vanished by recrystallization. In the next stage the deposit grows inward and upward i.e. adorally to form an oblique horn which is protruded as far as the level of the succeeding septal neck. The growth of this stage is clearly shown in section by a series of crescentic layers which reveals the cone-on-cone growth of the horn. In the adapical part of the section it is seen that a horn is intercalated between two horns showing the branching of radial canals.

In the camera the episepal deposit is more developed than the hyposeptal one. The pseudoseptum terminates inward in juxtaposition to the end of a radial canal.

*Comparison*:—This species is allied to *Ordosoceras quasilineatum* CHANG in the siphuncular structure, particularly the development of the oblique horns, but CHANG's species is a much smaller form which is quite distinct from this species in the subcentral position of the siphuncle, the conch expanding more rapidly in comparison with the siphuncular expansion and the circular but only slightly ovate cross section of the conch.

*Occurrence*:—Nantanchinkou area in the southwestern part of the Nanpiao coal-field, Jehol, Liaoning, Northeast China. TOKUDA's collection from the area contained *Tofangocericina*, *Armenoceras*, *Ormoceras* (?), *Polydesmia* and *Cameroceras*' siphuncle beside *Archaeoscyphia*, *Maclurites*, *Pagodispira* and *Isotelus* or *Isoteloides* by preliminary determination (KOBAYASHI and CHO, 1942). They were procured from Ordovician limestones in some horizons.

Among them the first to third cephalopods were already described under the names of *Tofangocerina nansiaoense* KOBAYASHI and MATUMOTO, *Jeholoceras robustum* KOBAYASHI and MATUMOTO and *Linormoceras centrale* KOBAYASHI and MATUMOTO (1942).

*Jeholoceras* is an orthoconic armenoceroïd with a broad submarginal siphuncle whose annuli are composed of vertical lamellae protruding inward in different length.

*Linormoceras* is an orthoconic ormoïd with a large subcentral siphuncle whose stereoplasmic deposits consist of annuli and endosipholinings. *Linormoceras centrale minor* was later described by CHANG (1965) from the Yingou Group of Yumen, Kansu.

These three cephalopods from Jehol are presumably younger, but *Archaeoscyphia* must be older than the present species.

#### Family Meitanoceratidae

KOBAYASHI, fam. nov.

*Diagnosis*:—Like Polydesmiidae siphuncular wall consists of middle annulation and a constriction on each side, but siphuncular segment is comparatively taller and narrower; annulus has no horn-shaped oblique projection; radial canals extending from central canal subrectangularly. (See *Meitanoceras subglobosum*, pl. 18, fig. 1)

*Remarks*:—Four species of *Ordosoceras* from the Chiatsun Group of the Himalayas (CHEN, 1975) belong probably to this family, although they may be generically distinguishable from *Meitanoceras*.

*Distribution*:—Llandeilian-Llanvirnian, Central China-Himalaya.

#### The age of the Maruyaman stage

When I proposed *Maruyamaceras* in 1931, I considered it a late Wolungian actinoceroïd, because *Maruyamaceras shimamurai*, *M. watanabei* and *M. sp.* beside *Cameroceras sp.* were collected from the Maruyama (Hwansan) limestone between the *Ormoceras*-bearing Toufangian limestone and the *Coreanoceras*-bearing Shorin Limestone in the Kyeomip'o-Hwangju (Kenjiho-Koshu) area, North Korea and because WATANABE's collection from Tungyuehuan, Pêshan-hsien, Shantung contained *Maruyamaceras peshanense*, *Stereoplasmoceras cf. machiakouense* and *Manchuroceras platyventrum*.

Subsequently SHIMIZU and OBATA (1937) pointed out that *Maruyamaceras* did not occur together with *Manchuroceras*, but did the former in a higher horizon than the latter in Pêshan-hsien, Shantung as well as the Liukiang coalfield, Hopei. They denominated the formation with the *Wutinoceras* zone containing *Wutinoceras*, *Maruyamaceras* and *Armenoceras* the Leichuang stage. In the same year TEICHERT ascertained the synonymy of *Maruyamaceras* with *Polydesmia*.

Then I examined in 1940 the WATANABE collection again and confirmed that the limestone slab containing *Manchuroceras platyventrum* and *Stereoplasmoceras cf. machiakouense* is different from the *Polydesmia peshanensis* bearing limestone in the lithological aspect. Therefore I distinguished the Maruyaman stage from the Wolungian series and noted that the stage is probably the equivalent of the Chazyan in North America or near it, provided *Armenoceras elegans* problem on which the reader is referred to a later page.

Later in 1956 OBATA distinguished the



upper or Wushan stage with *Armenoceras* (*Paramenoceras*) *onukii* and the lower or Leichuang stage s. str. with *Polydesmia kobayashi* (nom. nud.) in the Leichuang stage s.l. 1937 and correlated the two combined to the Chazyan of North America and the Llanvirnian of Europe.

In the mean time CHANG (1959, 1960) found the following four cephalopod zones in the Alashan-Chaotzushan area, western Ordos.

- II. Chaotzushan Limestone, 80-100 m thick
  3. *Chisiloceras undulatum* zone in the upper part
  2. *Ordosoceras quasilineatum* zone in the lower part
  1. *Polydesmia zuezhanshanensis* zone in the basal part
- I. Santaokan sandstone and limestone, 50 to 60 m thick
  0. *Wutinoceras* zone

In adding new facts CHEN (1976) summarized the Ordovician cephalopod biostratigraphy in North China in proposing Peianchuang suite for the unit having *Polydesmia* and *Ordosoceras* as its keys. This unit is underlain by the Liangchiashan Limestone containing *Coreanoceras* and *Manchuroceras*. The former is the approximate correlative of the Dawan suite and the latter that of the Hunghuayuan in Central China where the latter also yields *Manchuroceras* and *Coreanoceras* (CHEN and LIU, 1974). In Central China the international correlation can be made on the basis of rich graptolites, trilobites and others. There the Hunghuayuan Limestone is dated at the Arenigian exclusive of the *Azyograptus suecius* zone and the Dawan suite at the Llanvirnian in addition to the *suecius* zone (MU and CH'EN, 1962, LU, 1975). Because the Peianchuang suite is the *Polydesmia-Ordosoceras* age,

the age determination of the Maruyaman stage at the early Chazyan or the Whiterock is now thoroughly vindicated by these studies.

Incidentally, FLOWER, (1976a, b) shows in his correlation table that the Whiterock of North America is coeval with the Maruyaman, Wuting and Kangyao Formations in descending order, but the *Hystricurus* faunule of the Wuting fauna is Wolungian whereas some other Wuting fossils are pre-Kangyao or the Maruyaman in age, because the Kangyao is post-Wuting according to ENDO's emended sequence, 1953a, b.

*Polydesmia* and *Ordosoceras* constitute an early off-shoot of the Actinoceratida. They are, however, not the oldest of the group in Eastern Asia. As mentioned above, *Wutinoceras* appeared before them in Ordos. In Chinghai *Wutinoceras shihuigouense* CHANG and *Pararmenoceras* sp. 1 are reported together with *Manchuroceras tochuanshanense* CHANG from the Tochuanshan Limestone at Shihuigou (CHANG, 1965). The association of these three cephalopods indicates the transition from the Wolungian manchuroceroid age to the Toufangian actinoceroid age.

Now the age of *Armenoceras elegans* is to be discussed. ENDO (1932) described this species from the lower fossil horizon of the Ssuyen Formation at Penhsihu and Niuhsintai. He correlated the formation to the Black River of North America. This species was, however, referred to *Maruyamaceras* i.e. *Polydesmia* by TEICHERT (1933, 1937), KOBAYASHI (1934, 1936, 1940) and SHIMIZU and OBATA (1936). Therefore its reference to the Polydesmiidae, if not *Polydesmia*, is undeniable.

ENDO (1932) divided the Ordovician rocks inclusive of Ozarkian ones in South Manchuria into the Pingchou, Santao, Kangyao, Wuting and Ssuyen Formation

in ascending order. The first and second units correspond to the Wanwanian and Wolugnian Series (KOBAYASHI, 1931a, b, 1969). He correlated the Kangyao, Wuting and Ssuyen Formations to the Stones River, Blount and Black River respectively. Later (1953a, b), however, he replaced the Wuting below the Kangyao Formation by the reason that the Wuting fauna includes some Canadian elements (KOBAYASHI, 1935, 1966b).

According to ENDO (1932) the Kangyao fauna rich in *Lophospira* and other gastropods is older than the Ssuyen fauna rich in *Armenoceras* and other cephalopods. The type-localities of the Kangyao and Ssuyen Formations are, however, in separate basins of Yentai and Penhsihu, this status making difficult to verify the superposition of the latter on the former. On the contrary, the coexistence of such cephalopods with various gastropods including *Lophospira* is well known in the Machiakou Limestone in North China (GRABAU, 1922) as well as the Unkaku bed at Sunghoni (Shokori) near P'yeongyang, North Korea (KOBAYASHI, 1929, 1930). Therefore I think it quite probable that the difference of the faunal composition between the Kangyao and Ssuyen Formations depends much upon their facies. In other words, they are heteropic from but synchronous with each other at least to a certain extent. Nevertheless the occurrence of *Armenoceras elegans* in the Kangyao-Ssuyen suite indicates its being a post-Maruyaman survivor of the Polydesmiidae.

Finally, a few words are added on

this occasion about *Nybyoceras foerstei* ENDO, 1932, the type-species of *Wutinoceras* SHIMIZU and OBATA, 1936, from black banded limestone of the so-called Wuting Formation near Santaokangtzu near Penhsihu. I presume that the *foerstei*'s holotype was derived from a little higher horizon than the earthy limestone at Santao type-locality on the second railway tunnel of Santaokangtzu. However, this *foerstei* horizon must be already in the Maruyaman stage, namely, the Peianchuang of North China, and the Leichuang-Wushan suite of Hopei.

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### Explanation of Plate 17

*Ordosoceras jeholense* KOBAYASHI, sp. nov.

Figures 1, 2. Two longitudinal polished sections,  $\times 1.5$ . Holotype stored in University Museum, University of Tokyo (PM3894)



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## Place names in China (C) and Korea (K)

Alashan 賀蘭山 (C), Chaotzushan, Zueuzushan 棹子山 (C), Chiatsun 甲村 (C), Chinghai 青海 (C), Changkiu 章邱 (C), Dawan 大灣 (C), Honguez 河拐子 (C), Hopei 河北 (C), Hunghuayuan 紅花園 (C), Hwangho 黃河 (C), Hwangju, Kosu 黃州 (K), Jehol 熱河 (C), Kansu 甘肅 (C), Kanyao 缸窰 (C), Kilienshan, Qilianshan 祁連山 (C), Kuniutan 牯牛潭 (C), Kyeomip'o, Kenjiho 兼二浦 (K), Leichuang 雷莊 (C), Liangchiashan 亮家山 (C), Liaoning 遼寧 (C), Liukiang 柳江 (C), Machiakou 馬家溝 (C), Maruyama 丸山 (K), Minshankou 明山溝 (C), Nantanchinkou 南潭金溝 (C), Nanpiao 南票 (C), Niuhsintai 牛心台 (C), Nyalam 覈拉木 (C), Oketi 鄂托克旗 (C), Ordos 鄂爾多斯 (C), Peianchuang 北庵莊 (C), Peipiao 北票 (C), Penhsihu 本溪湖 (C), Pingchou 平州 (C), Pêshan-hsien, Poshan 博山 (C), P'yeongyang 平壤 (K), Santaokan 三道坎 (C), Santaokangtzu 三道崗子 (C), Shantung 山東 (C), Shihuigou 石灰溝 (C), Shorin-ri, Songnim-ni 松林里 (K), Ssuyen 四眼 (C), Sunghoni, Shokokri 勝湖里 (K), Tochuanshan 多泉山 (C), Toufangkou 豆腐溝 (C), Tungyüehyang 東岳陽 (C), Unkaku-ri, Unhak-ni 雲鶴里 (K), Vieheto 伊勒黑圖 (C), Wutingshan 五頂山 (C), Wushan 武山 (C), Yali 亞里 (C), Yentai 煙台 (C), Yingou 陰溝 (C), Yumen 玉門 (C)

## Explanation of Plate 18

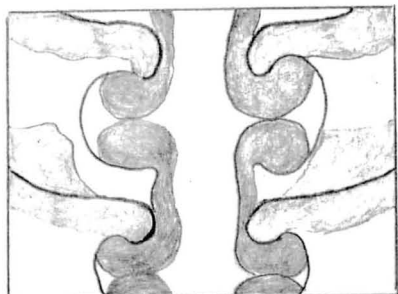
*Meitanoceras subglobosum* CHEN and LIU, 1974

Figure 1. Part of siphuncle in longitudinal section showing siphuncular sediments; drawn from CHEN and LIU, 1974, pl. 60, fig. 7.  $\times 4$ .

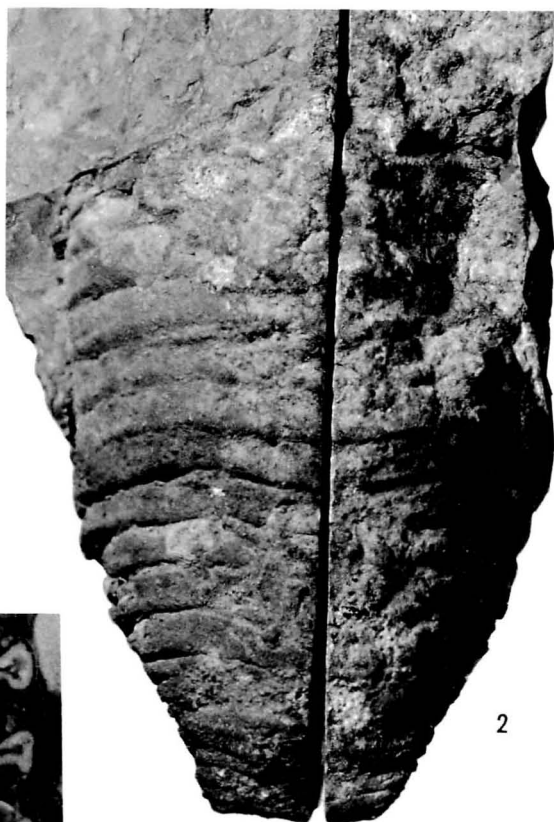
*Ordosoceras jeholense* KOBAYASHI sp. nov.

Figure 2. Ventral view of the holotype, showing septal sutures.  $\times 1.5$ .

Figures 3, 4. Part of longitudinal section of the holotype. (4: diagrammatic)  $\times 3$ .



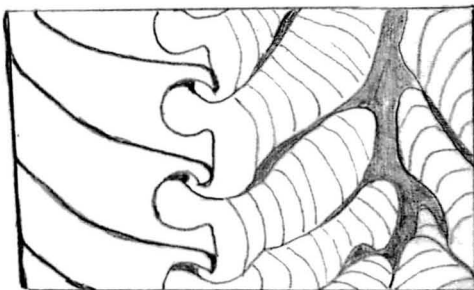
1



2



3



4

681. TAXONOMIC STUDIES ON SOME FOSSIL AND  
RECENT JAPANESE BALANOIDEA (PART 1)

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日本のいくつかの化石および現生フジツボ類の分類学的研究 (その 1): 化石フジツボ類は日本の新第三紀以降の地層から一般に殻のばらばらにはずれた破片として産出する。それらの破片から標本の全体像が復元され、現生標本との外部形態、殻構造の比較により種が同定された。しかし現生種の従来の分類には、種および種内の分類に大きな混乱があった。その主な理由は種以下の分類群が形態的差異の程度だけに基づいて研究者の主観によって分類されていたことにある。この論文では、日本の化石および現生フジツボ類の主要な種群である *Balanus amphitrite* グループが現生生物の外部形態、殻構造および軟体部の形態的特徴に加えて、地理的分布、生息域ならびに繁殖時期などに基づいて 4 種に分類された。またそれらの分類群の化石記録を層位学的に追跡することによって種分化や日本への移住の時期が検討された。

山口寿之

1. Introduction

DARWIN'S (1851a, 1854a) two monographs on living cirripeds are classics and are dependable even up to the present time. Following DARWIN, from the late 19th to the early 20th century, the collections of biological expeditions and other museum collections were studied by WELTNER (1897), HOEK (1883, 1913), KRÜGER (1911a, b), PILSBRY (1911, 1916, 1927), NILSSON-CANTELL (1921, 1932, 1934, 1938), BROCH (1922, 1931), and others. Most of these studies include taxonomic descriptions of Balanoidea from Japan and adjacent seas. Yet, a systematic description of Recent Japanese Balanoidea depends much upon a series of taxonomic publications made by UTINOMI (HIRO prior to 1939) (HIRO, 1932a, b; 1933, 1935; 1937; 1938; 1939a, b; UTINOMI, 1949a, b; 1954; 1955; 1958; 1962; 1967;

\* Received May 26, 1977; read Jan. 31, 1976 at Kawatabi.

