THE BARNACLES OF THE *BALANUS AMPHITRITE* COMPLEX (CIRRIPEDIA, THORACICA)

BY

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With 33 text-figures and 22 plates

Abstract. — A qualitative and quantitative study has been made of the Recent taxa assigned, or related, to *Balanus amphitrite* Darwin. All taxa of the complex have been redescribed and a key provided. Interspecific relationships have been evaluated statistically through the use of the generalized distance function and discriminant function analyses. Two well defined groups and three subgroups have been defined and a key proposed. The discriminant function has also been utilized as an aid in the identification of unknown specimens of a closely related pair of taxa.

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Introduction

In his monograph of the sessile Cirripedia, Darwin (1854) described *Balanus amphitrite,* which he considered one of the most variable and difficult species within the entire genus. Although initially he had believed that eight specifically distinct forms existed, he became convinced, after examining a large series of specimens, that all were merely varieties of a single species. Consequently he named, and briefly described, *communis, venustus, pallidus, niveus, modestus, stutsburi, obscurus, variegatus,* and *cirratus* as varieties of *B. amphitrite.* Darwin figured the shells of all of these varieties except *modestus* and *variegatus*; however, he illustrated the opercular valves only of *communis* and *stutsburi* and the tergum of *pallidus.* If known, Darwin did list the distributions of the different varieties, but he did not designate type specimens nor localities. Because of his incomplete descriptions, lack of adequate illustrations, and failure to select types, subsequent authors had great difficulty in referring specimens to Darwin's varieties of *B. amphitrite,* as may be seen by the following brief synopsis of the literature.

Although Hoek (1913), in his study of the "Siboga" collection, found specimens of *B. amphitrite* which resembled several of Darwin's (1854) varieties, he felt that he was only able to identify *B. a. communis* with assurance. He proposed a new variety, *B. a. malayensis,* for the remainder of the material.

Pilsbry (1916), in his emendation of the subgenus *Balanus,* designated eight named series to indicate how he interpreted the relationships of the species. In his *amphitrite* series, he included *B. amphitrite* Darwin, *B. poecilotheca* Krüger and, tentatively, *B. regalis* Pilsbry. He suggested that several species which he had not seen should also be included in the *amphitrite* series, i.e., *B. poecilus* Darwin, *B. violaceus* Gruvel, *B. dybowskii* Gruvel, *B. mirabilis* Krüger, and *B. minutus* Hoek. He placed *B. carenatus* Gruvel in synonymy with *B. amphitrite,* noting, however, that its exact status could not be determined until a revision of the oriental forms of *B. amphitrite* had been under-

taken. He did not discuss the status of Hoek's (1913) variety, *malayensis*. In addition, Pilsbry described two new subspecies, *B. a. albicostatus* and *B. a. inexpectatus,* gave subspecific rank in *B. amphitrite* to his previously (Pilsbry, 1909) described *B. peruvianus,* and amplified the earlier descriptions of *B. a. niveus; B. eburneus,* and *B. improvisus*. He also described a new subspecies of *B. concavus, B. c. pacificus*. From his study of *B. amphitrite,* Pilsbry concluded that definition of the subspecies was a very intricate problem and that, before a revision could be attempted, the Darwinian collection would have to be restudied and type localities selected for Darwin's varieties. Nearly fifty years elapsed, however, before Harding (1962) reexamined Darwin's type material of *B. amphitrite*.

In the interim, investigators continued, if possible, to refer specimens to Darwin's varieties or to erect additional subordinate taxa of *B. amphitrite*. These included *hawaiiensis* Broch (Broch, 1922), *denticulata* Broch (Broch, 1927a), *poeciloscul pta* Broch (Broch, 1931), *kruegeri* Nilsson-Cantell (Nilsson-Cantell, 1932c), *rafflesi* Nilsson-Cantell (Nilsson-Cantell, 1934a), *insignis* Nilsson-Cantell and *cochinensis* Nilsson-Cantell (Nilsson-Cantell, 1938), *formosanus* Hiro (Hiro, 1938), *fluminensis* Oliveira and *aeratus* Oliveira (Oliveira, 1941), *saltonensis* Rogers, *herzi* Rogers and *franciscanus* Rogers (Rogers, 1949), and *vladivostokensis* Tarasov & Zevina, *columaris* Tarasov & Zevina, and *kondakovi* Tarasov & Zevina (Tarasov & Zevina, 1957). Half of these new taxa were based on specimens having multidenticulate labra; whereas, according to Darwin (1854: 245) the labrum of *B. amphitrite* has from four to eight, generally six teeth. Nilsson-Cantell (1921), however, described a multidenticulate labrum for *B. a. communis*. Subsequently, he (Nilsson-Cantell, 1938) recognized *B. a. hawaiiensis,* which has a multidenticulate labrum, but stated that *B. a. denticulata* could not be distinguished from *B. a. communis* by its multidenticulate labrum, as the labrum in the latter taxon is variable. Utinomi (1960) placed *B. a. denticulata, B. a. franciscanus, B. a. herzi,* and questionably *B. a. saltonensis* in synonymy with *B. a. hawaiiensis*. He also enumerated eight diagnostic characters, in addition to the labrum, by which *B. a. hawaiiensis* could be differentiated from *B. a. communis*. As the name *communis* was preoccupied, Utinomi (1964) subsequently proposed the new name, *B. a. tesselatus,* for *B. a. communis* auct. (not Darwin).

Harding (1962) reexamined all of Darwin's type material of *B. amphitrite* available in the British Museum and, although the original collections were no longer complete, he was able to select lectotypes, complete with opercular valves and animal parts and locality data, for most of Darwin's varieties. On the basis of his findings, Harding divided *B. amphitrite* into four distinct

species, i.e., *B. amphitrite amphitrite* (= *B. a. communis*), *B. pallidus,* with subspecies, *B. p. stutsburi*; *B. venustus,* with subspecies, *B. v. niveus, B. v. modestus,* and *B. v. obscurus*; and *B. variegatus* with variety *cirratus.* He found that all of the species and subspecies, except *B. a. amphitrite,* had few teeth on the labrum. In the lectotype of *B. a. amphitrite,* the labrum had 12 or 13 teeth on each side, gradually decreasing in size downward along the sides of the notch. Not only does this labrum differ from Darwin's description of *B. a. communis,* but the figures (Harding, 1962, pl. 1 figs. a-g) of the shell and opercular valves differ from Darwin's figures (Darwin, 1854, pl. 5 fig. 2e, h, l). Consequently it must be concluded that Darwin's original material consisted of two distinct species which he confounded under the name *communis.*

As a result of Harding's (1962) revision, Utinomi & Kikuchi (1966) revised the taxa of the *amphitrite* complex from Japanese waters to include the following: *B. albicostatus albicostatus, B. amphitrite amphitrite, B. a. kruegeri, B. variegatus cirratus, B. variegatus tesselatus,* and *B. poecilotheca.* Subsequently, Utinomi (1966) removed *kruegeri* from *B. amphitrite* and assigned it subspecific rank in *B. pallidus.* He later raised it to specific status and gave the new names, *B. uliginosus* and *B. reticulatus,* to *B. a. kruegeri* and *B. v. tesselatus,* respectively, as the latter names were both preoccupied (Utinomi, 1967).

Stubbings (1967), using some of the diagnostic characters proposed by Utinomi (1960) to distinguish *B. a. hawaiiensis* from *B. a. communis,* found that some specimens could not be assigned to either taxon. He, therefore, concluded that *B. a. communis* (sensu Utinomi) and *B. a. hawaiiensis* were conspecific with *B. a. amphitrite.*

Although Harding's (1962) redescriptions and designations of lectotypes for Darwin's varieties clarified several ambiguities, the status of the non-Darwinian subspecies of *B. amphitrite* was still indeterminate. That many taxonomic problems remained became increasingly apparent when we attempted to refer specimens in our collections to the existing subspecies or closely allied species of the *amphitrite* complex. Consequently, we have undertaken a revision of all the described taxa of the complex, which is based, in part, on the *amphitrite* series proposed by Pilsbry (1916). In addition to descriptive taxonomy, cirripediologists occasionally have applied statistical analyses (e.g., Sandison, 1962; Matsui et al., 1964; Barnes & Healy, 1965, 1969, 1971); however, this revision is both classical and statistical in its approach to the complex.

As herein defined, the *amphitrite* complex includes the following Recent taxa.

B. abeli Lamy & André
B. albicostatus Pilsbry
B. amphitrite amphitrite Darwin
B. amphitrite saltonensis Rogers
B. citerosum Henry
B. concavus indicus Nilsson-Cantell
B. concavus mexicanus Henry
B. concavus pacificus Pilsbry
B. concavus sinensis Broch
B. dentivarians Henry
B. eburneus Gould
B. improvisus Darwin
B. inexpectatus Pilsbry
B. kondakovi Tarasov & Zevina
B. pallidus Darwin
B. patelliformis Bruguière
B. peruvianus Pilsbry
B. poecilotheca Krüger
B. reticulatus Utinomi
B. subalbidus Henry
B. suturaltus Henry
B. variegatus Darwin
B. venustus Darwin

Taxa formerly or herein assigned to, or considered closely related to *B. amphitrite* sensu lato, which have been placed in synonymy, or for which a replacement name or change in rank has been proposed, either previously or herein, and the taxa to which they are herein referred are listed in Table 1.

Three additional species, *B. poecilus* Darwin, *B. salaami* Nilsson-Cantell, and *B. regalis* Pilsbry, formerly were believed to be closely allied to the *amphitrite* complex; however, current evidence does not substantiate this belief. Darwin (1954) considered *B. poecilus* to be closest to *B. amphitrite,* but easily distinguished from it by the absence of the adductor ridge of the scutum and by the sharply truncate spur of the tergum. Although this species had not been seen since Darwin's original description, Pilsbry (1916) included it in his *amphitrite* series. Material from the Gulf of California (cf. Henry, 1960) and from Ecuador have provided evidence that this species is more closely allied to Pilsbry's *trigonus* series. Nilsson-Cantell (1932d) considered that his new species, *B. salaami,* from East Africa was closely related to *B. poecilus.* The diagnostic characters of this species also indicate that its closest affinity is with the *trigonus* series. Pilsbry (1916) provisionally included *B. regalis* in the *amphitrite* series because the walls of the shell suggested a relationship with *B. concavus,* i.e., *B. c. proteus,* from the Virginia Miocene. Subsequently, Kolosváry (1940, 1942a, b) referred *B. regalis* to *B. concavus* as a subspecies, presumably because of the ribbed parietes. His figures (Kolosváry, 1940, figs. 1d-f; 1942b, figs. 1-4) of the opercular valves clearly indicate that these specimens do not belong to *B. regalis* nor do they agree with any known form of *B. concavus.* Henry (1960) has since demonstrated the relationship of *B. regalis* to *B. aquila* Pilsbry.

The authors wish to express their sincere appreciation to the numerous individuals who contributed specimens used in this study, and in particular to

Table 1. Nomenclatural Changes for Taxa Formerly or Herein Assigned to, or Considered Close to, *Balanus amphitrite* Darwin

Prior Designation	Present Designation*
Balanus alatus Hoek	*Balanus poecilotheca* Krüger*
Balanus amphitrite albicostatus Pilsbry (in part)	*Balanus albicostatus* Pilsbry
Balanus amphitrite albicostatus Pilsbry (in part)	*Balanus kondakovi* Tarasov & Zevina*
Balanus amphitrite aeratus Oliviera	*Balanus amphitrite amphitrite* Darwin*
Balanus amphitrite cirratus Darwin	*Balanus variegatus* Darwin*
Balanus amphitrite cochinensis Nilsson-Cantell	*Balanus amphitrite amphitrite* Darwin*
Balanus amphitrite columnaris Tarasov & Zevina	*Balanus amphitrite amphitrite* Darwin*
Balanus amphitrite communis Darwin (in part)	*Balanus amphitrite amphitrite* Darwin
Balanus amphitrite communis Darwin (in part)	*Balanus reticulatus* Utinomi
Balanus amphitrite denticulata Broch (in part)	*Balanus amphitrite amphitrite* Darwin
Balanus amphitrite denticulata Broch (in part)	Species indeterminata*
Balanus amphitrite fluminensis Oliviera	*Balanus amphitrite amphitrite* Darwin*
Balanus amphitrite formosanus Hiro	*Balanus albicostatus* Pilsbry*
Balanus amphitrite franciscanus Rogers	*Balanus amphitrite amphitrite* Darwin
Balanus amphitrite hawaiiensis Broch (in part)	*Balanus amphitrite amphitrite* Darwin
Balanus amphitrite hawaiiensis Broch (in part)	*Balanus reticulatus* Utinomi*
Balanus amphitrite herzi Rogers	*Balanus amphitrite amphitrite* Darwin
Balanus amphitrite inexpectatus Pilsbry	*Balanus inexpectatus* Pilsbry*
Balanus amphitrite insignis Nilsson-Cantell	? *Balanus pallidus* Darwin
Balanus amphitrite kondakovi Tarasov & Zevina	*Balanus kondakovi* Tarasov & Zevina*
Balanus amphitrite krugeri Nilsson-Cantell	*Balanus kondakovi* Tarasov & Zevina*
Balanus amphitrite malayensis Hoek (in part)	*Balanus poecilotheca* Krüger*
Balanus amphitrite malayensis Hoek (in part)	Species indeterminata
Balanus amphitrite modestus Darwin	*Balanus venustus* Darwin*
Balanus amphitrite niveus Darwin	*Balanus venustus* Darwin*
Balanus amphitrite n. subsp. Zullo	*Balanus improvisus* Darwin*
Balanus amphitrite obscurus Darwin	*Balanus venustus* Darwin*
Balanus amphitrite pallidus Darwin	*Balanus pallidus* Darwin
Balanus amphitrite peruvianus Pilsbry	*Balanus peruvianus* Pilsbry*
Balanus amphitrite poeciloseulpta Broch	*Balanus poecilotheca* Krüger
Balanus amphitrite poecilotheca Krüger	*Balanus poecilotheca* Krüger
Balanus amphitrite rafflesi Nilsson-Cantell	*Balanus variegatus* Darwin*
Balanus amphitrite stutsburi Darwin	*Balanus pallidus* Darwin
Balanus amphitrite tesselatus Utinomi	*Balanus reticulatus* Utinomi
Balanus amphitrite variegatus Darwin	*Balanus variegatus* Darwin
Balanus amphitrite venustus Darwin	*Balanus venustus* Darwin
Balanus amphitrite vladivostokensis Tarasov & Zevina	*Balanus variegatus* Darwin*

Table 1 (Cont.). Nomenclatural Changes for Taxa Formerly or Herein Assigned to, or Considered Close to, *Balanus amphitrite* Darwin

Prior Designation	Present Designation
Balanus carenatus Gruvel	*Balanus variegatus* Darwin*
Balanus concavus pacificus brevicalcar Pilsbry	*Balanus concavus pacificus* Pilsbry*
Balanus concavus regalis Pilsbry	Species inquirenda*
Balanus democraticus DeKay	*Balanus eburneus* Gould
Balanus dybowskii Gruvel	*Balanus pallidus* Darwin
Balanus improvisus assimilis Darwin	*Balanus improvisus* Darwin
Balanus improvisus gryphicus Münter	*Balanus improvisus* Darwin
Balanus minutus Hoek	*Balanus poecilotheca* Krüger*
Balanus mirabilis Krüger	*Balanus albicostatus* Pilsbry*
Balanus pacificus Pilsbry	*Balanus concavus pacificus* Pilsbry*
Balanus pacificus brevicalcar Pilsbry	*Balanus concavus pacificus* Pilsbry*
Balanus pallidus krugeri Nilsson-Cantell	*Balanus kondakovi* Tarasov & Zevina*
Balanus patellaris Gmelin	*Balanus patelliformis* Bruguière
Balanus regalis Pilsbry	*Balanus aquila regalis* Pilsbry
Balanus tintinnabulum maroccana Broch	*Balanus venustus* Darwin*
Balanus uliginosus Utinomi	*Balanus kondakovi* Tarasov & Zevina*
Balanus variegatus cirratus Darwin	*Balanus variegatus* Darwin*
Balanus variegatus tesselatus Utinomi	*Balanus reticulatus* Utinomi
Balanus venustus modestus Darwin	*Balanus venustus* Darwin*
Balanus venustus niveus Darwin	*Balanus venustus* Darwin*
Balanus venustus obscurus Darwin	*Balanus venustus* Darwin*
Balanus violaceus Gruvel	*Balanus abeli* Lamy & André
Bastard, *Balanus improvisus assimilis* & *Balanus armatus* Müller	*Balanus venustus* Darwin

* Referred herein.

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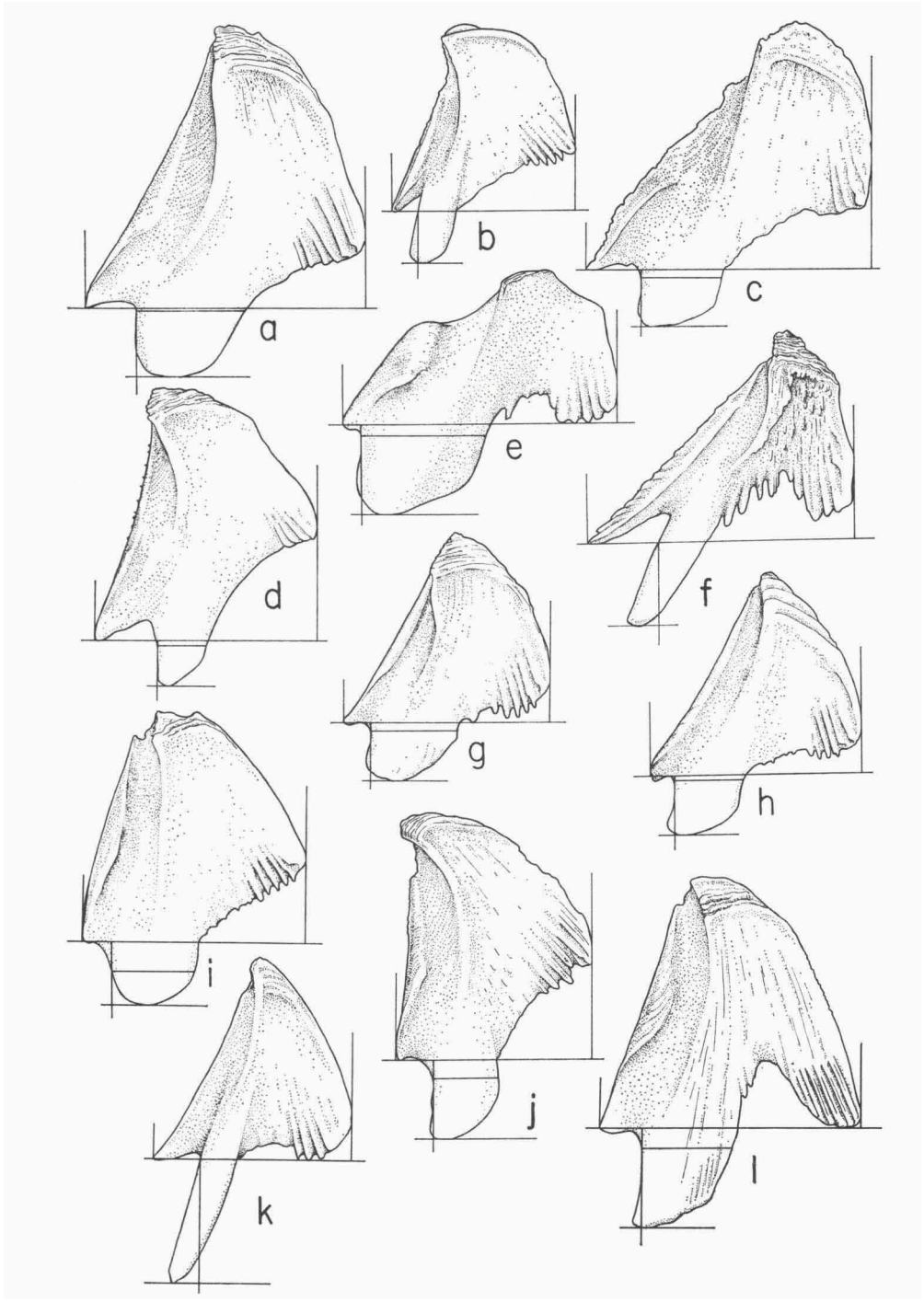

Fig. 1. Representative terga of the *amphitrite* complex, illustrating diversified configurations (see figure 3a for explanations of lines used in measurements for statistical analyses).

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METHODS

As previously indicated, both classical taxonomic and biometric methodology have been used in this study. The characters of the shells, opercular valves, and animals have been described in detail; those characters which could be measured or enumerated also have been treated statistically. Random samples of shells of each species were ground to permit examination of the structure of the tubes and septa of the parietes, particularly of the rostrum; similarly, samples of the sheath were ground and examined. Opercular valves were cleaned in full-strength commercial "Clorox"; the separated terga and scuta were dried and mounted in 28 ply microslides. The mouth parts and cirri were mounted in polyvinyl alcohol lactophenol. A series of specimens in each of several species were sectioned and polished to study the interlaminate figures; however, when it was found that the intraspecific variability and interspecific overlap of configurations were considerable, this procedure was not pursued. The description of the shell, opercular valves, mouth parts and cirri of each specimen, although undertaken in considerably greater detail, has followed Pilsbry (1916). Statistical treatment of species of the *amphitrite* complex has been patterned, in part, after Sandison's (1962) study of variation in populations of *B. amphitrite* var. *stutsburi* through the use of quantitative morphological characters. However, definition of characters has been altered, in this study, to permit the inclusion of numerous diversified tergal and scutal configurations occurring in taxa of the complex (figs. 1, 2). Regression and cononical analyses of valve shapes (cf. Barnes & Healy, 1965, 1969, 1971) could not be used in this study, as these techniques do not afford a measure of interspecific discrimination.

Sample size strongly influences any statistical analysis; therefore, the minimum sample size for any species of the complex was forty specimens. Although additional collections subsequently became available and have been included

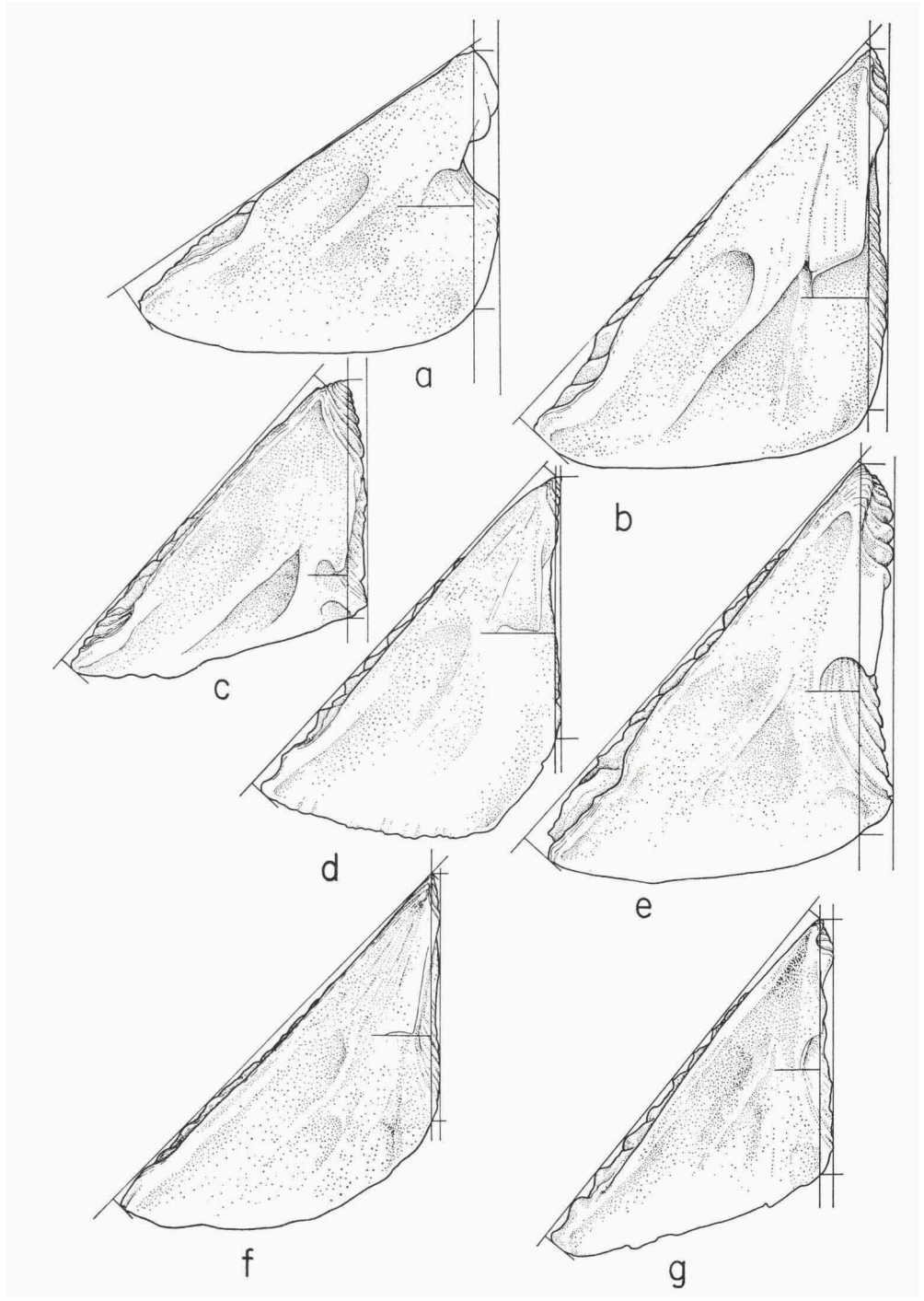

Fig. 2. Representative scuta of the *amphitrite* complex, illustrating diversified configurations (see figure 3b for explanation of lines used in measurements for statistical analyses).

in the descriptive study, at the time of the statistical evaluation of the species of the complex only the following 16 taxa were available in requisite sample size.

B. a. amphitrite (n = 272)
B. a. saltonensis (n = 201)
B. subalbidus (n = 95)
B. eburneus (n = 98)
B. improvisus (n = 93)
B. variegatus (n = 61)
B. reticulatus (n = 108)
B. kondakovi (n = 60)
B. citerosum (n = 90)
B. suturaltus (n = 41)
B. dentivarians (n = 52)
B. concavus pacificus (n = 71)
B. concavus mexicanus (n = 104)
B. venustus (n = 104)
B. inexpectatus (n = 151)
B. peruvianus (n = 87)

Fifteen morphological characters were utilized in the analyses of these 16 taxa; eight were obtained from the opercular valves and seven from the animal parts. Criteria for scutal and tergal measurements were developed from lines plotted on drawings of the valves enlarged 17.8 times. All drawings were done by one artist and checked for accuracy by the second author. All tergal measurements were obtained from such drawings. Following the establishment of suitable criteria for scutal measurements, these valves were measured using a stereomicroscope equipped with a 70 mm square grid divided into hundredths.

Four measurements were made for each tergum; use of these measurements in a series of six ratios provided the quantitative tergal characters. Three measurements from each scutum were used in a pair of ratios to define the scutal characters. All opercular valve measurements were made to the nearest 0.25 mm and were made by the second author.

The four tergal measurements (fig. 3a) are defined as follows:

1. The length of the basal margin (*a*) is defined by and measured on a line which intersects the basiscutal angle and is tangent to the basal margin on the carinal side of the spur at its most distant point from the apex of the valve. The origin of *a* is its point of intersection with a line constructed perpendicular to it at the apex of the basiscutal angle; *a* terminates at its point of intersection with a line constructed perpendicular to it and tangent to the carinal margin.

2. The spur length (*b*) is defined by and measured on a line constructed perpendicular to *a* and passed through *x*, the point on the scutal margin of the proximal half of the spur farthest from the line constructed perpendicular to *a* at the apex of the basiscutal angle. The origin of *b* is its point of intersection with *a*; *b* terminates at its point of intersection with a line constructed parallel to *a* and tangent to the most distal end of the spur.

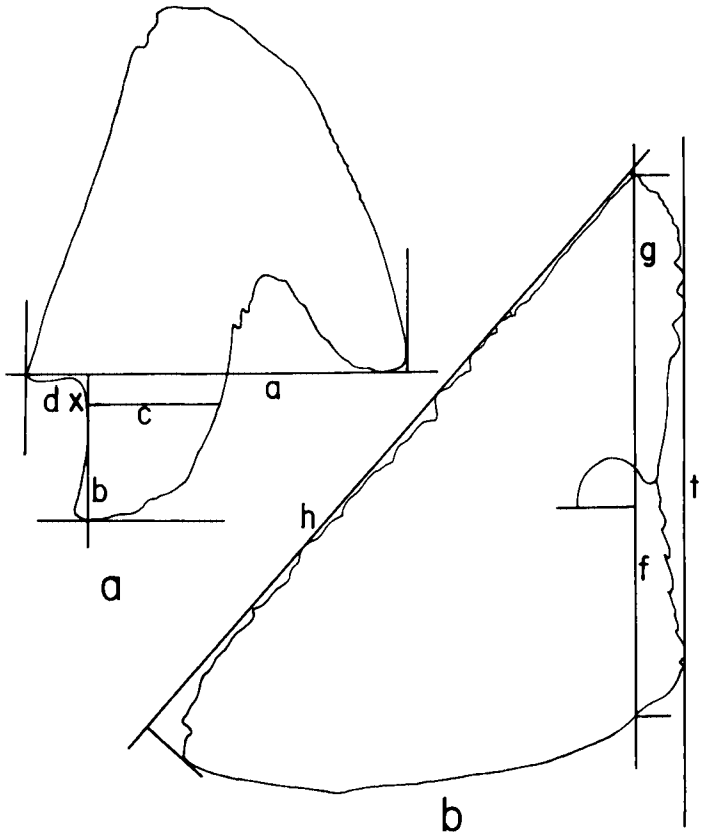

Fig. 3. Diagrams showing lines and points established for measurements used in statistical analyses — 3a, tergum: a, length of basal margin; x, point farthest from basiscutal angle on proximal half of scutal margin of spur; b, spur length; c, spur width; d, distance from basiscutal angle to spur. — 3b, scutum: t, initial line tangent to tergal margin; f, length of tergal margin; g, length of articular ridge; h, length of occludent margin.

3. The spur width (*c*) is defined by and measured on a line constructed parallel to or identical with *a* and passed through point *x*. The origin of *c* is point *x*; *c* terminates at its point of intersection with the carinal margin of the spur.

4. The distance from the basiscutal angle to the margin of the spur (*d*) is defined and measured on that part of *a* between its origin and the origin of *b*.

All scutal measurements (fig. 3b) are based on an intial line (*t*) which is constructed tangent to the tergal margin both above and below the insertion of the articular ridge.

1. The length of the tergal margin (*f*) is defined by and measured on a line constructed parallel to *t* and passed through the apex of the scutum. The origin

of *f* is its point of intersection with a line constructed perpendicular to it and tangent to the apex; *f* terminates at its point of intersection with the basal margin.

2. The length of the articular ridge (*g*) is defined by and measured on that part of *f* between its origin and its point of intersection with a line constructed perpendicular to it and passed through the point of insertion of the articular ridge.

3. The length of the occludent margin (*h*) is defined by and measured on a line constructed tangent to the occludent margin above and below the insertion of the articular ridge. The origin of *h* is its point of insertion with a line constructed perpendicular to it and tangent to the apex of the scutum; *h* terminates at its point of intersection with a line constructed perpendicular to it and tangent to the basioccludent angle.

Eight characters were obtained from ratios of the seven scutal and tergal measurements.

Character 1: spur width/basal margin
Character 2: spur length/spur width
Character 3: distance from angle/spur width
Character 4: distance from angle/spur length
Character 5: distance from angle/basal margin
Character 6: spur length/basal margin
Character 7: articular ridge/tergal margin
Character 8: articular ridge/occludent margin

Seven characters were obtained from the trophi and cirri and are defined as follows:

Character 9: number of teeth on labrum. — The average number of teeth on the two sides of the labrum, regardless of position, i.e., on the crest or on the sides of the notch.

Character 10: number of spines on the first maxilla. — The average number of spines between the upper and lower pairs of spines of the first maxillae.

Character 11: number of teeth on the mandible. — The average number of teeth on the mandibles.

Character 12: number of segments, cirrus I. — The average number of segments by which the anterior rami exceed (+), or fail to exceed (—) the posterior rami in length.

Character 13. number of segments, cirrus II. — Same criterion as 12.

Character 14. number of segments, cirrus III. — Same criterion as 12.

Character 15. number of paired setae, cirrus VI. — The average number

of paired setae on the median segments (i.e., where the maximum number of paired setae occurs) of the rami.

The parameters, i.e., range, mean, and standard deviation, for these 15 characters for the 16 taxa treated statistically are given in Appendix A.

In the application of statistical techniques to dynamic rather than static populations, one is invariably faced with problems of ecological diversity, bias, skewness, bimodal distributions, lack of normality, etc. To ascertain the extent of the effects of these problems on our statistical results, one species, *B. a. amphitrite,* was also subdivided into smaller population units and these units were subjected to analyses, as distinct taxa, in several tests (parameters for the populations of *B. a. amphitrite* are given in Appendix B). Tests for the significance between means, and analyses of variance tests were conducted to determine measurement bias, asymmetry, allometric growth, and homogeneity of variance (Appendix C), as well as tests of the significance of the results of the statistical analyses (Appendix D, E).

Two multivariate statistical techniques, which are appropriate for taxonomic analyses requiring simultaneous use of multiple characters having marked variability, have been applied in this study of the intra- and interspecific relationships of the taxa of the *amphitrite* complex. These techniques, the generalized distance function (Mahalanobis, 1930a, b; 1936) and the discriminant function (Fisher, 1936), each yield a single index of affinity, or divergence between pairs of taxa. Both functions are based on the assumption that the characters have multivariate normal distributions and that the populations have equal variances and covariances (homogeneity). Although there are no adequate tests for normality (cf. Fisher, 1944; Cochran, 1947), no radical departures from normality are apparent in the characters of the taxa (Appendix C-2: 1-14).

The generalized distance function (D^2 statistic) was designed to establish constellations of groups based on similarities of group characters. This resemblance is expressed in terms of Euclidian geometry as the square of the distance between groups in multidimensional space. The function was first applied to an anthropometric study of 22 interbreeding Indian castes (Mahalanobis, Majmmdar, and Rao, 1949), and has subsequently been applied to a variety of other biological studies for the determination of group affinities or divergences. Details of the mathematics of the generalized distance function are given by Rao (1952: 357). A summary of the computations used in the application of this function to the *amphitrite* complex is given in Appendix D-1. The resulting distances between pairs of taxa were then clustered to give indications of measures of affinity, and broader measures of relationship were obtained by grouping the resultant clusters into constellations

(figs. 4, 5). The techniques used in this study to obtain clusters and constellations are patterned after Rao (1952) and are detailed in Appendix D-2. Although the generalized distance function has been used satisfactorily in other studies, it was necessary to determine its applicability and efficacy in barnacle taxonomy. Using the five population subdivisions of *B. a. amphitrite* as distinct taxa, the function was applied to all taxa to ascertain whether intraspecific affinities among the populations of *B. a. amphititre* were greater

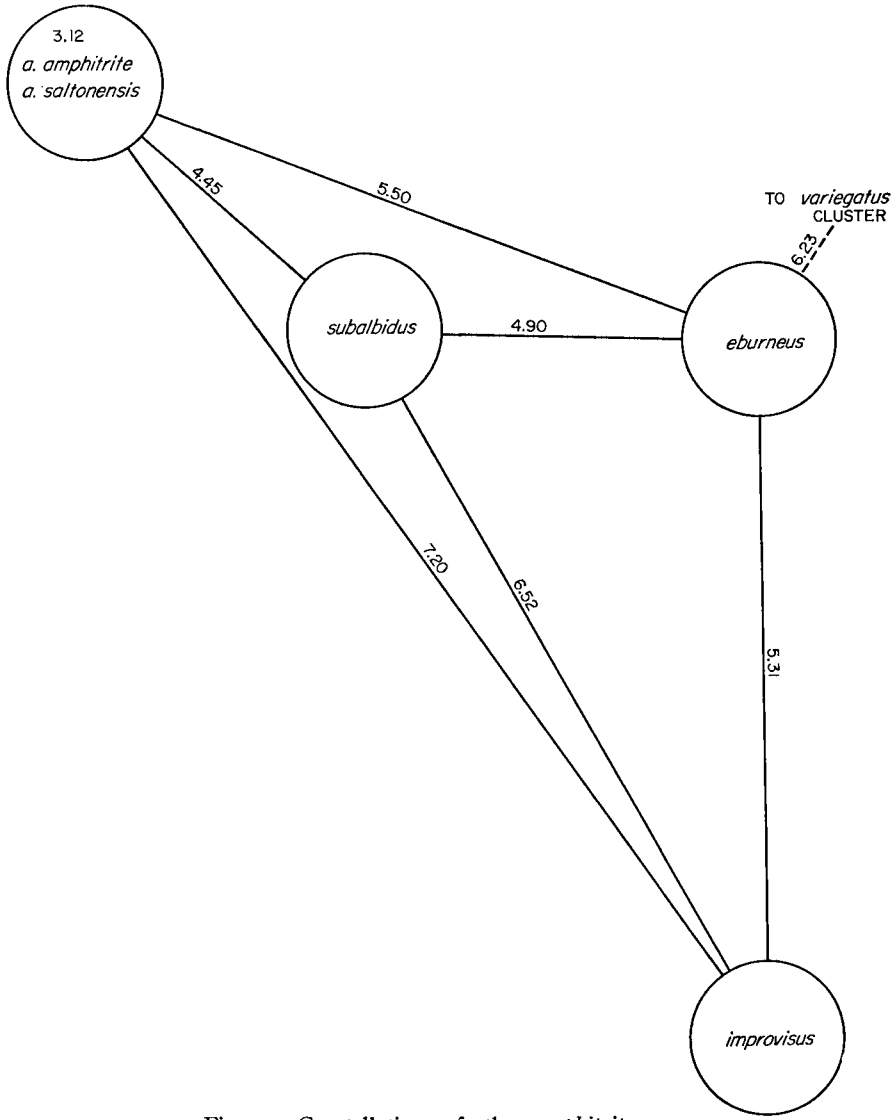

Fig. 4. Constellation of the *amphitrite* group.

than the interspecific affinities among the taxa in general. The results of these analyses are given in Appendix D-3.

The discriminant function was designed by Fisher (1936) for the separa-

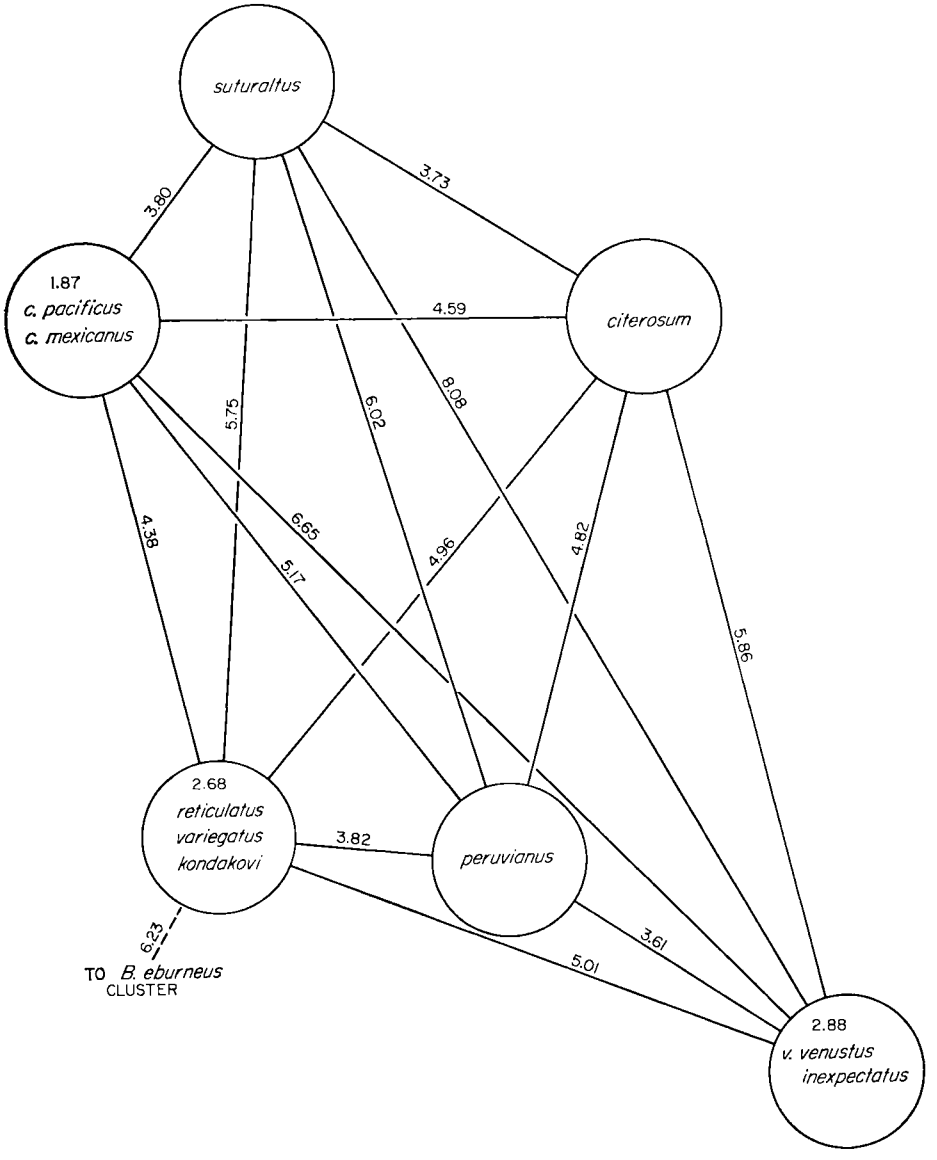

Fig. 5. Constellation of the *concavus, venustus,* and *variegatus* subgroups, and the *pallidus* (except *B. dentivarians*) group.

tion of two species of *Iris* on the basis of morphological characters, and subsequently has been used extensively in taxonomic studies. The function utilizes a series of characters in the construction of a linear function which has the property of discriminating between any chosen pair of classes (taxa) better than any other linear function, i.e., will give the smallest possible amount of overlap or frequency of misclassification (Mather, 1947). Rao (1949a) points out that the distance between two populations is an explicit function of the proportion of overlapping individuals. The discriminant function is closely related to the generalized distance function and develops the same square of the distance, D^2, which is the variance of the discriminant function treated as a linear combination of the measurements (Rao, 1952). In this study, the discriminant function was applied only to "closest neighbor pairs" of taxa, as determined by the D^2 values computed by the generalized distance function. The computations for the discriminant function and test for the significance of the results obtained from it are given in Appendices E-1 and E-2, respectively. Two additional applications of the discriminant function were made in this study. The first, the classification of individuals as members of one of a pair of given populations, was applied to a pair of very closely allied taxa, i.e., *B. variegatus* and *B. reticulatus*. The mathematical computations for this application of the discriminant function are given in Appendix E-3. The second was the objective assessment of the value of the taxonomic characters used (cf. Williams & Lambert, 1961). All morphological characters which could be reliably measured or enumerated were used in these analyses. However, if the discriminatory power gained by increasing the number of characters beyond a reasonable level of significance is not appreciable, such additions will not be commensurate with the work and computational procedures required to obtain them (cf. Rao, 1949b). Consequently, the discriminatory power of the 15 characters used in this study was tested, with a view toward future applications. The results are given in Appendix E-4.

Statistical analyses and tests were preformed on the IBM 709 computer at the University of Washington Computer Center. The generalized distance function was programmed by Mr. Paavo Kovala, Scientific Programmer, Department of Oceanography, University of Washington. The program for the discriminant function for two groups and the program for the analysis of variance were adapted by Mr. Kovala from BMD programs (BMD, 1964) BMD04M and BMD01V, respectively.

Morphology and Terminology

In general, the descriptive terms used in the descriptions of the species of the complex agree with those of Newman et al. (1969) and Newman & Ross

(1971). However, the complexities of specific identifications and interspecific relationships within the *amphitrite* complex have required the restriction or redefintion of certain terms and the introduction of several new terms. A few such terms, which were originally introduced by Henry (1974) in the descriptions of four new species of this complex, have been expanded, herein, to permit their application to the complex in its entirety.

The principal descriptive diagnostic characters afforded by the shell nad opercular valves have been described and illustrated by Pilsbry (1916) and Newman & Ross (1971) and need not be repeated. The supplemental characters used in the descriptions are defined in the glossary following. The mensural characters derived from the opercular valves have been defined previously (pp. 13-15); their application to the numerous configurations presented by taxa of the complex are illustrated in figures 1 and 2. The diagnostic significance of interlaminate figures (cf. Cornwall, 1959) of the shell, as purported by Read (1960), Harding (1962), and Davadie (1963), has not been substantiated for the species of this complex, where intraspecific variation and interspecific overlap in the figures were found to be considerable. Although most previous species descriptions have included at least brief references to some of the characters afforded by the trophi and cirri, few have considered these structures in detail. In the species of the complex, the structure, and particularly the armature, of the trophi and cirri have afforded numerous descriptive diagnostic characters. The characters of the animal used in the statistical analyses have previously been defined (pp. 15, 16); the general morphology of the trophi and cirri is described below. Intraspecific variation in these characters is discussed as it pertains to individual taxa. A list of abbreviations used in the text is given in Table 2.

Table 2. List of institutions with abbreviations used in the text

Academy of Natural Sciences, Philadelphia, U.S.A.	ANSP
Bernice P. Bishop Museum, Honolulu, Hawaii, U.S.A.	BPBM
British Museum (Natural History), London, England	BM
California Academy of Science, San Francisco, California, U.S.A.	CAS
Haifa Sea Fisheries Research Station, Haifa, Israel	HSFRS
Institute of Hydrobiology and Fisheries, Alexandria, Egypt	IHBF
Museum of Comparative Zoology, Harvard University, Cambridge, Mass., U.S.A.	MCZ
Massachusetts State College	MSC
New Zealand Oceanographic Institute, Wellington, New Zealand	NZOI
Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands	RMNH
Seto Marine Biological Laboratory, Japan	SMBL
National Museum of Natural History, Smithsonian Institution, Washington, D. C., U.S.A.	USNM
Zoological Museum, University of Berlin, Germany	ZMUB

Glossary of Supplemental Terms Used in the Species Descriptions

Shell

Parietal tubes: arranged in single row or in two or more rows between inner and outer lamina. Primary: tubes nearest inner lamina, if in more than one row. Subsidiary: tubes, in one or more rows, between primary tubes and outer lamina. Vesicular sheath: sheath composed of irregular, thin-walled calcareous vesicles, sometimes extending into furrow below overhanging lower margin of sheath.

Scutum

Tergal segment: narrowly inflected part of scutum near tergal margin.

Tergum

Carinal segment: part along carinal margin of tergum distinguished by upturned growth ridges, occasionally scarcely discernible or absent; sometimes protuberant in upper part and scarcely discernible, or rarely narrow, below protuberance; often delimited by ridge or groove.

Spur fasciole: nearly level, slight depression on outer surface of valve, extending to apex in line with spur; usually delimited on one or both sides by narrow groove.

Spur furrow: moderate to deep groove on outer surface of valve extending to apex in line with spur; with sides sometimes infolded.

Trophic and Cirral Setae

Simple: setae lacking lateral processes.

Feathered: setae with somewhat oblique, hair-like processes (setulae) on each side of shaft approximately equal in thickness to simple setae. Pinnate (fig. 6a): with short processes, usually restricted to apical third, or less, of shaft, rarely extending beyond apical half. Plumose (fig. 6b): with closely set, slightly longer processes, extending nearly to proximal end of shaft.

Complex cirral setae of Cirrus III: setae usually shorter and broader than simple or feathered setae, with single or double row of processes, usually thickened, on one side of shaft; or with apical branches. Pectinate (fig. 6c): with double row of short, usually fine, processes; shaft about same size as that of simple and feathered setae. Denticulate (fig. 6d): with single row of tooth-like processes. Bidenticulate (fig. 6e): with double row of tooth-like processes, varying in size and number. Bifurcate (fig. 6f): with 2 equal, or more frequently subequal, apical branches. Multifurcate (fig. 6g): with 1 long apical and 3 or 4 lateral branches (see also figs. 22, 23).

Fine Processes of Trophi and Cirri (fig. 7).

Scales: plate-like structures with margins unarmed (simple), or armed with minute spinules (spinulose) or denticles (denticulate).

Setulae: hair-like processes.

Spinules: fine processes with 1 (simple), 2 (bifid) or more (multifid) terminal points.

Teeth: tooth-like structures occuring on the labrum, mandible, and certain cirri; cirral teeth are conic, spike-like, or erect (below posterodistal angles).

General Morphology of Trophi and Cirri

Labrum (fig. 8a, b). — The labrum is either simple or multidenticulate. A simple labrum usually has a few teeth on the crest on either side of the notch, occasionally on only one side, or very rarely lacks teeth. Frequently, the

crest also bears setulae; however, their presence or numbers has not proved to be of significance. A multidenticulate labrum not only has few to numerous teeth on the crest on each side of the notch but also a series of teeth, progressively decreasing in size, extending down into the notch on either side. The presence of a multidenticulate labrum, as opposed to a simple labrum, is one of the principal diagnostic characters used to distinguish one group of the complex.

Palpus (fig. 8c, d). — No diagnostic characters have been determined conclusively; however, some differences in the type of setae on the upper

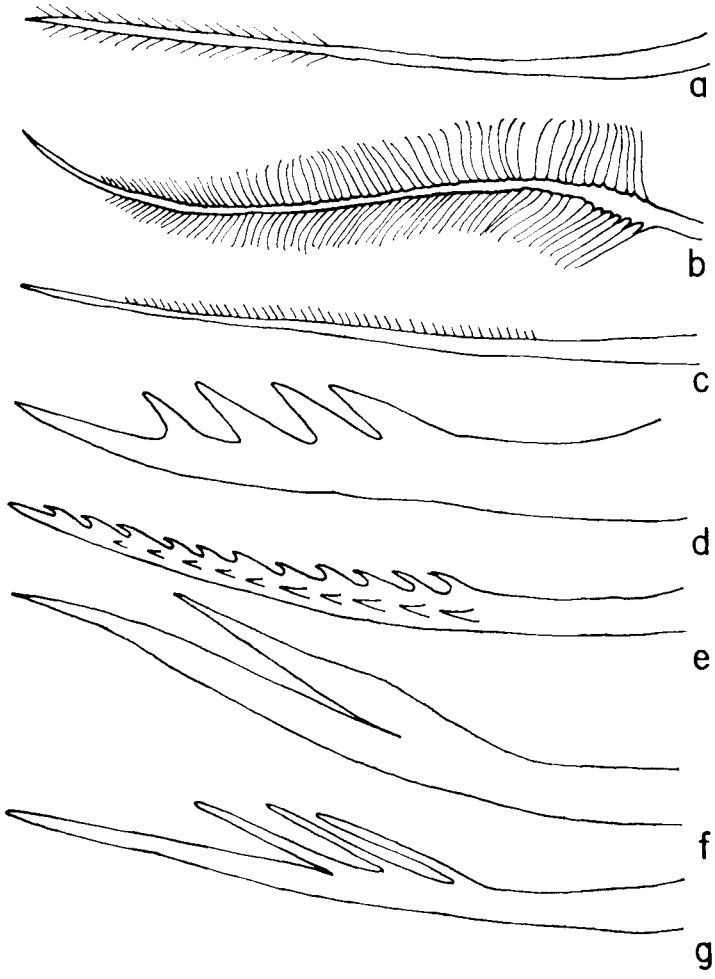

Fig. 6. Types of cirral setae: a, pinnate; b, plumose; c, pectinate (only 1 row of setulae illustrated); d, denticulate; e, bidenticulate; f, bifurcate; g, multifurcate.

margin and the type and position of setae on the labral face near the upper margin have been noted. The short setae on the upper margin may be finely pinnate, pinnate, or simple. Setae on the labral face near the upper margin, although usually pinnate, are variable in length and coarseness and sometimes may be curled at the tips.

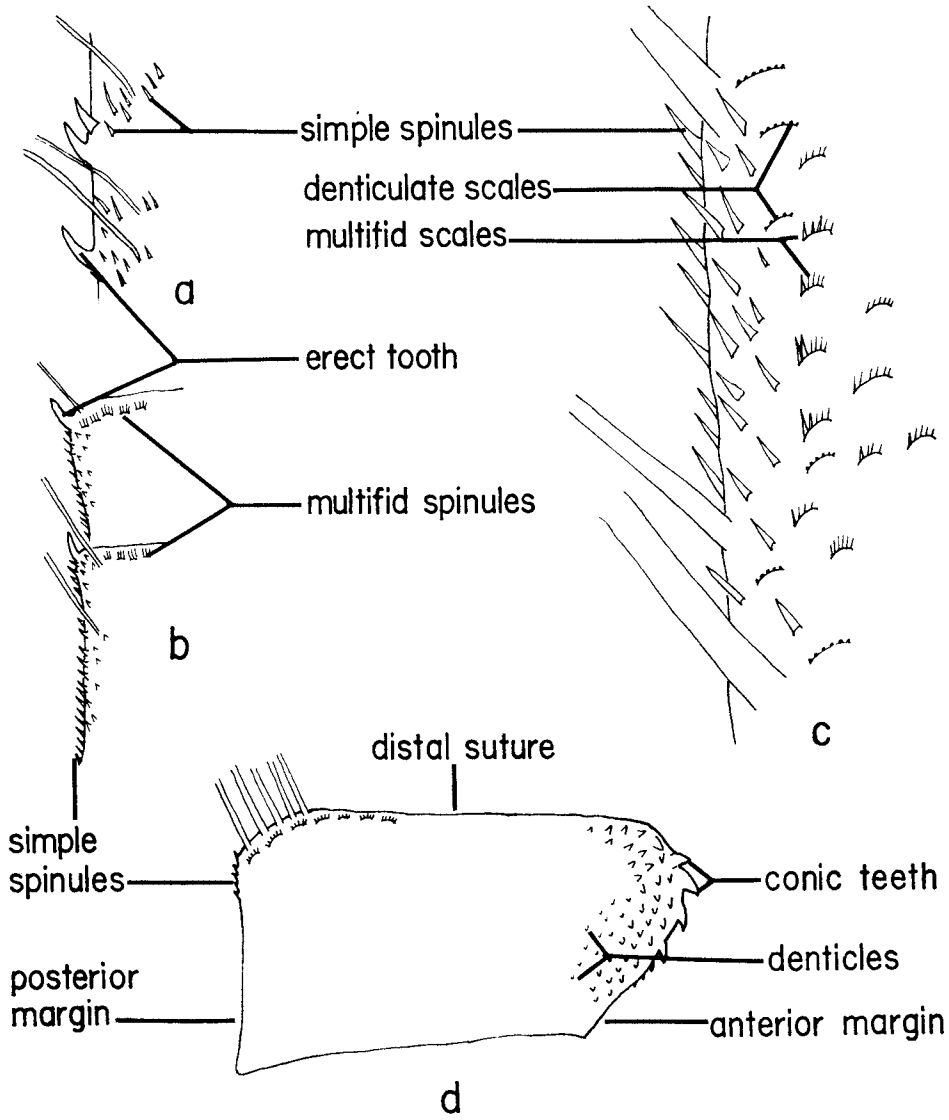

Fig. 7. Fine processes of cirri: a-c, posterior parts of segments of cirrus III; d, proximal segment of cirrus III.

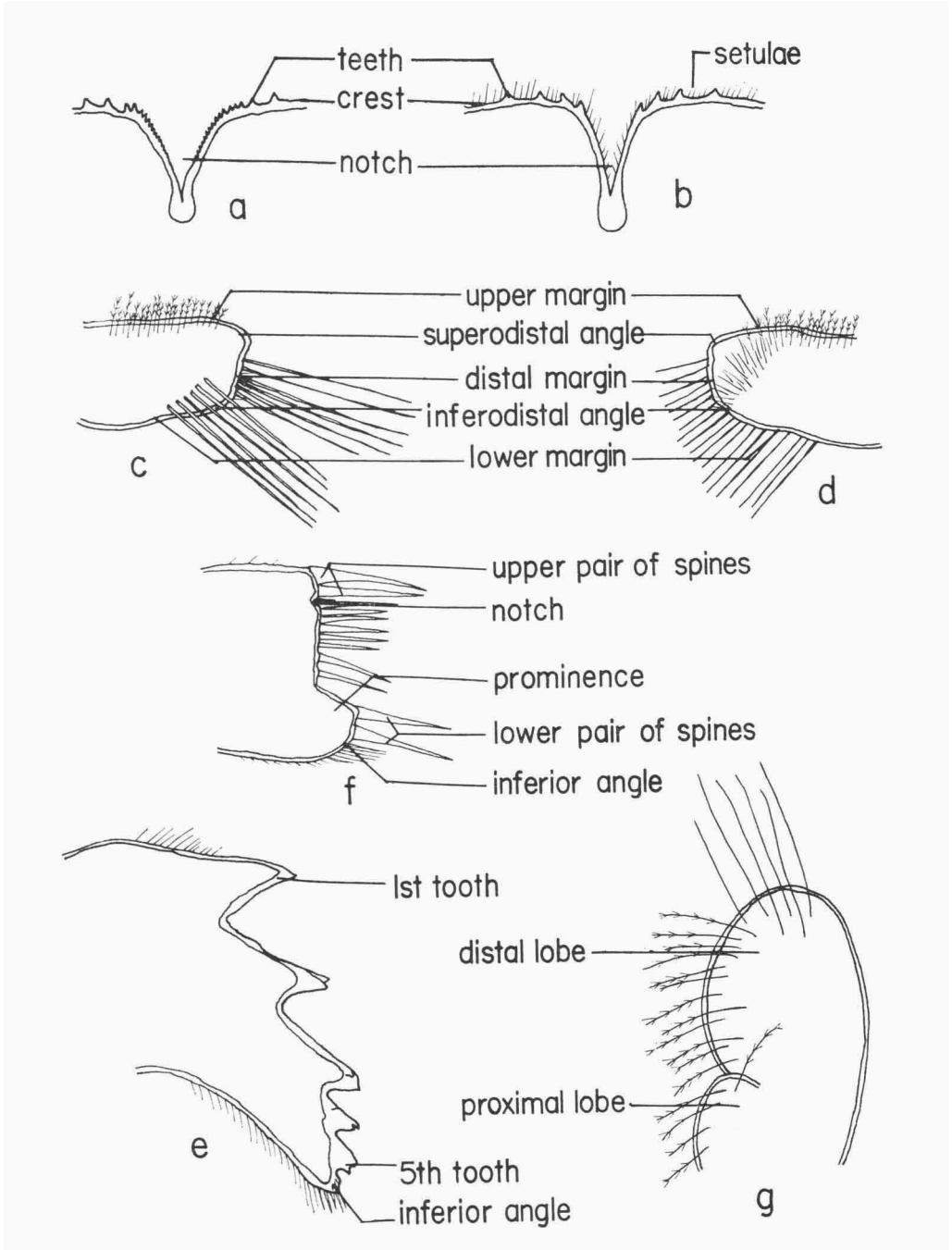

Fig. 8. Trophi. — a, b, labra: a. multidenticulate; b, simple; c, d, palpus: c, outer face; d, labral face; e, mandible; f, g, 1st and 2nd maxillae.

Mandible (fig. 8e). — The number of teeth varies from 4 to 7 for species of the complex. The lowest tooth may be confluent with the inferior angle, or if not confluent, the angle may or may not be spinose. As the mandible is subject to considerable wear during the intermolt period, the spines on the inferior angle and denticles on the lower teeth may not be apparent.

First maxilla (fig. 8f). — Several characters have proved of value in species identification, although their usefulness in closely allied species is restricted by the considerable intraspecific variation often observed. These characters include the presence or absence of a notch below the upper pair of spines, the number of spines between the upper and lower pairs, and to a lesser extent, the presence and strength or a prominence at the base of the lower pair of spines; in one species, *B. eburneus,* the intermediate spines are pectinate.

Second maxilla (fig. 8g). — No noteable differences have been observed in this structure among the species of the complex; some have setae with modified tips (bent) on the upper lobe.

Anterior cirri. — The number of segments in each cirral ramus often has been used as a character in species descriptions. We have found this character subject to both growth and external factors, and therefore, unreliable. We have chosen instead to use the segmental relationship between the two rami, that is, the number of segments by which the anterior ramus exceeds (+) or does not exceed (—) the posterior ramus. In the statistical analyses, this character is referred to simply as the number of segments of a given cirrus. The armature of each species is given in detail in the descriptions; however, a few general comments may be made regarding the cirri and the format used in these descriptions. The protopods, which are described collectively for the anterior cirri, all have some plumose setae posteriorly, in addition to pinnate and simple setae. With few exceptions, the rami of cirri I and II are not particularly distinctive; the distal sutures all have long setae; the outer faces are usually armed with a few spinules and scales near the anterior or posterior margins; and the inner faces are setose. In contrast, the rami of cirrus III are distinctively armed and, therefore, are treated in considerable detail in the descriptions. The format includes a general statement regarding the armature and setation, followed by a more specialized description of particular segments. The sequence followed includes the armature of 1) the distal sutures, 2) the anterior margins, 3) the outer faces near the anterior margins, 4) the inner faces near the anterior margins, 5) the posterior margins, 6) the outer faces near the posterior margins, and 7) the inner faces near the posterior margins. The teeth and denticles on the outer faces near the anterior margins and on the margins are usually

directed anteriorly or decurved; those near the anterodistal angle are usually also directed anteriorly or decurved; occasionally they may be directed distally. Some species have complex setae on the inner faces.

Posterior cirri. — Both the protopods and the cirri are described collectively with a general statement of the armature and setation, followed by a more detailed description of cirrus IV in the format given for the anterior cirri. The teeth on the outer faces near the anterior margins and on the anterior margins of cirrus IV are most frequently decurved, occasionally directed anteriorly; those near the anterodistal angles are usually directed anteriorly or anterodistally. As has been noted by previous investigators, the number of paired setae on the median segments of the rami of cirrus VI is frequently of diagnostic significance; this character is described separately.

Basidorsal point of penis (fig. 9). — Barnes & Klepal (1971) have attributed considerable taxonomic significance to the pedicel of the penis. We have not considered the penial girdle in the present study; however, the basidorsal point (referred to as the "horn" by Barnes & Klepal) is, at times, a useful diagnostic character. Setation of the basidorsal point, which is recorded for the first time for four species of the complex, appears to be variable; however, it is possible that the lack of setae in some specimens may be due to preservation or slide preparation.

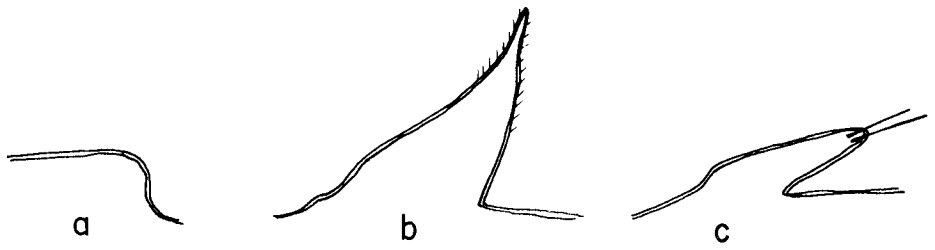

Fig. 9. Types of basidorsal points: a, very low, nude; b, spinulose; c, nude, with 2 subapical setae.

Interspecific Relationships within the *amphitrite* Complex

Although considerable similarity in morphology exists among the taxa of the complex, two presumably natural groupings can be readily recognized. The first, the nominal or *amphitrite* group, differentiated by the characteristic multidenticulate labrum, includes, in addition to *B. a. amphitrite, B. a. saltonensis, B. subalbidus, B. eburneus,* and *B. improvisus.* An identical grouping, or constellation, was arrived at through the use of the generalized distance function (fig. 4). The second, or *pallidus* group, is characterized by the

presence of subsidiary tubes in the parietes, by the vesicular structure of the sheath, and by the presence of complex setae on the inner faces of cirrus III. The *pallidus* group includes, in addition to the nominal species, *B. albisostatus, B. kondakovi, B. citerosum, B. suturaltus, B. dentivarians,* and provisionally, *B. abeli,* and *B. patelliformis.* The characters derived from the parietal tubes, the sheath, and the complex setae were not described for the latter two species and no material was available; however, the ribbed shell and the opercular valves suggest their close relationship to *B. albicostatus* and *B. kondakovi,* respectively.

The remaining species are distinguished, not by the particular characters that they share in common, but rather by the absence of the diagnostic characters of the first two groups (except for *B. inexpectatus* which does have complex setae on cirrus III). Further subdivisions, however, can be made on the basis of similarities in general morphology. Such subgroups, three in number, consist of 1) *B. concavus pacificus, B. c. mexicanus, B. c. indicus,* and *B. c. sinensis*; 2) *B. variegatus* and *B. reticulatus*; and 3) *B. venustus, B. poecilotheca, B. inexpectatus,* and *B. peruvianus.*

As neither *B. pallidus* nor the principal diagnostic characters of the *pallidus* group were included in the statistical analyses, the second and third constellations (fig. 5) derived from the generalized distance function do not accurately represent the interrelationships of the species of the *pallidus* group with the *concavus, variegatus,* or *venustus* subgroups. The interrelationships of the taxa within these subgroups, however, is clearly demonstrated by the function.

Key to the groups of the *amphitrite* complex

1. Labrum simple; parietes with or without subsidiary tubes; cirrus III with or without complex setae 2
— Labrum multidenticulate; parietes without subsidiary tubes; cirrus III without complex setae . . . . . *amphitrite* group
2. Parietes without subsidiary tubes; sheath solid; cirrus III rarely with complex setae 3
— Parietes with subsidiary tubes; sheath vesicular; cirrus III with complex setae . . . . . *pallidus* group
3. Parietal tubes with or without transverse septa; tergum with spur furrow or fasciole; cirri III-VI usually with simple spinules or erect teeth below posterodistal angles 4
— Parietal tubes without transverse septa; tergum with spur furrow; cirri III-VI without simple spinules or erect teeth below posterodistal angles . . *concavus* subgroup
4. Parietal tubes usually with transverse septa; tergum with spur furrow or fasciole, spur length greater than width, distance from basiscutal angle to spur usually greater than spur width; cirrus III without complex setae . . . *variegatus* subgroup
— Parietal tubes without transverse septa [with 1 exception]; tergum with spur fasciole, spur length less than spur width, distance from basiscutal angle to spur 1/2 or less spur width; cirrus III without [with 1 exception] complex setae *venustus* subgroup

Interrelationships may be seen among the subdivisions, particularly through the specialized characters shared by some members. For example, although none of the species of the *amphitrite* group have complex setae or more than a single row of parietal tubes, both *B. subalbidus* and *B. eburneus* frequently have the vesicular sheath characteristic of the *pallidus* group. Similarly, *B. inexpectatus* of the *venustus* subgroup has complex setae on cirrus III as do members of the *pallidus* group; however, it lacks the vesicular sheath and subsidiary tubes of the parietes. Although a multidenticulate labrum is restricted to the *amphitrite* group, *B. inexpectatus* and three species of the *pallidus* group may have more teeth on the crest than other species with simple labra, and a few teeth on the edge of the notch near the crest. The *concavus* subgroup is characterized by parietal tubes without transverse septa and by terga with spur furrows. The first character differentiates members of this subgroup only from those of the *pallidus* group, and the second, only from those of the *venustus* subgroup. Some characters which have been useful at the specific level, e.g., the presence of erect teeth below the posterior angles and the presence of teeth or simple spinules on cirrus II, occur in several subdivisions. Erect teeth are lacking in the *concavus* subgroup; teeth on cirrus II are found in one species of the *variegatus* subgroup and in three species of the *pallidus* group, and strongly spinulose cirri II occur in one species each in the *amphitrite* and *pallidus* groups and the *venustus* subgroup.

The *pallidus* group, on the basis of the development of the parietal tubes and the sheath, might be considered the most highly evolved of the complex, and the *concavus* subgroup, perhaps the least evolved; the latter is certainly the oldest in the geologic record. In the multiplication of the parietal tubes and the presence of complex setae on cirrus III, the *pallidus* group approaches the Tetraclitidae; however, *Balanus* (*Semibalanus*) *cariosus* (Pallas), which similarly has several rows of parietal tubes, also has several primitive characters. The *pallidus* group shows affinity with *Megabalanus,* the most highly evolved balanids, in the opercular valves and in the tendency, noted in *B. pallidus,* to have porose radii.

The multidenticulate labra of the *amphitrite* group might also indicate an advance in development; this charcter can not be accredited to environmental conditions as members of the group are found in extremely diverse habitats. Three of the species have a widespread distribution, being known from all oceans. In contrast, only two species of the *pallidus* group occur in more than one ocean; *B. pallidus* is known from both sides of the Atlantic and from the Indian Ocean, *B. kondakovi* is known from the Eastern Pacific and the Western Indian Ocean.

Key to the species of the *amphitrite*-complex

1. Labrum multidenticulate 2
— Labrum simple 6
2. Tergum with spur fasciole; radii narrow to wide, summits thick, crenulate or rough 3
— Tergum with spur furrow; radii narrow, summits thin, smooth, arched *B. improvisus*
3. Radii wide, summits crenulate; parietal tubes with or without transverse septa; cirri III-IV with erect teeth below posterodistal angles 4
— Radii narrow to wide, summits usually rough; parietal tubes without transverse septa; cirri III-IV without erect teeth below posterodistal angles 5
4. Parietal tubes usually without transverse septa; inner lamina with weak to moderate ribs; tergum usually with spur less than own width from basiscutal angle . . . . . *B. a. amphitrite*
— Parietal tubes usually with transverse septa; inner lamina with strong flat ribs; tergum usually with spur greater than own width from basiscutal angle . . . . . *B. a. saltonensis*
5. Scutum with fine longitudinal striae; tergum with carinal margin not protuberant, basal margin straight or slightly concave in carinal side . . . . *B. subalbidus*
— Scutum with strong longitudinal striae; tergum with carinal margin protuberant, basal margin concave, usually deeply excavated, on carinal side . . . . *B. eburneus*
6. Parietes usually longitudinally ribbed or folded 7
— Parietes usually smooth 9
7. Tergum externally with longitudinal furrows and grooves . . . . . *B. abeli*
— Tergum externally without longitudinal furrows or grooves 8
8. Parietes usually with coarse ribs, sometimes also with fine ribs: radii very wide, summits thick, rough; tergum with basal margin concave on carinal side *B. albicostatus*
— Parietes usually with few folds or numerous fine ribs; radii narrow, summits crenulate, arched; tergum with basal margin concave, sometimes deeply excavated, on carinal side . . . . . *B. patelliformis*
9. Parietal tubes in 2 or more rows; sheath vesicular; epicuticle usually persistent; cirrus III with complex setae, cirri III-VI without simple spinules or erect teeth below posterodistal angles 10
— Parietal tubes in single row; sheath solid; epicuticle sometimes persistent; cirrus III rarely with complex setae; cirri III-VI with or without simple spinules or erect teeth below posterodistal angles 14
10. Tergum with spur furrow, carinal margin rarely protuberant; sheath sometimes with calcareous vesicles in furrow below lower margin 11
— Tergum with spur fasciole, carinal margin protuberant; sheath without calcareous vesicles in furrow below lower margin . . . . . *B. kondakovi*
11. Tergum with apex not projecting above scutum, spur furrow usually open; scutum usually without pit below adductor ridge 12
— Tergum with apex projecting above scutum, spur furrow closed, nearly closed or closed above, open below; scutum with pit below adductor ridge 13
12. Epicuticle thin, usually persistent; radii with summits beveled; scutum with adductor ridge well separated from articular ridge; tergum with spur furrow occasionally almost closed . . . . . *B. pallidus*
— Epicuticle thick, persistent; radii with summits thick, smooth; scutum with adductor ridge close to articular ridge; tergum with spur furrow open . . . *B. citerosum*
13. Epicuticle thick; radii narrow, sunken; scutum with occludent margin greatly thickened in apical third, adductor ridge short; tergum with inner surface projecting below basal margin, carinal margin sometimes protuberant . . . . . *B. suturaltus*
— Epicuticle thin; radii very narrow, level; scutum with occludent margin normal, ad-

ductor ridge long; tergum with inner surface normal, carinal margin not protuberant . . . . . *B. dentivarians*

14. Parietes with or without transverse septa; tergum with spur furrow or spur fasciole 15
— Parietes usually without transverse septa; tergum with spur fasciole 20
15. Parietal tubes usually with transverse septa; scutum usually with apex recurved, without rostral pit; tergum without apex curved toward scutum 16
— Parietal tubes without transverse septa; scutum without recurved apex, usually with rostral pit; tergum with apex curved toward scutum 17
16. Radii with summits usually thick; scutum with adductor ridge close to articular ridge; tergum with spur furrow; cirrus II without spinules or teeth on outer faces near anterior margins; cirri III-VI without erect teeth below posterodistal angles . . . . . *B. variegatus*
— Radii with summits beveled; scutum with adductor ridge well separated from articular ridge; tergum usually with spur fasciole; cirrus II with simple spinules or teeth on outer faces near anterior margins; cirri III-VI with erect teeth below posterodistal angles . . . . . *B. reticulatus*
17. Scutum with adductor ridge long; tergum with spur furrow usually closed or almost so, spur own width or greater from basiscutal angle 18
— Scutum with adductor ridge short; tergum with spur furrow open, spur about 1/2 own width from basiscutal angle . . . . . *B. concavus indicus*
18. Parietes smooth; radii usually narrow, summits oblique; scutum with longitudinal striae fine 19
— Parietes rarely ribbed; radii moderately wide, summits subhorizontal to moderately oblique; scutum with longitudinal striae strong . . . . . *B. c. pacificus*
19. Shell cylindroconic; radii usually narrow; scutum with occludent margin sharply toothed, inner surface ridged . . . . . *B. c. mexicanus*
— Shell conic; radii extremely narrow; scutum with occludent margin weakly toothed, inner surface smooth . . . . . *B. c. sinensis*
20. Scutum usually with longitudinal striae; tergum with carinal margin protuberant; cirri III-VI with or without simple spinules or teeth below posterodistal angles . 21
— Scutum without longitudinal striae; tergum with carinal margin not protuberant; cirri III-VI with simple spinules or erect teeth below posterodistal angles 22
21. Parietes rarely ribbed; parietal tubes usually without transverse septa; sheath with basal margin overhanging; scutum with adductor ridge long, with pit below; cirrus III with simple spinules or erect teeth, cirri IV-VI with simple spinules below posterodistal angles . . . . . *B. venustus*
— Parietes smooth; parietal tubes without transverse septa; sheath with lower margin not overhanging; scutum with adductor ridge variable, without pit below; cirri III-VI without spinules or teeth below posterodistal angles . . . . . *P. poecilotheca*
22. Scutum with adductor ridge long, close to but not confluent with articular ridge, tergal segment usually not inflected, inner surface roughened; tergum with basal margin straight or slightly concave on scutal side; cirrus III with complex setae . . . . . *B. inexpectatus*
— Scutum with adductor ridge short, confluent with articular ridge, tergal segment narrowly inflected, inner surface strongly ridged; tergum with basal margin sloping to spur on scutal side; cirrus III without complex setae . . . . *B. peruvianus*

Balanus amphitrite amphitrite Darwin (text-figs. 10, 11, 13, pl. 1, pl. 5, fig. g, upper row right, pl. 9, figs. b, c)

Balanus amphitrite var. *communis* Darwin, 1854: 240 [in part; not pl. 5 fig. 2e, h, l (= *B. reticulatus* Utinomi); type locality by subsequent designation by Harding, 1962:

274; Natal, Republic of South Africa]. — Oliveira, 1941: 17, pl. 1 fig. 3, pl. 2 figs. 5, 6, pl. 3 fig. 1, pl. 8 fig. 7, pl. 9 figs. 5, 6, pl. 11 figs. 1-5. — Pope, 1945: 362, pl. 28 fig. 5, pl. 30 figs. 15, 16. — Karande & Palekar, 1966: 143, figs. 5, 6, pl. 1 fig. 4 (? in part; not pl. 4 row 2; see *B. reticulatus*).

Balanus amphitrite communis: Nilsson-Cantell, 1921: 311, fig. 64a-e (? in part; see *B. reticulatus*). — Nilsson-Cantell, 1932a: 110, 122, fig. 3a, b (? in part; not fig. 3c-f; see *B. reticulatus*). — Nilsson-Cantell, 1938: 36 (not fig. 7a, b; see remarks). — Zevina & Tarasov, 1954: 341, figs. 1-3. — Daniel, 1956: 20, pl. 4 figs. 15-21. — Tarasov & Zevina, 1957: 179, figs. 62a-g, 63a-d.

Balanus amphitrite forma *hawaiiensis* Broch, 1922: 314, figs. 56, 57a-e (in part; see *B. reticulatus*).

Balanus amphitrite var. *denticulata* Broch, 1927a: 133, fig. 14a-f, h-m (in part; not fig. 14g; see remarks). — Bishop, 1950: 409 [1] fig. — Millard, 1950: 266, pl. 11 figs. e, f. — Stubbings, 1961: 23 (in part; not fig. 4a-d; see *B. venustus* and *B. improvisus*).

Balanus amphitrite venustus: Sundra Raj, 1927: 113, pl. 12 figs. 1-8 (not *Balanus amphitrite venustus* Darwin, 1854: 240).

Balanus amphitrite hawaiiensis: Hiro, 1937: 432, figs. 20a-c, 21a-e. — Hiro, 1938: 304, fig. 4a, b. — Nilsson-Cantell, 1938: 40, fig. 9a, b. — Utinomi, 1956: 52, pl. 26 fig. 8. — Henry, 1958: 223, pl. 5 figs. c-e, pl. 9 figs. e-g. — Henry, 1960: 142. — Utinomi, 1960: 43, figs. 1a, b, e, 2a, b. — Ross, 1962: 12, figs. 1-5. — Utinomi, 1964: 52, pl. 26 fig. 8.

Balanus amphitrite cochinensis Nilsson-Cantell, 1938: 43, figs. 11a-e, 12a-e, pl. 1 figs. 2, 3.

Balanus amphitrite var. *fluminensis* Oliveira, 1941: 21, pl. 4 fig. 4, pl. 5 figs. 1, 2, pl. 8 figs. 1-5.

Balanus amphitrite var. *aeratus* Oliveira, 1941: 22, pl. 4 fig. 5, pl. 9 figs. 1-4.

Balanus amphitrite herzi Rogers, 1949: 8, pl. 1 figs. 6, 12-15.

Balanus amphitrite franciscanus Rogers, 1949: 9, pl. 1 figs. 5, 7, 16-19.

Balanus amphitrite var. *columnarius* Tarasov & Zevina, 1957: 179, 184, fig. 68a-e.

Balanus amphitrite denticulata: Henry, 1959: 192, pl. 1 fig. 5, pl. 3 fig. 7 upper row, right.

Balanus amphitrite amphitrite: Harding, 1962: 274, pl. 1 figs. a-h, pl. 2 figs. a-k. — Zullo, 1963: 8, figs. 53-58. — Stubbings, 1964b: 337. — Utinomi & Kikuchi, 1966: 5. — Zullo, 1966: 233. — Foster, 1967: 83, fig. 8a, b. — Stubbings, 1967: 271, fig. 14a (in part; not fig. 14b-f; see *B. reticulatus* and *B. improvisus*). — Utinomi, 1967: 200, pl. 6 fig. 1. — Utinomi, 1970: 355.

? *Balanus amphitrite amphitrite*: Davadie, 1963: 45, pl. 21 figs. 1a, b, 2a, b.

Balanus amphitrite var. *hawaiiensis*: Stubbings, 1963b: 15. — Karande & Palekar, 1966: 144, figs. 8, 9, pl. 1 fig. 5, pl. 4 row 3.

Balanus amphitrite: Southward & Crisp, 1963: 27, fig. 11.

Balanus amphitrite var. *cochinensis*: Karande & Palekar, 1966: 144, pl. 1 fig. 6, pl. 4 row 4.

not *Balanus amphitrite* var. *communis*: Krüger, 1911: 51, pl. 1 fig. 7, pl. 4 fig. 40a1-b2 (= *B. albicostatus*). — Hoek, 1913: 172 (see remarks). — Stubbings, 1963b: 14 (= *B. reticulatus*).

not *Balanus amphitrite* forma *communis*: Broch, 1922: 314 (see *B. reticulatus* and *B. poecilotheca*).

not *Balanus amphitrite communis*: Hiro, 1938: 301, fig. 1a, b. — Utinomi, 1956: 52, pl. 26 fig. 11. — Utinomi, 1960: 44, figs. 1c, d, 2c, d. — Stubbings, 1961: 22 (= *B. reticulatus*).

not *Balanus amphitrite* var. *denticulata*: Karande & Palekar, 1966: 145, fig. 7, pl. 1 fig. 7, pl. 4 row 5 (= *B. reticulatus*).

Lectotype. — BM 1961. 12.6.1a, b, c, by subsequent selection by Harding, 1962: 274.

