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

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1. Introduction

DARWIN's (1851a, 1854a) two monographs on living cirripedes 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;

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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 interspecific 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. volcanio).

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 N₂ 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 Balanomorpha 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 P. vespersis in the cultivating cages. Coll. Drs. K. Chineze & 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.
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 Matsuppu 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 Kagaizasawa 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 Toshisetsu 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 Usihogata Station, Rokumaibashi, Aomori City, Aomori Pref.; coarse sand. The Pliocene Kanita formation (UEMURA, et al., 1959).
Text-fig. 1. Sampling localities of fossil and living Balanoidea of Japan.

5a—b—Daishaka: a) a cliff (40°49.8' N., 140°38.5' E.) of right bank of the Amadai river, situated about 2.9 Km N80°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°43.5' N., 141°17.3' E.) same as Loc. 6, IWAI & SIOBARA, 1969; massive mud., b) a cliff (40°43.6' N., 141°16.1' E.) same as Loc. 9, IWAI & SIOBARA, 1969; massive mud., c) a cliff (40°43.4' N., 141°14.6' E.) same as Loc. 11, IWAI & SIOBARA, 1969; massive mud. The Pleistocene Numasaki mudstone.

7a—n—Mabuchi river valley: a) a road-cut (40°25.3' N., 141°16.8' E.) situated about
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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 Suwanota- taira 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 Kin- taichi 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 Tonesaki formation. a) The late Miocene Miyasawa sandstone (CHINZEI, 1966) of the Tonesaki formation. d, g, i & j) The late Miocene Metoki shell limestone (CHINZEI, 1966) of the Tonesaki 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—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 (HUSI- OKA, 1959).

9a—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 Takinue 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, Hanawa, et al., 1953; tuffaceous medium sand containing many quartz grains; Pliocene Tatsunokuchi formation (Hanawa, 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 (Hanawa, 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, Namekata-gun, Ibaraki Pref.; fossiliferous fine sand; Pleistocene Narita formation.

17a-e—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) Natsumida-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) Miyamotodai-Kaizuka (a shell-mound) (35°41.5' N., 140°0.2' E.), Miyamoto-cho, Funabashi City; late Jomon age (3500 Y.B.P.), c) Ebisagaku-Kaizuka (a shell-mound) (35°44.1' N., 140°2.5' E.), Ebisagaku, Oana-cho, Funabashi City; middle Jomon age (4200 Y.B.P.). Coll. Miss. H. Koike.

20a-b—Senata: a, b) cliffs same as Locs. 19a, 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 (Crasostrea gigas) and autochthonous Mya arenaria oongai; 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.,
28a—e—Tateyama: a) a cliff (34°58.1′ N., 139°49.4′ E.) same as Loc. 1, Yabe & Sugiyama, 1951; 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 nipponica). 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, Kumesawa-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 Ohfuno Station, Kasama.

31—Hitorizawa: a cliff (35°21.5'N., 139°36.6'E.) of rivulet, situated about 2 Km S30°E of Yokodai Station, Hitorizawa, Isogo-ku, Yokohama City, Kanagawa Pref.; cross-laminated pumiceous medium to coarse sand; Pleistocene Koshia formation (Otuka, 1930).

32a—Fujisawa: a) a cliff same as Loc. 25, Yamaguchi, 1973., b) a cliff (35°19.8'N., 139°30.7'E.) of Kashiyo 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—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 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, Yukinoshitawakaremichi, 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.


37a—Ninomiya: a) a cliff (35°18.7'N., 139°15.1'E.) situated about 2 Km N24°W of Ninomiya Station, Ushikoshi, 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—Kanagawa: below the ground (35°4'N., 138°56.6'E.) situated about 500 m north of Baraki Station, Nagasaki, Nira-yama-cho, Tagata-gun, Shizukuoka Pref.; mud; Holocene. Coll. Mr. Takahashi.

39—Nanao: a) 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—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 S.E 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—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 S7°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).


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.

Compartment
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 from 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 Tetractididae, 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.

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

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. statiburi by Harding (1962); in B. pallidus, B. albicostatus albicostatus (=B. albicostatus) and B. a. formosanus by Utinomi (1967) and in B. citerosum, B. suturalis and B. denivarians 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.
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. suturalis, 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 interpapulational 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 oblitterus [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 *Tetracitella karandei* [*Tetracitidae*] 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. Radii 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
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Table 1. Number of segments in each right cirrus of B. amphitrite, B. albicostatus, B. reticulatus and B. kondakovi.