1968; 1970).

Studies on fossils were also started by DARWIN (1851b, 1854b) and advanced by SEGUENZA (1873-76), ALESSANDRI (1906, 1907a, b), PILSBRY (1918, 1924, 1930), WITHERS (1923, 1924) and others. Recently, however, paleontologists have become increasingly interested in the study of appendage morphology, anatomy, ecology, etc. Thus the boundary between neontology and paleontology has become more and more obscure. NEWMAN, ROSS, ZULLO, and others are advancing the study of Balanoidea in uniting neontological and paleontological studies.

The Japanese fossil Balanoidea have not been studied in detail, though they are commonly found in association with molluscan fossils in the Neogene and Quaternary formations throughout Japan. In fact, "*Balanus* spp.", found at the end of faunal list of fossil molluscs, is usually the only mention of the *Balanus*

in stratigraphical or paleontological papers. Studies of Japanese fossil Balanoidea which have been published are summarized in YAMAGUCHI (1971). Species descriptions are frequently inadequate however so that it is difficult to determine whether or not these Japanese species have been correctly identified.

In this study, the writer attempts to refine the classification of some important species of Japanese living Balanoidea on the basis of distribution, ecology, habitat, biochemical characters and mechanism of reproductive isolation as well as morphological features. That is, the study has been conceived with inter-specific and infraspecific relations between living populations. From this vantage point it has been possible to more realistically interpret the fossil evidence.

## 2. Methods of Study

### *Sampling and preparation of fossil specimens*

Fossil barnacles are commonly found as fragmented skeletal remains. However, they are often attached to bank-forming oysters, other molluscan shells, and to solid materials in mud and sandstone. Therefore, prior to preparing a fossil specimen for study, the mode of occurrence should be observed in detail. Besides general observations on the nature of the sediments, note of the associated species is important for paleoecological considerations. This holds especially true in the case of the autochthonous occurrence of associated species (cf. *B. rostratus*). Knowledge of actual physical attachment between two closely related species is also indispensable for demonstrating microgeographical sympatry between two species (cf.

*Megabalanus rosa* and *M. volcano*).

To obtain fossil samples from loose sediments, they are sieved through a 1 mm or 2 mm mesh. The barnacles are then picked up from sieved remains. When articulated compartments are obtained, the interior cavities should carefully be examined to see if the opercular valves are present. If the specimens are buried in a matrix of hard sand or mudstone, they can be removed with hand tools. Specimens separated from a matrix can then be cleaned ultrasonically. Besides ordinary examination technique, X-ray photography can provide information on internal microstructure of compartments.

### *Laboratory techniques for living specimens*

For most field observations and laboratory techniques, the writer followed those explained by NEWMAN, ZULLO and WITHERS (1969). In addition, for samples to be prepared for the scanning electron microscope (SEM), appendages were dissected in 70% alcohol. Each appendage with then washed in an ultrasonic cleaner and then put separately into a small capsule with a net at each side. The alcohol was then gently replaced by distilled water, the appendage frozen in liquid N<sub>2</sub> and freeze-dried in a vacuum evaporator. Each appendage, placed on the specimen holder, was then coated with carbon and gold-palladium (Au 60%, Pd 40%), and observed under the SEM.

### *Depository, abbreviations and terminology*

Specimens are deposited in the collection of the University Museum, University of Tokyo (UMUT). Registration numbers are accompanied by prefix CA for Cenozoic Arthropoda and RA for Recent Arthropoda. Dissected appendages are mounted on glass slides, in the glycerin jelly and sealed with finger-nail polish. Other living specimens are kept



in 70% alcohol. Morphological terms in the present study are the same as those in NEWMAN, ZULLO and WITHERS (1969), HENRY and McLAUGHLIN (1975), and NEWMAN and ROSS (1976).

In the present study, the writer followed a new classification of Balanomorphs proposed by NEWMAN and ROSS (1976) based on comparative studies of surficial morphology, internal wall structure, trophi, chaetotaxis and intromittant organ.

### 3. Locality Register (Text-figure 1)

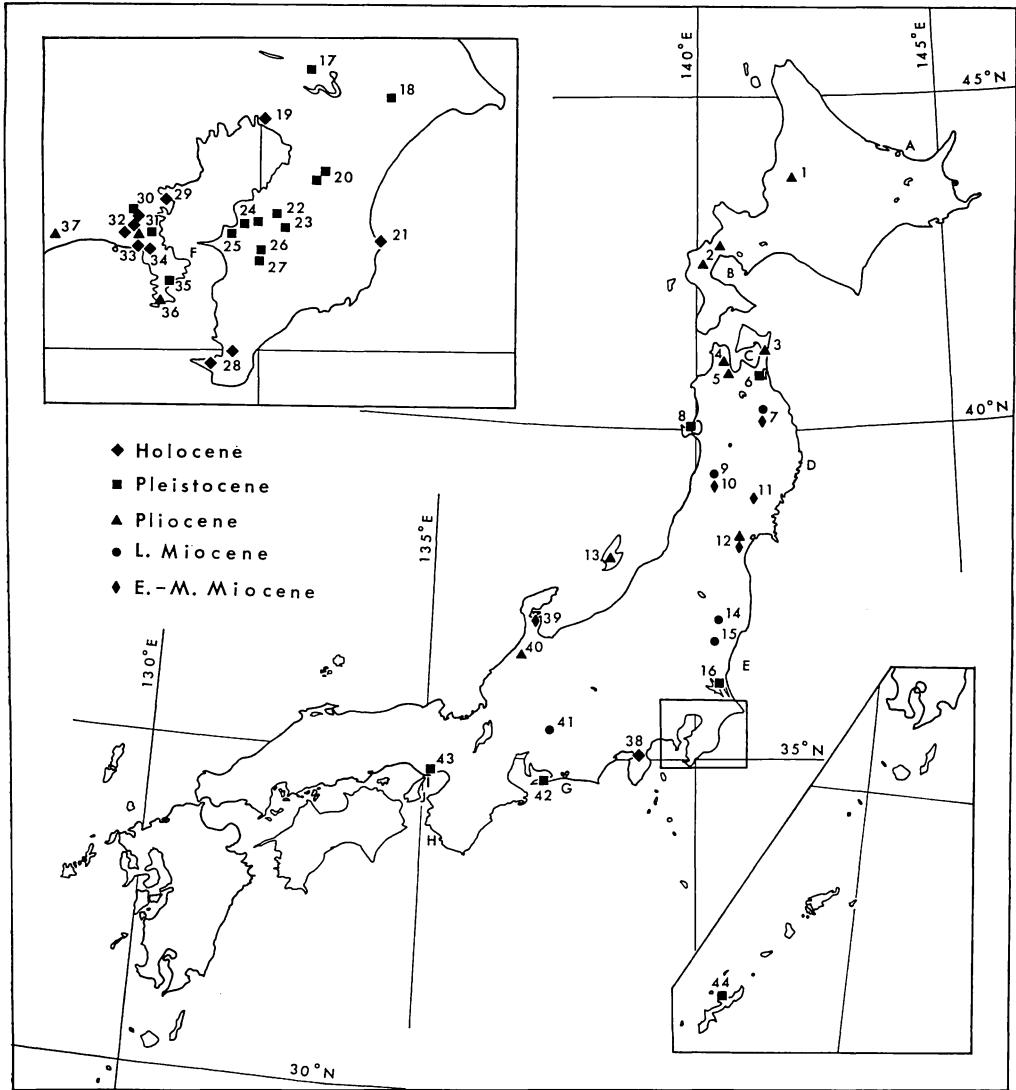
#### *Living specimens:*

- A**—Rocky shore (44°3.2' N., 144°16' E.) near Futatsu-iwa, Abashiri City, Hokkaido.
- B 1-3**—Dredge samples; Funka Bay, Hokkaido: B 1—(42°6' N., 140°48.1' E.); gravel; 40 m in depth., B 2—(42°15.4' N., 140°48.1' E.); mud containing gravel and pumice; 74 m in depth., B 3—(42°21.7' N., 140°21.4' E.); mud; 53 m in depth.
- C 1-3**—Mutsu Bay, Aomori Pref.: C 1—Dredge samples (42°5' N., 140°49.4' E.); mud; 60 m in depth., C 2—Kanita (42°2.4' N., 140°49.4' E.); on scallops *Patinopecten yesoensis* in the cultivating cages. Coll. Drs. K. CHINZEI & Y. IWASAKI., C 3—Rocky shore (45°54.2' N., 140°51.4' E.) near Asamushi Marine Biological Station.
- D**—Dredge samples (39°20.6' N., 141°56.4' E.); Otsuchi Bay, Iwate Pref.; mud; 35 m in depth. Coll. Mr. E. HONZA.
- E**—Dredge samples off Tokai-mura, Ibaragi Pref. Coll. Prof. N. NASU.
- F**—Dredge samples, same as Loc. B-2 of HORIKOSHI (1962), Tokyo Bay. Coll. Prof. M. HORIKOSHI.
- G**—On the test pile (34°44.2' N., 137°38' E.) submerged from Nov. 1973 to Aug. 1974, Hamana Lake. Coll. Dr. T. KAZIHARA.
- H**—Rocky shore (33°40.6' N., 135°21.8' E.) at Reisen bridge in the Tachigatani Inlet, Tanabe Bay, Shirahama, Wakayama Pref. Apr. 10, 1974.
- I**—Tanoshiro (34°34.5' N., 135°1.5' E.), Iwaya, Awajishima Is., Tsuna-gun, Hyogo Pref.

- J 1-2**—Dredge samples: J 1—Osaka Bay (34°29.5' N., 135°8' E.); mud; 38 m in depth., J 2—South of Tomogashima Channel (34°13' N., 134°57' E.); mud; 66 m in depth.

#### *Fossil specimens:*

- 1—Horoshin-Tachibetsu:** a cliff (43°49.7' N., 141°54.2' E.) of right bank of the Horoshin-Tachibetsu river, situated about 650 m S60°W of Matsupu Station, Numata, Uryu-gun, Hokkaido; light gray fine sand; Pliocene Horoshintachibetsu formation (OHARA, 1966); Coll. Dr. Y. IWASAKI.
- 2a-d—Setana:** a) a cliff (42°44.5' N., 140°24.9' E.) of right bank of the Kaigarasawa river, situated about 4.8 Km S68°W of Mena Station, Ran-etsu, Isoya-gun, Hokkaido; conglomeratic coarse sand., b) a cliff same as Loc. 12, YAMAGUCHI, 1973., c) a cliff (42°28.5' N., 140°11.8' E.) of left bank of the Toshihetsu river, situated about 950 m S48°W of Pirika Station, Pirika, Setana-gun, Hokkaido; pumiceous coarse sand., d) a cliff (42°26.8' N., 140°4.6' E.) of left bank of the Tanekawa river, situated about 3.3 Km N5°E of Tanekawa Station, Hikaridai, Setana-gun; coarse arkose sand. a-c) The Pliocene Setana formation (IKEYA & UEMATSU, 1968). d) The late Miocene Yakumo formation (IKEYA & UEMATSU, 1968).
- 3a-f—Shimokita:** a-d) cliffs same as Locs. 13a-d, YAMAGUCHI, 1973., e) a cliff (41°11.0' N., 141°16.6' E.) same as Loc. 6, HATAI, *et al.*, 1961; pumiceous silty sand., f) a cliff (41°10.0' N., 141°16.7' E.) of left bank of the mouth of the Maekawa river, Nakanosawa, Mutsu City, Aomori Pref.; pumiceous very coarse sand. The Pliocene Hamada formation (YAMAGUCHI, 1970).
- 4a-c—Tsugaru:** a, b) cliffs same as Locs. 14a, b, YAMAGUCHI, 1973., c) a cliff (45°55.4' N., 140°37.7' E.) of right bank of the Rokumaibashi river, situated about 3 Km S77°W of Ushirogata Station, Rokumai-bashi, Aomori City, Aomori Pref.; coarse sand. The Pliocene Kanita formation (UEMURA, *et al.*, 1959).



Text-fig. 1. Sampling localities of fossil and living Balanoida of Japan.

**5a-b—Daishaka:** a) a cliff ( $40^{\circ}49.8' N.$ ,  $140^{\circ}38.5' E.$ ) of right bank of the Amadai river, situated about 2.9 Km  $N80^{\circ}W$  of Tsugaru-Shinjo Station, Shinjo, Aomori City, Aomori Pref.; medium sand., b) a cliff same as Loc. 15, YAMAGUCHI, 1973. The Pliocene Daishaka formation (IWAI, 1965).

**6a-c—Kamikita:** a) a cliff ( $40^{\circ}43.5' N.$ ,  $141^{\circ}$

$17.3' E.$ ) same as Loc. 6, IWAI & SIOBARA, 1969; massive mud., b) a cliff ( $40^{\circ}43.6' N.$ ,  $141^{\circ}16.1' E.$ ) same as Loc. 9, IWAI & SIOBARA, 1969; massive mud., c) a cliff ( $40^{\circ}43.4' N.$ ,  $141^{\circ}14.6' E.$ ) same as Loc. 11, IWAI & SIOBARA, 1969; massive mud. The Pleistocene Numasaki mudstone.

**7a-n—Mabechi river valley:** a) a road-cut ( $40^{\circ}25.3' N.$ ,  $141^{\circ}16.8' E.$ ) situated about

3.1 Km N4°E of Sannohe Station, Sannohe-gun, Aomori Pref.; massive medium sandstone., b) a cliff (40°25.1' N., 141°17.7' E.) situated about 1.4 Km N68°W of Suwanotaira Station, Sannohe-gun; conglomeratic coarse sandstone., c) a road-cut (40°24.9' N., 141°16.8' E.) situated about 2.4 Km N6°E of Sannohe Station, Sannohe-gun; cross-laminated coarse sandstone containing gravel., d) a cliff (40°24.4' N., 141°15.8' E.) of right bank of the Sarube river, situated 1.9 Km N40°W of Sannohe Station, Sannohe-gun; barnacle limestone., e) a cliff (40°24.1' N., 141°17.1' E.) of right bank of the Mabechi river, situated about 1.1 Km N37°E of Sannohe Station, Sannohe-gun; ill-sorted coarse sandstone., f) a cliff (40°22.8' N., 141°15.5' E.) situated about 2 Km S34°W of Sannohe Station, Sannohe-gun; conglomeratic coarse sandstone., g) a road-cut (40°22.7' N., 141°16.3' E.) situated about 1.7 Km S16°W of Sannohe Station, Sannohe-gun; shell limestone containing gravel., h) a cliff (40°18.1' N., 141°18.7' E.) of right bank of the Mabechi river, situated about 2 Km S10°E of Kintaichi Station, Ninohe-gun, Iwate Pref.; ill-sorted conglomeratic coarse sandstone., i) a road-cut (40°17.7' N., 141°17.5' E.) along the branch of the Jumonji river, situated about 1.6 Km N14°W of Tomai Station, Ninohe-gun; conglomeratic coarse shell sandstone., j) a cliff (40°17.5' N., 141°17.5' E.) of left bank of the Jumonji river, situated about 1.3 Km N18°W of Tomai Station, Ninohe-gun; barnacle limestone and calcareous medium sandstone., k) a cliff (40°7' N., 141°8' E.) of left bank of the Mabechi river, situated about 300 m N53°E of Tomai Station, Ninohe-gun; ill-sorted silty sandstone containing gravel., l) a cliff (40°16.1' N., 141°18.2' E.) of right bank of the Mabechi river, situated about 1.7 Km N45°E of Kitafukuoka Station, Ninohe-gun; very coarse sandstone., m) a cliff (40°15.1' N., 141°18.6' E.) of left bank of the Shiratori river, situated about 1.9 Km N58°E of Kitafukuoka Station, Ninohe-gun; ill-sorted conglomeratic silty sandstone., n)

a road-cut (40°14.3' N., 141°18.4' E.) of the Namiuchi Pass, situated about 2.3 Km S35°E of Kitafukuoka Station, Ninohe-gun; cross-laminated pumiceous sandstone. f) The Pliocene Kamimetoki alternation (CHINZEI, 1966) of the Tomesaki formation. a) The late Miocene Miyasawa sandstone (CHINZEI, 1966) of the Tomesaki formation. d, g, i & j) The late Miocene Metoki shell limestone (CHINZEI, 1966) of the Tomesaki formation. b, c & e) The late Miocene Shinden sandstone (CHINZEI, 1966) of the Suenomatsuyama formation. k & n) The late Miocene Maisawa sandstone (CHINZEI, 1966) of the Suenomatsuyama formation. l) The late Miocene Aikawa andesite (CHINZEI, 1966) of the Suenomatsuyama formation. h & m) The late Miocene Anaushi conglomerate (CHINZEI, 1966) of the Suenomatsuyama formation.