Distribution. — Southeast Africa to Indian Union and Malaysia; Red, Black and Mediterranean seas; England and west Europe to south coast of Africa; Bermuda and southeast United States to Brazil; central California to southwest Mexico; Hawaii and Japan to Australia; east Asia from Vladivostok to China.

Material examined. — Table 3.

Diagnosis. — Shell with epicuticle usually not persistent; radii wide, summits thick, crenulate; sheath solid, lower margin slightly overhanging; parietal tubes in single row, usually without transverse septa. Scutum with growth ridges often crenulate; occasionally with fine longitudinal striae; articular ridge about 3/5 length of tergal margin; adductor ridge moderately long, well separated from articular ridge. Tergum with carinal margin protuberant in upper 1/3 to 1/2, with spur fasciole; spur length about 9/10 width; distance from basiscutal angle to spur usually less than own width; basal margin straight or slightly concave on carinal side. Labrum multidenticulate. Cirri III-VI with erect teeth below posterodistal angles; cirrus III without complex setae.

Description. — Shell usually conic or subcylindric, sometimes cylindric; orifice entire or slightly toothed, width usually more than 1/2 carinorostral diameter; surface smooth, often corroded; epicuticle thin, occasionally persistent. Radii wide, sometimes extremely wide, transversely striate; summits usually slightly oblique, sometimes horizontal, thick, crenulate; sutural edges with septa strongly denticulate on lower margins. Alae usually with summits moderately oblique, sometimes oblique, occasionally subhorizontal; sutural edges septate. Sheath solid, lower margin slightly overhanging. Inner lamina ribbed basally or sometimes to sheath; ribs low to moderately strong, weakly denticulate basally, sometimes ridged on sides near bases. Parietal tubes in single row, variable in size, 11-19 (14.2) in rostrum, usually without transverse septa and filled up in upper 1/5-1/2, occasionally filled up only at apex and with few, fine transverse septa in adjacent 1/5-1/4, or not filled up and with fine, approximate transverse septa in upper 1/4-1/3. Inner surface of outer lamina with 1-6 fine, occasionally strong, ribs between longitudinal septa; strong ribs denticulate basally, sometimes nearly reaching inner lamina. Basis with radial tubes and fine transverse septa, usually in 6 or 7 rows encircling original point of attachment, sometimes extending nearly to periphery.

Scutum flat or concave between apex and basal margin; apex sometimes slightly recurved; tergal segment usually narrowly inflected; basitergal angle obliquely truncate; occludent margin usually toothed; growth ridges low,

Table 3. *Balanus amphitrite amphitrite*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
California					
Berkely Aquatic Park	7	wood	---	23/5/52	Cornwall USNM
Venice	8	mussels	---	3/1/57	Pickens USNM
San Pedro	28	USS *Diligence*	---	27/9/61	Palumbo USNM
Cerritos Channel	2	---	---	31/12/55	Pickens USNM
Huntington Beach	12	mussels	*B. glandula, Ch. fissus*	3/11/56	Pickens USNM
Newport Bay	4	---	*B. glandula*	3/11/56	Pickens USNM
Newport Bay	3	mussels	*B. glandula*	-----	Cornwall USNM
La Jolla	2	wood	---	12/4/19	----- USNM 54740
Gulf of California					
Sonora	4	gastropods	*B. inexpectatus*	13/8/46	----- USNM 173807
Sonora	13	rocks	*Chthamalus* sp.	1/59	Eyerdam USNM
Guaymas	52	breakwater	---	5/5/62	Henry USNM,RMNH
Empalme	5	breakwater	*B. inexpectatus, Chthamalus* sp.	15/5/62	Henry USNM
Bocochibampo Bay	4	rocks	*B. inexpectatus, Ch. anisopoma*	7/5/62	Henry RMNH
Bocochibampo Bay	7	boat basin	*B. inexpectatus, Chthamalus* sp.	7/5/62	Henry USNM
Mexico, west coast					
San Carlos	19	mangroves	---	1963	Tripp USNM
Acapulco	1	boat lift	*B. inexpectatus, Chthamalus* sp.	17/5/60	Henry RMNH
Hawaii					
Off Oahu	8	surface buoys	---	24/1/44	----- BPBM 316
Off Oahu	2	surface buoy	---	26/9/44	----- BPBM 331
Pearl Harbor	4	piles	*B. reticulatus*	1931	----- BPBM 276
Pearl Harbor	3	*Anomia*	*B. reticulatus, B. trigonus*	11/3/48	----- BPBM 350
Pearl Harbor	1	lock	*B. eburneus*	-----	Sparks USNM
Honolulu Harbor	3	---	---	3/7/02	----- USNM 32517
Honolulu Harbor	1	---	*B. eburneus, B. reticulatus*	27/11/54	----- BPBM 396
Kaneohe Bay	16	limb	*B. eburneus, B. reticulatus, B. trigonus*	spring 59	Illg USNM,RMNH
Japan					
Yokosuka	5	test panel	*B. crenatus*	31/3/50	----- BPBM 371
Sagami Channel	6	limb	*B. kondakovi*	7/8/35	----- USNM 192694
Ago Bay	13	test panels	*B. reticulatus*	1/8/52	Mawatari USNM
China					
Tsingtao	2	test panel	*B. kondakovi*	1/51	----- BPBM 382

Table 3 (Continued). *Balanus amphitrite amphitrite*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
Philippine Islands					
Manila Bay, Novatas	2	---	---	4/49	---- USNM 182580
Malaysia					
Penang	∿100	rocks	---	27/7/73	Henry USNM,RMNH
Indian Union					
Bombay	51	---	*B.kondakovi,B.reticulatus,B.variegatus, B.tintinnabulum*	-----	Karande USNM,RMNH
Kenya					
Malindi	83	mangroves	---	7/3/72	Bennett USNM
Malindi	21	gastropods	---	7/3/72	Bennett RMNH
Mozambique					
Beira	1	pile	*B. reticulatus*	8/10/64	Gooding USNM
Republic of South Africa					
Bay of Natal	2	bamboo	*B. venustus*	----	Krauss RMNH 296
Durban Bay	6	shells, wood	*B. reticulatus*	30/7/64	Boss USNM
Knysna Estuary	1	---	---	-----	Rogers USNM
Salisbury I.	7	---	---	27/10/38	Brongersma RMNH 1130
Walvis Bay	9	---	---	22/1/69	---- RMNH 1252
Netherlands					
Scheveningen	1	---	---	19/9/55	Swennen RMNH 1131
Portugal					
Near Lagos	5	rock	---	4/5/71	---- RMNH 1253
Italy					
Bay of Naples	3	test blocks	*B. perforatus, B. trigonus*	9/57	Ray USNM
Yugoslavia					
Dalmatia	26	mussels	---	1940	---- USNM 89311
Egypt					
Alexandria, E. Harbor	2	glass, pile	*B. perforatus, B. trigonus*	-----	---- IHBF 123
Great Bitter Lake	∿50	---	---	8-9/50	Beets RMNH 1313
Suez, El-Shott	4	piles	*Ch. s. stellatus*	-----	---- IHBF 201
Israel					
Haifa	4	raft	*B. eburneus, B. trigonus*	27/5/56	---- HSFRS
Haifa	7	raft	*B. trigonus*	26/6/56	---- HSFRS
Haifa	3	buoy	*B.eburneus,B.reticulatus,B.tintinnabulum B.trigonus*	26/2/58	---- HSFRS

Table 3 (Continued). *Balanus amphitrite amphitrite*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
Israel (Cont.)					
Qishon River Anchorage	3	test panel	---	26/6/56	----- HSFRS
Bermuda					
Mill Creek	71	mangroves	---	5/8/62	Gooding USNM
Mill Creek	8	pecten	*B. eburneus*	5/8/62	Gooding RMNH
Pillars, Reach entry	6	---	*Ch. s. thompsoni*	summer 52	----- USNM
St. George's Harbor	7	---	*Ch. s. thompsoni*	summer 52	----- USNM 195758
Virginia					
Norfolk, Ocean Pk Br.	2	piles	*B. eburneus, B. crenatus, Ch. fragilis*	24/6/67	Gordon USNM
North Carolina					
Beaufort	5	---	---	-----	----- USNM 97625
Beaufort	15	---	*B. eburneus, Ch. fragilis*	-----	Costlow USNM
Florida, east coast					
Miami	10	M/V *Captiva*	*B. improvisus*	11/9/63	Southward USNM
Florida, west coast					
Fort Myers	1	mangrove	*B. eburneus*	-----	Stiles USNM
Tampa Bay	71	boat	*B. eburneus, B. venustus*	29/12/52	Yentsch USNM, RMNH
Port Tampa	5	rocks, piles	---	29/6/63	Ross USNM
Boca Ciega Bay	2	rock	*B. eburneus, Ch. fragilis*	8/10/55	----- USNM 209649
Saint Marks	1	oyster shell	*B. eburneus*	-----	Yentsch USNM
Panama City	3	jetty	*B. venustus*	6/11/64	Wells USNM
Mexico, southeast coast					
Bahía de Vergara	2	seawall	*B. eburneus*	17/3/65	McLaughlin RMNH
Veracruz Harbor	3	wreckage	*B. improvisus, Chthamalus* sp.	18/3/65	McLaughlin USNM
Boca del Rio	1	log	*B. eburneus, B. improvisus, B. subalbidus*	16/3/65	McLaughlin RMNH
Curaçao					
Willemstad	4	---	---	30/1/57	Holthuis RMNH 1177
Brazil					
Rio de Janeiro	16	rocks	*Chthamalus* sp.	1/2/70	Henry USNM, RMNH

fine, approximate, often crenulate; longitudinal striae sometimes present. Inner surface usually slightly roughened on upper part, sometimes smooth; articular ridge moderately reflexed, about 3/5 length of tergal margin and 2/5 length of occludent margin, end usually bluntly or sharply pointed, sometimes obliquely truncate or truncate; adductor ridge moderately long, usually

thick, sometimes acute, usually with shallow to moderate pit below bounded on tergal side by weak ridge, well separated from articular ridge; adductor muscle pit distinct; lateral depressor muscle pit small, usually shallow, sometimes moderately deep, occasionally absent.

Tergum with denticulate scutal margin; carinal margin protuberant in upper third to half, protuberance usually raised, sometimes separated from rest of valve by narrow groove; growth ridges fine, usually crenulate, often strongly so on scutal side; longitudinal striae occasionally present on carinal side; spur fasciole sometimes separated from scutal side, occasionally also from carinal side, by narrow groove; spur width about 3/10 length of basal margin; spur length about 9/10 spur width; distance from basiscutal angle about 9/10 spur width, about equal to spur length, and about 1/4 length of basal margin; spur length about 1/4 length of basal margin; end usually obliquely truncate, occasionally rounded; basal margin usually straight on both sides of spur, occasionally slightly concave on carinal side. Internally, scutal margin moderately high; articular ridge prominent, usually slightly, sometimes strongly, reflexed; articular furrow wide; crests for depressor muscle short, prominent, sometimes projecting slightly below basal margin; surface usually smooth, occasionally roughened on upper part.

Labrum with 8-25 (14.2) teeth, sometimes with setulae, on each side of deep notch.

Palpus with fine, short simple setae on upper margin, in narrow band parallel to upper margin, and in narrow band parallel to distal margin on upper half on outer face, also with long setae in tuft on lower half of distal margin and in oblique row near inferodistal angle; labral face with wide band of short, coarsely pinnate setae near upper margin, widest distally, abruptly narrowing to 2 or 3 rows proximally, few multifid setulae near distal margin, long setae near inferodistal angle, and wide band of setulae and fine simple spinules near lower margin.

Mandible with 4-6 (5.0) teeth and spinose inferior angle; 2nd tooth bifid, 3rd-6th with extra denticles.

First maxilla without notch below upper pair of spines, with 3-17 (7.1) spines between upper and lower pairs and few short spines on inferior angle; lower pair of spines usually on slight, sometimes moderately strong, occasionally strong, prominence.

Second maxilla without distinguishing characters.

Protopods of anterior cirri primarily with pinnate setae, some plumose setae posteriorly on coxopods; both segments of cirrus I with few spinules below posterodistal angles on outer faces, basipod sometimes with narrow subsutural band of simple spinules on posterior 1/3-1/2 on outer face, coxopod

sometimes with narrow band of simple scales near anterior margin on outer face; both segments of cirri II and III sometimes with few, fine simple and multifid spinules below anterodistal angles on outer faces, basipods each also with narrow subsutural band of simple spinules on outer face on posterior

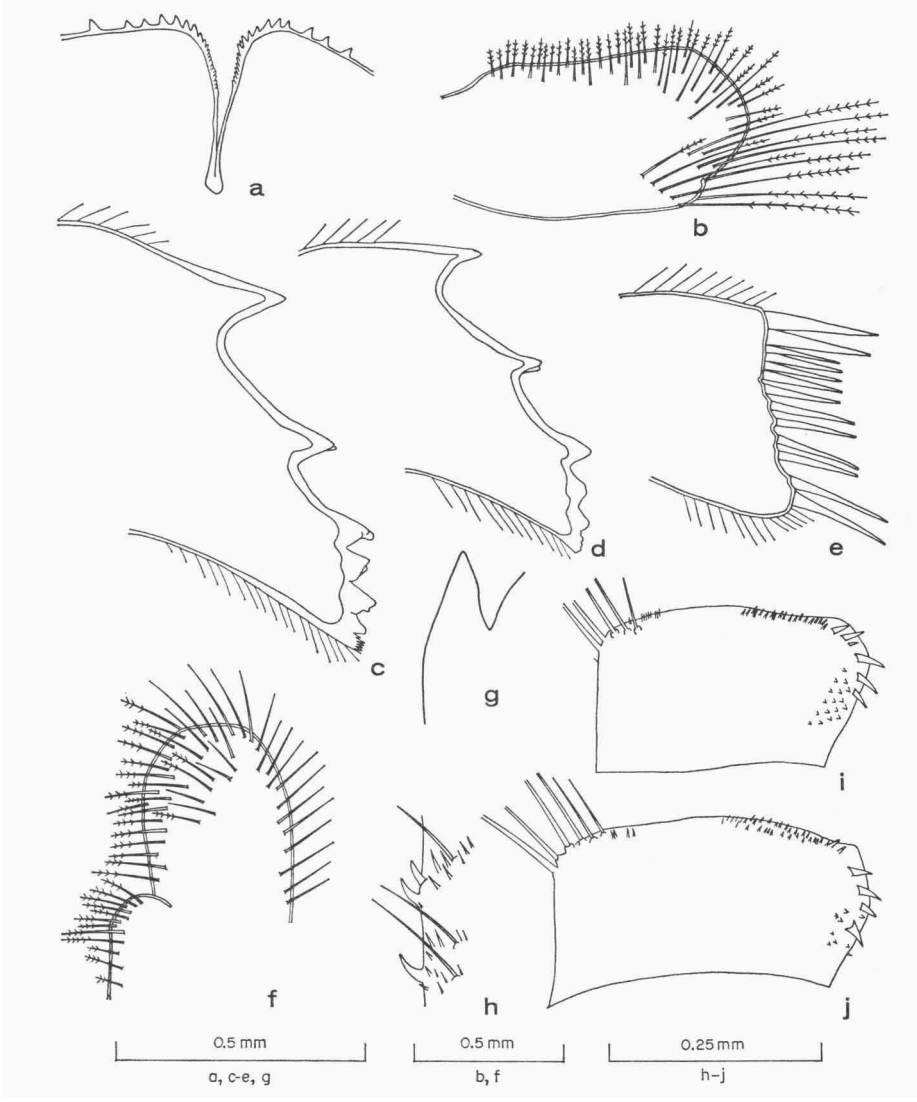

Fig. 10. *Balanus amphitrite amphitrite* Darwin. a, labrum; b, palpus; c, d, mandibles; e, f, 1st and 2nd maxillae; g, basidorsal point; h-j, anterior rami of cirrus III (h, posterior part of 2 proximal segments; i, j, 6th and 8th proximal segments) (a-j, Oahu, Hawaii: a-c, e-h, j, Kaneohe Bay, d, Honolulu Harbor; i, different specimen, Kaneohe Bay).

1/3-1/2, coxopods each with narrow band of simple scales near posterior margin.

Cirrus I with anterior ramus equal to or 1-11 (4.7) segments longer than posterior; posterior ramus with very protuberant segments; proximal segments of anterior ramus protuberant; distal sutures of both rami with long setae, also with multifid spinules on distal and some median segments, and with multifid and simple spinules near posterior margins on remaining segments; several proximal segments also with few simple spinules on inner face, near posterior margin.

Cirrus II with anterior ramus equal to or 1-6 (2.1) segments longer than posterior; both rami with protuberant segments; distal sutures with long setae, also with multifid spinules on distal and some median segments, and with multifid and simple spinules near posterior margins, occasionally also near anterior margins, on remaining segments; long proximal segments each with simple spinules on posterior margin, wide band of simple spinules on outer face and narrow band of simple spinules on inner face, near posterior margin; several adjacent segments each with 2 or 3 rows of simple spinules below posterodistal angle on outer face and few simple spinules on inner face near posterior margin.

Cirrus III with anterior ramus 1 segment shorter to 5 (2.7) segments longer than posterior; both rami with somewhat protuberant segments; distal sutures with short setae, spinules, and occasionally teeth; anterior margins and outer faces near anterior margins with conic teeth; posterior margins with erect teeth below short setae on distal angles; inner faces with band of spinules or teeth, without complex setae. Distal sutures each with multifid spinules and sometimes few simple spinules, occasionally also with 1 or 2 teeth, near anterior margin on distal segments, except ultimate; first 3 distal segments also with few short setae, remaining segments except 2 or 3 proximal segments each with multifid spinules near posterior margin and usually few spinules and 1-3 teeth near anterior margin, sometimes with teeth and simple spinules on anterior half of suture, 2 or 3 proximal segments each with multifid spinules near posterior margin and simple or multifid spinules near anterior margin. Anterior margins and outer faces near anterior margins on proximal and median segments on anterior ramus usually with teeth, sometimes with teeth on all but ultimate segment; long proximal segment usually without teeth, occasionally with few large teeth on outer face near anterodistal angle; remaining proximal and median segments each usually with 1-5 large teeth distally and several small teeth proximally on anterior margin, 2 or 3 large teeth near anterodistal angle and 2-6 rows of small teeth parallel to anterior margin on outer face, sometimes teeth in row

adjacent to anterior margin equally as large as marginal teeth; distal segments each sometimes with 1-4 large teeth on outer face near anterodistal angle; anterior margins of proximal segments of posterior ramus sometimes with 2-5 large teeth; outer faces near anterior margins of few proximal segments with few simple spinules or denticles, occasionally with few teeth, remaining proximal segments each with 2-6 rows of small teeth or 2 or 3 large teeth near anterodistal angle; median segments each sometimes with 2 or 3 large teeth near anterodistal angle. Posterior margins of both rami with 5 or 6 short setae on distal angles of all but 1 or 2 proximal segments, also with 1 or 2 large erect teeth, gradually decreasing in size distally, below distal angles of 2-7 proximal segments; long proximal segments with series of simple spinules, usually also with 1 or 2 erect teeth medially; posterior ramus occasionally with 1 or 2 erect teeth below distal angles on all but ultimate segment. Outer faces near posterior margins of both rami with narrow to wide band of simple spinules on long proximal segments. Inner faces near posterior margins with band of simple spinules or small erect teeth on long proximal segments; several adjacent segments sometimes with few denticles or spinules; each segment having erect teeth below distal angle usually with subsutural row of 6-10 simple spinules (anterior ramus), or erect teeth and simple spinules in oblique row (posterior ramus); occasionally segments of posterior ramus without erect teeth below posterodistal angle with oblique row of spinules or teeth.

Protopods of posterior cirri each usually with few, fine simple spinules near anteriodistal angle on outer face and narrow band of larger simple spinules near posterior margin on inner face.

Posterior cirri with fine multifid spinules on distal sutures; anterior ramus of cirrus IV also with simple spinules near anterior margins on proximal and some median segments, few proximal segments each occasionally also with 1 or 2 large teeth near anterior margin; posterior margins with 1 relatively long and 3 or 4 short setae, fewer proximally, on distal angles, also with 1 or 2 large erect teeth below; teeth usually on proximal halves of rami, sometimes on proximal two-thirds, occasionally only on few proximal segments; inner faces near posterior margins usually with few subsutural simple spinules on proximal segments; long proximal and 1 or 2 adjacent segments each occasionally also with 1 or 2 subsutural, large erect teeth and few rows of simple spinules parallel to margin. Anterior margins of few proximal segments of anterior ramus of cirrus IV occasionally with small teeth; posterior ramus without teeth. Outer faces near anterior margins of anterior ramus of cirrus IV usually with teeth on proximal, sometimes also on median segments, occasionally without teeth but with few simple spinules

below anterodistal angles of several proximal segments; each proximal segment usually with 2-6 rows of small teeth and denticles near anterior margin, sometimes also with 3 or 4 larger teeth near anterodistal angle; median segments each with 3 or 4 teeth near anterodistal angle, occasionally with 2-6 rows of small or large teeth and denticles near anterior margin; posterior ramus occasionally with 2 or 3 teeth, rarely also with few denticles on few proximal segments. Cirrus VI with 3-12 (7.2) pairs of setae on anterior margins of median segments. Basidorsal point of penis moderately large, nude.

Color. — Shell white or bluish-white with longitudinal lavender or purple stripes, variable in intensity and width; usually with broad medial and lateral interspaces on most parietes. Radii usually white with flecks of brownish-red, pink or purple, occasionally entirely white. Sheath generally purple or lavender, at least in part; laterals always colored, other parieties each usually colored or with colored striae or splotches; rostrum occasionally white. Scutum, externally, usually lavender or purple with narrow to wide white band near tergal margin, occasionally entirely white; internally, usually colored on lower part, occasionally entirely white. Tergum usually white with purple bands on scutal and carinal segments externally and scutal margin internally; occasionally colored except for white band on scutal margin and white articular ridge and spur; rarely entirely white.

Measurements. — Greatest diameter of lectotype 12.8 mm, height 12.2 mm. Basal diameter of largest paralectotype 30.2 mm.

Variations. — The specimens in the large lots from different localities exhibit, for the most part, all the variations noted in the description. Many of the variable characters are those characters listed by Utinomi (1960) to distinguish *B. a. hawaiiensis* (= *B. a. amphitrite*) from *B. a. communis* (sensu Utinomi). Harding (1962), in his examination of the Darwinian type material, noted variations in *B. a. amphitrite* in the color pattern of the parietes, in the summits of the radii, and in the width of the spur of the tergum. In addition to these variations, our material shows that the number of parietal tubes varies from 11-19 in the rostrum, in contrast to the 16 tubes described; the radii are not always wide with almost level summits, but may be narrow and the summits may be moderately oblique, or less often, oblique; the pit below the adductor ridge of the scutum is variable in size and shape. As pointed out by Stubbings (1967), all the characters of the tergum listed by Utinomi (1960) are highly variable.

Habitat. — Usually intertidal, often in brackish water, on rocks, shells, mangroves, shore installations, and ships. According to Hiro (1939a), this species occurs in the intertidal zone in Formosa; whereas, in the temperate

region, e.g., the mainland of Japan and the Yellow Sea, it is always on the bottoms of ships or on submerged objects but not on shore rocks.

Remarks. — As previously indicated, Darwin's (1854) description of *Balanus amphitrite* consisted of a rather detailed description of the species in general and only very brief diagnoses of the nine varieties he assigned to the taxon. Harding's (1962) subsequent designation of a lectotype and redescription of Darwin's *amphitrite* var. *communis* (= *B. amphitrite amphitrite*) has made it possible to review and at least partially resolve the confusion which exists in the literature pertaining to this species. Although earlier cirripediologists assigned specimens to var. *communis* and established numerous taxa for specimens differing from their interpretations of Darwin's typical variety, it was Utinomi (1967) who first suggested that Darwin had confounded two taxa under the name *communis*. Based on the specimens remaining in Darwin's collection, Harding described and figured the shell of the lectotype of *B. a. amphitrite* (Harding, 1962: 274, pl. 1 figs. a, b) and paralectotypes (Harding, 1962, pl. 1 fig. g) which all possess wide radii with subhorizontal summits and lack cross striations; these figures do not agree with Darwin's (1854, pl. 5 fig. 2a) figure of *B. a. communis*. As Utinomi (1967) has pointed out, Darwin's figure of the tergum (Darwin, 1854, pl. 5 fig. 2l) of *B. amphitrite* var. *communis* also does not agree with the tergum of the lectotype selected for *B. a. amphitrite* (Harding, 1962, pl. 1 figs. e, f) but does agree with *communis* sensu Utinomi (1960); to this latter species, Utinomi (1967) assigned the name *Balanus reticulatus*.

Harding (1962) listed only *B. amphitrite* var. *denticulata* as a synonym of *B. a. amphitrite* although Utinomi (1960) had clearly shown that Broch's variety was synonymous with *B. amphitrite hawaiiensis*. In addition, Utinomi (1960, 1967) pointed out that several earlier authors had confused this latter taxon with *B. amphitrite* var. *communis* [sensu Utinomi, 1938 (as Hiro), 1960, = *B. reticulatus*]

The material assigned by Nilsson-Cantell (1921) to *B. a. communis* appears to include specimens of both *B. a. amphitrite* and *B. reticulatus*. The figures (Nilsson-Cantell, 1921, fig. 64a-e) and his description of the mouth parts and cirri agree with *B. a. amphitrite*; however, his description of the shell resembles that of *B. reticulatus*. Nilsson-Cantell (1932a) commented on the marked variability of the terga of specimens he referred to *B. a. communis*. His figure (Nilsson-Cantell, 1932a, fig. 3a, b) of the opercular valves agree with those of *B. a. amphritrite*; however, his figures of specimens from the Mediterranean (Nilsson-Cantell, 1932a, fig. 3c-f) do not. As his material was dry, the latter specimens can not be assigned with certainity to any taxon, but it is probable that *B. reticulatus* was included.

Broch (1922, 1927) distinguished two new forms of *B. amphitrite* (*B. a. hawaiiensis* and *B. a. denticulata*), in part by the multidenticulate labrum; however, he questionably assigned two specimens with few labral teeth to the first taxon; these specimens are referred herein to *B. reticulatus*. Similarly, he noted that one specimen of *B. a. denticulata* had few teeth on the labrum; this specimen can not be assigned to any taxon as no further information was provided. Subsequently, Nilsson-Cantell (1938) recognized *B. a. hawaiiensis* but not *B. a. denticulata*. He stated (Nilsson-Cantell, 1938: 37) that the latter taxon could not be differentiated from *B. a. communis* which, as he had pointed out previously (Nilsson-Cantell, 1921), often had a multidenticulate labrum. He provided a figure of the opercular valves (Nilsson-Cantell, 1938, fig. 7a, b) to show the agreement with one of his earlier figures (Nilsson-Cantell, 1932a, fig. 3a, b; = *B. a. amphitrite*); however, figure 7a, does not agree with this latter figure. As he did not furnish a description of the specimen, this figure cannot be referred to any taxon.

Stubbings (1961), in the first of a series of papers on the West African barnacles, stated that he assigned specimens of *B. amphitrite* with only 3 teeth on each side of the labrum to *B. a. communis* and those with numerous teeth to *B. a. denticulata*. However, he provisionally assigned one lot from Atlantide station 50 to *B. a. denticulata* (cf. Stubbings, 1961, fig. 4a, b) although the specimens had only 4 teeth on each side of the notch. The characters of the shell and opercular valves indicate that these specimens should be referred to *B. venustus*. Anomalous specimens with multidenticulate labra from Lagos and Bathurst were referred to *B. a. denticulata*; however, several of the characters cited by Stubbings, as well as his figures of the opercular valves of the latter specimens (Stubbings, 1961, figs. 4c, d), indicate that both lots should be referred to *B. improvisus*. Subsequently, Stubbings (1963b) accepted Utinomi's (1960) diagnoses of *B. a. communis* and *B. a. hawaiiensis*, and Harding's (1962) definition of *B. a. amphitrite* (Stubbings, 1964b). Stubbings (1967), however, was apparently unaware that Utinomi (1964) had placed *B. a. hawaiiensis* in synonymy with *B. a. amphitrite* and had also proposed a new name for *communis* (sensu Utinomi), as he likewise placed *B. a. hawaiiensis* in synonymy and noted that Utinomi's *communis*, if valid, would need a new name. To test the validity of this latter taxon, Stubbings examined 28 specimens from 13 localities. Using the characters cited by Utinomi (1960) to distinguish *B. a. hawaiiensis* from *B. a. communis* (sensu Utinomi), he found that at least 8 specimens could not be assigned to either taxon. Consequently, he "... preferred to regard the West African *B. amphitrite*, ... as one rather variable form only, to which the name *B. amphitrite amphitrite* Darwin is applicable" (Stubbings, 1967: 276). We believe, how-

ever, that Stubbings' *B. a. amphitrite* definitely included two and possibly three distinct taxa. His failure to differentiate *B. a. communis* (sensu Utinomi) from *B. a. amphitrite* was due in part to the variability and thus limited usefulness of some of Utinomi's (1960) diagnostic characters. In addition, it is probably that some of Stubbings' "mixed categories" resulted from the inclusion of specimens of *B. improvisus* earlier misidentified as *B. a. denticulata* (cf. Stubbings, 1961). Stubbings (1967) also illustrated terga of *B. a. amphitrite* from five localities to show the range of spur form. Only one tergum (Stubbings, 1967, fig. 14a), with the data provided, can be referred to *B. a. amphitrite*; three terga (Stubbings, 1967, fig. 14d-f) are referred herein to *B. reticulatus* based, in part, on descriptions from their respective localities in previous papers (Stubbings, 1963b, 1961). The remaining terga (Stubbings, 1967, fig. 14b, c) can not be assigned with certainty to either taxon.

Sundra Raj (1927) reported *B. amphitrite venustus* with numerous teeth on the labrum. From the figures of the shell and opercular valves, however, this material should be referred to *B. a. amphitrite.*

In addition to recognizing both *B. a. communis* and *B. a. hawaiiensis,* Nilsson-Cantell (1938) described another subspecies, *B. a. cochinensis,* with a multidenticulate labrum. He primarily distinguished this subspecies, based on two specimens, by differences in the shell and tergum. As the differences described fall well within the observed variations of *B. a. amphitrite, B. a. cochinensis* herein is considered to be conspecific with *B. a. amphitrite.*

Karande & Palekar (1966) also referred specimens, presumably all with a multidenticulate labrum, to *B. a. communis, B. a. hawaiiensis,* and *B. a. cochinensis.* Our examination of some of Dr. Karande's material of *B. a. communis,* however, showed that *B. reticulatus* was included; the figure of the opercular valves of *B. a. communis* (cf. Karande & Palekar, 1966, pl. 4 row 2) tentatively is referred herein to the latter taxon. The figures of the other two species are referred to *B. a. amphitrite.*

Oliveira (1941) described two new varieties of *B. amphitrite*: *fluminensis* and *aeratus.* He distinguished *fluminensis* from his *communis* by the opercular valves and *aeratus* from *fluminensis* by color. Although the internal parts were not described for *aeratus* and the labrum was not described for *fluminensis,* the descriptions and figures indicate that both of these taxa should be referred to *B. a. amphitrite.*

Two subspecies, *B. a. herzi* and *B. a. franciscanus,* described by Rogers (1949) were reexamined by Henry (1959) and placed in synonymy with *B. a. denticulata.* As previously indicated, this latter taxon has been shown to be synonymous with *B. a. amphitrite.*

In describing the new variety, *B. amphitrite* var. *columnarius,* Tarasov & Zevina (1957) did not distinguish it from their *B. a.* var. *communis.* However, the description and their figures of the mouth parts, cirri, and opercular valves of both taxa agree with *B. a. amphitrite.*

The specimen assigned by Davadie (1963) to *B. a. amphitrite* only questionably can be referred to this species as little information was given. However, the figure of the tergum suggests that this material was correctly assigned.

Hoek (1913) expressed the difficulty he had in assigning the large Siboga collection of *B. amphitrite* to Darwin's (1854) varieties. Hoek recognized only var. *communis*; for those specimens which did not agree with his concept of this variety, he established a new variety, *malayensis* (see *B. poecilotheca*). None of this material can be referred to *B. a. amphitrite* as the labrum of both varieties had few teeth on the labrum. Nilsson-Cantell (1934a), who reexamined the Siboga collection, noted that many forms were included in Hoek's two varieties.

The superficial similarity of *B. a. amphitrite* and *B. reticulatus* is evident in the confusion that has persisted regarding their identities. Although only one character, the labrum, used in the statistical analyses readily distinguishes the two species, the 16 characters, used in combination in the distance function, show considerable divergence between the two (D-1:5). To eliminate the possibility that this large distance ($D^2 = 46.71$) was caused by the influence of other species in the simultaneous evaluation of multiple variables, the relationship of the same 108 specimens of *B. reticulatus* and the 272 specimens of *B. a. amphitrite* were tested with the discriminant function as though they were a "closest neighbor" pair of taxa. The resulting D^2 distance of 37.68 with only 0.11 error of misclassification is hightly significant at the 5 percent level [$F(15,364) = 187.94$], and exceeds, with one exception, the D^2 values obtained for all other "closest neighbor pairs" of taxa in the *amphitrite* complex (E-2:1). The summation of individual discriminant function Y values (fig. 11) shows minimal overlap of individuals. Similarly, when *B. reticulatus* was compared with the five populations of *B. a. amphitrite,* treated as distinct taxa (D-3:1), distances of $D^2 = 42.89$ and greater resulted, with percent of overlap of 0.05 and less, whereas the populations of *B. a. amphitrite* were separated by distances of $D^2 = 7.55$ and less, with percent of overlap, or error of misclassification, in excess of 8.5 percent. While most of the characters proposed by Utinomi (1960) for distinguishing *B. a. amphitrite* from *B. reticulatus* are too variable to be used, there can be no doubt that he was correct in recognizing two distinct taxa. Two diagnostic characters, not noted by Utinomi, are the rough versus beleved summits of the

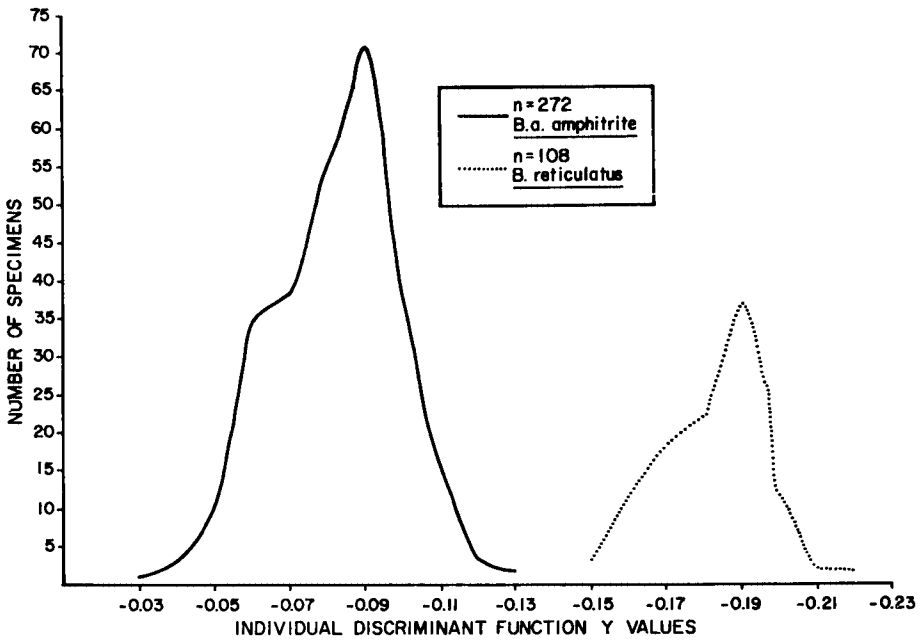

Fig. 11. Frequency distribution of individual Y values computed by the discriminant function for the populations of *Balanus amphitrite amphitrite* Darwin and *Balanus reticulatus* Utinomi.

radii and the color pattern of the sheath; unfortunately, like the color pattern of the parietes, these characters usually cannot be determined in corroded specimens.

As shown in the statistical analyses, *B. a. amphitrite* is most closely allied to the only other recognized subspecies, *B. a. saltonensis* ($D^2 = 5.01$) which is restricted to the Salton Sea (cf. fig. 13). *B. a. amphitrite* is associated with most of the other species of the complex and often with two other members of the subgenus *Balanus, B. crenatus* Bruguière and *B. trigonus* Darwin. *B. a. amphitrite* can usually be distinguished from the other species with a multidenticulate labrum by the color pattern of the parietes and sheath. Corroded or white forms can be differentiated from *B. eburneus* and *B. improvisus* and usually from *B. subalbidus* by the tergum (cf. pl. 5 fig. g). The occurrence of erect teeth below the posterodistal angles of some segments of cirri III-VI differentiates *B. a. amphitrite* from all but *B. a. saltonensis* in the *amphitrite* group. *B. a. amphitrite* may always be distinguished from the species in all other groups and subgroups of the complex, as well as from *B. crenatus* and *B. trigonus,* by the multidenticulate labrum. Corroded or white forms may be

differentiated readily from *B. crenatus* by the scutum, which in the latter species lacks an adductor ridge, and from corroded specimens of *B. albicostatus* and white or corroded forms of *B. pallidus* by the solid sheath. *B. a. amphitrite* also usually may be distinguished from corroded or white forms of *B. venustus* and *B. inexpectatus* by the opercular valves, but always from *B. venustus* by the presence of strong erect teeth below the posterodistal angles on cirri III-VI, and from *B. inexpectatus* by the lack of complex setae on cirrus III.

Balanus amphitrite saltonensis Rogers (text-figs. 12, 13, pl. 2)

Balanus amphitrite saltonensis Rogers, 1949: 5, pl. 1 figs. 2-4, 8-11 (type locality: Sandy Beach, Salton Sea, California). — Henry, 1959: 192, pl. 1 fig. 6.

Holotype. — CAS 9438.

Distribution. — Salton Sea and Wilmington Harbor, California (see remarks).

Material examined. — Table 4.

Table 4. *Balanus amphitrite saltonensis*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
California					
Salton Sea	5	---	---	-----	Bushman USNM
Salton Sea	3	twig	---	5/47	MacGinitie RMNH
Salton Sea	8	---	---	2/55	Newman USNM
Salton Sea	11	---	---	3/12/55	---- USNM 209162
Sandy Beach	4	---	---	12/47	Rogers USNM
Desert Beach	9	driftwood	---	10/44	Johnson USNM
Eiler's Resort	14	pier	---	13/5/45	Johnson USNM
Eiler's Resort	32	---	---	5/1/46	Johnson USNM
Fish Springs	2	driftwood	---	spring 47	Johnson USNM
Salton Sea Base	38	---	---	2/2/48	Johnson USNM
Salton Sea Base	15	ramp	---	28/4/49	Johnson USNM
Salton Sea Base	36	ramp	---	28/12/49	Johnson USNM
Sea View Beach	106	---	---	30/12/56	Johnson USNM,RMNH
Wilmington Harbor	2	piles	---	2/9/14	----- USNM 85042

Diagnosis. — Shell with epicuticle usually not persistent; radii extremely wide, summits thick, finely crenulate; sheath solid, lower margin overhanging; parietal tubes in single row, usually with transverse septa. Scutum with growth ridges finely crenulate; longitudinal striae rarely present; articular ridge about 3/5 length of tergal margin; adductor ridge usually moderately long, well separated from articular ridge. Tergum with carinal margin protuberant

in upper 1/3 to 1/2, with spur fasciole; spur length usually greater than width, distance from basiscutal angle to spur usually greater than own width; basal margin straight or slightly sloping on scutal side of spur, straight or concave on carinal side. Labrum multidenticulate. Cirri III-VI with erect teeth below posterodistal angles; cirrus III without complex setae.

Description. — Shell cylindric or subcylindric, often irregular in shape; orifice slightly toothed, width more than 1/2 carinorostral diameter, sometimes exceeding carinostral diameter; surface usually smooth, occasionally slightly rugose; epicuticle thin, usually not persistent. Radii extremely wide, with fine transverse striae; summits slightly oblique, thick, finely crenulate; sutural edges with septa strongly denticulate on lower margins, interspaces between septa usually not filled up solidly. Alae with moderately oblique summits; sutural edges septate. Sheath solid, lower margin overhanging. Inner lamina ribbed, usually to sheath; ribs strong, flat, weakly denticulate basally, finely ridged on sides near bases or sometimes nearly to sheath. Parietal tubes in single row, usually square, sometimes compressed, 11-16 (11.8) in rostrum; usually with few fine transverse septa in upper 1/5-1/2, occasionally almost to bases, sometimes without transverse septa and filled up in upper 1/5-1/4. Inner surface of outer lamina occasionally with 2-4 fine ribs between longitudinal septa. Basis with radial tubes and few, fine transverse septa near original point of attachment; often lengthened.

Scutum usually flat except for slightly recurved apex, occasionally concave between apex and basal margin; tergal segment occasionally very narrowly reflected; basitergal angle obliquely truncate; occludent margin toothed; growth ridges low, usually crenulate, often strongly so; longitudinal striae rarely present. Inner surface occasionally roughened on upper part; articular ridge usually moderately, sometimes slightly, reflexed, about 3/5 length of tergal margin and 2/5 length of occludent margin, end usually bluntly or sharply pointed, sometimes obliquely truncate, occasionally truncate; articular furrow deep; adductor ridge acute, usually moderately long, occasionally short, sometimes with narrow shallow pit below bounded on tergal side by weak ridge, well separated from articular ridge; adductor muscle pit distinct; lateral depressor muscle pit small, usually very shallow, occasionally moderately deep, sometimes absent.

Tergum with denticulate scutal margin; carinal margin protuberant in upper third to half, protuberance usually raised, sometimes separated from rest of valve by narrow groove; growth ridges fine, usually crenulate, stronger on protuberance; longitudinal striae sometimes present on one or both sides; spur fasciole sometimes separated from scutal side, occasionally

also from carinal side, by narrow groove; spur width about 1/5 length of basal margin; spur length about 1 1/5 spur width; distance from basiscutal angle to spur about 1 3/10 spur width, about 1 1/10 spur length, and about 1/4 length of basal margin; spur length about 1/4 length of basal margin; end usually obliquely truncate, occasionally rounded; basal margin usually straight on both sides of spur, sometimes sloping to spur on scutal side, occasionally slightly concave on carinal side. Internally, scutal margin usually low, sometimes moderately high; articular ridge prominent, usually slightly reflexed, occasionally not reflexed; articular furrow wide; crests for depressor muscle short, usually not very prominent, usually not projecting below basal margin; surface usually smooth, occasionally roughened on upper part.

Labrum with 9-25 (14.7) teeth, and usually setulae, on each side of notch.

Palpus generally as in *B. a. amphitrite*; short coarsely pinnate setae on labral face usually sparse.

Mandible with 4-6 (5.0) teeth and spinose inferior angle; 2nd tooth bifid; 3rd-6th with extra denticles.

First maxilla without notch below upper pair of spines, with 4-15 (6.8) spines between upper and lower pairs and few short spines on inferior angle; lower pair of spines usually on slight, occasionally on moderately strong, prominence.

Second maxilla without distinguishing characters.

Protopods of anterior cirri with primarily pinnate setae, some plumose setae posteriorly on coxopods; protopod of cirrus I with simple spinules below posterodistal angles on outer face, basipod sometimes with narrow band of simple spinules on outer face below distal suture on posterior 1/3, coxopod sometimes also with narrow band of simple scales on outer face near anterior margin; basipods of cirri II and III each with narrow band of simple spinules on outer face below distal suture on posterior 1/3-1/2, coxopods each with narrow band of simple scales on outer face near posterior margin.

Cirrus I with anterior ramus equal to or 1-10 (4.8) segments longer than posterior; posterior ramus with very protuberant segments; proximal segments of anterior ramus protuberant; distal sutures of both rami with long setae, also with multifid spinules on distal and some median segments and multifid and simple spinules near posterior margins on remaining segments; several proximal segments each with narrow to wide band of simple spinules near posterior margin on outer face; sometimes with few simple spinules near posterior margin on inner face.

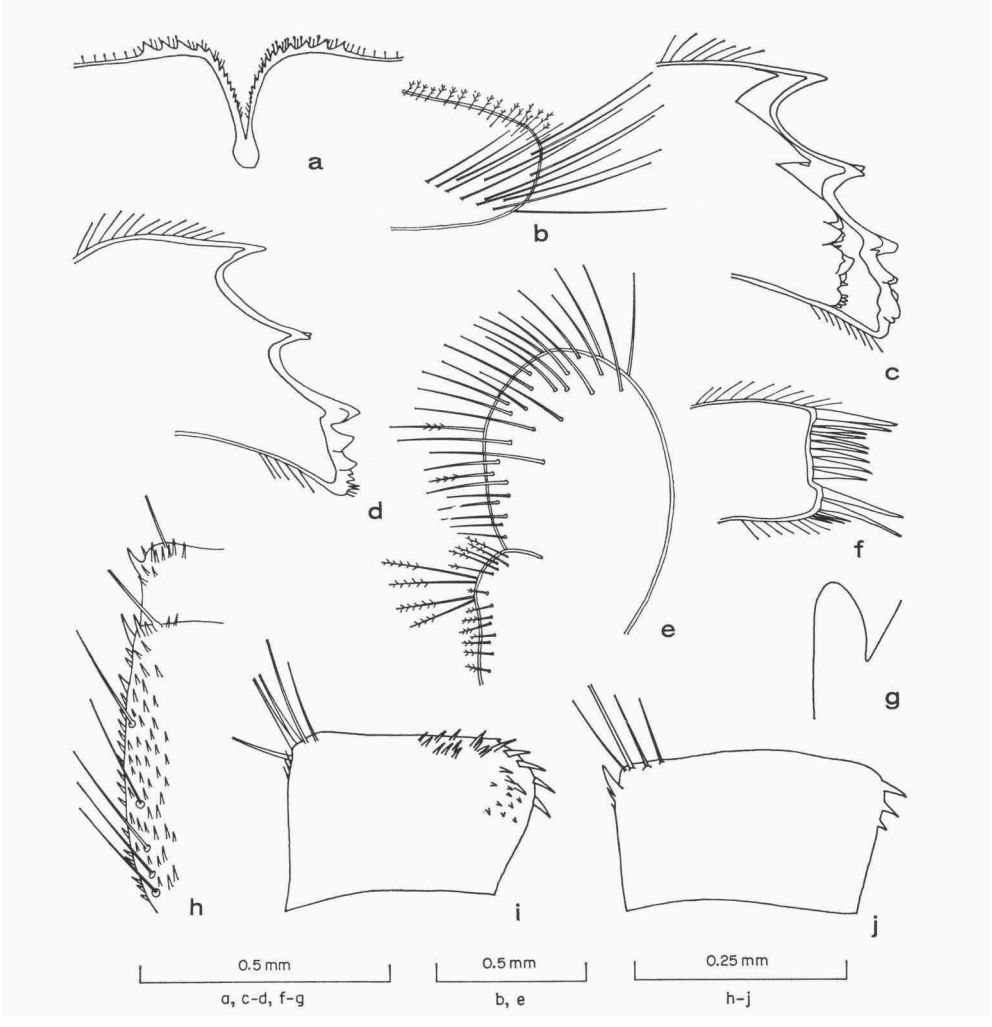

Fig. 12. *Balanus amphitrite saltonensis* Rogers. a, labrum; b, palpus; c, d, mandibles; e, f, 2nd and 1st maxillae; g, basidorsal point; h-j, anterior rami of cirrus III (h, posterior part of 2nd proximal segment; i, j, 9th and 5th proximal segments) (a-j, Salton Sea, California: a-c, i, j, Eiler's Resort; d-f, h, different specimen, Eiler's Resort; g, Fish Springs).

Cirrus II with anterior ramus 1 segment shorter to 4 (1.8) segments longer than posterior; both rami with protuberant segments; distal sutures with long setae, also with multifid spinules on distal and some median segments and multifid and simple spinules near posterior margins on remaining segments; long proximal segments each with simple spinules on posterior margin, narrow to wide band of simple spinules on outer face and narrow band of

simple spinules on inner face, near posterior margin; several adjacent segments each with 2 or 3 rows of simple spinules near posterodistal angle on outer face and few simple spinules on inner face, near posterior margin.

Cirrus III with anterior ramus 1 segment shorter to 4 (2.8) segments longer than posterior; both rami with somewhat protuberant segments; distal sutures with spinules and sometimes large conic teeth; outer faces near anterior margins with conic teeth; posterior margins with erect teeth below short setae on distal angles; inner faces without complex setae. Distal sutures with few short setae on 2-4 distal segments of posterior ramus; distal and some median segments of both rami with multifid spinules on posterior half and simple spinules on anterior half, except for 2 or 3 teeth close to anterior margin; remaining segments with multifid spinules near posterior margins and simple spinules near anterior margins. Anterior margins of anterior ramus with conic teeth on proximal and some median segments; long proximal segment sometimes with 3 or 4 teeth near distal angle; other proximal segments and some median segments each usually with 2-15 teeth, large near distal angle, remainder small or very small; posterior ramus occasionally with 1 or 2 teeth near distal angles of 1 or 2 proximal segments. Outer faces near anterior margins of anterior ramus usually with conic teeth on most segments; long proximal segment usually with few teeth near distal angle; other proximal and median segments with 2-6 rows of small teeth, sometimes also with row of large teeth adjacent to margin, and 2-4 large teeth near distal angle; each distal segment except ultimate usually with 1-4 large teeth near distal angle; posterior ramus usually with conic teeth on some proximal segments; few proximal segments usually with 2-6 rows of simple spinules or denticles; remaining proximal segments each usually with 2-6 rows of small teeth and 1-3 large teeth near distal angle, sometimes without teeth but with simple spinules on few proximal segments. Inner faces near anterior margins of long proximal segments each sometimes with scattered denticles on anterior third. Posterior margins with 3-6 short setae on distal angles of all but 1-3 proximal segments, usually with 1 or 2 large erect teeth below on 2-5 proximal segments; long proximal segments each also with series of simple spinules and 1 or 2 erect teeth medially. Outer faces near posterior margins of long proximal segments each with narrow band of simple spinules. Inner faces near posterior margins of each segment having erect teeth usually with subsutural row of 7-12 simple spinules; few adjacent segments without erect teeth sometimes also with subsutural row of spinules; posterior ramus with subsutural row directed obliquely from margin; long proximal segment usually with narrow band of simple spinules.

Protopods of posterior cirri each usually with few fine, simple and multifid spinules near anterodistal angle on outer face, few minute simple and multifid spinules near anterior margin and narrow band of simple spinules near posterior margin on inner face.

Posterior cirri usually without spinules on distal sutures of cirri V and VI and posterior ramus of cirrus IV, occasionally with fine simple and multifid spinules on most segments; anterior ramus of cirrus IV usually with fine simple and multifid spinules on distal and median segments, sometimes near anterior and posterior margins on proximal segments, occasionally without spinules. Posterior margins of posterior cirri usually with 2 or 3 moderately short fine setae, sometimes with 1 relatively long and 2 or 3 short setae on each distal angle, also with 1 or2 moderately large erect teeth below; teeth usually on proximal halves, sometimes on proximal two-thirds of rami; inner faces near posterior margins occasionally with 2 or 3 subsutural simple spinules or small erect teeth on each proximal segment; long proximal segments occasionally also with sparse row of simple spinules; long proximal segment of anterior ramus of cirrus IV occasionally with 2 rows of small conic teeth. Anterior margins of anterior ramus of cirrus IV occasionally with 1 or 2 small conic teeth on few proximal segments; posterior ramus without teeth. Outer faces near anterior margins on anterior ramus of cirrus IV usually with conic teeth on proximal and some median segments, occasionally without teeth; proximal and some median segments each usually with 2-7 rows of small teeth; proximal segments each sometimes with several rows of simple spinules or denticles and 1 or 2 large conic teeth near distal angle; long proximal and 1 or 2 adjacent segments usually without teeth; posterior ramus without teeth. Cirrus VI with 5-14 (10.1) pairs of setae on anterior margins of median segments. Basidorsal point of penis rather large, nude.

Color. — Shell white, bluish-white or occasionally pinkish-white, usually with lavender, pink, or purple longitudinal stripes of varying intensity and width, often confluent on carina and apices of laterals. Radii usually white with flecks of pink, lavender or purple, occasionally entirely colored or entirely white. Sheath usually purple or lavender, at least in part; laterals always colored, other parietes each usually colored or with colored stripes or splotches, rostrum usually white, sometimes with longitudinal purple stripe near margins, occasionally entirely colored. Scutum, externally, usually purple, occasionally pink or brownish-purple, often with white band on tergal and basal margins, sometimes entirely white; internally, usually purple or pink on lower part, occasionally entirely white. Tergum usually lavender, pink or purple with white bands on carinal and basal margins and spur fasciole, externally; internally, usually white with colored scutal margin, occasionally

colored with white carinal and basal margins, articular ridge and spur.

Measurements. — Diameter of largest specimen in type material 12 mm, height 15 mm. Carinorostral diameter of largest specimen in our material 20 mm, lateral diameter 25 mm, height 13 mm.

Variations. — Most of the specimens from the Salton Sea, as well as those from Wilmington Harbor, agree with the typical form is size, shape, and thinness of the parietes; the color pattern varies from all white to white with hyaline, pink, or lavender striae to white with colored splotches. Four specimens from two localities, collected in 1944 and 1947 on driftwood, are much larger (carinorostral diameter 20 mm), thick walled, with lavender striae and white bands on the rostrum and laterals; they lacked opercular valves. According to Hilton (1945) and Cockerell (1945) the barnacles, when they were first noticed in 1943 or 1944, were large, thick walled, and pink striped. Subsequently, they increased enormously in number, decreased in size, and lost the pink stripes.

Habitat. — Intertidal to 12 meters on submerged wood, pilings, wharfs, and rocks.

Remarks. — *B. a. saltonensis* is known only from the specialized habitat of the land-locked Salton Sea, with the exception of an anomalous lot from Wilmington Harbor collected in 1914. As shown in the summation of individual discriminant function Y values (fig. 13), *B. a. saltonensis* is very closely allied to *B. a. amphitrite*. Affinity between the two subspecies is particularly outstanding if the relation (D^2) of *B. a. saltonensis* to the individual populations of *B. a. amphitrite* is considered. It may be observed (D-3:1) that *B. a. saltonensis* is considerably closer ($D^2 = 5.65$) to the

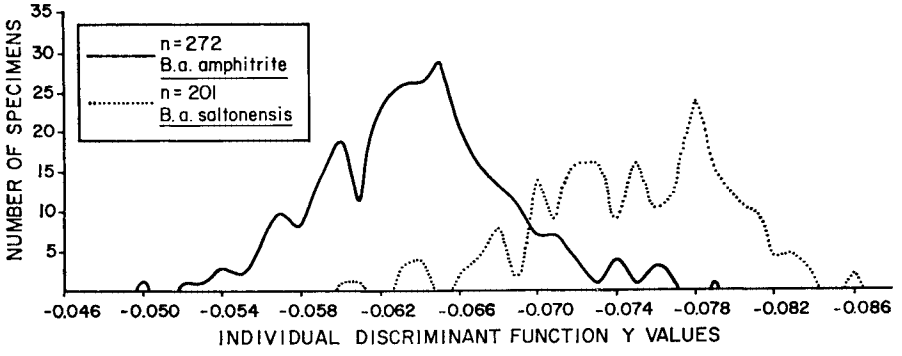

Fig. 13. Frequency distribution of individual Y values computed by the discriminant function for the populations of *Balanus amphitrite amphitrite* Darwin and *Balanus amphitrite saltonensis* Rogers.

Bermuda population than it is to any of the other *B. a. amphitrite* populations (D^2: 12.90-14.83). Although geographically distant, the Bermuda population shares several environmental factors with *B. a. saltonensis*. This Bermuda population was sampled from a bay nearly cut off by land development from the coastal environment; whereas, the other populations of *B. a. amphitrite* were taken from brackish and open coast environments. *B. a. saltonensis* and the Bermuda population, through geographic and gene-pool isolation, appear to be evolving along similar morphological lines in response to the presumably more severe environmental stresses. For example, *B. a. saltonensis* has had to adapt to the following physical and chemical conditions: annual and seasonal variations in the rates of water inflow and evaporation resulting in marked salinity changes, a wide seasonal temperature range, high sulfide and ammonia concentrations during the summer months, and an ionic concentration differing from that of marine waters (Carpelan, 1961). Furthermore, as the bottom is primarily mud, the surfaces for attachment are limited to the few rocks, pilings, submerged brush near the shore, and other barnacles. In addition, these barnacles are continually submerged, in contrast to most populations of *B. a. amphitrite* which are primarily intertidal.

Balanus subalbidus Henry (text-fig. 14, pls. 3, pl. 5 figs. f, g, lower row middle)

Balanus amphitrite pallidus: Henry, 1954: 443 (in part). — Henry 1959: 192, pl. 1 fig. 4, pl. 3 figs. 7 lower row, middle, 8 (not *Balanus amphitrite pallidus* Darwin, 1854: 240).
Balanus subalbidus Henry, 1974: 968, figs. 2a-i, 3a-j (type locality: Lake Pontchartrain, Louisiana).

Holotype. — USNM 85013.

Distribution. — Northeast United States from Massachusetts to Florida; Gulf of Mexico; Trinidad.

Material examined. — Table 5.

Diagnosis. — Shell with epicuticle usually persistent; radii narrow to wide, summits thick, rough; sheath vesicular, usually with calcareous vesicles in furrow below lower margin; parietal tubes in single row, with transverse septa. Scutum with growth ridges usually not crenulate; longitudinal striae fine; articular ridge about 3/5 length of tergal margin; adductor ridge short, close to but not confluent with articular ridge. Tergum with carinal margin convex; with spur fasciole; spur length about 9/10 width, distance from basiscutal angle to spur about 2/5 spur width; basal margin sloping to spur on scutal side, straight or slightly concave on carinal side. Labrum multidenticulate. Cirri III-VI without erect teeth below posterodistal angles; cirrus III without complex setae.

Table 5. *Balanus subalbidus*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
Massachusetts					
Boston, Charles River	5	tree branches	---	13/9/72	Taylor USNM
Maryland					
Annapolis, Sandy Pt.	10	piles	*B. improvisus*	21/6/67	Gordon USNM
South River	3	---	*B. improvisus*	winter 67	Gordon USNM
Piney Pt.	1	---	*B. improvisus*	31/5/37	---- USNM 79226
North Carolina					
Roanoke I.	3	---	*B. improvisus*	1/10/43	---- USNM 166137
Florida					
Bear Lake	20	mangroves	---	4/70	McLaughlin USNM,RMNH
Apalachee River	12	---	---	1965	Crisp USNM
Mississippi					
Pass Christian	1	---	---	9/28	Burkenroad USNM 104173
Louisiana					
Lake Pontchartrain	32	wood, shells	*B. improvisus*	----	---- USNM 200306
Rigolets, mouth	6	---	*B. improvisus*	19/1/54	---- USNM 77957
South Pt.	19	---	---	9/5/23	---- USNM 85103
Off Frenier Beach	90	---	*B. improvisus*	13/8/53	---- USNM 97958
Texas					
Mustang Bayou	1	---	---	----	---- ANSP
Port Aransas	6	twig	---	27/3/48	Hedgpeth USNM
Port Aransas	2	asphalt	*B. improvisus*	----	Hedgpeth USNM
Mexico, southeast coast					
Boca del Rio	2	log	*B.a.amphitrite,B.eburneus,B.improvisus*	16/3/65	McLaughlin USNM
Laguna Mandingo	78	mangroves	---	16/ /65	McLaughlin USNM,RMNH
Trinidad					
Maraca Bay	4	---	*B. eburneus,B. improvisus,B. reticulatus*	7/5/65	Henry RMNH

Description. — Shell conic or subcylindric; orifice sligthly toothed, width usually more than 1/2 carinorostral diameter; surface smooth, often corroded; epicuticle thick, sometimes persistent only basally. Radii narrow in conic, wide in subcylindric specimens, transversely striate; summits moderately oblique or oblique, thick, rough; sutural edges with septa weakly denticulate on lower margins. Alae with nearly horizontal summits; sutural edges septate. Sheath vesicular; usually with calcareous vesicles extending into

furrow below overhanging lower margin. Inner lamina ribbed to sheath; ribs weakly denticulate basally, ridged on sides near bases or occasionally nearly to sheath. Parietal tubes in single row, large, 11-19 (16) in rostrum, with transverse septa usually in upper half to third, sometimes to bases of some tubes. Inner surface of outer lamina sometimes with 1-6 fine, occasionally strong, ribs between longitudinal septa; strong ribs denticulate basally, sometimes almost reaching inner lamina. Basis with radial tubes and transverse septa.

Scutum with tergal segment narrowly inflected; occludent margin toothed; growth ridges low to moderately strong, sometimes crenulate in small specimens; longitudinal striae fine, usually present in small specimens; narrow longitudinal opaque stripes often present. Inner surface roughened on upper part; articular ridge high, somewhat reflexed, about 3/5 length of tergal margin and 2/5 length of occludent margin, end truncate; articular furrow deep; adductor ridge short, moderately strong, sometimes with shallow pit below usually bounded on tergal side by weak ridge, close to but not confluent with articular ridge; adductor muscle pit deep; lateral depressor muscle pit shallow, usually large.

Tergum moderately wide; scutal margin without denticles; carinal margin convex; growth ridges fine, stronger on carinal segment; latter widest medially; longitudinal striae absent; spur fasciole usually separated from scutal side by narrow groove; spur width about 1/3 length of basal margin; spur length about 9/10 spur width; distance from basiscutal angle to spur about 2/5 spur width, about 2/5 spur length, and about 1/10 length of basal margin; spur length about 1/3 length of basal margin; end obliquely truncate or rounded; basal margin sloping to spur on scutal side, straight or slightly concave on carinal side. Internally, scutal margin low; articular furrow wide; crests for depressor muscle sharp, approximate, projecting slightly below basal margin; surface roughened or ridged on carinal side, basally sometimes finely denticulate medially.

Labrum with 8-23 (14.3) teeth, usually with setulae on each side of wide notch; teeth on crest usually separated by slight space from teeth on edges of notch.

Palpus with fine, short simple setae on upper margin, in narrow band parallel to upper margin and in tuft near superodistal angle on outer face, also with long setae on distal end and in short oblique row near inferodistal angle; labral face with few long setae near distal margin, setulae on distal third, triangular patch of short finely pinnate setae, extending from upper margin to center of palpus on medial third, narrowing abruptly to 1 row proximally, and narrow band of fine simple scales along lower margin.

Mandible with 5-6 (5.1) teeth and spinose inferior angle; 1st and 2nd teeth bifid; 3rd-6th with extra denticles.

First maxilla usually without notch, occasionally with slight notch, below upper pair of spines; sometimes with short, thick simple or bifid spine on

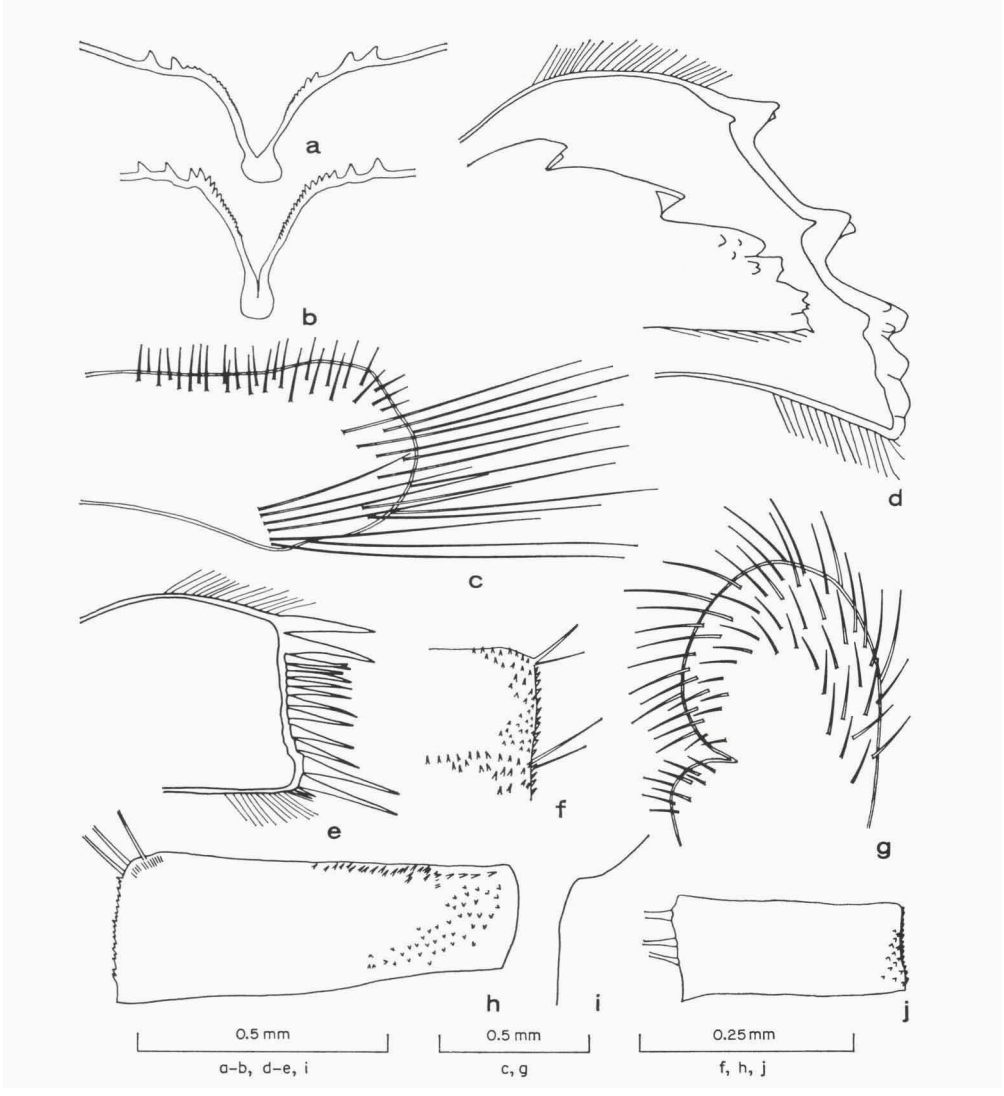

Fig. 14. *Balanus subalbidus* Henry. a, b, labra; c, palpus; d, mandible; e, 1st maxilla; f, h, anterior ramus of cirrus III [f, posterior part of 4th proximal segment (inner face); h, 6th proximal segment]; g, 2nd maxilla; i, basidorsal point; j, 4th proximal segment of cirrus IV (inner face) (a, c-h, j, holotype; b, paratype from 3/4 mile off Frenier Beach, Louisiana; i, paratype from type locality; after Henry, 1974).

outer face near lower spine of upper pair; with 5-14 (8.4) spines between upper and lower pairs and very few short spines on inferior angle; lower pair usually about same length but thicker than intermediate spines, lower pair longer than upper pair.

Second maxilla without distinguishing characters.

Protopods of anterior cirri with primarily simple setae, few plumose setae posteriorly; coxopod of cirrus I sometimes with narrow to wide band of simple scales near anterior margin; protopod of cirrus II without scales; cirrus III with few simple spinules near anterior margin on outer face of basipod, sometimes also with few simple scales medially; inner face sometimes with few simple spinules near posterior margin; coxopod with wide band of simple scales on outer face near posterior margin.

Cirrus I with anterior ramus 2-12 (5.0) segments longer than posterior; posterior ramus with very protuberant segments; proximal segments of anterior ramus protuberant; distal sutures of both rami with long setae, also with multifid spinules on several distal segments; few proximal segments each with narrow band of simple scales on outer face near posterior margin.

Cirrus II with anterior ramus equal to or 1-6 (2.0) segments longer than posterior; both rami with very protuberant segments; distal sutures with long setae, also with multifid spinules on several distal segments; proximal segments each with wide band of simple scales near posterior margin and few multifid spinules below posterodistal angle on outer face.

Cirrus III with anterior ramus 1-7 (3.4) segments longer than posterior; both rami with slightly protuberant segments; distal sutures with short setae and spinules; outer faces near anterior margins with conic teeth; posterior margins without teeth or spinules below short setae on distal angles; outer and inner faces near posterior margins with spinules and scales; inner faces without complex setae. Distal sutures with short setae, more numerous on posterior ramus, and multifid spinules on distal segments, simple spinules near anterior margins and multifid spinules near posterior margins on remaining segments. Anterior margins of several proximal segments of anterior ramus occasionally with teeth or simple spinules; posterior ramus without teeth or spinules. Outer faces near anterior margins of anterior ramus usually with teeth on proximal and median segments, occasionally on all but 2-4 distal segments; several proximal segments each with 2 or 3 rows of simple spinules near anterior margin and 3-5 teeth below anterodistal angle; remaining proximal and median segments each with 2-10 rows of teeth near anterior margin and 3-5 larger teeth below anterodistal angle; distal segments each occasionally with 1-3 sparse rows of teeth near anterior margin; posterior ramus usually with teeth on few proximal segments, some-

times on all proximal segments, occasionally without teeth but with simple spinules on few proximal segments; several proximal segments each usually with 3-5 teeth near distal angle, sometimes also with 1-6 rows of teeth, occasionally without teeth but with 1 or 2 rows of simple spinules; remaining proximal segments each sometimes with 3-5 large teeth near distal angle, also with 1 or 2 rows of teeth. Posterior margins on several proximal segments of anterior ramus usually with simple spinules, occasionally with small conic teeth; long proximal segment also with narrow band of simple, denticulate, or spinulose scales on outer face near posterior margin; inner face with narrow band of multifid spinules, sometimes also with few minute conic teeth near posterior margin; several adjacent segments each usually with narrow band of simple spinules or occasionally with narrow band of small conic teeth on inner face near posterior margin. Posterior margin on long proximal segment of posterior ramus occasionally with simple spinules; outer face with narrow band of simple, denticulate, or spinulose scales and inner face with narrow band of simple spinules, near posterior margin; several adjacent segments each usually with narrow band of spinulose scales, occasionally with 2 or 3 rows of teeth and denticulate scales near posterior margin on outer face.

Protopods of posterior cirri each with narrow band of simple spinules and denticles near anterior margin and narrow band of simple spinules near posterior margin, on inner face.

Posterior cirri with multifid spinules on distal sutures on proximal and median segments; posterior margins with 3 or 4 very short setae on each distal angle; several proximal segments of anterior rami each also with series of simple spinules; outer faces near posterior margins of several proximal segments of anterior rami each occasionally with narrow band of simple scales; inner faces near posterior margins of anterior rami with narrow band of denticles or denticulate scales; posterior rami each with narrow band of simple or denticulate scales on several proximal segments near posterior margins on both faces. Anterior ramus of cirrus IV without teeth on anterior margins; outer faces usually with conic teeth and denticles near anterior margins on proximal, occasionally on median, segments (small specimens usually without teeth, occasionally with few minute teeth); proximal segments each usually with 2-8 rows of minute teeth and denticles, or proximal and median segments each occasionally with 8-12 rows of small teeth near anterior margin and 3-7 larger teeth below anterodistal angle. Cirrus VI with 5-14 (8.0) pairs of setae on anterior margins of each median segment. Penis sparsely setose; basidorsal point very low, nude.

Color. — Parietes dirty white, occasionally with lavender longitudinal

stripes on carina; radii white; alae usually white, sometimes greyish or lavender with opaque white summits; epicuticle yellowish. Sheath white, usually with traces of adherent purple opercular membrane. Opercular valves white; scutum usually with opaque narrow, longitudinal or oblique stripes on outer surface. Opercular membrane color usually visible through thinner parts of scuta in small and some medium-sized specimens.

Measurements. — Carinorostral diameter of holotype 18 mm, height 10 mm. Diameter of largest specimen examined 20 mm, height 12 mm.

Variations. — The shell of corroded specimens is usually brownish and the radii are often very narrow and sunken. In small specimens, particularly, the scutum is especially thin on both sides of the adductor ridge; the tergum is noticeably thin medially near the base and has 4 or 5 opaque striae, in line with the crests for the depressor muscle on the outer surface, which extend from the apex to the base.

Frequently the lower pair of spines, and less often the upper pair of the first maxilla are represented by a single large spine or the 2 spines may be of subequal size. The intermediate spines often vary in size and occasionally are bifid.

Habitat. — Intertidal, on shells and wood, sometimes on mangrove roots; usually in brackish water.

Remarks. — Henry (1974) has shown that specimens previously referred to *B. a. pallidus* by Henry (1954) are, in part, *B. subalbidus* and, in part, *B. improvisus* (also see discussion under *B. improvisus*).

The material from Massachusetts greatly extends the previously known northern limit of *B. subalbidus*.

Results of the distance and discriminant function analyses indicate that *B. subalbidus* is most closely allied to *B. a. amphitrite* ($D^2 = 16.32$) and *B. eburneus* ($D^2 = 21.06$). However, a character not recognized at the time of the statistical analyses, the presence of a vesicular sheath, is common only to *B. subalbidus* and *B. eburneus* in the *amphitrite* group. The vesicular structure of the sheath, known elsewhere in the *amphitrite* complex only in the *pallidus* group, strongly suggests that *B. subalbidus* is more closely allied to *B. eburneus* than to *B. a. amphitrite*.

B. subalbidus may usually be easily distinguished from the other species with a multidenticulate labrum, except *B. a. amphitrite,* and from colorless forms of *B. venustus* by the tergum. *B. subalbidus* may usually be differentiated from *B. a. amphitrite* by the white sheath and opercular valves and always by the vesicular sheath and the lack of erect teeth below the posterodistal angles of cirri III-VI.

Balanus eburneus Gould (text-fig. 15, pl. 4, pl. 5 fig. g, lower row right)

Balanus eburneus Gould, 1841: 15, pl. 1 fig. 6 (type locality: Boston Bay, Massachusetts). — Darwin, 1854: 248, pl. 5 fig. 4a-d. — Pilsbry, 1916: 80, figs. 14, 16b, pl. 24 figs. 1-1c, 2. — Nilsson-Cantell, 1921: 309. — Neu, 1935: 93. — Neu, 1939: 216, fig. 5a-e. — Kolosváry, 1940: 36, figs. 3, 14, 18. — Kolosváry, 1947: 21, pl. 1 figs. 12-14, pl. 3 fig. i-i2. — Daniel, 1956: 18, pl. 4 figs. 7-11. — Tarasov & Zevina, 1957: 174, fig. 61. — Henry, 1959: 194, pl. 1 figs. 2, 3, pl. 3 fig. 7 lower row, right, pl. 4 figs. 1-6. — Davadie, 1963: 59, pl. 29 figs. 1-3, pl. 31 figs. 1a, b, 2a, b. — Southward & Crisp, 1963: 34, fig. 18a, b. — Zullo, 1963: 11, figs. 27-31. — Matsui, Shane & Newman, 1964: 141, fig. 1. — Utinomi, 1966: 36, fig. 1. — Stubbings, 1967: 270. — Utinomi, 1970: 353, figs. 8a-c, 9a-d, pl. 18 figs. 8-10. — Barnes & Healy, 1971: 83, figs. 1, 2.

B. [*alanus*] *democraticus* DeKay, 1844: 252.

Balanus amphitrite var. *niveus*: Oliveira, 1941: 19, pl. 3 figs. 3-6, pl. 4 figs. 2, 7 (in part; not *Balanus amphitrite* var. *niveus* Darwin, 1854: 240; also see *B. citerosum*).

Holotype. — MSC 253.

Distribution. — Northeast United States to Brazil; southwest Europe; Mediterranean, Black and Caspian seas; West Africa (Stubbings, 1967); Indian Union from Bombay to Madras; Japan to Hawaii; Gulf of California to coast of Panama.

Material examined. — Table 6.

Diagnosis. — Shell with epicuticle usually persistent; radii narrow to wide, summits thick, usually rough, occasionally crenulate; sheath usually vesicular, often with calcareous vesicles in furrow below lower margin; parietal tubes in single row, with transverse septa. Scutum with growth ridges strongly crenulate; longitudinal striae strong; articular ridge about 2/3 length of tergal margin; adductor ridge short, almost confluent with articular ridge. Tergum with carinal margin protuberant in upper 1/3 to 1/2; with spur fasciole; spur length greater than width, distance from basiscutal angle to spur about 3/4 spur width; basal margin concave or straight on scutal side, concave or deeply excavated on carinal side. Labrum multidenticulate. Cirri III-VI without erect teeth, with simple spinules, below posterodistal angles; cirrus III without modified setae.

Description. — Shell conic to cylindric; orifice toothed, width usually less than 1/2 carinorostral diameter in conic and cylindroconic specimens, more than 1/2 in subcylindric and cylindric specimens; surface smooth; epicuticle thin, usually persistent except on radii. Radii usually narrow in conic, moderate to wide in cylindric specimens; transversely striate; summits oblique, thick, usually rough, occasionally crenulate; sutural edges with septa strongly denticulate on lower margins. Alae with summits usually oblique, occasionally subhorizontal; sutural edges strongly septate. Sheath usually vesicular, frequently also with calcareous vesicles extending into furrow below over-

Table 6. *Balanus eburneus*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
Gulf of California					
Guaymas	9	dead mangrove	---	1959	Eyerdam USNM
Mexico, west coast					
Mazatlan, Sabalo Pt.	42	oyster shells	*B. improvisus*	23/5/68	Henry USNM,RMNH
Manzanillo lagoon	28	mussels	---	spring 63	Tripp USNM,RMNH
Hawaii					
Oahu	5	driftwood	---	2/1/56	----- BPBM 397
Pearl Harbor	6	rock oyster	---	1929	----- BPBM 271
Pearl Harbor	10	test panel	*B. trigonus*	20/3/45	----- BPBM 332
Pearl Harbor	3	lock	*B. a. amphitrite*	-----	Sparks USNM
Honolulu Harbor	1	test panel	*B. trigonus*	14/6/47	----- BPBM 339
Honolulu Harbor	2	boat hull	---	1950	----- BPBM 368
Honolulu Harbor	3	test panel	*B. trigonus*	21/11/54	----- BPBM 375
Honolulu Harbor	4	---	*B. a. amphitrite, B. reticulatus*	27/11/54	----- BPBM 396
Honolulu Harbor	11	---	---	14/1/56	----- BPBM 398
Honolulu Harbor	8	---	---	21/1/56	----- BPBM 401,402
Honolulu Harbor	6	test panels	---	28/1/56	----- BPBM 406
Honolulu Harbor	1	---	---	-----	----- BPBM 412
Kanoehe Bay	8	limb	*B.a.amphitrite,B.reticulatus,B.trigonus*	spring 59	Illg USNM
Japan					
Yokusuka	2	test panel	*B. crenatus*	1950	----- BPBM 372
Indian Union					
Bombay	3	---	---	-----	Karande USNM
Netherlands					
Terschelling I.	1	---	---	-----	Metz RMNH 1144
Egypt					
Alexandria	2	glass plates	---	-----	----- IHBF 971
Israel					
Haifa	9	raft	*B. a. amphitrite, B. trigonus*	27/5/56	----- HSFRS
Haifa	1	buoy	*B. a. amphitrite, B. reticulatus, B. tintinnabulum, B. trigonus*	26/2/58	----- HSFRS
Bermuda					
Mill Creek	9	pecten	*B. a. amphitrite*	5/8/62	Gooding USNM
New York					
Long I.	10	mussel, rocks	---	24/4/53	Holthuis RMNH 574

Table 6 (Continued). *Balanus eburneus*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
Maryland					
Isle of Wight Bay	16	sticks	---	2/9/52	Holthuis RMNH 576
Sinepuxent Inlet	∿50	---	---	29/9/52	Holthuis RMNH 577
Ridge	30	pier	---	13/2/66	McLaughlin RMNH
South Point	4	pier	---	20/2/66	Landrum USNM
Solomons I.	2	pier	*B. improvisus*	1/10/44	---- USNM 168649
Solomons I.	20	---	---	17/5/53	Holthuis RMNH 575
Off Point Lookout		---	---	22/5/60	Scheltema RMNH 648
Virginia					
Cape Charles Village	1	---	*B. crenatus*	23/6/67	Gordon USNM
York River bridge	2	piles	---	24/6/67	Gordon RMNH
Norfolk	6	piles	---	26/6/67	Gordon USNM
Ocean Park bridge	1	pile	*B.a.amphitrite,B.crenatus,Ch.fragilis*	24/6/67	Gordon RMNH
North Carolina					
Beaufort	2	---	*B. a. amphitrite, Ch. fragilis*	----	Costlow USNM
Wilmington	3	test block	*B. improvisus*	8/7/41	Clapp USNM
Wilmington	2	test block	---	16/8/41	Clapp USNM
South Carolina					
Sullivans I.	3	jetty	*B. venustus, Ch. fragilis*	31/12/52	Yentsch USNM
Florida, east coast					
Jacksonville	3	jetty	*B.improvisus,T.stalactifera,Ch.fragilis*	----	Yentsch USNM
Florida, west coast					
Gulf of Mexico	1	whistle buoy	*B. improvisus, B. venustus*	26/6/52	Yentsch USNM
Fort Myers	6	mangrove	*B. a. amphitrite*	----	Stiles RMNH
Tampa Bay	8	boat	*B. a. amphitrite, B. venustus*	29/12/52	Yentsch USNM
Boca Ciega Bay	6	rock	*B. a. amphitrite, Ch. fragilis*	8/10/55	---- USNM 209649
Boca Ciega Bay	1	gastropod	*B. venustus*	3/11/55	---- USNM 209649
Boca Ciega Bay	2	glass	*B. venustus*	4/11/55	---- USNM 209649
Saint Marks	37	oyster shells	*B. a. amphitrite*	----	Yentsch USNM
Alligator Harbor	2	mollusks	*B. venustus*	----	Yentsch USNM
Alligator Harbor	7	pelecypod	---	1961	Kohn USNM
Fort Walton	11	---	---	----	Yentsch USNM
Mississippi					
Biloxi	2	rock oysters	---	10/7/31	---- USNM 63905

Table 6 (Continued). *Balanus eburneus*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
Louisiana					
----	1	oyster shell	---	19/12/17	---- USNM 63905
New Orleans	3	---	---	1920	---- USNM 64982
Shell I.	1	---	---	1898	---- USNM 39409
Texas					
Galveston	1	---	---	1/3/40	---- USNM 159187
Mesquite Bay	2	rock oyster	*B. improvisus*	----	Hedgpeth USNM
Cedar Bayou	1	---	*C. patula*	----	Hedgpeth USNM
Copano Bay	1	pile	---	11/9/46	Hedgpeth USNM
Rockport	4	---	*B. improvisus, Ch. fragilis*	27/12/47	Hedgpeth USNM
Port Aransas	7	---	---	20/11/47	Hedgpeth USNM
Port Aransas	1	barge	*B. improvisus*	12/47	Hedgpeth USNM
Port Aransas	1	driftwood	---	27/3/48	Hedgpeth USNM
Laguna Madre	5	---	---	11/3/50	Hedgpeth USNM
Baffin Bay	3	piles	---	9/5/50	Hedgpeth USNM
Mexico, southeast coast					
Veracruz	1	seawall	*B. a. amphitrite*	17/3/65	McLaughlin RMNH
Boca del Rio	2	log	*B.a.amphitrite,B.subalbidus,B.improvisus*	16/3/65	McLaughlin RMNH
Puerto Rico					
San Juan	1	---	*T. stalactifera, Ch. fragilis*	9/42	NOL USNM
Guayanilla	1	pipe	*B. improvisus, B. reticulatus*	8/12/56	---- USNM 209901
Virgin Islands					
St. Croix	9	*Isonomen*	---	1849	Orsted/Zullo USNM
Guadeloupe					
Pte-à-Pitre	4	barge	---	8/49	---- USNM 187280
Trinidad					
Maraca Bay	4	---	*B.improvisus,B.reticulatus,B.subalbidus*	7/5/65	Henry RMNH

hanging lower margin of some compartments; sometimes solid. Inner lamina ribbed, usually to sheath; ribs denticulate basally, finely ridged on sides near bases. Parietal tubes in single row, usually moderately large, 11-21 (16.6) in rostrum, with transverse septa almost to bases. Inner surface of outer lamina usually with 2-4 fine ribs between longitudinal septa. Basis with radial tubes and transverse septa; sometimes lengthened.