<table>
<thead>
<tr>
<th></th>
<th>rCl</th>
<th>rCII</th>
<th>rCIII</th>
<th>rCIV</th>
<th>rCV</th>
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<td></td>
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<td>end</td>
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<td>3</td>
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<tr>
<td>x</td>
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<td>12.3</td>
<td>15.0 12.0</td>
<td>15.0 14.7</td>
<td>30.0 31.5</td>
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<td>15-18 12-16</td>
<td>16-19 13-17</td>
<td>29-33 32</td>
<td>33 34-36</td>
<td>36-37 34-38</td>
</tr>
<tr>
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<td>13.3</td>
<td>16.3 13.7</td>
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</tr>
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<td>18-19 16-17</td>
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<td>34-44 42</td>
<td>35-47 40-47</td>
</tr>
<tr>
<td>x</td>
<td>17.7</td>
<td>11.7</td>
<td>13.5 12.5</td>
<td>18.3 16.3</td>
<td>31.7 33.7</td>
<td>40.3 42</td>
</tr>
</tbody>
</table>

N: number of individuals examined. OR: observed range. X: arithmetic mean. Locality: B. amphitrite, B. albicostatus and B. reticulatus; Loc. H. B. kondakovi; Kasaoka Bay, Okayama Pref., Coll. Dr. S. Fuse.


B. rostratus may be a Japanese representative 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. Radii 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 *Pilsbr*, 1916
*B. amphitrite* peruvianus *Pilsbr*, 1916
*B. amphitrite* forma *hawaiensis Broch*, 1922
*B. amphitrite* var. *acutus* *Withers*, 1924
*B. amphitrite* var. *denticulata Broch*, 1927
*B. amphitrite* forma *poecilosculpta Broch*, 1931
*B. amphitrite* krügeri *Nilsson-Cantell*, 1932
*B. amphitrite* rafflesii *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* abundans *Kolosváry*, 1948
*B. amphitrite* archi-inexpectatus *Kolosváry*, 1948
*B. amphitrite* hungaricus *Kolosváry*, 1948
*B. amphitrite* helena *Kolosváry*, 1948
*B. amphitrite* var. *vladivosotakensis 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*, 1962
*B. amphitrite* longaensis *Kolosváry*, 1962

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

<table>
<thead>
<tr>
<th><strong>Darwin</strong> (1854 a)</th>
<th><strong>Harding</strong> (1962)</th>
</tr>
</thead>
<tbody>
<tr>
<td>B. amphitrite var. communis</td>
<td><em>B. amphitrite amphitrite Darwin</em></td>
</tr>
<tr>
<td>B. amphitrite var. pallidus</td>
<td><em>B. pallidus pallidus Darwin</em></td>
</tr>
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<td>B. amphitrite var. stuttsburi</td>
<td><em>B. pallidus stuttsburi Darwin</em></td>
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<td>B. amphitrite var. venustus</td>
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<tr>
<td>B. amphitrite var. niveus</td>
<td><em>B. venustus niveus Darwin</em></td>
</tr>
<tr>
<td>B. amphitrite var. modestus</td>
<td><em>B. venustus modestus Darwin</em></td>
</tr>
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<td>B. amphitrite var. obscurus</td>
<td><em>B. venustus obscurus Darwin</em></td>
</tr>
<tr>
<td>B. amphitrite var. variegatus</td>
<td><em>B. variegatus Darwin</em></td>
</tr>
<tr>
<td>B. amphitrite var. cirratus</td>
<td><em>B. variegatus var. cirratus Darwin</em></td>
</tr>
</tbody>
</table>
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Table 3

<table>
<thead>
<tr>
<th>Hiro (1938)</th>
<th>Utinomi (1967)</th>
</tr>
</thead>
<tbody>
<tr>
<td>B. a. forma communis Darwin</td>
<td>B. reticulatus Utinomi</td>
</tr>
<tr>
<td>B. c. forma cirrus Darwin</td>
<td>B. variegatus cirrus Darwin</td>
</tr>
<tr>
<td>B. a. forma poecilotheca Krüger</td>
<td>B. poecilotheca Krüger</td>
</tr>
<tr>
<td>B. a. forma albicostatus Pilssry</td>
<td>B. albicostatus albicostatus Pilssry</td>
</tr>
<tr>
<td>B. a. forma hawaiiensis Broch</td>
<td>B. amphitrite Darwin sensu Harding</td>
</tr>
<tr>
<td>B. a. forma krügeri Nilsson-Cantell</td>
<td>B. uliginosus Utinomi</td>
</tr>
<tr>
<td>B. a. forma formosanus Hiro</td>
<td>B. albicostatus formosanus Hiro</td>
</tr>
</tbody>
</table>