**8a-c—Oga:** a) a coastal cliff (39°58.3' N., 139°51.1' E.) situated about 300 m SW of Anden, Oga City, Akita Pref.; cross-laminated coarse to medium sand., b) a cliff (39°58.2' N., 139°51' E.) of coast situated about 450 m SW of Anden; cross-laminated and ill-sorted conglomeratic sand., c) a coastal cliff (39°58.1' N., 139°50.9' E.) situated about 550 m SW of Anden; coarse shell sand. a) The Pleistocene Anden formation (KITAZATO, 1975). b & c) The Pleistocene Shibikawa formation (HUZIOKA, 1959).

**9a-d—Ohmagari:** a) Shell quarry at Arasawa (39°24.3' N., 140°21.1' E.), Minami-Sotomura, Senpoku-gun, Akita Pref.; barnacle "coquina"., b) a cliff (39°21.6' N., 140°21.7' E.) same as fossil locality at Asizawa Pass of the Takinoue of OTUKA, 1936; massive ill-sorted tuffaceous sand containing carbonaceous matters., c) a cliff (39°22.1' N., 140°21.7' E.) of left bank of rivulet situated about 1 Km north of Loc. 9b; massive ill-sorted tuffaceous fine sand containing carbonaceous matters., d) a cliff (39°21.7' N., 140°21.4' E.) of right bank of rivulet, situated about 400 m west of Loc. 9b, Yasawagi, Hiraga-gun, Akita Pref.; massive ill-sorted tuffaceous fine

- sand containing carbonaceous matters. The early to middle Miocene Sugota formation (KATAYAMA, 1941).
- 10—**Ukibuta**: a cliff (39°18.8' N., 140°20.7' E.) same as fossil locality at Ukibuta of OTUKA, 1936, Higashi-Yuri-mura, Yuri-gun, Akita Pref.; ill-sorted tuffaceous medium sand; early to middle Miocene Sugota formation (KATAYAMA, 1941).
- 11—**Ichinoseki**: a cliff (38°55.7' N., 141°6.8' E.) of left bank of the Iwai river, situated about 2.5 Km N80°W of Ichinoseki Station, Ichinoseki City, Iwate Pref.; ill-sorted medium sand containing many pyroclastic rock fragments; middle to late Miocene Shimokurosawa formation (ONODERA, 1957).
- 12a—**b—Sendai**: a) a cliff (38°15.4' N., 140°49.6' E.) same as Loc. 1 of the Tatsunokuchi formation, HANZAWA, *et al.*, 1953; tuffaceous medium sand containing many quartz grains; Pliocene Tatsunokuchi formation (HANZAWA, *et al.*, 1953)., b) a cliff (38°12.8' N., 140°47.5' E.) situated about 200 m south of the Oide bridge across the Natori river, Moniwa, Sendai City, Miyagi Pref.; ill-sorted calcareous medium sand; early to middle Miocene Moniwa formation (HANZAWA, *et al.*, 1953).
- 13a—**c—Sawane**: a) a cliff (38°0.2' N., 138°16.1' E.) situated about 1.1 Km N85°W of Sawane-cho, Sawada-machi, Sado-gun, Niigata Pref.; ill-sorted conglomeratic very coarse sand., b) a cliff (38°0.9' N., 138°16.6' E.) situated about 1.4 Km N20°W of Sawane-cho; conglomeratic coarse shell sand., c) a cliff same as Loc. 17, YAMAGUCHI, 1973. The Pliocene Sawane formation.
- 14—**Tanakura**: a cliff (37°1.5' N., 140°25.6' E.) situated about 4.9 Km S57°W of Iwaki-Tanakura Station, Tanakura, Higashi-Shirakawa-gun, Fukushima Pref.; coarse arkose sand; late Miocene Kamitoyo formation (IWASAKI, 1970).
- 15—**Batoh**: a cliff (35°45.1' N., 140°8.7' E.) situated about 200 m east of the Shin-Naka bridge across the Nakagawa river, Nasu-gun, Tochigi Pref.; cross-laminated pumiceous conglomeratic coarse sand; late Miocene Kobana formation (KAWADA, 1953).
- 16—**Tamatsukuri**: a cliff (36°2.9' N., 140°27.1' E.) situated about 7.5 Km S25°E of Tamatsukuri-machi Station, Fujii, Namekatalogun, Ibaraki Pref.; fossiliferous fine sand; Pleistocene Narita formation.
- 17a—**c—Kioroshi**: a) a cliff (35°49.9' N., 140°9.6' E.) situated about 950 m S64°E of Kioroshi Station, Inzai-cho, Inba-gun, Chiba Pref.; fossiliferous well-sorted medium sand., b) a cliff (35°48.5' N., 140°12.2' E.) situated about 5.6 Km S58°E of fossiliferous well-sorted medium sand., c) a cliff (35°47.1' N., 141°14.4' E.) situated about 9.8 Km S55°E of Kioroshi Station; fossiliferous well-sorted medium sand. The Pleistocene Narita formation (KOZIMA, 1958).
- 18a—**b—Tako**: a, b) cliffs same as Locs. 18a, b, YAMAGUCHI, 1973.
- 19a—**c—Funabashi**: a) Natsumidai-Kofun (an ancient tomb) (35°41.8' N., 139°59.5' E.), Natsumi-cho, Funabashi City, Chiba Pref.; Kofun age (500-700 A.D.), b) Miyamoto-dai-Kaizuka (a shell-mound) (35°41.5' N., 140°0.2' E.), Miyamoto-cho, Funabashi City; late Jomon age (3500 Y. B. P.), c) Ebigasaku-Kaizuka (a shell-mound) (35°44.1' N., 140°2.5' E.), Ebigasaku, Oana-cho, Funabashi City; middle Jomon age (4200 Y. B. P.). Coll. Miss. H. KOIKE.
- 20a—**b—Semata**: a, b) cliffs same as Locs. 19 a, b, YAMAGUCHI, 1973.
- 21—**Taito**: a coastal cliff (35°19.3' N., 140°24.7' E.) situated about 2.4 Km N80°E of Taito Station, Shimonohara, Isumi-gun, Chiba Pref.; poorly sorted conglomeratic mud containing fossil oyster bank (*Crassostrea gigas*) and autochthonous *Mya arenaria oonogai*; Holocene Taito-zaki formation (OHARA & TAIRA, 1974).
- 22a—**c—Kamiizumi**: a-c) cliffs same as Locs. 20a-c, YAMAGUCHI, 1973.
- 23a—**b—Jizodo**: a) a cliff (35°22' N., 140°6.2' E.) same as Loc. 4, NAKAGAWA, 1960; pumiceous and scoriaceous fossiliferous medium sand., b) a cliff (35°21.4' N.,

- 140°5.4' E.) same as Loc. 5, NAKAGAWA, 1960; fossiliferous tuffaceous medium sand. The Pleistocene Jizodo formation (NAKAGAWA, 1960).
- 24a-m—Kisarazu:** a) a cliff (35°22.5' N., 140°0.7' E.) same as Loc. 52, KOZIMA, 1966; cross-laminated well-sorted medium sand., b) a cliff (35°23' N., 140°0.5' E.) same as Loc. 55, KOZIMA, 1966; cross-laminated well-sorted medium sand., c) a cliff (35°23.1' N., 140°0.5' E.) same as Loc. 56, KOZIMA, 1966; cross-laminated well-sorted medium sand., d) a cliff (35°23.1' N., 139°58.5' E.) same as Loc. 60, KOZIMA, 1966; fossiliferous coarse shell sand., e) a cliff (35°23.2' N., 139°57.8' E.) same as Loc. 63, KOZIMA, 1966; cross-laminated well-sorted medium sand., f) a cliff (35°22.7' N., 139°56.6' E.) same as Loc. 21a, YAMAGUCHI, 1973., g) a cliff (35°22.6' N., 139°56.6' E.) situated about 200 m south of Loc. 24f; fossiliferous pumiceous silty medium sand., h) a cliff (35°22.5' N., 139°56.5' E.) same as Loc. 69, KOZIMA, 1966; fossiliferous pumiceous silty medium sand., i) a cliff (35°22.5' N., 139°56.4' E.) same as Loc. 68, KOZIMA, 1966; fossiliferous pumiceous silty medium sand., j) a cliff (35°21.3' N., 139°55.1' E.) same as Loc. 78, KOZIMA, 1966; fossiliferous pumiceous silty medium sand., k) a cliff (35°21.3' N., 139°55.3' E.) same as Loc. 21b, YAMAGUCHI, 1973., l) a cliff (35°21.1' N., 139°54.7' E.) same as Loc. 80, KOZIMA, 1966; fossiliferous pumiceous silty medium sand., m) a cliff (35°20.8' N., 138°54.4' E.) same as Loc. 81, KOZIMA, 1966; fossiliferous pumiceous silty medium sand. a-k) The Pleistocene Narita formation (AOKI & BABA, 1972). 1-m) The Pleistocene Kamiizumi formation (AOKI & BABA, 1972).
- 25a-b—Futtsu:** a) a cliff (35°20.4' N., 139°52.8' E.) same as Loc. 85, KOZIMA, 1966; coarse shell sand containing gravel; Pleistocene Jizodo formation (AOKI & BABA, 1972)., b) a cliff (35°20.1' N., 139°52.2' E.) same as Loc. 86, KOZIMA, 1966; coarse shell sand containing gravel; Pleistocene Naruto formation (AOKI & BABA, 1972).
- 26—Nishiyatsu:** a cliff same as Loc. 22, YAMAGUCHI, 1973.
- 27—Ichijuku:** a cliff same as Loc. 23, YAMAGUCHI, 1973.
- 28a-c—Tateyama:** a) a cliff (34°58.1' N., 139°49.4' E.) same as Loc. 1, YABE & SUGIYAMA, 1931; fossiliferous muddy sand overlying reef-building corals., b) a cliff (34°58.1' N., 139°49.4' E.) situated about 150 m north of Loc. 28a; fossiliferous muddy sand containing fragments of corals., c) a cliff (35°0.4' N., 139°53.2' E.) same as Loc. 41, NOMURA, 1932; sandy silt containing fossil oyster bank (*Crassostrea nipponina*). The Holocene Numa formation (YOKOYAMA, 1911).
- 29—Yokohama:** 8 m below the ground (35°25.9' N., 139°37.3' E.) same as Loc. 17, MATSUSHIMA, 1973; massive mud; Holocene Sakuragi-cho formation (5110±125 Y. B. P.) (MATSUSHIMA, 1973).
- 30a-g—Totsuka:** a) a cliff (35°24.7' N., 139°32.4' E.) situated about 1.5 Km N10°E of Totsuka Station, Totsuka-cho, Totsuka-ku, Yokohama City, Kanagawa Pref.; mud containing bank forming oyster (*Crassostrea gigas*)., b) a road-cut (35°23.4' N., 139°31.7' E.) on the highway situated about 1 Km S45°W of Totsuka Station, Totsuka-cho, Totsuka-ku; mud containing bank forming oyster (*Crassostrea gigas*)., c) a cliff (35°23.5' N., 139°32.7' E.) situated about 100 m west of Loc. 30b; mud containing bank forming oyster (*Crassostrea gigas*)., d) a cliff (35°25' N., 139°32.9' E.) situated about 2.3 Km N26°E of Totsuka Station, Akiba-cho, Totsuka-ku; mud containing bank forming oyster (*Crassostrea gigas*)., e) 6.2 m (A) (6550±110 Y. B. P.; MATSUSHIMA, 1971) and 10 m (B) below the ground (35°22.8' N., 139°32.2' E.) same as Locs. 2A and B of MATSUSHIMA, 1972; lignitic sandy silt., f) a cliff (32°23.2' N., 139°30.9' E.) of rivulet situated about 2.4 Km S60°W of Totsuka Station, Kumisawa-cho, Totsuka-ku; mud containing bank forming oyster (*Crassostrea gigas*)., g) 0.5 m to 1 m below the Itachigawa river bed (35°21.7' N., 139°32.2' E.) situated about 1.2 Km N10°E of Ohfuna Station, Kasama-

- cho, Totsuka-ku; shell sand. e & g) The Holocene Ohfuna shell bed (MATSUSHIMA, 1972). a-d & f) The Pleistocene Nagayama formation (OTUKA, 1930).
- 31—**Hitorizawa**: a cliff (35°21.5' N., 139°36.6' E.) of rivulet, situated about 2 Km S30°E of Yōkōdai Station, Hitorizawa, Isogo-ku, Yokohama City, Kanagawa Pref.; cross-laminated pumiceous medium to coarse sand; Pleistocene Koshiha formation (OTUKA, 1930).
- 32a-b—**Fujisawa**: a) a cliff same as Loc. 25, YAMAGUCHI, 1973., b) a cliff (35°19.8' N., 139°30.7' E.) of Kashio river, situated about 2.2 Km S73°E of Fujisawa Station, Machiya, Fujisawa City, Kanagawa Pref.; very coarse shell sand containing gravel. The Holocene Ohfuna shell bed (MATSUSHIMA, 1972). Coll. Mr. Y. MATSUSHIMA.
- 33a-e—**Kamakura**: a) a cliff (35°20.6' N., 139°33.4' E.) same as Loc. 321, SHIKAMA & MASUJIMA, 1969; fossiliferous very coarse sand., b) a cliff (35°20.6' N., 139°33.2' E.) situated about 300 m west of Loc. 33a; pumiceous and scoriaceous coarse sand., c) 5 m below the ground (2600±80 Y.B.P., MATSUSHIMA; per. com.) (35°18.4' N., 139°33' E.) of the Namerikawa riverside, situated about 1 Km S20°W of Kamakura Station, Kamakura City, Kanagawa Pref.; coarse sand; Coll. Mr. MATSUSHIMA, d) 4 m below the ground (35°19.3' N., 139°34' E.) situated about 1.2 Km N65°E of Kamakura Station, Yukino-shita-Wakaremichi, Kamakura City; coarse sand containing gravel; Coll. Mr. MATSUSHIMA, e) a cliff (35°21.5' N., 139°31.4' E.) of rivulet, situated about 1.5 Km S45°W of Ohfuna Station, Okamoto-cho, Kamakura City; massive mud. c, d) The Holocene Kamakura shell bed (MATSUSHIMA, 1974). e) The Holocene Ohfuna shell bed (MATSUSHIMA, 1972). a, b) The Pliocene Nojima formation (SHIKAMA & MASUJIMA, 1969).
- 34—**Higashi-Zushi**: 5 m below the ground (35°17.7' N., 139°36.2' E.) same as Loc. Z-1 (5520±120 Y.B.P.; MATSUSHIMA, 1974) of MATSUSHIMA, 1974, Zushi City, Kanagawa Pref.; mud containing bank forming oyster (*Crassostrea gigas*); Holocene Zushi shell bed (MATSUSHIMA, 1974). Coll: Dr. Y. KANIE.
- 35—**Tsukuihama**: a cliff same as Loc. 26, YAMAGUCHI, 1973.
- 36—**Misaki**: a cliff same as Loc. 27, YAMAGUCHI, 1973.
- 37a-b—**Ninomiya**: a) a cliff (35°18.7' N., 139°15.1' E.) situated about 2 Km N24°W of Ninomiya Station, Uchikoshi, Ninomiya-cho, Naka-gun, Kanagawa Pref.; conglomeratic scoriaceous and pumiceous coarse shell sand., b) a cliff (35°18.9' N., 139°16.2' E.) same as Loc. ms (Mushikubo), OTUKA, 1929, Oiso-machi, Naka-gun; scoriaceous and pumiceous medium sand. The Pleistocene Ninomiya formation.
- 38—**Kanogawa**: below the ground (35°4' N., 138°56.6' E.) situated about 500 m north of Baraki Station, Nagasaki, Nirayama-cho, Tagata-gun, Shizuoka Pref.; mud; Holocene. Coll: Mr. TAKAHASHI.
- 39—**Nanao**: a cliff (37°2.4' N., 139°57.4' E.) same as Loc. 100, OTUKA, 1935, Nanao City, Ishikawa Pref.; cross-laminated conglomeratic coarse shell sand containing many bryozoans; early to middle Miocene Nanao formation (OTUKA, 1935).
- 40a-f—**Kanazawa**: a) a cliff (36°31.5' N., 136°41.2' E.) same as Loc. 31, KASENO & MATSUURA, 1965; coarse shell sand., b) a cliff (36°31.3' N., 136°42.3' E.) same as Loc. 20, KASENO & MATSUURA, 1965; massive fine sand., c) a cliff (36°32.8' N., 136°42.5' E.) same as Loc. 16, KASENO & MATSUURA, 1965; massive silty fine sand., d) a cliff (36°33.6' N., 136°42.6' E.) same as Loc. 9, KASENO & MATSUURA, 1965; conglomeratic coarse sand., e) a cliff (36°34.1' N., 136°42.1' E.) of a branch of the Kinppu river, situated about 100 m SE of Higashi-Nagae, Kanazawa City, Ishikawa Pref.; massive medium sand., f) a cliff (36°34.7' N., 136°41.4' E.) same as Loc. 2, KASENO & MATSUURA, 1965; massive medium sand. The Pliocene Omma formation (KASENO & MATSUURA, 1965).
- 41a-g—**Mizunami**: a) a cliff (35°24.9' N., 137°19.3' E.) same as Loc. L15, ITOIGAWA,