Scutum with tergal segment narrowly inflected; basitergal angle obliquely truncate; occludent margin toothed; growth ridges low to moderately strong,

strongly crenulate; longitudinal striae strong. Inner surface ridged on upper part, ridges sometimes crenulate; basal margin also sometimes crenulate; articular ridge very high, only slightly reflexed, about 2/3 length of tergal margin and 2/5 length of occludent margin, end truncate; articular furrow deep; adductor ridge short, usually high, without pit below, almost confluent with articular ridge; adductor muscle pit distinct; lateral depressor muscle pit extremely variable: often scarcely discernible, sometimes small, deep or shallow, occasionally large and shallow.

Tergum with scutal side ascending to high, usually denticulate scutal margin; carinal side usually concave medially; carinal margin strongly convex, protuberant in upper third to half, protuberance separated from rest of valve by narrow ridge; growth ridges moderate, often crenulate, except on protuberance, arched medially on carinal side of spur fasciole; longitudinal striae occasionally present on carinal side; spur fasciole usually separated from scutal side, occasionally also from carinal side, by narrow groove; spur width about 3/10 length of basal margin, spur length about 1 1/4 spur width; distance from basiscutal angle to spur about 3/4 spur width, about 3/5 spur length, and about 1/5 length of basal margin; spur length about 1/3 length of basal margin; end truncate; basal margin usually slightly concave, occasionally straight on scutal side of spur, concave, usually deeply excavated, on carinal side, sometimes crenulate on medial third. Internally, scutal margin moderately high; articular ridge low; articular furrow wide; crests for depressor muscle short but prominent, usually not projecting below basal margin; surface with crenulate ridges on upper part or often on entire carinal side.

Labrum with 6-32 (13.5) teeth and setulae on each side of deep notch.

Palpus with fine, short simple setae on upper margin, in narrow to moderately wide band parallel to upper margin and in tuft near superodistal angle on outer face, also with few long setae on distal end and in short oblique row near lower margin on distal fourth; labral face with short finely pinnate setae near upper margin on upper half distally, gradually decreasing to 3 or 4 rows proximally, long setae on lower half of distal margin and in row parallel to distal margin on distal fourth.

Mandible with 5-7 (5.9) teeth, inferior angle occasionally spinose; 2nd tooth bifid; 3rd-5th, sometimes 6th, with extra denticles; lowest tooth rarely confluent with inferior angle.

First maxilla without notch below upper pair of spines, with 5-14 (9.3) pectinate spines between upper and lower pairs and very few short spines on usually truncate inferior angle; lower pair of spines on strong prominence close to inferior angle; upper and lower pairs thicker but not much longer than some intermediate spines.

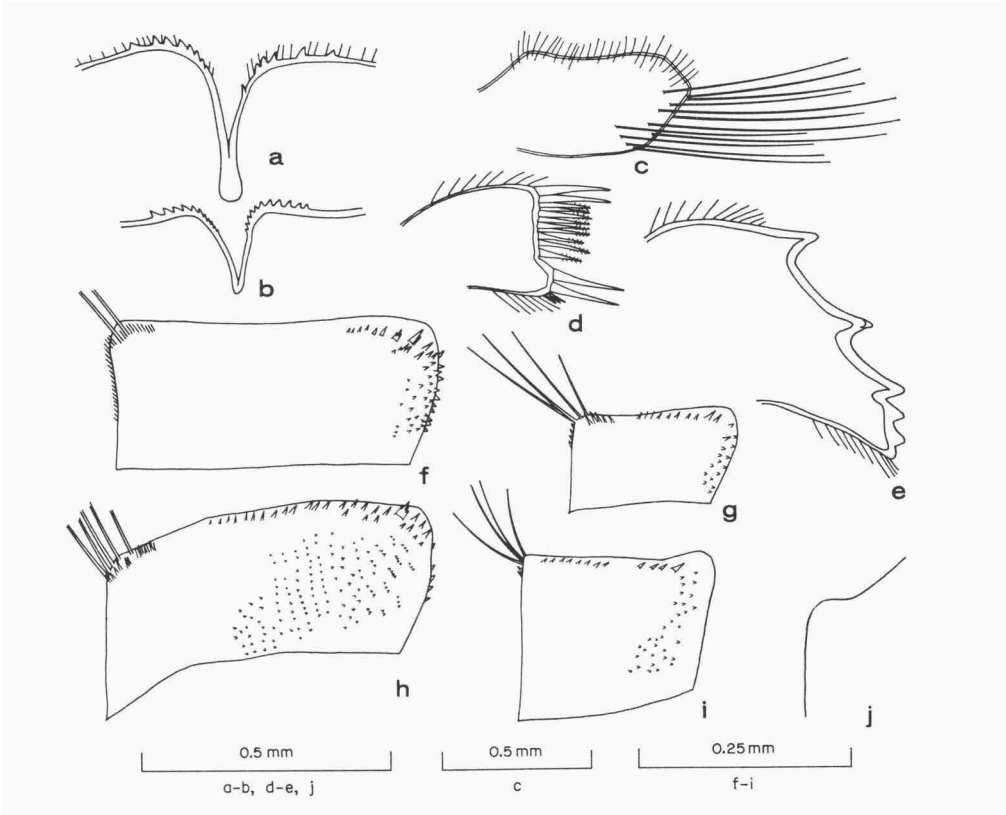

Fig. 15. *Balanus eburneus* Gould. a, b, labra; c, palpus; d, 1st maxilla; e, mandible; f-h, cirrus III (f, g, 6th proximal segments of anterior rami; h, 6th proximal segment of posterior ramus); i, 15th proximal segment of anterior ramus of cirrus IV; j, basidorsal point (a, Honolulu Harbor, Hawaii; b-e, g, Manzanillo, Mexico; f, h, j, Saint Marks, Florida; i, Jacksonville, Florida).

Second maxilla without distinguishing characters.

Protopods of anterior cirri with pinnate setae, numerous plumose setae posteriorly on coxopods; coxopod of cirrus I also with narrow band of fine simple scales on outer face near anterior margin; coxopods and occasionally basipods of cirri II and III each with narrow band or circular patch of fine simple scales on outer face near posterior margin.

Cirrus I with anterior ramus 2-14 (6.0) segments longer than posterior; posterior ramus with very protuberant segments; proximal segments of anterior ramus protuberant; distal sutures of both rami with long setae, few distal segments of posterior ramus also with multifid spinules; outer face near posterior margin of long proximal segments of both rami each with narrow band of simple scales.

Cirrus II with anterior ramus 1-8 (3.1) segments longer than posterior; both rami with very protuberant median segments. Distal sutures with long setae, and multified spinules near margins on anterior ramus and on posterior half on posterior ramus; posterior margins of 3 or 4 proximal segments of anterior ramus sparsely spinulose; remaining segments usually with few fine, sharp simple spinules below long setae on angle; several proximal segments of posterior ramus each occasionally with 1 or 2 sharp spinules below angle; outer face near posterior margin of each long proximal segment with narrow band of simple scales; remaining proximal and some median segments each with 2 or 3 short rows of multifid spinules near distal angle; anterior ramus also with narrow band of simple spinules near margin; inner face near posterior margin on anterior ramus with few simple spinules.

Cirrus III with anterior ramus equal to or 1-5 (2.8) segments longer than posterior; both rami with protuberant segments; distal sutures with short setae, spinules, and large conic teeth; outer faces near anterior margins with conic teeth; posterior margins with fine simple spinules below short setae on distal angles; outer and inner faces near posterior margins with scales or spinules; inner faces without complex setae. Distal sutures with few short setae, also with teeth on anterior half and multifid spinules on posterior half of few distal segments; remaining segments with teeth near anterior margins and spinules near posterior margins. Anterior margins of anterior ramus usually with small teeth on proximal segments; posterior ramus occasionally with 2 or 3 small or large teeth near distal angle of each proximal segment. Outer faces near anterior margins of anterior ramus usually with 2 or 3 rows of small teeth and 1-3 large teeth near distal angle on each segment except 1-4 distal segments, sometimes also with denticles; posterior ramus usually with wide band of denticles and 1-3 large teeth near distal angle of each proximal segment, sometimes with few small teeth close to margin. Inner faces near anterior margins of anterior ramus with few denticles or simple spinules on long proximal and 2 or 3 adjacent segments. Posterior margins of both rami with tuft of short setae on distal angles, also with simple spinules on 3 or 4 proximal segments and few, fine simple spinules below distal angle on each remaining proximal segment of anterior ramus; posterior ramus with fine simple spinules on long proximal segment and 1 or 2 fine simple spinules below distal angles on 2 or 3 adjacent segments, sometimes with 1 or 2 spinules below distal angles on remaining segments. Outer faces near posterior margins of both rami with narrow band of fine simple spinules on long proximal and 2 or 3 adjacent segments; remaining proximal segments usually with few multifid spinules near distal angles. Inner faces near posterior margins of anterior ramus usually with short subsutural row

of simple spinules on proximal segments; posterior ramus with narrow band of fine simple spinules on long proximal segment; 2 or 3 adjacent, sometimes remaining proximal segments each with short oblique subsutural row of simple spinules.

Protopods of posterior cirri each with fine simple spinules or denticles near anterior margin and usually with narrow band of fine simple spinules near posterior margin, on inner face.

Posterior cirri with simple spinules on distal sutures on proximal and some median segments; posterior margins with 3 or 4 short setae on each distal angle; proximal and median segments each also with 3 or 4 simple spinules below setae; several proximal segments with series of fine simple setae. Anterior margins of anterior ramus of cirrus IV occasionally with conic teeth on proximal segments; posterior ramus without teeth. Outer faces near anterior margins of anterior ramus of cirrus IV with conic teeth and denticles on proximal and median segments; long proximal and 2 or 3 adjacent segments each with 2-5 teeth below distal angle; remaining proximal and some median segments each usually with 2-6 large teeth near distal angle and wide band of small teeth on third to half proximally, gradually decreasing to few rows distally; posterior ramus without teeth, sometimes with 1-5 simple spinules below distal angles. Cirrus VI with 4-11 (7.0) pairs of setae on anterior margins of median segments. Basidorsal point of penis extremely low, nude.

Color. — Shell white; small specimens sometimes with hyaline longitudinal lines. Radii, alae, sheath, and opercular valves white. Epicuticle pale yellow.

Measurements. — Diameter of holotype 10 mm, height 8 mm. Largest specimen examined, diameter 40 mm, height 30 mm.

Variations. — The opercular valves vary considerably in thickness; sometimes they are thin in small and medium sized specimens or remarkably thick in large specimens. The tergum also varies in several other characters, i.e., the basal margin is usually not deeply excavated in small specimens; however, the degree of excavation is variable, even in large specimens, as is the width and length of the spur. Barnes and Healy (1971, fig. 1), who submitted terga from several localities to a biometrical analysis, found changes in the basal margin from the northerly to southern populations in the American Atlantic, and an anomalous type in one of the two southwest European populations examined. They suggested that this change in the configuration of the basal margin is related to temperature. However, we have found all of the configurations illustrated in a single lot from Saint Marks, Florida and all except Barnes and Healy's anomalous type in collections from Oahu, Hawaii. The terga of our Caribbean material most

closely resemble their type from Long Island, New York, in which the basal margin is strongly excavated, and the spur long and narrow. Thus it would appear that temperature is not a major influencing factor in tergal configuration.

The presence and degree of development of the vesiculation of the sheath is also variable. In 28 specimens of 53 examined, part of the sheath was found to be vesicular. Usually only the carina is vesicular; occasionally the carinal half of the shell is vesicular. The presence of a vesicular sheath does not appear to be related to geographic distribution of the species as it was represented in specimens from a wide range of localities.

Habitat. — Low water to 37 m, often in brackish water, on mollusk shells, wood, rocks, harbor installations, and ships.

Remarks. — Henry (1974) has shown that *B. a. niveus* of Oliveira (1941) should be referred in part to *B. eburneus* and in part to *B. citerosum* (also see remarks under the latter species).

As previously mentioned, both the statistical analyses and the mutual occurrence of a vesicular sheath indicate that *B. eburneus* is most closely allied to *B. subalbidus*. The characteristic configuration of the tergum, except in some small specimens, immediately distinguishes *B. eburneus* from other members of the *amphitrite* complex, except occasionally from *B. citerosum*. *B. eburneus* may be distinguished from the latter species by the thin epicuticle, by the single row of parietal tubes, by the multidenticulate labrum, and by the strong sculpturing of the scutum.

The record of *B. eburneus* from West Africa (Stubbings, 1967) was based on two specimens. Stubbings suggested that the lack of records of this species indicated that it had not yet been established, but was occasionally introduced by ships. *B. eburneus* has recently become established on the Japanese Sea side of central Japan (Utinomi, 1966). The first record from west American waters is that of Matsui et al (1964) for Balboa, Panama; it is recorded herein from two localities in Mexico. *B. eburneus* has become established at Manzanillo; however, its absence, during several years of collecting prior to 1968, suggests that it has been newly introduced in Mazatlan.

Balanus improvisus Darwin (text-fig. 16, pl. 5 figs. a-f, g, lower row left, h-j)

Balanus improvisus Darwin, 1854: 250, pl. 6 fig. 1a-c (type locality: not designated). — Pilsbry, 1916: 84, figs. 16a, 17a-e, pl. 24 figs. 3-3b, 5-5d. — Schaper, 1919-22: 227, figs. 22-30. — Nilsson-Cantell, 1921: 310. — Broch, 1924: 81, fig. 28a-c, pl. 1 fig. 7a, b, pl. 3 figs. 15a-d, 16. — Nilsson-Cantell, 1928: 33. — Neu, 1932: 143, fig. 3. — Ciurea, Monod & Dinulesco, 1933: 2, figs. 1, 2a-g, 3, 4a, b. — Neu, 1935: 94. — Neu, 1939: 214, figs. 3, 4a-c. — Henry, 1942: 119, fig. 1a-d, pl. 2 figs. 12, 13. — Tarasov & Zevina, 1957: 168, figs. 58-60. — Henry, 1959: 196, pl. 1 fig. 1, pl. 3 figs. 1-6, 7 lower row, left, 8. — Southward & Crisp, 1963: 33, fig. 17a, b. — Zullo, 1963: 11, figs. 36-

40. — Utinomi, 1968: 171. — Carlton & Zullo, 1969: 1. — Utinomi, 1970: 350, figs. 6a-e, 7a-f.

Balanus improvisus var. *assimilis* Darwin, 1854: 250. — Müller, 1867: 330, pl. 7 figs. 22, 32, pl. 8 figs. 50, 51. — Müller, 1868: 395, pl. 29 figs. 9, 17, 24.

Balanus improvisus var. *gryphicus* Münter, 1869: 9.

? *Balanus amphitrite pallidus*: Nilsson-Cantell,1932a: 111, 124, fig. 4a, b (? not *Balanus amphitrite pallidus* Darwin, 1854: 240).

Balanus amphitrite var. *denticulata*: Stubbings, 1961: 23, fig. 4c, d (in part; not fig. 4a, b; see *B. amphitrite* and *B. venustus*).

Balanus amphitrite var. *pallidus:* Stubbings, 1961: 27, fig. 6a, b (in part; see remarks).

Balanus amphitrite n. subsp. Zullo, 1963: 9, figs. 41-46 (see remarks).

? *Balanus amphitrite amphitrite*: Stubbings, 1967: 271 (in part; not fig. 14a-f; see *B. a. amphitrite* and *B. reticulatus*).

? *Balanus pallidus*: Stubbings, 1967: 277, fig. 16a (in part; not fig. 16b-e; see remarks).

not *Balanus improvisus*: Davadie, 1963: 61, pl. 29 fig. 5, pl. 32 figs. 1a, b, 2a, b (see remarks).

Type series. — BM.

Distribution. — Scotland and Baltic Sea to West Africa; Mediterranean, Black, Caspian, and Red seas; Nova Scotia to Patagonia; Oregon (Miller, 1965) to Peru; Japan; Australia (Bishop, 1951).

Material examined. — Table 7.

Diagnosis. — Shell with epicuticle usually persistent only on radii; radii narrow, summits thin, smooth, arched; sheath solid, lower margin not overhanging; parietal tubes in single row, with transverse septa. Scutum with growth ridges finely crenulate; longitudinal striae occasionally present; articular ridge about 3/4 length of tergal margin; adductor ridge long, separated from articular ridge by narrow groove. Tergum with carinal margin convex; with open spur furrow; spur length greater than width, distance from basiscutal angle to spur about 9/10 spur width; basal margin usually straight, occasionally slightly concave on carinal side of spur. Labrum multidenticulate. Cirri III-VI without simple spinules or erect teeth below posterodistal angles; cirrus III without complex setae.

Description. — Shell conic to cylindric; orifice usually slightly toothed, width usually more than 1/2 carinorostral diameter, sometimes exceeding carinorostral diameter; surface smooth unless ridged from replication of substratum; epicuticle thin, usually persistent only on radii. Radii narrow, transversely striate; summits oblique, thin, smooth, arched; sutural edges with septa usually weakly denticulate on lower margins, sometimes smooth. Alae with summits horizontal or slightly oblique; sutural edges finely septate. Sheath solid, lower margin not overhanging. Inner lamina ribbed to sheath; ribs finely denticulate basally, finely ridged on sides near bases or sometimes nearly to sheath. Parietal tubes in single row, usually moderately large, 14-24 (18.9) in rostrum, with transverse septa usually in upper 2/3, some-

Table 7. *Balanus improvisus*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
Eastern North Pacific Ocean					
----	4	S.S. *Colorado*	---	1/10/39	Townsend USNM
California					
San Pablo Bay	9	pile	---	----	Rogers USNM
San Francisco Bay	66	*Mya arenaria*	*B. crenatus*	9/12/12	*Albatross* USNM 170423
San Francisco Bay	1	oyster	---	25/2/39	---- CAS 29077
Gulf of California					
San Felipe	12	gastropods	---	25/4/67	Henry USNM, RMNH
30°28'N, 113°06'30"W	3	*Natica*	*B. c. mexicanus*	14/3/89	*Albatross* USNM
Mexico, west coast					
Mazatlan, Sabalo Pt.	7	oyster shells	*B. eburneus*	23/5/68	Henry USNM
San Blas	6	piles	*B. dentivarians*	5/5/64	Henry RMNH
Puerto Vallarta	6	oysters	*B. trigonus, Chthamalus* sp.	14/5/60	Henry USNM
Ecuador					
Carnero Pt.	1	gorgonian	*B.c.mexicanus, B.trigonus, B.masignotus*	9/5/63	Henry USNM
Playas	2	boat hull	*B. t. coccopoma, B. vinaceus*	13/5/63	Henry RMNH
Posorja	5	gastropod	---	13/5/63	Henry USNM
Posorja	8	boat hull	*B.dentivarians, B.t.coccopoma, Chth.* sp.	7/5/66	McLaughlin USNM
Posorja	2	piles	*B.inexpectatus, B.t.coccopoma, B.vinaceus*	7/5/66	McLaughlin USNM
Puna I.	5	gastropods	*Tetrabalanus polygenus, Chthamalus* sp. *B. inexpectatus*	22/12/34	---- USNM 131571
Peru					
Paita	2	*Pteria sterna*	*B. t. concinnus, B. trigonus*	10/26	---- USNM 93322
Netherlands					
IJselmeer, Oosterleek	∿50	pelecypods	---	22/7/32	---- RMNH 618
IJselmeer, Hoorn	4	---	---	28/4/66	---- RMNH 619
Egypt					
Lake Maryut	1	---	---	----	Cornwall USNM
Massachusetts					
Cape Cod, Cotuit	11	bridge	---	1964	Zullo USNM
Delaware					
Delaware Bay	∿50	mussel shell	---	27/4/57	Holthuis RMNH 617
Maryland					
Chesapeake Bay	2	driftwood	---	1961	McCrery USNM
Annapolis, Sandy Pt.	1	piles	*B. subalbidus*	21/6/67	Gordon USNM

Table 7 (Continued). *Balanus improvisus*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
Maryland (cont.)					
Kent Narrows	1	---	---	27/9/52	Holthuis RMNH 573
South River	1	---	*B. subalbidus*	winter 67	Gordan USNM
Patuxent River	5	---	---	16/7/34	----- USNM 79217
Solomons I.	5	pier	*B. eburneus*	11/10/44	----- USNM 168649
Solomons I.	1	---	---	17/5/53	Holthuis RMNH 572
Solomons I.	5	---	---	27/4/57	Scheltema RMNH 684
Piney Pt.	2	---	*B. subalbidus*	31/5/37	----- USNM 79226
Poseys Bluff Bar	3	---	---	30/11/42	----- USNM
Ragged Point Bar	5	---	---	19/11/42	----- USNM
Heron I. Bar	2	---	---	19/11/42	----- USNM
Coles Pt. Bar	2	---	---	26/11/42	----- USNM
Blake Creek Bar	2	---	---	27/11/42	----- USNM
Sheepshead Bar	2	---	---	1/12/42	----- USNM
Sheepshead Bar	5	---	---	7/12/42	----- USNM
Lower Cedar Pt. Bar	3	---	---	11/12/42	----- USNM
Swan Pt. Bar	3	---	---	15/12/42	----- USNM
Cords Flats Bar	2	---	---	11/1/43	----- USNM
Higgins Pt. Bar	3	---	---	26/1/43	----- USNM
Old Farms Bar	3	---	---	2/2/43	Frey USNM
North Carolina					
Roanoke I.	5	---	*B. subalbidus*	1/10/43	----- USNM 166137
Wilmington	1	test block	*B. eburneus*	8/7/41	Clapp USNM
Florida, east coast					
Jacksonville	7	jetty	*B. eburneus, T. stalactifera, Ch. fragilis*	-----	Yentsch USNM
Daytona Beach	5	test blocks	*B. venustus*	5/3/42	Clapp USNM
Miami	5	M/V *Captiva*	*B. a. amphitrite*	11/9/63	Southward USNM
Florida, west coast					
Gulf of Mexico	2	whistle buoy	*B. venustus, B. eburneus*	26/6/52	Yentsch USNM
Alligator Harbor	∿50	eel grass	---	-----	Yentsch USNM
Louisiana					
-----	2	oyster, crab	---	18/3/48	Hedgpeth USNM
Lake Pontchartrain	11	wood, clams	*B. subalbidus*	-----	----- USNM 200306
Rigolets, mouth	10	---	*B. subalbidus*	19/1/54	----- USNM 77955
Off Pointe Platte	7	---	---	27/11/53	----- USNM 97954
Off Frenier Beach	6	---	*B. subalbidus*	13/7/53	----- USNM 97956

Table 7 (Continued) *Balanus improvisus*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
Louisiana (cont.)					
Fort Livingston	10	---	---	4/5/48	Hedgpeth USNM
Texas					
Mesquite Bay	1	rock oyster	*B. eburneus*	15/7/46	Hedgpeth USNM
Mesquite Bay	7	turtle	*C. testudinaria*	15/7/46	Hedgpeth USNM
Rockport	4	---	*B. eburneus, Ch. fragilis*	27/12/47	Hedgpeth USNM
Port Aransas	1	asphalt	*B. subalbidus*	12/47	Hedgpeth USNM
Port Aransas	6	intake pipe	---	12/47	Hedgpeth USNM
Port Aransas	3	barge	*B. eburneus*	12/47	Hedgpeth USNM
Port Aransas	14	tank valve	---	26/3/48	Hedgpeth USNM
Port Aransas	3	piles	---	13/4/48	Hedgpeth USNM
Port Aransas	5	buoy	---	14/4/48	Hedgpeth USNM
Mexico, southeast coast					
Veracruz Harbor	2	rope	*B. trigonus*	17/3/65	McLaughlin RMNH
Veracruz Harbor	2	wreckage	*B. a. amphitrite, Chthamalus* sp.	18/3/65	McLaughlin USNM
Boco del Rio	4	log	*B.a.amphitrite, B.subalbidus, B.eburneus*	16/3/65	McLaughlin USNM
Honduras, Caribbean coast					
----	2	gastropod	---	----	---- USNM 51932
Costa Rica, Caribbean coast					
Portete	1	boat hull	*B. t. antillensis, T. stalactifera, Ch. fragilis*	23/2/65	Henry USNM
Puerto Rico					
Guayanilla	1	pipe	*B. eburneus, B. reticulatus*	8/12/56	---- USNM 209901
Trinidad					
Maraca Bay	5	---	*B.eburneus, B.reticulatus, B.subalbidus*	7/5/65	Henry RMNH
Brazil					
Bom Successo	1	---	---	14/2/35	---- USNM 85022
São Paulo, Cananéia	1	*Rhizophora*	*B. citerosum*	29/3/55	Gerlach USNM

times to bases. Inner surface of outer lamina sometimes with 1 or 2 fine ribs between longitudinal septa. Basis with radial tubes and transverse septa; sometimes lengthened.

Scutum with tergal segment narrowly inflected; basitergal angle obliquely truncate; occludent margin toothed; growth ridges low, occasionally finely crenulate; longitudinal striae sometimes present; narrow longitudinal groove close to occludent margin often present. Inner surface ridged on upper part,

occasionally with weak ridge between adductor ridge and tergal margin; articular ridge high, usually slightly reflexed, about 3/4 length of tergal margin and 2/5 length of occludent margin, end truncate; articular furrow narrow; adductor ridge high, long, usually extending above articular ridge, without pit below, separated, often by narrow groove, from articular ridge; adductor muscle pit usually small, deep, sometimes indistinct; lateral depressor muscle pit usually small, shallow, sometimes absent.

Tergum with scutal margin raised, not denticulate; carinal margin convex; growth ridges fine, slightly stronger on carinal segment; latter usually widest medially; longitudinal striae absent; spur furrow open, usually moderately deep, sometimes depressed on scutal side only; spur width about 1/5 length of basal margin; spur length about 1 3/5 spur width; distance from basi-scutal angle to spur about 9/10 spur width, about 1/2 spur length, and about 1/5 length of basal margin; spur length about 1/3 length of basal margin; end truncate, obtuse or rounded; basal margin usually straight on both sides of spur, sometimes slightly concave on carinal side. Internally, scutal margin low; articular ridge low; articular furrow wide; crests for depressor muscle very prominent and numerous, projecting slightly below basal margin; surface roughened or rugose on carinal side, sometimes with ridges projecting slightly below basal margin medially.

Labrum with setulae and 7-23 (15.1) teeth on each side of notch; 1 tooth on each side of crest sometimes separated by short space from series extending down side of notch.

Palpus with short finely pinnate setae on upper margin, sometimes also few near upper margin on outer face, with long setae in tuft and in oblique row near inferodistal angle and with few setulae near lower margin on distal third or half; labral face with narrow band of short pinnate setae along upper margin, fine short simple setae at distal end, more numerous near superodistal angle, and few long setae near inferodistal angle.

Mandible with 5-6 (5.9) teeth; inferior angle not spinose; 2nd tooth bifid; 3rd-5th with extra denticles; 6th small, sometimes bifid; lowest tooth usually confluent with inferior angle.

First maxilla without notch below upper pair of spines, with 3-15 (6.3) spines between upper and lower pairs and few short spines on inferior angle; lower pair of spines on usually strong prominence close to inferior angle.

Second maxilla without distinguishing characters.

Protopods of anterior cirri with simple and pinnate setae, also some plumose setae posteriorly on coxopods; cirrus I also with narrow band of simple scales on outer face near anterior margin; basipods of cirri II and III each sometimes with narrow band of simple scales on outer face near

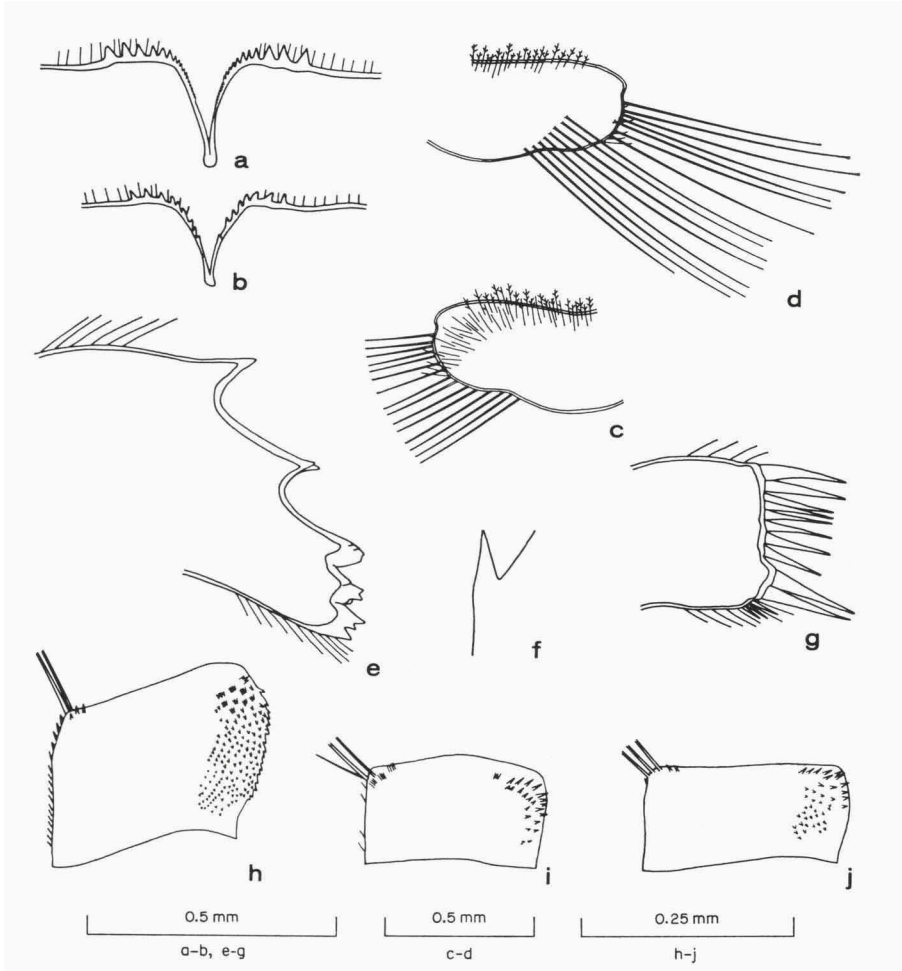

Fig. 16. *Balanus improvisus* Darwin. a, b, labra; c, d, palpus (labral and outer faces); e, mandible; f, basidorsal point; g, 1st maxilla; h-j, cirrus III (h, i, 5th and 4th proximal segments of anterior rami; j, proximal segment of posterior ramus) (a, c-e, g, h, San Pablo Bay, California; b, Fort Raleigh, North Carolina; f, Puna Island, Ecuador; i, j, Port Aransas, Texas).

posterior margin, coxopods each with narrow to wide band of simple scales on outer face near posterior margin.

Cirrus I with anterior ramus equal to or 1-6 (2.9) segments longer than posterior; posterior ramus with very protuberant segments; proximal segments of anterior ramus protuberant; distal sutures of both rami with long setae, occasionally also with multifid spinules on few distal segments of posterior ramus; outer faces near posterior margins on segments of both rami each sometimes with narrow band of simple scales.

Cirrus II with anterior ramus 2 segments shorter to 4 (1.6) segments longer than posterior; both rami with very protuberant segments; distal sutures with long setae, sometimes also with multifid spinules on few distal segments; posterior margins of several proximal segments of anterior ramus, sometimes also of posterior ramus, with fine simple spinules; several proximal segments each also with narrow band of simple scales on outer face near posterior margin.

Cirrus III with anterior ramus equal to or 1-7 (3.9) segments longer than posterior; both rami with somewhat protuberant segments; distal sutures with short setae and multifid spinules on several distal segments and with simple and multifid spinules near anterior and posterior margins on remaining segments; posterior margins without teeth or spinules below short setae on distal angles; inner faces without complex setae. Anterior margins sometimes with simple spinules or small conic teeth on proximal segments. Outer faces near anterior margins of proximal and median segments usually with simple spinules and denticles, sometimes with conic teeth; each segment usually with 3-10 spinules near distal angle and 3-10 rows of denticles, sometimes with 1-3 large spinules or teeth near distal angle and 3-10 rows of small teeth, occasionally without denticles or teeth, but with 1-4 rows of simple spinules; armature of posterior ramus usually stronger than anterior. Posterior margins usually with 4-6 short setae on distal angles; several proximal segments with few or no setae; long proximal, sometimes also several adjacent segments, with fine simple spinules. Inner faces near posterior margins of long proximal and usually several adjacent segments of anterior ramus each sometimes with narrow band of simple spinules, occasionally with 2 or 3 rows of denticles or small conic teeth; posterior ramus rarely with spinules or teeth on few proximal segments.

Protopods of posterior cirri each usually with fine simple spinules on anterior margin and in narrow band on inner face near anterior and posterior margins, sometimes also with narrow band of simple spinules and denticles on outer face and narrow band of simple spinules, denticles or simple scales on inner face, near anterior margin.

Posterior cirri with simple and multifid spinules on distal sutures; distal sutures of anterior ramus and sometimes of posterior ramus of cirrus IV also with several large simple spinules near anterior margins; posterior margins with 3-6 short setae on distal angles and simple spinules on long proximal and several adjacent segments. Anterior margins of anterior ramus of cirrus IV sometimes with fine spinules or small conic teeth on proximal segments; posterior ramus without spinules or teeth. Outer faces near anterior margins of anterior ramus of cirrus IV with large simple spinules near distal angles,

usually also with denticles or small conic teeth, on proximal segments; median and sometimes distal segments occasionally with spinules or teeth; proximal segments each with 3-5 spinules near distal angle, usually also with 8-10 rows of denticles or 2-6 rows of teeth and several rows of denticles; median segments each occasionally with teeth and denticles on distal third to half; posterior ramus usually without spinules or denticles, sometimes with 3-7 large simple spinules near each distal angle on few proximal segments, occasionally also with 8-10 rows of denticles. Cirrus VI with 5-8 (6.1) pairs of setae on anterior margin of each median segment. Basidorsal point of penis small, pointed.

Color. — Shell white, sometimes with hyaline longitudinal lines. Radii, alae, sheath, and opercular valves white. Epicuticle pale yellow.

Measurements. — Carinorostral diameter of largest specimen in type series 15 mm. Largest specimen examined, diameter 17 mm, height 9 mm.

Variations. — The shell and opercular valves of corroded specimens are frequently quite different from the typical form. The shell often is brownish or greyish in color and the radii may be obliterated. The upper parts of the opercular valves are usually corroded, the articulating margin worn, and the ridges on the inner surfaces less prominent.

Crowded specimens may be cylindric, irregular or funnel-shaped with extremely wide orifices; the bases may be lengthened; and the walls may be very thin. In both crowded and uncrowded specimens the thickness of the opercular valves is variable. When they are relatively thin, the tergal margins of the scuta are more strongly inflected, the pits for the depressor muscle are indistinct, and the inner surfaces are less rugose; the carinal margins of the terga are more strongly arched and the basal margins concave on the carinal sides of the spurs. Very occasionally the carina may have brownish striae.

The armature of cirri III and IV is quite variable. Small specimens usually lack teeth or denticles on the outer faces near the anterior margins and on the inner faces near the posterior margins. In some median and large specimens teeth and denticles are also absent. This variation in armature does not appear to be influenced by geographic location as specimens from the same lot may have many teeth or only a few spinules.

Habitat. — Intertidal to 46 m, often in brackish water, on rocks, wood, shore installations, ships, mollusk shells, crustaceans, fish, and algae.

Remarks. — Nilsson-Cantell (1932a) assigned colorless specimens from Patagonia to *B. a. pallidus,* primarily because the terga resembled Darwin's figure (Darwin, 1854, pl. 5 fig. 2k). Harding (1962) has shown that this figure does not agree with the tergum of the lectotype of *B. pallidus.* As

Nilsson-Cantell did not describe the internal parts, the specimens cannot, with certainty, be assigned to any taxon; however, the figures of the opercular valves (Nilsson-Cantell, 1932a, fig. 4a, b) suggests that his specimens may have been *B. improvisus,* known, according to Darwin (1854), from that area.

Although Stubbings (1967) did not believe that *B. improvisus* had established itself in quantity on the west coast of Africa as it was absent in his collections, we believe that there is strong evidence that it was not recognized in his collections from Bathurst, Gambia and Lagos, Nigeria. Certain specimens from Atlantide station 155 from Bathurst were referred by Stubbings (1961) to *B. amphitrite* var. *denticulata.* These specimens, which were white with hyaline lines, narrow radii, and characteristic scutum and tergum (Stubbings, 1961, fig. 4c, d), in our opinion should be assigned to *B. improvisus.* Other specimens from this station, also with a multidenticulate labrum, were assigned by Stubbings to *B. amphitrite* var. *pallidus.* The description and figures of the opercular valves (Stubbings, 1961, fig. 6a, b) clearly indicate that these also should be referred to *B. improvisus.* In a subsequent study, Stubbings (1967) used material from this Atlantide station in conjunction with other collections to show the variation in the tergum of *B. pallidus.* His figure (Stubbings, 1967, fig. 16a) is very similar to the figure (Stubbings, 1961, fig. 4d) of the specimen assigned to *B. a.* var. *denticulata,* and herein referred to *B. improvisus.* However, as there is no accompanying description, figure 16a can only questionably be assigned to the latter taxon. Material from Bathurst and Lagos provided two of Stubbings' three "mixed" categories of *B. a. amphitrite.* The listed characters of the anomalous specimens suggest that *B. improvisus* might have been included in the assemblages. Further, Stubbings (1967) noted that a large proportion of the West African *B. a. amphitrite* had white shells. We, therefore, must questionably assign *B. a. amphitrite* of Stubbingss (1967), in part, to *B. improvisus.*

Zullo (1963) suggested that the specimens, which Henry (1959) referred to *B. amphitrite pallidus,* should be considered a new subspecies as Harding (1962) had shown that the labrum of *B. pallidus* has only two or three teeth on each side of the notch. However, Henry (1974) subsequently explained that the material (USNM 79226), which Zullo used for the figures of the shell and opercular valves (Zullo, 1963, figs. 41-46) of this taxon, was actually *B. improvisus.*

The specimen from El Mankhar, which Davadie (1963) referred to *B. improvisus,* is obviously not this species as the wide radii and the short wide spur of the tergum (Davadie, 1963, pl. 29 fig. 5, pl. 32 fig. 1a, b) clearly

show. However, there are insufficient data to assign this specimen to any taxon.

Among the species of the *amphitrite* complex, *B. improvisus* is most nearly allied to *B. eburneus;* however, as indicated by the discriminant function, this relationship ($D^2 = 29.98$) is not actually close. The distinctive smooth, arched narrow radii and the spur furrow of the tergum clearly distinguish *B. improvisus* from the other species of the *amphitrite* group and from white forms of *B. venustus*. The arched radii, the solid sheath, and the single row of parietal tubes differentiate this taxon from *B. pallidus*.

Miller (1956) reported *B. improvisus* on crayfish at two localities at Astoria, Oregon. Prior to 1939, when Rogers reported this species from the San Francisco Bay region, the only records from the Eastern Pacific were those of Darwin (1854) from West Columbia and Quayaquil, Ecuador. Carlton & Zullo (1969) recorded *B. improvisus* from collections made between 1853 and 1934; twelve of the records were from the San Francisco Bay region and one was from San Pedro, California. The substrate, with two exceptions, was mollusk shells or pilings. These authors also listed the reports of *B. improvisus* subsequent to 1939; all were from the San Francisco Bay region with the exception of Miller's (1956) record from Oregon.

Cornwall (1941) reported *B. improvisus* from the Gulf of California. Our material extends the southern range in the Eastern Pacific to Peru, as well as providing additional records for the west coast of Mexico and Ecuador.

Bishop's (1951) report of *B. improvisus* was based on specimens from a ship, the itinerary of which showed that settlement of this species had to have occurred in southern Australia. He also recorded *B. improvisus* var. *assimilis* (= *B. improvisus*) from three localities in West Africa.

Balanus variegatus Darwin (text-fig. 17,pls. 6, 7)

Balanus amphitrite var. *variegatus* Darwin, 1854: 24 (type locality by subsequent designation by Harding, 1962: 291: Sydney, Australia). — Karande &Palekar, 1966: 143, figs. 3, 4, pl. 1 fig. 3, pl. 4 row 1.

Balanus amphitrite var. *cirratus* Darwin, 1854: 241, pl. 5 fig. 2b. — Pope, 1945: 362, pl. 28 fig. 6, pl. 29 fig. 6, pl. 30 figs. 13, 14. — Stubbings, 1963a: 331, fig. 3a-f.

Balanus carenatus Gruvel, 1907: 6, pl. 2 figs. 1-6.

Balanus amphitrite cirratus: Nilsson-Cantell, 1921: 316, fig. 65a-e. — Nilsson-Cantell, 1932b: 5. — Nilsson-Cantell, 1934a: 61. — Nilsson-Cantell, 1934b: 56. — Hiro, 1938: 302, fig. 2a, b. — Hiro, 1939a: 262. — Skerman, 1960: 610, figs. 1, 3.

Balanus amphitrite variegatus: Nilsson-Cantell, 1934a: 60. — Nilsson-Cantell, 1934b: 57, fig. 12a, b. — Foster, 1967: 83, fig. 7a, b.

Balanus amphitrite rafflesi Nilsson-Cantell, 1934a: 64, figs. 5a, b, 6a-e, pl. 5 figs. 5, 6. — Nilsson-Cantell, 1937: 95.

Balanus amphitrite venustus: Nilsson-Cantell, 1938: 37, fig. 8a, b (in part; see *B. venustus*).

Balanus amphitrite vladivostokensis Tarasov & Zevina, 1957: 179, 184, fig. 67a, b.
Balanus variegatus: Harding, 1962: 291, pl. 10 figs. a-k.
Balanus variegatus var. *cirratus*: Harding, 1962: 293, pl. 10 figs. 1-n. — Pope, 1966: 179.
Balanus variegatus cirratus: Utinomi & Kikuchi, 1966: 6. — Utinomi, 1967: 214, fig. 8a-e. — Utinomi, 1970: 357.
Balanus variegatus variegatus: Utinomi, 1968: 171.
not *Balanus amphitrite cirratus*: Zevina & Tarasov, 1963: 89, fig. 10a-e (= *B. reticulatus*).
not *Balanus amphitrite* var. *variegatus*: Stubbings, 1963a: 329, fig. 2a-e (= *B. reticulatus*).

Lectotype. — BM 1961. 12.6.80a, d, e, by subsequent selection by Harding, 1962: 291.

Distribution. — Australia and New Zealand to west Kyushu; east Asia from Vladivostok to Gulf of Siam; Sumatra to mouth of Indus.

Material examined. — Table 8.

Table 8. *Balanus variegatus*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
Philippine Islands					
Pandan, Antique	2	---	---	6/4/46	---- USNM 173906
Thailand					
----	2	*Thais* sp.	---	-----	Eyerdam USNM
Hua Hin		---	*T. squamosa*	19/1/54	---- USNM 200778
Singapore					
----	3	shell	---	-----	Deschamps USNM 51675
Malay Archipelago					
----	9	---	---	1826-32	Macklot RMNH 33
Malaysia					
Penang	1	test panel	*B. reticulatus*	8-10/60	Turner USNM
Sumatra					
Benkoelen	71	wood, shells	*B. reticulatus, B. kondakovi*	11/25	---- USNM
Indian Union					
Off Cochin	3	crab	---	12/4/64	Robertson USNM
Bombay	8	---	*B. a. amphitrite, B. reticulatus, B. tintinnabulum*	-----	Karande USNM

Diagnosis. — Shell with epicuticle usually persistent; radii narrow to wide, thick, occasionally slightly beveled. Sheath solid, lower margin slightly overhanging; parietal tubes in single row, rarely without transverse septa. Scutum with basitergal angle obliquely truncate; growth ridges usually conspicuously

crenulate; longitudinal striae fine; articular ridge about 7/10 length of tergal margin; adductor ridge usually short, separated from articular ridge by narrow groove. Tergum with carinal margin very slightly convex, with spur furrow usually open; spur length usually greater than spur width, distance from basiscutal angle to spur about 9/10 spur width; basal margin usually straight, occasionally slightly concave on scutal side of spur. Labrum simple. First maxilla with lower pair of spines usually on strong prominence. Cirrus II without simple spinules or teeth on outer face near anterior margin; cirri III-VI without erect teeth, with simple spinules, below posterodistal angles; cirrus III without complex setae.

Description. — Shell usually conic or cylindric, sometimes subcylindric; orifice slightly toothed, width equal to or more than 1/2 carinorostral diameter; surface smooth; epicuticle thin, usually persistent. Radii narrow to moderately wide in conic, wide in cylindric specimens, transversely striate; summits usually oblique, occasionally subhorizontal; usually thick, occasionally slightly beveled, rough; sutural edges with septa very strongly denticulate on lower margins. Alae with moderately oblique or oblique summits; sutural edges septate. Sheath solid, lower margin slightly overhanging. Inner lamina ribbed to sheath; ribs moderately strong, very weakly denticulate basally, usually finely ridged on sides near bases; lower margin between ribs sometimes with a denticle, occasionally with a fine stria. Parietal tubes in single row, variable in size, 13-17 (15.3) in rostrum, usually with fine, approximate transverse septa in upper 1/5-1/2, occasionally almost to bases of some tubes, rarely without transverse septa and filled up in upper 1/2. Inner surface of outer lamina sometimes with 1-4 fine ribs between longitudinal septa. Basis with radial tubes and transverse septa extending nearly to periphery; often lengthened, at least in part.

Scutum usually flat except for recurved apex; tergal segment occasionally narrowly inflected; basitergal angle obliquely truncate; occludent margin finely toothed; growth ridges low, usually conspicuously crenulate; longitudinal striae fine; narrow longitudinal groove close to occludent margin occasionally present. Inner surface usually with fine approximate ridges on upper part; articular ridge high, only slightly reflexed, about 7/10 length of tergal margin and about 1/2 length of occludent margin, end obliquely truncate, sometimes truncate; articular furrow narrow; adductor ridge high or moderately high, usually short, occasionally long, usually with shallow pit below sometimes bounded on tergal side by weak ridge, separated from articular ridge by narrow groove; adductor muscle pit well defined; lateral depressor muscle pit usually small and deep.

Tergum wide, with scutal margin finely denticulate, usually raised; some-

times with shallow longitudinal concavity or groove on scutal side; carinal margin very slightly convex; growth ridges fine, stronger medially on carinal segment; longitudinal striae often present on carinal side, occasionally also on scutal side; spur furrow usually open, moderately deep or sometimes shallow; spur width about 1/4 length of basal margin; spur length about 1 1/4 spur width; distance from basiscutal angle to spur about 9/10 spur width, about 3/5 spur length, and about 1/4 length of basal margin; spur length about 1/3 length of basal margin; end obliquely truncate; basal margin usually straight on both sides of spur, occasionally concave on scutal side. Internally, scutal margin low; articular ridge usually low, rarely slightly reflexed; articular furrow wide; crests for depressor muscle short but prominent, usually projecting slightly below basal margin; surface occasionally rough on upper part, basally sometimes denticulate medially.

Labrum with setulae and 1-4 (3.6) teeth on crest on each side of deep notch, usually 1 tooth on each side of crest near notch, occasionally 1 or 2 teeth on one or both edges of notch near crest.

Palpus with short finely pinnate setae on upper margin and setulae on lower margin; outer face with short simple setae in narrow band along upper margin, long setae on lower half of distal end and in oblique row near inferodistal angle, wide band of setulae along lower margin; labral face with band of strongly pinnate short setae along upper margin on upper third distally, gradually narrowing to 2 or 3 rows proximally, denticulate scales and setulae on distal fifth, row of long setae near distal margin on lower third, and wide band of denticulate and simple scales parallel to lower margin.

Mandible with 5-6 (5.4) teeth; inferior angle not spinose; 2nd tooth bifid; 3rd-6th with extra denticles; 5th tooth usually confluent with inferior angle, 6th, when present, confluent.

First maxilla with 1 or 2 fine spines in slight notch below upper pair of spines, sometimes with short thick spine on outer face near lower spine of upper pair, 5-10 (6.9) spines between upper and lower pairs and few short spines on inferior angle; lower pair of spines usually on strong or very strong, sometimes on moderate, occasionally on slight, prominence.

Second maxilla without distinguishing characters.

Protopods of anterior cirri primarily with pinnate setae, some plumose setae posteriorly; protopod of cirrus I with narrow band of simple scales near anterior margin and few multifid spinules below posterodistal angles, on outer face; protopods of cirri II and III each with narrow to wide band of simple scales on outer face near posterior margin; basipods and sometimes coxopods each also with narrow band of simple, denticulate, and spinulose scales on outer face near anterior margin.

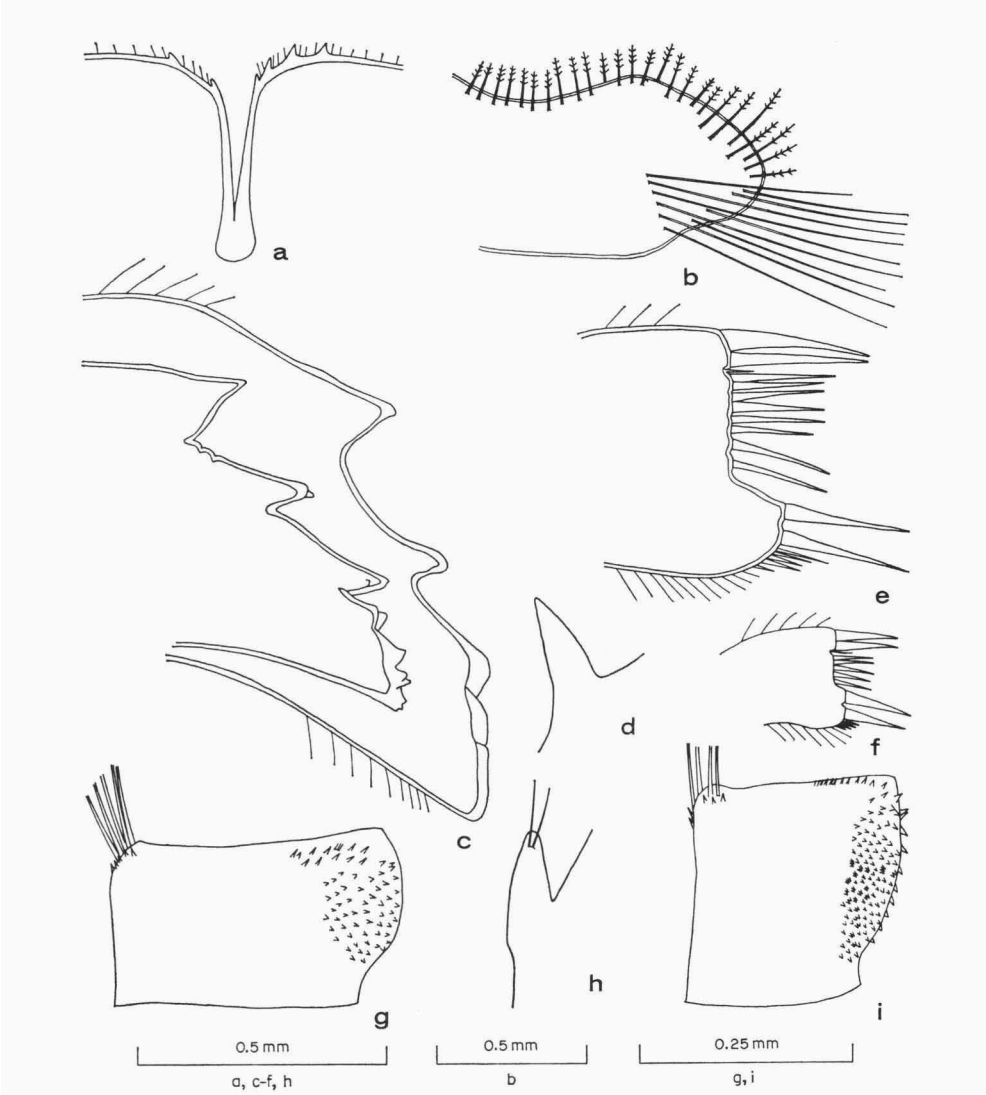

Fig. 17. *Balanus variegatus* Darwin. a, labrum; b, palpus; c, mandible; d, h, basidorsal points; e, f, 1st maxillae; g, 9th distal segment of anterior ramus of cirrus III; i, 10th proximal segment of anterior ramus of cirrus IV (a-i, Benkoelen, Sumatra: a-e, g, i, USNM 85026; f, different specimen, USNM 85026; h, USNM 85020).

Cirrus I with anterior ramus 3 segments shorter to 8 (3.8) segments longer than posterior; posterior ramus with extremely protuberant segments; proximal segments of anterior ramus protuberant; distal sutures of both rami with long setae, also with multifid spinules on distal segments; remaining segments with multifid spinules near posterior margin; several proximal seg-

ments each with narrow band of simple scales on outer face near posterior margin.

Cirrus II with anterior ramus 2 segments shorter to 4 (1.4) segments longer than posterior; both rami with moderately protuberant segments. Distal sutures with long setae, and multifid spinules generally near anterior and posterior margins on proximal and some median segments. Outer faces near anterior margins of long proximal segment of anterior ramus with narrow band of simple scales; few adjacent segments usually with few spinulose scales near distal angles; posterior ramus without scales on long proximal segment; few adjacent segments each with narrow band of spinulose scales or multifid spinules; remaining proximal segments sometimes with few multifid spinules near distal angles. Posterior margin of long proximal segment of posterior ramus with fine simple spinules. Outer faces near posterior margins of long proximal and several adjacent segments of both rami each with wide band of simple scales. Inner faces near posterior margins usually with narrow band of simple and spinulose scales.

Cirrus III with anterior ramus 1-5 (2.8) segments longer than posterior; both rami with slightly protuberant segments; distal sutures with short setae and spinules; posterior margins with simple spinules below relatively long setae on distal angles; inner faces occasionally with subsutural row of spinules, without complex setae. Distal sutures with few short setae and multifid spinules on 3-4 distal segments, simple and bifid spinules near anterior margins and multifid spinules near posterior margins on remaining distal and usually on median segments; multifid spinules near posterior margins on proximal and sometimes on median segments. Anterior margins of anterior ramus sometimes with conic teeth on proximal segments; posterior ramus usually without teeth, sometimes with teeth on 1 or 2 proximal segments. Outer faces near anterior margins of both rami usually with conic teeth and denticles on proximal and some median segments; long proximal segments each usually with few small teeth near distal angle, sometimes with narrow band of simple scales and few teeth or simple spinules near distal angle; remaining proximal and some median segments each usually with several rows of small teeth and denticles, sometimes also with 2-4 larger teeth near angle; remaining median segments each sometimes with few simple spinules near distal angle. Posterior margins with 5 or 6 relatively long setae, fewer proximally, on distal angles of most segments; proximal and some median segments of posterior ramus with 1-3 fine simple spinules below distal angles, sometimes with fine simple spinules on long proximal segments. Outer face near posterior margin of long proximal segment of anterior ramus with narrow to wide band of simple scales; 1 or 2 adjacent

segments each usually with 1 or 2 short subsutural rows of multifid spinules, occasionally also with few simple scales; remaining proximal segments each sometimes with 1 or 2 short subsutural rows of multifid spinules; posterior ramus with narrow band of simple scales on long proximal segment; few adjacent segments each with short subsutural row of multifid spinules. Inner face near posterior margin of long proximal segment of anterior ramus with narrow band of simple spinules or simple and spinulose scales; 1 or 2 adjacent segments usually with few short subsutural rows of simple or bifid spinules; posterior ramus with narrow band of simple spinules on long proximal segment; few adjacent segments each sometimes with short subsutural row of simple spinules.

Protopods of posterior cirri each with narrow band of simple, denticulate, or spinulose scales on inner face near anterior margin and narrow band of spinulose or denticulate scales on inner face near posterior margin.

Posterior cirri with simple spinules, usually larger near anterior margins, on distal sutures on proximal halves of rami; posterior margins with 1 relatively long and several short setae on each distal angle; cirri V and VI usually with 1 or 2 simple spinules below setae on each proximal segment, sometimes also on each median segment; cirrus IV without spinules below setae; inner faces near posterior margins of few proximal segments usually with 2 or 3 rows of denticulate scales; anterior ramus of cirrus IV sometimes, posterior ramus occasionally, also with 1 or 2 rows of denticles close to margin; proximal segments of cirri V and VI each usually with subsutural row of large simple spinules; median segments each sometimes with subsutural row of 3 or 4 smaller simple spinules. Anterior margins of anterior ramus of cirrus IV usually with small conic teeth on proximal, sometimes also on median, segments, occasionally without teeth; posterior ramus without teeth. Outer faces near anterior margins of anterior ramus of cirrus IV usually with small conic teeth on proximal segments, sometimes also on median segments; proximal segments each usually with 5 or 6 rows of teeth and denticles, occasionally with only 1 or 2 rows of teeth; median segments each usually with few simple spinules near distal angle, sometimes with 5 or 6 rows of teeth and denticles; posterior ramus usually without teeth, with few simple spinules below anterodistal angles on few proximal segments, occasionally without teeth on 5 or 6 proximal segments but with few small conic teeth on adjacent 2-10 segments. Cirrus VI with 4-6 (4.8) pairs of setae on anterior margins of median segments. Basidorsal point of penis narrow, usually with 2 subapical setae, sometimes with 1, occasionally without setae.

Color. — Shell usually reddish or bluish, or brownish purple, with approxi-

mate longitudinal stripes intersected by white or colored transverse stripes; stripes pinkish, bluish, reddish, purplish or brownish, occasionally entirely white. Alae usually white, occasionally purplish. Sheath usually white, occasionally brownish purple or red. Radii usually colored, occasionally white or white with color near parietes; color usually purplish, sometimes purple, pink, or red. Both sides of scutum usually colored except margins, sometimes white with color on middle or apex, occasionally entirely white; color usually purple or brownish purple, occasionally pink or red. Both sides of tergum usually white with brownish purple or purple, occasionally red, on carinal side, sometimes colored except for margins, occasionally entirely white.

Measurements. — Greatest diameter of lectotype 17 mm. Largest specimens examined with carinorostral diameter of 20 mm, height 15 mm; and diameter 10 mm, height 22 mm.

Variations. — The color of the shell is extremely variable. In the large series from Sumatra, the color varied from the brownish color attributed to *cirratus* by Darwin (1854) to the red or claret color of *variegatus*. Such color variation is represented both in the longitudinal and transverse stripes, which also vary in width and may be irregularly arranged. The scutum is always longitudinally striated unless corroded; however, the growth ridges may or may not be crenulated (beaded). In the material examined, the growth ridges were crenulated in 60% of the specimens. The adductor ridge is usually strong, but frequently short (73%).

According to Darwin (1854) the first maxilla of *cirratus* has the lower pair of spines on a strong prominence. Harding (1962) found a similar type of prominence on the first maxilla of *B. variegatus*. In approximately 25% of the material examined in this study the inferior angle of the first maxilla was not particularly prominent.

The material from Bombay, which was not available for the statistical analyses, agrees with the lectotype of *B. variegatus* in the color pattern, and only slightly crenulate growth ridges of the scutum; but the adductor ridge is long and strong, the tergal spur is narrower and farther from the basiscutal angle, and the spur furrow is partially closed. Many of the specimens in our material have striae or denticles basally on the inner lamina as described by Stubbings (1963a) and figured but not described by Utinomi (1966, fig. 8e) for *B. v. cirratus*.

Habitat. — Intertidal and upper subtidal; on shells, mangroves, fish traps, harbor installations, and ships. According to Pope (1966) *B. variegatus* can withstand widely varying salinities, silt, and chemical wastes.

Remarks. — Darwin (1854) distinguished var. *variegatus* from var. *cirratus* principally on the color of the shell; both, however, were described as being

transversely freckled with white. Darwin's supplemental characters included a conic shell and a small adductor ridge of the scutum in *variegatus* and, in *cirratus,* beaded growth lines on the scutum, a cup-formed basis, and a prominent inferior angle on the first maxilla. Harding (1962) was unable to find any specimens of *cirratus* with opercular valves and animal parts remaining in the Darwinian collection. He did, however, note that the color of shells of the two varieties, identified in Darwin's own hand writing, overlapped considerably. In addition, none of the remaining specimens of *cirratus* had a cup-shaped basis, but one specimen of *variegatus* did, and the inferior angle of the first maxilla of the lectotype was prominent. Harding raised *B. variegatus* to specific rank; however, he retained *cirratus* as a variety. As shown in this study, the characters used to separate *cirratus* from *variegatus* are highly variable. Therefore, we must consider the two taxa conspecific.

This conspecificity of the two taxa is substantiated by accounts of earlier authors. Nilsson-Cantell (1934b) described the shell of *B. a. variegatus* as conic and with violet longitudinal stripes; whereas, according to Utinomi (1968) the color agrees with Darwin's description, but the shell is tubuloconic. The shell of *B. a. cirratus* has been described as conic-cylindric, conic, or conic to tubuloconic by Nilsson-Cantell (1921), Stubbings (1963a), and Utinomi (1967), respectively. The transverse stripes may be of the same color as the longitudinal stripes instead of white (cf. Utinomi, 1967). The scutum of the specimens referred to *B. a. variegatus* by Nilsson-Cantell (1934a) and Utinomi (1968) had a distinct but short adductor ridge; the short adductor ridge was remarkably prominent in specimens recorded by Nilsson-Cantell (1934b). Harding (1962) described the adductor ridge of the lectotype as small. The scutum of Utinomi's (1968) *B. variegatus* did not have beaded growth ridges; neither did the scutum of Stubbings' (1963a) *B. a.* var. *cirratus.* The first maxilla of *B. variegatus* was not described by any of the above mentioned authors except Harding (1962), who described the inferior angle of the lectotype as prominent. Further evidence that the two taxa are not distinct is suggested by Nilsson-Cantell's (1934a) report of both taxa on the same mussel; this record was from Singapore.

A new subspecies, *B. a. rafflesi,* was also described from near Singapore by Nilsson-Cantell (1934a). He differentiated this subspecies from *B. a. communis* by the tergum, but did not mention the similarity of the tergum (Nilsson-Cantell, 1934a, fig. 5b) to that of *B. a. cirratus.* The shell of the larger specimen of *B. a. rafflesi* was entirely white; Nilsson-Cantell (1934b) also recorded white shells for *B. a. cirratus.* As the other characters described for *B. a. rafflesi* are well within the range of variation of *B.*

variegatus, Nilsson-Cantell's subspecies is considered herein to be synonymous with *B. variegatus.* Nilsson-Cantell (1938, fig. 8a, b) illustrated the opercular valves of some rose colored specimens which he referred to *B. a. venustus.* Both the scutum and tergum differ significantly from *B. venustus,* but do agree with *B. variegatus.*

Other taxa that are considered herein to be synonymous with *B. variegatus* are *B. carenatus* Gruvel and *B. a. vladivostokensis* Tarasov & Zevina. Gruvel (1907) distinguished his new species from *B. amphitrite* by the recurved carina, the form of the tergum, and the first maxilla. The shape of the carina, as noted by Pilsbry (1916), is not a diagnostic character; the form of the tergum, as well as the maxilla with the lower pair of spines on a strong prominence, agree with *B. variegatus.* Tarasov & Zevina (1957) related their new variety, which had a white shell, to *B. a. cirratus* but differentiated it by the straight rather than curved adductor ridge. This character is variable, as can be seen by the figures of the scutum (cf. Hiro, 1938, fig. 2a; Utinomi, 1967, fig. 8b); therefore, this cannot be considered a valid diagnostic character. Utinomi (1967) questionably referred *B. a. vladivostokensis* to *B. a. cirratus,* but subsequently (Utinomi, 1970) questionably referred it to *B. improvisus.*

As Stubbings (1963a) pointed out, the mouth parts and cirri of *B. a.* var. *variegatus* had not been fully described. However, his description of the cirri clearly shows that his specimens of *B. variegatus* should be referred to *B. reticulatus.* Similarly, the specimens assigned to *B. a. cirratus* by Zevina & Tarasov (1963) agree, in the armature of cirrus II, with *B. reticulatus.*

B. variegatus is most closely allied with *B. reticulatus* ($D^2 = 5.70$) and, at least superficially, the two species are often extremely difficult to differentiate. Using the discriminant function, a group of 45 small specimens known to belong to the *B. variegatus-B. reticulatus* pair were classified on the basis of the Y values computed for the individual specimens (E-3:1). Using the critical Y value (Y_0) obtained from the reference populations (E-2:1), specimens in the group were separated into their respective taxa, 22 specimens of *B. variegatus,* 23 specimens of *B. reticulatus.* The results of this statistical classification were compared with the group classification derived from the use of qualitative characters and found to be in agreement within the estimated error of misclassification ($< 10\%$).

The results of the generalized distance function suggest a close affinity also between *B. variegatus* and *B. kondakovi* on the basis of the 16 characters considered by the function. However, certain characters, which clearly place *B. kondakovi* in the *pallidus* group, were not used in the

statistical analyses. Therefore, the affinity suggested between these two species cannot be interpreted necessarily as a measure of phylogenetic relationship.

B. variegatus also exhibits a relatively high degree of affinity for the species pair, *B. c. pacificus-B. c. mexicanus,* and could well have been included in a cluster with this pair (D-2:1). This cluster, however, would have excluded *B. reticulatus,* its closest neighbor. Consequently, the cluster, *B. c. pacificus-B. c. mexicanus-B. variegatus* was not considered an adequate reflection of interspecific relationship. It is interesting to note, however, Darwin's (1854: 246) statement that *B. a. cirratus* (= *B. variegatus*) seemed to connect *B. amphitrite* and *B. concavus* very closely.

B. variegatus may usually be differentiated from *B. reticulatus* by the tergum, and always by the armature of cirrus II and the lack of erect teeth below the posterodistal angles on cirri III-VI in specimens greater than 5 mm in diameter. The difference in the convexity of the carinal margin of the tergum is the most reliable character to distinguish small specimens from *B. reticulatus.* Large cylindrical specimens of *B. variegatus* may resemble *B. kondakovi* in the color of the shell, but may be readily differentiated by the tergum. *B. variegatus* may be distinguished from all the subspecies of *B. concavus* by the less strongly sculptured scutum.

Balanus reticulatus Utinomi (text-figs. 11, 18, pl. 7 fig. d, pl. 8, pl. 9 figs. a, d, e)

Balanus amphitrite var. *communis* Darwin, 1854: 240, pl. 5 fig. 2e, h, l (in part; see *B. a. amphitrite*). — Stubbings, 1963b: 14.

? *Balanus amphitrite communis*: Nilsson-Cantell, 1921: 311 (in part; not fig. 64a-e). — Nilsson-Cantell, 1932a: 110, 122 (in part; not fig. 3a-f) (see *B. a. amphitrite*).

Balanus amphitrite forma *communis*: Broch, 1922: 314 (in part; not *Balanus amphitrite* var. *communis* Darwin, 1854: 240; see *B. poecilotheca*).

Balanus amphitrite forma *hawaiiensis* Broch, 1922: 314 (in part; not figs. 56, 57a-e; see *B. a. amphitrite*).

Balanus amphitrite communis: Hiro, 1938: 301, fig. 1a, b. — Utinomi, 1956: 52, pl. 26 fig. 11. Utinomi, 1960: 44, figs. 1c, d, 2c, d. — Stubbings, 1961: 22 (not *Balanus amphitrite communis* Darwin, 1854: 240).

Balanus amphitrite cirratus: Zevina & Tarasov, 1963: 89, fig. 10a-e (not *Balanus amphitrite cirratus* Darwin, 1854: 241).

Balanus amphitrite var. *variegatus*: Stubbings, 1963a: 329, fig. 2a-e (not *Balanus amphitrite* var. *variegatus* Darwin, 1854: 241).

Balanus amphitrite variety: Southward & Crisp, 1963: 43, fig. 23.

Balanus amphitrite tesselatus Utinomi, 1964: 52, pl. 26 fig. 11 (not *Balanus tesselatus* Sowerby, 1818, pl. 84).

? *Balanus amphitrite* var. *communis:* Karande & Palekar, 1966: 143, pl. 4 row 2 (in part; not figs. 5, 6, pl. 1 fig. 4; see *B. a. amphitrite*).

Balanus amphitrite var. *denticulata*: Karande & Palekar, 1966: 145, fig. 7, pl. 1 fig. 7, pl. 4 row 5 (not *Balanus amphitrite* var. *denticulata* Broch, 1927a: 133).

Balanus variegatus tesselatus: Utinomi & Kikuchi, 1966: 5 (not *Balanus tesselatus* Sowerby, 1818, pl. 84).

Balanus amphitrite amphitrite: Stubbings, 1967: 271, fig. 14d-f (in part; not fig. 14a-c; see *B. a. amphitrite* and *B. improvisus*).

Balanus reticulatus Utinomi, 1967: 216, figs. 9a, b, 10a, b, 11a-e, pl. 6 figs. 7, 8 (type locality: Tatigatani, Tanabe Bay, Japan). — Utinomi, 1970: 356.

Holotype. — SMBL 199.

Distribution. — Japan and Hawaii to Malay Archipelago; east Asia from Yellow Sea to Gulf of Siam; Malaysia to southeast Africa; Mediterranean Sea; West Africa; southeast United States to West Indies.

Material examined. — Table 9.

Diagnosis. — Shell with epicuticle sometimes persistent; radii narrow to moderately wide; summits beveled; sheath solid, lower margin slightly overhanging; parietal tubes in single row, rarely without transverse septa. Scutum with basitergal angle truncate; growth ridges occasionally crenulate; longitudinal striae fine; articular ridge about 2/3 length of tergal margin; adductor usually short, well separated from articular ridge. Tergum with carinal margin slightly convex, sometimes narrowly protuberant in upper 1/3, usually with spur fasciole, occasionally with open furrow; spur length greater than width, distance from basiscutal angle to spur about equal to spur width; basal margin usually straight, occasionally slightly concave on scutal side of spur. Labrum simple. First maxilla with lower pair of spines usually on slight prominence. Cirrus II with simple spinules or conic or spike-like teeth on outer face near anterior margin; cirri III to VI with erect teeth below posterodistal angles; cirrus III without complex setae.

Description. — Shell usually subcylindric or cylindric, sometimes conic; orifice toothed, width usually more than 1/2 carinorostral diameter; surface smooth; epicuticle thin, sometimes persistent. Radii with fine transverse striae, usually narrow, sometimes moderately wide, occasionally slightly sunken; summits oblique, beveled; sutural edges with septa strongly denticulate on lower margins. Alae with moderately oblique or oblique summits; sutural edges septate. Sheath solid, lower margin slightly overhanging. Inner lamina ribbed, usually to sheath; ribs low, weakly denticulate basally, usually finely ridged on sides near bases; lower margin between ribs sometimes with 1-6 minute denticles, occasionally with 1-6 fine longitudinal striae. Parietal tubes in single row, usually large, sometimes compressed, 11-19 (13.5) in rostrum, with fine approximate transverse septa usually in upper 1/5-1/3, occasionally almost to bases, rarely without transverse septa, filled up in upper 1/4. Inner surface of outer lamina sometimes with 1-6 fine ribs between longitudinal septa. Basis with radial tubes and fine transverse septa usually extending nearly to or to periphery, occasionally in 5 or 6 rows encircling original point of attachment; sometimes lengthened in part.

Scutum usually flat except for recurved apex; tergal segment narrowly inflected, basitergal angle truncate; occludent margin finely toothed; growth ridges moderate, occasionally crenulate; longitudinal striae fine. Inner surface usually moderately roughened on upper part; articular ridge high,

Table 9. *Balanus reticulatus*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
Hawaii					
Off Oahu	17	buoys	---	24/1/44	---- BPBM
Off Oahu	2	buoy	---	28/4/44	---- BPBM 325
Oahu	2	rocks	---	1929	---- BPBM 268
Pearl Harbor	5	---	---	----	---- BPBM 233
Pearl Harbor	6	piles	*B. a. amphitrite*	1931	---- BPBM 276
Pearl Harbor	1	*Anomia* sp.	*B. a. amphitrite, B. trigonus*	11/3/48	---- BPBM 350
Honolulu Harbor	1	---	*B. a. amphitrite, B. eburneus*	27/11/54	---- BPBM 396
Kaneohe Bay	73	limb	*B. a. amphitrite, B. eburneus, B. trigonus*	spring 59	Illg USNM, RMNH
Japan					
Ago Bay, Hamajima	19	test panels	*B. trigonus*	1/8/52	Mawatari USNM
Tanabe Bay	4	---	---	4/4/65	Utinomi USNM
Formosa					
Keelung Harbor	5	freighter	---	3/5/64	Schmitt USNM
Thailand					
Langsuan	1	bamboo	---	22/9/23	---- USNM 59198
Malaysia					
Penang	57	test panels	*B. variegatus*	8-10/60	Turner USNM
Java					
Besoeki	21	gastropod	---	1865	Semmelink RMNH 34
Sumatra					
Benkoelen	2	shell, wood	*B. variegatus, B. kondakovi*	11/25	---- USNM 85026
Indian Union					
Bombay	15	---	*B. a. amphitrite, B. variegatus B. tintinnabulum*	----	Karande USNM
Mozambique					
Beira	20	piles	*B. a. amphitrite*	8/10/64	Gooding USNM
Republic of South Africa					
Durban Bay	15	shells, wood	*B. a. amphitrite*	30/7/64	Boss USNM
Indo-Atlantic					
----	4	M.S. *Arnham*	---	14/2/57	Schuitema RMNH 623

Table 9 (Continued). *Balanus reticulatus*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
Israel					
Haifa	1	buoy	*B. a. amphitrite, B. eburneus, B. tintinnabulum, B. trigonus*	26/2/58	---- HSFRS
Florida, east coast					
Miami	50	test panel	*B. trigonus*	----	Moore USNM,RMNH
Puerto Rico					
Guayanilla	1	pipe	*B. eburneus, B. improvisus*	8/12/56	---- USNM 209901
Trinidad					
Maraca Bay	1	---	*B. eburneus,B. improvisus,B. subalbidus*	7/5/65	Henry RMNH

only slightly reflexed, about 2/3 length of tergal margin and about 1/2 length of occludent margin, end truncate; articular furrow deep; adductor ridge usually short and high, sometimes moderately long, low or moderately high, usually with shallow pit below occasionally bounded on tergal side by weak ridge, well separated from articular ridge; adductor muscle pit distinct; lateral depressor muscle pit usually small and shallow, sometimes moderately deep, occasionally large, elongate.

Tergum with scutal margin raised, denticulate; carinal margin slightly convex, sometimes narrowly protuberant in upper third; growth ridges fine, sometimes finely crenulate, stronger on protuberance; latter sometimes, entire carinal segment occasionally, delimited by narrow groove or ridge; longitudinal striae occasionally present on carinal side; usually spur fasciole separated from scutal side, usually also from carinal side, by narrow groove, or occasionally open shallow spur furrow; spur width about 1/4 length of basal margin; spur length about 1 1/4 spur width; distance from basi-scutal angle to spur about equal to spur width, about 4/5 spur length, and about 1/5 length of basal margin; spur length about 3/10 length of basal margin, end obliquely truncate; basal margin usually straight on both sides of spur, occasionally slightly concave on scutal side. Internally, scutal margin low; articular ridge usually prominent, somewhat reflexed; articular furrow wide; crests for depressor muscle short, prominent, usually projecting slightly below basal margin; surface sometimes roughened on upper part, occasionally roughened on entire carinal side, basally sometimes denticulate medially.

Labrum with setulae and 0-5 (3.8) teeth on crest on each side of deep notch; usually 1 tooth of each side on crest near notch, occasionally 1 tooth on one or both edges of notch near crest.

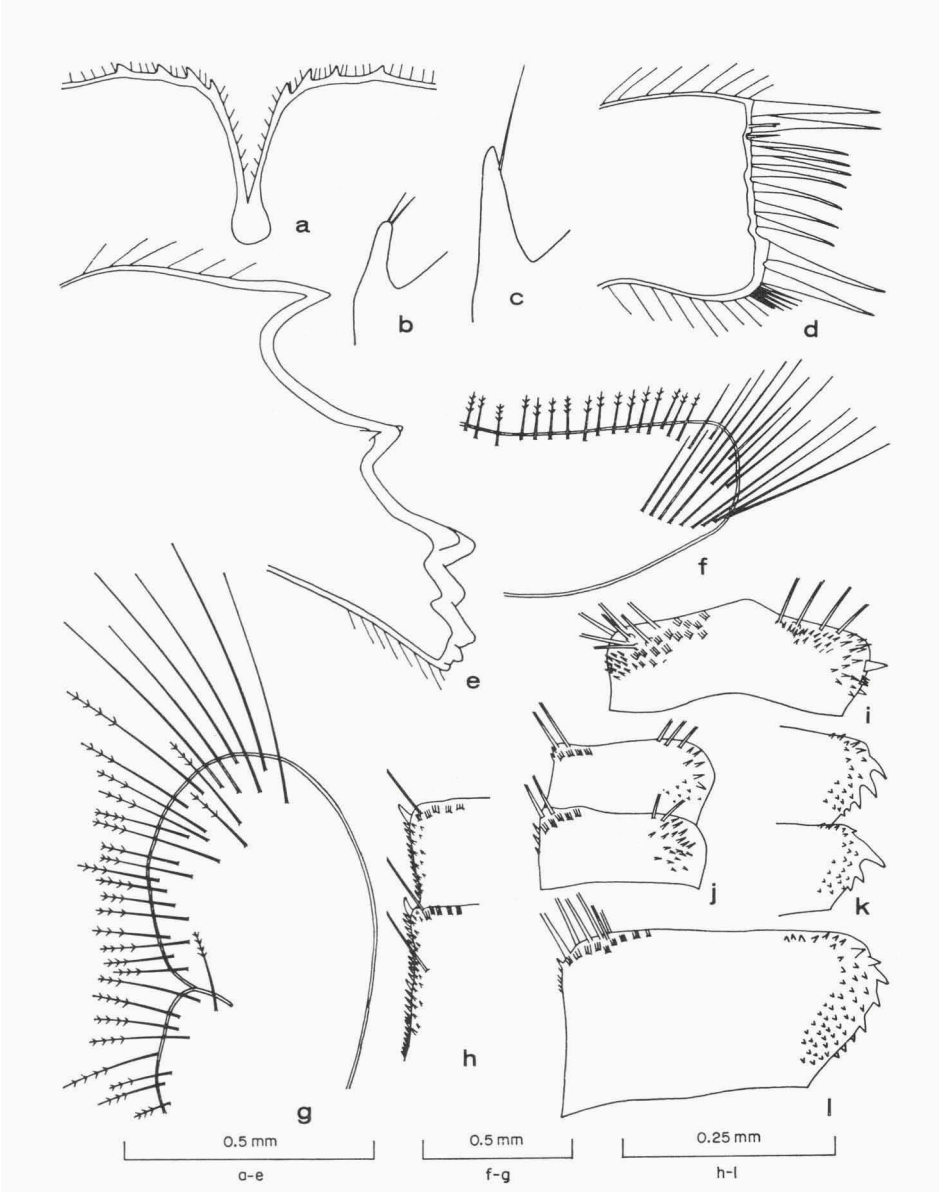

Fig. 18. *Balanus reticulatus* Utinomi. a, labrum; b, c, basidorsal points; d, g, 1st and 2nd maxillae; e, mandible; f, palpus; h, k, l, anterior rami of cirri III (h, posterior part of 2 proximal segments; k, 10th and 11th distal segments; l, 8th distal segment); i, j, posterior rami of cirrus II (i, 6th proximal segment; j, 5th and 6th proximal segments) (a-l, Oahu, Hawaii: a, c-f, h, l, BPBM 268; b, Kaneohe Bay; g, BPBM 314; i, k, BPBM 116; j, BPBM 318).