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 Okino Bay, 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 cirrus from Iki Is. and Ariake Bay was reported first by Hiro (1938). This form was later called B. variegatus var. cirrus by Harding (1962) and B. variegatus cirrus by Utinomi (1967). Thus it seems necessary to clarify the relation between B. variegatus variegatus and B. variegatus var. cirrus; 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.


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 *McLaughlin* (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)
slopes towards the occulident 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.
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

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**Explanation of Plate 19**

Fig. 1. *Balanus amphitrite* Darwin (UMUT-RA8263) from Tanabe Bay (Loc. H). 1a-b. whole wall, ×2, 1c-d. exterior and interior views of right scutum, ×6, 1e-f. exterior and interior views of right tergum, ×6.

Fig. 2. *Balanus amphitrite* Darwin (UMUT-RA8264) from Tanabe Bay (Loc. H). 2a-b. exterior and interior views of rostrum, ×2.5, 2c-d. exterior and interior views of left lateral, ×2.5, 2e-f. exterior and interior views of left carinolateral, ×2.5, 2g-h. exterior and interior views of carina, ×2.5.

Fig. 3. *Balanus albicostatus* Pilsbry (UMUT-RA8265) from Tanabe Bay (Loc. H). 3a-b. whole wall, ×2, 3c-d. exterior and interior views of right scutum, ×5, 3e-f. exterior and interior views of right tergum, ×5.

Fig. 4. *Balanus albicostatus* Pilsbry (UMUT-RA8266) from Tanabe Bay (Loc. H). 4a-b. exterior and interior views of rostrum, ×2, 4c-d. exterior and interior views of left lateral, ×2, 4e-f. exterior and interior views of carinolateral, ×2, 4g-h. exterior and interior views of carina, ×2.

Fig. 5. *Balanus reticulatus* Utinomi (UMUT-RA8267) from Tanabe Bay (Loc. H). 5a-b. whole wall, ×1.5, 5c-d. exterior and interior views of right scutum, ×4, 5e-f. exterior and interior views of right tergum, ×4, 5g-h. exterior and interior views of rostrum, ×1.5, 5i-j. exterior and interior views of left lateral, ×1.5, 5k-l. exterior and interior views of left carinolateral, ×1.5, 5m-n. exterior and interior views of carina, ×1.5.

Fig. 6. *Balanus kondakovi* Tarasov and Zevina (UMUT-RA8268) from Hamana Lake (Loc. G). 6a-b. whole wall, ×1.5, 6c-d. exterior and interior views of right scutum, ×4, 6e-f. exterior and interior views of right tergum, ×4.

Fig. 7. *Balanus kondakovi* Tarasov and Zevina (UMUT-RA8269) from Hamana Lake (Loc. G). 7a-b. exterior and interior views of rostrum, ×1.5, 7c-d. exterior and interior views of left carinolateral, ×1.5, 7g-h. exterior and interior views of carina, ×1.5.

[Descriptions to be published in Part 2]
are all warm water inhabitants. Their geographical range extends from southeast 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); Abaratubo Bay, Misaki, Kanagawa Pref.; Mukashima 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.
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 challengeri zone of the uppermost intertidile. 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.; Mukishima 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

Explanation of Plate 20

(Figs. 1-4. anterior view of rostrum)
Fig. 1. Balanus amphitrite Darwin (UMUT-RA8264) from Tanabe Bay (Loc. H), ×5.
Fig. 2. Balanus albicostatus Pilsbry (UMUT-RA8266) from Tanabe Bay (Loc. H), ×5.
Fig. 3. Balanus reticulatus Utinomi (UMUT-RA8267) from Tanabe Bay (Loc. H), ×2.
Fig. 4. Balanus kondakovi Tarasov and Zevina (UMUT-RA8269) from Hamana Lake (Loc. G), ×4.