1960; massive medium sandstone., b) a cliff (35°23.9' N., 137°14.8' E.) situated about 3.7 Km N12°W of Mizunami Station, Hongo, Mizunami City, Gifu Pref.; conglomeratic very coarse sandstone., c) a cliff (35°23.6' N., 137°16.9' E.) situated about 3.9 Km N38°E of Mizunami Station, Nataki, Mizunami City; conglomeratic very coarse sandstone., d) cliffs (35°23.6' N., 137°16.6' E.) situated about 3.5 Km N32°E of Mizunami Station, Dan, Mizunami City; conglomeratic very coarse sandstone., e) a cliff (35°22.5' N., 137°16.5' E.) same as Loc. S 45-5, ITOIGAWA, 1960; conglomeratic very coarse sandstone., f) a cliff (35°23.3' N., 137°12.8' E.) situated about 4.2 Km N37°E of Tokishi Station, Shizuhora, Toki City, Gifu Pref.; conglomeratic very coarse sandstone., g) a cliff (35°21' N., 137°12.7' E.) situated about 2.5 Km S72°E of Tokishi Station, Nakahida, Toki City; conglomeratic very coarse sandstone. The late Miocene Shukunohora sandstone of the Oidawara formation (ITOIGAWA, 1960).

42a-e—Atsumi: a) a cliff (34°39' N., 137°22' E.) same as Loc. 2, HAYASAKA, 1961; mud containing bank forming oyster (*Crassostrea gigas*); Pleistocene Akasawa siltstone (HAYASAKA, 1961)., b) a cliff (34°37.1' N., 137°14.7' E.) same as Loc. 139, HAYASAKA, 1961; conglomeratic medium sand., c) a cliff (34°37.1' N., 137°14.7' E.) same as Loc. 138, HAYASAKA, 1961; conglomeratic medium sand., d) a cliff (34°37.1' N., 137°14.8' E.) same as Loc. 137, HAYASAKA, 1961; conglomeratic medium sand., e) a cliff (34°14.8' N., 137°14.8' E.) same as Loc. 28, YAMAGUCHI, 1973. b-e) The Pleistocene Toshima sand (HAYASAKA, 1961).

43—Akashi: exact locality unknown, Akashi City, Hyogo Pref.; Pleistocene Maiko shell bed (SHIKAMA, 1936). Repository: Osaka City Museum Natural History.

44—Okinawa-jima Is.: a road-cut (26°40.4' N., 127°59.9' E.) situated about 500 m S20°E of Nakasone, Nakijin-son, Nago City, Okinawa Pref.; calcareous fine sand; Pleistocene Nakoshi sand.

#### 4. Evaluation of Morphological Characters

Before entering into discussion of systematics, some morphological characters of balanoids are taxonomically evaluated. Taxonomy based on an adequate evaluation of morphological characters at the species level may provide evidence of evolutionary processes, and contribute to the determination of higher categories.

##### Compartments

##### External surface of shell wall:

That the nature of external surface of shell wall is often affected by the microtopography of substratum has been shown in the following examples; living *B. porcatus* (= *B. balanus*), *B. crenatus* and *B. patellaris* (= *B. patelliformis*) (DARWIN, 1854a); living *B. rostratus apertus* and *B. balanus* (PILSBRY, 1916); *B. shilohensis* (PILSBRY, 1930); living *B. eburneus* and fossil *B. concavus* (GREGG, 1948), etc. In fossil of *B. rostratus* growing on *Chlamys nipponensis* and *Chirona (Chirona) evermanni* on *Chlamys islandicus*, external surfaces of shell walls have a fine relief which in effect is a replicate of ribs of the scallop. It is well known that the external surface of shell wall is also influenced by other ecological factors, such as population density (KATO, *et al.*, 1960a, b) and wave action.

*Solidobalanus (Hesperibalanus) hesperius nipponensis* was originally distinguished from *S. (H.) hesperius* s.s. by a smooth rather than ribbed external surface (PILSBRY, 1916). However, living Japanese specimens of *S. (H.) hesperius* growing on the same substratum show a wide range of individual variation; the external surface ranging from smooth to

ribbed (pl. 27\*, figs. 4, 5). Thus this morphological character can hardly be regarded as useful in distinguishing *S. (H.) hesperius* s.s. from *S. (H.) h. nipponensis*.

In conclusion, since the external surface of the shell wall may be modified by ecological factors, such as the nature of substratum, population density, etc., care must be taken in how this character is used in the classification of the barnacles.

#### *Radii:*

In his revision of the Tetraclitidae, it was emphasized by ROSS (1969) that the mode of shell growth is significant in taxonomy. Two modes of shell growth were distinguished in one family as follows: diametric shell growth (which produces enlargement of radii) and monometric shell growth (which does not induce enlargement of radii).

The summits of radii both in *Megabalanus rosa* and *M. volcano* as well as other members of "*Megabalanus tintinnabulum*" species group are nearly parallel to the base (YAMAGUCHI, 1973). But in a few species of *Megabalanus*, the summits are oblique. Therefore, this morphological character can't be a subgeneric character of this group.

In four living species of *B. amphitrite* species group from Japan, the nature of summits of radii ranges from horizontal to oblique, and the degree of inclination seems to reflect specific difference.

In conclusion, the width and nature of summits of radii are important character in taxonomy, but differences may or may not be useful above the species level.

#### *Internal structure of compartment* *Longitudinal tubes, transverse septa and subsidiary tubes:*

PILSBRY (1916) interpreted the mode of distribution of transverse septa in longitudinal tubes and the number of longitudinal tubes in rostrum as useful criteria in distinguishing subspecies of *B. rostratus*. However, PILSBRY's subspecific designations are not necessarily acceptable in the light of modern species concepts, because the entire range of diagnostic characters utilized are to be found within the population of Japanese *B. rostratus*. On the other hand, living Japanese *B. amphitrite* can be distinguished from three other species of *B. amphitrite* group by the absence of transverse septum in longitudinal tubes.

DARWIN (1854a) described that the longitudinal septa of *B. amphitrite* occasionally bifurcate at the base and make irregular minute tubes (subsidiary tubes). Subsequently, the presence of subsidiary tubes has been shown by following authors: in *B. amphitrite albicostatus* (= *B. albicostatus*) by PILSBRY (1916); in *B. pallidus pallidus* and *B. p. stutsburi* by HARDING (1962); in *B. pallidus*, *B. albicostatus albicostatus* (= *B. albicostatus*) and *B. a. formosanus* by UTINOMI (1967) and in *B. citerosum*, *B. suturaltus* and *B. dentivarians* of *B. amphitrite*-complex by HENRY (1973).

Taxonomic evaluation on the mode of distribution of transverse septa and number of longitudinal tubes should be made through the examination of individual and geographical variations. The absence of transverse septa and the presence of subsidiary tubes are considered to be important morphological characters for classification; especially the latter may represent a close relationship among species.

\*pls. 23-27 to be published in part 2.



*Nature of cavity between sheath and inner lamina:*

HENRY (1973) attached importance to the presence of calcareous vesicles filling the cavity between sheath and inner lamina, and pointed out that *B. citerosum*, *B. suturaltus*, *B. dentivarians*, *B. crenatus*, *B. glandula*, *Semibalanus cariosus* and *S. balanoides* possess calcareous vesicles. In living Japanese *B. amphitrite* species group, transverse septa (=calcareous vesicles) are developed in the cavity between sheath and inner lamina in *B. albicostatus* and *B. kondakovi*, but absent in *B. amphitrite* and *B. reticulatus*.

This morphological character also seems to be taxonomically important, although ecophenotypic variation needs to be examined.

*Opercular valves*

*Proportion of tergal and basal length of scutum:*

*Solidobalanus (Hesperibalanus) hesperius nipponensis* was distinguished from *S. (H.) hesperius* s. s. by a difference in the proportions of tergal and basal length of scuta (PILSBRY, 1916). The difference is, however, intrapopulational in Japan. Therefore, this character is not adopted as a criterion for subspecific distinction. On the other hand, in an examination of shell growth of living Japanese *B. amphitrite*, *B. albicostatus* and *B. reticulatus*, it was observed that growth of the tergal and basal margins of the scutum of *B. albicostatus* and *B. reticulatus* is isometric, but that in *B. amphitrite* it is allometric. Therefore, there are cases where the shape of scutum changes with age as well as with ecological factors.

*Ratio of the width of spur to the distance between basiscutal angle and anterior face of spur:*

Ratios of the width of spur to the basal margin have been noted in the systematic descriptions by some authors. But the extent of individual and geographical variations is rarely taken into consideration. Closely related species *Megabalanus rosa* and *M. volcano* are biometrically distinguished by the ratio of the width of spur and distance between basiscutal angle and anterior face of spur (YAMAGUCHI, 1973). On the other hand in three living species from Japan, *B. amphitrite*, *B. albicostatus* and *B. reticulatus* of *B. amphitrite* group, the ratio shows wide ranges of intra- and interpopulational variations which overlap each other.

In summary, these examples again illustrate that a particular morphological character may be important in some groups but not in others. The value of a character must be judged in each case. *Outline of basal margin of tergum:*

The nature of the basal margin of tergum of *Megabalanus rosa* is clearly different from that of *M. volcano* (YAMAGUCHI, 1973). HENRY (1973) regarded the nature of basal margin of tergum as a diagnostic character in the establishment of four new species in *B. amphitrite*-complex. In living *B. amphitrite*, *B. albicostatus*, *B. reticulatus* and *B. kondakovi* from Japan, the nature of basal margin is also important for the species level classification.

*Appendages*

*Number of segments in each cirrus:*

NEWMAN (1967) reported that *Tetrachthamalus oblittertus* [Chthamalidae] collected from three localities shows a narrow range of individual variation but a wide range of geographical variation in length and number of segments of exopodite of cirrus III. However, it has since been noted that the exopod of the

third cirrus ranges between normal and antenniform on a seasonal basis in the same population (NEWMAN, pers. com.).

YAMAGUCHI (1973) demonstrated that the range of the number of segments of cirri I to III in *Megabalanus rosa* and *M. volcano* show narrow ranges of individual and geographical variations, but those of cirri IV to VI show wide ranges of individual variations; those in the exopodite of cirrus I and in both rami of cirrus III are distinctly different between two species; and these differences aid in discriminating between species. In four living species of *B. amphitrite* group from Japan, the numbers of segments in cirri I to III show narrow ranges of individual variation, but they overlap each other to the degree that it is impossible to discriminate between these four species by this morphological character alone (Table 1).

Thus, taxonomical significance of this morphological character must be evaluated in accordance with individual, seasonal and geographical variations.

*Mandible:*

ROSS (1971) noted the mandible of *Tetraclitella karandei* [Tetraclitidae] differs from that of other species of this genus in the degree of development and number of subsidiary cusps of the second to fourth teeth. YAMAGUCHI (1973) demonstrated that the nature of the fourth and fifth teeth of mandible is clearly distinct between *Megabalanus rosa* and *M. volcano* and represents a specific character. On the other hand, four living species *B. amphitrite* group from Japan are difficult to separate by this morphological character. In summary, it is again difficult to generalize taxonomical importance of these morphological characters.

Applying the morphological evaluation

discussed above, it is possible to demonstrate various degrees of morphological divergence between related forms in balanoids of Japanese area. When the divergence is such that a significant gap appears between species groups, subgenera and genera may be formed. When the gap is recognizable, but not fully defined or substantiated, the complex can be refined as a species group. The following groups, occurring in Japanese waters, form basis of the present study.

“*Balanus amphitrite*” group (excluding *B. eburneus* and *B. improvisus*) is characterized by the followings: Shell wall externally with colored longitudinal stripes and sometimes with colored horizontal lines. External surface of scutum smooth and with weakly prominent growth lines. Adductor ridge of scutum weakly to strongly prominent but not very long; and sometimes with shallow pit below. Distal border of each proximal intermediate segment of cirrus III (frequently to VI) with several small spinules. The group includes the following closely related species: *B. amphitrite*, *B. albicostatus*, *B. reticulatus* and *B. kondakovi*.

“*Megabalanus tintinnabulum*” group is readily distinguishable from the other balanoids by the following characters: Parietes with longitudinal tubes and transverse septa. Rarii wide with tubes and their summits usually parallel to the base. Basis calcareous and tubiferous. Scutum with beaked apex and with broad basal border. Basal margin of tergum roughly straight on both sides of the spur. Intermediate segments of cirri III and IV with short spinules on the distal borders. The group includes two species, *M. rosa* and *M. volcano*.

*Solidobalanus (Hesperibalanus) hesperius* is mainly characterized by the following

Table 1. Number of segments in each right cirrus of *B. amphitrite*, *B. albicostatus*, *B. reticulatus* and *B. kondakovi*.

		rCI		rCII		rCIII		rCIV		rCV		rCVI	
		exo	end	exo	end	exo	end	exo	end	exo	end	exo	end
<i>B. amphitrite</i>	RA8274	23	13	16	13	16	16	31	34	32	33	35	34
	RA8365	21	12	15	12	15	14	29	29	33	33	35	36
	RA8370	21	12	14	11	14	14	—	—	35	37	36	37
	N	3	3	3	3	3	3	2	2	3	3	3	3
	OR	21-23	12-13	14-16	11-13	14-16	14-16	29-31	29-34	32-35	33-37	35-36	34-37
	$\bar{x}$	21.7	12.3	15.0	12.0	15.0	14.7	30.0	31.5	33.3	34.3	35.3	35.7
<i>B. albicostatus</i>	RA8275	23	13	14	12	16	12	26	29	24+	21+	24+	24+
	RA8366	17	13	13	13	16	12	26	28	28	29	25	24
	RA8371	19	13	15	13	17	17	33	35	32	38	39	40
	N	3	3	3	3	3	3	3	3	2	2	2	2
	OR	17-23	13	13-15	12-13	16-17	12-17	26-33	28-35	28-32	29-38	25-39	24-40
	$\bar{x}$	19.7	13	14.0	12.7	16.3	13.7	28.3	30.7	30.0	33.5	32.0	32.0
<i>B. reticulatus</i>	RA8276	23	15	18	16	19	17	33	32	33	36	36	37
	RA8367	19	13	15	12	16	13	29	32	33	34	37	38
	RA8372	20	12	16	13	17	16	26+	12+	—	—	36	34
	N	3	3	3	3	3	3	2	2	2	2	3	3
	OR	19-23	12-15	15-18	12-16	16-19	13-17	29-33	32	33	34-36	36-37	34-38
	$\bar{x}$	20.7	13.3	16.3	13.7	17.3	15.3	31.0	32.0	33.0	35.0	36.3	36.3
<i>B. kondakovi</i>	RA8362	17	13	13	12	18	17	31	33	34	22+	35	40
	RA8363	19	10	14	8+	19	16	30	38	44	35+	47	47
	RA8364	17	12	14+	13	18	16	34	30	43	42	46	45
	N	3	3	2	2	3	3	3	3	3	1	3	3
	OR	17-19	10-13	13-14	12-13	18-19	16-17	30-34	30-38	34-44	42	35-47	40-47
	$\bar{x}$	17.7	11.7	13.5	12.5	18.3	16.3	31.7	33.7	40.3	42	42.7	44.0

N: number of individuals examined. OR: observed range.  $\bar{x}$ : arithmetic mean. Locality: *B. amphitrite*, *B. albicostatus* and *B. reticulatus*; Loc. H. *B. kondakovi*; Kasaoka Bay, Okayama Pref., Coll. Dr. S. FUSE.

characters: Wall solid. Radii narrow with oblique summits and denticulated sutural edges. Scutum flat with weak growth ridges. Faint callus-like projections observable between articular and adductor ridges in some specimens. Tergum with wide spur. Crests for depressor muscle strongly developed.