Palpus with setulae on distal fifth to half of lower margin, short finely pinnate setae on upper margin and in narrow band near upper margin on outer face, also with long setae on lower half of distal margin and in oblique row near inferodistal angle; narrow to wide band of setulae on distal half, and sometimes narrow band of simple scales on proximal half near lower margin; labral face with band of strongly pinnate short setae along upper margin on upper third distally, abruptly narrowing to 1 or 2 rows proximally, denticulate scales and setulae on distal fifth, row of long setae near distal margin on lower third, narrow band of setulae on distal half and of simple scales on proximal half parallel to lower margin.

Mandible with 4-7 (5.7) teeth, inferior angle not spinose; 2nd tooth bifid; 3rd-7th with extra denticles; 4th or 5th teeth not confluent with inferior angle; 6th or 7th, if present, confluent with inferior angle.

First maxilla with 1 or 2 fine spines in slight notch below upper pair of spines, short thick spine on outer face near lower spine of upper pair, 2-15 (6.6) spines between upper and lower pairs, and few short spines on inferior angle; lower pair of spines usually on slight, sometimes on moderate, rarely on strong, prominence.

Second maxilla without distinguishing characters.

Protopods of anterior cirri primarily with pinnate setae, some plumose setae posteriorly on coxopods; both segments of cirrus I with narrow band of simple scales near anterior margin and few multifid spinules below posterodistal angles on outer faces; inner faces usually with few simple spinules below posterodistal angles; protopods of cirri II and III each with narrow to wide band of simple scales near posterior margin and simple and multifid spinules below anterodistal angle on outer face; inner faces with few simple spinules below posterodistal angles and sometimes also below anterodistal angles.

Cirrus I with anterior ramus 2-9 (4.4) segments longer than posterior; posterior ramus with very protuberant segments; proximal segments of anterior ramus protuberant; distal sutures of both rami with long setae, also with multifid spinules on most segments of anterior ramus and on few distal segments of posterior ramus; several proximal segments of both rami each also with wide band of simple and multifid spinules on outer face, and sometimes with narrow band of simple spinules on inner face, near posterior margin.

Cirrus II with anterior ramus 1 segment shorter to 4 (1.3) segments longer than posterior; both rami with protuberant segments; distal sutures with long setae and multifid spinules, usually near anterior and posterior margins of proximal and some median segments; outer faces near anterior

margins with simple spinules or teeth; outer and inner faces near posterior margins with spinules or scales. Anterior margins of few proximal segments of posterior ramus each with 1 large conic tooth or several spike-like teeth near distal angle. Outer faces near anterior margins of several proximal segments of anterior ramus sometimes with few simple spinules, occasionally with 1 or 2 small conic teeth on 1 or 2 segments; posterior ramus with narrow to wide band of simple spinules on 3 or 4 proximal segments; 1-3 adjacent segments each usually with small conic teeth in 2 or 3 rows parallel to margin and 1-3 large conic or spike-like teeth near distal angle, sometimes with few small conic teeth or simple spinules near distal angles. Outer faces near posterior margins on several proximal segments of both rami each with wide band of simple and spinulose scales; remaining proximal and some median segments each with 2 or 3 short rows of multifid spinules below distal angle. Inner faces near posterior margins each with narrow band of simple spinules.

Cirrus III with anterior ramus equal to or 1-6 (2.9) segments longer than posterior; both rami with slightly protuberant segments; distal sutures with spinules and short setae, sometimes also with conic teeth; outer faces near anterior margins with conic teeth; posterior margins with erect teeth below short setae on distal angles; inner faces with subsutural spinules or teeth, without complex setae. Distal sutures usually with simple spinules and 1-6 teeth on anterior third to half, with multifid spinules near posterior margin on all distal segments except ultimate and on median segments; first 2 or 3 distal segments also with few short setae; proximal segments with multifid spinules near posterior margins; anterior ramus sometimes with teeth near anterior margins on all segments including ultimate; posterior ramus occasionally without teeth. Anterior margins usually with conic teeth on proximal, occasionally also on some median, segments of anterior ramus; posterior ramus usually without teeth, sometimes with teeth on few proximal segments; long proximal segment of anterior ramus usually without teeth, sometimes with 1 or 2 small teeth below distal angle, occasionally with series of small teeth; remaining proximal and few median segments each usually with 1-4 large teeth, sometimes with large teeth distally and 2 or 3 small teeth proximally, occasionally with crowded series of small teeth; long proximal segment of posterior ramus occasionally with 1 or 2 small teeth below distal angle, few adjacent segments each sometimes with 1 or 2 large teeth below distal angle, occasionally with 3-5 small teeth. Outer faces near anterior margins of both rami usually with teeth on all except few distal segments, sometimes on all except ultimate; long proximal segments each usually with few small teeth near anterodistal angle, sometimes with 2 or 3

rows of small teeth near margin; remaining proximal, median, and few distal segments each usually with numerous small and few large teeth on anterior third, large teeth usually near anterodistal angle, sometimes in row adjacent to margin; remaining distal segments, except ultimate, each usually with few, large simple or bifid spinules, sometimes also with few teeth, near anterodistal angle. Inner face near anterior margin of long proximal segment of anterior ramus occasionally with few simple spinules and scales; several adjacent segments sometimes with few simple spinules; posterior ramus sometimes with few simple spinules on long proximal segment. Posterior margins of both rami with 5 or 6 short setae on most distal angles, fewer proximally, sometimes lacking on 1 or 2 proximal segments; anterior ramus with 1-3 large erect teeth below distal angles on most proximal segments except long proximal; sometimes also on median segments; long proximal segment, usually with series of simple spinules; long proximal and several adjacent segments occasionally with series of small conic teeth; long proximal segment of posterior ramus with simple spinules. Outer faces near posterior margins of several proximal segments of anterior ramus occasionally with few simple spinules and scales, rarely with few small conic teeth; posterior ramus occasionally with narrow band of simple and spinulose scales on long proximal segment. Inner faces near posterior margins of each segment of anterior ramus having erect teeth below distal angle usually with subsutural row of several simple spinules and 2-4 teeth, occasionally without teeth, sometimes with 2 or 3 rows of simple spinules below subsutural row; long proximal segment usually with narrow band of simple spinules, sometimes with several rows of simple spinules and conic teeth; each segment of posterior ramus having erect teeth below distal angle with few subsutural simple spinules, sometimes also with narrow band of simple spinules or spinulose scales on long proximal segment.

Protopods of posterior cirri each usually with few simple spinules near anterodistal angle on outer face, occasionally also with narrow band of fine multifid spinules near anterior margin; inner face with narrow to wide band of simple or multifid spinules near anterior margin and narrow band of larger simple spinules, usually also with several subsutural, large simple spinules or erect teeth near posterior margin; coxopods sometimes and basipods occasionally with fine simple spinules on posterior margins.

Posterior cirri usually with simple spinules on distal sutures near anterior margins on proximal halves, sometimes with simple spinules, larger near anterior margin on each suture of all but few distal segments; distal sutures of anterior ramus also with several large teeth near anterior margins of most segments; few distal segments sometimes with large simple spinules;

posterior margins of posterior cirri with 1 long and few short setae on each distal angle, also with 1 or 2 large erect teeth below setae usually on few proximal segments; remaining proximal and some median segments each sometimes with large erect teeth below setae; inner faces near posterior margins of proximal and some median segments with subsutural erect teeth or simple spinules; proximal segments usually with 3-5 teeth, sometimes with 1 or 2 teeth and 2 or 3 spinules, occasionally without teeth; median segments with 3-5 teeth; long proximal and 1-6 adjacent segments of anterior rami each usually also with 2 or 3 rows of small conic teeth, sometimes with 2 or 3 rows of denticulate scales or simple spinules, sometimes without scales or spinules, occasionally with few small conic teeth. Anterior margins of few proximal segments of anterior ramus of cirrus IV sometimes with numerous small or 1-4 large conic teeth; posterior ramus without teeth. Outer faces near anterior margins of anterior ramus of cirrus IV with teeth on proximal, sometimes also on median, and occasionally on all but 2 or 3 distal, segments; each proximal segment usually with 3 or 4 large teeth near anterodistal angle and numerous small teeth near anterior margin, rarely with only 3 or 4 teeth near anterodistal angle; median and distal segments each with 3 or 4 teeth near anterodistal angle; posterior ramus usually without teeth, rarely with few, small conic teeth on few proximal segments. Cirrus VI with 4-7 (5.0) pairs of setae on anterior margins of median segments. Basidorsal point of penis narrow, usually with 2 apical or subapical setae, sometimes with 1 seta, occasionally without setae.

Color. — Shell of holotype reddish gray, bluish in upper part, with moderately broad, dark purple, equidistant longitudinal stripes, intersected by many alternating reddish brown and white transverse lines (Utinomi, 1967). In our material, shell sometimes buff or white; longitudinal stripes usually purple, sometimes lavender, pinkish, or hyaline; transverse lines usually same color as interspaces between longitudinal stripes, never noticeably alternating with white lines. Longitudinal stripes often narrow, sometimes lacking on middle or edges of parietes, occasionally confluent; transverse lines sometimes not discernible. Radii usually white, sometimes with purple on parietal edges, occasionally purple. Alae usually purplish, sometimes white; sheath white with purple longitudinal bands with one band on alar part of laterals and on middle of other compartments. Scutum, externally and internally, usually purple except for white margins and ridges, occasionally white or white with small splotches of color. Tergum, externally and internally, usually purple except for white margins and spur, occasionally white with traces of color.

Measurements. — Carinorostral diameter of holotype 26 mm, height

15 mm. Largest specimens examined, carinorostral diameter 18 mm, rostral height 10 mm; carinorostral diameter 14 mm, greatest height 18 mm.

Variations. — As indicated in the description, the characters of the shell and opercular valves are highly variable; yet Utinomi (1960) used some of these characters to differentiate *B. a. communis* (= *B. reticulatus*) from *B. a. hawaiiensis* (= *B. a. amphitrite*). Unfortunately, some of his characters are also highly variable in *B. a. amphitrite*. The color of the shell and opercular valves varies even within a single clump of specimens (Hawaiian) or on a single shell (Durban Bay). The longitudinal stripes, in the material from Bombay, vary from pink to purple and on two shells are confluent. The number of parietal tubes in specimens from the type locality is 9-11 (10), whereas, in the remainder of our material the number varies from 11-17 (13.5). The radii may be moderately wide with moderately oblique or oblique summits; the width appears not to be related to the shape of the shell, nor is it associated exclusively with one type of tergum. Our specimens from the type locality all have narrow radii with very oblique summits; the spur of the tergum is narrow, longer than wide, but differing from the typical form in being less than its own width from the basiscutal angle in most specimens. In contrast, the specimens from Bombay, with one exception, have moderately wide radii with moderately oblique summits; the narrow spur of the tergum is more than its own width from the basiscutal angle in all specimens.

Utinomi (1967) described *B. reticulatus* from material collected at two localities in Japan. Although our material includes specimens from his two localities, variations in several characters, in addition to the color variations mentioned previously, have been noted. In Utinomi's material, the parietal tubes lacked transverse septa; in the present collections, they were rarely lacking. He did not mention denticles or striae basally on the inner lamina of his specimens; however, these occur in some specimens from most of the localities represented in our collection. Utinomi described the adductor ridge of the scutum as low and short; we have found it usually high and less frequently moderately high or low, and short to moderately long. While the spur is most frequently characterized by a spur fasciole, occasionally a spur furrow has been observed. According to Utinomi (1967) the labrum invariably has 3 teeth on each side of the notch; we found the number to vary from 0 to 5 (3.8). Only 3% of our specimens had a strong prominence on the first maxilla, as described by Utinomi; in 36% of the specimens the prominence was moderate and in 61% it was slight.

Utinomi (1967) did not describe the characteristic armature of cirrus II, the presence of erect teeth below the posterodistal angles of cirri III-VI, the

presence of teeth on cirrus IV, nor the basidorsal point of the penis, thus no comparisons can be made. He did describe cirrus VI with 6 paris of setae on the median segments; in our specimens the number varied from 4 to 7 (4.9). In a random sample of 30 specimens, 40% were found to have 1 or 2 setae on the basidorsal point of the penis.

Habitat. — Intertidal to 18 m, on mollusk shells, crabs, wood, rocks, harbor installations, and ships. In Japanese waters, apparently confined to upper subtidal in highly saline bays (Utinomi, 1967).

Remarks. — As previously discussed, Darwin's figures of the shell and tergum of *B. a.* var. *communis* (Darwin, 1854, pl. 5 fig. 2e, l) do not agree with *B. a. amphitrite* sensu stricto, as restricted by lectotype selection by Harding (1962). These figures, however, do agree with *B. reticulatus,* which also has a simple labrum as described by Darwin for var. *communis.*

The description and figures of the opercular valves, mouth parts, and cirri of the specimens referred by Nilsson-Cantell (1921) to *B. a. communis* agree with *B. a. amphitrite*; however, the color pattern of the shells and the narrow radii with very oblique summits suggests that his material included specimens of *B. reticulatus.* Subsequently, Nilsson-Cantell (1932a) referred specimens to *B. a. communis* only on the basis of the opercular valves as the specimens had been dried. He noted that the tergum was variable; the Mediterranean specimens, as he had pointed out in his earlier paper (Nilsson-Cantell, 1921), had narrower terga than the Malayan or South African specimens. Although his figures of the tergum (Nilsson-Cantell, 1932a, fig. 3c-f) can not be assigned, with certainty, to any taxon, it seems probable that this Mediterranean material also included specimens of *B. reticulatus.*

Unaware that Nilsson-Cantell (1921) had described a multidenticulate labrum in *B. a. communis,* Broch (1922) described a new subspecies, *B. a. hawaiiensis,* which he distinguished from Darwin's (1854) var. *communis* by the labrum. However, Broch doubtfully included in *B. a. hawaiiensis* two specimens, from Mindanao, which had few teeth on the labrum; from the description of the shell and opercular valves, these specimens should be referred to *B. reticulatus.* Broch's (1922) *B. amphitrite* forma *communis* included specimens from 20-30 fathoms, which differed in the color pattern from typical *communis* (= *B. reticulatus*) but agree with that of *B. poecilotheca.*

Utinomi (1960) was the first to clearly differentiate the forms with a multidenticulate labrum from var. *communis.* After Harding's (1962) redescription of *B. a. amphitrite,* Utinomi (1964) proposed a new name, *B. amphitrite tesselatus,* for var. *communis* auct. (not Darwin). Subsequently, Utinomi & Kikuchi (1966) listed this taxon as *B. variegatus tesselatus* and

Utinomi (1967), having found that the specific name *tesselatus* was preoccupied by *B. tesselatus* Sowerby, proposed the name *reticulatus* and raised the taxon to specific rank.

Zevina & Tarasov (1963) assigned specimens to *B. a. cirratus* and Stubbings (1963a) referred specimens to *B. a. variegatus* which, because of the armature of cirrus II, clearly must be referred to *B. reticulatus.*

Karande & Palekar (1966) assigned specimens with simple labra to *B. a.* var. *denticulata.* The description and figures (Karande & Palekar, 1966, pl. 1 fig. 7, pl. 4 row 5) indicate that this material should be referred to *B. reticulatus.* As previously indicated, Dr. Karande's material of *B. a. communis* that we examined, included specimens of *B. reticulatus;* the figures of the opercular valves (Karande & Palekar (1966, pl. 4 row 2) for the former taxon resemble those of *B. reticulatus.*

Stubbings (1967), after an examination of 26 specimens, from 13 localities, of the *communis* and *hawaiiensis* types differentiated by Utinomi (1960), concluded that *communis* sensu Utinomi was not a valid taxon, as Stubbings found 8 specimens with a "mixed" assemblage of characters. As previously noted, we believe that Stubbings' failure to distinguish between these two taxa was due, in part, to the variability of the characters used, and in part, to the inclusion of specimens of *B. improvisus* in his material. We refer, on the basis of his earlier descriptions of specimens from Freetown (Stubbings, 1963b: 15) and from Lagos (Stubbings, 1961: 22), the figures of the tergum of Stubbings' (1967, fig. 14d-f) *B. a. amphitrite* from these localities to *B. reticulatus.*

Utinomi (1967) did not give the distribution of *B. reticulatus* but remarked that it is probably widely distributed. Our material confirms this belief, as our records show that it occurs on both sides of the Atlantic and in the Indian Ocean; the range is also extended in the western Pacific. Prior to World War II, *B. reticulatus* was more prevalent than *B. a. amphitrite* in Japanese bays and harbors but now is apparently not found on the Japan Sea coast; it occurs in stenohaline habitats only (cf. Utinomi, 1967, 1970).

As previously discussed, *B. reticulatus* is superficially very similar to *B. a. amphitrite;* however, comparison of Y values of members of the species (fig. 11) indicates minimal overlap. Similarly, in the statistical comparison of taxa of the complex, these two species were found to be quite diverse ($D^2 = 46.71$). In contrast, the distance between *B. reticulatus* and *B. variegatus* was only $D^2 = 4.44$ when the taxa of the complex were considered simultaneously and $D^2 = 4.06$ when closest neighbor pairs were analysed. Although the characters afforded by the shells and opercular valves are highly variable in both species, two characters of the cirri will distinguish

the two species in specimens larger than 5 mm in diameter. In *B. reticulatus,* cirrus II is armed on the outer face near the anterior margin with simple spinules or conic or spike-like teeth; spinules and teeth are absent from the outer faces near the anterior margins in *B. variegatus.* Similarly, erect teeth are present below the posterodistal angles in cirri III-VI in *B. reticulatus*; erect teeth are absent in *B. variegatus.*

B. reticulatus can be differentiated from both *B. variegatus* and *B. a. amphitrite* by the carinal segment of the tergum. In *B. reticulatus* the carinal segment can be distinguished along the entire carinal margin; the upper third is sometimes narrowly protuberant and the growth ridges are only slightly stronger than those on the rest of the valve. The carinal segment is narrower, often scarcely discernible in *B. variegatus*; the growth ridges are stronger medially. In contrast, the protuberance is sharply delimited in *B. a. amphitrite* and usually extends nearly to the middle of the margin; the growth ridges on the protuberance are much stronger than those on the rest of the valve while those below the protuberance are scarcely discernible.

B. reticulatus can usually be distinguished from *B. variegatus* and always from *B. a. amphitrite* by the beveled, rather than rough, summits of the radii. The sheath, which is almost always colored in *B. reticulatus,* is white in *B. variegatus.* The color pattern is different in *B. reticulatus* and *B. a. amphitrite*; particularly distinctive is the purple longitudinal alar band on the lateral part of the sheath in *B. reticulatus.* In *B. a. amphitrite* the laterals, at least, are always entirely colored.

Balanus pallidus Darwin (text-fig. 19, pl. 10 figs. a-g)

Balanus amphitrite var. *pallidus* Darwin, 1854: 240, pl. 5 fig. 2c (in part; not pl. 5 fig. 2k; see remarks; type locality: unknown). — Stubbings, 1961: 27 (in part; not fig. 6a, b, see *B. improvisus*). — Stubbings, 1963b: 15, figs. 4a-e.

Balanus amphitrite var. *stutsburi* Darwin, 1854: 240, pl. 5 figs. 2d, i, m-o. — Stubbings, 1959: 1282, fig. 1. — Stubbings, 1961: 24 (in part; not fig. 5; see *B. venustus*). — Sandison, 1962: 517, figs. 4, 5, 7, 8, 12. — Stubbings, 1963b: 19, fig. 6a-d.

Balanus dybowskii Gruvel, 1903a: 24. — Gruvel, 1903c: 143, pl. 1 figs. 1-9, pl. 4 fig. 14.

Balanus amphitrite venustus: Nilsson-Cantell, 1925: 28, fig. 11a-h, pl. 1 fig. 3 (not *Balanus amphitrite venustus* Darwin, 1854: 240).

Balanus amphitrite stutsburi: Nilsson-Cantell, 1932a: 111, 125, fig. 5a-e.

? Balanus amphitrite insignis Nilsson-Cantell, 1938: 41, fig. 10a-h, pl. 1 fig. 1.

Balanus pallidus stutsburi: Harding, 1962: 281, pl. 4 figs. a-h. — Stubbings, 1964a: 109.

Balanus pallidus: Stubbings, 1964b: 338, fig. 4a-d. — Stubbings, 1965: 887. — Stubbings, 1967, fig. 16b-e (? in part; not fig. 16a; see *B. improvisus*). — Utinomi, 1967: 206, fig. 3a-c.

Balanus amphitrite var. *venustus*: Karande & Palekar, 1966: 145, fig. 13, pl. 2 fig. 9, pl. 4 row 7 (not *Balanus amphitrite* var. *venustus* Darwin, 1854: 240).

not *Balanus amphitrite* var. *stutsburi*: Krüger, 1927: 13, 16 (= *B. kondakovi*).

not *Balanus amphitrite pallidus*: Nilsson-Cantell, 1932a: 111, 124, fig. 4a, b (? = *B. improvisus*). — Henry, 1959: 192, pl. 1 fig. 4, pl. 3 figs. 7, 8 (= *B. subalbidus*).

Lectotype. — BM 1961. 12.6.36a-c, by subsequent selection by Harding, 1962: 278.

Distribution. — West Indies to north coast of south America; Panama Canal; West Africa from Morocco to mouth of Congo; Mediterranean Sea; Zanzibar; Bombay, Indian Union; ? Sumatra (Nilsson-Cantell, 1938).

Material examined. — Table 10.

Diagnosis. — Shell with epicuticle usually persistent; radii narrow to wide, summits beveled; sheath vesicular, often with calcareous vesicles in furrow below lower margin; parietal tubes usually in 2 or more rows. Opercular valves with epicuticle thin, persistent. Scutum usually flat, sometimes externally concave; longitudinal striae fine; articular ridge about 3/5 length of tergal margin; adductor ridge long, well separated from articular ridge. Tergum with carinal margin convex, with spur furrow, usually open; spur length greater than twice width, distance from basiscutal angle to spur greater than spur width; basal margin concave, often deeply excavated on carinal side. Labrum simple. Cirrus II with simple spinules or conic teeth

Table 10. *Balanus pallidus*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
Zanzibar					
----	~50	---	---	1864	Salmin RMNH 35
Sicily					
----	1	---	---	----	---- USNM 51678
Nigeria					
Lagos, Tarquah Bay	11	test panels	---	21/11/57	Stubbings USNM
Niger Delta	8	---	---	5-8/60	Beets RMNH 1176
Port Harcourt	4	---	---	19/12/53	Stubbings USNM
Bonny River	4	buoy	---	30/11/57	Stubbings USNM
Panama Canal					
Miraflores Locks (upper chamber)	23	---	---	17/1/72	Jones USNM
Venezuela					
Lake Maracaibo	9	---	---	1963	Stubbings USNM
Surinam					
Suriname River	~50	---	---	24/6/48	Geijskes RMNH 181
Wia Wia Bank	~100	wood	---	12/11/48	---- RMNH 734
French Guiana					
Mahury Estuary	8	---	---	----	Stubbings USNM

on outer face near anterior margin; cirrus III with complex setae, without erect teeth below posterodistal angles; cirrus VI with 3-5 (4.2) paired setae on median segments.

Description. — Shell conic to cylindric; orifice usually toothed; width about 1/2 carinorostral diameter in conic specimens, more than 1/2 carinorostral diameter in cylindric; surface smooth unless ridged from replication of substratum; epicuticle thin, usually persistent. Radii narrow in conic, usually wide in cylindric specimens, usually with inconspicuous transverse striae; summits oblique, beveled, rough; sutural edges with septa usually smooth, sometimes weakly denticulate on lower margins. Alae with nearly horizontal summits; sutural edges septate. Sheath vesicular, often with calcareous vesicles extending into furrow below lower margin. Inner lamina ribbed to sheath; ribs weakly denticulate basally, occasionally finely ridged on sides near bases. Parietal tubes usually in 2 or more rows, arranged with small or moderately large tube on each side of primary longitudinal septa, sometimes with minute tube on each side of some subsidiary longitudinal septa; primary parietal tubes large, 16-22 (18.8) in rostrum, with transverse septa, usually in upper 1/3 to 1/2, occasionally to bases; subsidiary tubes extending apically to about middle of parietes, with fine transverse septa to bases. Inner surface of outer lamina occasionally with 1 or 2 ribs between primary longitudinal septa; ribs sometimes denticulate basally. Basis thin, with radial tubes and transverse septa.

Scutum usually flat, sometimes externally concave between apex and basal margin; basitergal angle rounded; occludent margin toothed; growth ridges low; longitudinal striae fine, approximate, sometimes indistinct. Inner surface sometimes roughened on upper part; articular ridge high; reflexed, about 3/5 length of tergal margin and about 1/3 length of occludent margin, end truncate or pointed; articular furrow deep; adductor ridge long, prominent, acute, without pit below, very well separated from articular ridge; adductor muscle pit indistinct; lateral depressor muscle pit small, shallow, sometimes absent.

Tergum with scutal margin raised, denticulate; carinal margin convex; growth ridges fine, slightly arched medially on carinal side of spur furrow, stronger on narrow to wide carinal segment; latter usually delimited by shallow groove; longitudinal striae occasionally present on carinal side; spur furrow usually open, occasionally almost closed, shallow or moderately deep; spur width about 1/5 length of basal margin; spur length about 2 2/3 spur width; distance from basiscutal angle to spur about 1 2/5 spur width, about 1/2 spur length, and about 1/5 length of basal margin; spur length about 2/5 length of basal margin; end usually rounded, sometimes obliquely trun-

cate; basal margin concave on both sides of spur, often deeply excavated on carinal side. Internally, scutal margin high; articular ridge prominent, reflexed at apex; articular furrow deep; crests for depressor muscle very prominent and numerous, usually projecting below basal margin; surface roughened on upper part, sometimes ridged medially on lower part; ridges occasionally projecting below basal margin.

Labrum with setulae and 1-5 (3.0) large teeth on crest on each side of notch; 1 tooth on each side usually on edge of crest near notch.

Palpus with short finely pinnate setae on upper margin; outer face with short simple setae in tuft on superodistal angle, in narrow band near upper margin on distal half, denticulate scales on distal fifth, more numerous near lower margin, long setae on lower half of distal margin and in oblique row

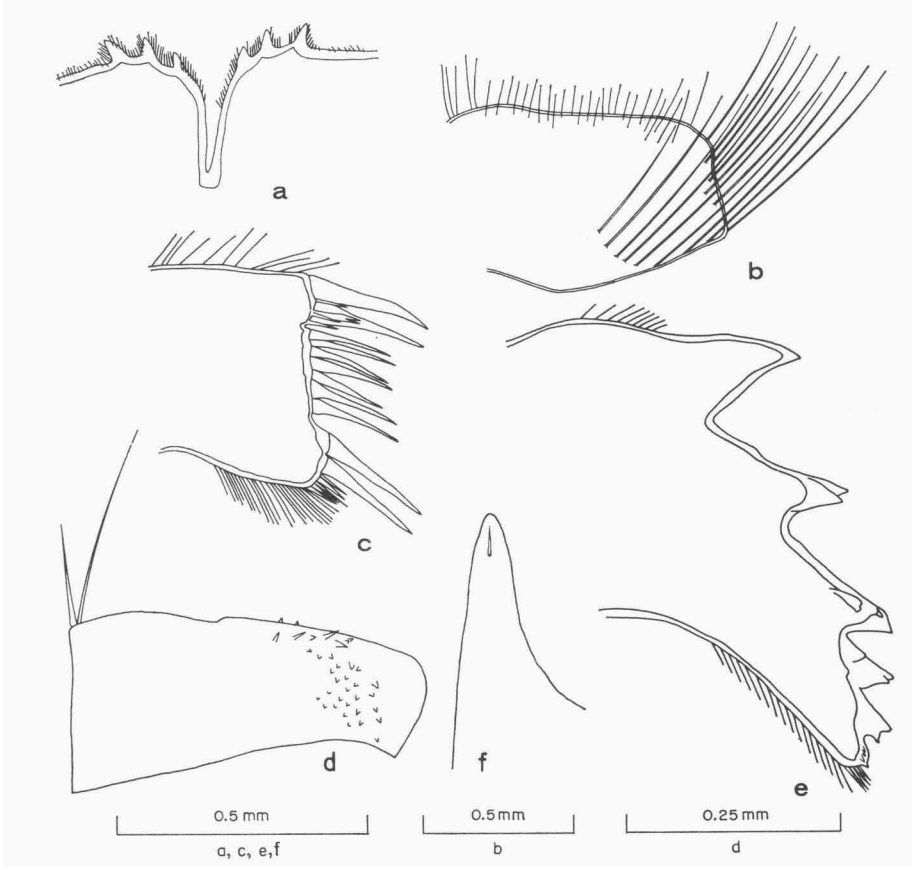

Fig. 19. *Balanus pallidus* Darwin. a, labrum; b, palpus; c, 1st maxilla; d, 6th proximal segment of anterior ramus of cirrus III; e, mandible; f, basidorsal point (a-e, Sicily; f, Port Harcourt, Nigeria).

near inferodistal angle, also with narrow band of setulae near lower margin on proximal 3/4; labral face with coarsely pinnate short setae near upper margin in 6-10 rows distally, gradually decreasing to 1 or 2 sparse rows proximally.

Mandible with 5-6 (5.0) teeth and spinose inferior angle; 2nd tooth bifid; 3rd-5th with many extra denticles; lower tooth not confluent with inferior angle.

First maxilla with 2-6 fine spines in notch below upper pair of spines, sometimes with 2 or 3 short thick spines on outer face near lower spine of upper pair, 3-10 (6.5) spines between upper and lower pairs and few short fine spines on inferior angle; lower pair of spines usually on slight prominence.

Second maxilla without distinguishing characters.

Protopods of anterior cirri with primarily pinnate setae, some plumose setae posteriorly on coxopods; both segments of cirrus I each with wide band of simple scales near anterior margin and narrow band of denticulate scales near posterior margin, on outer face; protopods of cirri II and III each with narrow band of simple, spinulose, and denticulate scales near posterior margin on outer face; basipods each sometimes with narrow band of simple and multifid spinules near anterior margin on inner face.

Cirrus I with anterior ramus equal to or 1-6 (3.4) segments longer than posterior; posterior ramus, and anterior ramus proximally, with very protuberant segments; distal sutures of both rami with long setae and multifid spinules; several proximal segments each with fine simple spinules on posterior margin and narrow band of simple and spinulose scales on outer face near posterior margin; long proximal segment and sometimes also 1 or 2 adjacent segments each with narrow band of multifid spinules on inner face near posterior margin.

Cirrus II with anterior ramus 2 segments shorter to 3 (1.2) segments longer than posterior; both rami with very protuberant segments; distal sutures with long setae and multifid spinules; outer faces near anterior margins with spinules and sometimes also teeth; posterior margins with simple spinules and short setae; outer and inner margins with scales near posterior margins. Distal sutures usually also with few simple spinules near anterior margins on posterior ramus. Outer faces near anterior margins of few proximal segments of both rami each with narrow band of multifid spinules; remaining proximal segments each with several rows of multifid spinules and few large simple spinules and conic teeth near distal angle; median and most distal segments each with wide band of simple and multifid spinules. Posterior margins of proximal segments with simple spinules.

Outer and inner faces near posterior margins each with band of simple and spinulose scales.

Cirrus III with anterior ramus 2-5 (3.3) segments longer than posterior; both rami with protuberant segments; distal sutures with short setae and spinules; outer faces near anterior margins with conic teeth; posterior margins with short setae and spinules; inner faces with complex setae. Distal sutures with setae and multifid spinules on 3 or 4 distal segments; simple and multifid spinules near anterior margins and multifid spinules near posterior margins on remaining segments. Anterior margins of anterior ramus sometimts with teeth on proximal segments; posterior ramus without teeth. Outer faces near anterior margins of anterior ramus with teeth on proximal and median, sometimes on distal, segments; proximal and median segments each with 2 or 3 and 2-7 large teeth, respectively, near distal angle, sometimes also with 2-8 rows of small teeth; distal segments sometimes with 2 or 3 large teeth, occasionally with few small teeth near distal angle; posterior ramus usually with teeth on proximal segments, sometimes also on median segments, occasionally without teeth but with spinules near distal angles on proximal segments; proximal segments each usually with 2-7 large teeth near distal angle, sometimes also with 2-8 rows of small teeth, occasionally with only few simple and multifid spinules near distal angles. Posterior margins with tufts of short setae, fewer proximally, on distal angles; long proximal segment, occasionally also few adjacent segments of anterior ramus, with fine simple spinules. Outer faces near posterior margins of few proximal segments each with narrow band of simple or denticulate scales. Inner faces near posterior margins each sometimes with narrow band of spinulose or denticulate scales, also with complex setae below each distal angle; anterior ramus usually with few pectinate setae on 3 or 4 distal segments; posterior ramus with several pectinate setae on most segments, frequently also with 1 or 2 multifurcate setae on few segments or 3 or 4 bifurcate setae usually on all but ultimate and 1 or 2 proximal segments, occasionally on only few segments, rarely absent. Pectinate setae with pectination variable in length and thickness; multifurcate setae with apical ends long or short, usually with 2 or 3 long teeth, sometimes with 3-7 slightly shorter and thinner teeth.

Protopods of posterior cirri each with narrow band of denticulate scales near anterior margin and narrow band of simple and multifid spinules near posterior margin, on inner face.

Posterior cirri with multifid spinules on distal sutures; proximal and median segments of both rami also with simple spinules near posterior margins; posterior margins of anterior ramus with 3 relatively long and several short setae

on each distal angle; outer faces near posterior margins each with narrow band of simple scales usually on proximal half of each ramus, sometimes on only few proximal segments. Anterior ramus of cirrus IV also with conic teeth on outer faces near anterior margins on proximal segments, occasionally without teeth; few proximal segments each usually with 2-5 large teeth near anterodistal angle; remaining proximal segments each sometimes with 2-5 large teeth near distal angle, occasionally also with 4 or 5 rows of small teeth near anterior margin; posterior ramus usually without teeth, occasionally with 2 or 3 large teeth near distal angle on few proximal segments. Cirrus VI with 3-5 (4.2) pairs of setae on anterior margins of median segments. Basidorsal point of penis spinulose, also usually with 1 or 2 subapical setae.

Color. — Shell entirely white or white with pink, red, or purple longitudinal, sometimes confluent, stripes, frequently colored only basally or apically, often only with color on edges of parietes. Radii white, often with splotches of color, or colored like parietes. Alae white or with pink or purple near parietes or on summits. Epicuticle pale yellow. Sheath usually entirely white, occasionally with pink or purple alae. Scutum, externally and internally, usually dark purple with white band on tergal margin, sometimes also with white band on occludent margin; occasionally entirely white or white with splotch of color near base medially. Tergum, externally and internally, usually white or white with apex purple or pink; occasionally with carinal side purple or pink; outer surface often with light or opaque striae from apex to base in line with crests for depressor muscle.

Measurements. — Carinorostral diameter of lectotype 8.2 mm, height 13.8 mm. Diameter of largest specimen examined 17 mm, height 10 mm.

Variation. — As both Sandison (1962) and Stubbings (1961, 1963) have pointed out, *B. pallidus* is an extremely variable species. In addition to the variations noted in the description, the shell is often very fragile, particularly in colorless specimens, and the radii may be incompletely calcified. In these specimens, the opercular valves are thin; the articular ridge of the scutum is usually short; the spur is very narrow, often tapering to a point; the carinal side of the basal margin is greatly excavated. Dr. Stubbings (personal communication) has also seen the radii not filled up in poorly calcified West African specimens.

The mouth parts and cirri of the specimens described herein differ somewhat from Sandison's (1962) description of specimens from eight localities on the Guinea coast. The intermediate spines of the first maxilla of her Port Harcourt specimens varied from 8-13 (9.9) and of the other seven localities, from 6-11 (7.7). The maximun number of paired setae on cirrus

VI was always 4 in the Port Harcourt material; whereas, the number in six other localities ranged from 3-9 (5.1).

Complex setae on the third cirrus have not previously been reported for *B. pallidus*. Pectinate setae were present in all the specimens examined and some bifurcate or multifurcate setae were seen in most of the West African, Venezuelan, and Panamic specimens, but only in one of the French Guianan specimens.

Habitat. — Intertidal to 6 m, often in brackish water; on mangrove roots, shells, harbor installations, and ships. According to Sandison (1962), in Lagos Harbor, white forms are more common in the dry season and purple forms more common in the wet season; she suggests that color may be related to the type of food available. *B. pallidus* can withstand fluctuations in salinity (Sandison & Hill, 1966).

Remarks. — Part of the difficulties that various investigators have had in recognizing *B. pallidus* has been due to the fact that Darwin's (1854) description of the tergum of var. *pallidus* and his figure (Darwin, 1854, pl. 5 fig. 2k) do not agree. Harding (1962) has shown that Darwin's description, and not his figure, correctly applied to *B. pallidus*. Harding raised *pallidus* to specific rank, with Darwin's var. *stutsburi* as a subspecies. He was unable to differentiate the two taxa except by color, but noted that, unlike Darwin's other varieties, both had subsidiary parietal tubes. This character was also noted by Darwin (1854) for *B. amphitrite* and by Pilsbry (1916) for *B. a. albicostatus*.

Nilsson-Cantell (1932a) and Henry (1959) both assigned specimens to *B. a. pallidus* primarily on the similarity of their material to Darwin's figure of the tergum. Nilsson-Cantell's (1932a) specimens agree, for the most part, with *B. improvisus*; however, as he did not describe the mouth parts and cirri, these specimens can be assigned only tentatively to this taxon. Henry's (1959) specimens, which had multidenticulate labra, were subsequently referred to *B. subalbidus* Henry, 1974.

Stubbings (1961) doubtfully assigned some specimens from Bathurst, Gambia to *B. a. pallidus*; however, the characters of the shell and opercular valves (Stubbings, 1961, fig. 6a, b) and the multidenticulate labra clearly indicate that these specimens should have been referred to *B. improvisus*. Subsequently, Stubbings (1967, fig. 16a) included a tergum from this station in a series of figures showing the range of variability of the tergum of *B. pallidus*. Figure 16a, based on the above cited description of the specimens of *B. pallidus* and the figure of the tergum of a specimen from the same station, referred to *B. a.* var. *denticulata* (Stubbings, 1961, fig. 4d), should also be referred to *B. improvisus*. The description of the tergum

(Stubbings, 1961, fig. 5) and color pattern of the shells indicate that the lot of specimens tentatively referred to *B. a.* var. *stutsburi* should have been assigned to *B. venustus*. Subsequently, Stubbings (1963b) placed *B. dybowskii* Gruvel, and in a latter paper (Stubbings, 1964b), *B. pallidus stutsburi* in synonymy with *B. pallidus*. In both these actions, we concur with Stubbings' conclusions.

In a redescription of *B. v. venustus,* Stubbings (1967) pointed out that Nilsson-Cantell's description and figures (Nilsson-Cantell, 1925: 28, figs. 11a-h, pl. 1 fig. 3) of *B. a. venustus* should have been referred to *B. pallidus*; however, he did not include it in his synonymy of the latter species. Karande & Palekar (1966) accepted Nilsson-Cantell's (1925) interpretation of *B. a. venustus*; their material is also referred herein to *B. pallidus*.

Nilsson-Cantell (1938) described a new subspecies, *B. a. insignis,* based on one corroded specimen. Utinomi (1967) questionably referred this taxon to *B. pallidus* without comment. The description of the shell and mouth parts and cirri agree with *B. pallidus*. The opercular valves have a somewhat different configuration; however, this probably can be explained by the corrosion of the articulating margins. Therefore, we also questionably refer *B. a. insignis* to *B. pallidus*.

As previously indicated, insufficient numbers of specimens of *B. pallidus* were available to be included in the statistical analyses; therefore, a quantitative evaluation of its relationship to other taxa of the complex cannot be made. However, the presence of more than a single row of parietal tubes in the parietes, a vesicular sheath, and complex setae on cirrus III clearly indicate the affinity of *B. pallidus* to the other taxa assigned to the *pallidus* group.

B. pallidus appears to be most closely related to *B. citerosum*; they may be most readily differentiated by the tergum. In addition, the epicuticle of *B. citerosum* is very thick and the summits of the radii are smooth rather than rough and are not beveled.

The records from Venezuela, Surinam, and French Guiana extend the range of *B. pallidus* in the western Atlantic, but may not indicate that this species is spreading, as this area has not been extensively studied. The record from the locks of the Panama Canal, however, is notable. If *B. pallidus* establishes itself in the eastern Pacific, as *B. eburneus* has recently done, this record will substantiate the route of the invasion (cf. Matsui et al., 1964).

Balanus albicostatus Pilsbry (text-figs. 20, 22a, pl. 10 figs. h-k, pl. 11 figs. m, n)

Balanus amphitrite var. *communis*: Krüger, 1911: 51, pl. 1 fig. 7, pl. 4 fig. 40a1-b2 [as 34 in text] (not *Balanus amphitrite* var. *communis* Darwin, 1854: 240).
Balanus mirabilis Krüger, 1912: 11, pl. 2 fig. 6.

Balanus amphitrite albicostatus Pilsbry, 1916: 90, fig. 18a, b, pl. 20 figs. 1-4 (in part, see *B. kondakovi*; type locality: Japan). — Nilsson-Cantell, 1921: 314. — Hiro, 1937: 342. — Hiro, 1938: 303, fig. 3a-d. — Hiro, 1939a: 261, fig. 8a, b. — Hiro, 1939b: 209. — Utinomi, 1956: 52, pl. 26 fig. 19. — Zevina & Tarasov, 1963: 91, fig. 11a-e. — Utinomi, 1964: 52, pl. 26 fig. 10.

Balanus amphitrite form *formosanus* Hiro, 1938: 306, figs. 6a-h, 7a-c.

Balanus albicostatus albicostatus: Utinomi & Kikuchi, 1966: 5. — Utinomi, 1967: 209, figs. 4a-c, 5a-g, pl. 6 fig. 2. — Utinomi, 1970: 356.

Balanus albicostatus formosanus: Utinomi, 1967: 212, figs. 6a-c, 7a-d, pl. 6 fig. 3.

Holotype. — USNM 32950.

Distribution. — Japan; southeast Asia from Korea to Formosa and Hong Kong; California (see remarks).

Material examined. — Table 11.

Table 11. *Balanus albicostatus*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
California					
Morro Bay	1	*Ostrea* sp.	---	15/6/43	----- USNM 165407
Japan					
Shinagawa Bay	1	---	*B. kondakovi*	-----	----- USNM 32951
China					
Minhow	9	-----	---	-----	----- USNM

Diagnosis. — Shell with epicuticle not persistent; parietes ribbed; radii very wide, summits thick, rough; sheath vesicular, sometimes with calcareous vesicles in furrow below lower margin; parietal tubes in 2 or more rows. Opercular valves with epicuticle thin, usually persistent. Scutum flat; longitudinal striae fine; articular ridge about 2/3 length of tergal margin; adductor ridge short, well separated from articular ridge. Tergum with carinal margin convex, with spur fasciole; spur length about 4/5 width; distance from basiscutal angle to spur about 1/2 spur width; basal margin usually straight, occasionally concave, on scutal side, concave on carinal side. Labrum simple. Cirrus II without spinules or teeth on outer face near anterior margin; cirrus III with complex setae, without erect teeth below posterodistal angles; cirrus VI with 4 or 5 (4.1) paired setae on median segments.

Description. — Shell conic or cylindroconic; orifice moderately toothed, width more than 1/2 carinorostral diameter; surface usually ribbed, occasionally without ribs; epicuticle not persistent. Radii usually very wide, occasionally moderately wide, transversely striate; summits usually moderately

oblique, occasionally oblique, thick, rough; sutural edges with septa strongly denticulate on lower margins. Alae with moderately oblique summits; sutural edges septate. Sheath vesicular, sometimes with calcareous vesicles extending into furrow below overhanging lower margin. Inner lamina ribbed, usually only on lower half; ribs denticulate basally, occasionally ridged on sides near bases. Parietal tubes in 2 or more rows, arranged with usually small, sometimes large, tube on one or both sides of few primary longitudinal septa, occasionally also with minute tube on one or both sides of few subsidiary longitudinal septa; primary tubes large, 15-20 (16.5) in rostrum, with transverse septa usually in upper 2/3, occasionally to bases; subsidiary tubes extending apically to middle of parietes, with transverse septa nearly to bases. Inner surface of outer lamina sometimes with 1 or 2 ribs between primary longitudinal septa. Basis thin, with fine radial tubes and transverse septa.

Scutum flat; occludent margin toothed; growth ridges low; longitudinal striae fine. Inner surface usually roughened on upper part; articular ridge high, reflexed, about 2/3 length of tergal margin and about 1/2 length of occludent margin, end truncate; articular furrow wide; adductor ridge short, moderately prominent, without pit below, well separated from articular ridge; adductor muscle pit well defined; lateral depressor muscle pit shallow, sometimes absent.

Tergum narrow; scutal margin raised, denticulate; carinal margin convex; growth ridges fine, stronger on narrow carinal segment; longitudinal striae absent; spur fasciole separated from scutal side, usually also from carinal side, by narrow groove; spur width about 3/10 length of basal margin; spur length about 4/5 spur width; distance from basiscutal angle to spur about 1/2 spur width, about 2/3 spur length, and about 1/5 length of basal margin; spur length about 1/4 length of basal margin; end rounded or obliquely truncate; basal margin usually straight, occasionally concave, on scutal side of spur, concave on carinal side. Internally, scutal margin high, articular ridge high, reflexed; articular furrow deep; crests for depressor muscle strong, usually projecting below basal margin; surface rugose medially, at least on upper part, ridges sometimes projecting below basal margin.

Labrum with setulae and 2-4 (3.0) teeth on crest on each side of notch; 1 tooth on each side occasionally on edge of notch near crest.

Palpus with short pinnate setae on upper margin and in band, widest distally, parallel to upper margin on outer face, also with long setae on distal end and in short oblique row near inferodistal angle; labral face with curved, short pinnate setae in band on distal fifth, gradually narrowing to few rows proximally, parallel to upper margin.

Mandible with 5 teeth and spinose inferior angle; 2nd tooth bifid; 3rd-5th with extra denticles; 5th tooth not confluent with inferior angle.

First maxilla with 2 or 3 fine spines in slight notch below upper pair of spines, short thick spine, often bifid, on outer face near lower spine of upper pair, 5-9 (6.9) spines between upper and lower pairs, few fine spines on

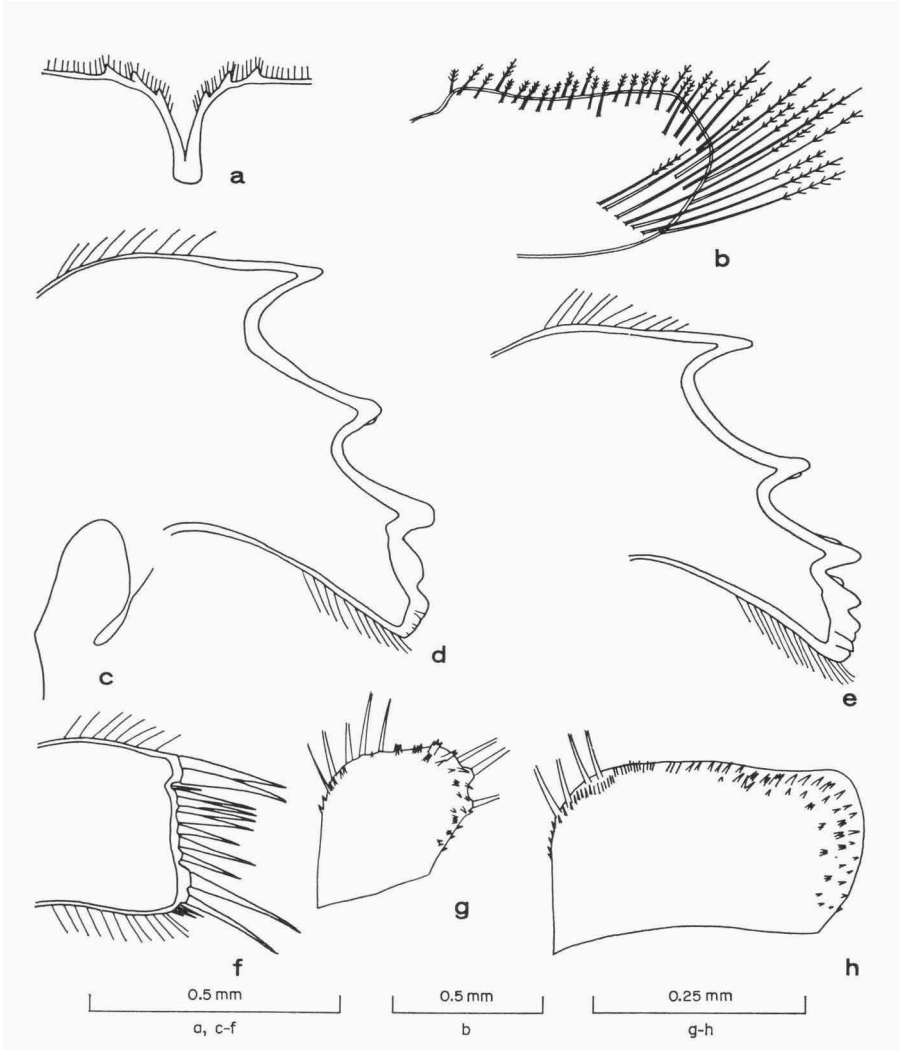

Fig. 20. *Balanus albicostatut* Pilsbry. a, labrum; b, palpus; c, basidorsal point; d, e, mandibles (of 2 specimens); f, 1st maxilla; g, h, 2nd and 6th distal segments of anterior ramus of cirrus III (a-h, Minhow, China: a, b, e, f from same specimen, c, d, second specimen; g, h, third specimen).

inferior angle, 2 adjacent to lower pair longer, often with pectinate tips; lower pair of spines on slight prominence.

Second maxilla without distinguishing characters.

Protopods of anterior cirri primarily with pinnate setae, some plumose setae posteriorly on coxopods; coxopod of cirrus I with narrow band of simple scales on outer face near anterior margin; coxopods and sometimes basipods of cirri II and III each with narrow band of simple scales on outer face near posterior margin.

Cirrus I with anterior ramus 2-5 (3.5) segments longer than posterior; posterior ramus with moderately protuberant segments; proximal segments of anterior ramus protuberant; distal sutures of both rami with long setae, sometimes also with multifid spinules on few distal segments.

Cirrus II with anterior ramus equal to or 1 or 2 (1.1) segments longer than posterior; both rami with protuberant segments; distal sutures with long setae, also with multifid spinules on distal segments and near anterior and posterior margins on median segments.

Cirrus III with anterior ramus 1-4 segments longer than posterior; both rami with slightly protuberant segments; distal sutures with spinules and short setae; outer faces near anterior margins with spinules, rarely with few teeth; posterior margins with short setae; inner faces with complex setae. Distal sutures with simple, bifid, and multifid spinules and few short setae on 3 or 4 distal segments; remaining segments with multifid spinules near posterior margins, sometimes also with simple spinules near anterior margins. Anterior margins without teeth. Outer faces near anterior margins with spinules, usually near distal angles, sometimes parallel to margins; proximal segments occasionally with several rows of simple, bifid, and multifid spinules; median and distal segments each with few simple, bifid, and multifid spinules near distal angles, sometimes also with 1 or 2 rows of simple spinules, occasionally with 2 or 3 large conic teeth near angles and 1 or 2 sparse rows of large and small conic teeth; 4-6 distal segments with larger and more numerous spinules. Posterior margins with 3-6 short setae, fewer proximally, on distal angle; long proximal segments occasionally with fine simple spinules. Inner faces with complex setae on distal segments of anterior ramus and most segments of posterior ramus; several distal segments of both rami with few pectinate setae; anterior ramus also with 1-3 denticulate setae; posterior ramus with 1-8 denticulate setae on all but 3 or 4 proximal segments. Denticulate setae usually with 4-6 large teeth, sometimes with numerous small teeth in row on one side, less often with teeth in double row on one side (fig. 22a).

Protopods of posterior cirri each with few simple and multifid spinules on outer face near anterodistal angles; coxopods each also with narrow band

of simple spinules on outer face near anterodistal angles; coxopods each also with narrow band of simple spinules on outer face near posterior margin.

Posterior cirri with multifid spinules, more numerous on distal segments, on distal sutures and 3-6 short setae on posterodistal angles. Anterior ramus of cirrus IV occasionally with few small conic teeth or simple spinules on outer faces near anterodistal angles on few proximal segments; posterior ramus without teeth or spinules. Cirrus VI with 3-5 (4.0) pairs of setae on anterior margins of median segments. Basidorsal point of penis nude.

Color. — Shell purple, reddish purple, or deep pink with white longitudinal ribs or bands. Radii purplish or pink. Alae lavender with white summits. Sheath purple. Scutum externally purple with white band on tergal margin; internally, white with splotches of purple. Tergum externally purple, with white spur fasciole and ray adjacent to carinal segment; internally, purple with white spur, articular ridge, crests, and carinal segment.

Measurements. — Carinorostral diameter of largest specimen in type series 16.5 mm, height 10 mm.

Variations. — Considerable variation exists in the development of the ribs on the exterior of the parietes, and in rare instances the shell may be without ribs. Similarly, variation was observed in the size and arrangement of the accessory parietal tubes.

All of the material examined in the present study have pectinate setae on the inner faces of the distal segments of both rami of cirrus III and denticulate setae on the posterior ramus, and less frequently on the anterior ramus. Nilsson-Cantell (1921), who first recorded modified setae on cirrus III in this species, described two types, one with fine double pectination and one with thick teeth. Both types are illustrated by Zevina & Tarasov (1963, fig. 11d); the denticulate setae are thick, with 3-7 very large teeth on one side; occasionally specimens from the same lot lacked denticulate setae.

Habitat. — Usually intertidal, often in brackish water, on rocks, mollusk shells, and sticks; occasionally on submerged wood and iron plates. In the Inland Sea, this species is widely distributed in the intertidal zone; whereas, in Tanabe Bay, on the Pacific coast, it occurs above mid-tide level in rather small protected areas (cf. Hiro, 1937: 432).

Remarks. — Pilsbry (1916) placed the *B. a.* var. *communis* and questionably the *B. a.* var. *niveus* (= *B. kondakovi*) of Krüger (1911) in synonymy with his new subspecies, *B. a. albicostatus*. In the lot from Shinagawa Bay, Pilsbry noted that with the exception of one specimen, the shells were not ribbed and the radii were narrow; however, the opercular valves were missing. In reexamining this lot, we found one specimen with the opercular

valves. Comparison of this specimen with typical *B. albicostatus* has shown conclusively that Pilsbry's anomalous specimens are *B. kondakovi* (pl. 11 fig. m). At the same time, Pilsbry (1916: 92) pointed out that Krüger's (1912) *B. mirabilis* had the characters of *B. amphitrite* and might be an old specimen of *B. a. albicostatus*. Krüger's species was based on a large corroded specimen; however, it agrees with similarly corroded specimens in the present collections. *B. mirabilis* is a senior subjective synonym of *B. albicostatus*; however, this name is preoccupied by *B. perforatus mirabilis* Darwin.

Hiro (1938) named a new form of *B. amphitrite, B. a.* form *formosanus,* and subsequently (Hiro, 1939a) placed this form in synonymy with *B. a. albicostatus*. Utinomi & Kikuchi (1966) raised *albicostatus* to specific rank and Utinomi (1967) recognized *formosanus* as a subspecies. He distinguished this subspecies primarily on the less prominent ribs of the parietes. The strength of the ribs in *B. albicostatus* is highly variable; Hiro's figure of the tergum of *formosanus* (Hiro, 1938, fig. 6d) agrees more with the holotype of *B. albicostatus,* than does his own figure (Hiro, as Utinomi, 1967, fig. 5c, d) of the latter species. Under the circumstances, we do not believe that *formosanus* can be considered a distinct subspecies.

A single specimen of *B. albicostatus* from Morro Bay, California is present in the collections of the National Museum of Natural History, Smithsonian Institution. As a subsequent examination of oysters from Morro Bay failed to reveal any additional specimens of this species, it appears that *B. albicostatus* has not become established in California.

Specimens of *B. albicostatus* were not available in sufficient numbers to permit inclusion of this species in the statistical analyses; however, the presence of more than a single row of parietal tubes in the parietes, a vesicular sheath, and complex setae on cirrus III clearly show its relationship to other species of the *pallidus* group.

Corroded specimens of *B. albicostatus* may be differentiated from *B. a. amphitrite* and *B. reticulatus* by the tergum, as well as by the above mentioned characters. *B. abeli* and ribbed forms of *B. patelliformis* may also be distinguished from *B. albicostatus* by the tergum.

Balanus kondakovi Tarasov & Zevina (text-figs. 21, 22b, c, f, pl. 11 figs. a-m)

Balanus amphitrite var. *niveus*: Krüger, 1911: 51, figs. 102-104, pl. 4 fig. 35a-b_2 (not *Balanus amphitrite* var. *niveus* Darwin, 1854: 240).

Balanus amphitrite var. *stutsburi*: Krüger, 1914: 437. — Krüger, 1927: 13, 16 (not *Balanus amphitrite* var. *stutsburi* Darwin, 1854: 240).

Balanus amphitrite albicostatus Pilsbry, 1916: 90 (in part; not fig. 18a, b, pl. 20 figs. 1-4; see *B. albicostatus*).

Balanus amphitrite krügeri Nilsson-Cantell, 1932c: 24, fig. 10a-g, pl. 1 figs. 5-7. — Hiro, 1938: 305, fig. 5a-d. — Hiro, 1939a: 263. — Utinomi, 1956: 52, pl. 26 fig. 9. — Zevina & Tarasov, 1963: 93, fig. 12a, b.

Balanus amphitrite var. *kondakovi* Tarasov & Zevina, 1957: 179, 191, fig. 76a-d (type locality: Japan).

Balanus amphitrite var. *insignis*: Karande & Palekar, 1966: 145, figs. 10-12, pl. 2 fig. 8, pl. 4 row 6 (not *Balanus amphitrite* var. *insignis* Nilsson-Cantell, 1938: 41).

Balanus pallidus krügeri: Utinomi, 1966: 38.

Balanus uliginosus Utinomi, 1967: 202, figs. 1a-c, 2a-e, pl. 6 figs. 4-6. — Utinomi, 1970: 356.

Holotype. — ZMUB.

Distribution. — Japan and Yellow Sea to Gulf of Siam; New Zealand; southwest Australia to Sumatra; Bombay, Indian Union.

Material examined. — Table 12.

Diagnosis. — Shell with epicuticle persistent; radii usually wide, summits beveled; sheath vesicular, without calcareous vesicles in furrow below lower margin; parietal tubes in 2 or more rows. Opercular valves with epicuticle thin, persistent. Scutum usually flat except for recurved apex, occasionally with narrowly inflected tergal margin; usually with fine to moderate longitudinal striae; articular ridge about 3/5 length of tergal margin; adductor ridge variable, well separated from articular ridge. Tergum with carinal margin convex, narrowly protuberant in upper third; with spur fasciole;

Table 12. *Balanus kondakovi*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
Japan					
Shinagawa Bay	8	---	*B. albicostatus*	----	---- USNM 32951
Sagami Channel	13	limb	*B. a. amphitrite*	7/8/35	---- USNM 192694
China					
----	22	twigs	---	1923	---- USNM 58162
Tsingtao	2	test panel	*B. a. amphitrite*	1/51	---- BPBM 382
Thailand					
Samut Prakan	46	*Nipa* sp.	*Chthamalus* sp.	28/5/39	---- USNM 85023
New Zealand					
Auckland	21	---	*Elminius modestus*	----	---- NZOI
Sumatra					
Benkoelen	2	wood, shell	*B. variegatus, B. reticulatus*	11/25	---- USNM
Indian Union					
Bombay	8	wood	---	----	Karande USNM,RMNH

spur length greater than width; distance from basiscutal angle to spur greater than spur width; basal margin excavated, often deeply, on both sides of spur; inner surface sometimes projecting below basal margin. Labrum simple. Cirrus II usually with simple spinules and conic teeth on outer faces near anterior margins; cirrus III with modified setae, without erect teeth on posterodistal angles; cirrus VI with 3-8 (5.1) paired setae on median segments.

Description. — Shell usually subcylindric or cylindric, occasionally conic; orifice toothed, width more than 1/2 carinorostral diameter; surface usually smooth, sometimes slightly rugose; epicuticle thin, persistent. Radii usually wide, transversely striate; summits oblique, beveled, rough; sutural edges with septa denticulate on lower margins. Alae with oblique summits; sutural edges septate. Sheath vesicular, without calcareous vesicles in furrow below overhanging lower margin. Inner lamina strongly ribbed, usually to sheath; ribs denticulate basally, ridged on sides near bases or sometimes nearly to sheath. Parietal tubes usually in 2 or more rows, arranged usually with small tube on each side of primary longitudinal septa, occasionally with minute tube on each side of subsidiary longitudinal septa; primary tubes 13-18 (15.2) in rostrum, with transverse septa usually in upper half, occasionally nearly to bases; subsidiary tubes extending apically to middle of parietes, with few transverse septa in upper part; large subsidiary tubes occasionally with inner lamina [= outer lamina of primary tube] ribbed on lower part; ribs denticulate basally. Inner surface of outer lamina sometimes with 2-6 ribs between primary longitudinal septa; 1 or 2 ribs sometimes strongly denticulate at bases, almost reaching inner lamina. Basis thin, with radial tubes and transverse septa.

Scutum usually flat except for recurved apex, sometimes externally concave between apex and basal margin; tergal segment occasionally very narrowly inflected; basitergal angle obliquely truncate; occludent margin toothed; epicuticle usually persistent; growth ridges low to moderate; longitudinal striae fine to moderate, occasionally absent; narrow longitudinal groove, close to occludent margin, sometimes indistinct near apex, often present. Inner surface sometimes roughened on upper part; articular ridge prominent, usually slightly reflexed, about 3/5 length of tergal margin and about 2/5 length of occludent margin, end truncate or pointed; articular furrow narrow; adductor ridge usually moderately strong, long or short, rarely with shallow pit below bounded on tergal side by weak ridge, well separated from articular ridge; adductor muscle pit distinct; lateral depressor muscle pit shallow or moderately deep.

Tergum with scutal margin raised, strongly denticulate; carinal side often

concave medially; carinal margin convex, narrowly protuberant in upper third; growth ridges moderate, strongly arched medially on both sides of spur fasciole, very strong on protuberance, upturned along carinal margin; longitudinal striae absent; spur fasciole well defined, usually with narrow groove on each side; spur width about 1/4 length of basal margin; spur length about 1 1/4 spur width; distance from basiscutal angle to spur about 1 1/10 spur width, about 9/10 spur length, and about 1/4 length of basal margin; spur length about 3/10 length of basal margin; end rounded; basal margin excavated, often deeply, on both sides of spur; inner surface sometimes projecting slightly below basal margin on carinal side. Internally, scutal margin high; articular ridge moderately reflexed in upper part; articular furrow deep; crests for depressor muscle long, strong, sometimes projecting below basal margin; surface rugose, at least in upper part, basally smooth on scutal side, sometimes denticulate or irregularly toothed medially on carinal side.

Labrum with setulae and 0-7 (4.0) teeth on crest on each side of notch; 1 tooth on each side usually on edge of crest near notch; 1-3 teeth occasionally on one or both edges of notch near crest.

Palpus with short finely pinnate setae on upper margin; outer face with short simple setae in tuft near superodistal angle and in 2 or 3 rows near upper margin, long setae on distal third and in oblique row near inferodistal angle, narrow band of denticulate scales near distal margin; labral face with narrow band of short pinnate setae parallel to upper margin on proximal three-fourths and denticulate scales near inferodistal angle.

Mandible with 5 or 6 (5.1) teeth and spinose inferior angle; 1st and 2nd teeth bifid; 3rd-5th with extra denticles.

First maxilla usually with 1-3 fine spines in slight notch below upper pair, short thick spine on outer face near lower spine of upper pair, 2-10 (6.1) spines between upper and lower pairs, and few fine spines on inferior angle; lower pair of spines usually on slight prominence.

Second maxilla without distinguishing characters.

Protopods of anterior cirri with primarily pinnate setae, some plumose setae posteriorly on coxopods; protopod of cirrus I with narrow band of simple scales on outer face near anterior margin; both segments of cirri II and III each with wide band of denticulate scales on outer face near posterior margin.

Cirrus I with anterior ramus equal to or 1-8 (3.8) segments longer than posterior; posterior ramus with very protuberant segments; proximal segments of anterior ramus protuberant; distal sutures of both rami with long setae, also with multifid spinules on few distal segments of anterior ramus.

Cirrus II with anterior ramus 1 segment shorter to 5 (1.6) segments longer than posterior; both rami with moderately protuberant segments; distal sutures with long setae, also with multifid spinules on 3 or 4 distal segments and multifid and simple spinules near anterior margins on 2-4 adjacent segments, sometimes with few large conic teeth near anterior margins on several distal segments, occasionally with few multifid and large simple spinules anteriorly on all but ultimate segment; outer faces near anterior margins each usually with multifid and simple spinules and few large conic teeth; posterior ramus sometimes with spinules and teeth on all but 3 or 4 distal segments.

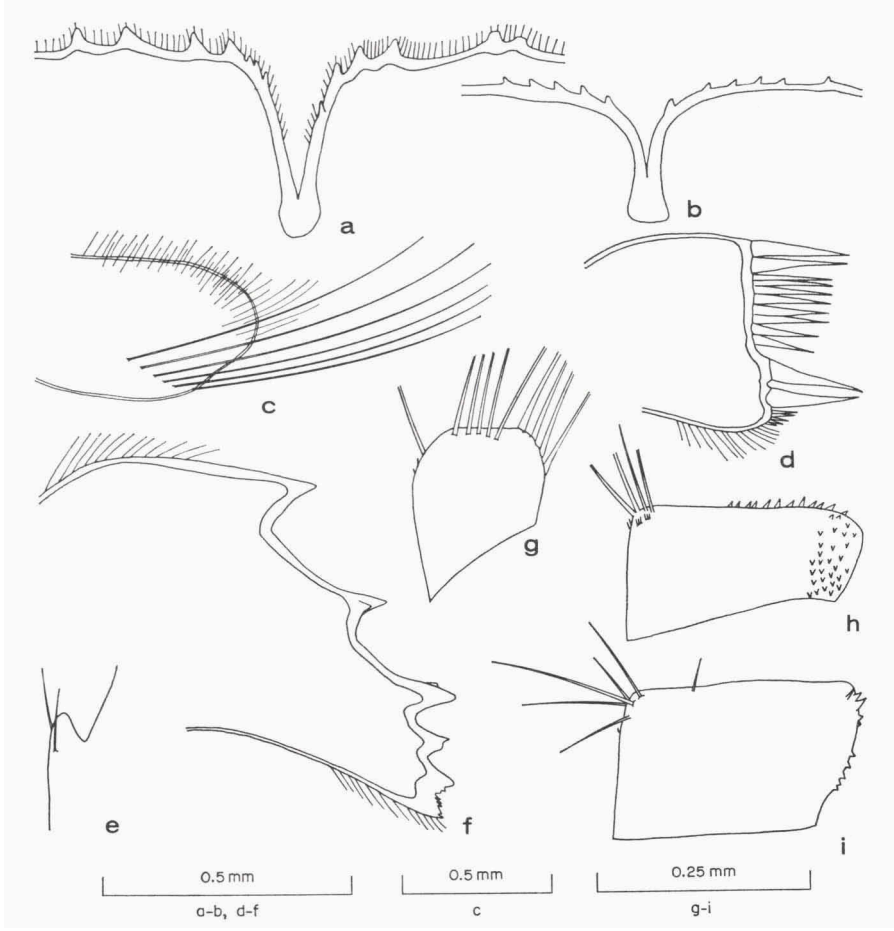

Fig. 21. *Balanus kondakovi* Tarasov & Zevina. a, b, labra; c, palpus; d, 1st maxilla; e, basidorsal point; f, mandible; g-i, anterior rami of cirrus III (g, 3rd distal segment; h, 7th proximal segment; i, 4th proximal segment) (a, China, UNSM 58162; b-g, i, Samut Prakan, Thailand; h, Auckland, New Zealand).

Cirrus III with anterior ramus equal to or 1-4 (3.0) segments longer than posterior; both rami with slightly protuberant segments; distal sutures with short setae and spinules; anterior margins and outer faces near anterior margins with conic teeth; posterior margins with short setae on distal angles; outer and inner faces near posterior margins with scales or spinules; inner faces also with complex setae. Distal sutures with multifid spinules and few short setae on 2-5 distal segments; remaining segments each with simple spinules, sometimes also with 1 or 2 large conic teeth near anterior margins and multifid spinules near posterior margins. Anterior margins with small teeth on proximal segments, occasionally also on median segments. Outer faces near anterior margins of proximal segments each usually with 1 or 2 rows of large or small teeth, occasionally with 3-6 rows of small teeth, also with 3-10 large teeth near distal angle; median segments each sometimes with 3 or 4 large teeth near distal angle, occasionally with armature like proximal segments; distal segments each occasionally with 3 or 4 large teeth near distal angle. Posterior margins with tuft of short setae, fewer proximally, on distal angles. Outer faces near posterior margins of proximal segments with narrow band of simple scales. Inner faces near posterior margins of proximal segments each with narrow band of spinules; inner faces of anterior ramus with few pectinate setae on 1 or 2 distal segments; posterior ramus usually with few pectinate setae on most segments, sometimes with 2-8 denticulate setae on each segment but ultimate and 1 or 2 proximal segments; distal segments occasionally with 1 or 2 bifurcate setae. Pectinate setae on anterior ramus with only fine pectinations, on posterior ramus with fine or coarse pectinations; denticulate setae with 4-7 large teeth or 10-20 small teeth usually in double row on one side, occasionally in single row (fig. 22b, c, f).

Protopods of posterior cirri each usually with narrow band of multifid spinules near anterior margin and wide band of denticulate scales near posterior margin on outer face; inner face with wide band of multifid spinules near posterior margin.

Posterior cirri usually with multifid and simple spinules on distal sutures near anterior margins of most segments; with 1 relatively long and several shorter setae on posterodistal angles; proximal segments each with narrow band of denticulate scales on inner face, occasionally also on outer face, near posterior margin. Anterior ramus of cirrus IV occasionally with small conic teeth on anterior margins of few proximal segments; outer faces near anterior margins of several proximal segments with conic teeth, usually with large conic teeth and simple spinules near distal angles, sometimes also with 2-4 rows of small conic teeth; posterior ramus usually with few large simple spinules, sometimes also 1 or 2 large conic teeth, near distal angles on each

of few proximal segments. Cirrus VI with 3-8 (5.1) pairs of setae on anterior margins of median segments. Basidorsal point of penis large, sometimes with 2 subapical setae.

Color. — Shell usually lavender, bluish purple, or reddish with lighter or darker, narrow or wide longitudinal stripes; sometimes also with irregular horizontal striae or splotches; occasionally white with only traces of color. Radii white or white with varying amounts of pink or purple, occasionally entirely pink or purple. Alae usually pink or purple with white summits, sometimes white. Epicuticle straw colored. Sheath usually white with purple or pink splotches, sometimes entirely purple. Scutum externally dull purple or pink with narrow white band along tergal margin and narrow to wide lighter colored or white band on occludent side, sometimes entirely white; internally usually either colored medially or entirely white, sometimes purple or pink with white band along tergal margin. Tergum externally purple or pink except for white margins, spur, and longitudinal fasciole, or entirely white; internally, purple or pink with white band along carinal margin and white crests and spur, white except for purple or pink band on carinal side of articular ridge, or entirely white.

Measurements. — Carinorostral diameter of holotype 12 mm, height 8 mm. Diameter of largest specimen from type locality 19 mm, height 14 mm.

Variations. — Very occasionally the shell may be slightly ribbed. In conic specimens the radii are frequently narrow with thin edges. Variability in the occurrence of accessory parietal tubes has been noted, particularly in specimens from New Zealand. These specimens also were found to vary from the typical form in several other characters. The parietes were thin walled with large square parietal tubes; the labra, with one exception, had 3 teeth on the crest on each side of the notch; and cirri III lacked bifurcate or denticulate setae.

Habitat. — Intertidal, on sticks, bamboo, shells, and buoys. According to Utinomi (1967) this species usually occurs on sticks set on muddy beds for oyster culture in brackish bays and estuaries and is rare on intertidal rocks and stones in Japan and Korea.

Remarks. — Pilsbry (1916), without comment, placed Krüger's *B. a.* var. *niveus* in synonymy with *B. a. albicostatus*. Nilsson-Cantell (1932c), however, named the new subspecies, *Balanus amphitrite krügeri*, for this taxon. As pointed out by Utinomi (1967), the name *kruegeri* is preoccupied by *Balanus krügeri* Pilsbry, 1916. He proposed the new name *B. uliginosus* as a replacement name and raised the taxon to specific rank. However, in the course of this study, it has been found that the species, *B. kondakovi* Tarasov & Zevina, is synonymous with Nilsson-Cantell's *B. a. kruegeri*. The

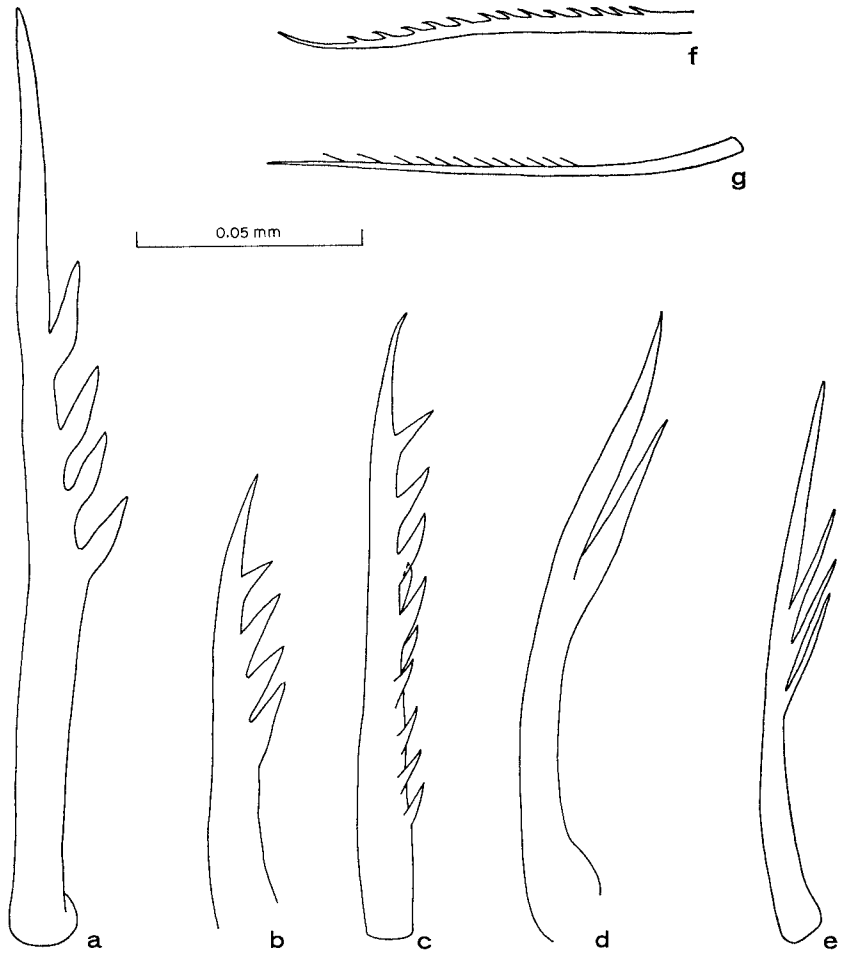

Fig. 22. Complex setae, *Balanus pallidus* group. a, b, f, denticulate; c, bidenticulate below, denticulate above; d, bifurcate; e, multifurcate; g, pectinate (only 1 row of setulae drawn) (a, *Balanus albicostatus*; b, c, f, *Balanus kondakovi*; d, e, g, *Balanus citerosum).*

character of the number of teeth on the labrum (up to 7 on each side of the notch) was used by Tarasov & Zevina (1957) to differentiate *B. kondakovi* from *B. a. kruegeri;* however, this number is within the range of variation of the latter taxon. Consequently, as the first available synonym of a pre-occupied name (article 60, Code of Zoological Nomenclature), *B. kondakovi* Tarasov & Zevina must be used for this species.

Krüger (1914) referred specimens from Australia with shells colored like *B. a. variegatus* and opercular valves like *B. a. stutsburi* to the latter taxon; subsequently he (Krüger, 1927) recorded similar specimens from a ship from

Australia. It is apparent that these specimens should be referred to *B. kondakovi.*

In material of *B. a. albicostatus,* Pilsbry (1916) noted that, with one exception, specimens from Shinagawa Bay differed from the typical form in the color pattern of the shell and in lacking ribs. As he did not find opercular valves in these specimens he was uncertain about their identity. Upon re-examination of the material, one specimen was found with opercular valves. The color patterns of the shells and the opercular valves (pl. 11 fig. m) indicate that these specimens are *B. kondakovi.*

Karande & Palekar (1966) assigned specimens from Bombay to *B. a. insignis* (also see remarks under *B. pallidus*). The opercular valves illustrated

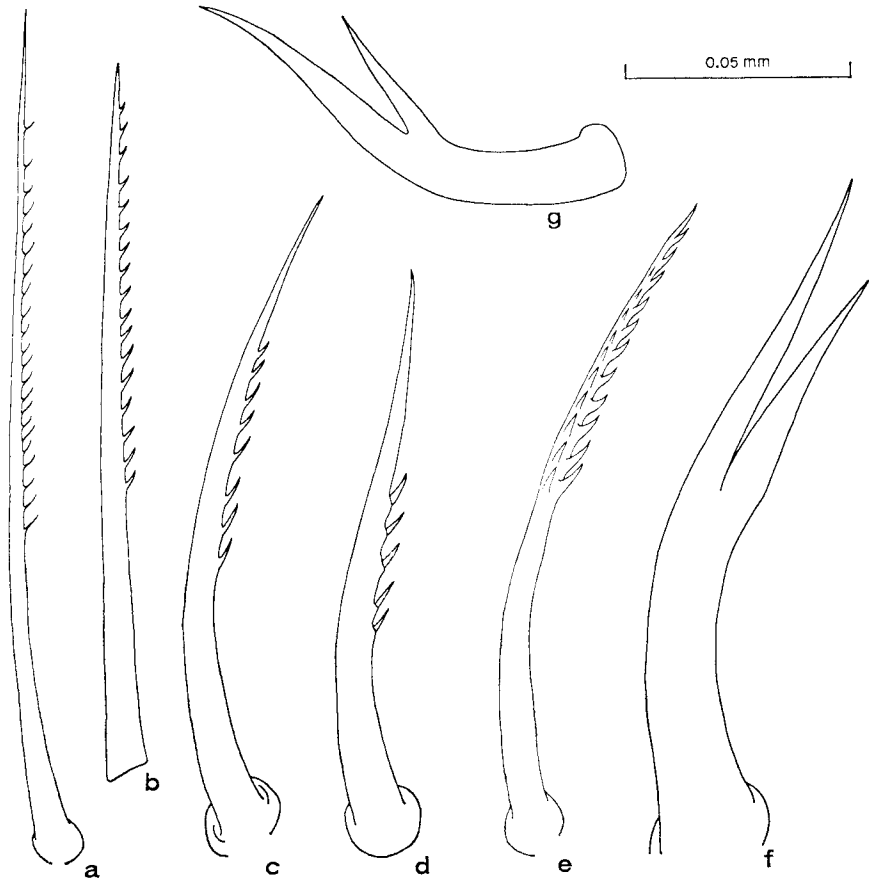

Fig. 23. Complex setae, *Balanus inexpectatus.* a, pectinate (only 1 row of setuale drawn); b-d, denticulate; e, bidenticulate; f, g, bifurcate.

(Karande & Palekar, 1966, pl. 4 row 6) clearly indicate that these specimens should have been referred to *B. kondakovi.* Material in the present study also includes similar specimens of *B. kondakovi* from Bombay.