(Figs. 5-8. longitudinal section)
Fig. 5. Balanus amphitrite Darwin (UMUT-RA8270) from Tanabe Bay (Loc. H), rostrum, ×6.
Fig. 6. Balanus albicostatus Pilsbry (UMUT-RA8271) from Tanabe Bay (Loc. H), right lateral, ×5.
Fig. 7. Balanus reticulatus Utinomi (UMUT-RA8272) from Tanabe Bay (Loc. H), right lateral, ×4.
Fig. 8. Balanus kondakovi Tarasov and Zevina (UMUT-RA8273) from Hamana Lake (Loc. G), right lateral, ×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), ×3.
Fig. 10. Balanus albicostatus Pilsbry (UMUT-RA8275) from Tanabe Bay (Loc. H), ×2.
Fig. 11. Balanus reticulatus Utinomi (UMUT-RA8276) from Tanabe Bay (Loc. H), ×1.5.
Fig. 12. Balanus kondakovi Tarasov and Zevina (UMUT-RA8269) from Hamana Lake (Loc. G), ×2.

[Description to be published in Part 2]
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 Balanoida are hermaphrodites, with the exception of four species of commensal forms (Henry and McLaughlin, 1967; McLaughlin and Henry, 1972) which have complemental 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. tintinabulum, 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 Hidnaga 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., ×100, 1b. 8th segment of right cirrus III, lv., ×300, 1c. 8th segment of right cirrus IV, lv., ×250.

Fig. 2. Balanus albicostatus Pilsbry from Tanabe Bay (Loc. H). 2a. labrum, av., ×100, 2b. 8th segment of right cirrus III, lv., ×200, 2c. 10th segment of right cirrus IV, lv., ×300.

Fig. 3. Balanus reticulatus Utinomi from Tanabe Bay (Loc. H). 3a. labrum, av., ×100, 3b. 8th segment of right cirrus III, lv., ×200, 3c. 10th segment of right cirrus IV, lv., ×300.

Fig. 4. Balanus kondakovi Tarasov and Zevina from Kasaoka Bay, Okayama Pref. 4a. labrum, av., ×100, 4b. 12th segment of right cirrus III, lv., ×250, 4c. 11th segment of right cirrus IV, lv., ×250.

[Description to be published in Part 2]
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. 2a, 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 sympathy 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 hawaiensis* (=*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*

*ÔHARA (1969) reported on occurrence of* *B. amphitrite* *from the Pleistocene Senata 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), ×2., 2a-b. exterior and interior views of right scutum (UMUT-CA8314), ×5., 3a-b. exterior and interior views of right tergum (UMUT-CA8315), ×5., 4a-b. exterior and interior views of rostrum (UMUT-CA8316), ×3., 5a-b. exterior and interior views of left lateral (UMUT-CA8317), ×3.

Figs. 6-10. _Balanus reticulatus_ UTINO MI from the Holocene Numa Formation (Loc. 28a). 6a-b. whole wall (UMUT-CA8318), ×2.5., 7a-b. exterior and interior views of left scutum (UMUT-CA8319), ×5., 8a-b. exterior and interior views of right tergum (UMUT-CA8320), ×5., 9a-b. exterior and interior views of rostrum (UMUT-CA8321), ×3., 10a-b. exterior and interior views of right lateral (UMUT-CA8322), ×3.

Fig. 11. _Balanus reticulatus_ UTINO MI (UMUT-CA8323) on _Cerithideopsilla djadjariensis_ (MARTIN) from the Holocene Ofuna Shell Bed (Loc. 30e), ×1.

Fig. 12. _Balanus reticulatus_ UTINO MI (UMUT-CA8324) on coral from the Holocene Taito-zaki Formation (Loc. 21), ×1.

Figs. 13-18. _Balanus kondakovi_ TARASOV and ZEVINA from the Pleistocene Akasawa Silt (Loc. 42a). 13a-b. whole wall (UMUT-CA8325), ×1.5., 14a-b. exterior and interior views of right scutum (UMUT-CA8326), ×5., 15a-b. exterior and interior views of right tergum (UMUT-CA8327), ×5., 16a-b. exterior and interior views of left lateral (UMUT-CA8328), ×2.5., 17a-b. exterior and interior views of left carinolateral (UMUT-CA8329), ×2.5., 18. shell wall (UMUT-CA8329) on _Crassostrea gigas_ (THÜNBERG), ×1.

[Description to be published in Part 2].