*B. rostratus* may be a Japanese re-

presentative of *B. balanus* group of the Atlantic and is characterized by the followings: Shell with smooth external surface. Carinolaterals narrow. Rostrum well developed. Radii narrow with oblique summits. Scutum with prominent growth ridges and distinct longitudinal striations. Pit for adductor muscle weakly developed or hardly visible.

Tergum with wide and blunt spur.

*B. crenatus* may consist of several geographic races or subspecies and is characterized by the following characters: External surface of shell wall smooth. Raddi narrow with steeply oblique summits and denticulated sutural edges. Calcareous vesicles develop in the cavity between sheath and inner lamina. Scutum with very weak growth ridges. Articular ridge very prominent and reflexed. Adductor ridge very weak or hardly visible. Pit for adductor muscle deep.

In the following pages, the writer intends to evaluate the species level classification of some important groups of Japanese barnacles.

### 5. Revision of *Balanus* *amphitrite* group

*Necessity of a species revision of the B. amphitrite group*

*B. amphitrite* was originally described by DARWIN (1854a). He divided it into nine varieties. However, his descriptions are brief and incomplete. The type specimen, type-locality and "type" for variety were not designated by DARWIN.

After that, the following varieties, forma or subspecies were additionally described as infraspecific taxa of *B. amphitrite*.

- B. amphitrite* var. *malayensis* HOEK, 1913
- B. amphitrite* *albicostatus* PILSBRY, 1916

- B. amphitrite inexpectus* PILSBRY, 1916
- B. amphitrite peruvianus* PILSBRY, 1916
- B. amphitrite* forma *hawaiiensis* BROCH, 1922
- B. amphitrite* var. *acutus* WITHERS, 1924
- B. amphitrite* var. *denticulata* BROCH, 1927
- B. amphitrite* forma *poecilosculpta* BROCH, 1931
- B. amphitrite kriegeri* NILSSON-CANTELL, 1932
- B. amphitrite rafflesi* NILSSON-CANTELL, 1934
- B. amphitrite* forma *formosanus* HIRO, 1938
- B. amphitrite* var. *fluminensis* OLIVEIRA, 1941
- B. amphitrite* var. *aeratus* OLIVEIRA, 1941
- B. amphitrite litoralis* KOLOSVÁRY, 1948
- B. amphitrite abundantus* KOLOSVÁRY, 1948
- B. amphitrite archi-inexpectatus* KOLOSVÁRY, 1948
- B. amphitrite hungaricus* KOLOSVÁRY, 1948
- B. amphitrite helenae* KOLOSVÁRY, 1948
- B. amphitrite* var. *vladivostokensis* TARASOV and ZEVINA, 1957
- B. amphitrite* var. *columnaris* TARASOV and ZEVINA, 1957
- B. amphitrite* var. *kondakovi* TARASOV and ZEVINA, 1957
- B. amphitrite karakumiensis* KOLOSVÁRY, 1961
- B. amphitrite merklini* KOLOSVÁRY, 1962a
- B. amphitrite tongaensis* KOLOSVÁRY, 1962b

Recently, from a modern taxonomic standpoint, HARDING (1962) reexamined and redescribed the specimens which had been studied by DARWIN. HARDING allocated the taxonomic position of DARWIN's nine varieties of *B. amphitrite* in accordance with the degree of morphological difference, as shown in Table 2.

Table 2

DARWIN (1854 a)	HARDING (1962)
<i>B. amphitrite</i> var. <i>communis</i> .....	<i>B. amphitrite amphitrite</i> DARWIN
<i>B. amphitrite</i> var. <i>pallidus</i> .....	<i>B. pallidus pallidus</i> DARWIN
<i>B. amphitrite</i> var. <i>stutsburi</i> .....	<i>B. pallidus stutsburi</i> DARWIN
<i>B. amphitrite</i> var. <i>venustus</i> .....	<i>B. venustus venustus</i> DARWIN
<i>B. amphitrite</i> var. <i>niveus</i> .....	<i>B. venustus niveus</i> DARWIN
<i>B. amphitrite</i> var. <i>modestus</i> .....	<i>B. venustus modestus</i> DARWIN
<i>B. amphitrite</i> var. <i>obscurus</i> .....	<i>B. venustus obscurus</i> DARWIN
<i>B. amphitrite</i> var. <i>variegatus</i> .....	<i>B. variegatus</i> DARWIN
<i>B. amphitrite</i> var. <i>cirratus</i> .....	<i>B. variegatus</i> var. <i>cirratus</i> DARWIN

Table 3

HIRO (1938)	UTINOMI (1967)
<i>B. a.</i> forma <i>communis</i> DARWIN	<i>B. reticulatus</i> UTINOMI
<i>B. c.</i> forma <i>cirratus</i> DARWIN	<i>B. variegatus cirratus</i> DARWIN
<i>B. a.</i> forma <i>poecilotheca</i> KRÜGER	<i>B. poecilotheca</i> KRÜGER
<i>B. a.</i> forma <i>albicostatus</i> PILSBRY	<i>B. albicostatus albicostatus</i> PILSBRY
<i>B. a.</i> forma <i>hawaiiensis</i> BROCH	<i>B. amphitrite</i> DARWIN sensu HARDING
<i>B. a.</i> forma <i>krügeri</i> NILSSON-CANTELL	<i>B. uliginosus</i> UTINOMI
<i>B. a.</i> forma <i>formosanus</i> HIRO	<i>B. albicostatus formosanus</i> HIRO

UTINOMI (1967) also revised his (1938) seven forms *B. amphitrite* from Japanese and its adjacent waters, as shown in Table 3.

HARDING (1962) and UTINOMI (1967) proposed their classifications for this species group mainly on the basis of degree of morphological difference. Other criteria, at the species level, were in general not utilized in the classification. Therefore, a reexamination of *B. amphitrite* group from biological standpoint could be of value.

#### Taxonomic problems concerning the Japanese *B. amphitrite* group

Excluding species from Formosa in UTINOMI's (1967) list, there are six species of *B. amphitrite* group described from Japanese waters.

*B. poecilotheca* was described by KRÜGER (1911a) from Okinose Bank, Sagami Bay. HIRO (1938) once placed this species in *B. amphitrite* group and called *B. a.* forma *poecilotheca*, but in his 1967's paper, he excluded this species from his list of *B. amphitrite* complex.

Occurrence of *B. amphitrite* forma *cirratus* from Iki Is. and Ariake Bay was reported first by HIRO (1938). This form was later called *B. variegatus* var. *cirratus* by HARDING (1962) and *B. variegatus cirratus* by UTINOMI (1967). Thus it seems necessary to clarify the relation between *B. variegatus variegatus* and *B.*

*variegatus* var. *cirratus*; are they mere variations of one species or are they representatives of two geographically definable subspecies. Unfortunately this species is too rare in Japanese waters to ascertain its taxonomic status.

*B. albicostatus* and *B. uliginosus* (= *B. kondakovi*) present no taxonomic problem (UTINOMI, 1970; HENRY and MCLAUGHLIN, 1975).

In order to clarify the taxonomic status of *B. amphitrite* and *B. reticulatus*, it is necessary to examine descriptions, and illustrations of both DARWIN (1854a) and HARDING (1962) in some detail.

HARDING (1962) examined the specimens of *B. amphitrite* which was originally described by DARWIN (1854a). The majority of DARWIN's specimens are incompletely preserved, and their localities in many cases unknown. However, HARDING found many complete individuals of *communis* and *venustus* together on a single bamboo fragment from Natal. These specimens are accompanied with handwriting of DARWIN as *B. amphitrite*. In fact, as pointed by HARDING (1962), DARWIN (1854a, p. 246) had described *B. a.* var. *venustus* and *B. a.* var. *communis* from Natal. Among the *communis* on the bamboo, a complete specimen was selected as the lectotype of *B. amphitrite* by HARDING, because the type specimens of *B. amphitrite* had not yet been designated by DARWIN and

later authors. Thus, *B. a. var. communis* of DARWIN (1854a) was designated as *B. a. amphitrite* by HARDING (1962).

UTINOMI (1967) interpreted that the illustrated specimen of *B. a. var. communis* (DARWIN, 1854a, pl. 5, figs. 2e, 2h and 2l) differed morphologically from the lectotype of *B. a. amphitrite* (HARDING, 1962, pl. 1, figs. a-h), and that the difference deserves specific distinction. Therefore, he gave a new specific name *B. reticulatus* to the former.

Now it becomes necessary to reexamine the figures and descriptions of both DARWIN and HARDING to find out whether *B. a. var. communis* of DARWIN and *B. a. amphitrite* described by HARDING are conspecific with each other or different species.

DARWIN's (1854a, p. 240) description of the radii and tergum of *B. a. var. communis* can be summarized as follows: 1) Summits of radii oblique or nearly parallel to the base; 2) basal shape of spur square or bluntly pointed. DARWIN illustrated a specimen which is characterized by the oblique summits of radii and the bluntly pointed basal shape of spur (DARWIN, 1854a, pl. 5, figs. 2e, 2h and 2l). DARWIN did not describe any more details about radii and tergum.

HARDING's (1962, p. 277, 278) description of the radii and tergum of *B. a. amphitrite* can also be summarized as follows: 1) Summits of radii in specimens including the lectotype (pl. 1, figs. a-b) are almost parallel to the base, but in some other specimens more oblique; 2) many specimens labelled by DARWIN as *B. a. var. communis*, which were later called *B. a. amphitrite* by HARDING, have short and wider spur, but one or two individuals have such narrow spur as DARWIN's figure (pl. 5, fig. 2l).

Now it is obvious from the DARWIN's and HARDING's descriptions that there

exist two distinct forms in one species. One is characterized by the oblique summits of radii and a narrow spur of tergum, the other has the summits of radii which are parallel to the base and wider spur of tergum.

Although DARWIN and HARDING interpreted these morphological difference as infraspecific, UTINOMI (1967) considered these differences as interspecific.

The writer interpreted from the DARWIN's figures (pl. 5, figs. 2e, 2h and 2l) that *B. a. var. communis* carries the following morphological characters in addition to the characters already described by DARWIN and HARDING: Wider distance between anterior face of spur and basiscutal angle than width of spur; slightly concave basal margin at carinal side of spur in tergum.

From the figures (HARDING, 1962, pl. 1, figs. e-f) of the lectotype of *B. a. amphitrite*, the tergum of *B. a. amphitrite* can be characterized by the followings: Distance between anterior face of spur and basiscutal angle approximately half width of spur; basal margin both sides of spur straight. Therefore, the illustrated figures (DARWIN, 1854a, pl. 5, figs. 2e, 2h and 2l) of *B. a. var. communis* DARWIN is clearly different from those (pl. 1, figs. a-f) of HARDING's lectotype of *B. a. amphitrite* in the nature of summits of radii, width, shape and position of spur of tergum.

Thus it appears that the two forms are different species, as was pointed out by UTINOMI (1967) and confirmed by SOUTHWARD (1975), by HENRY and MC-LAUGHLIN (1975), and by the present investigation. The form characterized by a oblique summits of radii and a narrow spur is *B. reticulatus*.

*Comparison of morphological characters of the B. amphitrite group of Japan*

In order to evaluate the conclusions based on the literature survey explained in the foregoing lines, the morphology of the Japanese specimens will be examined systematically.

#### Shell wall

##### 1) Nature of external ornamentation, color and stripes of shell wall

In *B. amphitrite*, *B. reticulatus* and *B. kondakovi*, the external surface of shell wall is smooth with coloration of longitudinal stripes. Each stripe is always found between two adjacent primary longitudinal septa.

In *B. amphitrite* (pl. 19, figs. 1a-b, 2a-h), the ground color of the shell is dirty white, and the color of stripes is grayish blue to purplish blue or reddish purple. The colored stripes are found on all the external surface except the central trapezoidal areas of rostrum and lateral compartments.

In *B. reticulatus* (pl. 19, figs. 5a-b, 5g-n), the ground color of shell wall is dirty white to gray, light purplish red or purplish red. These longitudinal colored stripes are intersected by white or colored horizontal stripes.

In *B. kondakovi* (pl. 19, figs. 6a-b, 7a-h), the ground color of shell wall is dirty white. The stripes are purple, or reddish to bluish purple. These longitudinal colored stripes are occasionally intersected by white horizontal stripes.

In *B. albicostatus* (pl. 19, figs. 3a-b, 4a-h), the external surface of shell wall has white longitudinal ribs, which are variable in length and width and always correspond to primary longitudinal septa. But the septa do not always correspond to the ribs. The ground color of shell is purple, reddish purple or violet.

##### 2) Radii and their summits

In *B. amphitrite*, the radii are well developed, and their summits are approximately parallel to the base. In *B.*

*albicostatus* and *B. reticulatus*, the radii are moderately developed, but their summits are oblique to the base. In *B. kondakovi*, the radii are narrow and their summits are steeply oblique to the base.

#### 3) Shell structure

##### a) Longitudinal tubes (Text-fig. 2)

In *B. amphitrite* (pl. 20, figs. 5, 9a-d), the longitudinal tubes have no transverse septum. The longitudinal tubes in *B. albicostatus* (pl. 20, figs. 6, 10a-d), *B. kondakovi* (pl. 20, figs. 8, 12a-d) and *B. reticulatus* (pl. 20, figs. 7, 11a-d) have transverse septa which are parallel to the base. However, the transverse septa of the first two species are arranged regularly, while in the last they are irregularly spaced.

##### b) Subsidiary tubes (Text-fig. 2)

In *B. albicostatus* (pl. 20, fig. 2), each of the longitudinal tubes is very often accompanied by small (subsidiary) tubes. They are formed by secondary longitudinal septum which projects from the outer lamina and join to the wall of the primary longitudinal septum.

In *B. amphitrite* (pl. 20, fig. 1), *B. reticulatus* (pl. 20, fig. 3) and *B. kondakovi* (pl. 20, fig. 4), no subsidiary tubes are found.

##### c) Cavity between sheath and inner lamina

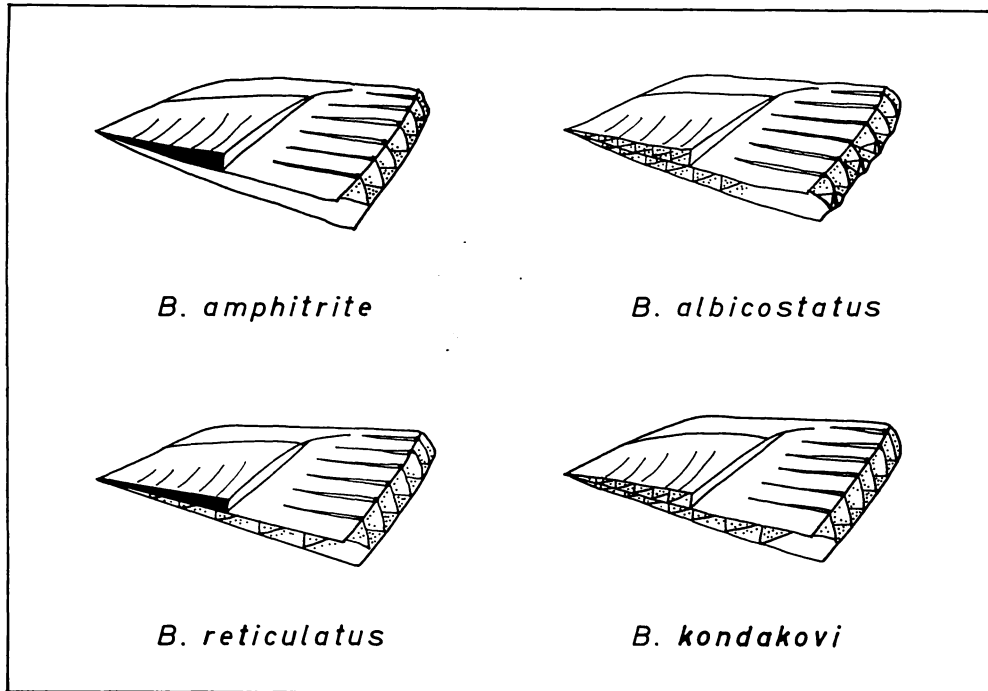
In *B. amphitrite* (pl. 20, fig. 5) and *B. reticulatus* (pl. 20, fig. 7), the cavity between sheath and inner lamina is filled up by calcareous matter, while those of *B. albicostatus* (pl. 20, fig. 6) and *B. kondakovi* (pl. 20, fig. 8) have calcareous vesicles.