Results of the statistical analyses suggest that *B. kondakovi* is most closely allied with *B. variegatus* ($D^2 = 6.82$) and *B. reticulatus* ($D^2 = 10.68$); however, as previously mentioned, three characters shared by members of the *pallidus* group were not included in the analyses. The presence of subsidiary tubes in the parietes, vesicular sheath, and complex setae on cirrus III clearly indicate the relationship of *B. kondakovi* to the other members of the *pallidus* group. The affinity of this species to *B. variegatus* and *B. reticulatus* in the other 16 characters, however, suggest that *B. kondakovi* may provide a link between the *pallidus* group and other groups or subgroups within the complex.

According to Utinomi (1967) the distribution of *B. kondakovi* is restricted to southern Japan and Korea, China, and Taiwan. We have extended the southern range to New Zealand, and our material indicates that *B. kondakovi* has a wide distribution in the Indian Ocean.

White forms and those with a similar color pattern can easily be distinguished from *B. variegatus* by the tergum which, in *B. kondakovi,* has the basal margin excavated on both sides of the spur and a spur fasciole instead of a spur furrow. White forms of *B. kondakovi* may also be distinguished from *B. pallidus* by the spur fasciole and the shorter spur of the tergum. Within the *pallidus* group, *B. kondakovi* has its greatest affinity to *B. suturaltus,* as the inner surface of the tergum sometimes projects below the basal margin in these two species. As far as is known, in the genus *Balanus,* this character is restricted to *B. kondakovi* and *B. suturaltus.*

Balanus citerosum Henry (text-figs. 22 d, e, g, 24, pl. 12)

Balanus amphitrite var. *niveus*: Oliveira, 1941: 19 [in part; not pl. 3 figs. 3-6, pl. 4 figs. 2, 7 (= *B. eburneus*); not *Balanus amphitrite* var. *niveus* Darwin, 1854: 240].
Balanus citerosum Henry, 1974: 976, figs. 4a-i, 5a-k (type locality: Rio Nobrega, São Paulo, Cananéia, Brazil).

Holotype. — USNM 143834.

Distribution. — Brazil.

Material examined. — Table 13.

Diagnosis. — Shell with epicuticle thick, persistent; radii narrow to moderately wide, summits thick, smooth; sheath vesicular, usually with calcareous vesicles in furrow below lower margin; parietal tubes in 2 or more rows. Opercular valves with epicuticle thick, persistent. Scutum flat except for sharply inflected tergal segment; longitudinal striae fine; articular

Table 13. *Balanus citerosum*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
Brazil					
Rio Nobrega	78	*Rhizophora*	*Chthamalus* sp.	28/3/55	Gerlach USNM
Rio Nanaù	21	*Rhizophora*	*B. improvisus*	29/3/55	Gerlach USNM
Rio Baguassù	59	*Laguncularia*	---	3/3/55	Gerlach USNM
Cananéia	4	*Rhizophora*	---	18/8/66	Smith/Zullo USNM

ridge about 2/3 length of tergal margin; adductor ridge moderately long, close to but not confluent with articular ridge. Tergum with carinal margin convex, with open spur furrow; spur length greater than width; distance from basiscutal angle to spur about 3/5 spur width; basal margin usually slightly concave, occasionally deeply excavated on carinal side. Labrum simple. Cirrus II without simple spinules or teeth on outer face near anterior margin; cirrus III with complex setae, without erect teeth below posterodistal angles; cirrus VI with 4-9 (5.8) paired setae on median segments.

Description. — Shell conic or subcylindric; orifice slightly toothed, width 1/2 or less carinorostral diameter in small and medium-sized specimens, usually more than 1/2 in large specimens; surface smooth, often corroded; epicuticle thick, persistent. Radii narrow or moderately wide, level, transversely striate, usually corroded; summits oblique, thick, smooth; septa strongly denticulate on lower margins. Alae with horizontal summits; sutural edges septate. Sheath vesicular, usually with calcareous vesicles extending into deep furrow below overhanging lower margin. Inner lamina usually strongly ribbed to sheath; ribs denticulate basally, ridged on sides near bases. Parietal tubes in 2 or more rows, arranged with large tube on each side of primary longitudinal septa and small tube on each side of subsidiary longitudinal septa; sometimes also with 1 or 2 rows of minute tubes close to outer lamina; primary parietal tubes, larger in small specimens, 16-18 (17) in rostrum; with transverse septa usually nearly to bases, sometimes to bases; subsidiary tubes usually entending to middle of parietes, sometimes to apical third, with transverse septa nearly to or to bases; largest subsidiary tubes with inner lamina [= outer wall of primary tube] ribbed on lower part; ribs denticulate basally, occasionally almost reaching outer lamina of parietes. Basis thin, with radial tubes and numerous transverse septa; sometimes lengthened in part.

Scutum with narrow tergal segment sharply inflected, basitergal angle obliquely truncate, occludent margin toothed, not thickened; growth ridges low; longitudinal striae fine; slightly oblique or longitudinal opaque stripes some-

times also present; epicuticle thick, persistent. Inner surface roughened on upper part; articular ridge high, reflexed, about 2/3 length of tergal margin and 2/5 length of occludent margin, end truncate or pointed; articular furrow narrow; adductor ridge moderately long, prominent, upper part thick, lower part acute, occasionally with shallow pit below bounded on tergal side by weak ridge, close to but not confluent with articular ridge; adductor muscle pit shallow; lateral depressor muscle pit shallow, usually small, sometimes absent.

Tergum moderately wide; scutal margin denticulate; carinal margin slightly convex; growth ridges fine, slightly stronger on very narrow carinal segment; longitudinal striae absent; spur furrow open, shallow; spur width about 1/4 length of basal margin; spur length about 1 1/2 spur width; distance from basiscutal angle to spur about 3/5 spur width, about 2/5 length, and about 1/5 length of basal margin; spur length about 2/5 length of basal margin; end rounded or obliquely truncate; basal margin usually slightly concave, sometimes concave, on both sides of spur, occasionally deeply excavated on carinal side. Internally, scutal margin moderately high; articular ridge moderate, reflexed near apex in small specimens; articular furrow wide; crests for depressor muscle strong, projecting below basal margin; surface roughened or rugose medially; basally usually denticulate medially.

Labrum with setulae and 0-4 (3.0) strong teeth on crest on each side of deep notch, 1 tooth on each side usually on edge of crest near notch.

Palpus with setulae on lower margin near distal end, fine short simple setae on upper margin and on distal third on outer face near upper margin, also with denticulate scales near distal margin and long setae medially on distal end and in slightly oblique row near inferodistal angle; labral face with band of strongly pinnate short setae near upper margin on upper third distally, abruptly narrowing to 2-4 rows proximally.

Mandible with 5 or 6 (5.03) teeth and sometimes with spinose inferior angle; 2nd tooth bifid, 3rd-6th with extra denticles; 5th tooth not confluent with inferior angle; 6th tooth, if present, confluent with inferior angle.

First maxilla usually with slight notch below upper pair of spines, 1 or 2 fine spines in notch, 3-19 (6.0) spines between upper and lower pairs, and tuft of fine spines on inferior angle; lower pair of spines usually on slight prominence.

Second maxilla without distinguishing characters.

Protopods of anterior cirri with pinnate or simple setae, some plumose setae posteriorly; both segments of cirrus I with few multifid spinules near posterior margin on outer faces; coxopod also with band of simple scales near anterior margin; coxopod of cirrus II with few multifid spinules and narrow

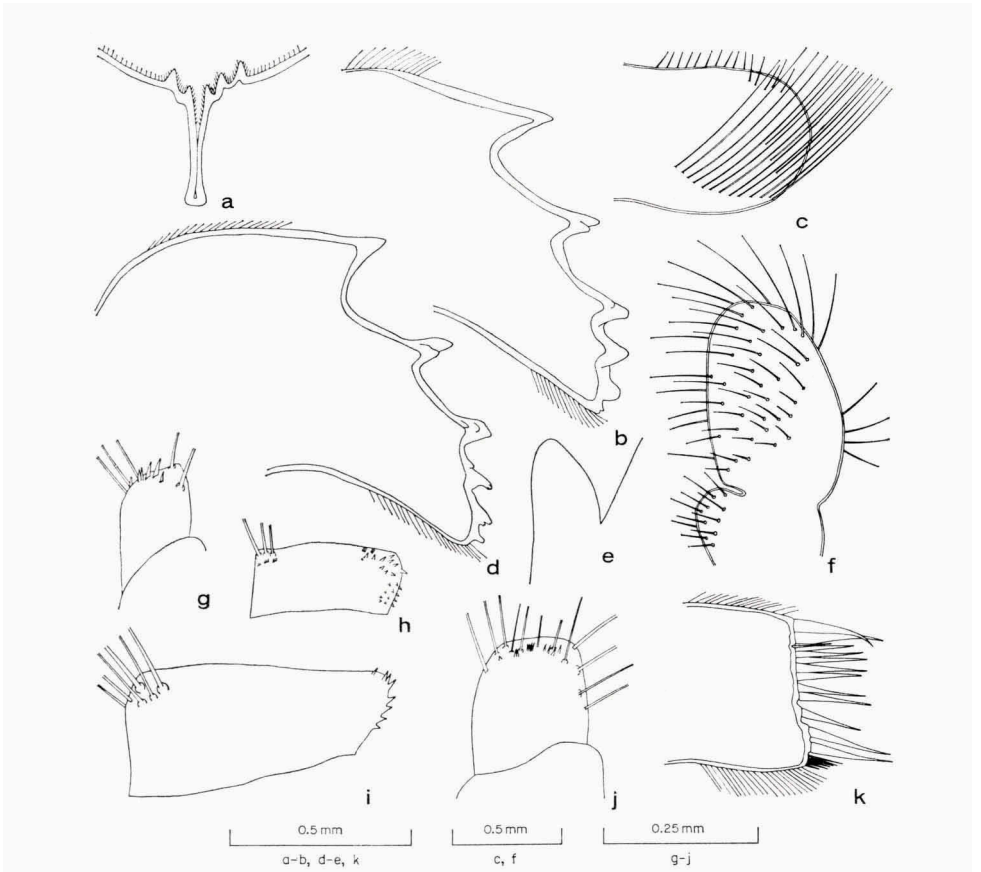

Fig. 24. *Balanus citerosum* Henry. a, labrum; b, d, mandibles; c, palpus; e, basidorsal point; f, 2nd maxilla; g-j, anterior ramus of cirrus III (g, j, 3rd distal segments; h, i, 6th proximal segments); k, 1st maxilla (a, b, k, holotype, c, d, g, i, paratype from Rio Nobrega, Cananéia, Brazil; e, f, j, paratype from Rio Baguassù, Cananéia, Brazil; h, paratype from Rio Nanaù, Cananéia, Brazil; after Henry, 1974).

band of simple scales near posterior margin on outer face; protopod of cirrus III with narrow to wide band of simple scales on posterior margin on outer face.

Cirrus I with anterior ramus 1-9 (4.0) segments longer than posterior; posterior ramus with very protuberant segments; proximal segments of anterior ramus protuberant; distal sutures of both rami with multifid spinules, more numerous on distal segments, and long setae; few proximal segments each with narrow band of simple and spinulose scales on outer face near posterior margin.

Cirrus II with anterior ramus 2 segments shorter to 4 (0.7) segments longer than posterior; both rami with very protuberant segments; distal sutures

with long setae, also with multifid spinules on several distal segments and near anterior and posterior margins on median and proximal segments; few proximal segments each with narrow band of spinulose scales on outer face near posterior margin.

Cirrus III with anterior ramus equal to or 1-5 (2.7) segments longer than posterior; both rami with slightly protuberant segments; distal sutures with short setae and multifid spinules; outer faces near anterior margins with conic teeth; posterior margins with few short and several longer setae on distal angles; outer and inner faces near posterior margins with scales; inner faces with complex setae. Distal sutures with short setae and multifid spinules on several distal segments; 4-6 distal segments of anterior ramus each also with several large teeth or simple spinules near anterior margin. Anterior margins and outer faces near anterior margins on proximal segments of anterior ramus usually with teeth, occasionally median segments also with teeth; proximal and median segments each with 3-5 teeth below anterodistal angle, proximal segments usually also with teeth on anterior margin and in 2 or 3 rows near margin; median segments occasionally with teeth on anterior margin and few teeth near margins. Anterior margins of posterior ramus without teeth; outer faces near anterior margins of proximal, sometimes also median, segments with teeth; proximal segments each with 3-5 teeth below anterodistal angle, sometimes also with 1 or 2 rows of teeth near anterior margins on several proximal segments; median segments each with few simple spinules and 1 or 2 teeth near anterodistal angle. Posterior margins of both rami with few short and several longer setae on distal angle; long proximal segments sometimes with simple spinules. Outer faces near posterior margins of long proximal segments each with narrow band of spinulose scales; several adjacent segments each with few spinulose scales. Inner faces near posterior margins with complex setae and spinules; long proximal segments each with narrow band of simple and multifid spinules; several adjacent segments each with few multifid spinules; anterior ramus usually with 1 or 2 pectinate setae on several distal segments, occasionally also with 1 or 2 multifurcate setae on 1 or 2 distal segments; posterior ramus with 2 or 3 pectinate setae on most segments, 1-6 bifurcate setae on 1-12 segments, occasionally also with 1 or 2 multifurcate on few segments; multifurcate setae with 3 or 4 thin branches on one side (fig. 22 d-f).

Protopods of posterior cirri each with narrow band of multifid spinules near anterior margin on both faces.

Posterior cirri with simple and multifid spinules on distal sutures and 1-3 long and 3-5 short setae on each posterodistal angle, usually also with

simple spinules on posterior margin and in narrow band on inner face near posterior margin on proximal half of each ramus; several proximal segments each sometimes with narrow band of simple scales on outer face near posterior margin. Anterior ramus of cirrus IV also with conic teeth and simple spinules on outer faces near anterior margins on proximal and sometimes median segments; proximal segments each usually with 2 or 3 large teeth or simple spinules below anterodistal angle, occasionally also with 2 or 3 sparse rows of small teeth and denticles near anterior margins; posterior ramus usually without teeth or spinules on outer faces near anterior margins; proximal segments each sometimes with few simple spinules, occasionally with 3-5 large conic teeth, near anterodistal angle. Cirrus VI with 4-9 (5.8) pairs of setae on anterior margin of each median segment. Basidorsal point of penis large, nude.

Color. — Shell white with lavender, red, or purple stripes, sometimes confluent; radii white; alae white, sometimes with purplish summits; epicuticle brown. Sheath white, sometimes with purple alae. Scutum usually purple on outer and inner surfaces except for narrow white band along tergal margin; inner surface sometimes entirely white; outer surface often irregularly striped with lighter or darker longitudinal or slightly oblique stripes. Tergum usually purple on carinal side of both surfaces, sometimes entirely white on inner or both surfaces.

Measurements. — Carinorostral diameter of holotype 23 mm, height 16 mm; diameter of largest specimen 32 mm, height 19 mm.

Variations. — Specimens of all sizes are frequently corroded; sometimes the vesicular sheath and parietal tubes are exposed, the radii are very poorly differentiated, and the sutures are sunken. In corroded specimens the opercular valves are usually very narrow in the upper part and the basal margins of the terga are more deeply excavated on the carinal side than are those of noncorroded or young specimens.

Habitat. — Intertidal, on mangrove roots in brackish water.

Remarks. — As Matsui et al. (1964) pointed out, the figures of *Balanus amphitrite* var. *niveus* of Oliveira (1941) are referable to *B. eburneus*; however, Henry (1974) showed that the description of his specimens indicated that *B. citerosum* was included in his material.

Among the taxa of the *pallidus* group, the results of the statistical analyses suggest that *B. citerosum* is most closely allied with *B. suturaltus* (D^2 = 17.11). However, as *B. pallidus* was not included in these analyses, the relationship of *B. citerosum* to *B. suturaltus* is misleading. Morphological evidence suggests that *B. citerosum* is actually most closely allied to *B. pallidus*. *B. citerosum* may be distinguished from the latter species by the thick

epicuticle on the shell and by the opercular valves. The adductor ridge is close to the articular ridge instead of being separated as in *B. pallidus*; the spur is shorter and closer to the basiscutal angle in *B. citerosum.*

Balanus suturaltus Henry (text-fig. 25, pls. 13, pl. 15 fig c)

Balanus suturaltus Henry, 1974: 983, figs. 6a, 7a-h, 8a-k (type locality: Boca de Barranca, Costa Rica).

Holotype. — USNM 143835.

Distribution. — West Costa Rica.

Material examined. — Table 14.

Table 14. *Balanus suturaltus*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
Costa Rica, Pacific coast					
Barranca River	7	rocks	*B. inexpectatus, B. peruvianus, T. polygenus*	18/2/65	Henry USNM
Boca de Barranca	38	boulder	*B. inexpectatus, B. t. coccopoma, Chthamalus* sp.	18/2/65	Henry USNM
Boca de Barranca	57	boulder	*B. inexpectatus, B. t. coccopoma, Tetraclita* sp., *Chthamalus* sp.	14/5/68	Henry RMNH
Bahia de Barranca	1	rock	*B. inexpectatus, B. t. coccopoma Tetraclita* sp., *Chthamalus* sp.	18/2/65	Henry USNM

Diagnosis. — Shell with epicuticle thick, persistent; radii narrow, sunken; summits thin, smooth, arched; sheath vesicular, sometimes with calcareous vesicles in furrow below lower margin; parietal tubes in 2 or more rows. Opercular valves with epicuticle thick, persistent. Scutum flat except for recurved apex; occludent margin greatly thickened in apical third; longitudinal striae fine; articular ridge about 7/10 length of tergal margin; adductor ridge short, well separated from articular ridge. Tergum with carinal margin convex; with closed or nearly closed spur furrow; spur length greater than width; distance from basiscutal angle to spur about 9/10 spur width; basal margin concave on scutal side, deeply excavated on carinal side; inner surface projecting below margin on carinal side. Labrum simple. Cirrus II with simple spinules, also usually with spike-like or conic teeth on outer face near anterior margins and usually with teeth on anterior margins; cirrus III with complex setae, without erect teeth below posterodistal angles; cirrus VI with 7-11 (8.6) paired setae on median segments.

Description. — Shell conic; orifice toothed, width about 1/3 carinorostral diameter; surface roughened; epicuticle thick, persistent. Radii narrow, sunken, transversely striate; summits oblique, thin, smooth, arched; sutural edges with septa strongly denticulate on lower margins, sometimes also on upper margins. Alae with oblique summits; sutural edges finely septate.

Sheath vesicular; sometimes with calcareous vesicles extending into deep furrow below overhanging lower margin. Inner lamina ribbed to sheath; ribs finely denticulate basally, finely ridged on sides near bases. Parietal tubes in 2 or more rows, usually arranged with small tube on each side of primary longitudinal septa and smaller tube on each side of subsidiary longitudinal septa, sometimes also with few minute tubes close to outer lamina, occasionally arranged with 4 or 5 rows of subsidiary tubes on outer side of only few primary tubes; primary tubes large, 12-17 (14.0) in rostrum, with transverse septa almost to bases; subsidiary tubes extending almost to apex, with transverse septa almost to or to bases; largest subsidiary tubes usually with inner lamina [= outer wall of primary tubes] ribbed on lower part; ribs denticulate basally. Inner surface of outer lamina without ribs. Basis with radial tubes and numberous transverse septa.

Scutum thick, flat, except for recurved apex; basitergal angle rounded; occludent margin toothed, greatly thickened on apical third; epicuticle thick, persistent; growth ridges moderately prominent, occasionally finely crenulate; longitudinal striae fine, approximate. Inner surface roughened on upper part, sometimes thickened between pit below adductor ridge and lateral depressor muscle pit; articular ridge high, reflexed, about 7/10 length of tergal margin and 2/5 length of occludent margin, end usually truncate, occasionally obliquely truncate or rounded; articular furrow narrow; adductor ridge short, usually strong, either thick or acute, with moderate pit below, well separated, occasionally by narrow groove, from articular ridge; adductor muscle pit shallow; lateral depressor muscle pit deep, usually large; small rostral depressor muscle pit usually present.

Tergum narrow; apex projecting slightly above scutum; scutal side usually with narrow longitudinal groove close to spur furrow; scutal margin finely denticulate; carinal side usually concave medially, carinal margin thin, sometimes narrowly protuberant in upper third; epicuticle thick, persistent; growth ridges approximate, fine, usually crenulate, strongly arched medially on both sides of spur furrow, stronger on protuberance, upturned on carinal margin; longitudinal striae absent; spur furrow closed or almost closed; spur width about 1/4 length of basal margin; spur length about 1 4/5 spur width; distance from basiscutal angle to spur about 9/10 spur width, about 1/2 spur length, and about 1/4 length of basal margin; spur length about 1/2 length of basal margin; end rounded; basal margin concave on scutal side of spur, deeply excavated on carinal side; inner surface projecting below basal margin on carinal side, slightly to strongly excavated close to spur. Internally, scutal margin high; articular ridge low or moderate; articular furrow wide, rather deep; crests for depressor muscle moderately prominent, short, occasionally

projecting slightly below basal margin; surface usually roughened medially, sometimes ridged on upper part, basally smooth.

Labrum with crest sloping to shallow notch; with setulae and 1-7 (4.0) teeth on crest and usually on one or both edges of notch near crest.

Palpus with setulae on distal half of lower margin; short finely pinnate setae on upper margin, in narrow band along upper margin and superior half of distal margin on outer face, also with long setae in tuft on distal end and in oblique row near inferodistal angle; wide band of setulae near lower margin;

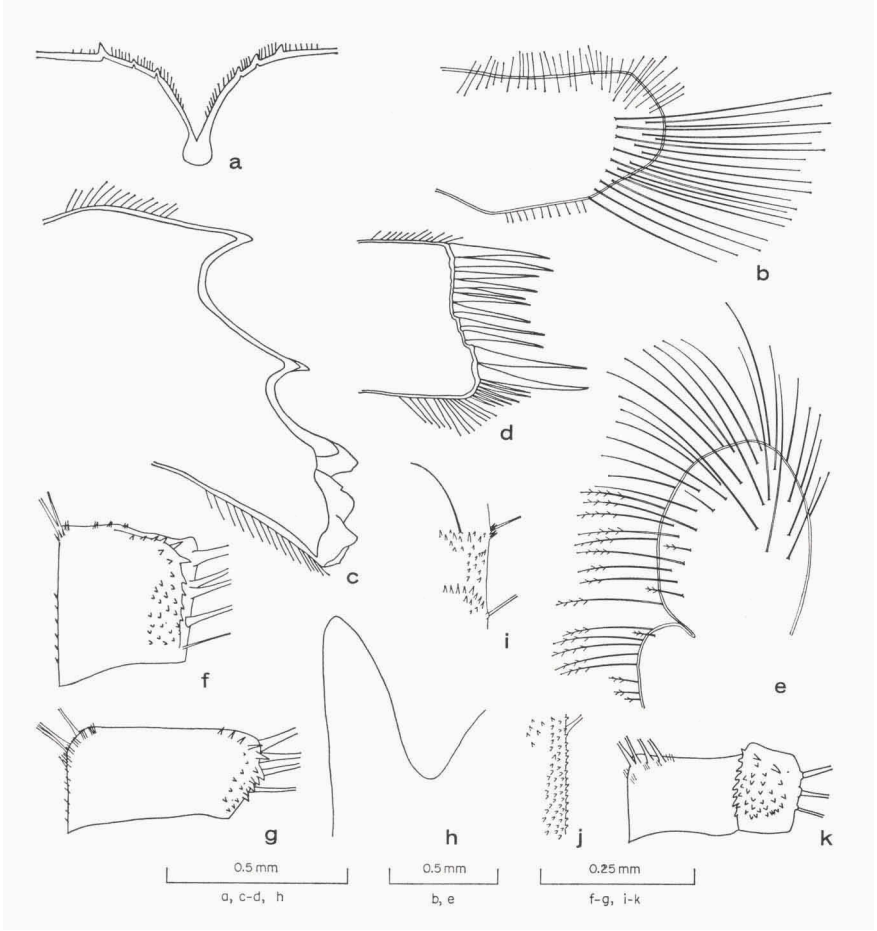

Fig. 25. *Balanus suturaltus* Henry. a, labrum; b, palpus; c, mandible; d, 1st maxilla; e, 2nd maxilla; f, median segment of anterior ramus of cirrus IV; g, i, j, anterior ramus of cirrus III [g, median segment; i, j, posterior parts of 2nd proximal segment and of distal portion of long proximal segment (inner face)]; h, basidorsal point; k, 4th proximal segment of posterior ramus of cirrus III (a-g, i-k, holotype; h, paratype from Boca de Barranca, Costa Rica; after Henry, 1974).

labral face with short coarsely pinnate setae in band near upper margin on proximal three-fourths, broad in distal third to half, abruptly narrowing to 1 or 2 rows proximally; spinulose scales on upper half and multifid setulae on lower half of distal fourth; narrow band of simple scales along lower margin on proximal three-fourths.

Mandible with 5 teeth; inferior angle not spinose; 1st tooth occasionally bifid or with extra denticle; 2nd bifid; 3rd-5th with extra denticles; 5th tooth usually confluent with inferior angle.

First maxilla without notch below upper pair of spines, with short thick spine on outer face near lower spine of upper pair, 6-12 (8.4) spines between upper and lower pairs, and tuft of short spines on inferior angle; lower pair on slight prominence.

Second maxilla without distinguishing characters.

Protopods of anterior cirri with primarily pinnate setae, some plumose setae posteriorly on coxopods; both segments of cirrus I with narrow band of multifid spinules near posterior margin on outer face, coxopod also with wide band of simple scales near anterior margin; protopods of cirrus II without spinules or scales; coxopod of cirrus III with wide band of simple scales on outer face near posterior margin.

Cirrus I with anterior ramus 2-11 (5.0) segments longer than posterior; posterior ramus with very protuberant segments; proximal segments of anterior ramus protuberant; distal sutures of both rami with long setae and multifid spinules, more numerous on proximal segments; several proximal segments each also with simple spinules on posterior margin and narrow band of multifid spinules on outer face near posterior margin.

Cirrus II with anterior ramus 1 segment shorter to 6 (1.3) segments longer than posterior; both rami with very protuberant segments; distal sutures with long setae and multifid spinules; posterior ramus also with few simple spinules near anterior margins on proximal segments; anterior margins and outer faces near anterior margins of anterior ramus without spinules or teeth; posterior ramus with spinules or strong teeth; posterior margins of several proximal segments with simple spinules, longer on anterior ramus; outer faces near posterior margins of several proximal segments each with narrow band of simple and multifid spinules; long proximal segments each also with narrow to wide band of simple scales; inner faces near posterior margins of several proximal segments each with narrow band of simple spinules. Anterior margins of posterior ramus sometimes with spike-like or conic teeth on proximal segments, except long proximal, occasionally also on some median segments; outer face near anterior margin of long proximal segment usually with 2 or 3 rows of large simple spinules; remaining

proximal segments each usually with 2 or 3 rows of simple spinules and few larger simple spinules or spike-like teeth, sometimes with 2-4 rows of small conic teeth and few simple spinules, occasionally with few large simple spinules or 1 or 2 rows of small simple spinules; some median segments each usually with few large simple spinules or large teeth near distal angle, occasionally also with 1 or 2 rows of small conic teeth near margin.

Cirrus III with anterior ramus 1-6 (4.1) segments longer than posterior; both rami with slightly protuberant segments; distal sutures with short setae, spinules, and conic teeth; anterior margins and outer faces near anterior margins with conic teeth; posterior margins with tuft of short setae. Distal sutures with multifid spinules, also few large teeth or simple spinules near anterior margins on distal segments, 2-4 distal segments also with short setae. Anterior margins with large teeth, largest near distal angles, on all but 2 or 3 distal segments. Outer faces near anterior margins with 4-7 rows of large or small teeth and few denticulate scales, usually on proximal and median segments, sometimes on all but 2 or 3 distal segments. Inner faces near anterior margins of proximal segments of anterior ramus sometimes with narrow to wide band of denticles and multifid spinules; remaining proximal segments occasionally with few denticles; posterior ramus without denticles or spinules. Posterior margins of proximal segments of anterior ramus with conic teeth or simple spinules; posterior ramus sometimes with simple spinules, occasionally with small teeth, on several proximal segments. Outer faces near posterior margins of proximal segments of anterior ramus each with several rows of denticulate scales and few simple and multifid spinules; posterior ramus occasionally with few simple and multifid spinules. Inner faces near posterior margins of proximal segments of anterior ramus with teeth and spinules; several proximal segments each usually with several rows of simple spinules, sometimes also with small teeth; remaining proximal segments each usually with simple spinules on distal half, sometimes with few simple spinules near distal angle; median segments sometimes with few simple spinules near distal angles. Inner faces of anterior ramus without complex setae; posterior ramus with complex setae; distal segments, except ultimate, each usually with 1-3 pectinate setae, sometimes also with 1, less often 2, bifurcate setae; median segment occasionally with 1 or 2 bifurcate setae.

Protopods of posterior cirri each with several rows of simple spinules, occasionally also with denticulate scales on inner faces near anterior margins; basipods each sometimes also with short subsutural row of small simple spinules near posterodistal angle, occasionally with narrow band of simple spinules near posterior margin on inner face; coxopods each with 1 or 2

short subsutural rows of large simple spinules near posterodistal angle on inner face.

Posterior cirri with several short and 1 or 2 longer setae on each posterodistal angle and multifid spinules on distal sutures; distal sutures of cirrus IV, occasionally of cirrus V, also with few simple spinules near anterior margins; anterior ramus, occasionally posterior ramus, of cirrus IV each also with 2 or 3 conic teeth near anterior margin on proximal and median segments; inner faces near posterior margins of several segments of posterior cirri each with subsutural row of 4-6 large simple spinules near distal angle, and usually with several rows of simple spinules, occasionally also with 1 or 2 sparse rows of small conic teeth; remaining proximal and some median segments each usually with subsutural row of 4-6 large simple spinules near distal angle, sometimes with only few small simple spinules, or without spinules. Anterior ramus of cirrus IV with conic teeth on anterior margins on proximal segments; outer faces near anterior margins with teeth and denticulate scales on proximal segments, usually also on some median segments, occasionally on all but distal segments; long proximal segment with few teeth near distal angle; remaining segments with 2-10 rows of teeth and scales, fewer proximally and distally; posterior ramus without teeth on anterior margins; outer faces near anterior margins usually without teeth, occasionally with conic teeth on few proximal segments, rarely on most proximal and some median segments; several proximal segments without teeth; adjacent 2-4 segments each occasionally with few minute teeth proximally and 1 or 2 larger teeth near distal angle; some proximal and few adjacent median segments rarely with 2-10 rows of teeth and denticulate scales. Anterior ramus of cirrus V occasionally with 2-5 rows of conic teeth and denticulate scales on outer faces near anterior margins on each proximal segment except long proximal and several adjacent segments. Cirrus VI with 3-5 (4.2) pairs of setae on anterior margin of each median segment. Basidorsal point of penis large, nude.

Color. — Parietes bluish purple, sometimes with darker, narrow stripes, radii white with narrow band of color near parietes or occasionally entirely white; alae bluish near parietes, white near sutures; epicuticle yellowish brown. Sheath purplish; growth ridges fringed with brownish membrane. Scutum, on both surfaces, usually purple medially with white near occludent and tergal margins, sometimes purple except for white band along tergal margin. Tergum white with purple on all or part of carinal side on both surfaces, sometimes with 1-4 darker longitudinal striae, usually confluent apically, on outer surface near carinal margin.

Measurements. — Carinorostral diameter of holotype 24 mm, height 15 mm. Diameter of largest specimen 33 mm, height 20 mm.

Variations. — The amount of excavation of the carinal side of the basal margin of the tergum appears to be, as in other species of the complex, a function of size. In small specimens the basal margin is frequently only slightly concave; however, even in these specimens the projecting inner surface is prominent. The arrangement of the teeth on the labrum is subject to considerable variation. Teeth may be present only on the crest or frequently teeth are present both on the crest and on the edges of the notch.

Habitat. — Intertidal, on rocks and boulders near river mouth.

Remarks. — The results of the distance function analysis suggest that *B. suturaltus* is most closely allied to *B. c. pacificus* ($D^2 = 15.17$) and *B.citerosum* ($D^2 = 16.58$). However, as previously noted, the characters, the presence of a vesicular sheath, and complex setae on cirrus III, were not used in the statistical analyses. Neither were two species of the *pallidus* group available in sufficient numbers to be included in the analyses. Consequently, the interspecific relationship of *B. suturaltus* to other members of the complex cannot be accurately determined. This species is readily distinguished from all other species, except *B. kondakovi,* by the development of the inner surface of the tergum. The thickening of the apical portion of the scutum and the presence of a spur furrow on the tergum distinguish *B. suturaltus* from *B. kondakovi.*

Balanus dentivarians Henry (text-fig. 26, pl. 14, pl. 15 figs a, b, d)

Balanus dentivarians Henry, 1974: 992, figs. 6b, 9, 10a-f, 11 a-j (type locality: San Cristóbal Estuary, San Blas, Mexico).

Holotype. — USNM 143836.

Distribution. — West Central America and South America from Mexico to Ecuador.

Material examined. — Table 15.

Diagnosis. — Shell with epicuticle thin, persistent; radii very narrow, summits thin, smooth; sheath vesicular, sometimes with calcareous vesicles in furrow below lower margin; parietal tubes in 2 or more rows. Opercular valves with epicuticle thin, persistent. Scutum flat except for narrowly inflected tergal segment; longitudinal striae fine; articular ridge about 2/3 length of tergal margin; adductor ridge long, usually separated by narrow groove from articular ridge. Tergum with carinal margin convex, with closed spur furrow or closed above, open below; spur length usually nearly three times width; distance from basiscutal angle to spur greater than spur width; basal margin straight on scutal side, concave on carinal side. Labrum simple. Cirrus II with simple spinules on outer face near anterior margin;

Table 15. *Balanus dentivarians*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
Mexico, west coast					
San Blas	55	piles	*B. improvisus*	7/5/64	Henry USNM,RMNH
Panama, Pacific coast					
Sabana River	10	oyster reef	---	1966	Phelps USNM
Ecuador					
Posorja	1	boat hull	*B. improvisus, B. t. coccopoma Chthamalus* sp.	7/5/66	McLaughlin USNM
Guayaquil	32	piles	*T. polygenus*	1,2/5/66	McLaughlin USNM
Guayaquil	41	channel buoy	---	9/5/66	McLaughlin USNM
Guayaquil	∿500	marker buoys	*T. polygenus*	9/5/66	McLaughlin USNM,RMNH
Guayaquil	24	marker buoys	---	12/5/66	McLaughlin RMNH

cirrus III with complex setae, without erect teeth below posterodistal angles; cirrus VI with 7-11 (8.6) paired setae on median segments.

Description. — Shell usually cylindroconic, occasionally cylindric; orifice toothed, width about 1/3 carinorostral diameter; surface usually smooth unless ridged from replication of substratum, occasionally roughened in part; epicuticle thin. Radii very narrow, level, transversely striate; summits extremely oblique, thin, smooth; sutural edges denticulate on lower margins. Alae with oblique summits; sutural edges finely septate. Sheath vesicular; sometimes with calcareous vesicles extending into furrow below overhanging lower margin. Inner lamina ribbed to sheath; ribs finely denticulate basally, occasionally finely ridged on sides near bases. Parietal tubes in 2 or more rows, usually arranged with small tube on each side of primary longitudinal septa and minute tube on each side of subsidiary longitudinal septa, sometimes also with row of minute tubes close to outer lamina; primary tubes large, 16-22 (190) in rostrum, with transverse septa in upper 2/3; subsidiary tubes extending apically to about middle of parietes, with transverse septa almost to or to bases; largest subsidiary tubes sometimes with inner lamina [= outer wall of primary tube] ribbed on lower part; ribs denticulate basally. Inner surface of outer lamina occasionally with 1 or 2 fine ribs between longitudinal septa of subsidiary tubes. Basis with radial tubes and numerous transverse septa; sometimes lengthened in part.

Scutum thin, with narrowly inflected tergal segment; basitergal angle rounded, strongly ascending; occludent margin toothed, not thickened; growth ridges low; longitudinal striae fine, approximate. Inner surface slightly to moderately roughened on upper part, thickened between pit below

adductor ridge and lateral depressor muscle pit; articular ridge high, not reflexed; about 2/3 length of tergal margin and about 1/3 length of occludent margin, end usually rounded, occasionally truncate; articular furrow narrow; adductor ridge long, moderately strong, acute, with deep pit below, separated from articular ridge usually by narrow groove; lateral depressor muscle pit large, deep.

Tergum wide, apex projecting slightly above scutum; scutal side occasionally with narrow longitudinal groove close to spur furrow; scutal margin denticulate; carinal side sometimes with medial longitudinal groove, carinal margin thin; growth ridges fine, sometimes stronger medially on very narrow carinal segment; longitudinal striae occasionally present on carinal side; spur furrow closed or closed above, open below; spur width about 1/5 length of basal margin; spur length about 2 9/10 spur width; distance from basiscutal angle to spur about 1/5 spur width, about 2/5 spur length, and about 1/4 length of basal margin; spur length about 3/5 length of basal margin; end rounded; basal margin straight on scutal side of spur, concave on carinal side. Internally, scutal margin low; articular ridge very low; articular furrow moderately wide; crests for depressor muscle prominent, short, usually projecting below basal margin; surface sometimes roughened on carinal side, basally occasionally with 1-3 denticles adjacent to spur.

Labrum with setulae and 2-7 (3.4) teeth on crest on each side of notch; usually with teeth only on crest, sometimes with teeth on crest and on each edge of notch near crest.

Palpus with short finely pinnate setae on upper margin and in narrow band parallel to upper margin on outer face, also with long setae in tuft on distal end and in oblique row near inferodistal angle, narrow band of setulae parallel to lower margin; labral face with band of coarsely pinnate short setae near upper margin on proximal three-fourths, broad in distal third to half, abruptly narrowing to 1 or 2 rows proximally.

Mandible with 5 or 6 (5.9) teeth; inferior angle not spinose; 1st tooth usually bifid or with extra denticle; 2nd bifid; 3rd-6th with extra denticles; lowest confluent with inferior angle.

First maxilla usually without notch below upper pair of spines, with short thick spine on outer face near lower spine of upper pair, 4-14 (9.5) spines between upper and lower pairs, tuft of fine spines on inferior angle; lower pair of spines usually on slight, sometimes on moderate, prominence.

Second maxilla without distinguishing characters.

Protopods of anterior cirri with primarily pinnate setae, some plumose setae posteriorly on coxopods; both segments of cirrus I each with wide band of simple scales near anterior margin on outer face; basipod of cirrus II

with few multifid spinules near anterior margin on outer face, coxopod with few denticulate scales near posterodistal angle on outer face; basipod of cirrus III with narrow band of denticulate and spinulose scales near posterior margin on outer and inner faces.

Cirrus I with anterior ramus equal to or 1-11 (6.4) segments longer than posterior; posterior ramus with very protuberant segments; proximal segments of anterior ramus protuberant; distal sutures of both rami with long setae and multifid spinules; posterior margins of long proximal segments

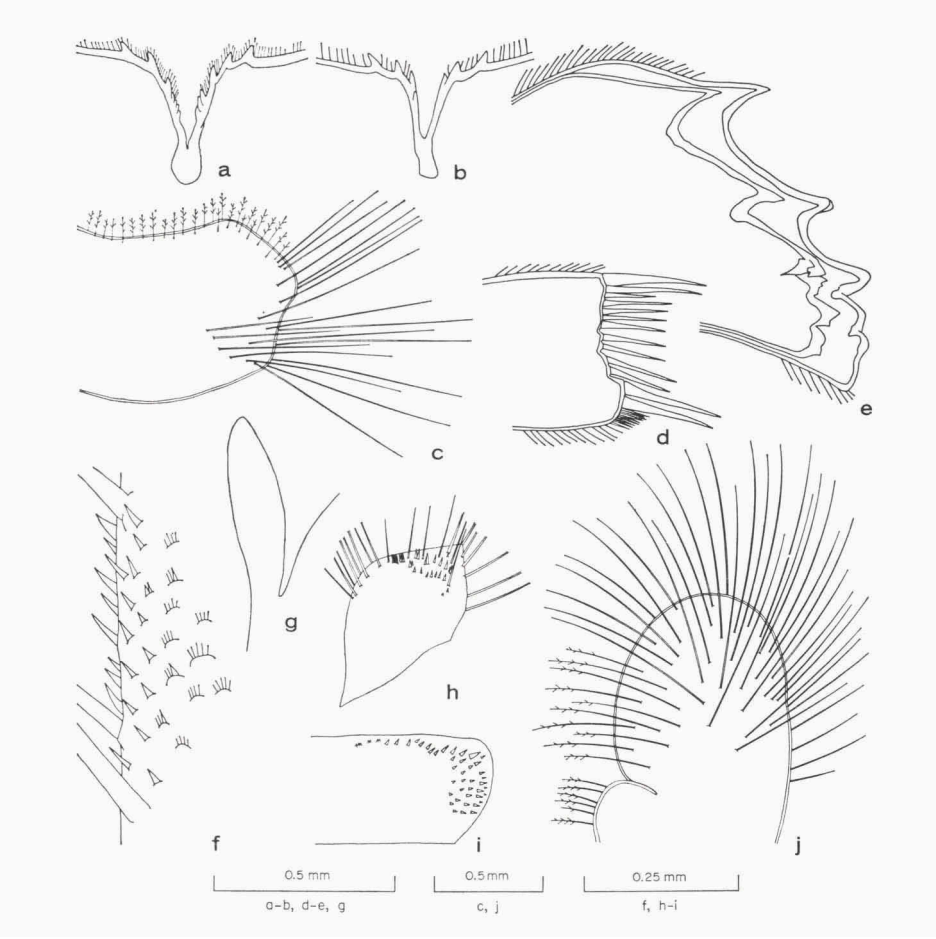

Fig. 26. *Balanus dentivarians* Henry. a, b, labra; c, palpus; d, 1st maxilla; e, mandible; f, h, i, anterior ramus of cirrus III (f, posterior part of long proximal segment; h, 2nd distal segment; i, anterior part of 6th proximal segment); g, basidorsal point; j, 2nd maxilla (a, c-e, g, j, holotype; b, f, h, i, paratype from San Cristôbal Estuary, San Blas, Mexico; after Henry, 1974).

with simple spinules; outer face near posterior margin of several proximal segments each with narrow band of spinulose and denticulate scales.

Cirrus II with anterior ramus 2 segments shorter to 5 (1.9) segments longer than posterior; both rami with protuberant segments; distal sutures with long setae and multifid spinules; outer faces near anterior margins of proximal segments each usually with few simple spinules; posterior ramus occasionally with very wide band of larger simple spinules; median segments of both rami with multifid spinules, more numerous on posterior ramus below angles; posterior margins of anterior ramus with simple spinules on proximal segments; outer faces near posterior margins of proximal segments each with simple, denticulate and spinulose scales on posterior half; median segments with multifid spinules, more numerous on posterior ramus, below angles; inner faces near posterior margins of several proximal segments of anterior ramus each with narrow band of simple spinules and denticulate scales.

Cirrus III with anterior ramus 2-6 (4.4) segments longer than posterior; both rami with protuberant segments; distal sutures with large conic teeth or simple spinules near anterior margins and multifid spinules near posterior margins, also with few short setae on 2-4 distal segments; outer faces near anterior margins with conic teeth; posterior margins with short setae and simple spinules; both faces with spinules and scales near posterior margin; inner face of posterior ramus also with complex setae Anterior margins of proximal segments of both rami sometimes with conic teeth. Outer faces near anterior margins of long proximal segments each usually without teeth but with 4 or 5 rows of simple spinules; other proximal and some median segments each with 5 or 6 teeth near distal angle, usually also with wide band of teeth and few denticulate scales, occasionally with only 1 or 2 rows of teeth; remaining median segments each usually with 3-6 teeth near distal angles. Posterior margins with short setae, fewer proximally, on distal angles, also with simple spinules on proximal segments. Outer faces near posterior margins with narrow band of simple spinules and spinulose and denticulate scales on each proximal segment. Inner faces of posterior ramus with complex setae; both rami with narrow band of simple spinules near posterior margin on all segments except few distal; posterior ramus with 3 or 4 pectinate setae, sometimes also with few bifurcate setae on each distal segment except ultimate, and 1-16 bifurcate setae usually on each median and proximal segment except long proximal, occasionally only on 3 or 4 proximal segments

Protopods of posterior cirri each sometimes with narrow band of simple and multifid spinules on outer face and narrow band of simple spinules on

inner face near posterior margin; both faces with wide band of simple spinules near posterior margins.

Posterior cirri with simple and multifid spinules, decreasing in number distally, on distal sutures, 3 or 4 short setae and 1 longer seta on each posterodistal angle, and narrow band of simple spinules on inner face near posterior margin of each segment on proximal half. Anterior ramus of cirrus IV also with conic teeth on outer faces near anterior margins on proximal segments, sometimes also on median segments, occasionally on all but few distal segments; proximal segments each with 3-7 teeth near distal angle, usually also with 2-5 sparse rows of teeth and few denticulate scales on anterior third to half; median segments each usually with 3-7 teeth near distal angle, sometimes also with teeth on anterior third; distal segments, except ultimate, each occasionally with 3-7 teeth near distal angle; posterior ramus usually without teeth on outer faces near anterior margins; proximal segments each usually with 3-5 simple spinules near distal angle, occasionally also with 2-6 rows of teeth near anterior margin. Cirrus VI with 7-11 (8.6) pairs of setae on anterior margin of each median segment. Basidorsal point of penis large, usually elongate, nude.

Color. — Parietes usually lavender with dull purplish brown, approximate stripes; stripes sometimes confluent at center or edges of parietes; occasionally entirely white; radii usually white, occasionally lavender; alae white; epicuticle yellowish brown. Sheath usually white or white on rostral half, purplish on carinal half; occasionally entirely purplish. Scutum usually purplish brown with white tergal segment and narrow adjacent band on external surface, occasionally occludent half white or white with purplish brown margin, less frequently entirely purple; inner surface usually greyish lavender with white tergal segment, sometimes white with color apically or medially on lower half, occasionally purplish with white articular and adductor ridges. Tergum usually white on spur and scutal side, purplish brown on all or part of carinal side on both surfaces; occasionally inner surface entirely white.

Measurements. — Carinorostral diameter of holotype 23 mm, rostral height 16 mm. Diameter of largest specimen 47 mm.

Variations. — Crowded specimens are usually cylindric, often with lengthened bases. Variation in certain of the characters of the internal parts appears to be related both to geographic distribution and size. As noted by Henry (1974) specimens from Ecuador were usually larger than those from Mexico and Panama, and had fewer teeth on the labra, fewer spines between the upper and lower pairs of spines on the first maxilla and fewer paired setae on cirrus VI. However, the armature of the posterior ramus of cirrus

II was stronger in large than in small specimens from both Ecuador and Panama.

Habitat. — Intertidal, on piles, buoys, oyster reefs, in brackish water.

Remarks. — Although clearly allied with the species of the *pallidus* group, *B. dentivarians* is not closely related to any of the known species in the group. The results of the discriminant function analysis indicate that although *B. dentivarians*' closest neighbor is *B. suturaltus* ($D^2 = 94.94$), the distance separating them is more than three times greater than for any of the other pairs of taxa analysed. In superficial appearance, *B. dentivarians* is also most similar to *B. suturaltus*; however, it may be distinguished from the latter species by the greater width of the tergum, longer spur which is also farther removed from the basiscutal angle, and by the normal development of the inner surface of the tergum.

Balanus patelliformis Bruguière (text-fig. 27, pl. 16, pl. 17 figs f-j)

[Die Stern-patellenförmige Meereichel] Spengler, 1780: 106, pl. 5 fig. 4. — Chemnitz, 1785: 316, pl. 98 fig. 839.

Balanus patelliformis Bruguière, 1789: 169 (type locality: south coast of India). — Bruguière, 1792, pl. 165 fig. 3. — Lamy & André, 1932: 132.

Lepas patellaris Gmelin, 1790: 3213.

Balanus patellaris: Darwin, 1854: 259, pl. 6 fig. 5a-c. — Gruvel, 1903c: 139. — Gruvel, 1905: 238, fig. 265. — Nilsson-Cantell, 1921: 328. — Nilsson-Cantell, 1929: 4, figs. 1a, b, 3a-f. — Nilsson-Cantell, 1938: 46, pl. 1 figs. 4, 5. — Utinomi, 1968: 174, figs. 5, 6a, b. (not *Balanus patellaris* Lamarck, 1818: 395).

Holotype. — Presumably no longer extant.

Distribution. — Southwest coast of India to Strait of Malacca; Philippine Archipelago to Java Sea.

Material examined. — None.

Diagnosis. — Parietes longitudinally folded, ribbed, or smooth; radii narrow, summits crenulate, arched; sheath with lower margin not overhanging. Scutum flat; longitudinal striae absent; articular ridge about 1/2 length of tergal margin; adductor ridge short to moderately long, widely separated from articular ridge. Tergum with carinal margin convex, with open furrow; spur length about equaling width; distance from basiscutal angle to spur equaling spur width; basal margin straight or concave on scutal side, concave, sometimes deeply excavated on carinal side. Labrum simple. Cirrus VI with 3 paired setae.

Description. — Shell conic to subcylindric; orifice slightly toothed, width more than 1/2 carinorostral diameter; surface with longitudinal folds, incompletely or regularly ribbed, or smooth. Radii narrow, sometimes trans-

versely striate; summits oblique, arched, crenulate; sutural edges bluntly denticulate. Alae wide; summits subhorizontal; sutural edges septate. Sheath with lower margin not overhanging. Inner lamina strongly ribbed; ribs slightly denticulate basally. Parietal tubes rather large; without transverse septa. Basis thin, usually with radial tubes, at least near periphery; sometimes solid.

Scutum flat; growth ridges low; longitudinal striae absent. Inner surface without ridges; articular ridge prominent, reflexed, about 1/2 length of tergal margin, end pointed or truncate; articular furrow apparently deep, adductor ridge short, low, well separated from articular ridge; adductor muscle pit shallow; lateral depressor muscle pit shallow or absent.

Tergum with carinal margin protuberant; longitudinal striae absent; spur furrow open; spur width about 1/4 length of basal margin; spur width about equal to spur length; distance from basiscutal angle to spur about equal to spur width; end bluntly pointed; basal margin straight or slightly concave on scutal side of spur, straight, concave, or deeply excavated on carinal side. Internally, articular ridge extremely prominent; crests for depressor muscle strong.

Labrum with setulae and 3-5 teeth on crest on each side of notch.

Palpus with pinnate setae on upper margin; outer face with short setae in tuft near superodistal angle, long setae in tuft on distal margin on inferior third and in oblique row near inferodistal angle.

Mandible with 5 teeth and pointed inferior angle; 2nd-5th teeth indistinctly double.

First maxilla with few fine spines in notch below upper pair of spines, 5 spines between upper and lower pairs, few fine spines on inferior angle; lower pair of spines on prominence

Second maxilla without distinguishing characters.

Cirrus I with unequal rami; posterior ramus with very protuberant segments.

Cirrus II with subequal rami; both rami with protuberant segments.

Cirrus VI with 3 pairs of setae on anterior margins of median segments.

Description modified from Darwin (1854) and Nilsson-Cantell (1929).

Color. — Shelly dirty brown or dirty white, color sometimes in longitudinal bands; young specimens regularly banded longitudinally with violet-brown and dirty white. Radii usually dull red or violet. Color of sheath and opercular valves unknown.

Measurements. — Diameter of Darwin's (1854) specimen 23 mm; diameter of Nilsson-Cantell's (1929) larger specimen 18 mm, height 7 mm.

Variation. — The shape and surface of the shell are both extremely

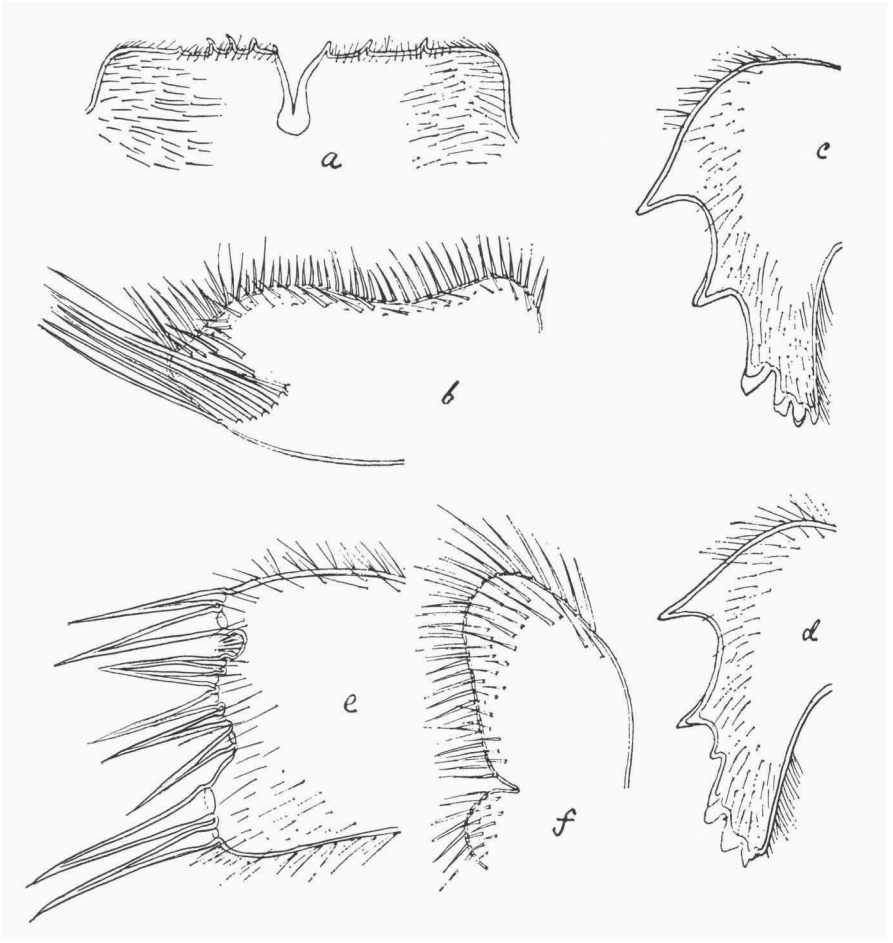

Fig. 27. *Balanus patelliformis* Bruguière. a, labrum; b, palpus; c, d, mandibles; e, f, 1st and 2nd maxillae (after Nilsson-Cantell, 1929).

variable. According to Darwin (1845), the shell is depressed, usually smooth, but in older specimens slightly folded longitudinally. The specimens described or figured by Nilsson-Cantell (1921, 1929, 1938, pl. 1 figs 4, 5) are conic and folded or occasionally finely ribbed. In Utinomi's (1968) material, the shell is usually subcylindric and smooth but sometimes subcylindric or depressed conic and folded or finely ribbed.

The tergum is also extremely variable. The basal margin of the tergum figured by Nilsson-Cantell (1929, fig. 1a) is deeply excavated on the carinal side, close to the spur; the carinal side of the basal margin in Utinomi's (1968, fig. 6b) figure is broadly excavated. Darwin's (1954, pl. 6 fig. 5b) tergum, however, has a straight basal margin and the spur is shorter than the spur in Nilsson-Cantell's and Utinomi's figures.

Remarks. — Darwin (1854) was apparently unaware that Bruguière (1789) had given the name, *B. patelliformis,* to the specimen figured by Spengler (1780, pl. 5, fig. 4) and reproduced by Chemnitz (1785) without binomen, as he used Gmelin's (1790) proposed name, *patellaris,* for the species. However, although Darwin cited *Lepas patellaris* Gmelin, he credited Spengler with the autorship of *B. patellaris.* The few subsequent investigators who have recorded this species have followed Darwin's usage of Gmelin's specific name. Lamy & André, (1932), however, correctly pointed out that *B. patellaris* is an objective junior synonym of *B. patelliformis.*

The status of Lamarck's (1818) *B. patellaris* cannot be determined from his incomplete description. It was recorded from France and he questioned whether it was synonymous with *Chthamalus stellatus* (Poli).

Darwin (1854) assigned *B. patellaris* to his section D (basis without pores), although he remarked that it had almost as strong a claim for being ranked in his section C as the basis sometimes had tubes near the periphery and that it showed more affinity to *B. improvisus* than to any other species. Contrary to Darwin's findings, the basis of the specimens referred to *B. patellaris* by Nilsson-Cantell (1929) and Utinomi (1968) have radial tubes.

We believe, however, that several characters, particularly those of the labrum and tergum and, to a lesser extent, the surface of the shell indicate that *B. patelliformis* is more closely allied to *B. albicostatus* and *B. kondakovi* than to *B. improvisus.* The figure of the tergum (Nilsson-Cantell, 1929, fig. 1a) is very similar to figures of the tergum of *B. kondakovi* (cf. Nilsson-Cantell, 1932b, fig. 10f; Zevina & Tarasov, 1963, fig. 12a; Utinomi, 1967, fig. 1b). Utinomi's (1968) fig. 6b of the tergum of *B. patellaris* agrees well with the tergum of our specimen of *B. kondakovi* from Thailand (pl. 11 fig. c), and also shows a certain resemblance to the tergum of the holotype of *B. albicostatus* (cf. Pilsbry, 1916, pl. 20 fig. 2a).

Specimens of *B. patelliformis* with longitudinally folded walls are easily differentiated from *B. kondakovi* and *B. albicostatus,* but shells with narrower ribs resemble the shells of strongly ribbed specimens of the latter species.

The description and figures of the mouth parts and cirri (cf. Nilsson-Cantell, 1929, fig. 3a-f) give further evidence for the close relationship of *B. patelliformis* with *B. kondakovi* and *B. albicostatus.* Therefore, we tentavively include *B. patelliformis* in the *pallidus* group, although several diagnostic characters, such as the occurrence of subsidiary parietal tubes, a vesicular sheath, and complex setae are not known.

Balanus abeli Lamy & André (pl. 17 figs a-e)

Balanus violaceus Gruvel, 1993a: 24 (type locality: unknown). — Gruvel, 1903b: 297. — Gruvel, 1903c: 133, pl. 1 figs. 11-14, pl. 4 fig. 12.
Balanus abeli Lamy & André, 1932: 218 (footnote).
not *Lepas violacea* Gmelin, 1791: 3213 (see remarks).

Holotype. — BM.

Distribution. — Unknown.

Material examined. — None.

Diagnosis. — Parietes finely ribbed; radii wide, summits thick. Scutum flat; longitudinal striae absent; articular ridge about 3/4 length of tergal margin; adductor ridge short, widely separated from articular ridge. Tergum with carinal margin convex, with deep longitudinal furrow on each side of spur fasciole and 2 longitudinal grooves on carinal side medially; spur length about equaling width; distance from basiscutal angle to spur about 1/2 spur width; basal margin concave on scutal side, straight on carinal side. Labrum without teeth.

Description. — Shell conic; orifice strongly toothed, width more than 1/2 carinorostral diameter; surface with numerous, narrow longitudinal ribs. Radii wide; summits oblique, thick; sutural edges denticulate. Alae wide; summits oblique. Inner lamina ribbed; ribs laterally ridged, more strongly basally. Parietal tubes without transverse septa, not filled up near apex. Basis with radial tubes.

Scutum flat except for recurved apex; growth ridges low; longitudinal striae absent. Inner surface rugose on upper part; articular ridge high, reflexed, about 3/4 length of tergal margin, end truncate; articular furrow deep; adductor ridge short, low, well separated from articular ridge; adductor muscle pit deep; lateral depressor muscle pit small, deep.

Tergum with apex slightly reflexed; growth ridges low; longitudinal striae absent; deep longitudinal furrow on each side of spur, 2 shallower longitudinal grooves on carinal side [described by Gruvel as deep fold each side of spur, two folds carinal side], fasciole raised, separated from each side by narrow ridge; spur width about 3/10 width of basal margin; spur length about equaling spur width; distance from basiscutal angle to spur about 1/2 spur width; end rounded; basal margin strongly concave on scutal side; straight or slightly concave on carinal side. Internally, scutal margin high; articular ridge low, slightly reflexed; articular furrow deep; crests for depressor muscle strong, projecting below basal margin; surface basally denticulate medially.

Labrum with setulae, without teeth.

Mandible with 4 teeth and spinose inferior angle.

First maxilla with 6 spines in slight notch below upper pair of spines, few fine spines on inferior angle; lower pair of spines on prominence.

Second maxilla without distinguishing characters.

Cirri I and II short and thick.

Posterior cirri long. Penis very long, about 3 times length of cirrus VI, sparsely spinose.

Color. — Shell violaceous with clear, greyish violet ribs. Scutum and tergum, externally, greyish violet with pale longitudinal bands; internally, with violet splotches.

Measurements. — Carinorostral diameter 16 mm, height 11 mm.

Variations. — Unknown.

Habitat. — Unknown.

Remarks. — The specific name, *violacea,* was first used by Gmelin (1790: 3213) for the figure of Chemnitz's Lepas Indiae orientalis ex violaceo radiata (Chemnitz, 1785, pl 99 fig. 842). Previously, however, Bruguière (1789) had proposed the name *Balanus radiatus,* and Spengler (1790) the name, *Lepas purpurea,* for this same specimen figured by Chemnitz (1785). Darwin (1854) apparently was unaware that Gmelin had given a name to this specimen, but he remarked (Darwin, 1854: 241) that it was impossible to identify Bruguière's and Spengler's species. Similarly, Gruvel (1903a) apparently was not aware of Gmelin's use of the specific name when he named his new violet-colored species *Balanus violaceus.* Subsequently Pilsbry (1916) questionably placed *B. radiatus* and *Lepas purpurea* in synonymy with *B. amphitrite* and considered that *B. violaceus* Gruvel should be given subspecific status in *B. amphitrite.* He pointed out that the name *violaceus* was preoccupied by *L. violacea* Gmelin, a species which he considered a balanid; however, he did not propose a replacement name for Gruvel's species.

Ross (1969) placed *L. violacea* Gmelin, but not Gruvel's species, *L. purpurea,* and *B. radiata* in synonymy with *Tetraclita radiata* Darwin and designated *B. radiata* Bruguière the type species of a new genus, *Newmanella,* a tetraclitid. In the interim, Lamy & André (1932) had placed *L. violacea* in synonymy with *B. radiata* and, noting that Gruvel's name was preoccupied, proposed the replacement name, *B. abeli* for Gruvel's species. Although incorrect in retaining Bruguière's *radiata* in *Balanus,* Lamy & André's proposition of a new name is legal under the Code of Zoological Nomenclature, and since this action took place prior to 1960, the name *B. violaceus* Gruvel cannot be restored (L. B. Holthuis, personal communication).

Pilsbry (1916) stated that his new subspecies, *B. a. albicostatus,* the only ribbed form of *B. amphitrite,* might prove to be close to, or even synonymous

with Gruvel's *B. violaceus* because of its ribbed parietes. However, he pointed out that this latter species differed from *B. a. albicostatus* in several minor details of the scutum and particularly by the series of external folds [designated furrows and grooves herein to conform with the other taxa] on the tergum. Utinomi (1967) apparently agreed that Gruvel's species might be conspecific with *B. albicostatus* as he included *?Balanus violaceus* Gruvel in the synonymy of *B. albicostatus albicostatus.* Since Pilsbry's original description, many specimens of *B. albicostatus,* covering a wide geographic range, have been recorded and a tergum with longitudinal furrows has never been noted.

The shell of *B. abeli* also resembles the specimens of *B. patelliformis* with finely ribbed shells but both the scutum and, to a lesser extent, the tergum differ. The tergum resembles that of *B. kondakovi* in the deep excavation on the scutal side of the spur and the denticulate basal margin on the carinal side. We, tentatively, have included *B. abeli* in the *pallidus* group although several of the diagnostic characters of the group are unknown. *B. abeli,* like *B. patelliformis,* differs from the other members of the *pallidus* group by lacking transverse septa in the parietal tubes.

Balanus concavus pacificus Pilsbry (text-fig. 28, pl. 18, figs a-e)

Balanus concavus: Darwin, 1854: 235 [in part; not pl. 4 fig. 4a-c (= *B. c. mexicanus*); not *Balanus concavus* Bronn, 1831: 127; 1838: 1155, pl. 36 fig. 12a-e].
Balanus concavus pacificus Pilsbry, 1916: 104, fig. 25a-e, pl. 23 figs. 1-1c (type locality: San Diego, California). — Giltay, 1934: 1, figs. 1-4. — Henry, 1942: 104, pl. 2 figs. 1-4. — Cornwall, 1951: 328, pl. 4 figs. d, e. — Henry, 1959: 200, pl. 2 figs. 1-6. — Ross, 1962: 16.
Balanus concavus pacificus form *brevicalcar* Pilsbry, 1916: 337, fig. 26a-c, pl. 23 figs. 2-2c.
Balanus pacificus: Ross, 1964: 489.
Balanus pacificus brevicalcar: Ross, 1964: 489.

Holotype. — USNM 32953.

Distribution. — Central California to southwest Baja California, Mexico.

Material examined. — Table 16.

Diagnosis. — Shell with epicuticle usually persistent; radii moderately wide, level; summits subhorizontal to moderately oblique; sheath solid, lower margin overhanging; parietal tubes in single row, without transverse septa. Scutum with growth ridges usually crenulate; longitudinal striae strong; articular ridge about 7/10 length of tergal margin; adductor ridge long, separated from articular ridge; lateral depressor muscle pit bounded on occludent side by high ridge sometimes folded over in upper part. Tergum with closed or nearly closed spur furrow; spur length greater than spur width, distance from basiscutal angle to spur about equaling spur width; basal margin straight on both sides of spur. Labrum simple. Cirri III-VI

Table 16. *Balanus concavus pacificus*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
California					
Goleta	14	rocks	*B. aquila*	6/57	Connell USNM
Off Port Hueneme	12	stomatopods	---	14/4/64	MacGinitie RMNH
Off Point Mugu	4	decapods	---	6/7/62	MacGinitie RMNH
Off Point Mugu	6	bottle	---	10/10/62	MacGinitie USNM
Off Mugu pier	2	decapod	---	29/8/62	MacGinitie USNM
Off Mugu pier	6	sand dollar	---	5/12/62	MacGinitie USNM
Off Mugu pier	9	decapod	---	7/1/63	MacGinitie RMNH
Off Mugu pier	4	---	---	21/1/63	MacGinitie USNM
Off Mugu pier	6	decapod	---	19/3/63	MacGinitie USNM
Off Mugu pier	2	sand dollar	---	21/3/63	MacGinitie USNM
Off Mugu pier	5	---	---	13/8/63	MacGinitie USNM
Off Mugu pier	13	pelecypods	---	6/10/63	MacGinitie USNM
Off Catalina Harbor	5	*Polinices* sp.	---	23/6/51	----- USNM 205678
Off Pt. Loma light	3	*Neptunea* sp.	---	12/3/04	----- USNM
Baja California, west coast					
San Antonio del Mar	3	sand dollar	*B. aquila, B. t. californicus*	1/8/39	Henry RMNH
Santa Maria Beach	13	sand dollars	---	31/7/39	Henry USNM
Socorro	24	crabs	*B. glandula, Ch. fissus*	28/7/39	Henry RMNH
12 mi N of Rosario	1	gastropod	*B.aquila,B.t.californicus,T.s.rubescens*	31/7/39	Henry USNM

without erect teeth below posterodistal angles; cirrus III without complex setae, with 1 or 2 thick curved setae on posterodistal angles.

Description. Shell conic to cylindric; orifice usually slightly toothed, width less than 1/2 carinorostral diameter; surface smooth, occasionally ribbed at base; epicuticle thin, usually persistent. Radii moderately wide, usually with fine transverse striae, sometimes also with fine longitudinal striae; summits subhorizontal to moderately oblique, thick, rough; sutural edges with septa strongly denticulate on lower margins. Alae with oblique summits; sutural edges smooth. Sheath solid, lower margin overhanging. Inner lamina ribbed, sometimes to sheath; ribs denticulate basally, finely ridged on sides near bases. Parietal tubes in single row, usually numerous, 13-47 (28) in rostrum; without transverse septa, filled up in upper 1/6-1/4. Inner surface of outer lamina occasionally with 1 or 2 ribs between longitudinal septa. Basis with radial tubes and fine transverse septa, occasionally without transverse septa near periphery, often with vesicular layer below; sometimes lengthened.

Scutum usually level, sometimes slightly concave between apex and basal margin; tergal segment usually narrowly inflected; basitergal angle rounded; occludent margin strongly toothed; growth ridges moderately prominent, usually denticulate; longitudinal striae strong, unequal, approximate, sometimes indistinct in large specimens. Inner surface strongly ridged on upper part, sometimes roughened or with 1 or 2 longitudinal ridges between adductor ridge and tergal margin, sometimes crenulate basally; articular ridge high, reflexed, about 7/10 length of tergal margin and about 1/2 length of occludent margin, end truncate; articular furrow narrow; adductor ridge strong, long, extending from above end of articular ridge almost to basal margin, without pit below, separated from articular ridge by deep narrow groove; adductor muscle pit shallow; lateral depressor muscle pit deep, bounded on occludent side by high thin ridge sometimes folded over in upper part; rostral muscle pit small.

Tergum usually wide; apex curved toward scutum; scutal margin denticulate; carinal margin slightly convex; growth ridges moderately prominent, not upturned along carinal margin; longitudinal striae often present on carinal side, sometimes also on scutal side; spur furrow closed or almost closed except occasionally in small specimens; spur width about 3/10 length of basal margin; spur length about 1 3/5 spur width; distance from basiscutal angle to spur about equal to spur width, about 2/3 spur length, and about 1/4 length of basal margin; spur length about 2/5 length of basal margin; end obliquely truncate or rounded, occasionally denticulate on folded over scutal side; basal margin straight on both sides of spur. Internally, scutal margin low; articular ridge low, reflexed in small specimens; articular furrow shallow, moderately wide; crests for depressor muscle low, sometimes long, not projecting below basal margin; surface strongly ridged between articular ridge and carinal margin.

Labrum with setulae and 0-4 (2.6) small teeth on crest on each side of notch.

Palpus with setulae on inferior half of distal margin and on distal third to half of lower margin, pinnate short setae on upper margin and on outer face, in tuft near superodistal angle and usually in narrow band, sometimes with only few setae near upper margin, also with long setae on distal end and in 3 or 4 short rows extending proximally from inferior fourth of distal margin, usually parallel, sometimes oblique to lower margin, and narrow band of setulae near lower margin; labral face with short pinnate setae near upper margin on proximal four-fifths, usually arranged in narrow band, wider distally and proximally, sometimes with few setae along margin or in distal and proximal tufts.

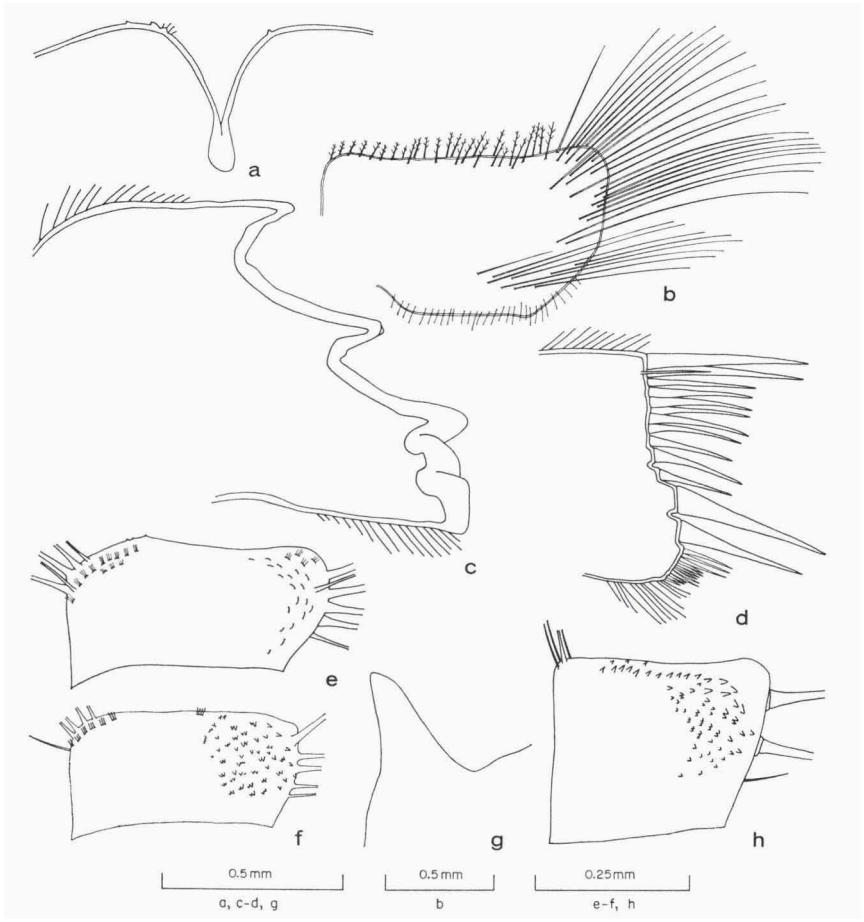

Fig. 28. *Balanus concavus pacificus* Pilsbry. a, labrum; b, palpus; c, mandible; d, 1st maxilla; e, f, cirrus III (e, 12th distal segment of anterior ramus; f, 10th distal segment of posterior ramus); g, basidorsal point; h, 17th distal segment of cirrus IV (a-h, Point Mugu, California).

Mandible with 5 teeth; inferior angle not spinose; 2nd, sometimes also 1st, tooth bifid; 3rd-5th with extra denticles; 5th tooth usually confluent with inferior angle.

First maxilla usually with slight notch below upper pair of large spines, 2 or 3 fine spines in notch, with short spine on outer face near lower spine of upper pair, 3-11 (7.2) spines between upper and lower pairs, and tuft of fine spines on inferior angle; lower pair of spines on moderate prominence.

Second maxilla without distinguishing characters.

Protopods of anterior cirri with primarily pinnate setae, some plumose setae posteriorly on coxopods; both segments of cirrus I each with wide

band of simple scales on outer face near anterior margin; protopods of cirri II and III each with wide band of simple scales near posterior margin.

Cirrus I with anterior ramus 1 segment shorter to 7 (3.3) segments longer than posterior; posterior ramus with extremely protuberant segments; proximal segments of anterior ramus protuberant; distal sutures of both rami with long setae and multifid spinules, decreasing in number proximally; proximal segments each with narrow band of simple scales on outer face near posterior margin.

Cirrus II with anterior ramus 2 segments shorter to 4 (0.5) segments longer than posterior; both rami with very protuberant segments; distal sutures with long setae and multifid spinules, decreasing in number proximally; proximal segments each with narrow to wide band of simple scales on outer face near posterior margin; long proximal segment of anterior ramus with simple spinules on posterior margin.

Cirrus III with anterior ramus equal to or 1-7 (2.9) segments longer than posterior; both rami with slightly protuberant segments; distal sutures with multifid spinules and few short setae on few distal segments; remaining segments with stronger multifid spinules, usually only near anterior and posterior margins; posterior margins with short setae and fine simple spinules; inner faces without complex setae. Anterior margins of 1 or 2 proximal segments sometimes with few small conic teeth. Outer faces near anterior margins usually with numerous small conic teeth and scales and few spinules on proximal and median segments; distal segments usually with few scales and spinules; anterior ramus sometimes without teeth but with numerous scales and few spinules; posterior ramus occasionally without teeth but with few scales and spinules; proximal and median segments of both rami each usually with several simple, bifid, and multifid spinules near anterodistal angle and wide band of teeth and scales, arranged with 2-6 rows of teeth close to margin, 4-6 rows of denticulate scales adjacent to teeth and several rows of simple scales mesiad, sometimes occupying anterior half or more; distal segments each usually with narrow band of simple, occasionally also few denticulate, scales; few simple, bifid, and multifid spinules near distal angle. Posterior margins with tuft of short setae, fewer proximally, on distal angles; proximal segments with fine simple spinules. Outer faces near posterior margins of proximal segments each usually with narrow to wide band of simple and denticulate scales, more numerous on anterior ramus. Inner faces near posterior margins of long proximal and 1 or 2 adjacent segments each sometimes with narrow band of simple scales.

Protopods of posterior cirri each with narrow to wide band of simple

scales on outer face and narrow band of simple and spinulose scales on inner face near posterior margin; usually also with few simple and spinulose scales on inner face near anterior margin; posterior margins without short thick setae on distal angles; coxopods each with simple and multifid spinules, also with few short setae near posterodistal angles on outer and inner faces.

Posterior cirri with simple and multifid spinules on distal sutures, with 1-3 relatively long setae and 5-7 shorter thinner setae on each posterodistal angle except on few proximal segments; long proximal and few adjacent segments of cirrus IV and anterior rami of cirri V and VI without short setae, but with 1-3 long setae; 5-9 proximal segments of posterior rami of cirri V and VI each usually with 1, occasionally 2, thicker, slightly curved setae; inner faces near posterior margins of long proximal segments each sometimes with narrow band of simple scales; several adjacent segments each sometimes with narrow band of simple scales, also with 3-7 simple spinules on distal suture. Anterior margins of anterior ramus of cirrus IV occasionally with small conic teeth; posterior ramus without teeth. Outer faces near anterior margins of anterior ramus of cirrus IV usually with small conic teeth on proximal and median, sometimes also on distal segments, occasionally without teeth, but with few simple scales on proximal segments; posterior ramus usually without teeth, occasionally with small conic teeth and denticulate scales on proximal, rarely on median segments; proximal segments of anterior ramus each usually with teeth and simple and denticulate scales in 2 or 3 rows near distal angle; median, as well as proximal segments, each sometimes with teeth and denticulate scales on anterior third to half, usually arranged with several rows of teeth close to margin and several adjacent rows of scales, fewer proximally and distally; few distal segments each sometimes with 3 or 4 teeth or simple spinules near distal angle; posterior ramus usually with few simple spinules near distal angles on proximal segments, each sometimes also with subsutural row of simple spinules on anterior third and few simple spinules near margin, occasionally with few teeth and simple spinules near distal angle and in subsutural row on anterior third and 2 or 3 rows of denticulate scales, or rarely 6-10 rows of teeth and scales, near margin; median segments occasionally with simple spinules near distal angle or in subsutural row on anterior third; few median segments each rarely with 6-10 rows of teeth and scales. Cirrus VI with 3-5 (4.0) pairs of setae on anterior margins of median segments. Basidorsal point of penis large, nude.

Color. — Shell white, pink, or pinkish purple with narrow to wide pink or red longitudinal stripes, occasionally yellowish or entirely white. Radii white or yellowish, with or without pink or red transverse or longitudinal

striae. Alae usually white, occasionally white with pink near sutural edges. Epicuticle yellowish. Sheath usually white or white with splotches of pink; color usually confined to alar and radial parts of compartments, stronger on carinal half. Scutum usually entirely white or white externally and white with pink near apex internally. Tergum usually white with upper part pink or pinkish-purple externally and internally, sometimes entirely white or white with traces of pink, occasionally pinkish-purple except for white ridges and spur.

Measurements. — Carinorostral diameter of holotype 34 mm, height 20.5 mm.

Variations. — Occasionally specimens with colorless shells have been noted; however, longitudinal striae are differentiated. These specimens also are thinner walled and the bases less firmly attached to the substrata than usually observed. Specimens on living sand dollars are more deeply colored that those on other substrata. Although the opercular valves are usually moderately wide, a few specimens have moderately narrow opercular valves. The degree of development of the pit for the lateral depressor muscle of the scutum varies considerably, as does the rugosity between the adductor ridge and the pit. Some specimens from all localities have a slight ridge, very occasionally two ridges basally between the adductor ridge and the pit for the lateral depressor muscle. Ross (1962) noted a secondary ridge in the scutum of specimens from the southwest coast of Baja California; the ridge in these specimens was longer, with the upper end between the adductor and articular ridges. In most small and also in unworn specimens, the upper part of the articular ridge of the tergum is more strongly reflexed toward the scutum.

Habitat. — Intertidal to 91 m, on living or dead sand dollars, mollusk shells, crustaceans, and rocks.

Remarks. — Darwin (1854) referred Recent material from three localities in the eastern Pacific to *B. concavus* and, with little or no description, additional specimens from the Philippines and Australia. Pilsbry (1916) included Darwin's Panamic (Darwin, 1854, pl. 4 fig. 4a-c) and Peruvian *B. concavus,* as well as his California specimens in the new subspecies *B. c. pacificus.* However, we have referred Darwin's Panamic specimens to *B. c. mexicanus* (see discussion of that species) and, herein, restrict the distribution of *B. c. pacificus* to California and the west coast of Baja California. The occurrence of this species in Tampa Bay, Florida, as recorded by Ross (1962), is doubtful; the material upon which this record was based has been lost (Ross, personal communication).

Pilsbry (1916) also distinguished form *brevicalcar* from typical *B. c. paci-*

ficus by the narrower opercular valves. More specifically, he cited the shorter adductor ridge which does not extend above the articular ridge, the tubular shaped lateral depressor muscle pit, and the shorter spur of the tergum as distinguishing characters of this form. As all of these specific characters also may be associated with wide opercular valves, the distinctness of this form can not be recognized.