#### Opercular valve

##### 1) Scutum

##### a) Adductor ridge

The adductor ridge of *B. amphitrite* (pl. 19, fig. 1d), *B. reticulatus* (pl. 19, fig. 5d) and *B. kondakovi* (pl. 19, fig. 6d)



Text-fig. 2. Schematic profiles of compartments of *B. amphitrite*, *B. albicostatus*, *B. reticulatus* and *B. kondakovi*.

slopes towards the occludent margin. However, that of *B. albicostatus* (pl. 19, fig. 3d) projects subvertically from the inner surface of scutum.

## 2) Tergum

### a) Spur

In *B. amphitrite* (pl. 19, figs. 1e-f), the spur is wide, and squarish at the end. The spur of *B. albicostatus* (pl. 19, figs. 3e-f) is narrow and obliquely truncated at the end. The spur of *B. reticulatus* (pl. 19, figs. 5e-f) is moderately wide but becomes narrow toward the end and rounded or obliquely truncated at the extremity. The spur of *B. kondakovi* (pl. 19, figs. 6e-f) is narrow, becomes narrower toward the end and is sharply pointed at the extremity.

### b) Basal margin of tergum

In *B. amphitrite*, the basal margin at

the scutal side of spur is straight, and at the carinal side of spur it is straight or slightly concave. In *B. albicostatus*, the basal margin at the carinal side of spur is slightly concave. The basal margin of both sides of spur of *B. reticulatus* is approximately straight. The basal margin at the carinal side of spur of *B. kondakovi* is deeply notched.

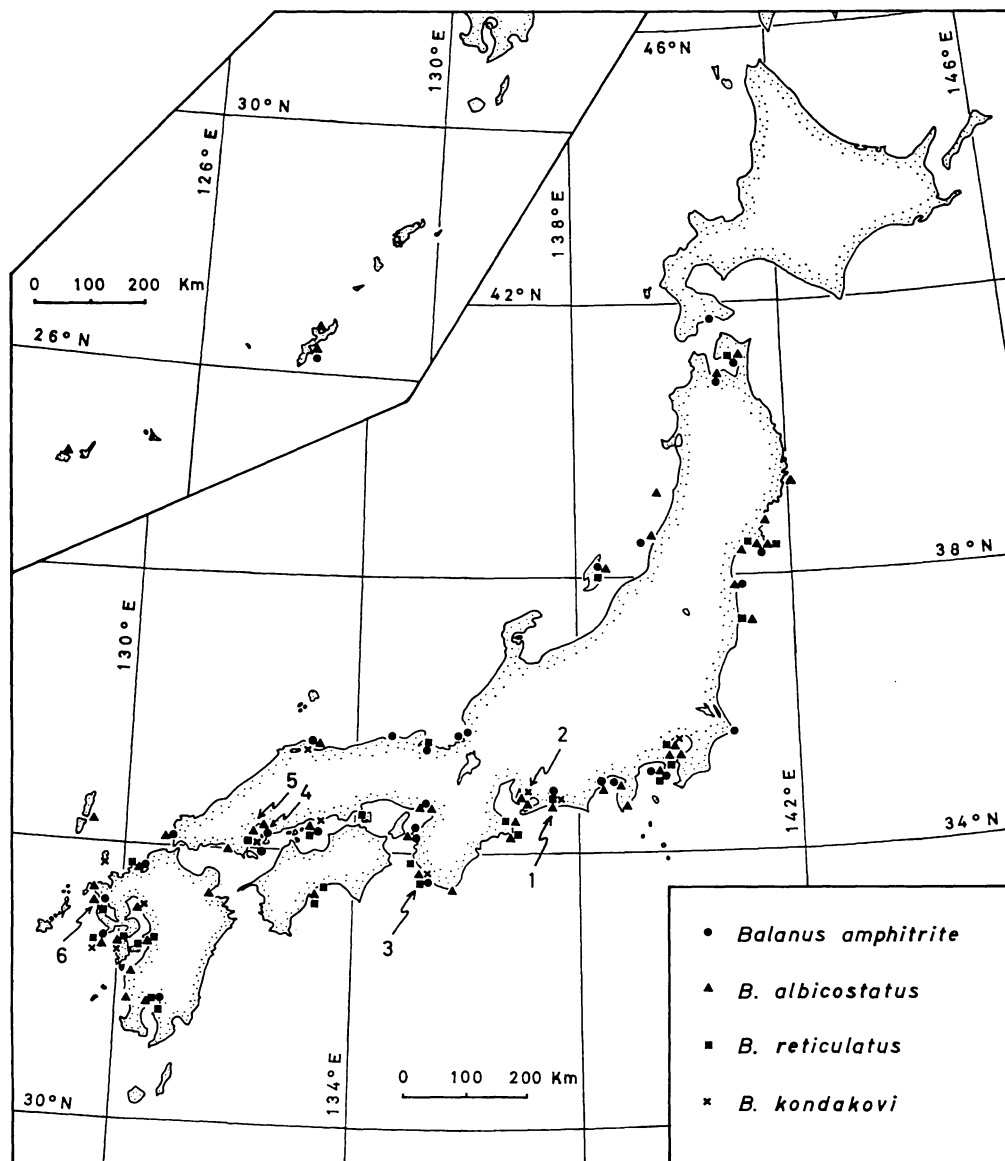
## Animal parts

### 1) Cirri

#### a) Nature of anterior faces of cirri III and IV

In *B. amphitrite* (pl. 21, figs. 1b-c), the exopodite of cirrus III is provided with many short and blunt spines (hook-like spines) on the anterior face of each segment, but exopodite of cirrus IV has a few short and fine spinules instead.





Text-fig. 3. Distribution of *B. amphitrite*, *B. albicostatus*, *B. reticulatus* and *B. kondakovi* in the Recent sea. [Compiled from ARAKAWA; 1973, HIRO; 1933, 1939a, b, IGA; 1973, MAWATARI; 1967, MAWATARI and KOBAYASHI; 1954a, b, MIZUNO, HARADA and MIZUNO; 1964, TOYOSIMA and IRIE; 1962, UTINOMI; 1949, 1955, 1962, 1970, UTINOMI and KIKUCHI; 1966, YAMAGUCHI; 1972MS, 1974MS, YAMAMURA; 1971, YAMAMURA, KUWATANI and NISHII; 1969]. 1. Hamana Lake, 2. Mikawa Bay, 3. Tanabe Bay, 4. Kure, 5. Hiroshima Bay, 6. Sasebo.

In *B. albicostatus* (pl. 21, figs. 2b-c), spinules on the anterior face of each segment of the exopodite of cirri III and IV become obscure. The exopodite of cirri III and IV of *B. reticulatus* (pl. 21, figs. 3b-c) has dense short spinules at the anterior face of each segment, while in *B. kondakovi* (pl. 21, figs. 4b-c) it has a few short spinules near the anterodistal corner of each segment.

#### 2) Labrum

The labrum of *B. amphitrite* (pl. 21, fig. 1a) has 11 or more teeth, while the labrum of *B. albicostatus* (pl. 21, fig. 2a), *B. reticulatus* (pl. 21, fig. 3a) and *B. kondakovi* (pl. 21, fig. 4a) has only 3 or 4 teeth on both sides of the labrum notch.

In conclusion, four species discussed above are morphologically distinct from each other. Degree of morphological difference between the three species, *B. amphitrite*, *B. reticulatus* and *B. kondakovi*, seems similar. *B. albicostatus*, however, seems different from the above three species in having characteristic ornamentation and shell structure.

#### Distribution

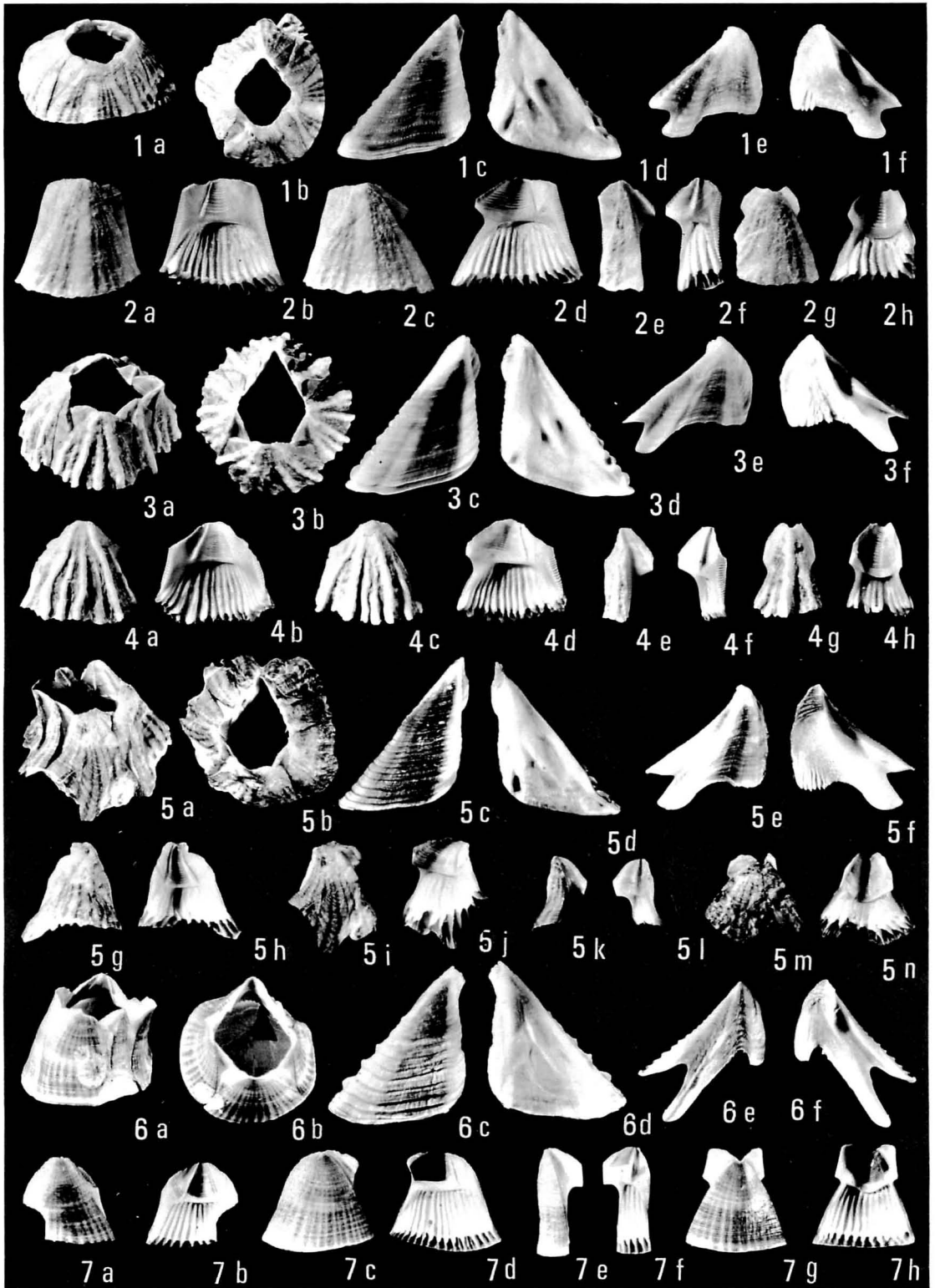
A conclusion is that in general in the Japanese waters, the four species occur in macrogeographically sympatric relationship. Now it becomes important to examine whether or not this macrogeographical sympatry includes physical contact between species.

Members of the *B. amphitrite* group

### Explanation of Plate 19

- Fig. 1. *Balanus amphitrite* DARWIN (UMUT-RA8263) from Tanabe Bay (Loc. H). 1a-b. whole wall,  $\times 2.$ , 1c-d. exterior and interior views of right scutum,  $\times 6.$ , 1e-f. exterior and interior views of right tergum,  $\times 6.$
- Fig. 2. *Balanus amphitrite* DARWIN (UMUT-RA8264) from Tanabe Bay (Loc. H). 2a-b. exterior and interior views of rostrum,  $\times 2.5.$ , 2c-d. exterior and interior views of left lateral,  $\times 2.5.$ , 2e-f. exterior and interior views of left carinolateral,  $\times 2.5.$ , 2g-h. exterior and interior views of carina,  $\times 2.5.$
- Fig. 3. *Balanus albicostatus* PILSBRY (UMUT-RA8265) from Tanabe Bay (Loc. H). 3a-b. whole wall,  $\times 2.$ , 3c-d. exterior and interior views of right scutum,  $\times 5.$ , 3e-f. exterior and interior views of right tergum,  $\times 5.$
- Fig. 4. *Balanus albicostatus* PILSBRY (UMUT-RA8266) from Tanabe Bay (Loc. H). 4a-b. exterior and interior views of rostrum,  $\times 2.$ , 4c-d. exterior and interior views of left lateral,  $\times 2.$ , 4e-f. exterior and interior views of carinolateral,  $\times 2.$ , 4g-h. exterior and interior views of carina,  $\times 2.$
- Fig. 5. *Balanus reticulatus* UTINOMI (UMUT-RA8267) from Tanabe Bay (Loc. H). 5a-b. whole wall,  $\times 1.5.$ , 5c-d. exterior and interior views of right scutum,  $\times 4.$ , 5e-f. exterior and interior views of right tergum,  $\times 4.$ , 5g-h. exterior and interior views of rostrum,  $\times 1.5.$ , 5i-j. exterior and interior views of left lateral,  $\times 1.5.$ , 5k-l. exterior and interior views of left carinolateral,  $\times 1.5.$ , 5m-n. exterior and interior views of carina,  $\times 1.5.$
- Fig. 6. *Balanus kondakovi* TARASOV and ZEVINA (UMUT-RA8268) from Hamana Lake (Loc. G). 6a-b. whole wall,  $\times 1.5.$ , 6c-d. exterior and interior views of right scutum,  $\times 4.$ , 6e-f. exterior and interior views of right tergum,  $\times 4.$
- Fig. 7. *Balanus kondakovi* TARASOV and ZEVINA (UMUT-RA8269) from Hamana Lake (Loc. G). 7a-b. exterior and interior views of rostrum,  $\times 1.5.$ , 7c-d. exterior and interior views of left carinolateral,  $\times 1.5.$ , 7g-h. exterior and interior views of carina,  $\times 1.5.$

[Descriptions to be published in Part 2]



are all warm water inhabitants. Their geographical range extends from south-east Asia to the Japanese coast.

The northern limit of distribution of *B. amphitrite*, *B. albicostatus* and *B. reticulatus* is the Tsugaru Strait, but that of *B. kondakovi* is Tokyo Bay on the Pacific side and Nakanoumi Lake on the Japan Sea side. The first three species are widely distributed throughout the Japanese coast, but the last scattered.