Ross (1964) raised *B. c. pacificus* to specific rank and form *brevicalcar* to subspecific rank; for the latter taxon he designated the specimen represented by Pilsbry's (1916) plate 23 figures 2 and 2a as the lectotype of *B. pacificus brevicalcar*. Ross noted, however, that none of the remaining specimens in the type lot agreed with Pilsbry's description of the taxon. As previously indicated, all of Pilsbry's presumably diagnostic characters of this taxon are variable; therefore, we refer these specimens to *B. c. pacificus*. Because of the uncertain status of Darwin's (1854) Philippine, Peruvian, and Australian specimens of *B. concavus* and *B. concavus regalis* of Kolosváry (1940, 1942a, b; see remarks for *B. c. mexicanus*), we cannot agree with Ross (1964) that *B. c. pacificus* should be accorded specific rank at this time.

Results of the generalized distance function show that *B. c. pacificus* is most closely allied to *B. c. mexicanus* ($D^2 = 3.50$) and *B. suturaltus* ($D^2 = 12.30$). As previously indicated, three diagnostic characters of the *pallidus* group, which distinguish *B. suturaltus,* were not included in the statistical analyses. Consequently, the relationship between *B. c. pacificus* and *B. suturaltus* may be misleading. In determining interspecific relationships, a cluster, which includes *B. c. pacificus. B. c. mexicanus,* and *B. variegatus,* can be generated (D-2:1). However, such a cluster would exclude *B. reticulatus* and, therefore, has not been considered an adequate reflection of relationships.

B. c. pacificus can be differentiated from *B. c. mexicanus* by several characters not used in the statistical analyses, e.g., the color pattern of the shell, the summits of the radii, the color pattern of the opercular valves, stronger striae of the scutum, and by the more open lateral depressor muscle pit.

Balanus concavus mexicanus Henry (text-fig. 29, pl. 18 figs f-j)

Balanus concavus: Darwin, 1854: 235, pl. 4 fig. 4a-c (in part, see *B. c. pacificus*; not *Balanus concavus* Bronn, 1831: 127; 1838: 1155, pl. 36 fig. 12a-e).

Balanus concavus mexicanus Henry, 1941: 109, pl. 13 figs. 1-5 (type locality: Magdalena Bay, Baja California, Mexico). — Henry, 1960: 141, pl. 5 figs. a, e-h.

Holotype. — MCZ 11333.

Distribution. — Southwest Baja California, Mexico and Gulf of California to north Peru.

Material examined. — Table 17.

Diagnosis. — Shell with epicuticle not persistent; radii usually narrow, slightly sunken, summits oblique; sheath solid, lower margin overhanging; parietal tubes in single row, without transverse septa. Scutum with growth

Table 17. *Balanus concavus mexicanus*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
Baja California, west coast					
Santa Maria Bay	5	gastropods	---	7/3/34	---- USNM 128939
24°31'N, 111°59'W	3	gastropods	*B. trigonus*	2/5/88	*Albatross* USNM
Gulf of California					
10 m S., San Felipe	1	*Natica* sp.	---	2/49	---- USNM 182863
30°28'N, 113°06'30"W	5	*Natica* sp.	*B. improvisus*	14/3/89	*Albatross* USNM
Off Tiburon I.	2	*Natica* sp.	---	11/3/36	---- USNM 139772
Guaymas	~100	gastropods	---	1/59	Eyerdam USNM,RMNH
Mexico, west coast					
Mazatlan	1	*Macron* sp.	---	----	Eyerdam USNM
Mazatlan	1	gastropod	*B. trigonus*	11/5/62	Henry RMNH
Tangola Bay	2	gastropods	*B. trigonus*	28/2/34	---- USNM 128938
Costa Rica, Pacific coast					
Salinas Bay	3	gastropod	*B. trigonus*	11/12/35	---- USNM 131571
Culebra Bay	14	gastropods	*B. trigonus*	24/2/34	---- USNM 128938
Panama, Pacific coast					
Bay of Panama	58	gastropods	*B. trigonus*	1/62	Eyerdam USNM,RMNH
Cobbe Beach	7	---	---	2/62	Eyerdam USNM
Chorrero Beach	16	*Semele* sp.	---	1/62	Eyerdam USNM
Pedro Gonzales I.	1	*Strombus* sp.	*B. trigonus*	1943	Eyerdam USNM
Pedro Gonzales I.	1	*Pecten* sp.	*B. trigonus*	1/62	Eyerdam USNM
El Rey I.	9	mollusks	---	1943	Eyerdam USNM,RMNH
Ecuador					
Ballenita	45	*Murex* sp.	*B. trigonus*	3/5/66	McLaughlin USNM
Off La Libertad	3	*Turritella* sp.	---	19/1/33	---- USNM 122445
Off La Libertad	3	gastropods	---	9/2/34	---- USNM
Carnero Point	2	gorgonian	*B. improvisus*,*B. masignotus*,*B. trigonus*	9/5/63	Henry RMNH
Chanduy	17	gastropods	*B. trigonus*	5/5/66	McLaughlin RMNH
Posorja	5	gastropod	---	7/5/66	McLaughlin USNM
Peru					
04°51'S, 81°17'W	5	stick	---	6/66	McLaughlin USNM

ridges sometimes crenulate; basitergal angle obliquely truncate; longitudinal striae fine; articular ridge about 7/10 length of tergal margin; adductor ridge long, well separated from articular ridge; lateral depressor muscle pit bounded on occludent side by high ridge usually folded over. Tergum with spur furrow; spur length greater than spur width, distance from basiscutal angle to spur greater than spur width; basal margin straight on both sides of spur. Labrum simple. Cirri III-VI without erect teeth below posterodistal angles; cirrus III without modified setae; posterior cirri with 1 or 2 thick curved setae on posterodistal angles.

Description. — Shell cylindroconic; orifice toothed, width less than 1/2 carinorostral diameter; surface smooth unless ridged from replication of substratum; epicuticle not persistent. Radii usually narrow, slightly sunken, with fine transverse striae; summits oblique, thick, rough; sutural edges with septa strongly denticulate on lower margins. Alae with very oblique summits; sutural edges smooth. Sheath solid, lower margin overhanging. Inner lamina ribbed, usually only in lower part; ribs denticulate basally, usually finely ridged on sides near bases. Parietal tubes in single row, usually numerous, 12-41 (23) in rostrum; without transverse septa, filled up in upper 1/5-1/3. Inner surface of outer lamina sometimes with 1-4 fine ribs between longitudinal septa; 1 or 2 ribs occasionally denticulate at bases, almost reaching inner lamina. Basis with radial tubes and fine transverse septa, usually few near original point of attachment, occasionally extending almost to periphery; sometimes with vesicular layer below; sometimes lengthened.

Scutum often slightly concave between apex and basal margin; tergal segment narrowly inflected; basitergal angle obliquely truncate; occludent margin sharply toothed; growth ridges low, sometimes crenulate; longitudinal striae fine, approximate, sometimes absent. Inner surface finely ridged on upper part, sometimes spiculate or with 1 or 2 ridges medially; often with shallow excavation, occasionally finely spiculate, larger than adductor muscle pit, basally between adductor ridge and occludent margin; articular ridge high, slightly reflexed, about 7/10 length of tergal margin and about 2/5 length of occludent margin, end truncate; articular furrow narrow; adductor ridge high, acute, long, extending from above end of articular ridge almost to basal margin, without pit below, well separated from articular ridge by deep, moderately wide groove; adductor muscle pit shallow; lateral depressor muscle pit deep, bounded on occludent side by thin ridge usually folded over; rostral muscle pit small.

Tergum wide, apex curving toward and projecting slightly above scutum; scutal margin sharply denticulate; carinal margin slightly convex; growth

ridges fine, sometimes crenulate, not upturned along carinal margin; longitudinal striae occasionally present on carinal side, with 3 or 4 longitudinal ridges sometimes also near margin; spur furrow usually almost closed, open in small specimens; spur width about 1/4 length of basal margin; spur length about 1 7/10 spur width; distance from basiscutal angle to spur about 1 1/10 spur width, about 2/3 spur length, and about 1/4 length of basal margin; spur length about 2/5 length of basal margin; end obliquely truncate, usually denticulate on folded-over scutal side; basal margin straight on both sides of spur, occasionally finely crenulate on carinal side. Internally, scutal margin low; articular ridge long, low, reflexed; articular furrow narrow; crests for depressor muscle moderate, not projecting below basal margin; surface strongly ridged between articular ridge and carinal margin.

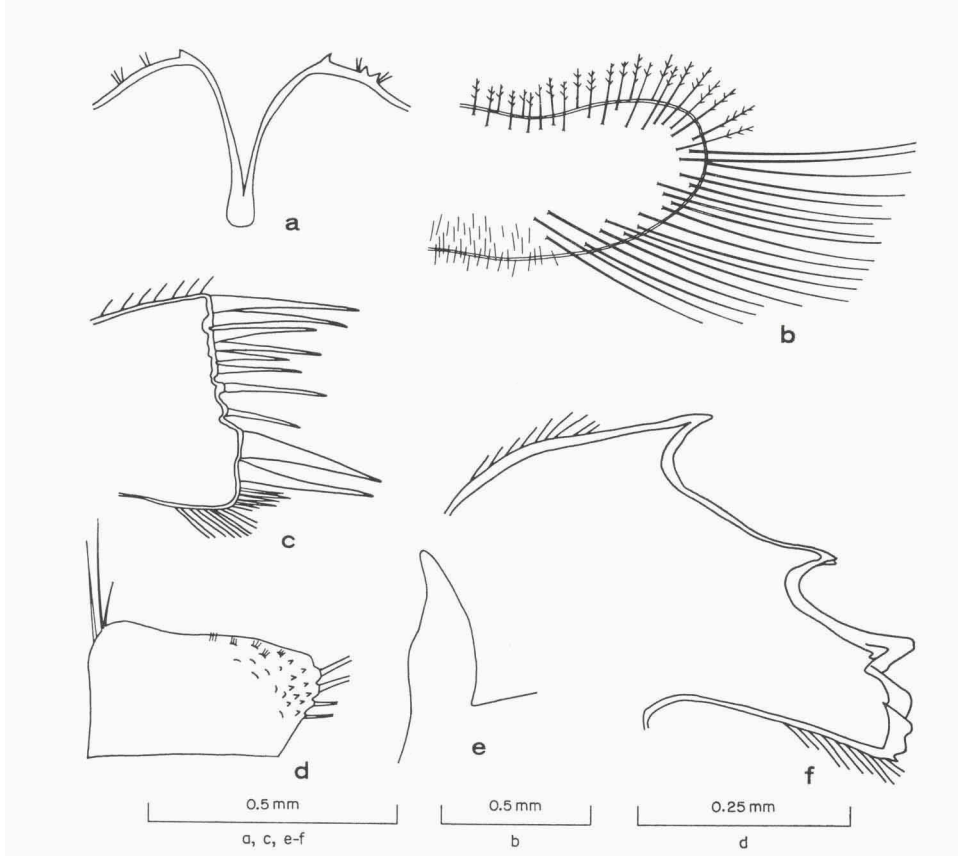

Fig. 29. *Balanus concavus mexicanus* Henry. a, labrum; b, palpus; c, 1st maxilla; d, fourth proximal segment of posterior ramus of cirrus III; e, basidorsal point; f, mandible (a-f, Bay of Panama).

Labrum with setulae and 0-3 (2.7) moderately large teeth on crest on each side of notch.

Palpus similar to that of *B. c. pacificus* except for long setae on outer face in 1 or 2 instead of 3 or 4 rows.

Mandible with 5 teeth; inferior angle not spinose; 2nd tooth bifid; 3rd-5th with extra denticles; 5th tooth confluent with inferior angle.

First maxilla usually with slight notch below upper pair of spines, 1 or 2 fine spines sometimes in notch, with short spine on outer face near lower spine of upper pair, 1-9 (5.3) spines between upper and lower pairs and tuft of fine spines on inferior angle; lower pair of spines on slight prominence.

Second maxilla without distinguishing characters.

Protopods of anterior cirri with primarily pinnate setae, some plumose setae posteriorly on coxopods; protopods of cirrus I each with narrow band of simple scales on outer face near anterior margin; protopods of cirri II and III each with wide band of simple scales on outer face near posterior margin.

Cirrus I with anterior ramus equal to or 1-6 (2.5) segments longer than posterior; posterior ramus with extremely protuberant segments; proximal segments of anterior ramus protuberant; distal sutures of both rami with long setae and few multifid spinules; several proximal segments each with narrow band of simple scales on outer face near posterior margin.

Cirrus II with anterior ramus 3 segments shorter to 2 (0.2) segments longer than posterior; both rami with very protuberant segments; distal sutures with long setae and multifid spinules; proximal segments each with wide band of simple scales on outer face near posterior margin; long proximal segments and several adjacent segments of anterior ramus with simple spinules on posterior margins.

Cirrus III with anterior ramus equal to or 1-7 (2.4) segments longer than posterior; both rami with slightly protuberant segments; distal sutures with multifid spinules and few short setae on few distal segments, remaining segments usually with stronger multifid and simple spinules near anterior margins and multifid spinules near posterior margins; median segments each sometimes with simple and multifid spinules on anterior half; posterior margins with short setae and spinules; inner faces without complex setae. Anterior margins usually with 1-5 conic teeth, occasionally with 5-15 small teeth, on proximal and median segments; distal segments rarely with 1 or 2 large teeth; occasionally without teeth. Outer faces near anterior margins usually with small conic teeth on proximal and median segments, occasionally also on distal segments, sometimes without teeth but with few simple and multifid spinules near distal angles on proximal, occasionally also on median seg-

ments; proximal and median segments each usually with 1-3 subsutural rows of simple, bifid, and multifid spinules and 2 or 3 rows of simple scales on anterior half, sometimes also with few teeth, occasionally with few multifid spinules near distal angle, occasionally also with few teeth near margin. Posterior margins with 2-6 short setae, fewer proximally, on distal angles; proximal segments with fine simple spinules. Outer faces near posterior margins of proximal segments each with narrow band of simple and spinulose scales. Inner faces near posterior margins of long proximal segments each occasionally with narrow band of simple spinules; several adjacent segments occasionally with few simple and multifid spinules near distal angles.

Protopods of posterior cirri each with 2 thick short setae on posterodistal angle and narrow band of simple spinules on inner face near posterior margin of basipods; coxopods each with 1 or 2 rows of simple scales near anterior margins on outer face; short thick setae on posterodistal angle, sometimes with fine simple spinules on posterior margin, and narrow band of simple scales on outer face near posterior margin; inner face with narrow band of simple and multifid spinules and spinulose scales near anterior margin, 1-6 short thick setae on distal suture and narrow band of conic teeth and simple spinules near posterior margin.

Posterior cirri with simple and multifid spinules on distal sutures and 1 or 2 relatively long setae and 3-5 shorter, much thinner setae on each posterodistal angle except on few proximal segments; long proximal and 1 or 2 adjacent segments of cirrus IV and 5-7 proximal segments of cirri V and VI usually with 1, occasionally 2, short, thick, slightly curved setae; outer faces near posterior margins of long proximal and several adjacent segments each occasionally with narrow band of simple scales; inner faces near posterior margins of long proximal segments each usually with narrow band of simple spinules, occasionally with adjacent narrow band of simple scales; several adjacent segments each usually with 5-7 simple spinules on distal suture, sometimes also with narrow band of simple scales. Anterior margins of anterior ramus of cirrus IV occasionally with small conic teeth on proximal and some median segments; outer faces sometimes with teeth; long proximal and 1 or 2 adjacent segments each usually without teeth or spinules, occasionally with few simple spinules near distal angle; remaining proximal and some median segments each usually with simple spinules in short subsutural row and in 2 or 3 rows near margin on distal third to half, sometimes with subsutural row of simple spinules, also few small teeth and denticulate scales on distal third to half, or 2-4 sparse rows of teeth and denticles close to margin, occasionally with subsutural row of small teeth and 2-8 rows of small teeth and denticulate

scales near margin; posterior ramus usually without spinules or teeth; proximal segments each sometimes with few simple spinules, occasionally with few small conic teeth near distal angle; proximal and median segments each occasionally with spinules below distal angle and subsutural row of simple spinules on anterior third to half. Cirrus VI with 2-5 (3.6) pairs of setae on anterior margins of median segments. Basidorsal point of penis large, usually narrow, nude.

Color. — Shell reddish purple or purple, only rarely with fine longitudinal stripes; stripes usually confined to apex; small specimens frequently rose or pink. Radii red or pink with lighter transverse striae. Alae white. Sheath usually white, occasionally white with radial parts of compartments pink. Scutum externally dark red or reddish purple, often with translucent spots opposite depressor and rostral muscle pits; occasionally white near apex or basal margin; internally red or reddish purple with white adductor and articular ridges, lateral depressor muscle pit and ridges. Tergum externally red, reddish purple, or pink except for white margins, spur, and spur furrow; internally red, reddish purple, or pink except for white carinal and basal margins, spur, and spur prominence; usually lighter colored than scutum.

Measurements. — Carinorostral diameter of holotype 22 mm, height 16 mm; carinorostral diameter of largest specimen examined 25 mm, height 20 mm (Ecuador).

Variations. — Although the color of the parietes of the specimens from Ecuador is dark, the opercular valves are paler than in the typical form. The longitudinal striae of the scuta are sometimes, especially in large specimens, stronger than in the typical form. The development of the spiculate or ridged inner surface of the scutum appears to be restricted to the Panamic specimens. Occasionally in very small specimens the pit for the lateral depressor muscle is long but not tubular.

Habitat. — Intertidal (?) or subtidal to 73 m, on mollusk shells, wood, and dead gorgonians.

Remarks. — Darwin's (1854) specimens of *B. concavus* from Panama are referred herein to *B. c. mexicanus*; however, the status of his Peruvian specimen is uncertain. It differs from *B. c. mexicanus* in the only characters mentioned by Darwin, i.e., the shell is white and rugged and the scutum is very strongly sculptured.

Kolosváry (1940: 106, fig. 1d-f) also recorded a specimen from Peru; he referred this specimen to *B. regalis* Pilsbry, which he reduced to a subspecies of *B. concavus,* presumably because of its ribbed parietes, as the opercular valves and internal parts were not known. The status of this

specimen likewise cannot be determined as he did not describe it and his figures are inadequate. The figure of the finely striated rostrum does not show the radii; those of the scutum indicate only that it is striated and that the adductor ridge is long. Subsequently, Kolosváry (1942a, b) referred specimens from Chile to *B. c. regalis*. These specimens differ greatly from *B. c. mexicanus*. The strongly ribbed shell is yellowish; the radii are wide with oblique summits; the scutum has a coarsely latticed structure and a short adductor ridge; the narrow tergum has a short spur close to the basiscutal angle and an open spur furrow. Kolosváry's taxon agrees in many characters with Nilsson-Cantell's (1932d) *B. c. indicus* from East Africa; however, it differs in the strongly ribbed parietes, the color of the shell, and the narrow tergum. As Kolosváry did not describe the parietal tubes nor the trophi and cirri, the status of his specimens, like Darwin's Peruvian specimens, cannot be determined, but must await a thorough review of the Recent taxa assigned to *B. concavus*. If Kolosváry's Chilean material proves to be a new taxon, it will require a new name, as Henry (1960) referred *B. regalis* to *B. aquila* Pilsbry as a subspecies.

As previously indicated, results of the statistical analyses indicate the close relationship between *B. c. mexicanus* and *B. c. pacificus* ($D^2 = 3.50$). This D^2 value is smaller than among any of the other taxa considered in the analyses; however, it is, with one exception, larger than the distances measured among the populations of *B. a. amphitrite*.

B. c. mexicanus can be differentiated from *B. c. pacificus* by several characters of the shell and opercular valves. The habitats of the two subspecies also appear to differ, as *B. c. mexicanus* rarely has been collected intertidally.

Balanus concavus sinensis Broch (pl. 19)

Balanus concavus forma *sinensis* Broch, 1931 : 63, fig. 23a-f (type locality : Hong Kong).

Holotype. — Deposition unknown.

Distribution. — Known only from type locality.

Material examined. — None.

Diagnosis. — Shell with radii very narrow, almost rudimentary, summits extremely oblique. Scutum with growth ridges crenulate; longitudinal striae fine; articular ridge about 1/2 length of tergal margin; adductor ridge long, well separated from articular ridge. Tergum with spur furrow; spur length about twice width, distance from basiscutal angle to spur slightly greater than spur width; basal margin straight on both sides of spur. Labrum simple.

Description. — Shell conic; orifice distinctly toothed; surface smooth. Radii extremely narrow, almost rudimentary; summits very oblique. Alae

well developed; summits somewhat oblique, smooth. Inner lamina ribbed, with 2 or 3 very distinct, longitudinal white striae between ribs; some striae terminating in denticle basally. Parietal tubes moderately large, up to 14 in rostrum; without transverse septa, not filled up near apex.

Scutum with basitergal angle rounded; occludent margin toothed; growth ridges low; longitudinal striae fine, approximate. Inner surface smooth; articular ridge low, reflexed, about 1/2 length of tergal margin, end truncate; adductor ridge high, long, extending from above end of articular ridge nearly to basal margin, well separated from articular ridge; adductor muscle pit deep; lateral depressor muscle pit large, deep.

Tergum wide; growth ridges very low; longitudinal striae present on carinal side; spur furrow deep, narrow, usually almost closed; spur width about 1/5 length of basal margin; spur length about twice spur width; distance from basiscutal angle to spur slightly greater than spur width; end obliquely rounded; basal margin straight on both sides of spur. Internally, scutal margin inflected; articular ridge low; crests for depressor muscle prominent, not projecting below basal margin.

Labrum with 3 teeth on crest on each side of deep notch.

Mandible with 3 strong and 2 small teeth; 2nd tooth bifid, 4th and 5th with extra denticles; 5th confluent with inferior angle.

First maxilla without notch below upper pair of spines, with 7 or 8 spines between upper and lower pairs, few fine spines on inferior angle; lower pair of spines on slight prominence close to inferior angle.

Cirrus I with anterior ramus 4 segments longer than posterior. Armature of cirri like subspecies *pacificus* except for fewer teeth on anterior ramus of cirrus III. Penis with well developed basidorsal point.

Color. — Shell white with brown or lilac longitudinal stripes, sometimes also with transverse striations producing spotted appearance. Color of radii, alae, sheath, and opercular valves not stated.

Measurements. — Carinorostral diameter of largest specimen 16 mm.

Variations. — Unknown.

Habitat. — Unknown.

Remarks. — *B. c. sinensis* is distinguished from other Recent subspecies of *B. concavus* by the extremely narrow radii with very oblique summits and by the parietal tubes not being filled up at the apex. The presence of striae and denticles on the inner lamina of the wall may indicate affinities with the *variegatus* subgroup. Darwin (1854) recorded *B. concavus* from two localities in the western Pacific, i.e., Australia, without any description, and a single specimen from the Philippine Archipelago. The status of these specimens is uncertain. The latter specimen differs from *B. c. sinensis*

in the strong sculpturing and the less prominent adductor ridge of the scutum and in the wider of the tergum. It also appears to differ from the other known subspecies of *B. concavus,* and is the largest specimen of this species recorded by Darwin, having a diameter of 31 mm.

Balanus concavus indicus Nilsson-Cantell (pl. 20)

Balanus concavus indicus Nilsson-Cantell, 1932d: 2, fig. 1a-i, pl. 1 fig. 1 (type locality: Dar-es-Salaam, Tanzania).

Holotype. — Deposition unknown.

Distribution. — Known only from type locality.

Material examined. — None.

Diagnosis. — Shell with radii wide, summits moderately oblique; parietal tubes in single row, without transverse septa. Scutum with growth ridges coarsely crenulate; longitudinal striae strong; articular ridge slightly greater than 1/2 length of tergal margin; adductor ridge short, close to but not confluent with articular ridge. Tergum with open spur furrow; spur length about twice width, distance from basiscutal angle to spur equal to spur width; basal margin slightly concave on scutal side of spur, straight on carinal side. Labrum simple.

Description. — Shell conic; orifice rhomboidal, moderately wide; surface smooth. Radii wide; summits moderately oblique. Parietal tubes without transverse septa. Basis with radial tubes and transverse septa; lengthened in part.

Scutum with narrowly inflected tergal segment; basitergal angle obliquely truncate; occludent margin strongly toothed; growth lines well defined; longitudinal striae strong, fewer than in *B. c. pacificus.* Inner surface strongly ridged on upper part; articular ridge high, reflexed, slightly greater than 1/2 length of tergal margin, end truncate; adductor ridge very low, short, close to but not confluent with articular ridge; adductor muscle pit distinct; lateral depressor muscle pit small; basal margin crenulate.

Tergum wide; apex curving toward scutum; longitudinal striae present on carinal side; spur furrow open; spur width about 1/5 length of basal margin; spur length about twice spur width; distance from basiscutal angle to spur about equal to spur width; end rounded; basal margin slightly concave on scutal side of spur, straight on carinal side. Internally, scutal margin low; articular ridge low; crests for depressor muscle moderately well developed, not projecting below basal margin.

Labrum with setulae and 3 small teeth on crest on each side of notch.

Mandible with 5 teeth and spinose inferior angle; 2nd-4th teeth with extra denticles.

First maxilla with 1 or 2 fine spines in slight notch below upper pair of spines, 5 spines between upper and lower pairs of spines, few fine spines on inferior angle; lower pair of spines on slight prominence.

Second maxilla without distinguishing characters.

Cirrus I with anterior ramus 4 segments longer than posterior; segments not as protuberant as in *B. c. pacificus*

Cirrus II with anterior ramus 2 segments longer than posterior; segments not as protuberant as in *B. c. pacificus.*

Cirrus III with anterior ramus 2 segments longer than posterior; anterior ramus with strong decurved teeth on anterior margin.

Posterior cirri with 4 pairs of setae on anterior margins.

Color. — Shell reddish white with violet longitudinal stripes. Radii white or colored. Color of alae, sheath, and opercular valves not given.

Measurements. — Carinorostral diameter of holotype 12 mm, height 15 mm.

Variations. — Known from single specimen.

Habitat. — On buoy.

Remarks. — This subspecies is distinguished from other Recent subspecies of *B. concavus* by the weak and short adductor ridge of the scutum; the sculpturing on the external surface of the scutum appears to be stronger; the spur is closer to, rather than its own width or greater from, the basiscutal angle of the tergum. *B. c. indicus* resembles Kolosváry's (1942a, b) *B. concavus regalis* from Chile in these characters except that in the latter, the short adductor ridge of the scutum is strong.

Balanus venustus Darwin (text-fig. 30, pl. 21 figs a-f)

Balanus amphitrite var. *venustus* Darwin, 1854: 240, pl. 5 fig. 2a (in part, see remarks; type locality by subsequent designation by Harding, 1962: 283: Natal, Republic of South Africa). — Stubbings, 1961: 29. — Stubbings, 1963b: 21.

Balanus amphitrite var. *niveus* Darwin, 1854: 240, pl. 5 fig. 2f.

Balanus amphitrite var. *modestus* Darwin, 1854: 240.

Balanus amphitrite var. *obscurus* Darwin, 1854: 241, pl. 5 fig. 2g.

[Bastard] *Balanus armatus* and *Balanus improvisus* var. *assimilis*: Müller, 1867: 348, pl. 7 figs. 29-31, 33-43, pl. 8 figs. 45, 49. — Müller, 1868: 406, pl. 20 figs. 4-6, 8, 11-13, 18, 20, 23.

Balanus amphitrite niveus: Pilsbry, 1916: 92, figs. 19a-f, 20a-e, 21a-c, 22, pl. 19 figs. 1-2e. — Nilsson-Cantell, 1921: 318. — Nilsson-Cantell, 1925: 31. — Nilsson-Cantell, 1928: 33. — Nilsson-Cantell, 1939: 4. — Pilsbry, 1953: 25. — Henry, 1959: 192, pl. 3 fig. 7, upper row, left.

Balanus tintinnabulum forma *maroccana* Broch, 1927b: 21, pl. 1 figs. 4-6, pl. 2 figs. 7, 8.

Balanus amphitrite inexpectatus: Nilsson-Cantell, 1933: 506, fig. 2a-g (not *Balanus amphitrite inexpectatus* Pilsbry, 1916: 97).

Balanus amphitrite venustus: Nilsson-Cantell, 1938: 37 (in part; not fig. 8a, b; see *B. variegatus*). — Daniel, 1956: 21, pl. 5 figs. 1-6.

Balanus amphitrite var. *denticulata*: Stubbings, 1961: 23, fig. 4a, b (in part; not fig. 4c, d; see *B. a. amphitrite* and *B. improvisus).*
Balanus amphitrite var. *stutsburi*: Stubbings, 1961: 24, fig. 5 (in part; see *B. pallidus*).
Balanus venustus venustus:Harding, 1962: 283, pl. 6 figs. a-p. — Stubbings, 1965: 887, figs. 2c, 3a-f. — Stubbings, 1967: 280, fig. 17a-f. — Utinomi, 1970: 355, pl. 18 fig. 11.
Balanus venustus niveus: Harding, 1962: 286, pl. 7 figs. a-r. — Zullo, 1963: 12, figs. 47-52. — Stubbings, 1964b: 340. — Zullo, 1966: 232, fig. 3a, b.
Balanus venustus modestus: Harding, 1962: 287, pl. 8 figs. a-p.
Balanus venustus obscurus: Harding, 1962: 289, pl. 9 figs. a-q.
not *Balanus amphitrite* var. *niveus*: Krüger, 1911: 51, figs. 102-104, pl. 4 fig. 35a-b_2 (= *B. kondakovi*). — Oliveira, 1941: 19, pl. 3 figs. 3-6, pl. 4 figs. 2, 7 (see *B. citerosum* and *B. eburneus*).
not *Balanus amphitrite venustus*: Nilsson-Cantell, 1925: 28, fig. 11a-h, pl. 1 fig. 3 (= *B. pallidus*). — Sundra Raj, 1927: 113, pl. 12 figs. 1-8 (= *B. a. amphitrite*).
not *Balanus amphitrite* var. *venustus*: Karande & Palekar, 1966: 145, fig. 13, pl. 2 fig. 9, pl. 4 row 7 (= *B. pallidus*).

Lectotype. — BM 1961. 12.2.24a, b, c by subsequent selection by Harding, 1962: 283.

Distribution. — Southeast Africa and Madagascar to Persian Gulf; east coast of India; southwest Europe to Cape of Good Hope; northeast United States to Brazil; Japan (Utinomi, 1970).

Material examined. — Table 18.

Diagnosis. — Shell with epicuticle sometimes persistent; parieties rarely ribbed; radii moderate to wide, summits thick, rough; sheath solid, lower margin overhanging; parietal tubes in single row, usually without transverse septa. Scutum usually flat except for narrowly inflected tergal segment, sometimes with recurved apex; basitergal angle obliquely truncate; longitudinal striae sometimes absent; articular ridge about 3/4 length of tergal margin; adductor ridge long, well separated from articular ridge. Tergum with carinal margin convex, narrowly protuberant in upper 1/3 to 1/2; with spur fasciole; spur length about 4/5 width; distance from basiscutal angle to spur about 1/2 spur width; basal margin sloping to spur or straight on scutal side of spur, slightly concave or straight on carinal side. Labrum simple. Cirrus III with erect teeth or simple spinules below posterodistal angles, without complex setae; posterior cirri with simple spinules below posterodistal angles.

Description. — Shell usually conic, sometimes cylindric or subcylindric, occasionally cylindroconic; orifice toothed, width usually equal to or more than 1/2 carinorostral diameter; surface usually smooth unless ridged from replication of substratum, very occasionally ribbed; epicuticle thin, sometimes persistent. Radii moderately wide or wide, sometimes with fine longitudinal striae, occasionally with fine transverse striae; summits moderately oblique or oblique, thick, rough; sutural edges with septa strongly denticulate on lower

Table 18. *Balanus venustus*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
Morocco					
----	5	---	---	----	Broch/Zullo USNM
Republic of South Africa					
Bay of Natal	11	bamboo	*B. a. amphitrite*	----	Krause RMNH 296
Salisbury I.	1	---	*B. a. amphitrite*	27/10/38	Brongersma RMNH 1130
Virginia					
Cape Henry	3	test plate	---	1/59	---- USNM 54833
Core Banks	100	mollusks	*B. calidus*	3/4/61	Wells USNM,RMNH
Beaufort	2	---	---	----	---- USNM 79253
Wilmington	1	test block	---	8/7/41	Clapp USNM
South Carolina					
Sullivans I.	1	jetty	*B. eburneus, Ch. fragilis*	31/12/52	Yentsch USNM
Florida, east coast					
Daytona Beach	1	test block	---	4/2/42	Clapp USNM
Daytona Beach	1	test block	*B. improvisus*	5/3/42	Clapp USNM
Florida, west coast					
Dry Tortugas	5	---	---	4/8/58	---- USNM
----	6	whistle buoy	*B. eburneus, B. improvisus*	26/6/52	Yentsch USNM
Fish Hawk sta. 7108	4	---	---	----	---- USNM 51537
Sanibel I.	1	gastropod	---	1/1/13	---- USNM 59597
Marco I.	13	*Strombus* sp.	---	----	Hemphill USNM 6950
Tampa Bay	3	pier	---	27/9/52	Yentsch USNM
Tampa Bay	1	boat	*B. a. amphitrite, B. eburneus*	29/12/52	Yentsch USNM
Tampa Bay	1	portunid	---	1901-02	---- USNM 25579
Boca Ciega Bay	3	---	---	3/1/84	---- USNM 6481
Boca Ciega Bay	1	gastropod	*B. eburneus*	3/11/55	---- USNM 209649
Boca Ciega Bay	9	glass	*B. eburneus*	4/11/55	---- USNM 209649
Boca Ciega Bay	3	pelecypods	---	16/11/55	---- USNM 209649
Boca Ciega Bay	8	pelecypods	---	18/11/55	---- USNM 209649
Cedar Keys	20	gastropods	---	12/83	---- USNM 13910
Cedar Keys	5	*C. patula*	---	27/10/49	---- USNM 184533
St. Teresa	12	*Caretta* sp.	---	23/4/64	Wells USNM
Alligator Harbor	83	mollusks	*B. eburneus*	----	Yentsch USNM,RMNH
Alligator Harbor	7	*Venus* sp.	---	1961	Kohn USNM
Panama City	7	jetty	*B. a. amphitrite*	6/11/64	Wells USNM

Table 18 (Continued). *Balanus venustus*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
Texas					
Heald Bank	2	---	---	-----	----- USNM 54833
Mexico, southeast coast					
Campeche Bay	54	*Busycon* sp.	*C. patula*	6/62	Eyerdam USNM, RMNH
Panama, Caribbean coast					
Galeta	6	*Pteria* sp.	*B. t. antillensis, B. trigonus, Newmanella radiata*	16/8/71	Birkeland USNM
Trinidad					
NE end of island	∿50	gastropods	---	18/2/71	Theunissen RMNH 1251
Venezuela					
Off Coche I.	52	gastropods	*B. trigonus*	15/4/39	----- USNM 85011
Brazil					
Off Patros I.	3	---	*B. spongicola*	-----	----- USNM 14144
Itajai, Santa Catarina	8	gastropods	---	-----	----- USNM 59097

margins. Alae with moderately oblique or oblique summits; sutural edges finely septae. Sheath solid, lower margin overhanging. Inner lamina weakly ribbed, usually to sheath; ribs denticulate basally, occasionally finely ridged on sides near bases. Parietal tubes in single row, variable in size and shape, 11-15 (12.5) in rostrum, usually without transverse septa, filled up in upper 1/3-1/2, sometimes with fine approximate transverse septa in upper 1/5-1/4. Inner surfaces of outer lamina sometimes with 1-5 fine ribs between longitudinal septa; 1 or 2 occasionally stronger, denticulate at bases, almost reaching inner lamina. Basis with radial tubes and transverse septa near original point of attachment.

Scutum sometimes with slightly recurved apex; tergal segment narrowly inflected; basitergal angle obliquely truncate; basal margin sometimes excavated close to basitergal angle; occludent margin weakly toothed; growth ridges low; longitudinal striae fine, sometimes absent. Inner surface usually slightly roughened on upper part; articular ridge high, slightly reflexed, about 3/4 length of tergal margin and 1/2 length of occludent margin, end usually obliquely truncate, sometimes truncate; articular furrow moderately deep; adductor ridge high, long, extending slightly above end of articular ridge, with pit below sometimes bounded on tergal side by weak ridge, well separated from articular ridge; adductor muscle pit deep; lateral depressor muscle pit small, deep; small rostral pit sometimes present.

Tergum with scutal margin prominently raised, occasionally finely denticulate; carinal margin convex, narrowly protuberant on upper third to half; growth ridges fine, stronger on protuberance; longitudinal striae absent; spur fasciole usually separated from scutal side and occasionally also from carinal side by narrow groove; spur width about 3/10 length of basal margin; spur length about 4/5 spur width; distance from basiscutal angle to spur about 1/2 spur width, about 1/2 spur length, and about 1/10 length of basal margin; spur length about 1/4 length of basal margin; end usually obliquely truncate, occasionally rounded; basal margin usually sloping slightly to spur, sometimes straight on scutal side, usually slightly concave, occasionally straight on carinal side. Internally, scutal margin low; articular ridge low, not reflexed; articular furrow rather wide and deep; crests for depressor muscle strong, usually numerous, projecting below basal margin; surface sometimes roughened on upper part, basally usually finely denticulate medially.

Labrum with 0-3 (2.9) teeth on crest on each side of notch; 1 tooth on each side usually on edge of notch near crest; sometimes setulose.

Palpus with very finely pinnate short setae on upper margin and setulae on distal third to half of lower margin; outer face with narrow band of short simple setae along upper margin, long setae on distal margin and in oblique row near inferodistal angle; setulae in tuft near inferodistal angle and in double row on proximal three-fourths near lower margin; labral face with band of strongly pinnate short setae along upper margin on mediodistal third abruptly narrowing to few rows proximally; fine denticulate scales on upper half of distal third; setulae on lower half of distal third and in narrow band along lower margin on distal two-thirds.

Mandible with 5 or 6 (5.1) teeth; inferior angle not spinulose; 1st tooth usually with denticle near tip, occasionally bifid; 3rd-6th with extra denticles; 5th tooth usually close to but not confluent with inferior angle, 6th tooth, if present, confluent.

First maxilla without notch below upper pair of spines, with 3-7 (4.6) spines between upper and lower pairs and few fine spines on inferior angle; lower pair close to inferior angle, occasionally on slight prominence.

Second maxilla without distinguishing characters.

Protopods of anterior cirri with primarily pinnate setae, some plumose setae posteriorly; protopod of cirrus I with narrow band of simple scales near anterior margin, sometimes also spinulose scales near posterodistal angle on outer face; both segments of cirri II and III each with narrow band of simple scales near posterior margin, sometimes with simple spinules near anterodistal angle, on outer face.

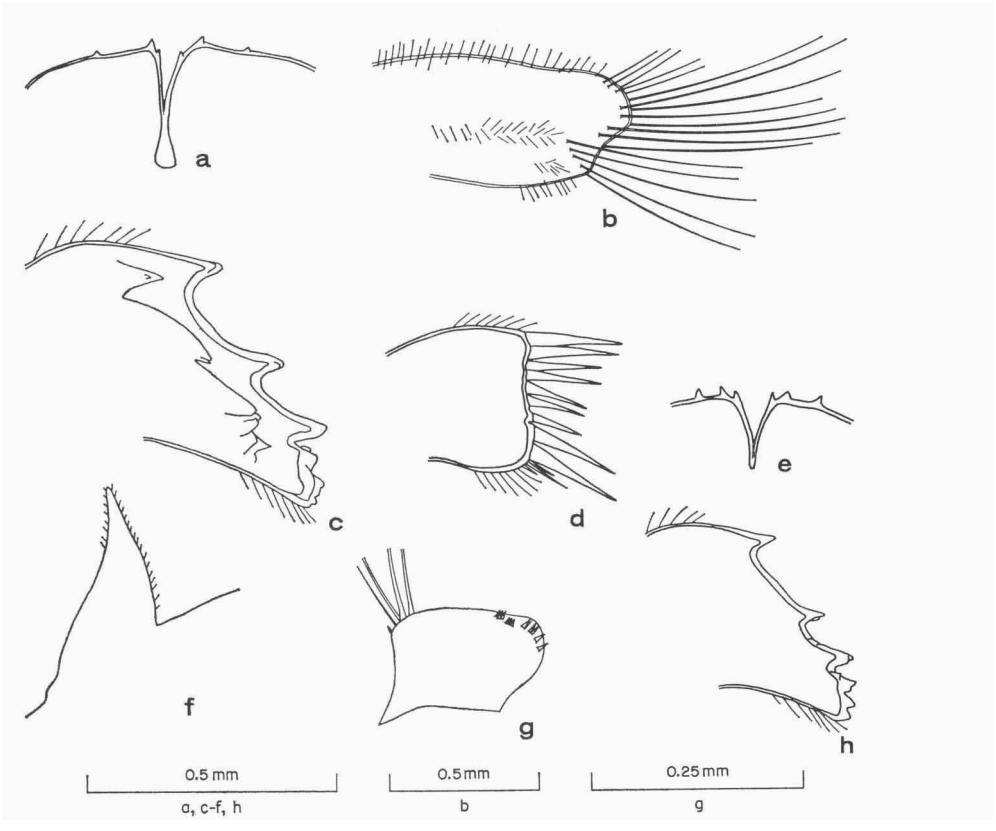

Fig. 30. *Balanus venustus* Darwin. a, e, labra; b, palpus; c, h, mandibles; d, 1st maxilla; f, basidorsal point; g, sixth distal segment of anterior ramus of cirrus III [a-d, g, Coche Island, Venezuela; e, h, Campeche, Mexico (different specimens); f, Alligator Harbor, Florida].

Cirrus I with anterior ramus 2-9 (5.3) segments longer than posterior; posterior ramus with very protuberant segments; proximal segments of anterior ramus protuberant; distal sutures of both rami with long setae and with multifid spinules generally near posterior margins on median and proximal segments; long proximal segments each with narrow band of simple scales on outer face near posterior margin; 2 or 3 adjacent segments of posterior ramus each sometimes with multifid spinules on outer face near posterodistal angle.

Cirrus II with anterior ramus 1 segment shorter to 3 (1.4) segments longer than posterior; both rami with moderately protuberant segments; distal sutures with long setae and with multifid spinules generally near anterior and posterior margins proximally; long proximal segments eacs usually with narrow band of simple scales on outer face near posterior margin.

Cirrus III with anterior ramus 1 segment shorter to 4 (2.2) segments longer than posterior; both rami with slightly protuberant segments; distal sutures usually with multifid and simple spinules near posterior angles on 1 or 2 distal segments and multifid spinules on few distal segments, also usually with multifid and simple spinules near anterior margins and multifid spinules near posterior margins on remaining segments; outer faces near anterior margins with conic teeth and denticles; posterior margins with short setae; inner faces without complex setae. Anterior margins of proximal segments of anterior ramus sometimes with small conic teeth; posterior ramus without teeth. Outer faces near anterior margins of proximal segments each with 1-3 large teeth and several large spinules near distal angle, usually also with 2-8 rows of small teeth or denticles, occasionally without large teeth and spinules near angle, but with 4-8 rows of small teeth near anterior margin; median segments each usually with 1 or 2 large teeth and several large simple or bifid spinules near distal angles, sometimes without teeth, occasionally without teeth or spinules. Posterior margins with tuft of short setae on distal angles on all but few proximal segments; anterior ramus usually with 2 or 3 large simple spinules or erect teeth, occasionally with 1-3 fine simple spinules below each distal angle on few proximal segments; long proximal segment also with series of simple spinules; long proximal and 1 or 2 adjacent segments of posterior ramus each usually with 1-3 fine simple spinules below distal angle, occasionally without spinules. Inner faces near posterior margins of few proximal segments of anterior ramus sometimes with 1-3 large subsutural spinules, occasionally with 3-6 large spinules or teeth in subsutural row; long proximal segment sometimes also with 3 or 4 rows of fine simple spinules or 2 or 3 rows of small conic teeth; long proximal and 1 or 2 adjacent segments of posterior ramus each sometimes with 3 or 4 subsutural fine simple spinules.

Protopods of posterior cirri each with narrow band of simple spinules on inner face near anterior and posterior margins, occasionally with narrow band of simple scales on outer face near posterior margin; coxopods each with subsutural row of 4-8 fine short setae and 4-8 large, simple spinules on inner face near posterior margin.

Posterior cirri without spinules on distal sutures of cirri V and VI; anterior, sometimes also posterior ramus of cirrus IV with simple and multifid spinules on distal sutures near anterior margins; posterior margins with tufts of short setae on distal angles, usually with 2 or 3 small or large simple spinules below setae on some proximal segments; long proximal and 2 or 3 adjacent segments of cirrus IV each usually with 2 small simple spinules below distal angle, sometimes with 2 large simple spinules; long

proximal and 5-7 adjacent segments of cirri V and VI sometimes with 2 or 3 spinules below distal angles; outer faces near posterior margins of cirrus IV sometimes with 2 or 3 rows of simple spinules on each long proximal segment; proximal and median segments each occasionally with 2 or 3 rows of denticles and denticulate scales; anterior ramus sometimes with 2 subsutural large simple spinules or 2 or 3 subsutural erect teeth on few proximal segments; 5-7 adjacent segments of cirri V and VI each usually with 2 or 3 subsutural erect teeth, occasionally with 2 or 3 subsutural, large simple spinules. Anterior margins of anterior ramus of cirrus IV with small conic teeth on proximal and median segments, occasionally without teeth; posterior ramus without teeth. Outer faces near anterior margins of anterior ramus of cirrus IV with conic teeth on proximal segments, sometimes also on median segments, occasionally without teeth; proximal segments each usually with 1-3 large teeth near distal angle and 2-6 rows of small teeth and denticles, sometimes with only 1-3 teeth near each distal angle, occasionally also with few denticles; median segments each usually with 1-3 small teeth near distal angle, sometimes also with 2-6 rows of smaller teeth, denticles, and denticulate scales; posterior ramus usually without teeth, occasionally with few small teeth near distal angles on proximal segments, or 3 or 4 rows of denticles on proximal and median segments. Cirrus VI with 3-7 (4.9) pairs of setae on anterior margins of median segments. Basidorsal point of penis long, narrow, spinulose.

Color. — Shell usually white or colored with narrow, approximate, longitudinal, colored or hyaline stripes; stripes sometimes faint or confluent on some or all parietes; sometimes white above and colored, with or without stripes, below or vice-versa; occasionally entirely white. Ground color pale pink or bluish gray; stripes pink, reddish purple, lavender, red, or dark gray. Radii white, colored like parietes, or with one or two colored stripes near parietes. Alae white. Epicuticle pale yellow. Sheath usually entirely white, occasionally bluish near lower margin or pinkish or purplish in middle of carina. Inner lamina usually white, occasionally bluish. Scutum usually white with some color on outer surface; sometimes colored except for narrow white band on tergal or basal margins; occasionally entirely white. Inner surface usually white with some color; sometimes entirely white; occasionally colored except for white apex and narrow white band on tergal and basal margins. Tergum usually white on outer and inner surfaces; sometimes white with small or large splotches of color on carinal side; very occasionally with color on carinal side except for narrow white band on tergal and basal margins. Color of opercular valves usually pink, sometimes pinkish or reddish purple.

Measurements. — Greatest diameter of lectotype 8.9 mm, of paralectotype 14.8 mm. Carinorostral diameter of largest specimens recorded 20 mm (Bombay, Karande & Palekar, 1966); 16 mm (West Africa, Stubbings, 1965).

Variations. — In addition to the variations noted in the description, the color pattern of the opercular valves varies considerably. Specimens with white shells and hyaline or pale colored stripes appear to be commoner on the southeast coast of the United States and in certain localities in the Gulf of Mexico, i.e., Boca Ciega and Alligator Bays, Florida; pink or bluish shells with dark stripes are more frequent in Campeche Bay and Venezuela. However, all of the recorded color patterns occur in the latter localities. Color patterns of 25 specimens on a gastropod shell from Venezuela vary from white, pink, or bluish gray with hyaline, pink, lavender, or reddish purple stripes to white above and colored below or colored above and white below. As pointed out by Pilsbry (1916) and Stubbings (1967), there is no relationship between the color of the shell and that of the opercular valves. Stubbings (1965, 1967) also noted considerable variation in color in his West African specimens.

Habitat. — Usually subtidal to 62 m, on mollusk shells, crustaceans, gorgonians, and polychaete tubes; very occasionally lowest intertidal zone on harbor installations.

Remarks. — Harding (1962) raised Darwin's (1854) var. *venustus* to specific rank, with the varieties, *niveus, modestus,* and *obscurus* as subspecies. Darwin had differentiated these varieties by the color pattern of the shells, only adding for *venustus* that the carinal half of the basal margin of the tergum is sometimes much hollowed out and for *niveus* that the epidermis is not persistent (Darwin, 1854: 240). Although Harding (1962) described and figured the opercular valves, trophi, and cirri, he also was unable to differentiate these taxa by any other characters than the color pattern. We have shown that the color pattern is highly variable in specimens from one locality or even on one gastropod shell; therefore, we believe that Darwin's (1854) varieties, *niveus, modestus,* and *obscurus* are synonymous with *B. venustus.* The distribution of these taxa in what remains of Darwin's type material also corroborates this belief. Harding (1962) designated the following type localities: Natal for *venustus,* Madagascar for *niveus,* and the West Indies for *obscurus*; he inferred that *modestus* was also from the West Indies or the Gulf coast of the United States from the distribution of the gastropod on which the specimens had settled. The type material also included specimens of *venustus* from West Africa and Ceylon, *niveus* from the West Indies and Portugal; Darwin also listed Florida, South Africa,

the Mediterranean, and the Red Sea for the latter taxon. Harding (1962: 228) noted that some specimens of *B. v. niveus* were on the gasropod shell with *B. v. modestus.*

As previously mentioned, Darwin (1854) described the tergum of *venustus* as hollowed out on the carinal half of the basal margin. Harding (1962: 285) described the tergum as "... the carinal half of the valve is less developed than the scutal half so that the carinal edge is very much shorter than the scutal edge, or in Darwin's words, 'The carinal half of the basal margin is much hollowed out". Harding's figures (pl. 6 figs. f, g; pl. 7 figs. d, e; pl. 8 figs. f, g; pl. 9 figs. e, f), however, show that the basal margin is straight or only slightly concave on the carinal side. It would appear that Harding misinterpreted Darwin's phrase "hollowed out". Darwin's use of this phrase also strongly suggests that he confounded two taxa under the name *venustus,* and perhaps explains the reason that Nilsson-Cantell (1925) referred specimens of *B. pallidus* to *B. a. venustus* (cf. Stubbings, 1967).

Pilsbry (1916) considered both Müller's (1867) hybrid species and his *B. improvisus* var. *assimilis* synonymous with *B. a. niveus.* We concur with his judgement regarding the "hybrid" of *B. armatus-B. improvisus* var. *assimilis*; however, Müller's description clearly indicates that *B. improvisus* var. *assimilis* (sensu stricto) should be referred to *B. improvisus.*

Broch (1927b) named a new forma, *B. tintinnabulum maroccana,* for small specimens (greatest diameter, 13 mm), colored like *B. tintinnabulum,* but with markedly different opercular valves. As we have been able to reexamine some of this material, we herein refer Broch's (1927b) *B. t. maroccana* to *B. venustus.* The radii lack tubes, the scutum has a long high adductor ridge, and the tergum has a wide spur, close to the basiscutal angle, and a spur fasciole.

Other taxa which are referred to *B. venustus,* at least in part, are the *B. a. inexpectatus* of Nilsson-Cantell (1933), and the *B. a. denticulata* and *B. a.* var. *stutsburi* of Stubbings (1961). The characters noted by Nilsson-Cantell for his specimens from the Caribbean agree with those of *B. venustus* from that area; *B. inexpectatus* is restricted to the eastern Pacific. Stubbings (1961, fig. 4a, b) tentatively assigned some specimens with a simple labrum to *B. a.* var. *denticulata.* The description of the shell and the opercular valves clearly indicate that these specimens should be referred to *B. venustus.* He also tentatively referred small specimens from another locality to *B. a.* var. *stutsburi.* The tergum (Stubbings, 1961, fig. 5) does not agree with that of *B. pallidus*; however, both the tergum and the color pattern of the shells do agree with *B. venustus.*

Nilsson-Cantell (1938) assigned some rose colored specimens from the

Gulf of Mannar to *B. a. venustus*. However, the short articular ridge of the scutum and several characters of the tergum shown in the figures of the opercular valves (Nilsson-Cantell, 1938, fig. 8a, b) indicate that this specimen should be referred to *B. variegatus*. Previously, Nilsson-Cantell (1925) assigned specimens from West Africa to *B. a. venustus*. We concur with Stubbings (1967), who referred these specimens to *B. pallidus*, but we do not agree, as indicated above, with his retention of Nilsson-Cantell's (1938) figures of the opercular valves in *B. venustus*. Karande & Palekar (1966) accepted Nilsson-Cantell's interpretation of *B. a. venustus* and their specimens of this taxon are also referrable to *B. pallidus*.

Utinomi's (1970) record of *B. venustus* from two localities on the Japan Sea coast is the first authentic record of this species in Japan. Weltner's (1897) record from Nagasaki has never been confirmed.

Results of the statistical analyses indicate that *B. venustus* is most closely allied to *B. inexpectatus* ($D^2 = 8.31$). In general morphology, *B. venustus* is also closely allied to *B. poecilotheca*; however, the latter species was not available in sufficient numbers to be included in the analyses.

B. venustus can be distinguished from *B. inexpectatus* both statistically and through characters not considered in the analyses. Both the alae and radii are oblique in *B. venustus*, whereas in *B. inexpectatus* only the radii are oblique. Consequently, the orifice is entire instead of toothed as in *B. venustus*. The scutum of *B. venustus* usually has longitudinal striae; the adductor ridge is farther from the articular ridge; cirrus III lacks complex setae; and cirri IV-VI lack erect teeth below the posterodistal angles. The habitat and distribution are also different. *B. venustus* is mainly found subtidally, *B. inexpectatus* intertidally. *B. venustus* occurs on both sides of the Atlantic, and in the Indian Ocean and the western Pacific; whereas, *B. inexpectatus* is restricted to the eastern Pacific.

Balanus poecilotheca Krüger (text-fig. 31, pl. 21 figs. g-l)

Balanus poecilotheca Krüger, 1911: 48, figs. 95-97, pl. 1 fig. 2c-e, pl. 3 fig. 32a-e3 (type locality: Okinose Bank, Sagami Bay, Japan). — Pilsbry, 1916: 119. — Barnard, 1924: 65. — Utinomi, 1958: 294.

Balanus amphitrite var. *malayensis* Hoek, 1913: 172, pl. 14 figs. 8, 9, 10a-d, 11a, b, 12*, 13-15, 17 (in part; see remarks). — Broch, 1916: 5, pl. 1 figs. 1, 8a-d.

Balanus alatus Hoek, 1913: 175, pl. 15 figs. 1, 2a-d, 3, 4, 4*, 5, 6, 6*, 7, 8. — Pilsbry, 1916: 110.

Balanus minutus Hoek, 1913: 177, pl. 15 figs. 9, 10a-c, 11-16. — Broch, 1922: 317, figs. 58, 59a-d, 60a-c. — Nilsson-Cantell, 1925: 31, fig. 12a-e, pl. 1 fig. 4. — Utinomi, 1968: 173.

Balanus amphitrite forma *communis*: Broch, 1922: 314 (in part; see *B. reticulatus*; not *Balanus amphitrite* var. *communis* Darwin, 1854: 240).

Balanus amphitrite forma *poecilosculpta* Broch, 1931: 59, fig. 21a-e.

Balanus amphitrite poeciloscutata: Nilsson-Cantell, 1934a: 61, figs. 3a, b, 4a-e, pl. 5 fig. 4.
Balanus amphitrite poecilotheca: Hiro, 1937: 435, figs. 22a-e, 23a-g. — Hiro, 1938: 393.

Holotype. — Deposition unknown.

Distribution. — Japan and South China to Malay Archipelago; southwest Australia to southwest Africa.

Material examined. — Table 19.

Table 19. *Balanus poecilotheca*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
Philippine Islands					
Off Sulada I.	22	twigs	---	16/2/08	---- USNM 85024
Off Observation I.	16	gorgonians	*B. ciliatus*	----	*Albatross* USNM 67302

Diagnosis. — Shell with epicuticle not persistent; radii very wide, summits thick, rough; sheath solid, lower margin not overhanging; parietal tubes in single row, without transverse septa. Scutum flat; basitergal angle oblique; longitudinal striae fine; articular ridge about 2/3 length of tergal margin; adductor ridge variable, separated usually by narrow groove from articular ridge. Tergum with carinal margin very narrowly protuberant in upper 1/3; with spur fasciole; spur length about 4/5 spur width; distance from basiscutal angle to spur about 1/2 spur width; basal margin usually straight, occasionally concave on carinal side of spur. Labrum simple. Cirri III-VI without erect teeth below posterodistal angles; cirrus III without complex setae.

Description. — Shell subcylindric, often laterally compressed; orifice toothed, width more than 1/2 carinorostral diameter; surface smooth; epicuticle not persistent. Radii very wide, transversely striate; summits oblique, thick, rough; sutural edges with septa strongly denticulate on lower margins. Alae with summits usually oblique, occasionally slightly oblique; sutural edges septate. Sheath solid, lower margin not overhanging. Inner lamina strongly ribbed on lower part; ribs denticulate basally, ridged on sides. Parietal tubes in single row, small, 8-10 (9.2) in rostrum, without transverse septa, filled up in upper half. Inner surface of outer lamina occasionally with 1-3 strong ribs between longitudinal septa. Basis with radial tubes, except near original point of attachment, without transverse septa.

Scutum flat; basitergal angle oblique; growth ridges fine; longitudinal striae fine, sometimes only on lower part. Inner surface smooth; articular ridge high, not reflexed, about 2/3 length of tergal margin and about 1/2

length of occludent margin, end obliquely truncate; articular furrow deep; adductor ridge extremely variable, short to moderately long, weak to moderately strong, without pit below, separated usually by narrow groove from articular ridge; adductor and lateral depressor muscle pits shallow, sometimes indistinct.

Tergum with scutal margin raised, sharply denticulate; carinal margin very narrowly protuberant in upper third, protuberance separated from rest of valve by narrow groove; growth ridges fine, stronger on protuberance; longitudinal striae absent; spur fasciole separated from scutal side by narrow groove; spur width about 1/4 length of basal margin; spur length about 4/5 spur width; distance from basiscutal angle to spur about 1/2 spur width, about 3/5 spur length, and about 1/10 length of basal margin; spur length about 1/5 length of basal margin; end rounded; basal margin usually straight on both sides of spur, sometimes slightly concave on carinal side. Internally, scutal margin moderately high; articular ridge usually high, sometimes low, reflexed; articular furrow moderately deep; crests for depressor muscle prominent, usually projecting slightly below basal margin; surface smooth.

Labrum with setulae and 3-5 (4.0) large teeth on crest on each side of notch.

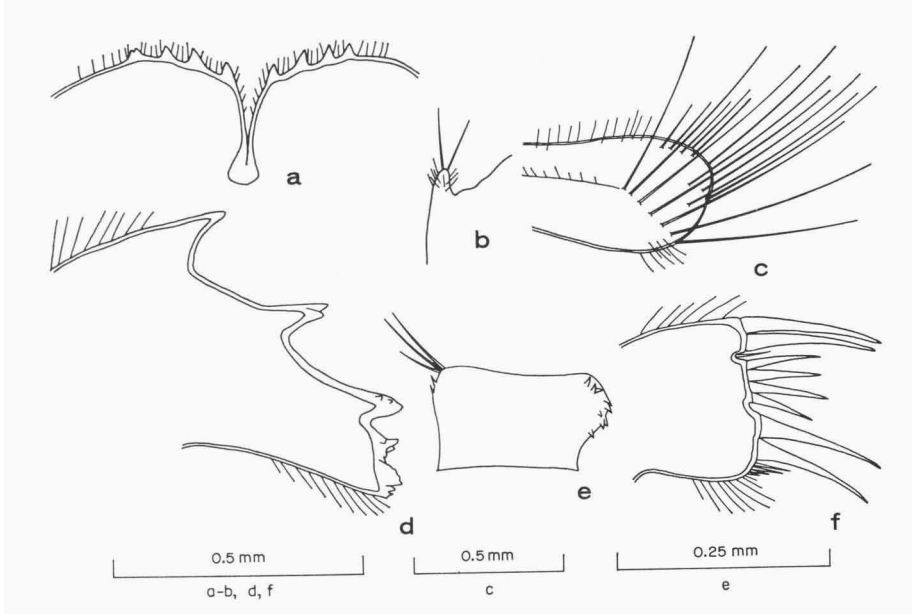

Fig. 31. *Balanus poecilotheca* Krüger. a, labrum; b, basidorsal point; c, palpus; d, mandible; e, 4th proximal segment of anterior ramus of cirrus III; f, 1st maxilla (a-f, Sulada Island, Philippine Islands).

Palpus with short, thin finely pinnate setae on upper margin and setulae on lower margin near distal end; outer face with few short simple setae near superodistal angle, long setae in tuft at distal end and in oblique row extending mediad from inferodistal angle, and also with row of setulae medially on proximal three-fourths; labral face with narrow band of short strongly pinnate setae near upper margin on proximal four-fifths and tuft of setulae near inferodistal angle.

Mandible with 5 or 6 (5.2) teeth; inferior angle not spinose; 2nd tooth bifid; 3rd-5th with extra denticles; lowest tooth not confluent with inferior angle.

First maxilla with 1 or 2 fine spines in slight notch below upper pair of spines, 2-5 (3.6) spines between upper and lower pairs, and few slender spines on rounded inferior angle; lower pair close to angle, occasionally on slight prominence.

Second maxilla without distinguishing characters.

Protopods of anterior cirri with primarily pinnate setae, many plumose setae posteriorly on coxopods; coxopod of cirrus I also with narrow band of simple scales on outer face near anterior margin; protopods of cirri II and III each with narrow band of simple scales on outer face near posterior margin.

Cirrus I with anterior ramus 2-6 (3.7) segments longer than posterior; both rami with protuberant segments; distal sutures of both rami with long setae and multifid spinules; proximal segments each with narrow to wide band of simple scales on outer face near posterior margin.

Cirrus II with anterior ramus 1-3 (2.1) segments longer than posterior; both rami with protuberant segments; distal sutures with long setae, also with multifid spinules on distal segments and near posterior margins on median and proximal segments.

Cirrus III with anterior ramus 1-5 (2.2) segments longer than posterior; both rami with slightly protuberant segments; distal sutures with multifid spinules near anterior and posterior margins on distal segments, also few short setae near posterior margins on 1 or 2 distal segments; posterior margins with few short setae on distal angles; inner faces without complex setae. Anterior margins of median segments usually with small conic teeth, anterior ramus usually with 2-6 teeth on each segment and 2 or 3 simple spinules below distal angles of some distal segments, occasionally with 1 or 2 teeth on each distal segment except ultimate; posterior ramus usually with 1-6 teeth on each median segment, occasionally without teeth. Outer faces near anterior margins occasionally with 1-3 sparse rows of small conic teeth

on median segments; some distal segments each with 2 or 3 simple spinules near distal angles; posterior ramus without teeth, sometimes with 2 or 3 simple spinules near each distal angle of median segments. Posterior margins with short setae, fewer proximally, on distal angles; anterior ramus occasionally also with 2 fine sharp spinules below setae on proximal and median segments. Outer faces near posterior margins of long proximal segments of both rami each with narrow band of simple scales.

Protopods of posterior cirri sometimes with narrow band of simple spinules near anterior margin and narrow band of simple scales near posterior margin, on inner face on each basipod; coxopods each usually with narrow band of multifid spinules near anterior margin, narrow band of simple or denticulate scales near posterior margin, and 3-6 large conic teeth near posterodistal angle, on inner face.

Posterior cirri each with very few simple spinules on distal sutures near anterior margins and 1 or 2 relatively long and 3 or 4 short setae on posterodistal angles. Cirrus IV sometimes with 2 or 3 small conic teeth or spinules on outer faces near anterodistal angles of few proximal segments of anterior ramus; posterior ramus usually without teeth or spinules, occasionally with 2 or 3 conic teeth or simple spinules near anterodistal angles of few proximal segments. Cirrus VI with 4 or 5 (4.1) pairs of setae on anterior margins of median segments. Basidorsal point of penis narrow, sparsely spinulose, with 2 apical setae.

Color. — Shell usually white or pink with reddish brown or purple longitudinal stripes crossed by irregularly arranged splotches, sometimes white with color on edges or apices of parietes. Radii and alae white or colored like parietes. Sheath white or white with splotches of pink or red. Scutum externally white with pink or red margins, sometimes with color also near apex or medially; internally, white or white with colored margins, occasionally colored except for white pits. Both surfaces of tergum usually white with pink or red band near carinal margin, sometimes with color also near apex medially.

Measurements. — Carinorostral diameter of largest specimen from type locality 11.0 mm, height 9.0 mm. Carinorostral diameter of largest specimens recorded by other authors 10.5 mm (*malayensis,* Hoek, 1913, pl. 14 fig. 8); 10 mm *poeciloscultpta* Broch, 1931).

Variations. — The adductor ridge of the scutum varies from weak or scarcely discernible to thin, sharp, and moderately long; in most specimens less than 4 mm in diameter it is weak. The articular ridge of the tergum varies in prominence; in one specimen in our material, the development of the articular

ridge approached that of the tergum of *B. minutus* illustrated by Broch (1922, fig. 59a, b).

Teeth on cirrus IV have not been described previously; of the 25 specimens examined, 2 had teeth on the anterior ramus, 1 specimen had teeth on both rami.

Remarks. — Krüger (1911) described a new species, *B. poecilotheca,* distinguished by the color pattern of the shell, and the variation in the prominence of the adductor ridge of the scutum; often is was scarcely discernible. Subsequently, Hoek (1913) described three new taxa, *B. alatus B. minutus,* and *B. a. malayensis,* all with a distinctive color pattern. *B. alatus* and *B. minutus* were distinguished from *B. amphitrite* by the absence of the adductor ridge, and from each other by minor differences in the opercular valves and mouth parts, and by their depth distribution (564 m and 80 m, respectively). *B. a. malayensis* was distinguished from Darwin's (1854) *B. a. communis,* in part, by the less prominent adductor ridge. Although Hoek noted Krüger's (1911) description of a new species, he did not discuss the relationship of *B. poecilotheca* with his new taxa.

Similarly, Broch (1931) who described a new form *B. a. poeciloscul pta,* with a scutum having a very reduced adductor ridge, did not compare this taxon with *B. poecilotheca,* nor did Nilsson-Cantell (1934a). Nilsson-Cantell noted, however, that in his examination of Hoek's Siboga material, some specimens of *B. a. malayensis* resembled *B. a. poeciloscul pta.* He also stated (Nilsson-Cantell, 1934a: 61) that *B. minutus,* which both he (Nilsson-Cantell, 1925) and Broch (1922) had reidentified, was also very similar to *B. poeciloscul pta.* The opercular valves, particularly of one specimen of *B. minutus,* figured by Broch (1922, fig. 59a-d) resemble those of the specimen from West Australia which Broch (1916) referred to *B. a. malayensis* much more than they do Hoek's figures of the opercular valves of *B. minutus* (cf. Hoek, 1913, pl. 15 fig. 10a-c).

Hiro (1937) assigned *poecilotheca* to *B. amphitrite* as a subspecies and put *B. a. poeciloscul pta* in synonymy with it. Later, he (as Utinomi, 1968) reconsidered and reinstated specific rank for *B. poecilotheca.*

Both Pilsbry (1916) and Broch (1922) examined material from the Sulu Archipelago. Pilsbry referred specimens to *B. alatus* and to *B. poecilotheca.* In contrast, Broch referred specimens to *B. a. communis* and *B. minutus*; his description of *B. a. communis,* from a station, where he also recorded *B. minutus,* agrees with *B. poecilotheca.* On the basis of our reexamination of the specimens which Pilsbry referred to *B. alatus* and one lot ("Albatross" station 5146) referred to *B. poecilotheca,* as well as evidence from the literature, *B. a. malayensis, B. alatus, B. minutus,* and *B. poeciloscul pta* are, herein, considered synonymous with *B. poecilotheca.*

Specimens of *B. poecilotheca* were not available in sufficient numbers to permit inclusion of this species in the statistical analyses of interspecific relationships; however, qualitative data indicate that this species is most closely allied to species of the *venustus* subgroup. *B. poecilotheca* agrees with *B. venustus* in the subtidal habitat; however, it occurs at a far greater depth than any of the other members of the complex. This species also apparently does not reach as large a size as other species in the complex.

Balanus inexpectatus Pilsbry (text-fig. 23, 32, pl. 22 figs. a-e)

Balanus amphitrite inexpectatus Pilsbry, 1916: 97, pl. 20 figs. 5-5e (type locality: Gulf of California). — Henry, 1943: 368, pl. 31 figs. 15, 16. — Henry, 1959: 192. — Henry, 1960: 142.

not *Balanus amphitrite inexpectatus*: Nilsson-Cantell, 1933: 506, fig. 2a-g (= *B. venustus*). — Kolosváry, 1947: 20, pl. 3 figs. h, h_1 (see remarks).

Holotype. — USNM 12398.

Distribution. — Gulf of California and southwest Baja California to Ecuador.

Material examined. — Table 20.

Diagnosis. — Shell with epicuticle sometimes persistent; radii moderately wide, summits thick, rough; sheath solid, lower margin sometimes overhanging; parietal tubes in single row, without transverse septa. Scutum usually flat, occasionally with narrowly inflected tergal segment; basitergal angle occasionally obliquely truncate; longitudinal striae absent; articular ridge about 3/4 length of tergal margin; adductor ridge long, close to but not confluent with articular ridge. Tergum with carinal margin slightly convex; with spur fasciole; spur length about 2/3 spur width, distance from basiscutal angle to spur about 1/3 spur width; basal margin usually straight, occasionally concave on scutal side of spur. Labrum simple. Cirri III-VI with erect teeth below posterodistal angles; cirrus III with complex setae.

Description. — Shell usually conic, occasionally cylindric; orifice entire, width less than 1/2 carinorostral diameter; surface smooth; epicuticle thin, sometimes persistent at base. Radii moderately wide, transversely striate; summits moderately oblique, thick, rough; sutural edges with septa strongly denticulate on lower margins. Alae with horizontal summits; sutural edges finely septate. Sheath solid, lower margin sometimes overhanging. Inner lamina ribbed, usually only on lower half; ribs denticulate basally, finely ridged on sides. Parietal tubes in single row, variable in size and shape, 14-18 (16.5) in rostrum, without transverse septa, filled up in upper 1/3-1/2. Inner surface of outer lamina usually with 2-4 fine ribs between longitudinal septa, 1 or 2 ribs sometimes stronger, denticulate basally, occasionally al-

Table 20. *Balanus inexpectatus*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
Gulf of California					
San Felipe	2	rocks	*T. stalactifera, Ch. anisopoma*	30/5/63	Paine USNM
Sonora	4	gastropods	*B. a. amphitrite*	13/8/46	----- USNM 173807
Puerto Peñasco	4	gastropod	---	30/11/52	----- USNM 205678
Puerto Peñasco	35	gastropods	---	-----	Causey USNM
Puerto Peñasco	2	gastropods	---	27/4/55	----- USNM 205678
Guaymas	3	pelecypod	---	1/59	Eyerdam USNM
Empalme	2	breakwater	*B. a. amphitrite, Chthamalus* sp.	15/5/62	Henry USNM
Bocochibampo Bay	6	---	*B. a. amphitrite, Ch. anisopoma*	7/5/62	Henry RMNH
Bocochibampo Bay	53	boat basin	*B. a. amphitrite, Chthamalus* sp.	7/5/62	Henry RMNH
Estero de la Luna	4	gastropod	---	10/4/40	Ricketts USNM
Agiabampo Estuary	12	gastropod	*B. trigonus*	11/4/40	Ricketts USNM
Topolobampo Bay	12	rocks	*B. trigonus, Chthamalus* sp.	9/5/62	Henry RMNH
Baja California, west coast					
Magdelena Bay	14	---	---	-----	----- USNM
Mexico, west coast					
Mazatlan	1	breakwater	*B. trigonus, Chthamalus* sp.	11/5/62	Henry USNM
San Blas	3	jetty	*Chthamalus* sp.	2/4/63	Tripp USNM
San Blas	12	coconut roots	*Chthamalus* sp.	2/4/63	Tripp RMNH
Acapulco	10	boat lift	*B. a. amphitrite, Chthamalus* sp.	17/5/60	Henry RMNH
El Salvador					
Near Gorda Pt.	11	rocks	*Chthamalus* sp.	28/4/63	Henry USNM
Catuco	39	piles, rocks	*Chthamalus* sp.	28/4/63	Henry USNM,RMNH
La Union	2	---	*B. tintinnabulum*	14/5/39	----- USNM 145652
Honduras, Pacific coast					
-----	15	oyster shells	---	1938	Eyerdam USNM
Costa Rica, Pacific coast					
Cedro I.	12	rocks, shells	*B. t. coccopoma, Chthamalus* sp.	19/2/65	Henry USNM
Puntarenas	5	piles	*B.peruvianus,B.t.coccopoma,B.vinaceus, Ch.panamensis*	17/2/65	Henry RMNH
Barranca River	5	rocks	*B.peruvianus,B.suturaltus,T.polygenus, Chthamalus* sp.	18/2/65	Henry USNM
Boca de Barranca	∿100	boulder	*B. suturaltus, B. t. coccopoma, Chthamalus* sp.	18/2/65	Henry USNM
Boca de Barranca	70	boulder	*B. suturaltus, B. t. coccopoma, Tetraclita* sp., *Chthamalus* sp.	14/5/68	Henry USNM,RMNH
S. of Boca de Barranca	30	rocks	*B. suturaltus, B. t. coccopoma, Tetraclita* sp., *Chthamalus* sp.	18/2/65	Henry USNM,RMNH
S. of Boca de Barranca	70	---	*B. t. coccopoma, Tetraclita* sp., *Chthamalus* sp.	14/5/68	Henry USNM
Golfito	74	cobbles	*Ch. panamensis*	2/3/62	Eyerdam USNM

Table 20 (Continued). *Balanus inexpectatus*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
Panama, Pacific coast					
Cobbe Beach	11	oyster, coral	*B. trigonus*	2/62	Eyerdam USNM
San Francisco Beach	20	rocks	*Ch. panamensis*	3/5/63	Henry USNM,RMNH
Ecuador					
Santa Elena Bay	26	oyster shells	---	-----	Eyerdam USNM
Playas	1	pelecypod	---	13/5/63	Henry RMNH
Posorja	30	mangroves	---	13/5/63	Henry USNM
Posorja	58	piles	*B.improvisus,B.t.coccopoma,B.vinaceus, T.polygenus,Chthamalus* sp.	7/5/66	McLaughlin RMNH
Puna I.	8	shells, rocks	---	23/12/34	----- USNM
Puna I.	15	gastropods	*B. improvisus*	22/12/34	----- USNM 131571

most reaching inner lamina. Basis with radial tubes except near original point of attachment; with few transverse septa, not extending to periphery.

Scutum usually flat, occasionally with narrow tergal segment slightly inflected; basitergal angle occasionally obliquely truncate; occludent margin toothed; growth ridges low; longitudinal striae absent. Inner surface usually roughened in upper part; articular ridge high, slightly reflexed; about 3/4 length of tergal margin and 1/2 length of occludent margin, end truncate or pointed; articular furrow deep; adductor ridge high, long, with deep pit below occasionally bounded on tergal side by weak ridge, close to but not confluent with articular ridge; adductor muscle pit moderately deep; lateral depressor muscle pit small, shallow.

Tergum with scutal margin raised, often strongly, occasionally finely denticulate; carinal margin slightly convex; growth ridges fine, stronger on narrow carinal segment; longitudinal striae absent; spur fasciole with narrow groove on each side; spur width about 2/5 length of basal margin; spur length about 2/3 spur width; distance from basiscutal angle to spur about 1/3 spur width, about 1/2 spur length, and about 1/10 length of basal margin; spur length about 1/4 length of basal margin; end usually rounded or truncate, occasionally obliquely truncate; basal margin usually straight on both sides of spur, occasionally concave on scutal side. Internally, scutal margin high; articular ridge prominent, somewhat reflexed; articular furrow moderately wide and deep; crests for depressor muscle strong, numerous, occasionally extending from carinal margin to spur, projecting below basal margin; surface usually roughened on carinal side, basally sometimes finely to strongly denticulate medially.

Labrum with setulae and 0-8 (2.9) teeth on crest on each side of notch;

1 tooth of each side usually on crest near notch, 1-4 teeth occasionally on one or both edges of notch near crest.

Palpus with very finely pinnate short setae on upper margin and setulae on lower margin; outer face with several rows of simple short setae near upper margin, decreasing in number proximally, long setae on distal margin and in oblique row near inferodistal angle; narrow band of setulae near lower margin; labral face with narrow band of strongly pinnate short setae near upper margin on proximal three-fourths, setulae near distal margin and in narrow band along lower margin.

Mandible with 5-7 (5.0) teeth, occasionally with spinose inferior angle; 1st and 2nd teeth bifid, 3rd-7th with extra denticles, lowest tooth usually confluent with inferior angle.

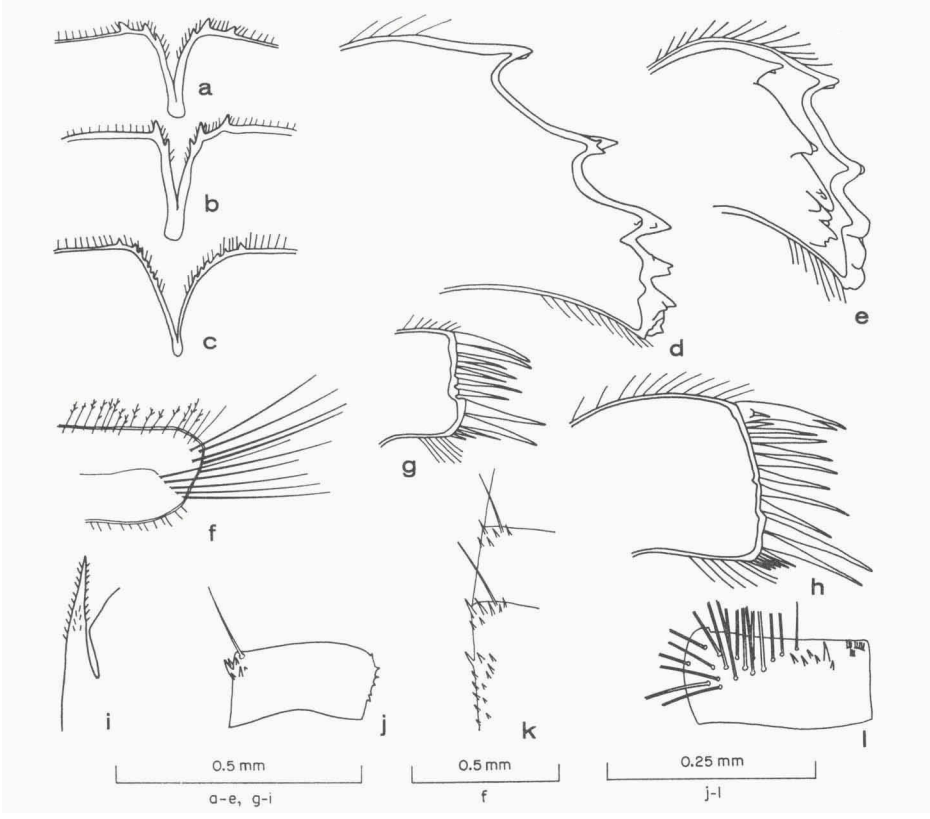

Fig. 32. *Balanus inexpectatus* Pilsbry. a-c, labra; d, e, mandibles; f, palpus; g, h, 1st maxillae; i, basidorsal point; j, 4th proximal segment of anterior ramus of cirrus III; k, l, posterior ramus of cirrus III (k, posterior part of proximal segments; 1, inner face of 3rd proximal segment) (a, e-g, i, j, Posorja, Ecuador, USNM; b, d, h, San Blas, Mexico; c, k, l, Catuco, El Salvador).

First maxilla without notch below upper pair of spines, with 2-14 (5.9) spines between upper and lower pairs and few fine spines on inferior angle; lower pair of spines slightly larger than upper pair, close to inferior angle, usually on slight prominence.

Second maxilla without distinguishing characters.

Protopods of anterior cirri with pinnate setae, few plumose setae posteriorly; coxopods of cirrus I with narrow band of simple scales near anterior margin on outer face; both segments sometimes with few simple spinules below posterodistal angles on outer faces; protopods of cirri II and III each with wide band of simple scales near posterior margin on outer face, sometimes also with few simple spinules below anterodistal angles.

Cirrus I with anterior ramus equal to or 1-10 (4.9) segments longer than posterior; posterior ramus with very protuberant segments; proximal segments of anterior ramus protuberant; distal sutures with long setae and with multifid spinules generally near posterior margins proximally; long proximal segments each sometimes with narrow band of simple spinules, occasionally with adjacent narrow band of simple scales, on outer face near posterior margin.

Cirrus II with anterior ramus 2 segments shorter to 3 (1.2) segments longer than posterior; both rami with moderately protuberant segments; distal sutures with long setae, also with multifid spinules on distal and some median segments, usually near anterior and posterior margins on median segments, sometimes with simple spinules near posterior margins on proximal segments of posterior ramus; long proximal segments each occasionally with narrow to wide band of simple scales on outer face near posterior margin.

Cirrus III with anterior ramus equal to or 1-5 (2.5) segments longer than posterior; both rami with slightly protuberant segments; distal sutures with multifid spinules on several distal segments, usually with multifid spinules near posterior margins and simple and multifid spinules near anterior margins on remaining segments; outer faces near anterior margins with conic teeth; posterior margins with erect teeth below short setae on distal angles. Anterior margins of anterior ramus usually with 1-5 small or large teeth on proximal and median segments; posterior ramus occasionally with teeth on proximal segments. Outer faces near anterior margins with teeth on proximal segments, usually also with teeth on median segments of anterior ramus; long proximal segments of both rami each with few small teeth near anterodistal angle; remaining proximal segments each usually with 3-5 larger teeth near anterodistal angle and 2-6 rows of small teeth, occasionally with 5-7 large teeth in subsutural row; median segments of anterior ramus usually with similar armature, occasionally with only few small teeth or

denticles on proximal half of each segment. Inner faces near anterior margins of several proximal segments of anterior ramus usually with few denticles or fine spinules. Posterior margins with tuft of short setae on distal angles, fewer or lacking on some proximal segments, several large erect teeth and simple and multifid spinules below distal angles on few proximal segments, 1-3 smaller teeth or fine sharp spinules below distal angles on most or all remaining segments; long proximal segments of anterior ramus occasionally with fine spinules; long proximal segment of posterior ramus sometimes with series of fine simple spinules, few proximal segments each with 1 or 2 moderately large erect teeth below angle, remaining proximal and median segments usually with 2 or 3 sharp simple spinules below angles, occasionally also with erect teeth, teeth and spinules decreasing in size distally. Outer faces near posterior margins of segments having erect teeth below distal angles sometimes also with several teeth and simple or multifid spinules; long proximal segment of anterior ramus sometimes with 2 or 3 rows of small conic teeth or simple spinules; posterior ramus occasionally with few spinules on long proximal segment. Inner faces near posterior margins usually with subsutural row of 3 or 4 teeth on proximal segments, occasionally on some median segments; long proximal segment of anterior ramus usually also with 2 or 3 rows of small conic teeth, several adjacent segments each sometimes with few conic teeth; long proximal segment of posterior ramus usually with several rows of simple spinules, occasionally without spinules; proximal segments having large erect teeth below distal angles each usually with subsutural row of large and small teeth and few simple spinules; proximal segments lacking erect teeth below angles sometimes with subsutural row of teeth or spinules. Inner faces of both rami with complex setae below distal sutures near posterior margins; anterior ramus usually with few pectinate setae on several distal segments, occasionally with single denticulate seta on 1 or 2 segments, rarely with 1-4 bifurcate setae on 1-5 segments; posterior ramus usually with few pectinate setae on most segments; 5 or 6 distal segments, except ultimate, usually with 1-6, occasionally 1-14 bifurcate setae; 1 or 2 distal segments occasionally also with denticulate or multifurcate setae; remaining segments except 1 or 2 proximal segments sometimes with bifurcate setae; rarely with bifurcate setae only on 1 or 2 distal segments or without bifurcate setae. Denticulate setae with short apical ends and single or double row of 15-20 small teeth; multifurcate setae with relatively long apical ends and 2-9, occasionally with only 2 or 3, long teeth; bifurcate setae arched, anteriorly directed, position changing from posteriorly on distal segments to medially on proximal segments.

Protopods of posterior cirri each with narrow band of multifid and simple spinules near anterior margin, sometimes with few multifid and simple spinules near anterodistal angle on outer face, larger simple spinules near anterodistal angle; basipods each with 4 or 5 large simple spinules in subsutural row near posterior margin, occasionally also with 1-3 erect teeth medially; coxopods each sometimes with narrow band of simple scales near posterior margin on outer face; 5-7 large erect teeth and simple spinules in subsutural row near posterior margin on inner face, sometimes with band of simple and multifid spinules and few teeth near posterior margin.

Posterior cirri with fine simple and multifid spinules on distal sutures of median segments; inner faces near anterior margins of anterior rami with sparsely scattered denticles on long proximal segments; posterior margins with several short setae on distal angles of cirri V and VI and 1 or 2 longer and 5 or 6 short setae on cirrus IV; proximal, occasionally also some median, segments of cirri IV-VI usually with several erect teeth, sometimes with few simple spinules, below setae. Anterior margins of anterior ramus of cirrus IV sometimes with conic teeth; outer faces near anterior margins sometimes with conic teeth and spinules on some proximal segments, occasionally without teeth or spinules; long proximal and adjacent segment usually without teeth or spinules; next 3-9 segments with 1 or 2 sparse rows of small teeth or less often with several rows of moderately large teeth or spinules, rarely with few conic teeth on 2 or 3 proximal segments. Cirrus VI with 4-7 (5.6) pairs of setae on anterior margins of median segments. Basidorsal point of penis rather long and narrow; spinulose.

Color. — Shell usually dull purplish blue with white or lighter blue longitudinal stripes; sometimes with upper part white, lower part purplish blue or blue, or white except for few purplish blue splotches or longitudinal stripes on some compartments; occasionally purplish or grayish blue with lighter longitudinal stripes; infrequently with indistinct transverse stripes. Radii white, white with splotches of color, or colored like parietes. Alae usually dull blue or purplish blue, sometimes white. Epicuticle yellowish brown. Sheath usually with purple, sometimes dull blue, band in middle of each compartment. Inner lamina of rostrum and carina sometimes purple or blue near edge of sheath. Scutum usually colored except for white band along tergal margin; inner surface occasionally white except for colored occludent margin and pit below adductor ridge; color usually dark purple, or blackish, brownish, or pinkish purple; occasionally blue. Tergum usually white with some color, occasionally entirely white; outer surface usually with colored striae opposite crest for depressor muscle and narrow to wide colored band along occludent margin, sometimes with colored band along

carinal margin; inner surface usually with wide colored band along occludent margin and splotch of color above crests, sometimes colored except for narrow white basal band; color usually reddish purple, sometimes lavender, or blackish, brownish, or bluish purple.

Measurements. — Carinorostral diameter of holotype 14 mm. Carinorostral diameter of largest specimen examined 19 mm, height 12 mm (Puntarenas, Costa Rica).

Variations. — The shell and the upper parts of the opercular valves are often corroded. In one lot from Golfito, the specimens are all corroded. Most of the specimens from San Blas are white with little color; a few are bluish with indistinct longitudinal striae; none are corroded. In most lots, there are a few white with little color or entirely white specimens, but most of the specimens are colored; usually some are corroded, at least on the upper part.

Considerable variation was noted in the occurrence and the number of bifurcate setae on the posterior ramus of cirrus III. The frequency of occurrence varied from 100% to 73% in specimens from Panama, the Gulf of California, west coast of Mexico, and Costa Rica and from 42% to 24% in specimens from Ecuador and El Salvador. Specimens from the latter localities had fewer bifurcate setae (1 to 3 or 4) on 5 or 8 segments, respectively. Specimens from the Gulf of California had bifurcate setae (1-14) on all segments; those from the west coast of Mexico had fewer setae (1-6) on all but ultimate and 1 or 2 proximal segments. Specimens from Costa Rica and Panama had 1 to 4 or 5 setae on 5 or 6 segments.

Habitat. — Intertidal on rocks, mollusk shells, shore installations, and mangroves.

Remarks. — Henry (1960) referred the *B. a. inexpectatus* of Nilsson-Cantell (1933) from Bonaire and of Kolosváry (1947) from the Adriatic Sea to this taxon; however, as a result of our present studies, we herein restrict the distribution of *B. inexpectatus* to the eastern Pacific and refer Nilsson-Cantell's (1933) *B. a. inexpectatus* to *B. venustus*. From Kolosváry's description and figures, it is impossible to refer his *B. a. inexpectatus* to any taxon.

Results of the statistical analyses indicate that *B. inexpectatus* is most closely allied to *B. venustus* ($D^2 = 8.31$) and forms a cluster with it. *B. inexpectatus* is also closely related to *B. peruvianus* ($D^2 = 12.08$). As previously noted (p. 174) several characters not used in the statistical analyses also can be used to differentiate *B. inexpectatus* from *B. venustus*. The former species can be distinguished from *B. peruvianus*, a much larger barnacle occupying a similar geographic range, by the color pattern of the shell

and by the entire rather than toothed orifice. Corroded specimens can be differentiated by the opercular valves, particularly the scutum. In *B. peruvianus* the adductor ridge is united to the very prominent articular ridge and the upper part is strongly ridged.

Balanus peruvianus Pilsbry (text-fig. 33, pl. 22 figs. f-j)

Balanus peruvianus Pilsbry, 1909: 69, fig. 1, pl. 19 figs. 1-4 (type locality: La Palasada, Peru).

Balanus amphitrite peruvianus: Pilsbry, 1916: 97, figs. 23, 24a-f, pl. 24 fig. 4, pl. 37 figs. 2-2c. — Zullo, 1968: 227.

Lectotype — USNM 38691, by subsequent selection by Zullo, 1968: 227.

Distribution — Costa Rica to Peru.

Material examined. — Table 21.

Diagnosis — Shell with epicuticle usually persistent basally; radii moderately wide, summits thick, rough; sheath solid, lower margin overhanging; parietal tubes in single row, without transverse septa. Scutum flat except for narrowly inflected tergal segment; basitergal angle obliquely truncate; longitudinal striae absent; articular ridge about 7/10 length of tergal margin; adductor ridge short, confluent with articular ridge. Tergum with carinal margin convex; with spur fasciole; spur length about 9/10 spur width, distance from basiscutal angle to spur about 1/2 spur width; basal margin sloping to spur on scutal side. Labrum simple. Cirri III to VI with erect teeth or simple spinules below posterodistal angles; cirrus III without complex setae.

Description. — Shell conic or subcylindric; orifice toothed, width about 1/2 carinorostral diameter; surface smooth; epicuticle thin, usually presistent only at base; radii moderately wide, with fine transverse striae; summits oblique, thick, rough; sutural edges with septa strongly denticulate on lower margins. Alae with oblique summits; sutural edges finely septate. Sheath

Table 21. *Balanus peruvianus*, Material Examined

Locality	n	Substrate	Association	Date	Collector / Deposition
Costa Rica, Pacific coast					
San Lucas I.	9	---	*Chthamalus* sp.	6/1/30	----- USNM 64753
Puntarenas	28	piles	*B.inexpectatus, B.t.coccopoma, B.vinaceus, Ch.panamensis*	17/2/65	Henry RMNH
Puntarenas, inner hbr.	27	rocks	---	19/2/65	Henry USNM
Barranca River	24	rocks	*B.inexpectatus, B.suturaltus, T.polygenus, Chthamalus* sp.	18/2/65	Henry USNM
Panama, Pacific coast					
Chorrero Beach	98	mangroves	*B. t. peninsularis, Chthamalus* sp.	2/62	Eyerdam USNM, RMNH
Chorrero Beach	17	rocks	*Chthamalus* sp.	2/62	Eyerdam USNM

solid, lower margin overhanging. Inner lamina ribbed, usually only on lower half; ribs finely ridged on sides. Parietal tubes in single row, small, 12-18 (15.1) in rostrum, without transverse septa, filled up in upper half. Inner surface of outer lamina usually with 1 strong rib, sometimes with 2 or 3 strong ribs, between longitudinal septa; ribs denticulate basally, sometimes almost reaching inner lamina. Basis with narrow radial tubes, except sometimes near original point of attachment; with fine transverse septa except near periphery.

Scutum with narrowly inflected tergal segment; basitergal angle obliquely truncate; occludent margin weakly toothed; growth ridges low; longitudinal striae absent. Inner surface strongly ridged on upper part, ridges often projecting below articular ridge; articular ridge high, slightly reflexed, about 7/10 length of tergal margin and about 1/2 length of occludent margin, end truncate or pointed; articular furrow deep; adductor ridge strong but short, with deep pit below bounded on tergal side by well defined ridge, confluent with articular ridge; adductor muscle pit moderately deep; lateral depressor muscle pit small, shallow, sometimes indistinct.

Tergum with scutal margin raised, not denticulate; carinal margin convex; growth ridges fine, stronger on usually wide carinal segment; longitudinal striae occasionally present on carinal side; spur fasciole separated from scutal side, occasionally also from carinal side, by narrow groove; spur width about 1/3 length of basal margin; spur length about 9/10 spur width; distance from basiscutal angle to spur about 1/2 spur width, about 1/2 spur length, and about 1/5 length of basal margin; spur length about 3/10 length of basal margin; end truncate; basal margin sloping to spur on scutal side, straight on carinal side. Internally, scutal margin low; articular furrow deep; crests for depressor muscle short, sharp, projecting slightly below basal margin; surface usually ridged between articular ridge and carinal margin, ridges strongest near carinal margin, sometimes projecting below basal margin medially.

Labrum with 0-4 (2.5) small teeth on crest on each side of deep notch, sometimes sparsely setulose.

Palpus with fine, short simple setae on upper margin, in tuft near superodistal angle, and sometimes in narrow band near upper margin on outer face, also with long setae at distal end and in short oblique row near inferodistal angle, wide band of curled setulae near lower margin and few multifid spinules near distal margin; labral face with band of short, curved pinnate setae near upper margin on distal half, abruptly narrowing to few rows proximally, few long setae at distal end, multifid spinules in wide band near distal margin and in narrow band, sometimes also with row of long setulae

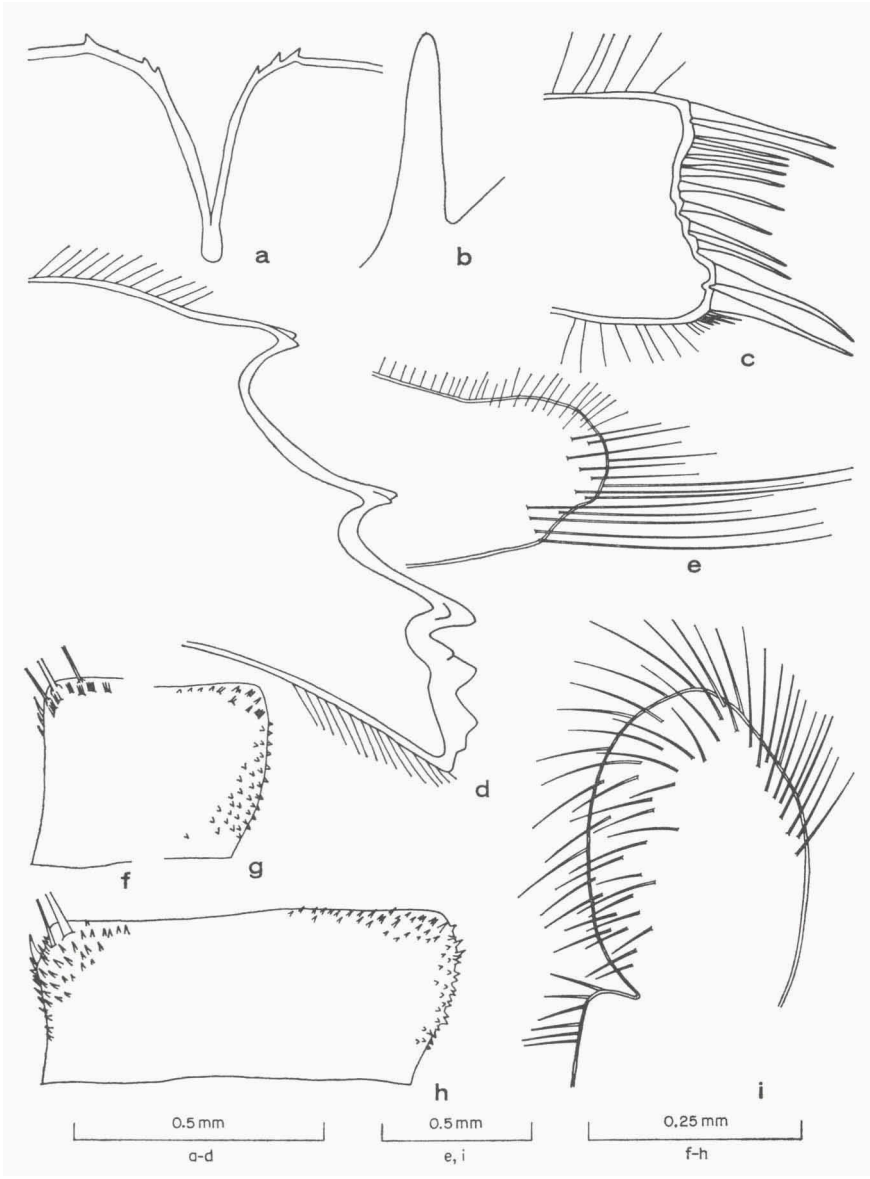

Fig. 34. *Balanus peruvianus* Pilsbry. a, labrum; b, basidorsal point; c, i, 1st and 2nd maxillae; d, mandible; e, palpus; f-h, anterior ramus of cirrus III (f, g, posterior and anterior parts of 8th proximal segment; h, 4th proximal segment) (a-i, Chorrero Beach, Panama: a, c-e, i, same specimen; b, second specimen; f-h, third specimen).

near upper margin of band, along lower margin on distal half and narrow band of simple scales near lower margin on proximal half.

Mandible with 5 or 6 (5.0) teeth, inferior angle sometimes spinose; 1st and 2nd teeth bifid; 3rd-5th with extra denticles; 5th tooth not confluent with inferior angle, 6th tooth, when present, confluent.

First maxilla sometimes with 1 or 2 fine spines in slight notch below upper pair of spines, with 4-13 (7.9) spines between upper and lower pairs and very few fine spines on inferior angle; lower pair of spines usually on moderate, occasionally on slight, prominence close to inferior angle.

Second maxilla without distinguishing characters.

Protopods of anterior cirri with primarily pinnate setae, some plumose setae posteriorly; basipods of cirrus I with few simple scales near anterior margin on outer face, also with narrow band of multifid and simple spinules and simple scales near posterior margin; inner face with few multifid and simple spinules near anterior and posterior margins; coxopod with narrow band of simple scales near anterior margin on outer face and multifid and subtural narrow band of relatively long simple spinules near posterior margin on outer and inner faces; protopod of cirrus II with narrow band of simple scales near posterior margin on outer face; basiopod also with multifid spinules or spinulose scales near posterodistal angle on outer face, sometimes with few multifid spinules near posterodistal angle on inner face; protopod of cirrus III with wide band of small conic teeth near posterior margin on inner face; basipod usually also with narrow band of denticulate scales or multifid spinules near anterior margin and few simple and multifid spinules near anterodistal angle on outer and inner faces.

Cirrus I with anterior ramus 3-18 (8.7) segments longer than posterior; posterior ramus with very protuberant segments; proximal segments of anterior ramus protuberant; distal sutures of both rami with long setae, also multifid spinules. Outer face near anterior margin of anterior ramus with wide band of simple scales on long proximal segment. Posterior margin of long proximal segment of posterior ramus with simple spinules. Outer faces near posterior margins of anterior ramus with wide band of relatively long simple and multifid spinules, also with few simple scales on long proximal segment; most proximal segments each with wide band of primarily simple spinules, decreasing in number and size distally; posterior ramus with wide band of simple and multifid spinules and simple scales on long proximal segment; several adjacent segments each with narrow band of multifid spinules and simple scales, decreasing in number distally. Inner faces near posterior margins of long proximal segments of both rami each with narrow band of simple spinules.

Cirrus II with anterior ramus 1 segment shorter to 5 (1.9) segments longer than posterior; both rami with protuberant segments; distal sutures with long setae and multifid spinules. Outer faces near anterior margins of long proximal segments each with narrow band of multifid and simple spinules. Inner faces near anterior margins with narrow band of large simple spinules on each of several proximal segments except long proximal. Posterior margin of long proximal segment of anterior ramus with simple spinules; several adjacent segments each with simple spinules on distal half. Outer faces near posterior margins of long proximal segment of both rami with wide band of simple scales and spinules; several adjacent segments of anterior ramus with 5 or 6 short rows of multifid spinules, also with relatively large simple spinules near angle; remaining segments each with 2-4 subsutural short rows of multifid spinules; posterior ramus with 2 or 3 subsutural short rows of multifid spinules on several proximal segments; remaining segments each with few multifid spinules near distal angle. Inner faces near posterior margins of long proximal segments of both rami with narrow band of large simple spinules and simple and denticulate scales.

Cirrus III with anterior ramus 1-6 (3.3) segments longer than posterior; both rami with slightly protuberant segments; distal sutures with multifid spinules, larger near anterior margins, also with few short setae on 2 or 3 distal segments of anterior ramus and on 5 or 6 of posterior ramus; outer faces near anterior margins of both rami with small conic teeth; posterior margins with erect teeth or large simple spinules below short setae on distal angles; inner faces without complex setae, but with small conic teeth near posterior margins. Anterior margins of anterior ramus with small conic teeth on proximal and some median segments; posterior ramus rarely with teeth on proximal segments. Outer faces near anterior margins of both rami with teeth usually on proximal segments, occasionally only on few proximal segments; some median segments of anterior ramus usually, and of posterior ramus occasionally, with teeth; proximal segments each usually with simple spinules near distal angle, usually also with 1 or 2 rows of teeth, sometimes with 5-8 rows of teeth and denticles; long proximal and 1 or 2 adjacent segments each sometimes without teeth but with 1 or 2 rows of simple spinules; few median segments sometimes with armature of proximal segments, occasionally with only few simple spinules near distal angles; remaining median segments usually with few simple spinules near distal angles, sometimes without spinules. Posterior margins with tuft of short setae, fewer proximally, usually on each distal angle, sometimes absent on few proximal segments of anterior ramus, and series of simple spinules on long proximal and few adjacent segments; remaining proximal and few median

segments each sometimes with simple spinules on distal half; anterior ramus also with 2 erect teeth below distal angle on each proximal segment; median segments each with 2 teeth or large simple spinules below distal angles; posterior ramus with 2 large simple spinules below distal angle of each proximal segment. Outer faces near posterior margins of few proximal segments of both rami each with narrow band of simple and multifid spinules; anterior ramus usually also with wide band of small conic teeth, denticulate scales, and simple spinules. Inner faces near posterior margins of few proximal segments of anterior ramus each sometimes with subsutural band of teeth or spinules; posterior ramus with narrow band of conic teeth and simple spinules.

Protopods of posterior cirri each usually with fine simple spinules on posterior margin and below distal angle on anterior margin; inner face with narrow band of simple spinules and small conic teeth near anterior and posterior margins; armature weaker on basipods, also on coxopods of cirrus IV.

Posterior cirri with few simple spinules on distal sutures of proximal and some median segments; posterior margins with series of fine simple spinules on proximal and some median segments, also usually with 3 or 4 short setae, fewer proximally, on each distal angle, sometimes lacking on several proximal segments; 5 or 6 proximal segments each usually with 2-4 large spinules or erect teeth below distal angle; remaining proximal and some median segments each with 2 smaller simple spinules below setae; outer faces near posterior margins of proximal and some median segments each usually with 2 or 3 rows of simple spinules, sometimes without spinules; inner faces near posterior margins of proximal and some median segments each usually with 2-8 rows of small conic teeth or simple spinules, decreasing in number and size distally; teeth and spinules more numerous on cirri V and VI, teeth usually larger on anterior rami. Anterior margins of few proximal segments of anterior ramus of cirrus IV sometimes with small conic decurved teeth; posterior ramus without teeth. Outer faces near anterior margins of proximal segments of anterior ramus of cirrus IV each occasionally with 1-5 sparse rows of small conic decurved teeth; posterior ramus without teeth. Cirrus VI with 4-9 (6.0) pairs of setae on anterior margins of median segments. Basidorsal point of penis long, narrow, nude.

Color. — Shell dirty white, usually with edges of parietes purple or with purple striae on one or more compartments, sometimes dull purple. Radii usually purple, sometimes white with purple splotches, less often entirely white. Alae purple with white summits. Epicuticle yellowish brown. Sheath

dull purple or grayish purple. Scutum externally purple, usually with white band at base or medially; color sometimes limited to 1 or 2 bands along tergal margin; internally, lower half usually purple, upper half white; sometimes purple except for white ridges and pits. Tergum externally purple with white spur fasciole, usually with longitudinal hyaline lines between spur fasciole and carinal segment; internally, purple with white articular ridge and spur, crests for depressor muscle also usually white.

Measurements. — Carinorostral diameter of holotype 31 mm, height 23 mm. Diameter of largest specimen examined 33 mm, greatest height 21 mm.

Variations. — Other than in the degree of corrosion, specimens from Costa Rica and Panama show no consistent differences. Specimens from both localities, however, differed somewhat from Pilsbry's (1916) description of Peruvian specimens. In our material, the bases have radial tubes, except sometimes near the original point of attachment, with fine transverse septa; the bases in the type material have tubes only near the periphery. Pilsbry did not mention transverse septa. The number of parietal tubes in the rostrum varies from 12, as noted by Pilsbry, to 18. Pilsbry's Peruvian specimens are dirty purplish white or pale dull purple without longitudinal stripes, whereas many of the Panamic and most of the Costa Rican specimens are striped, at least on some compartments.

Habitat. — Intertidal; on mangroves, rocks, and pilings.

Remarks. — Although Pilsbry (1909) described *B. peruvianus* as a distinct species, he subsequently (Pilsbry, 1916) assigned it as a subspecies of *B. amphitrite*. In view of the current interpretation of *B. a. amphitrite* we recognize *B. peruvianus* as a distinct species.

The northern limit of *B. peruvianus* has been extended to Costa Rica. The absence of this species in the relatively extensive collections from Ecuador can not be explained as collections were made in habitats similar to those in which *B. peruvianus* occurs over the rest of its range.

Results of the distance and discriminant functions indicate that *B. peruvianus* is most closely allied to *B. inexpectatus* ($D^2 = 12.08$), but is sufficiently distinct to be excluded from the cluster, *B. venustus* — *B. inexpectatus* (D-2:1). As previously mentioned, *B. peruvianus* can usually be readily distinguished from *B. inexpectatus* by the characters of the opercular valves. It is always distinguished from the latter species by the lack of complex setae on cirrus III. Pilsbry (1916) stressed the colored sheath in *B. a. peruvianus* as a diagnostic character to differentiate this taxon from other subspecies of *B. amphitrite*. However, *B. inexpectatus*, as well as some other species of the *amphitrite* complex, also have a colored sheath.

In our material from Costa Rica, *B. peruvianus* was associated with

Tetrabalanus polygenus Cornwall. The opercular valves of this species are very similar to *B. peruvianus* (cf. Zullo, 1969, figs. 7-10), as are the mouth parts and cirri. Zullo's figures were of a specimen from Costa Rica; however, neither he nor Cornwall (1941) noted the associations of *T. polygenus* with other species. In Ecuador, where, as we have stated, we failed to find *B. peruvianus, T. polygenus* was associated with other species of the complex, i.e., *B. inexpectatus, B. dentivarians,* and *B. improvisus.*

ZOOGEOGRAPHY

The past uncertainty and ambiguity of the status of many of the taxa has made it difficult to assess the geographic distribution of members of the *B. amphitrite* complex. Generally the distribution is limited to tropical and warm temperate provinces. Only *B. improvisus* has a notable latitudinal distribution. With the exception of the *B. concavus* subgroup, the groups and subgroups recognized herein have one or more representatives with broad distributions. Three of the species of the *amphitrite* group virtually have world-wide distributions, i.e., *B. a. amphitrite, B. eburneus,* and *B. improvisus.* One of the other two taxa of this group is endemic in the Salton Sea, California; the second is apparently restricted to the Americas' Atlantic. One member of each of the remaining groups or subgroups, i.e., *B. pallidus, B. reticulatus,* and *B. venustus,* also has a wide distribution but, unlike the three species of the *amphitrite* group, these species have not been recorded from the eastern Pacific. However, two of these divisions are represented in the latter region by the endemic species, *B. inexpectatus* and *B. peruvianus* of the *venustus* subgroup and *B. suturaltus* and *B. dentivarians* of the *pallidus* group The latter group also has an endemic representative, *B. citerosum,* in Brazil, and two species in the western Pacific, i.e., *B. albicostatus,* limited to the Japanese and East Asian seas, and *B. kondakovi,* with a wider range, extending to New Zealand and to the western part of the Indian Ocean. *B. variegatus* has a range similar to that of *B. kondakovi.* The other member of its subgroup, *B. reticulatus,* although only recently recognized in the Americas' Atlantic, appears, at least in some parts of south Florida, to be replacing *B. a. amphitrite;* whereas, in Japanese waters the reverse situation has occurred (cf. Utinomi, 1967). The *concavus* subgroup is well represented in the eastern Pacific where *B. c. pacificus* is found in the warm temperate region and is replaced in the tropics by *B. c. mexicanus.* As the other two subspecies recognized in the *concavus* subgroup are known only from the type localities of Hong Kong and Dar-es-Salaam, respectively, and the status of other taxa formerly referred to *B. concavus* is uncertain, the distribution of this subgroup remains in doubt. Although most members

of the *amphitrite* complex occupy intertidal habitas, some extend into the upper part of the subtidal; one species, *B. poecilotheca,* of the *venustus* subgroup, however, occurs at depths ranging from 80 to greater than 500 meters in the Malay Archipelago and Indian Ocean.

SUMMARY

During the course of this study, all taxa formerly assigned to, or thought to be related to, *Balanus amphitrite* Darwin have been reviewed. A number of taxa have been placed in synonymy or otherwise suppressed, with the result that twenty-three species or subspecies are considered herein to represent the *B. amphitrite* complex. All taxa have been redescribed in detail and, within the complex, two morphologically distinct groups and three additional subgroups have been established, i.e., the *amphitrite* and *pallidus* groups and the subgroups, *variegatus, concavus,* and *venustus.*

The availability of large samples in the majority of the taxa has made it possible to qualitatively and quantitatively evaluate intraspecific variation in characters presumed to be diagnostic. Consequently, certain characters, such as shell color, strength of the adductor ridge of the scutum, and number of teeth on the mandible, have been found to be little or no taxonomic value. However, a number of characters, heretofore not reported for species of the complex, have been recognized; they have aided considerably in species differentiation and in the evaluation of relationships.

In addition, quantitative characters and interspecific affinities and divergences have been examined with the use of multivariate statistical tools of the generalized distance and discriminant functions. The discriminant function has also been found useful in the separation of members of a closely related species-pair, and in the evaluation of diagnostic characters.

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APPENDICES

APPENDIX A. PARAMETERS FOR 15 QUANTITATIVE CHARACTERS OF 16 TAXA OF THE *AMPHITRITE*-COMPLEX

A-1. Parameters for 15 Quantitative Characters of *B. amphitrite amphitrite* (n = 272)

	Character	Character Range	Mean	Standard Deviation
1.	spur width/basal margin	0.14-0.48	0.28	0.06
2.	spur length/spur width	0.47-1.76	0.91	0.23
3.	distance from angle/spur width	0.24-2.11	0.88	0.32
4.	distance from angle/spur length	0.36-1.65	0.96	0.22
5.	distance from angle/basal margin	0.11-0.34	0.23	0.04
6.	spur length/basal margin	0.17-0.34	0.24	0.04
7.	articular ridge/tergal margin	0.46-0.84	0.63	0.06
8.	articular ridge/occludent margin	0.32-0.55	0.44	0.04
9.	average number of teeth on labrum	8.00-23.00	14.18	2.81
10.	average number of spines on first maxilla	4.00-15.00	7.07	1.43
11.	average number of teeth on mandible	4.00-6.00	5.01	0.11
12.	average number of segments, cirrus I	0.00-9.50	4.68	1.29
13.	average number of segments, cirrus II	0.00-6.00	2.10	0.93
14.	average number of segments, cirrus III	-1.00 to 4.50	2.66	0.84
15.	average number of paired setae, cirrus VI	3.00-12.00	7.23	1.61

A-2. Parameters for 15 Quantitative Characters of *B. amphitrite saltonensis* (n = 201)

	Character	Character Range	Mean	Standard Deviation
1.	spur width/basal margin	0.13-0.36	0.22	0.04
2.	spur length/spur width	0.64-2.00	1.21	0.26
3.	distance from angle/spur width	0.42-2.65	1.30	0.37
4.	distance from angle/spur length	0.48-2.00	1.07	0.24
5.	distance from angle/basal margin	0.15-0.39	0.27	0.04
6.	spur length/basal margin	0.16-0.41	0.26	0.04
7.	articular ridge/tergal margin	0.47-0.76	0.63	0.05
8.	articular ridge/occludent margin	0.33-0.54	0.43	0.04
9.	average number of teeth on labrum	9.50-23.50	14.72	2.40
10.	average number of spines on first maxilla	4.50-12.00	6.77	1.05
11.	average number of teeth on mandible	4.50-6.00	5.02	0.16
12.	average number of segments, cirrus I	2.50-8.00	4.75	1.06
13.	average number of segments, cirrus II	-1.00 to 4.00	1.76	0.75
14.	average number of segments, cirrus III	0.00-4.00	2.78	0.66
15.	average number of paired setae, cirrus VI	5.00-14.00	10.09	1.82

APPENDIX A (Continued).

A-3. Parameters for 15 Quantitative Characters of *B. subalbidus* (n = 95)

	Character	Character Range	Mean	Standard Deviation
1.	spur width/basal margin	0.26-0.49	0.36	0.05
2.	spur length/spur width	0.45-1.27	0.91	0.18
3.	distance from angle/spur width	0.05-0.73	0.38	0.16
4.	distance from angle/spur length	0.08-0.70	0.41	0.13
5.	distance from angle/basal margin	0.02-0.21	0.13	0.04
6.	spur length/basal margin	0.19-0.44	0.32	0.05
7.	articular ridge/tergal margin	0.05-0.69	0.60	0.05
8.	articular ridge/occludent margin	0.35-0.48	0.41	0.03
9.	average number of teeth on labrum	8.50-23.00	14.29	3.35
10.	average number of spines on first maxilla	5.00-12.00	8.38	1.64
11.	average number of teeth on mandible	5.00-6.00	5.08	0.21
12.	average number of segments, cirrus I	2.00-11.00	4.96	1.48
13.	average number of segments, cirrus II	0.00-5.50	2.04	1.24
14.	average number of segments, cirrus III	1.00-6.00	3.43	0.98
15.	average number of paired setae, cirrus VI	5.50-13.50	8.02	1.53

A-4. Parameters for 15 Quantitative Characters of *B. eburneus* (n = 98)

	Character	Character Range	Mean	Standard Deviation
1.	spur width/basal margin	0.16-0.40	0.28	0.05
2.	spur length/spur width	0.77-2.25	1.29	0.26
3.	distance from angle/spur width	0.31-1.55	0.74	0.24
4.	distance from angle/spur length	0.34-0.97	0.60	0.13
5.	distance from angle/basal margin	0.12-0.28	0.20	0.03
6.	spur length/basal margin	0.26-0.47	0.34	0.04
7.	articular ridge/tergal margin	0.56-0.76	0.65	0.04
8.	articular ridge/occludent margin	0.38-0.51	0.44	0.03
9.	average number of teeth on labrum	7.00-30.50	13.49	4.33
10.	average number of spines on first maxilla	7.00-12.00	9.34	1.38
11.	average number of teeth on mandible	5.00-7.00	5.87	0.32
12.	average number of segments, cirrus I	3.00-13.00	6.03	1.59
13.	average number of segments, cirrus II	1.50-6.50	3.13	0.83
14.	average number of segments, cirrus III	0.00-5.00	2.81	1.13
15.	average number of paired setae, cirrus VI	4.50-10.50	6.97	1.47

APPENDIX A (Continued).

A-5. Parameters for 15 Quantitative Characters of *B. improvisus* (n = 93)

	Character	Character Range	Mean	Standard Deviation
1.	spur width/basal margin	0.12-0.36	0.21	0.05
2.	spur length/spur width	0.73-2.44	1.59	0.37
3.	distance from angle/spur width	0.29-1.80	0.87	0.31
4.	distance from angle/spur length	0.27-0.91	0.54	0.13
5.	distance from angle/basal margin	0.09-0.25	0.17	0.04
6.	spur length/basal margin	0.24-0.47	0.32	0.04
7.	articular ridge/tergal margin	0.60-0.89	0.74	0.06
8.	articular ridge/occludent margin	0.33-0.56	0.45	0.04
9.	average number of teeth on labrum	7.50-21.50	15.11	2.94
10.	average number of spines on first maxilla	4.00-10.00	6.32	1.00
11.	average number of teeth on mandible	5.00-6.00	5.88	0.30
12.	average number of segments, cirrus I	1.00-5.50	2.89	1.16
13.	average number of segments, cirrus II	-2.00 to 4.00	1.55	1.01
14.	average number of segments, cirrus III	1.00-7.00	3.86	1.06
15.	average number of paired setae, cirrus VI	5.00-8.00	6.09	0.89

A-6. Parameters for 15 Quantitative Characters of *B. variegatus* (n = 61)

	Character	Character Range	Mean	Standard Deviation
1.	spur width/basal margin	0.15-0.35	0.27	0.04
2.	spur length/spur width	0.80-2.19	1.26	0.24
3.	distance from angle/spur width	0.56-2.10	0.93	0.27
4.	distance from angle/spur length	0.50-1.06	0.73	0.12
5.	distance from angle/basal margin	0.17-0.31	0.24	0.03
6.	spur length/basal margin	0.25-0.42	0.33	0.03
7.	articular ridge/tergal margin	0.59-0.86	0.71	0.06
8.	articular ridge/occludent margin	0.38-0.56	0.48	0.04
9.	average number of teeth on labrum	1.50-4.00	3.64	0.54
10.	average number of spines on first maxilla	5.00-10.00	6.89	0.98
11.	average number of teeth on mandible	5.00-6.00	5.43	0.45
12.	average number of segments, cirrus I	2.00-7.00	3.80	1.13
13.	average number of segments, cirrus II	-0.50 to 3.50	1.43	0.85
14.	average number of segments, cirrus III	1.00-5.00	2.84	0.84
15.	average number of paired setae, cirrus VI	4.00-6.00	4.80	0.62

APPENDIX A (Continued).

A-7. Parameters for 15 Quantitative Characters of *B. reticulatus* (n = 108)

	Character	Character Range	Mean	Standard Deviation
1.	spur width/basal margin	0.12-0.34	0.23	0.04
2.	spur length/spur width	0.77-2.05	1.25	0.29
3.	distance from angle/spur width	0.51-1.81	0.97	0.28
4.	distance from angle/spur length	0.52-1.03	0.77	0.11
5.	distance from angle/basal margin	0.15-0.30	0.22	0.03
6.	spur length/basal margin	0.20-0.38	0.28	0.03
7.	articular ridge/tergal margin	0.55-0.80	0.67	0.05
8.	articular ridge/occludent margin	0.36-0.56	0.46	0.04
9.	average number of teeth on labrum	0.50-5.00	3.77	0.60
10.	average number of spines on first maxilla	3.00-15.00	6.56	1.51
11.	average number of teeth on mandible	4.50-7.00	5.67	0.48
12.	average number of segments, cirrus I	2.00-9.00	4.42	1.19
13.	average number of segments, cirrus II	-0.50 to 4.00	1.27	0.76
14.	average number of segments, cirrus III	0.00-4.00	2.85	0.71
15.	average number of paired setae, cirrus VI	4.00-6.00	4.95	0.56

A-8. Parameters for 15 Quantitative Characters of *B. kondakovi* (n = 60)

	Character	Character Range	Mean	Standard Deviation
1.	spur width/basal margin	0.16-0.33	0.24	0.04
2.	spur length/spur width	0.80-1.93	1.27	0.27
3.	distance from angle/spur width	0.52-1.96	1.11	0.41
4.	distance from angle/spur length	0.35-1.79	0.87	0.23
5.	distance from angle/basal margin	0.14-0.44	0.25	0.06
6.	spur length/basal margin	0.22-0.42	0.30	0.04
7.	articular ridge/tergal margin	0.50-0.74	0.61	0.05
8.	articular ridge/occludent margin	0.31-0.51	0.41	0.05
9.	average number of teeth on labrum	0.50-6.00	4.01	0.99
10.	average number of spines on first maxilla	3.50-8.50	6.06	1.09
11.	average number of teeth on mandible	5.00-6.00	5.07	0.25
12.	average number of segments, cirrus I	0.50-6.00	3.82	1.36
13.	average number of segments, cirrus II	0.00-4.00	1.63	0.92
14.	average number of segments, cirrus III	0.00-4.00	2.98	0.91
15.	average number of paired setae, cirrus VI	3.00-7.25	5.10	1.35

APPENDIX A (Continued).

A-9. Parameters for 15 Quantitative Characters of *B. citerosum* (n = 90)

	Character	Character Range	Mean	Standard Deviation
1.	spur width/basal margin	0.18-0.39	0.27	0.05
2.	spur length/spur width	0.80-2.71	1.54	0.36
3.	distance from angle/spur width	0.22-1.04	0.61	0.19
4.	distance from angle/spur length	0.19-0.61	0.39	0.09
5.	distance from angle/basal margin	0.08-0.26	0.16	0.03
6.	spur length/basal margin	0.25-0.52	0.40	0.05
7.	articular ridge/tergal margin	0.50-0.76	0.65	0.05
8.	articular ridge/occludent margin	0.33-0.51	0.41	0.04
9.	average number of teeth on labrum	0.00-4.00	2.77	0.55
10.	average number of spines on first maxilla	3.00-18.50	6.41	1.99
11.	average number of teeth on mandible	5.00-6.00	5.03	0.15
12.	average number of segments, cirrus I	1.00-8.50	4.11	1.44
13.	average number of segments, cirrus II	-1.00 to 3.50	0.67	1.02
14.	average number of segments, cirrus III	0.00-5.00	2.70	0.97
15.	average number of paired setae, cirrus VI	4.00-9.00	5.79	1.25

A-10. Parameters for 15 Quantitative Characters of *B. suturaltus* (n = 41)

	Character	Character Range	Mean	Standard Deviation
1.	spur width/basal margin	0.19-0.40	0.27	0.04
2.	spur length/spur width	1.14-2.45	1.79	0.32
3.	distance from angle/spur width	0.49-1.56	0.87	0.23
4.	distance from angle/spur length	0.33-0.68	0.48	0.07
5.	distance from angle/basal margin	0.15-0.30	0.23	0.03
6.	spur length/basal margin	0.39-0.58	0.47	0.04
7.	articular ridge/tergal margin	0.54-0.82	0.69	0.06
8.	articular ridge/occludent margin	0.32-0.51	0.42	0.04
9.	average number of teeth on labrum	1.50-7.00	4.00	1.35
10.	average number of spines on first maxilla	6.00-11.50	8.40	1.16
11.	average number of teeth on mandible	.....	5.00	0.00
12.	average number of segments, cirrus I	2.50-8.50	4.98	1.30
13.	average number of segments, cirrus II	-1.00 to 4.50	1.28	1.12
14.	average number of segments, cirrus III	1.50-6.00	4.09	0.99
15.	average number of paired setae, cirrus VI	3.50-5.00	4.24	0.52

APPENDIX A (Continued).

A-11. Parameters for 15 Quantitative Characters of *B. dentivarians* (n = 52).

	Character	Character Range	Mean	Standard Deviation
1.	spur width/basal margin	0.15-0.24	0.19	0.02
2.	spur length/spur width	2.09-4.46	2.90	0.40
3.	distance from angle/spur width	0.74-1.73	1.21	0.22
4.	distance from angle/spur length	0.26-0.55	0.42	0.06
5.	distance from angle/basal margin	0.16-0.28	0.23	0.03
6.	spur length/basal margin	0.44-0.70	0.56	0.05
7.	articular ridge/tergal margin	0.53-0.73	0.65	0.04
8.	articular ridge/occludent margin	0.32-0.41	0.36	0.02
9.	average number of teeth on labrum	2.00-6.50	3.44	0.74
10.	average number of spines on first maxilla	6.00-12.00	9.49	0.96
11.	average number of teeth on mandible	5.00-6.00	5.88	0.28
12.	average number of segments, cirrus I	0.00-9.50	6.36	1.81
13.	average number of segments, cirrus II	-2.00 to 5.00	1.88	1.60
14.	average number of segments, cirrus III	2.00-6.00	4.38	0.87
15.	average number of paired setae, cirrus VI	7.00-11.00	8.58	0.75

A-12. Parameters for 15 Quantitative Characters of *B. concavus pacificus* (n = 71)

	Character	Character Range	Mean	Standard Deviation
1.	spur width/basal margin	0.17-0.38	0.28	0.05
2.	spur length/spur width	1.13-2.40	1.57	0.24
3.	distance from angle/spur width	0.66-1.75	1.00	0.24
4.	distance from angle/spur length	0.40-1.12	0.64	0.11
5.	distance from angle/basal margin	0.21-0.33	0.27	0.03
6.	spur length/basal margin	0.25-0.58	0.43	0.06
7.	articular ridge/tergal margin	0.54-0.88	0.72	0.07
8.	articular ridge/occludent margin	0.35-0.58	0.47	0.05
9.	average number of teeth on labrum	0.00-3.50	2.56	0.68
10.	average number of spines on first maxilla	3.00-10.00	7.18	1.76
11.	average number of teeth on mandible	.....	5.00	0.00
12.	average number of segments, cirrus I	0.00-6.50	3.33	1.04
13.	average number of segments, cirrus II	-2.00 to 3.00	0.61	1.01
14.	average number of segments, cirrus III	1.00-6.00	2.90	0.95
15.	average number of paired setae, cirrus VI	3.00-5.00	3.99	0.46

APPENDIX A (Continued).

A-13. Parameters for 15 Quantitative Characters of *B. concavus mexicanus* (n = 104)

Character		Character Range	Mean	Standard Deviation
1.	spur width/basal margin	0.15-0.33	0.24	0.03
2.	spur length/spur width	1.11-2.77	1.71	0.28
3.	distance from angle/spur width	0.58-2.36	1.11	0.30
4.	distance from angle/spur length	0.41-0.92	0.65	0.11
5.	distance from angle/basal margin	0.15-0.36	0.26	0.04
6.	spur length/basal margin	0.29-0.54	0.41	0.05
7.	articular ridge/tergal margin	0.50-0.88	0.69	0.06
8.	articular ridge/occludent margin	0.32-0.58	0.45	0.05
9.	average number of teeth on labrum	0.00-3.00	2.65	0.57
10.	average number of spines on first maxilla	2.50-8.50	5.32	1.30
11.	average number of teeth on mandible	.....	5.00	0.00
12.	average number of segments, cirrus I	0.50-4.50	2.54	0.82
13.	average number of segments, cirrus II	-2.00 to 2.00	0.20	0.85
14.	average number of segments, cirrus III	0.00-5.00	2.40	0.80
15.	average number of paired setae, cirrus VI	2.75-4.50	3.56	0.51

A-14. Parameters for 15 Quantitative Characters of *B. venustus* (n = 104)

Character		Character Range	Mean	Standard Deviation
1.	spur width/basal margin	0.17-0.42	0.30	0.06
2.	spur length/spur width	0.50-1.58	0.81	0.23
3.	distance from angle/spur width	0.14-1.33	0.45	0.23
4.	distance from angle/spur length	0.25-1.11	0.53	0.16
5.	distance from angle/basal margin	0.06-0.24	0.12	0.04
6.	spur length/basal margin	0.17-0.31	0.24	0.03
7.	articular ridge/tergal margin	0.61-0.92	0.76	0.06
8.	articular ridge/occludent margin	0.42-0.63	0.53	0.04
9.	average number of teeth on labrum	1.00-3.00	2.86	0.37
10.	average number of spines on first maxilla	3.00-6.50	4.60	0.80
11.	average number of teeth on mandible	5.00-6.00	5.06	0.23
12.	average number of segments, cirrus I	2.00-9.00	5.31	1.40
13.	average number of segments, cirrus II	-0.50 to 3.00	1.40	0.64
14.	average number of segments, cirrus III	0.00-4.00	2.21	0.58
15.	average number of paired setae, cirrus VI	4.00-6.25	4.88	0.67

APPENDIX A (Continued).

A-15. Parameters for 15 Quantitative Characters of *B. inexpectatus* (n = 151).

	Character	Character Range	Mean	Standard Deviation
1.	spur width/basal margin	0.25–0.50	0.38	0.05
2.	spur length/spur width	0.42–1.00	0.67	0.12
3.	distance from angle/spur width	0.07–0.69	0.32	0.13
4.	distance from angle/spur length	0.11–0.90	0.47	0.15
5.	distance from angle/basal margin	0.04–0.19	0.11	0.03
6.	spur length/basal margin	0.19–0.32	0.25	0.03
7.	articular ridge/tergal margin	0.62–0.87	0.74	0.05
8.	articular ridge/occludent margin	0.33–0.58	0.49	0.04
9.	average number of teeth on labrum	0.50–7.00	2.89	0.65
10.	average number of spines on first maxilla	3.00–10.00	5.91	1.09
11.	average number of teeth on mandible	5.00–6.50	5.01	0.12
12.	average number of segments, cirrus I	0.50–9.00	4.88	1.24
13.	average number of segments, cirrus II	0.00–3.00	1.16	0.77
14.	average number of segments, cirrus III	1.00–4.50	2.53	0.72
15.	average number of paired setae, cirrus VI	4.25–7.00	5.62	0.58

A-16. Parameters for 15 Quantitative Characters of *B. peruvianus* (n = 87).

	Character	Character Range	Mean	Standard Deviation
1.	spur width/basal margin	0.24–0.48	0.33	0.05
2.	spur length/spur width	0.60–1.58	0.93	0.17
3.	distance from angle/spur width	0.17–0.95	0.50	0.16
4.	distance from angle/spur width	0.19–0.98	0.54	0.14
5.	distance from angle/basal margin	0.07–0.25	0.16	0.04
6.	spur length/basal margin	0.21–0.44	0.30	0.04
7.	articular ridge/tergal margin	0.58–0.83	0.72	0.05
8.	articular ridge/occludent margin	0.45–0.65	0.52	0.04
9.	average number of teeth on labrum	1.00–3.00	2.49	0.57
10.	average number of spines on first maxilla	5.00–12.00	7.88	1.49
11.	average number of teeth on mandible	5.00–6.00	5.01	0.05
12.	average number of segments, cirrus I	3.50–18.00	8.65	2.28
13.	average number of segments, cirrus II	0.00–4.00	1.86	1.03
14.	average number of segments, cirrus III	1.00–5.00	3.26	1.03
15.	average number of paired setae, cirrus VI	4.00–8.50	5.95	0.77

APPENDIX B. PARAMETERS FOR 15 QUANTITATIVE CHARACTERS OF 5 POPULATIONS OF *B. AMPHITRITE AMPHITRITE*

B-1. Parameters for 15 Quantitative Characters of *B. a. amphitrite* from the Central and West Pacific (n = 28)

Character	Character Range	Mean	Standard Deviation
1. spur width/basal margin	0.16–0.38	0.29	0.05
2. spur length/spur width	0.63–1.35	0.91	0.19
3. distance from angle/spur width	0.46–1.88	0.84	0.31
4. distance from angle/spur length	0.58–1.39	0.91	0.19
5. distance from angle/basal margin	0.15–0.31	0.23	0.04
6. spur length/basal margin	0.21–0.32	0.25	0.03
7. articular ridge/tergal margin	0.50–0.75	0.64	0.06
8. articular ridge/occludent margin	0.34–0.55	0.45	0.05
9. average number of teeth on labrum	8.00–20.00	14.75	3.43
10. average number of spines on first maxilla	4.00–13.00	6.93	1.66
11. average number of teeth on mandible	5.00–6.00	5.04	0.19
12. average number of segments, cirrus I	2.50–8.00	5.11	1.45
13. average number of segments, cirrus II	0.50–5.00	2.18	1.08
14. average number of segments, cirrus III	1.00–4.00	2.75	0.80
15. average number of paired setae, cirrus VI	4.50–10.00	6.23	1.38

B-2. Parameters for 15 Quantitative Characters of *B. a. amphitrite* from the East Pacific (n = 64)

Character	Character Range	Mean	Standard Deviation
1. spur width/basal margin	0.14–0.48	0.32	0.07
2. spur length/spur width	0.47–1.68	0.79	0.22
3. distance from angle/spur width	0.24–2.00	0.70	0.32
4. distance from angle/spur length	0.36–1.32	0.86	0.23
5. distance from angle/basal margin	0.11–0.29	0.20	0.04
6. spur length/basal margin	0.17–0.33	0.24	0.03
7. articular ridge/tergal margin	0.52–0.80	0.64	0.06
8. articular ridge/occludent margin	0.37–0.55	0.44	0.04
9. average number of teeth on labrum	10.00–23.00	15.12	2.65
10. average number of spines on first maxilla	5.00–15.00	7.67	1.57
11. average number of teeth on mandible	5.00–6.00	5.02	0.14
12. average number of segments, cirrus I	2.00–9.50	5.33	1.41
13. average number of segments, cirrus II	0.00–4.50	2.16	0.94
14. average number of segments, cirrus III	-1.00 to 4.50	2.63	0.97
15. average number of paired setae, cirrus VI	3.50–10.25	7.48	1.28

APPENDIX B (Continued).

B-3. Parameters for 15 Quantitative Characters of *B. a. amphitrite* from the Gulf of Mexico (n = 59)

	Character	Character Range	Mean	Standard Deviation
1.	spur width/basal margin	0.15-0.38	0.25	0.05
2.	spur length/spur width	0.62-1.76	1.07	0.22
3.	distance from angle/spur width	0.40-2.11	1.07	0.31
4.	distance from angle/spur length	0.64-1.52	1.00	0.19
5.	distance from angle/basal margin	0.14-0.34	0.25	0.03
6.	spur length/basal margin	0.17-0.34	0.26	0.03
7.	articular ridge/tergal margin	0.46-0.80	0.61	0.05
8.	articular ridge/occludent margin	0.35-0.53	0.42	0.04
9.	average number of teeth on labrum	9.50-22.50	14.77	2.86
10.	average number of spines on first maxilla	4.00-13.50	6.71	1.29
11.	average number of teeth on mandible	4.00-5.00	4.98	0.13
12.	average number of segments, cirrus I	2.00-6.50	4.17	1.02
13.	average number of segments, cirrus II	1.00-4.00	2.51	0.90
14.	average number of segments, cirrus III	1.00-4.00	2.80	0.60
15.	average number of paired setae, cirrus VI	5.00-8.25	6.21	0.78

B-4. Parameters for 15 Quantitative Characters of *B. a. amphitrite* from Bermuda (n = 66)

	Character	Character Range	Mean	Standard Deviation
1.	spur width/basal margin	0.16-0.37	0.26	0.05
2.	spur length/spur width	0.56-1.58	0.94	0.24
3.	distance from angle/spur width	0.46-1.83	0.98	0.30
4.	distance from angle/spur length	0.62-1.65	1.04	0.23
5.	distance from angle/basal margin	0.15-0.31	0.24	0.04
6.	spur length/basal margin	0.17-0.34	0.23	0.03
7.	articular ridge/tergal margin	0.51-0.75	0.63	0.05
8.	articular ridge/occludent margin	0.37-0.55	0.45	0.04
9.	average number of teeth on labrum	9.50-17.00	12.93	1.96
10.	average number of spines on first maxilla	4.50-10.50	7.23	1.06
11.	average number of teeth on mandible	.....	5.00	0.00
12.	average number of segments, cirrus I	1.50-6.50	4.41	1.02
13.	average number of segments, cirrus II	1.00-3.50	1.78	0.56
14.	average number of segments, cirrus III	1.50-4.00	2.67	0.67
15.	average number of paired setae, cirrus VI	6.50-12.00	8.83	0.13

APPENDIX B (Continued).

B-5. Parameters for 15 Quantitative Characters of *B. a. amphitrite* from the Mediterranean (n = 37)

	Character	Character Range	Mean	Standard Deviation
1.	spur width/basal margin	0.21-0.39	0.30	0.04
2.	spur length/spur width	0.57-1.35	0.83	0.18
3.	distance from angle/spur width	0.41-1.44	0.82	0.23
4.	distance from angle/spur length	0.51-1.55	0.99	0.21
5.	distance from angle/basal margin	0.16-0.32	0.23	0.03
6.	spur length/basal margin	0.19-0.33	0.24	0.04
7.	articular ridge/tergal margin	0.58-0.84	0.66	0.05
8.	articular ridge/occludent margin	0.35-0.55	0.44	0.04
9.	average number of teeth on labrum	9.00-20.00	13.14	2.37
10.	average number of spines on first maxilla	4.00-11.00	6.64	1.49
11.	average number of teeth on mandible	.....	5.00	0.00
12.	average number of segments, cirrus I	3.00-8.00	4.65	1.09
13.	average number of segments, cirrus II	0.00-3.50	1.64	0.74
14.	average number of segments, cirrus III	-0.50 to 4.00	2.34	1.14
15.	average number of paired setae, cirrus VI	3.00-11.00	7.05	1.61

APPENDIX C. TESTS FOR VALIDITY OF STATISTICAL TECHNIQUES

C-1. Test for Bias in Tergal and Scutal Measurements.

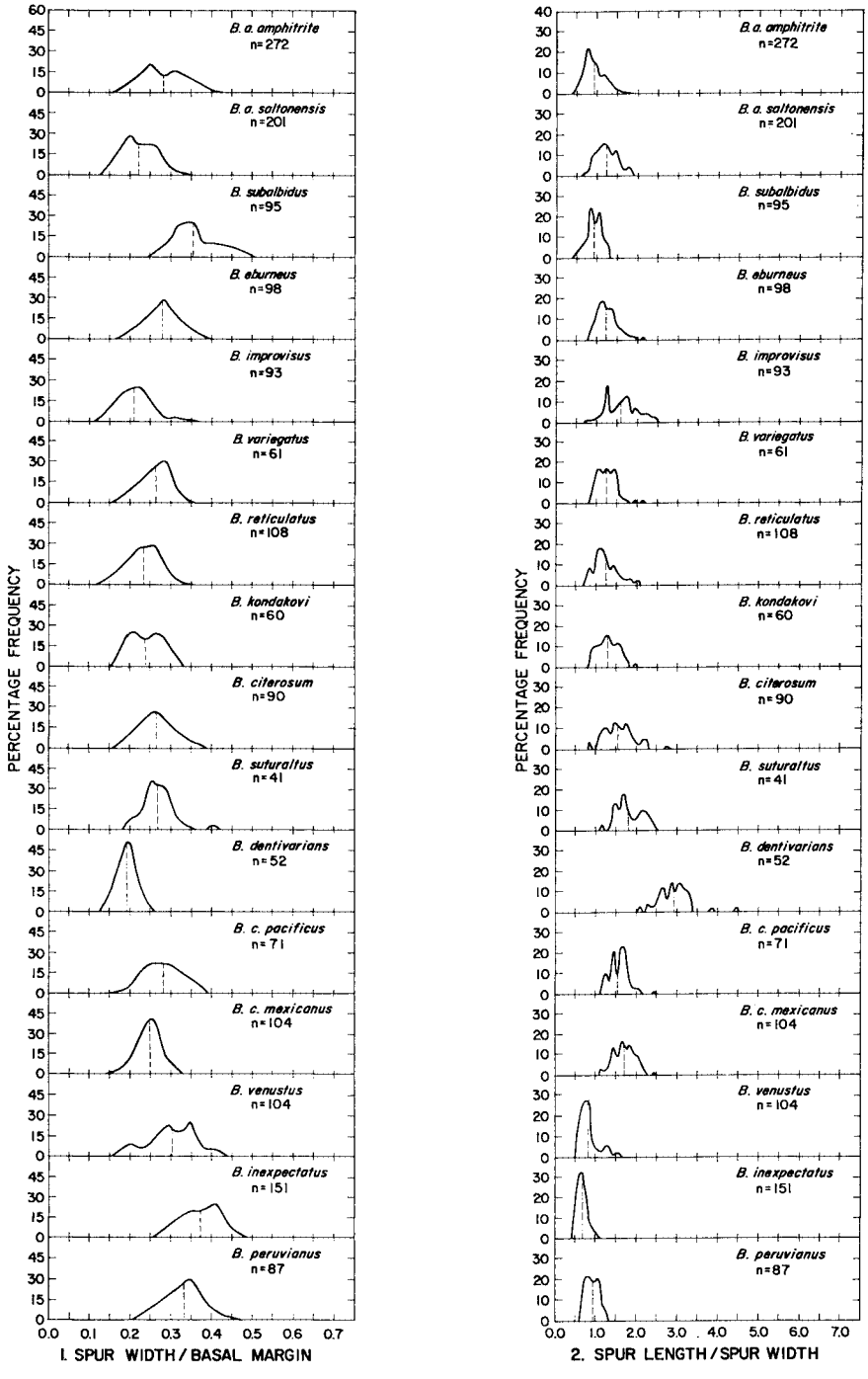
From a random sample of previously drawn terga, new drawings were made by the same artist. Measurements were made on the second series and compared with the measurements obtained from the original drawings. Mean differences between measurements from the two sets of drawings did not exceed 1.5 mm and were less than 0.5 mm in 40% of the samples. Although all tergal measurements were made by one individual, it was still necessary to test personal measurement bias; therefore, replicate measurements were made from a random sample of the original drawings. Results of these measurements had a mean average difference of less than 1.0 mm. Further, as all measurements were converted to ratios for the statistical analyses, tests for significant differences were made between ratios obtained from: 1) measurements of original and second drawings, 2) replicate measurements, and 3) measurements of a random sample of actual terga and their drawings. Results, using the t-test of significant differences between two means (Snedecor & Cochran, 1967), indicated significance at the 5 percent level for only character 2 in three taxa, for character 6 in two taxa and characters 1, 3, and 4 in one taxon. Therefore, the bias present in the tergal characters is not sufficient to have resulted in serious errors in the statistical analyses.

Similar tests were conducted to determine the amount of personal measurement bias inherent in the scutal measurements; random samples of scuta measurements was less than 0.5 mm and the test of significant differences between means of the ratios obtained for the two sets of measurements was not significant at the 5 percent level.

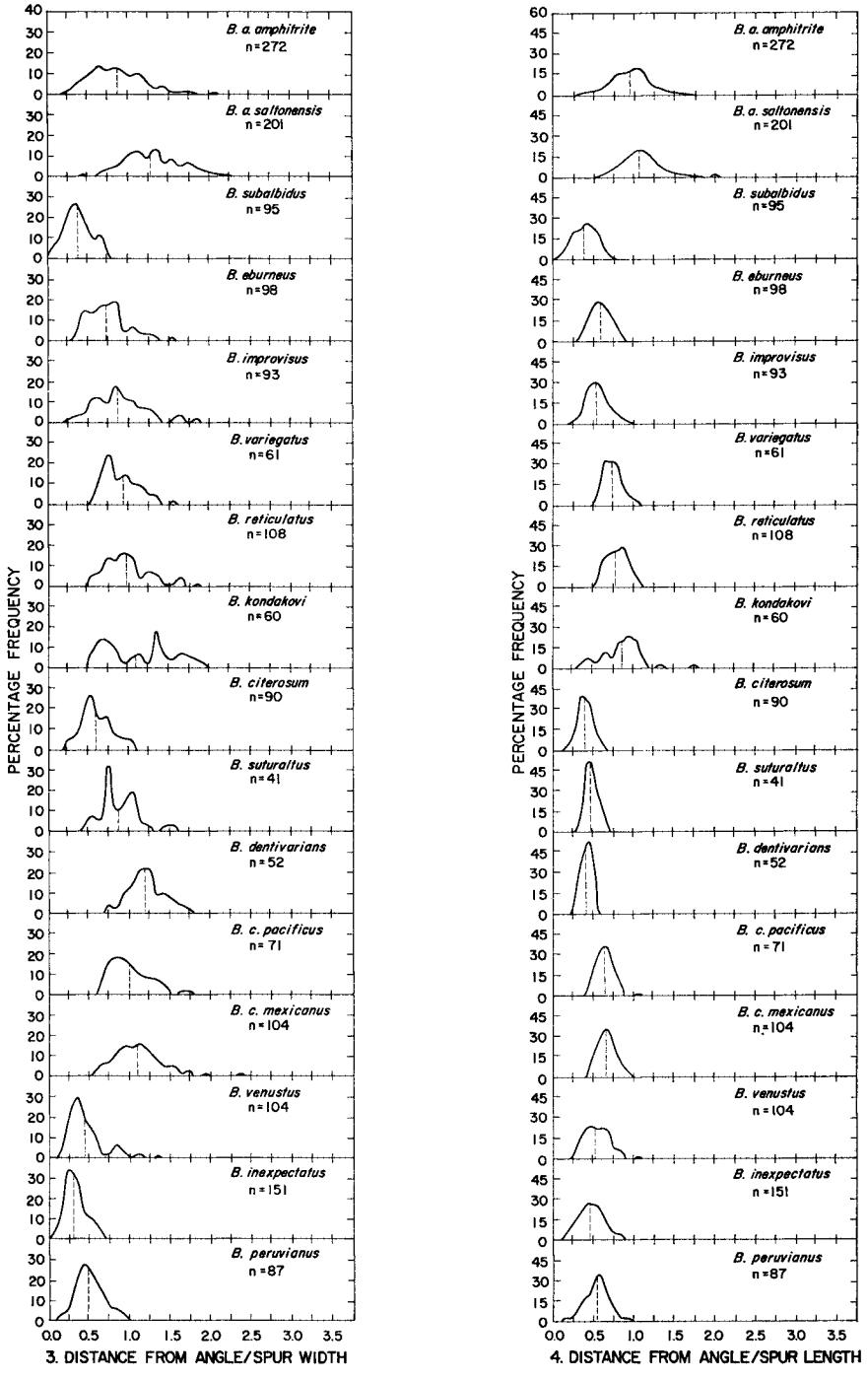
C-2. Frequency Distributions of 14 Characters of 16 Taxa of the *amphitrite* complex.

The majority of these quantitative characters show considerable intraspecific variation and interspecific overlap of ranges. Indications of skewness and bimodal distributions may be observed from an examination of the frequency distributions of 14 characters for the 16 taxa. In all taxa, deviations from the means in the remaining character, number of teeth on the mandible, were negligible. One explanation for the observed asymetry is possible allometry within the taxa. The data in the study have been obtained from samples with heterogenous size categories and unequal sample numbers within these categories; therefore, it has been necessary to determine whether allometry occurs, and if so, to assess its effect on the results of the generalized distance and discriminant functions.

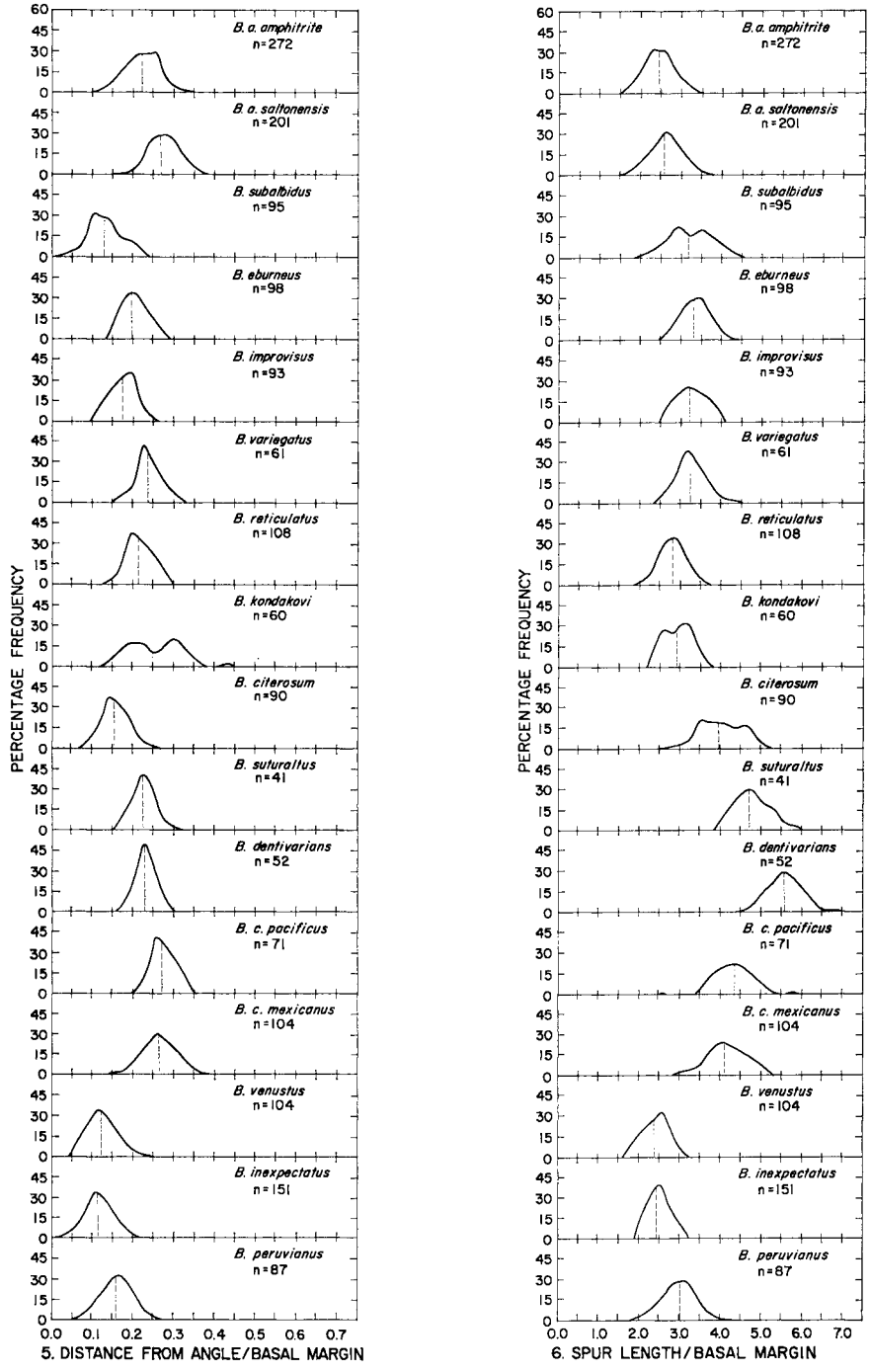
Appendix C-2 (Continued).



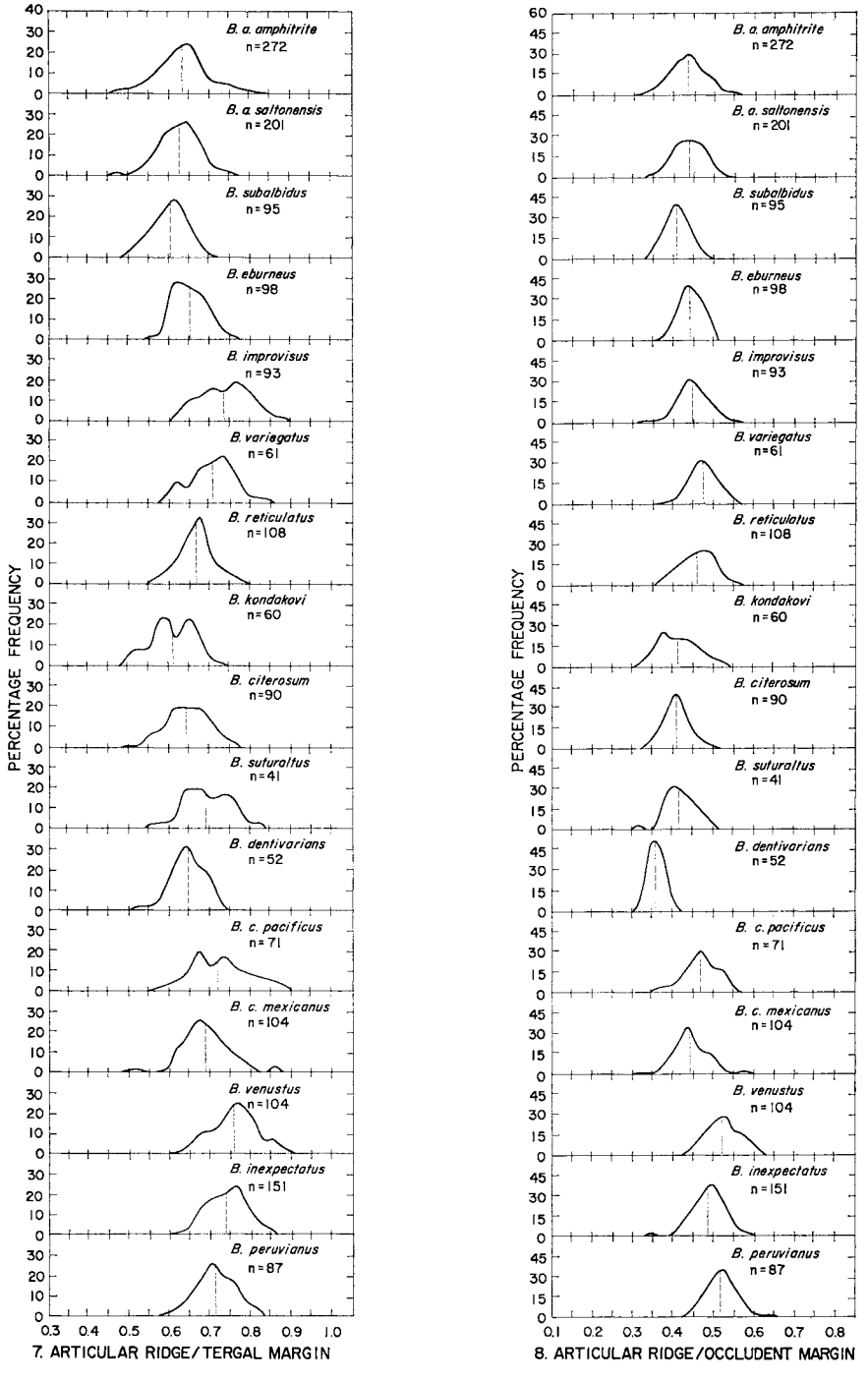
Appendix C-2 (Continued).



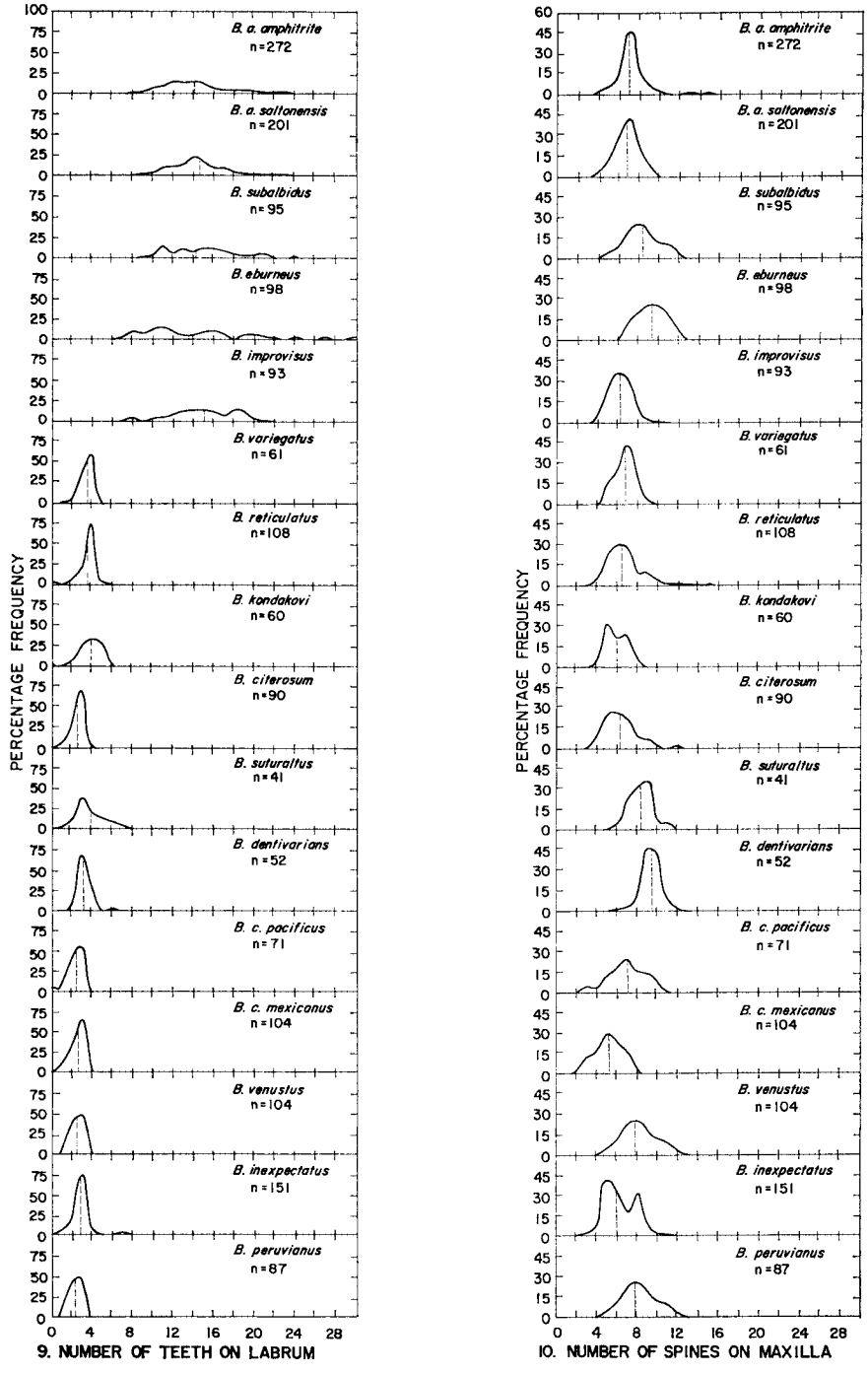
Appendix C-2 (Continued).



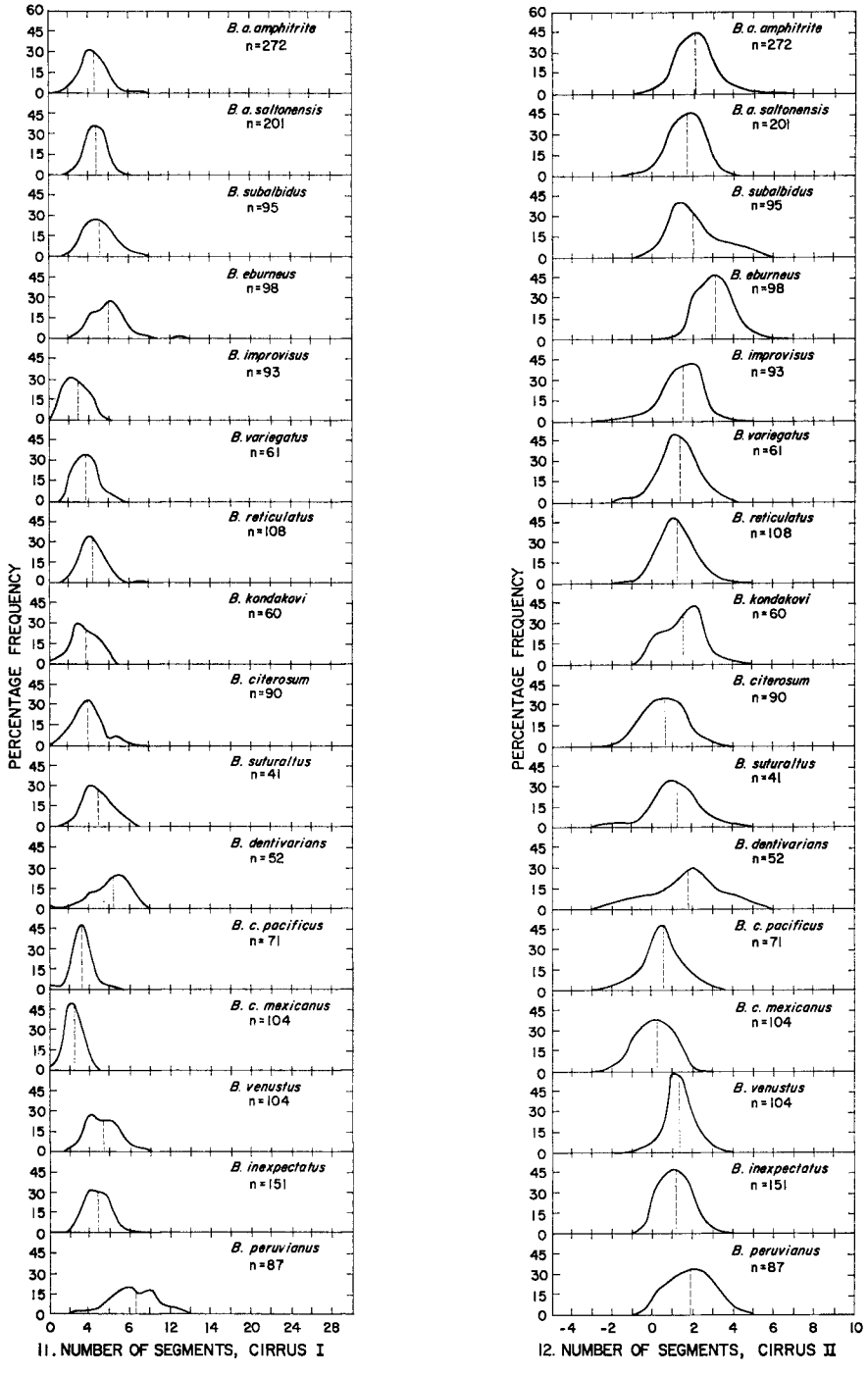
Appendix C-2 (Continued).