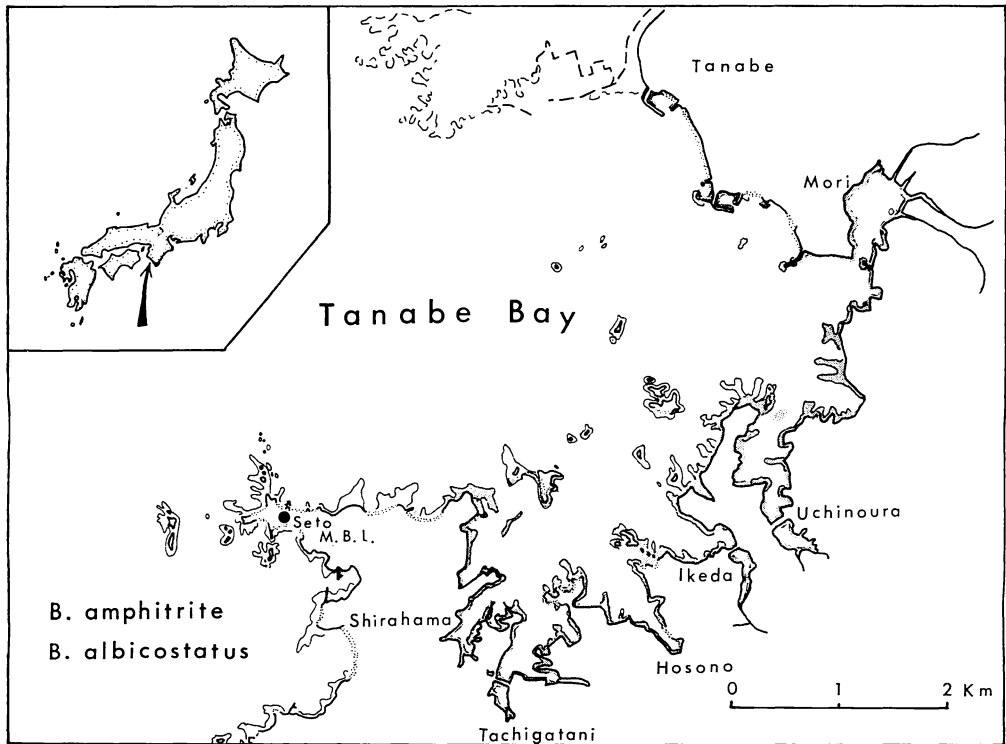
*B. amphitrite*, *B. albicostatus* and *B. reticulatus* have been reported from the same general area at the following localities: Ominato, Mutsu Bay (HIRO, 1938, 1939b); Aburatsubo Bay, Misaki, Kanagawa Pref.; Mukaishima Is., Hiroshima Pref.; Kagoshima, Kagoshima Pref.; Nomosaki Penin. (UTINOMI, 1962)

and Sasebo Bay, Nagasaki Pref.; Hakata Bay, Fukuoka Pref. (HIRO, 1938; UTINOMI, 1970). *B. kondakovi* was reported, together with the above three species, from the same general area at the following localities: Hamana, Lake, Shizuoka Pref.; Mikawa Bay, Aichi Pref.; Tanabe Bay, Shirahama (HIRO, 1937, 1938; UTINOMI, 1967); Hiroshima Bay, Hiroshima Pref. (ARAKAWA, 1973).

The distribution of this species group so far known in Japan is summarized in Text-figure 3.

#### Habitat

The writer had an opportunity, in March to April, 1974, to observe the habitat at Tanabe Bay (Text-figs. 4 and 5), where four species, *B. amphitrite*, *B.*



Text-fig. 4. Distribution of *B. amphitrite* and *B. albicostatus* in Tanabe Bay.

*albicostatus*, *B. reticulatus* and *B. kondakovi* had been reported to occur by UTINOMI (1967).

*B. amphitrite* and *B. albicostatus* were found side by side and widely distributed from the lower to upper levels of intertidal zone in the inner bay. The upper part of the *B. amphitrite* and *B. albicostatus* zone overlaps the lower part of the *Chthamalus challengerii* zone of the uppermost intertide. They are, however, especially abundant in the middle level. Less commonly, these two species are also found 1) on the rocky shore of the middle to lower tidal zone facing the open sea, but not where there is strong wave action, 2) in the estuarine regions temporarily influenced by fresh water at the lower tide, and 3) attached to buoys and other floating objects in the inner bay.

*B. reticulatus* is mainly found on floating objects, but sometimes in the

lower level of intertidal zone of rocky shores. On rocky shores, however, this species is rather rare in comparison with *B. albicostatus* and *B. amphitrite*. Therefore, in the lower intertidal zone of Tanabe Bay, *B. amphitrite*, *B. albicostatus* and *B. reticulatus* are found side by side, a sympatric relationship in microgeographical sense. The same relationship was detected in Yokohama and Aburatsubo, Kanagawa Pref.; Heta and Hamana Lake, Shizuoka Pref.; Mukai-shima Is., Kure harbor and Kurahashi-jima Is., Hiroshima Pref.; Kagoshima Bay, Kagoshima Pref.; Tomioka, Amakusa Is., Kumamoto Pref.; Sasebo Bay, Nagasaki Pref.

Another species, *B. kondakovi*, was reported from the Tachigatani Inlet in the Tanabe Bay by UTINOMI (1967). At Tachigatani Inlet, *B. amphitrite*, *B. albicostatus* and *B. reticulatus* were common, but the writer was unable to

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#### Explanation of Plate 20

(Figs. 1-4. anterior view of rostrum)

- Fig. 1. *Balanus amphitrite* DARWIN (UMUT-RA8264) from Tanabe Bay (Loc. H),  $\times 5$ .  
 Fig. 2. *Balanus albicostatus* PILSBRY (UMUT-RA8266) from Tanabe Bay (Loc. H),  $\times 5$ .  
 Fig. 3. *Balanus reticulatus* UTINOMI (UMUT-RA8267) from Tanabe Bay (Loc. H),  $\times 2$ .  
 Fig. 4. *Balanus kondakovi* TARASOV and ZEVINA (UMUT-RA8269) from Hamana Lake (Loc. G),  $\times 4$ .

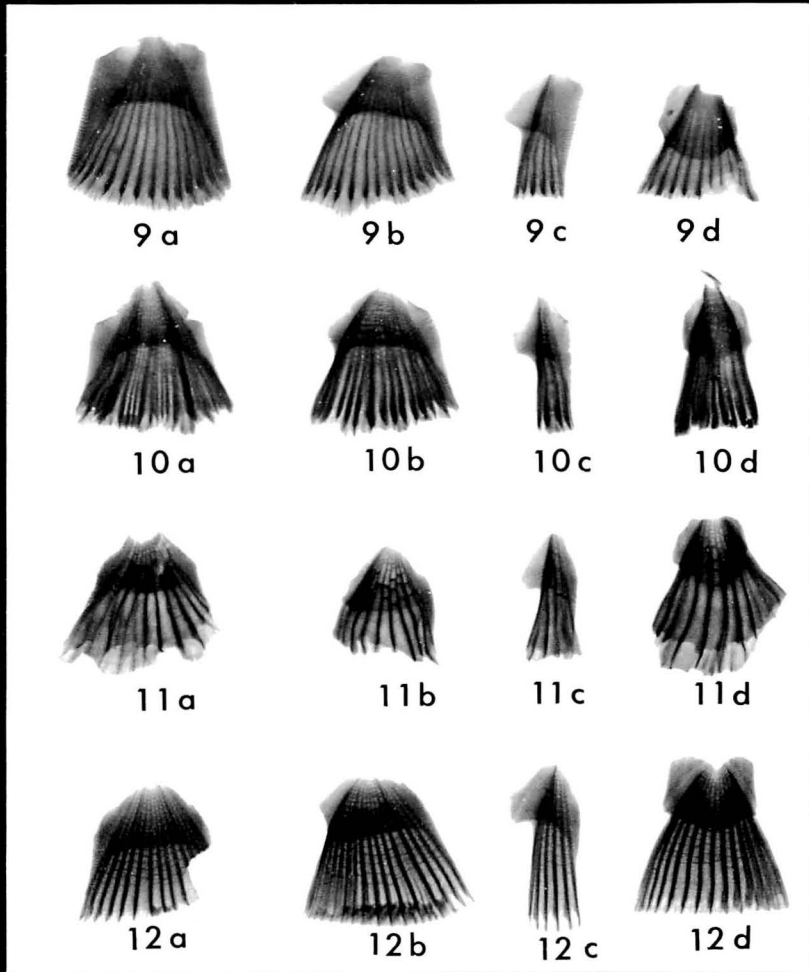
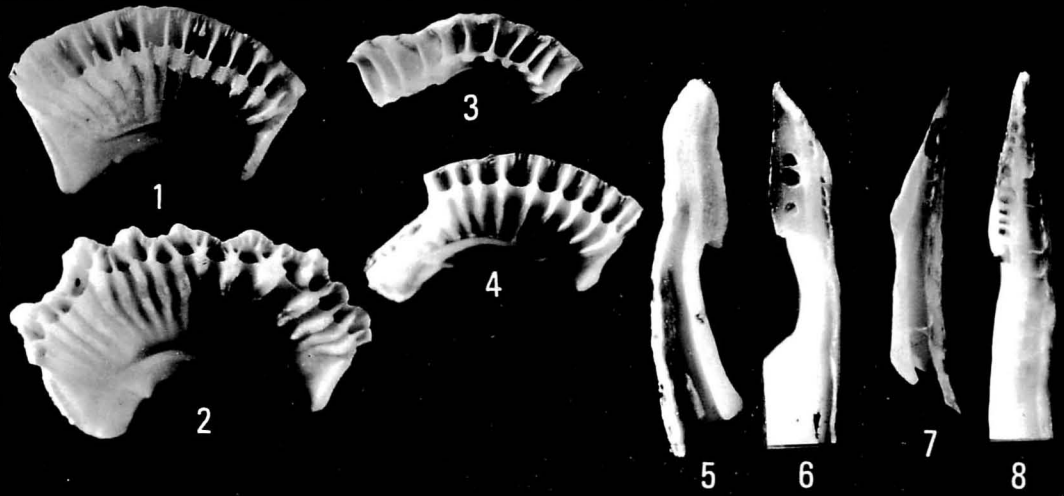
(Figs. 5-8. longitudinal section)

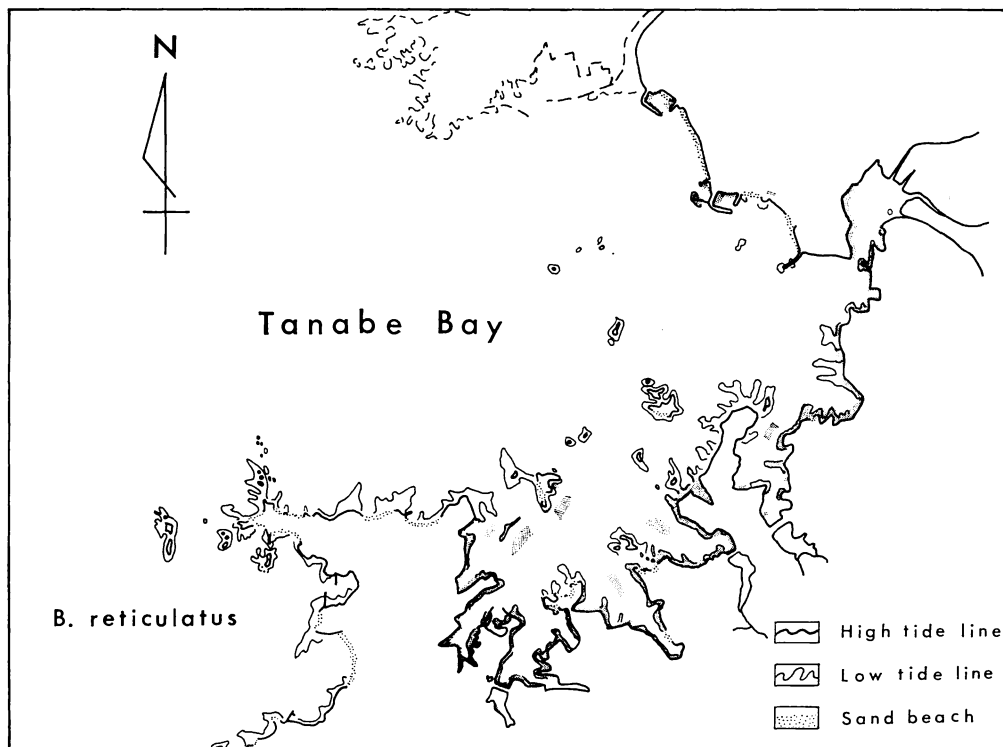
- Fig. 5. *Balanus amphitrite* DARWIN (UMUT-RA8270) from Tanabe Bay (Loc. H), rostrum,  $\times 6$ .  
 Fig. 6. *Balanus albicostatus* PILSBRY (UMUT-RA8271) from Tanabe Bay (Loc. H), right lateral,  $\times 5$ .  
 Fig. 7. *Balanus reticulatus* UTINOMI (UMUT-RA8272) from Tanabe Bay (Loc. H), right lateral,  $\times 4$ .  
 Fig. 8. *Balanus kondakovi* TARASOV and ZEVINA (UMUT-RA8273) from Hamana Lake (Loc. G), right lateral,  $\times 6$ .

(Figs. 9-12. photo by soft x-ray. a. rostrum, b. right lateral, c. right carinolateral, d. carina)

- Fig. 9. *Balanus amphitrite* DARWIN (UMUT-RA8274) from Tanabe Bay (Loc. H),  $\times 3$ .  
 Fig. 10. *Balanus albicostatus* PILSBRY (UMUT-RA8275) from Tanabe Bay (Loc. H),  $\times 2$ .  
 Fig. 11. *Balanus reticulatus* UTINOMI (UMUT-RA8276) from Tanabe Bay (Loc. H),  $\times 1.5$ .  
 Fig. 12. *Balanus kondakovi* TARASOV and ZEVINA (UMUT-RA8269) from Hamana Lake (Loc. G),  $\times 2$ .

[Description to be published in Part 2]



Text-fig. 5. Distribution of *B. reticulatus* in Tanabe Bay.

find *B. kondakovi* on the rocky shore, floating objects or piles there.

In Hiroshima Bay, four species, *B. amphitrite*, *B. albicostatus*, *B. reticulatus* and *B. kondakovi*, were found together on the cultured oyster (*Crassostrea gigas*) (ARAKAWA, 1973). The writer found an association between *B. kondakovi* and *B. albicostatus* near Yanagawa, Saga Pref., in Ariake Bay, and between *B. kondakovi*, *B. amphitrite* and *B. reticulatus* in Hamana Lake, in both cases on the stakes of bamboo. *B. kondakovi* is generally not found on rocky shores, but rather on piles, oysters and stems of plants etc., in the innermost part of the bay. *B. kondakovi* may be ecologically different from three other species.

In conclusion, the distribution of *B.*

*kondakovi* does not completely coincide with that of the other three species in geographic sense, and the range of *B. reticulatus* does not completely agree with that of *B. amphitrite* and *B. albicostatus* in vertical sense. However, a strictly sympatric relation between these four species of *B. amphitrite* group can be observed not only in the Tanabe Bay but also at many other localities in Japan. Therefore, geographical variation (subspecies) and/or ecophenotypic effect do not explain the morphological differences. It is clear these four taxa are distinct at the species level.

#### *Mechanisms of reproductive isolation*

Because of the definition of species (MAYR, 1963), reproductive isolation is

the most important criterion for the discrimination at the species level. Species of superfamily Balanoidea are hermaphrodites, with the exception of four species of commensal forms (HENRY and McLAUGHLIN, 1967; McLAUGHLIN and HENRY, 1972) which have complementary male. Though there are some evidences of self-fertilization (CRISP, 1954; BARNES and CRISP, 1956; BARNES and BARNES, 1958, etc), method of reproduction of hermaphrodite is in general cross fertilization. Fertilized eggs hatch into nauplius larvae and are kept in the mantle cavity of adult individual until the larvae reach a certain developmental stage. Therefore, the period when mature eggs or nauplius larvae are found in the mantle cavity of adults may be regarded roughly as breeding season. Whether or not the eggs attain the mature stage can be judged by the darkness in color of eggs. The difference in breeding seasons of closely related species *Megabalanus rosa* and *M. volcano*, which had been previously treated as two subspecies of *M. tintinnabulum*, were interpreted as a possible mechanism of reproductive isolation

(YAMAGUCHI, 1973). In fact, the breeding season of *M. rosa* is in March to May (Spring) when the water temperature begin to rise, while that of *M. volcano* corresponds to the period of maximum water temperature in July to October (Summer to Autumn).

Reproductive seasons of members of the *B. amphitrite* group in Japan has not yet been sufficiently examined. However, nauplius and cyprid larvae of *B. amphitrite* and *B. albicostatus* were reared in the following seasons: May to August (*B. albicostatus*) at Misaki by ISHIDA and YASUGI (1937), July to September (*B. amphitrite*) at Akiho, Yamaguchi Pref. by HUDINAGA and KASAHARA (1942). Larval settlements of *B. amphitrite*, *B. albicostatus* and *B. reticulatus* were observed in the following seasons: April to December (*B. reticulatus*) by MAWATARI and KOBAYASHI (1954a, b), May to November (*B. amphitrite* and *B. reticulatus*) by YAMAMURA, KUWATANI and NISHII (1969), April to December by YAMAMURA (1972). All the above three observations made at Ago Bay agreed that the larval settlements of three species

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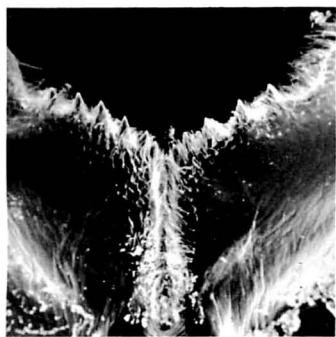
#### Explanation of Plate 21

(Photo by scanning electron microscope (SEM).)

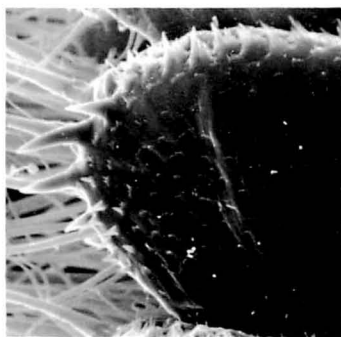
- Fig. 1. *Balanus amphitrite* DARWIN from Tanabe Bay (Loc. H). 1a. labrum, av.,  $\times 100.$ , 1b. 8th segment of right cirrus III, lv.,  $\times 300.$ , 1c. 8th segment of right cirrus IV, lv.,  $\times 250.$
- Fig. 2. *Balanus albicostatus* PILSBRY from Tanabe Bay (Loc. H). 2a. labrum, av.,  $\times 100.$ , 2b. 8th segment of right cirrus III, lv.,  $\times 200.$ , 2c. 10th segment of right cirrus IV, lv.,  $\times 300.$
- Fig. 3. *Balanus reticulatus* UTINOMI from Tanabe Bay (Loc. H). 3a. labrum, av.,  $\times 100.$ , 3b. 8th segment of right cirrus III, lv.,  $\times 200.$ , 3c. 10th segment of right cirrus IV, lv.,  $\times 300.$
- Fig. 4. *Balanus kondakovi* TARASOV and ZEVINA from Kasaoka Bay, Okayama Pref. 4a. labrum, av.,  $\times 100.$ , 4b. 12th segment of right cirrus III, lv.,  $\times 250.$ , 4c. 11th segment of right cirrus IV, lv.,  $\times 250.$

[Description to be published in Part 2]

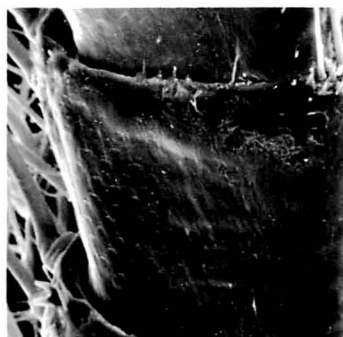




1a



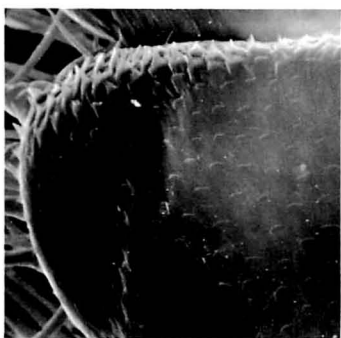
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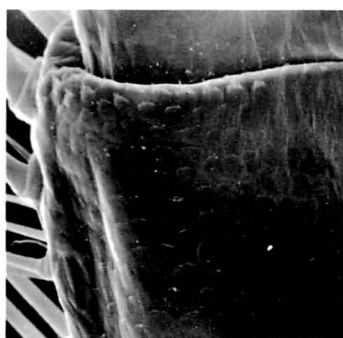
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2a



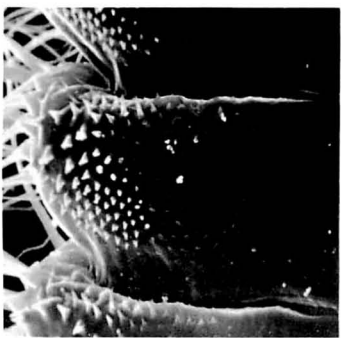
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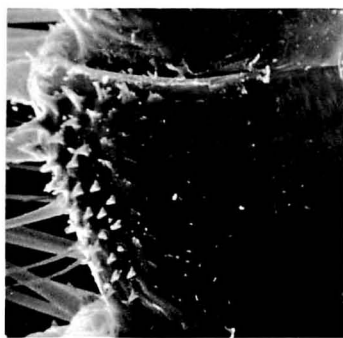
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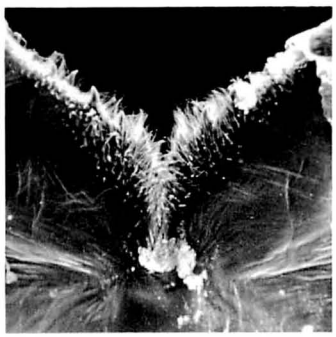
3a



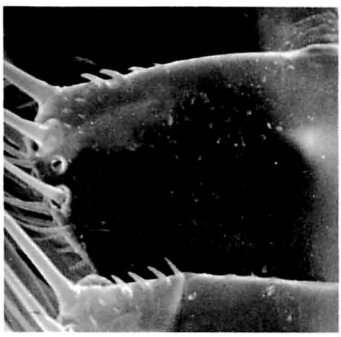
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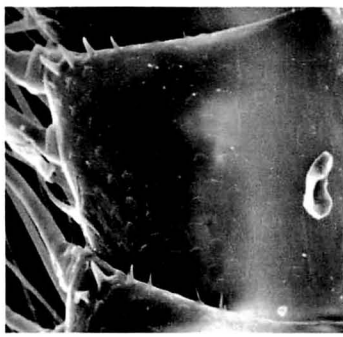
3c



4a



4b



4c

attain their maximum activity in June to October. Unfortunately, the exact breeding seasons of these species were not mentioned by these authors. Some of these may breed all the year round. However, the breeding seasons of these three species seem to be in summer and roughly coincide with each other.

Morphological difference between these three species cannot be explained by polymorphism, because only one of them is represented at some places. Hybrids have never been found. Therefore, it is interpreted that these three species are distinct from one another. If they are not reproductively isolated by differences in breeding seasons, it must be by some other unknown mechanism.

#### *Stratigraphic distribution*

The oldest fossil of *B. amphitrite* group so far known from Japan is traced back to the Pleistocene.

Fossil *B. kondakovi* has been found attached to the bank forming oysters in the Pleistocene and the Holocene sediments at Locs. 24a, 30d, and 34. They are, however, not associated with other species of *B. amphitrite* group. Fossil oyster bank which is represented by autochthonous *Crassostrea gigas* suggests an environment of the innermost portion of the embayment. Thus, the habitat of *B. kondakovi* has been unchanged since the Pleistocene.

Fossil *B. albicostatus* has been found in association with *B. reticulatus* in the Pleistocene and the Holocene sediments at Locs. 21, 28a-b and 30a, g. Thus, the sympatry of these two species was already established before the Pleistocene.

Living *B. amphitrite* is found in association with *B. albicostatus* and/or *B. reticulatus* in various bays of Japan. *B. albicostatus* and *B. reticulatus* are found on the shells from the shell mounds of

the Jomon age (3500-4200 Y. B. P.) (Locs. 19b, c) and the Kofun age (500-700 A. D.) (Loc. 19a). Yet, fossil or even semifossil *B. amphitrite*\* has never been found in Japan. Therefore, it is highly probable that *B. amphitrite* is a new comer to the Japanese coasts sometimes in the historical age, as was assumed by HIRO (1938).

According to the trustworthy observation made by HIRO (1938) before the World War II, *B. amphitrite hawaiiensis* (= *B. amphitrite*) and *B. amphitrite communis* (= *B. reticulatus*) live on the shore below the low tide line, while *B. amphitrite albicostatus* (= *B. albicostatus*) are always found in the intertidal zone. In detail, *B. amphitrite* is dominant and *B. reticulatus* is rare in such bays under little influence of oceanic water as Kure and Sasebo harbors. On the other hand, *B. amphitrite* is extremely rare and *B. reticulatus* is a common species in the bays faced on Pacific Ocean.

The recent observations made by the writer in Japanese embayments, including Kure and Sasebo harbors, clarified the fact that *B. amphitrite* as well as *B. albicostatus* becomes abundant in the intertidal zone. *B. reticulatus*, however, is still found to the lower level of intertidal zone of shore or on floating objects. In conclusion, *B. amphitrite* seemingly extended its habitat into the intertidal zone in various bays of Japan during the past half century. The apparent shift in the vertical distribution of *B. amphitrite* may be interpreted as a result of the combination of two factors, first, the increase in individual number of *B. amphitrite* over the general area of *B. albicostatus* and *B. reticulatus*

\* OHARA (1969) reported on occurrence of *B. amphitrite* from the Pleistocene Semata formation; however, it seem that the identification is incorrect.

in the intertidal zone and the zone below the low tide, and second, the thin out of *B. amphitrite* in the zone below the low tide, due to the competitive advantage of *B. reticulatus* over *B.*

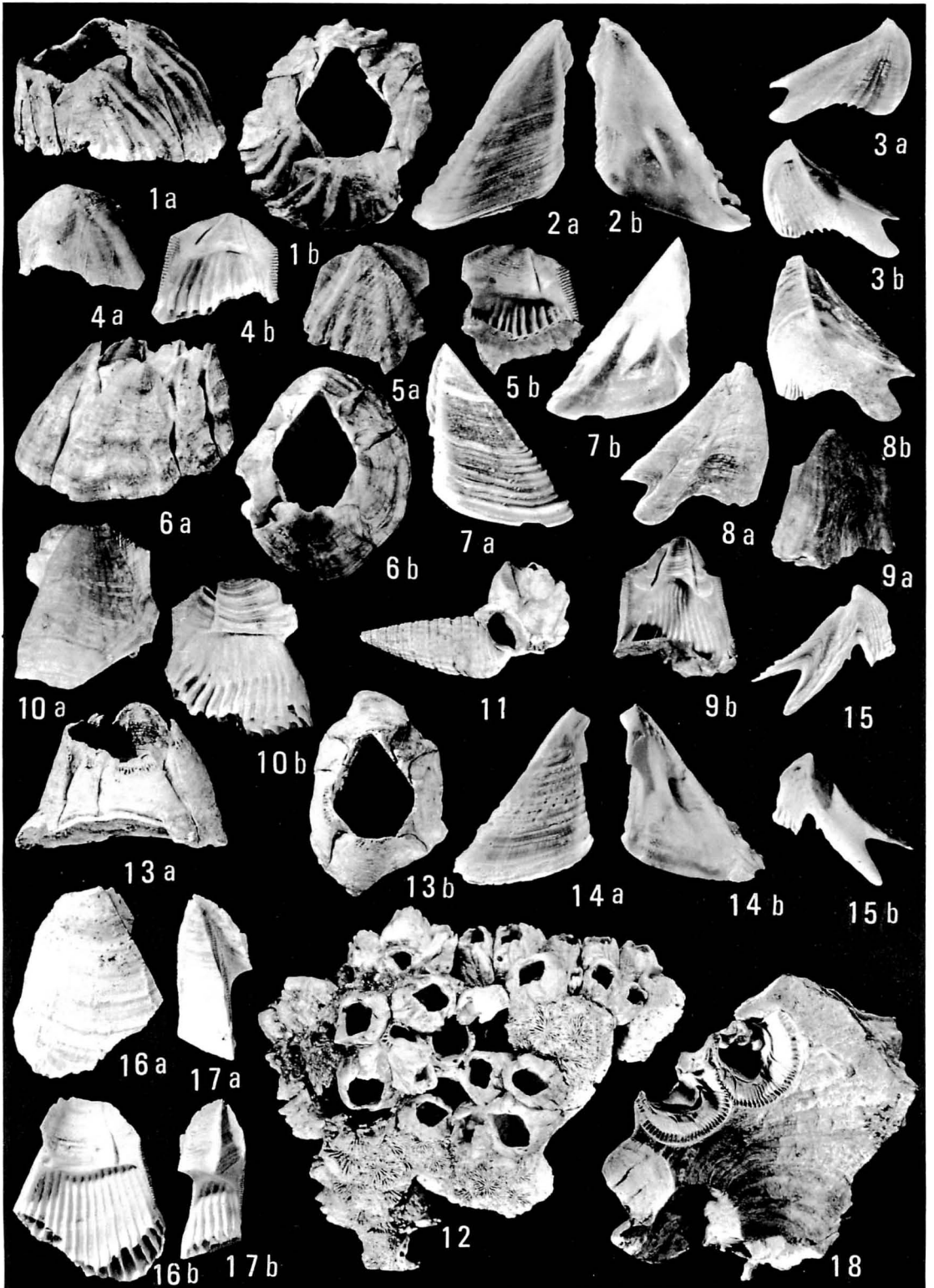
*amphitrite*. This assumption seems interesting but entrust its proof to further observation.

[to be continued]

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#### Explanation of Plate 22

- Figs. 1-5. *Balanus albicostatus* PILSBRY from the Holocene Numa Formation (Loc. 28a). 1a-b. whole wall (UMUT-CA8313),  $\times 2.$ , 2a-b. exterior and interior views of right scutum (UMUT-CA8314),  $\times 5.$ , 3a-b. exterior and interior views of right tergum (UMUT-CA8315),  $\times 5.$ , 4a-b. exterior and interior views of rostrum (UMUT-CA8316),  $\times 3.$ , 5a-b. exterior and interior views of left lateral (UMUT-CA8317),  $\times 3.$
- Figs. 6-10. *Balanus reticulatus* UTINOMI from the Holocene Numa Formation (Loc. 28a). 6a-b. whole wall (UMUT-CA8318),  $\times 2.5.$ , 7a-b. exterior and interior views of left scutum (UMUT-CA8319),  $\times 5.$ , 8a-b. exterior and interior views of right tergum (UMUT-CA8320),  $\times 5.$ , 9a-b. exterior and interior views of rostrum (UMUT-CA8321),  $\times 3.$ , 10a-b. exterior and interior views of right lateral (UMUT-CA8322),  $\times 3.$
- Fig. 11. *Balanus reticulatus* UTINOMI (UMUT-CA8323) on *Cerithideopsisilla djadjariensis* (MARTIN) from the Holocene Ofuna Shell Bed (Loc. 30e),  $\times 1.$
- Fig. 12. *Balanus reticulatus* UTINOMI (UMUT-CA8324) on coral from the Holocene Taito-zaki Formation (Loc. 21),  $\times 1.$
- Figs. 13-18. *Balanus kondakovi* TARASOV and ZEVINA from the Pleistocene Akasawa Silt (Loc. 42a). 13a-b. whole wall (UMUT-CA8325),  $\times 1.5.$ , 14a-b. exterior and interior views of right scutum (UMUT-CA8326),  $\times 5.$ , 15a-b. exterior and interior views of right tergum (UMUT-CA8327),  $\times 5.$ , 16a-b. exterior and interior views of left lateral (UMUT-CA8328),  $\times 2.5.$ , 17a-b. exterior and interior views of left carinolateral (UMUT-CA8328),  $\times 2.5.$ , 18. shell wall (UMUT-CA8329) on *Crassostrea gigas* (THÜNBERG),  $\times 1.$
- [Description to be published in Part 2]



行 事 予 定

	開 催 地	開 催 日	講 演 申 込 締 切
120 回 例 会	熊 本 大 学	1977年10月 16 日	1977年 8 月15日
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お 知 ら せ

○本会名誉会員の早坂一郎君は昭和52年8月19日に逝去されました。ここにつつしんで哀悼の意を表します。

日本古生物学会

編 集 係 より

○1978年度発行予定の本誌 No. 109 より、短報を除く各原著論文に内容を簡潔に示す英文アブストラクトをつけることになりました。今後投稿される方は原稿に添えて従来の和文要約とは別に、300語以内の英文アブストラクト原稿をお送り下さい。

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