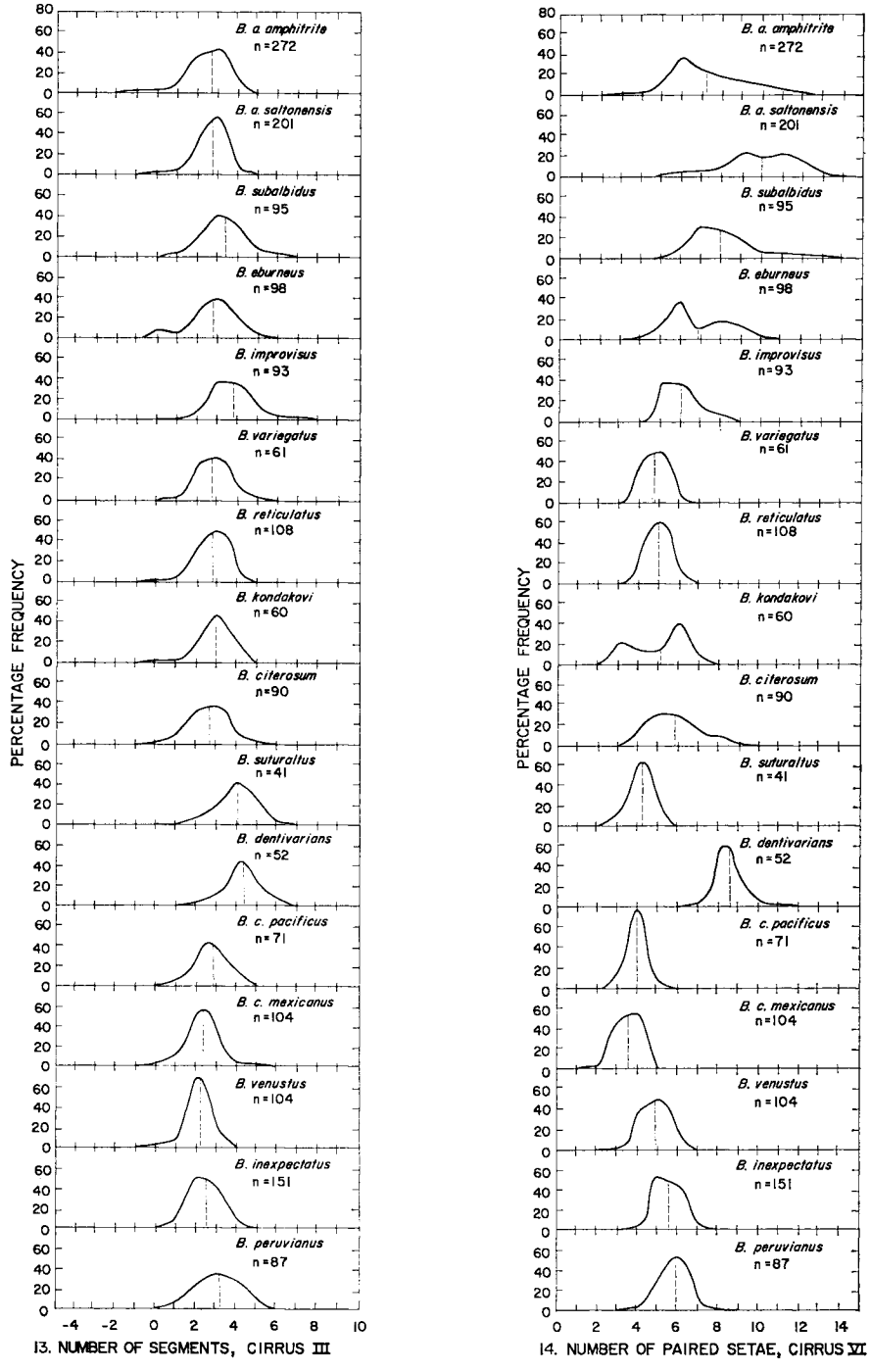
Appendix C-2 (Continued).



Appendix C-2 (Continued).



Appendix C-2 (Continued).



C-3. Test for Allometry.

Using the one-way analysis of variance (Snedecor and Cochran, 1967), we tested the null hypothesis: Allometry does not occur in the samples of the 16 taxa of the *amphitrite* complex. The results of the analyses showed significant F values at the 5 percent level for 11 of the 16 taxa in at least 50% of the characters (C-3:1). The parameters for the characters of the taxa, divided into size categories, as well as the results of the one-way analyses of variance are given in C-3:2-15.

To assess the effect of this presumed allometry on the results obtained from the distance and discriminant functions, each taxon, subdivided into its available size categories of small, medium, and large and treated as distinct populations, was analyzed using the generalized distance function. Comparison of these D^2 values with those obtained from the taxa as a whole showed no significant differences in inter- and intra-specific relations among the taxa. Therefore, it was concluded that the presumed allometry present in the samples did not affect the analyses adversely and that extensive manipulation of the original data was not required.

APPENDIX C-3.

C-3:1. Summary of Effect of Size on 14 Quantitative Characters of 16 Taxa of the *amphitrite*-complex, tested by the One-way Analysis of Variance. * Indicates Significance at the 5 Percent Level.

	Character	*B. a. amphitrite*	*B. a. saltonensis*	*B. subalbidus*	*B. eburneus*	*B. improvisus*	*B. variegatus*	*B. reticulatus*	*B. kondakovi*	*B. citerosum*	*B. subtilis*	*B. denticulatus*	*B. c. pacificus*	*B. c. mexicanus*	*B. venustus*	*B. inexpectatus*	*B. perviscanus*
1.	spur width/basal margin	*	*	*			*	*	*	*			*		*		*
2.	spur length/spur width	*	*	*			*		*	*			*		*		*
3.	distance from angle/spur width	*	*	*			*		*	*			*		*		*
4.	distance from angle/spur length	*	*	*	*				*				*	*	*		
5.	distance from angle/basal margin	*		*	*	*			*						*		*
6.	spur length/basal margin												*	*			*
7.	articular ridge/tergal margin												*	*	*		
8.	articular ridge/occludent margin								*				*	*			
9.	number of teeth on labrum	*	*	*	*					*	*		*	*	*		
10.	number of spines on first maxilla	*	*	*	*	*	*	*	*	*	*		*	*	*	*	*
12.	number of segments, cirrus I		*	*	*	*	*	*		*	*		*	*			*
13.	number of segments, cirrus II	*	*	*	*	*			*	*						*	*
14.	number of segments, cirrus III	*	*	*	*	*	*			*			*	*	*		*
15.	number of paired setae, cirrus VI	*					*		*	*		*	*				

APPENDIX C-3 (Continued). Parameters for 14 Quantitative Characters of 16 Taxa of the *amphitrite*-complex, divided into Size Categories, with Results of Analyses of Variance.

C-3:2. Parameters for spur width/basal margin and analysis of variance F-value

Taxa	Carinorostral diameter (mm)	Sample size	Character range	Mean	Standard deviation	Analysis of variance F-value
B. a. amphitrite	<8	106	0.14-0.36	0.25	0.05	*27.00
	8-15	146	0.16-0.48	0.30	0.06	
	>15	20	0.24-0.41	0.33	0.05	
B. a. saltonensis	<8	118	0.13-0.36	0.21	0.04	*18.81
	8-15	83	0.15-0.35	0.24	0.04	
	>15	..	.....	....	....	
B. subalbidus	<8	43	0.26-0.43	0.33	0.03	*24.91
	8-15	43	0.27-0.49	0.37	0.06	
	>15	9	0.37-0.48	0.43	0.03	
B. eburneus	<12	70	0.19-0.40	0.28	0.05	0.34
	12-20	28	0.16-0.36	0.29	0.05	
	>20	..	.....	....	....	
B. improvisus	<7	39	0.13-0.34	0.21	0.05	1.00
	7-11	50	0.12-0.36	0.22	0.05	
	>11	4	0.20-0.27	0.23	0.03	
B. variegatus	<8	23	0.15-0.31	0.23	0.04	*19.18
	8-15	31	0.20-0.35	0.28	0.03	
	>15	7	0.25-0.35	0.31	0.03	
B. reticulatus	<8	32	0.15-0.34	0.22	0.04	*3.29
	8-15	72	0.12-0.33	0.24	0.04	
	>15	4	0.23-0.30	0.26	0.03	
B. kondakovi	<8	33	0.20-0.33	0.26	0.03	*14.60
	8-15	16	0.20-0.30	0.23	0.03	
	>15	11	0.16-0.26	0.20	0.03	
B. citerosum	<12	69	0.18-0.39	0.26	0.04	*6.93
	12-20	13	0.20-0.38	0.28	0.05	
	>20	8	0.22-0.38	0.32	0.06	
B. suturaltus	<12	..	.....	....	....	1.42
	12-20	13	0.21-0.30	0.26	0.03	
	>20	28	0.19-0.40	0.27	0.04	
B. dentivarians	<12	1	.....	0.17	....	0.00
	12-20	22	0.15-0.24	0.20	0.02	
	>20	29	0.16-0.23	0.20	0.02	
B. c. pacificus	<12	45	0.17-0.38	0.26	0.04	*21.47
	12-20	16	0.26-0.38	0.32	0.04	
	>20	10	0.28-0.36	0.33	0.03	
B. c. mexicanus	<12	89	0.15-0.33	0.24	0.03	3.00
	12-20	14	0.21-0.31	0.26	0.03	
	>20	1	.....	0.28	....	
B. venustus	<7	69	0.17-0.40	0.29	0.06	*11.25
	7-11	35	0.25-0.42	0.33	0.04	
	>11	..	.....	....	....	
B. inexpectatus	<8	58	0.25-0.46	0.37	0.05	1.53
	8-15	90	0.28-0.50	0.38	0.05	
	>15	3	0.35-0.42	0.38	0.03	
B. peruvianus	<12	23	0.24-0.37	0.30	0.04	*6.98
	12-20	42	0.25-0.42	0.33	0.05	
	>20	22	0.29-0.48	0.35	0.05	

* Indicates significance at 5 percent level.

APPENDIX C-3 (Continued).

C-3:3. Parameters for spur length/spur width and analysis of variance F-value

Taxa	Carinorostral diameter (mm)	Sample size	Character range	Mean	Standard deviation	Analysis of variance F-value
	<8	106	0.47-1.76	1.01	0.26	
B. a. amphitrite	8-15	146	0.52-1.53	0.86	0.20	*17.70
	>15	20	0.51-1.00	0.76	0.13	
	<8	118	0.64-1.80	1.25	0.27	
B. a. saltonensis	8-15	83	0.72-2.00	1.16	0.23	*6.59
	>15	..	.....	....	....	
	<8	43	0.69-1.27	0.98	0.15	
B. subalbidus	8-15	43	0.45-1.25	0.88	0.18	*9.41
	>15	9	0.54-1.00	0.75	0.14	
	<12	70	0.82-1.76	1.23	0.22	
B. eburneus	12-20	28	0.77-2.25	1.24	0.32	0.01
	>20	..	.....	....	....	
	<7	39	0.89-2.44	1.67	0.40	
B. improvisus	7-11	50	0.73-2.30	1.53	0.35	1.57
	>11	4	1.22-1.96	1.55	0.31	
	<8	23	1.06-2.19	1.44	0.25	
B. variegatus	8-15	31	0.80-1.44	1.16	0.16	*15.71
	>15	7	0.92-1.40	1.10	0.15	
	<8	32	0.77-1.92	1.34	0.28	
B. reticulatus	8-15	72	0.77-2.05	1.21	0.28	2.59
	>15	4	0.88-1.31	1.13	0.19	
	<8	33	0.80-1.60	1.14	0.20	
B. kondakovi	8-15	16	0.85-1.65	1.36	0.25	*15.38
	>15	11	1.12-1.93	1.54	0.24	
	<12	69	1.00-2.71	1.60	0.34	
B. citerosum	12-20	13	1.07-2.18	1.50	0.34	*5.00
	>20	8	0.80-1.81	1.20	0.39	
	<12	..	.....	....	....	
B. suturalitus	12-20	13	1.59-2.45	1.91	0.29	2.68
	>20	28	1.14-2.31	1.74	0.32	
	<12	1	.....	3.00	....	
B. dentivarians	12-20	22	2.20-4.46	2.92	0.48	0.12
	>20	29	2.09-3.83	2.88	0.35	
	<12	45	1.13-2.40	1.62	0.25	
B. C. pacificus	12-20	16	1.26-2.09	1.51	0.20	*3.49
	>20	10	1.23-1.61	1.44	0.13	
	<12	89	1.11-2.77	1.71	0.28	
B. c. mexicanus	12-20	14	1.27-2.18	1.75	0.28	0.23
	>20	1	.....	1.41	....	
	<7	69	0.50-1.58	0.85	0.25	
B. venustus	7-11	35	0.55-1.13	0.74	0.15	*5.88
	>11	..	.....	....	....	
	<8	58	0.42-0.98	0.69	0.13	
B. inexpectatus	8-15	90	0.46-1.00	0.66	0.11	0.95
	>15	3	0.62-0.70	0.66	0.04	
	<12	23	0.83-1.58	1.09	0.15	
B. peruvianus	12-20	42	0.67-1.29	0.89	0.14	
	>20	22	0.60-1.08	0.83	0.13	*21.30

* Indicates significance at 5 percent level.

APPENDIX C-3 (Continued).

C-3:4. Parameters for distance from angle/spur width and analysis of variance F-value

Taxa	Carinorostral diameter (mm)	Sample size	Character range	Mean	Standard deviation	Analysis of variance F-value
	<8	106	0.51-2.00	1.02	0.33	
B. a. amphitrite	8-15	146	0.24-2.11	0.81	0.29	*23.87
	>15	20	0.33-1.00	0.63	0.18	
	<8	118	0.42-2.65	1.37	0.39	
B. a. saltonensis	8-15	83	0.65-1.83	1.18	0.30	*13.87
	>15	..	.....	....	....	
	<8	43	0.27-0.73	0.47	0.13	
B. subalbidus	8-15	43	0.08-0.67	0.33	0.14	*25.73
	>15	9	0.05-0.26	0.17	0.07	
	<12	70	0.31-1.28	0.76	0.22	
B. eburneus	12-20	28	0.38-1.55	0.69	0.27	1.53
	>20	..	.....	....	....	
	<7	39	0.33-1.69	0.96	0.32	
B. improvisus	7-11	50	0.29-1.80	0.82	0.29	2.98
	>11	4	0.52-1.24	0.75	0.33	
	<8	23	0.68-2.10	1.07	0.30	
B. variegatus	8-15	31	0.56-1.53	0.86	0.20	*7.84
	>15	7	0.57-1.09	0.72	0.18	
	<8	32	0.51-1.69	1.03	0.28	
B. reticulatus	8-15	72	0.53-1.81	0.95	0.29	1.48
	>15	4	0.63-1.01	0.83	0.18	
	<8	33	0.52-1.60	0.90	0.32	
B. kondakovi	8-15	16	0.64-1.65	1.23	0.35	*19.30
	>15	11	1.18-1.96	1.56	0.29	
	<12	69	0.28-1.04	0.64	0.18	
B. citerosum	12-20	13	0.22-0.93	0.56	0.21	*3.73
	>20	8	0.24-0.80	0.46	0.18	
	<12	..	.....	....	....	
B. suturaltus	12-20	13	0.70-1.40	0.93	0.20	1.34
	>20	28	0.49-1.56	0.84	0.24	
	<12	1	.....	1.60	....	
B. dentivarians	12-20	22	0.74-1.73	1.21	0.27	0.00
	>20	29	0.91-1.52	1.20	0.16	
	<12	45	0.67-1.75	1.10	0.24	
B. c. pacificus	12-20	16	0.66-1.18	0.86	0.16	*13.16
	>20	10	0.69-0.99	0.80	0.10	
	<12	89	0.58-2.36	1.13	0.31	
B. c. mexicanus	12-20	14	0.73-1.23	1.02	0.15	1.84
	>20	1	.....	0.86	....	
	<7	69	0.20-1.33	0.50	0.26	
B. venustus	7-11	35	0.14-0.59	0.34	0.11	*13.01
	>11	..	.....	....	....	
	<8	58	0.08-0.69	0.35	0.14	
B. inexpectatus	8-15	90	0.07-0.58	0.30	0.12	2.45
	>15	3	0.29-0.37	0.33	0.04	
	<12	23	0.42-0.95	0.62	0.13	
B. peruvianus	12-20	42	0.19-0.88	0.49	0.16	*12.40
	>20	22	0.17-0.64	0.40	0.13	

* Indicates significance at 5 percent level.

APPENDIX C-3 (Continued).

C-3:5. Parameters for distance from angle/spur length and analysis of variance F-value

Taxa	Carinorostral diameter (mm)	Sample size	Character range	Mean	Standard deviation	Analysis of variance F-value
B. a. amphitrite	<8	106	0.62-1.65	1.02	0.21	
	8-15	146	0.36-1.50	0.93	0.23	*10.45
	>15	20	0.36-1.04	0.82	0.17	
B. a. saltonensis	<8	118	0.48-2.00	1.10	0.26	
	8-15	83	0.58-1.45	1.02	0.20	*5.35
	>15	..	.....	....	....	
B. subalbidus	<8	43	0.27-0.70	0.48	0.09	
	8-15	43	0.14-0.62	0.37	0.12	*23.77
	>15	9	0.08-0.36	0.24	0.10	
B. eburneus	<12	70	0.34-0.97	0.61	0.14	
	12-20	28	0.40-0.80	0.55	0.11	*4.18
	>20	..	.....	....	....	
B. improvisus	<7	39	0.27-0.91	0.57	0.12	
	7-11	50	0.28-0.82	0.53	0.13	2.15
	>11	4	0.36-0.63	0.47	0.12	
B. variegatus	<8	23	0.56-1.03	0.74	0.12	
	8-15	31	0.50-1.06	0.74	0.12	1.85
	>15	7	0.53-0.78	0.65	0.10	
B. reticulatus	<8	32	0.57-0.98	0.77	0.11	
	8-15	72	0.52-1.03	0.78	0.11	0.26
	>15	4	0.61-0.92	0.74	0.13	
B. kondakovi	<8	33	0.35-1.79	0.80	0.27	
	8-15	16	0.40-1.05	0.90	0.16	*4.06
	>15	11	0.84-1.15	1.02	0.09	
B. citerosum	<12	69	0.25-0.61	0.40	0.09	
	12-20	13	0.19-0.50	0.37	0.08	0.78
	>20	8	0.30-0.50	0.38	0.07	
B. suturaltus	<12	..	.....	....	....	
	12-20	13	0.37-0.61	0.49	0.07	0.07
	>20	28	0.33-0.68	0.48	0.08	
B. dentivarians	<12	1	.....	0.53	....	
	12-20	22	0.26-0.50	0.41	0.06	0.25
	>20	29	0.32-0.55	0.42	0.05	
B. c. pacificus	<12	45	0.48-1.12	0.68	0.11	
	12-20	16	0.40-0.78	0.57	0.08	*9.96
	>20	10	0.43-0.64	0.56	0.06	
B. c. mexicanus	<12	89	0.41-0.92	0.66	0.12	
	12-20	14	0.48-0.69	0.58	0.06	*5.05
	>20	1	.....	0.61	....	
B. venustus	<7	69	0.30-1.11	0.57	0.16	
	7-11	35	0.25-0.68	0.46	0.12	*12.92
	>11	..	.....	....	....	
B. inexpectatus	<8	58	0.16-0.90	0.50	0.15	
	8-15	90	0.11-0.89	0.45	0.15	1.85
	>15	3	0.42-0.56	0.50	0.08	
B. peruvianus	<12	23	0.44-0.82	0.57	0.11	
	12-20	42	0.25-0.98	0.54	0.15	1.85
	>20	22	0.19-0.78	0.49	0.15	

* Indicates significance at 5 percent level.

APPENDIX C-3 (Continued).

C-3:6. Parameters for distance from angle/basal margin and analysis of variance F-value

Taxa	Carinorostral diameter (mm)	Sample size	Character range	Mean	Standard deviation	Analysis of variance F-value
B. a. amphitrite	<8	106	0.15–0.32	0.24	0.03	
	8–15	146	0.11–0.34	0.22	0.04	*14.38
	>15	20	0.13–0.24	0.20	0.03	
B. a. saltonensis	<8	118	0.15–0.39	0.27	0.04	
	8–15	83	0.20–0.36	0.27	0.04	1.51
	>15	..	.....	....	....	
B. subalbidus	<8	43	0.09–0.21	0.15	0.03	
	8–15	43	0.03–0.21	0.12	0.04	*23.71
	>15	9	0.02–0.10	0.07	0.03	
B. eburneus	<12	70	0.12–0.28	0.20	0.03	
	12–20	28	0.13–0.26	0.19	0.03	*4.89
	>20	..	.....	....	....	
B. improvisus	<7	39	0.10–0.25	0.18	0.03	
	7–11	50	0.09–0.22	0.16	0.03	*4.24
	>11	4	0.14–0.25	0.17	0.05	
B. variegatus	<8	23	0.18–0.31	0.24	0.03	
	8–15	31	0.17–0.31	0.24	0.03	1.95
	>15	7	0.19–0.27	0.22	0.03	
B. reticulatus	<8	32	0.16–0.28	0.22	0.03	
	8–15	72	0.15–0.30	0.22	0.03	0.07
	>15	4	0.19–0.23	0.21	0.02	
B. kondakovi	<8	33	0.14–0.44	0.22	0.06	
	8–15	16	0.14–0.33	0.28	0.05	*11.15
	>15	11	0.27–0.36	0.30	0.03	
B. citerosum	<12	69	0.11–0.26	0.16	0.03	
	12–20	13	0.08–0.19	0.15	0.03	1.83
	>20	8	0.09–0.17	0.14	0.03	
B. suturaltus	<12	..	.....	....	....	
	12–20	13	0.19–0.29	0.24	0.03	1.49
	>20	28	0.15–0.30	0.22	0.04	
B. dentivarians	<12	1	.....	0.28	....	
	12–20	22	0.16–0.28	0.23	0.03	0.18
	>20	29	0.20–0.27	0.23	0.02	
B. c. pacificus	<12	45	0.21–0.33	0.28	0.03	
	12–20	16	0.22–0.31	0.27	0.03	1.94
	>20	10	0.23–0.30	0.26	0.02	
B. c. mexicanus	<12	89	0.15–0.36	0.27	0.05	
	12–20	14	0.23–0.29	0.26	0.02	0.30
	>20	1	.....	0.24	....	
B. venustus	<7	69	0.07–0.24	0.13	0.04	
	7–11	35	0.06–0.15	0.11	0.02	*13.47
	>11	..	.....	....	....	
B. inexpectatus	<8	58	0.04–0.19	0.12	0.03	
	8–15	90	0.03–0.18	0.11	0.03	2.40
	>15	3	0.11–0.14	0.13	0.02	
B. peruvianus	<12	23	0.14–0.25	0.18	0.03	
	12–20	42	0.07–0.23	0.16	0.04	*10.95
	>20	22	0.07–0.19	0.14	0.04	

* Indicates significance at 5 percent level.

APPENDIX C-3 (Continued).

C-3:7. Parameters for spur length/basal margin and analysis of variance F-value

Taxa	Carinorostral diameter (mm)	Sample size	Character range	Mean	Standard deviation	Analysis of variance F-value
B. a. amphitrite	<8	106	0.17-0.34	0.24	0.04	
	8-15	146	0.17-0.33	0.24	0.04	0.39
	>15	20	0.20-0.31	0.25	0.03	
B. a. saltonensis	<8	118	0.16-0.41	0.26	0.04	
	8-15	83	0.18-0.41	0.27	0.04	3.38
	>15	..	.....	....	....	
B. subalbidus	<8	43	0.24-0.43	0.32	0.05	
	8-15	43	0.19-0.44	0.32	0.06	0.01
	>15	9	0.23-0.41	0.32	0.06	
B. eburneus	<12	70	0.26-0.47	0.34	0.04	
	12-20	28	0.28-0.43	0.34	0.04	0.20
	>20	..	.....	....	....	
B. improvisus	<7	39	0.26-0.41	0.33	0.04	
	7-11	50	0.24-0.47	0.32	0.04	1.24
	>11	4	0.30-0.39	0.35	0.04	
B. variegatus	<8	23	0.26-0.42	0.33	0.03	
	8-15	31	0.25-0.42	0.32	0.04	0.42
	>15	7	0.29-0.37	0.33	0.03	
B. reticulatus	<8	32	0.20-0.34	0.28	0.03	
	8-15	72	0.23-0.38	0.28	0.03	0.68
	>15	4	0.25-0.33	0.29	0.04	
B. kondakovi	<8	33	0.22-0.42	0.29	0.05	
	8-15	16	0.25-0.35	0.31	0.03	1.60
	>15	11	0.27-0.34	0.30	0.02	
B. citerosum	<12	69	0.25-0.52	0.40	0.05	
	12-20	13	0.33-0.47	0.41	0.05	2.66
	>20	8	0.29-0.45	0.36	0.05	
B. suturaltus	<12	..	.....	....	....	
	12-20	13	0.42-0.56	0.49	0.04	2.41
	>20	28	0.39-0.58	0.46	0.04	
B. dentivarians	<12	1	.....	0.52	....	
	12-20	22	0.49-0.66	0.56	0.04	0.02
	>20	29	0.44-0.70	0.56	0.05	
B. c. pacificus	<12	45	0.25-0.52	0.41	0.05	
	12-20	16	0.38-0.58	0.47	0.06	*12.61
	>20	10	0.42-0.58	0.47	0.05	
B. c. mexicanus	<12	89	0.29-0.50	0.41	0.05	
	12-20	14	0.37-0.54	0.45	0.04	*7.75
	>20	1	.....	0.39	....	
B. venustus	<7	69	0.18-0.30	0.23	0.03	
	7-11	35	0.17-0.31	0.24	0.03	0.13
	>11	..	.....	....	....	
B. inexpectatus	<8	58	0.19-0.30	0.25	0.03	
	8-15	90	0.19-0.32	0.25	0.03	0.05
	>15	3	0.23-0.26	0.25	0.02	
B. peruvianus	<12	23	0.25-0.44	0.33	0.04	
	12-20	42	0.21-0.41	0.29	0.04	*7.37
	>20	22	0.22-0.36	0.29	0.04	

* Indicates significance at 5 percent level.

APPENDIX C-3 (Continued).

C-3:8. Parameters for articular ridge/tergal margin and analysis of variance F-value

Taxa	Carinorostral diameter (mm)	Sample size	Character range	Mean	Standard deviation	Analysis of variance F-value
B. a. amphitrite	<8	106	0.48-0.84	0.63	0.06	
	8-15	146	0.46-0.80	0.64	0.06	1.22
	>15	20	0.50-0.74	0.61	0.06	
B. a. saltonensis	<8	118	0.48-0.74	0.63	0.05	
	8-15	83	0.47-0.76	0.62	0.05	0.04
	>15	..	.....	....	....	
B. subalbidus	<8	43	0.50-0.69	0.61	0.04	
	8-15	43	0.52-0.69	0.60	0.05	0.47
	>15	9	0.52-0.65	0.60	0.04	
B. eburneus	<12	70	0.56-0.76	0.65	0.04	
	12-20	28	0.61-0.73	0.66	0.03	1.71
	>20	..	.....	....	....	
B. improvisus	<7	39	0.64-0.89	0.73	0.07	
	7-11	50	0.60-0.85	0.74	0.06	1.04
	>11	4	0.63-0.86	0.77	0.10	
B. variegatus	<8	23	0.61-0.78	0.69	0.05	
	8-15	31	0.59-0.86	0.72	0.06	2.10
	>15	7	0.65-0.80	0.71	0.06	
B. reticulatus	<8	32	0.55-0.74	0.66	0.04	
	8-15	72	0.58-0.80	0.67	0.05	0.12
	>15	4	0.62-0.73	0.66	0.04	
B. kondakovi	<8	33	0.50-0.74	0.61	0.06	
	8-15	16	0.50-0.69	0.60	0.05	0.85
	>15	11	0.57-0.67	0.63	0.03	
B. citerosum	<12	69	0.50-0.76	0.64	0.06	
	12-20	13	0.59-0.72	0.66	0.05	0.42
	>20	8	0.56-0.72	0.64	0.06	
B. suturaltus	<12	..	.....	....	....	
	12-20	13	0.57-0.75	0.68	0.05	0.67
	>20	28	0.54-0.82	0.70	0.06	
B. dentivarians	<12	1	.....	0.65	....	
	12-20	22	0.53-0.71	0.64	0.05	2.04
	>20	29	0.57-0.73	0.66	0.04	
B. c. pacificus	<12	45	0.54-0.87	0.69	0.06	
	12-20	16	0.59-0.86	0.74	0.07	*17.20
	>20	10	0.74-0.88	0.81	0.04	
B. c. mexicanus	<12	89	0.50-0.88	0.68	0.06	
	12-20	14	0.68-0.85	0.74	0.05	*13.99
	>20	1	.....	0.87	....	
B. venustus	<7	69	0.61-0.92	0.75	0.06	
	7-11	35	0.65-0.89	0.78	0.05	*4.52
	>11	..	.....	....	....	
B. inexpectatus	<8	58	0.66-0.85	0.74	0.05	
	8-15	90	0.62-0.87	0.74	0.05	0.16
	>15	3	0.69-0.75	0.73	0.03	
B. peruvianus	<12	23	0.64-0.83	0.71	0.05	
	12-20	42	0.58-0.83	0.72	0.05	0.27
	>20	22	0.61-0.81	0.72	0.05	

* Indicates significance at 5 percent level.

APPENDIX C-3 (Continued).

C-3:9. Parameters for articular ridge/occludent margin and analysis of variance F-value

Taxa	Carinorostral diameter (mm)	Sample size	Character range	Mean	Standard deviation	Analysis of variance F-value
B. a. amphitrite	<8	106	0.32-0.55	0.44	0.04	
	8-15	146	0.34-0.55	0.44	0.04	0.06
	>15	20	0.37-0.55	0.43	0.05	
B. a. saltonensis	<8	118	0.34-0.52	0.44	0.04	
	8-15	83	0.33-0.54	0.43	0.04	1.55
	>15	..	.....	....	....	
B. subalbidus	<8	43	0.35-0.45	0.41	0.02	
	8-15	43	0.37-0.48	0.41	0.03	0.59
	>15	9	0.36-0.48	0.42	0.03	
B. eburneus	<12	70	0.38-0.51	0.44	0.02	
	12-20	28	0.38-0.50	0.45	0.03	2.92
	>20	..	.....	....	....	
B. improvisus	<7	39	0.33-0.56	0.44	0.04	
	7-11	50	0.35-0.51	0.45	0.04	0.39
	>11	4	0.42-0.50	0.46	0.03	
B. variegatus	<8	23	0.41-0.51	0.46	0.02	
	8-15	31	0.38-0.56	0.48	0.04	2.66
	>15	7	0.43-0.51	0.48	0.03	
B. reticulatus	<8	32	0.36-0.54	0.46	0.04	
	8-15	72	0.38-0.56	0.46	0.04	0.02
	>15	4	0.42-0.50	0.46	0.04	
B. kondakovi	<8	33	0.31-0.51	0.40	0.05	
	8-15	16	0.36-0.51	0.42	0.05	*7.13
	>15	11	0.42-0.51	0.45	0.03	
B. citerosum	<12	69	0.33-0.51	0.41	0.03	
	12-20	13	0.35-0.49	0.40	0.04	0.41
	>20	8	0.37-0.48	0.41	0.03	
B. suturaltus	<12	..	.....	....	....	
	12-20	13	0.32-0.48	0.40	0.04	3.13
	>20	28	0.37-0.51	0.43	0.04	
B. dentivarians	<12	1	.....	0.34	....	
	12-20	22	0.32-0.41	0.36	0.02	0.00
	>20	29	0.33-0.39	0.36	0.02	
B. c. pacificus	<12	45	0.35-0.55	0.45	0.04	
	12-20	16	0.45-0.53	0.49	0.03	*10.53
	>20	10	0.46-0.58	0.51	0.04	
B. c. mexicanus	<12	89	0.32-0.58	0.44	0.04	
	12-20	14	0.41-0.57	0.47	0.05	*4.33
	>20	1	.....	0.58	....	
B. venustus	<7	69	0.42-0.63	0.52	0.05	
	7-11	35	0.47-0.59	0.53	0.03	1.39
	>11	..	.....	....	....	
B. inexpectatus	<8	58	0.41-0.58	0.49	0.04	
	8-15	90	0.33-0.57	0.48	0.03	1.39
	>15	3	0.44-0.52	0.47	0.05	
B. peruvianus	<12	23	0.45-0.62	0.51	0.04	
	12-20	42	0.45-0.65	0.53	0.03	1.62
	>20	22	0.47-0.58	0.52	0.03	

* Indicates significance at 5 percent level.

APPENDIX C-3 (Continued).

C-3:10. Parameters for number of teeth on labrum and analysis of variance F-value

Taxa	Carinorostral diameter (mm)	Sample size	Character range	Mean	Standard deviation	Analysis of variance F-value
B. a. amphitrite	<8	106	8.00-19.00	12.35	1.94	
	8-15	146	8.00-22.50	15.17	2.62	*54.09
	>15	20	10.50-23.00	16.62	2.68	
B. a. saltonensis	<8	118	9.50-21.50	14.26	2.24	
	8-15	83	10.50-23.50	15.37	2.48	*10.89
	>15	..	.....	....	....	
B. subalbidus	<8	43	8.50-19.00	12.56	2.44	
	8-15	43	10.00-23.00	15.24	3.26	*17.57
	>15	9	14.50-21.50	18.00	2.90	
B. eburneus	<12	70	7.00-24.00	12.74	3.51	
	12-20	28	7.00-30.50	15.39	5.53	*8.10
	>20	..	.....	....	....	
B. improvisus	<7	39	7.50-20.00	14.45	3.24	
	7-11	50	8.00-21.50	15.66	2.67	1.96
	>11	4	11.50-16.50	14.62	2.18	
B. variegatus	<8	23	3.00-4.00	3.85	0.32	
	8-15	31	1.50-4.00	3.52	0.63	3.04
	>15	7	2.50-4.00	3.43	0.53	
B. reticulatus	<8	32	3.00-4.50	3.92	0.26	
	8-15	72	0.50-5.00	3.73	0.68	2.77
	>15	4	2.00-4.00	3.25	0.87	
B. kondakovi	<8	33	0.50-5.50	4.21	1.06	
	8-15	16	3.00-5.00	3.78	0.58	1.58
	>15	11	2.00-6.00	3.73	1.19	
B. citerosum	<12	69	1.00-3.50	2.88	0.34	
	12-20	13	1.00-3.00	2.46	0.72	*7.02
	>20	8	0.00-4.00	2.31	1.13	
B. suturaltus	<12	..	.....	....	....	
	12-20	13	2.50-7.00	4.73	1.59	*6.31
	>20	28	1.50-6.50	3.66	1.10	
B. dentivarians	<12	1	.....	3.00	....	
	12-20	22	3.00-4.50	3.39	0.60	0.29
	>20	29	2.00-6.50	3.50	0.85	
B. c. pacificus	<12	45	2.00-3.50	2.81	0.37	
	12-20	16	0.00-3.00	2.19	0.89	*11.33
	>20	10	0.00-3.00	2.00	0.85	
B. c. mexicanus	<12	89	0.00-3.00	2.70	0.55	
	12-20	14	1.50-3.00	2.32	0.67	*5.51
	>20	1	.....	3.00	....	
B. venustus	<7	69	1.50-3.00	2.91	0.27	
	7-11	35	1.00-3.00	2.74	0.49	*5.21
	>11	..	.....	....	....	
B. inexpectatus	<8	58	0.50-7.00	2.89	0.73	
	8-15	90	1.00-5.00	2.89	0.60	0.01
	>15	3	2.50-3.00	2.83	0.29	
B. peruvianus	<12	23	1.00-3.00	2.46	0.58	
	12-20	42	1.00-3.00	2.58	0.52	1.13
	>20	22	1.00-3.00	2.36	0.66	

* Indicates significance at 5 percent level.

APPENDIX C-3 (Continued).

C-3:11. Parameters for number of spines on first maxilla and analysis of variance F-value

Taxa	Carinorostral diameter (mm)	Sample size	Character range	Mean	Standard deviation	Analysis of variance F-value
B. a. amphitrite	<8	106	4.00-13.50	6.44	1.28	
	8-15	146	5.00-15.00	7.40	1.41	*21.51
	>15	20	7.00-10.00	8.05	0.99	
B. a. saltonensis	<8	118	4.00-12.00	6.45	1.00	
	8-15	83	5.00-11.00	7.23	0.93	*31.14
	>15	..	.....	....	....	
B. subalbidus	<8	43	5.00-9.50	7.40	1.00	
	8-15	43	5.00-12.00	9.05	1.67	*22.29
	>15	9	8.00-11.50	9.94	1.21	
B. eburneus	<12	70	7.00-12.00	9.07	1.38	
	12-20	28	7.00-12.00	10.02	1.13	*10.37
	>20	..	.....	....	....	
B. improvisus	<7	39	4.00-10.00	5.91	1.15	
	7-11	50	5.00-8.00	6.59	0.74	*6.83
	>11	4	6.00-8.00	7.00	0.82	
B. variegatus	<8	23	5.00-10.00	6.39	1.10	
	8-15	31	5.50-9.00	7.03	0.73	*9.13
	>15	7	7.00-8.50	7.93	0.53	
B. reticulatus	<8	32	3.00-8.00	5.59	1.04	
	8-15	72	4.50-15.00	6.94	1.48	*11.82
	>15	4	5.50-9.50	7.62	1.75	
B. kondakovi	<8	33	3.50-8.50	5.44	0.95	
	8-15	16	5.50-8.00	6.91	0.69	*19.70
	>15	11	5.00-7.50	6.68	0.72	
B. citerosum	<12	69	3.00-9.00	5.72	1.11	
	12-20	13	6.00-18.50	8.73	3.15	*27.91
	>20	8	6.50-10.50	8.50	1.31	
B. suturaltus	<12	..	.....	....	....	
	12-20	13	6.00-9.00	7.85	0.97	*4.81
	>20	28	7.00-11.50	8.66	1.16	
B. dentivarians	<12	1	.....	6.00	....	
	12-20	22	8.50-11.00	9.68	0.81	0.84
	>20	29	7.50-12.00	9.47	0.85	
B. c. pacificus	<12	45	3.00-9.00	6.26	1.43	
	12-20	16	7.00-10.00	8.50	1.00	*33.60
	>20	10	8.50-10.00	9.20	0.59	
B. c. mexicanus	<12	89	2.50-7.50	5.11	1.25	
	12-20	14	5.00-8.50	6.57	0.85	*17.87
	>20	1	.....	7.00	....	
B. venustus	<7	69	3.00-6.00	4.38	0.79	
	7-11	35	4.00-6.50	5.01	0.65	*16.56
	>11	..	.....	....	....	
B. inexpectatus	<8	58	3.00-9.50	5.40	0.96	
	8-15	90	4.00-10.00	6.23	1.06	*11.64
	>15	3	5.50-7.00	6.17	0.76	
B. peruvianus	<12	23	5.00-8.00	6.20	0.99	
	12-20	42	5.00-10.00	8.17	1.03	*47.37
	>20	22	7.00-12.00	9.09	1.09	

* Indicates significance at 5 percent level.

APPENDIX C-3 (Continued).

C-3:12. Parameters for number of segments, cirrus I and analysis of variancr F-value

Taxa	Carinorostral diameter (mm)	Sample size	Character range	Mean	Standard deviation	Analysis of variance F-value
B. a. amphitrite	<8	106	1.50-9.00	4.48	1.14	
	8-15	146	0.00-9.50	4.82	1.29	2.13
	>15	20	2.00-9.00	4.70	1.80	
B. a. saltonensis	<8	118	2.50-8.00	6.23	1.06	
	8-15	83	2.50-7.50	4.93	1.02	*4.01
	>15	..	.....	....	....	
B. subalbidus	<8	43	2.00-8.00	4.57	1.22	
	8-15	43	3.00-8.00	5.12	1.43	*4.52
	>15	9	4.00-11.00	6.06	2.23	
B. eburneus	<12	70	3.00-13.00	5.66	1.56	
	12-20	28	3.00-10.00	6.96	1.49	*15.26
	>20	..	.....	....	....	
B. improvisus	<7	39	1.00-4.50	2.41	1.06	
	7-11	50	1.00-5.50	3.21	1.11	*6.83
	>11	4	2.00-4.50	3.62	1.18	
B. variegatus	<8	23	2.00-4.50	3.17	0.65	
	8-15	31	2.00-6.00	3.84	0.91	*23.73
	>15	7	3.50-7.00	5.71	1.19	
B. reticulatus	<8	32	2.50-7.00	3.92	1.06	
	8-15	72	2.00-9.00	4.67	1.20	*5.24
	>15	4	3.50-4.00	3.88	0.25	
B. kondakovi	<8	33	0.50-6.00	3.67	1.50	
	8-15	16	3.00-6.00	4.19	1.00	0.80
	>15	11	2.00-6.00	3.77	1.37	
B. citerosum	<12	69	1.00-7.50	3.77	1.23	
	12-20	13	3.50-7.00	5.35	1.18	*9.97
	>20	8	2.50-8.50	5.00	2.09	
B. suturaltus	<12	..	.....	....	....	
	12-20	13	2.50-6.00	4.38	1.04	*4.26
	>20	28	3.00-8.50	5.25	1.33	
B. dentivarians	<12	1	.....	2.50	....	
	12-20	22	0.00-9.50	6.52	2.25	0.08
	>20	29	4.00-8.50	6.38	1.28	
B. c. pacificus	<12	45	0.00-4.50	3.20	0.86	
	12-20	16	0.00-6.50	3.22	1.45	*3.37
	>20	10	3.00-5.00	4.10	0.81	
B. c. mexicanus	<12	89	0.50-4.50	2.45	0.80	
	12-20	14	1.50-4.00	3.14	0.77	*9.22
	>20	1	.....	2.50	....	
B. venustus	<7	69	2.50-8.00	5.33	1.35	
	7-11	35	2.00-9.00	5.26	1.52	0.07
	>11	..	.....	....	....	
B. inexpectatus	<8	58	3.00-7.50	4.95	1.00	
	8-15	90	0.50-8.50	4.82	1.31	0.58
	>15	3	3.50-9.00	5.50	3.04	
B. peruvianus	<12	23	4.50-10.00	7.02	1.30	
	12-20	42	3.50-13.00	8.99	2.04	*10.65
	>20	22	5.50-18.00	9.70	2.65	

* Indicates significance at 5 percent level.

APPENDIX C-3 (Continued).

C-3:13. Parameters for number of segments, cirrus II and analysis of variance F-value

Taxa	Carinorostral diameter (mm)	Sample size	Character range	Mean	Standard deviation	Analysis of variance F-value
B. a. amphitrite	<8	106	0.00-4.00	1.56	0.58	
	8-15	146	0.00-5.00	2.39	0.89	*41.03
	>15	20	0.00-6.00	2.85	1.26	
B. a. saltonensis	<8	118	-1.00-3.50	1.60	0.75	
	8-15	83	0.50-4.00	1.98	0.71	*12.78
	>15	..	.....	....	....	
B. subalbidus	<8	43	0.00-3.00	1.55	0.77	
	8-15	43	0.50-5.50	2.46	1.38	*7.09
	>15	9	0.00-5.00	2.39	1.60	
B. eburneus	<12	70	1.50-5.00	2.89	0.72	
	12-20	28	2.50-6.50	3.73	0.80	*25.67
	>20	..	.....	....	....	
B. improvisus	<7	39	-1.00-2.50	1.24	0.95	
	7-11	50	-2.00-4.00	1.70	0.98	*5.03
	>11	4	1.50-3.50	2.62	0.85	
B. variegatus	<8	23	0.00-3.00	1.17	0.63	
	8-15	31	-0.50-3.50	1.50	0.92	2.49
	>15	7	0.00-3.00	1.93	0.93	
B. reticulatus	<8	32	-0.50-3.00	1.25	0.66	
	8-15	72	0.00-4.00	1.27	0.78	0.19
	>15	4	0.00-3.00	1.50	1.29	
B. kondakovi	<8	33	0.00-3.00	1.29	0.88	
	8-15	16	1.00-3.50	1.88	0.62	*7.26
	>15	11	0.50-4.00	2.32	0.93	
B. citerosum	<12	69	-1.00-2.00	0.47	0.85	
	12-20	13	-2.00-3.00	1.15	1.39	*6.58
	>20	8	0.00-3.50	1.56	1.08	
B. suturaltus	<12	..	.....	....	....	
	12-20	13	0.00-3.00	1.23	0.93	0.04
	>20	28	-1.00-4.50	1.30	1.21	
B. dentivarians	<12	1	.....	1.50	....	
	12-20	22	-2.00-5.00	1.70	1.56	0.46
	>20	29	-1.50-5.00	2.02	1.67	
B. c. pacificus	<12	45	-1.00-2.00	0.48	0.78	
	12-20	16	-2.00-3.00	0.62	1.55	1.85
	>20	10	0.00-2.50	1.15	0.78	
B. c. mexicanus	<12	89	-2.00-2.00	0.22	0.86	
	12-20	14	-1.00-1.50	0.11	0.84	0.23
	>20	1	.....	-0.50	....	
B. venustus	<7	69	-0.50-3.00	1.41	0.65	
	7-11	35	-0.50-2.50	1.37	0.65	0.10
	>11	..	.....	....	....	
B. inexpectatus	<8	58	0.00-3.00	0.96	0.70	
	8-15	90	0.00-3.00	1.27	0.80	*3.08
	>15	3	1.00-2.00	1.50	0.50	
B. peruvianus	<12	23	0.00-2.50	1.04	0.77	
	12-20	42	0.00-4.00	2.07	0.98	*13.00
	>20	22	0.50-4.00	2.30	0.90	

* Indicates significance at 5 percent level.

APPENDIX C-3 (Continued).

C-3:14. Parameters for number of segments, cirrus III and analysis of variance F-value

Taxa	Carinorostral diameter (mm)	Sample size	Character range	Mean	Standard deviation	Analysis of variance F-value
B. a. amphitrite	<8	106	-0.50-4.00	2.26	0.80	*24.95
	8-15	146	-1.00-4.50	2.90	0.77	
	>15	20	2.00-4.00	3.10	0.66	
B. a. saltonensis	<8	118	0.00-4.00	2.67	0.67	*8.33
	8-15	83	1.00-4.00	2.94	0.60	
	>15	..	.....	....	....	
B. subalbidus	<8	43	1.00-4.50	2.92	0.84	*18.75
	8-15	43	2.00-5.50	3.71	0.79	
	>15	9	3.00-6.00	4.56	0.98	
B. eburneus	<12	70	0.00-4.50	2.55	1.14	*14.99
	12-20	28	2.00-5.00	3.46	0.82	
	>20	..	.....	....	....	
B. improvisus	<7	39	1.00-5.00	3.27	0.85	*13.51
	7-11	50	3.00-7.00	4.31	0.95	
	>11	4	2.50-6.00	3.88	1.55	
B. variegatus	<8	23	1.00-4.00	2.39	0.66	*8.77
	8-15	31	1.00-5.00	3.00	0.82	
	>15	7	3.00-5.00	3.64	0.75	
B. reticulatus	<8	32	1.00-4.00	2.62	0.62	2.37
	8-15	72	0.00-4.00	2.95	0.73	
	>15	4	2.00-4.00	2.88	0.85	
B. kondakovi	<8	33	1.50-4.00	2.97	0.68	0.37
	8-15	16	1.50-4.00	3.12	0.81	
	>15	11	0.00-4.00	2.82	1.54	
B. citerosum	<12	69	0.00-4.00	2.51	0.84	*5.99
	12-20	13	2.00-5.00	3.35	0.97	
	>20	8	1.00-5.00	3.25	1.49	
B. suturaltus	<12	..	.....	....	....	0.83
	12-20	13	2.50-5.50	3.88	0.87	
	>20	28	1.50-6.00	4.19	1.04	
B. dentivarians	<12	1	.....	3.00	....	2.11
	12-20	22	2.50-6.00	4.20	0.78	
	>20	29	2.00-6.00	4.55	0.89	
B. c. pacificus	<12	45	1.00-6.00	2.64	0.86	*6.90
	12-20	16	1.50-4.50	3.09	0.93	
	>20	10	2.50-5.00	3.75	0.92	
B. c. mexicanus	<12	89	0.00-5.00	2.26	0.70	*22.23
	12-20	14	2.00-5.00	3.25	0.91	
	>20	1	.....	3.00	....	
B. venustus	<7	69	0.50-3.00	2.10	0.47	*7.24
	7-11	35	0.00-4.00	2.41	0.70	
	>11	..	.....	....	....	
B. inexpectatus	<8	58	1.00-4.50	2.40	0.74	2.03
	8-15	90	1.00-4.00	2.59	0.69	
	>15	3	2.00-4.00	3.00	1.00	
B. peruvianus	<12	23	1.00-4.00	2.39	0.81	*14.94
	12-20	42	2.00-5.00	3.50	0.80	
	>20	22	1.00-5.50	3.70	1.13	

* Indicates significance at 5 percent level.

APPENDIX C-3 (Continued).

C-3:15. Parameters for number of paired setae, cirrus VI and analysis of variance F-value

Taxa	Carinorostral diameter (mm)	Sample size	Character range	Mean	Standard deviation	Analysis of variance F-value
B. a. amphitrite	<8	106	3.00-12.00	7.64	1.72	*5.82
	8-15	146	3.50-11.00	6.95	1.47	
	>15	20	5.00-10.50	7.14	1.58	
B. a. saltonensis	<8	118	5.00-13.50	10.26	1.64	2.74
	8-15	83	5.00-14.00	9.83	2.03	
	>15	..	.....	....	....	
B. subalbidus	<8	43	5.50-11.75	8.10	1.37	0.15
	8-15	43	6.00-13.50	7.92	1.65	
	>15	9	6.50-12.50	8.03	1.83	
B. eburneus	<12	70	4.75-10.50	6.91	1.48	0.35
	12-20	28	4.50-9.25	7.11	1.47	
	>20	..	.....	....	....	
B. improvisus	<7	39	5.00-8.00	5.97	0.99	1.50
	7-11	50	5.00-8.00	6.13	0.77	
	>11	4	5.00-8.00	6.75	1.26	
B. variegatus	<8	23	4.00-6.00	4.47	0.58	*9.01
	8-15	31	4.00-6.00	4.91	0.53	
	>15	7	5.00-6.00	5.39	0.50	
B. reticulatus	<8	32	4.00-6.00	5.01	0.66	0.54
	8-15	72	4.00-6.00	4.91	0.53	
	>15	4	5.00-5.50	5.12	0.25	
B. kondakovi	<8	33	4.50-7.25	6.05	0.65	*58.86
	8-15	16	3.00-6.50	4.34	1.14	
	>15	11	3.00-4.00	3.36	0.44	
B. citerosum	<12	69	4.00-9.00	6.07	1.17	*8.64
	12-20	13	4.00-8.00	5.06	1.13	
	>20	8	4.00-7.00	4.62	1.06	
B. suturaltus	<12	..	.....	....	....	0.04
	12-20	13	3.50-5.00	4.27	0.56	
	>20	28	3.50-5.00	4.23	0.50	
B. dentivarians	<12	1	.....	8.00	....	*7.41
	12-20	22	7.00-9.50	8.28	0.54	
	>20	29	8.00-11.00	8.83	0.81	
B. c. pacificus	<12	45	3.00-5.00	4.10	0.35	*3.84
	12-20	16	3.00-5.00	3.80	0.54	
	>20	10	3.00-4.50	3.80	0.63	
B. c. mexicanus	<12	89	2.75-4.50	3.52	0.51	3.42
	12-20	14	3.00-4.00	3.79	0.43	
	>20	1	.....	4.25	....	
B. venustus	<7	69	3.50-6.25	4.86	0.70	0.39
	7-11	35	4.00-6.00	4.94	0.61	
	>11	..	.....	....	....	
B. inexpectatus	<8	58	4.25-7.00	5.64	0.60	0.41
	8-15	90	4.25-7.00	5.62	0.56	
	>15	3	5.00-6.00	5.33	0.58	
B. peruvianus	<12	23	4.00-7.75	5.86	0.80	0.27
	12-20	42	4.75-8.50	5.97	0.81	
	>20	22	5.00-7.50	6.02	0.69	

* Indicates significance at 5 percent level.

C-4. Test for Homogeneity of Variance.

Barlett's test for homogeneity of variance (Bartlett, 1937) has been applied for the joint testing of variances for all characters of the taxa. The results indicate significant inequalities in the variances of all characters. However, as pointed out by Bishop & Nair (1939), the significance levels of Bartlett's test are strongly influenced by inequalities in the degrees of freedom of the samples; these levels may also be seriously distorted by pooled variance error (cf. Cochran, 1947). Although the efficiency of functions is reduced by heterogeneity of variances and covariances, the contributions made by the characters toward the separation of the taxa exceed the disadvantages of the loss of efficiency.

APPENDIX D. GENERALIZED DISTANCE FUNCTION ANALYSIS

D-1. Computation of Generalized Distance Function.

The method of computation of the generalized distance function consisted of the construction of an orthogonal set of variables from the original set of characters. The first step involved the construction of a table of normalized means (D-1:1), $\overline{X}_1 \ldots \overline{X}_p$, for p characers in each group. The normalized means were then transformed, by the use of pooled intragroup correlations (D-1:2), into values, $F_1 \ldots F_p$, which are uncorrelated variables. The $F_1 \ldots F_p$ values were then transformed into $f_1 \ldots f_p$ variables having unit variance. The formula for D^2 between two groups thus becomes:

$$D^2 = \sum_{i=1}^{p} (f_{i1} - f_{i2})^2 \qquad (1)$$

where f_{i1} andf_{i2} are transformed values (D-1:3) of the ith character in groups 1 and 2, respectively, and p is the number of characters (Worlund, unpublished).

Unless the populations under study are all represented by large samples, corrections for bias, which depends upon sample size, variance and covariance, must be made before D^2 values among groups can be compared (D-1:4). When the sample size is the same for all characters in each group, the bias is simply:

$$p \frac{n_1 + n_2}{n_1 n_2} \qquad (2)$$

where n_1 and n_2 are the sample sizes of populations 1 and 2, respectively, and p is the number of characters (Rao, 1952: 364). Variance and covariance are accounted for in the dispersion matrix of the D^2 computations. The resulting corrected D^2 values and percents of overlap between pairs (D-1:5) reveals the general pattern of relationships among the taxa. When the distance between certain pairs of taxa is much less than the distance between either member of the pair and the next closest taxon, such pairs are termed clusters (Rao, 1952:352).

Appendix D-1 (Continued).

D-1:1. Normalized Mean Values of 15 Characters

Taxa	spur width/ basal margin	spur length/ spur width	distance from angle/ spur width	distance from angle/ spur length	distance from angle/ basal margin	spur length/ basal margin	articular ridge/ tegal margin	articular ridge/ occludent margin	number of teeth on labrum	number of spines on first maxilla	number of teeth on mandible	number of segments, cirrus I	number of segments, cirrus II	number of segments, cirrus III	number of paired setae, cirrus VI
B. a. amphitrite	0.169	-1.686	0.187	1.972	0.677	-2.373	-0.844	-0.290	3.569	0.027	-1.086	0.120	0.651	-0.439	1.035
B. a. saltonensis	-1.068	-0.521	1.685	2.660	1.824	-1.966	-0.985	-0.359	3.825	-0.200	-1.011	0.170	0.278	-0.302	3.417
B. subalbidus	1.734	-1.673	-1.629	-1.342	-2.013	-0.527	-1.383	-0.971	3.622	1.014	-0.737	0.241	0.585	0.452	1.689
B. eburneus	0.206	-0.451	-0.332	-0.202	-0.139	-0.063	-0.489	-0.103	3.244	1.735	2.736	0.920	1.757	-0.270	0.814
B. improvisus	-1.242	0.936	0.169	-0.507	-0.794	-0.410	1.072	-0.061	4.011	-0.538	2.800	1.125	0.055	0.944	0.082
B. variegatus	-0.148	-0.340	0.358	0.607	0.867	-0.359	0.561	0.734	-1.447	-0.108	0.780	-0.490	-0.076	-0.231	-0.995
B. reticulatus	-0.791	-0.394	0.519	0.878	0.359	-1.448	-0.218	0.402	-1.385	-0.356	1.846	-0.059	-0.241	-0.222	-0.872
B. kondakovi	-0.700	-0.292	1.036	1.430	1.313	-1.108	-1.219	-0.880	-1.271	-0.737	-0.815	-0.475	0.146	-0.070	-0.741
B. citrosum	-0.126	0.760	-0.795	-1.410	-1.292	1.415	-0.616	-0.972	-1.862	-0.475	-0.963	-0.279	-0.892	-0.399	-0.167
B. subnatus	-0.078	1.718	0.165	-0.876	0.629	3.210	0.275	-0.748	-1.275	1.028	-1.111	0.327	-0.233	1.220	-1.459
B. denticulatus	-1.615	5.985	1.399	-1.268	0.771	5.359	-0.517	-2.260	-1.540	1.847	2.770	1.295	0.406	1.550	2.162
B. a. pacificus	0.184	0.863	0.637	0.045	1.824	2.304	0.795	0.578	-1.962	0.105	-1.111	-0.819	-0.958	-0.165	-1.671
B. a. mexicanus	-0.572	1.406	1.041	0.106	1.643	1.783	0.239	-0.029	-1.916	-1.291	-1.111	-1.368	-1.392	-0.744	-2.028
B. venustus	0.647	-2.074	-1.385	-0.567	-2.112	-2.583	1.475	2.090	-1.819	-1.838	-0.834	0.558	-0.106	-0.973	-0.924
B. inexpectatus	2.181	-2.617	-1.861	-0.969	-2.381	-2.281	1.182	0.990	-1.804	-0.848	-1.067	0.261	-0.367	-0.601	-0.310
B. peruvianus	1.219	-1.619	-1.195	-0.557	-1.175	-0.952	0.672	1.878	-1.991	0.634	-1.085	0.742	0.386	0.251	-0.031

Appendix D-1 (Continued).

D-1:2. Pooled Intragroup Correlations

	spur width/ basal margin	spur length/ spur width	distance from angle/ spur width	distance from angle/ spur length	distance from angle/ basal margin	spur length/ basal margin	articular ridge/ tergal margin	articular ridge/ occludent margin	number of teeth on labrum	number of spines on first maxilla	number of teeth on mandible	number of segments, cirrus I	number of segments, cirrus II	number of segments, cirrus III	number of paired setae, cirrus VI
spur width/ basal margin		-0.7076	-0.8172	-0.5519	-0.5985	0.0998	0.1504	0.1516	0.1457	0.2759	0.0130	0.1292	0.1363	0.1213	-0.0604
spur length/ spur width	-0.7076		0.7091	0.0967	0.4896	0.5101	-0.1227	-0.1518	-0.0617	-0.1760	-0.0117	-0.0696	-0.0783	-0.0728	-0.0270
distance from angle/ spur width	-0.8172	0.7091		0.7004	0.8329	-0.0410	-0.1187	-0.1395	-0.1172	-0.2274	-0.0226	-0.1229	-0.1144	-0.1094	0.0245
distance from angle/ spur length	-0.5519	0.0967	0.7004		0.7624	-0.4916	-0.0528	-0.0594	-0.1023	-0.1817	-0.0154	-0.1066	-0.1005	-0.0968	0.0686
distance from angle/ basal margin	-0.5985	0.4896	0.8329	0.7624		0.0683	-0.0550	-0.0985	-0.1032	-0.1949	-0.0210	-0.0907	-0.0967	-0.0986	-0.0422
spur length/ basal margin	0.0998	0.5101	-0.0410	-0.4916	0.0683		0.0024	-0.0359	0.0290	0.0509	0.0041	0.0718	0.0370	0.0432	-0.1141
articular ridge/ tergal margin	0.1504	-0.1227	-0.1187	-0.0528	-0.0550	0.0024		0.6953	-0.0351	0.1213	-0.0165	0.0367	-0.0455	0.0097	0.0148
articular ridge/ occludent margin	0.1516	-0.1518	-0.1395	-0.0594	-0.0985	-0.0359	0.6953		0.0173	0.1835	-0.0105	0.0564	-0.0421	0.0482	0.0508
number of teeth on labrum	0.1457	-0.0617	-0.1172	-0.1023	-0.1032	0.0290	-0.0351	0.0173		0.1267	0.0426	0.0878	0.1421	0.0889	-0.1191
number of spines on first maxilla	0.2759	-0.1760	-0.2274	-0.1817	-0.1949	0.0509	0.1213	0.1835	0.1267		0.0734	0.1519	0.1669	0.2614	0.0180
number of teeth on mandible	0.0130	-0.0117	-0.0226	-0.0154	-0.0210	0.0041	-0.0165	-0.0105	0.0426	0.0734		0.0495	0.0193	0.0697	0.0060
number of segments, cirrus I	0.1292	-0.0696	-0.1229	-0.1066	-0.0907	0.0718	0.0367	0.0564	0.0878	0.1519	0.0495		0.1392	0.0701	0.0608
number of segments, cirrus II	0.1363	-0.0783	-0.1144	-0.1005	-0.0967	0.0370	-0.0455	-0.0421	0.1421	0.1669	0.0193	0.1392		0.1895	-0.1153
number of segments, cirrus III	0.1213	-0.0728	-0.1094	-0.0968	-0.0986	0.0432	0.0097	0.0482	0.0889	0.2614	0.0697	0.0701	0.1895		0.0024
number of paired setae, cirrus VI	-0.0604	-0.0270	0.0245	0.0686	-0.0422	-0.1141	0.0148	0.0508	-0.1191	0.0180	0.0060	0.0608	-0.1153	0.0024	

Appendix D-1 (Continued).

D-1:3. Mean Values of Transformed Characters

Taxa	spur width/ basal margin	spur length/ spur width	distance from angle/ spur width	distance from angle/ spur length	distance from angle/ basal margin	spur length/ basal margin	articular ridge/ tergal margin	articular ridge/ occludent margin	number of teeth on labrum	number of spines on first maxilla	number of teeth on mandible	number of segments, cirrus I	number of segments, cirrus II	number of segments, cirrus III	number of paired setae, cirrus VI
B. a. amphitrite	0.169	-2.217	1.347	0.832	-0.119	-0.802	-0.989	0.307	3.614	-0.170	-1.225	0.076	0.255	-0.579	1.375
B. a. saltonensis	-1.068	-1.807	2.101	0.153	0.123	0.006	-0.921	0.461	4.125	-0.162	-1.136	0.223	-0.045	-0.324	3.813
B. eubalidus	1.734	-0.632	-0.175	-1.337	-0.988	0.565	-1.582	-0.262	3.424	0.348	-0.962	-0.182	-0.231	-0.057	2.064
B. ebumeus	0.206	-0.432	-0.152	-0.435	0.534	0.220	-0.542	0.292	3.305	1.501	2.492	0.405	1.100	-1.229	1.303
B. improvisus	-1.242	0.081	-1.577	-0.530	-1.022	-0.740	1.349	-1.112	4.300	-0.632	2.693	-1.324	-0.060	0.909	0.473
B. variegatus	-0.148	-0.629	0.648	-0.304	1.203	-0.242	0.514	0.519	-1.352	0.017	0.869	-0.405	0.235	-0.164	-1.052
B. reticulatus	-0.791	-1.350	0.224	-0.625	0.117	-0.552	-0.134	0.743	-1.266	-0.062	1.926	0.127	0.059	-0.122	-1.233
B. kondakovi	-0.700	-1.115	1.228	-0.381	0.832	-0.349	-1.209	-0.019	-1.144	-0.274	-0.734	-0.134	0.420	0.220	-0.795
B. citerosum	-0.126	0.950	-1.967	0.225	-0.770	1.298	-0.495	-0.791	-1.917	-0.276	-0.930	-0.196	-0.733	-0.146	-0.503
B. auturalis	-0.078	2.353	-0.612	1.046	0.981	1.946	0.323	-1.135	-1.227	1.259	-1.170	0.151	-0.335	1.131	-1.446
B. dentivarians	-1.615	6.854	-2.178	4.908	-2.033	-0.478	-0.140	-2.143	-1.948	2.734	2.619	1.072	0.182	1.151	2.211
B. c. pacificus	0.184	1.406	0.966	0.378	2.521	1.109	0.693	0.242	-1.894	0.182	-1.013	-0.831	0.665	0.053	-1.515
B. c. mexicanus	-0.572	1.417	0.569	0.097	1.801	0.415	0.277	-0.054	-1.818	-1.024	-0.933	-1.117	-0.868	-0.131	-1.923
B. venustus	0.647	-2.288	-0.794	-1.691	-1.269	-0.975	1.441	1.218	-1.875	-2.257	-0.593	0.938	0.393	-0.513	-1.547
B. inexpectatus	2.181	-1.520	0.372	-1.527	-1.643	-1.300	0.914	-0.069	-2.119	-1.429	-0.880	0.474	-0.196	-0.296	-0.767
B. peruvianus	1.219	-1.071	-0.002	-0.810	-0.267	-0.120	0.504	1.802	-2.207	0.244	-1.022	0.723	0.489	0.100	-0.458

Appendix D-1 (Continued).

D-1:4. Uncorrected D^2 (upper triangle) and Bias (lower triangle) Computed for 16 Taxa

	B.a.amphitrite	*B.a.saltonensis*	*B.subalbidus*	*B.eburneus*	*B.improvisus*	*B.variegatus*	*B.reticulatus*	*B.kondakovi*	*B.citerosum*	*B.suturaltus*	*B.dentivarians*	*B.c.pacificus*	*B.c.mexicanus*	*B.venustus*	*B.inexpectatus*	*B.peruvianus*
B.a.amphitrite		9.86	16.07	26.66	47.10	44.14	46.90	33.03	63.20	74.10	183.8	76.85	65.89	63.46	56.99	50.27
B.a.saltonensis	0.13		23.25	34.40	57.08	66.07	69.41	52.42	85.14	95.57	193.4	89.24	89.20	94.17	86.65	74.35
B.subalbidus	0.21	0.23		24.35	42.88	51.99	54.69	43.36	49.42	64.58	168.6	70.57	69.97	68.11	53.89	49.81
B.eburneus	0.21	0.23	0.31		28.46	37.25	35.62	44.75	60.07	65.46	139.1	66.84	69.41	74.98	72.06	55.37
B.improvisus	0.22	0.24	0.32	0.31		55.36	50.47	66.19	66.15	77.24	139.6	87.38	77.05	79.70	81.91	83.04
B.variegatus	0.30	0.32	0.40	0.40	0.41		4.44	73.14	23.53	28.09	136.7	13.60	12.74	25.16	24.31	12.68
B.reticulatus	0.19	0.21	0.30	0.29	0.30	0.38		11.06	27.84	41.54	140.5	30.22	25.21	22.48	26.02	16.93
B.kondakovi	0.30	0.32	0.41	0.40	0.41	0.50	0.39		23.74	31.17	150.1	19.50	15.90	29.09	25.37	15.24
B.citerosum	0.22	0.24	0.32	0.32	0.33	0.41	0.31	0.42		14.45	98.88	23.96	18.85	37.14	32.18	23.57
B.suturaltus	0.42	0.44	0.52	0.52	0.53	0.61	0.50	0.62	0.53		87.71	12.88	16.94	66.95	57.33	36.77
B.dentivarians	0.34	0.36	0.45	0.44	0.45	0.53	0.43	0.54	0.46	0.65		132.1	132.7	200.9	179.7	155.4
B.c.pacificus	0.27	0.29	0.37	0.36	0.37	0.46	0.35	0.46	0.38	0.58	0.50		3.86	52.15	45.08	26.27
B.c.mexicanus	0.20	0.22	0.30	0.30	0.31	0.39	0.28	0.39	0.31	0.51	0.43	0.36		42.33	38.69	27.80
B.venustus	0.20	0.22	0.30	0.30	0.31	0.39	0.28	0.39	0.31	0.51	0.43	0.36	0.29		8.56	14.34
B.inexpectatus	0.15	0.17	0.26	0.25	0.26	0.35	0.24	0.35	0.27	0.46	0.39	0.31	0.24	0.24		12.35
B.peruvianus	0.23	0.25	0.33	0.33	0.33	0.42	0.31	0.42	0.34	0.54	0.46	0.38	0.32	0.32	0.27	

D-1:5. Corrected D^2 (upper triangle) and Percent of Overlap (lower triangle) Computed for 16 Taxa

	B.a.amphitrite	*B.a.saltonensis*	*B.subalbidus*	*B.eburneus*	*B.improvisus*	*B.variegatus*	*B.reticulatus*	*B.kondakovi*	*B.citerosum*	*B.suturaltus*	*B.dentivarians*	*B.c.pacificus*	*B.c.mexicanus*	*B.venustus*	*B.inexpectatus*	*B.peruvianus*
B.a.amphitrite		9.73	16.49	26.45	46.89	43.84	46.71	32.72	62.98	73.68	183.5	67.59	65.69	63.26	56.83	50.04
B.a.saltonensis	5.94		23.02	34.17	56.84	65.75	69.20	52.10	84.89	95.13	193.0	88.96	88.99	93.96	86.48	74.11
B.subalbidus	2.12	0.82		24.04	42.56	51.59	54.39	42.96	49.10	64.06	168.2	70.20	69.66	67.81	53.63	49.48
B.eburneus	0.51	0.18	0.71		28.15	36.85	35.33	44.35	59.75	64.94	138.7	66.47	69.12	74.68	71.81	55.05
B.improvisus	0.03	0.01	0.06	0.40		54.95	50.17	65.78	65.82	76.71	139.1	87.00	76.75	79.39	81.65	82.70
B.variegatus	0.05	<0.01	0.02	0.12	0.01		4.06	6.82	23.12	27.48	136.1	13.14	12.35	24.77	23.97	12.26
B.reticulatus	0.03	<0.01	0.01	0.15	0.02	15.62		10.68	27.53	41.03	140.0	29.87	24.93	22.20	25.78	16.61
B.kondakovi	0.21	0.02	0.05	0.04	<0.01	9.51	5.05		23.32	30.55	149.6	19.04	15.51	28.70	25.02	14.82
B.citerosum	<0.01	<0.01	0.02	0.01	<0.01	0.82	0.44	0.80		13.91	98.43	23.58	18.54	36.83	31.91	23.23
B.suturaltus	<0.01	<0.01	<0.01	<0.01	<0.01	0.44	0.07	0.29	3.14		87.06	12.30	16.42	66.44	56.86	36.23
B.dentivarians	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01		131.6	132.3	200.5	179.4	155.0
B.c.pacificus	<0.01	<0.01	<0.01	<0.01	<0.01	3.51	0.32	1.46	0.75	4.01	<0.01		3.50	51.79	44.77	25.89
B.c.mexicanus	<0.01	<0.01	<0.01	<0.01	<0.01	3.92	0.62	2.44	1.58	2.12	<0.01	17.36		42.05	38.45	27.49
B.venustus	<0.01	<0.01	<0.01	<0.01	<0.01	0.64	0.91	0.37	0.12	<0.01	<0.01	0.02	0.06		8.31	14.02
B.inexpectatus	0.01	<0.01	0.01	<0.01	<0.01	0.71	0.55	0.62	0.24	0.01	<0.01	0.04	0.10	7.49		12.08
B.peruvianus	0.02	<0.01	0.02	0.01	<0.01	4.01	2.07	2.74	0.80	0.13	<0.01	0.55	0.44	3.07	4.09	

D-2. Computational Procedures for Determination of Clusters.

As there are no formal rules for finding clusters, Rao (1952:363) utilizes a method which begins with a pair of closely related groups to which a third with the smallest average D^2 from the first two is added. This procedure is followed until the average D^2 obtained by adding a group is particularly high. The latter group is therefore considered to lie outside the cluster. This method is then repeated until all groups have been clustered. In clustering the 16 taxa of the *amphitrite*-complex, clusters defined with average D^2 values of less than 10.00 were found to give the most realistic groupings (D-2:1), with only the position of *B. variegatus* not precisely defined. Constellations, representing intercluster relationships, were then developed in terms of the square root of the average square of the distance (D^2).

APPENDIX D-2. Computational Procedures for Determining Clusters and Constellations

D-2:1. Computations of Clusters

Taxon added to cluster	Sum of corrected D^2	No. of terms (n)	Increase in D^2 / Increase in n	Average corrected D^2 ($\Sigma D^2/n$)	Resulting cluster
B. variegatus - *B. reticulatus*	4.06	1	-----	4.06	*variegatus-reticulatus kondakovi*
B. kondakovi	29.00	3	8.75	7.19	
B. peruvianus	65.25	6	14.56	10.88	
B. c. pacificus - *B. c. mexicanus*	3.50	1	-----	3.50	*c. pacificus-c. mexicanus* [*variegatus*]*
B. variegatus	29.00	3	12.75	9.66	
B. kondakovi	70.36	6	13.79	11.73	
B. venustus - *B. inexpectatus*	8.31	1	-----	8.32	*venustus-inexpectatus*
B. peruvianus	34.41	3	13.05	11.47	
B. peruvianus - *B. inexpectatus*	12.08	1	-----	12.08	*peruvianus*
B. suturaltus - *B. c. pacificus*	12.30	1	-----	12.30	*suturaltus*
B. citerosum - *B. suturaltus*	13.91	1	-----	13.91	*citerosum*
B. dentivarians - *B. suturaltus*	87.06	1	-----	87.06	*dentivarians*
B. a. amphitrite - *B. a. saltonensis*	9.73	1	-----	9.73	*a. amphitrite-a. saltonensis*
B. subalbidus	49.24	3	19.76	16.41	
B. subalbidus - *B. a. amphitrite*	16.49	1	-----	16.49	*subalbidus*
B. eburneus - *B. subalbidus*	24.04	1	-----	24.04	*eburneus*
B. improvisus - *B. eburneus*	28.15	1	-----	28.15	*improvisus*

* Not included in cluster, see text.

D-2:2. Constellations, with Intra- and Inter-cluster Average Corrected D^2

	Cluster	(a)	(b)	(c)	(d)		
	Constellation I						
(a)	*B. a. amphitrite* - *B. a. saltonensis*	9.73	19.76	30.31	51.86		
(b)	*B. subalbidus*	19.76	-----	24.04	42.56		
(c)	*B. eburneus*	30.31	24.04	-----	28.15		
(d)	*B. improvisus*	51.86	42.56	28.15	-----		
	Constellation II						
	Cluster	(e)	(f)	(g)	(h)	(i)	(j)
(e)	*B. variegatus* - *B. reticulatus* - *B. kondakovi*	7.19	19.14	14.56	25.07	24.63	33.02
(f)	*B. c. pacificus* - *B. c. mexicanus*	19.14	3.50	26.69	44.26	21.06	14.36
(g)	*B. peruvianus*	14.56	26.69	-----	13.05	23.23	36.23
(h)	*B. venustus* - *B. inexpectatus*	25.07	44.26	13.05	8.31	34.37	65.27
(i)	*B. citerosum*	24.63	21.06	23.23	34.37	-----	13.91
(j)	*B. suturaltus*	33.02	14.36	36.23	65.27	13.91	-----
	Constellation III						
(k)	*B. dentivarians*	-----					

D-3. Test of the Efficacy of the Generalized Distance Function.

Using data from five geographic populations of *B. a. amphitrite,* the hypothesis, the distance between geographic populations of a species would be significantly less (indicating greater affinity) than the distances between any of these populations and the other taxa of the complex, was tested (D-3:1).

APPENDIX D-3. Results of Generalized Distance Function Analysis of Selected* Taxa of the *amphitrite*-complex and 5 Populations of *B. a. amphitrite*: Corrected D^2 (upper triangle) and Percent of Overlap (lower triangle)

	B. a. amphitrite														
	(1) Central and West Pacific	(2) East Pacific	(3) Gulf of Mexico	(4) Bermuda	(5) Mediterranean	*B. a. saltonensis*	*B. subalbidus*	*B. eburneus*	*B. improvisus*	*B. variegatus*	*B. reticulatus*	*B. kondakovi*	*B. venustus*	*B. inexpectatus*	*B. peruvianus*
B. a. amphitrite															
Population (1)		2.25	1.45	6.45	2.10	14.79	24.88	24.50	42.71	41.63	42.89	32.51	58.42	55.01	49.28
Population (2)	22.66		6.57	4.70	2.81	12.94	20.84	26.93	50.06	52.54	53.31	42.78	66.99	56.64	53.72
Population (3)	27.43	10.03		7.55	5.71	12.90	25.43	26.51	44.77	44.80	46.83	31.65	68.91	66.01	57.12
Population (4)	10.20	14.01	8.53		4.30	5.65	25.75	29.88	53.31	48.90	49.43	37.45	68.92	62.28	50.07
Population (5)	23.58	20.05	11.51	14.92		14.83	28.46	30.66	49.14	40.51	43.52	31.67	58.43	50.34	46.81
B. a. saltonensis	2.74	3.59	3.59	11.70	2.68		28.92	33.67	57.21	66.96	68.77	53.70	94.71	87.39	71.59
B. subalbidus	0.64	1.13	0.59	0.55	0.38	0.36		23.71	53.29	54.92	59.33	47.28	75.55	58.77	51.46
B. eburneus	0.68	0.48	0.51	0.32	0.28	0.14	0.75		28.87	37.64	36.31	45.75	75.33	72.81	54.23
B. improvisus	0.05	0.02	0.04	0.01	0.02	0.01	0.01	0.36		55.84	50.99	66.99	80.40	83.55	85.07
B. variegatus	0.06	0.01	0.04	0.02	0.07	<0.01	0.01	0.11	0.01		3.86	7.22	25.66	26.20	13.34
B. reticulatus	0.05	0.01	0.03	0.02	0.05	<0.01	0.01	0.13	0.02	16.35		10.31	22.28	27.04	16.65
B. kondakovi	0.22	0.05	0.25	0.11	0.25	0.01	0.03	0.04	<0.01	9.01	5.37		29.80	27.63	16.68
B. venustus	0.01	<0.01	<0.01	<0.01	0.01	<0.01	<0.01	<0.01	<0.01	0.57	0.91	0.32		8.95	14.59
B. inexpectatus	0.01	0.01	<0.01	<0.01	0.02	<0.01	0.01	<0.01	<0.01	0.52	0.47	0.43	6.68		14.47
B. peruvianus	0.02	0.01	0.01	0.02	0.03	<0.01	0.02	0.01	<0.01	3.36	2.07	2.07	2.81	2.87	

* Taxa with $D^2 > 60$ and percent of overlap <0.01 are excluded.

APPENDIX E. DISCRIMINANT FUNCTION ANALYSES

E-1. Computation of Discriminant Function.

Discrimination between pairs of taxa requires the selection of the best linear function of the original variables whose coefficients will maximize the value of the statistic to be used. This has been accomplished by the construction of a linear compound in the form:

$$Y = \sum_{i=1}^{p} \lambda_i x_i \qquad (1)$$

where x_i is the value of the i^{th} character with its corresponding coefficient λ_i, and p is the number of characters. Rao (1952:247) has shown that the best linear compound for two multivariate normal populations is such that the coefficients λ_i are obtained by solving the following series of simultaneous equations:

$$\begin{aligned} \lambda_1 W_{11} + \lambda_2 W_{12} + \lambda_3 W_{13} + \ldots + \lambda_p W_{1p} &= d_1 \\ \lambda_1 W_{21} + \lambda_2 W_{22} + \lambda_3 W_{23} + \ldots + \lambda_p W_{2p} &= d_2 \\ \cdot \qquad\qquad\qquad\qquad\qquad\qquad &\cdot \\ \cdot \qquad\qquad\qquad\qquad\qquad\qquad &\cdot \\ \cdot \qquad\qquad\qquad\qquad\qquad\qquad &\cdot \\ \lambda_1 W_{p1} + \lambda_2 W_{p2} + \lambda_3 W_{p3} + \ldots + \lambda_p W_{pp} &= d_p \end{aligned} \qquad (2)$$

where d_i is the difference between the estimated population means of the i^{th} character, W_{ij} is the pooled covariance between the i^{th} and j^{th} characters, and p is the number of characters. D^2 is given by:

$$D^2 = \lambda_1 d_1 + \lambda_2 d_2 + \lambda_3 d_3 + \ldots + \lambda_p d_p \qquad (3)$$

For pairs of taxa of the *amphitrite*-complex, the discriminant function is:

$$Y = \lambda_1 x_1 + \lambda_2 x_2 + \lambda_3 x_3 + \ldots + \lambda_{15} x_{15} \qquad (4)$$

where x_1 is spur width/basal margin, x_2 is spur length/spur width, x_3 is distance from angle/spur width, x_4 is distance from angle/spur length, x_5 is distance from angle/basal margin, x_6 is spur length/basal margin, x_7 is articular ridge/tergal margin, x_8 is articular ridge/occludent margin, x_9 is number of teeth on labrum, x_{10} is number of spines on first maxilla, x_{11} is number of teeth on mandible, x_{12} is number of segments, cirrus I, x_{13} is number of segments, cirrus II, x_{14} is number of segments, cirrus III, and x_{15} is number of paired setae, cirrus VI (E-1:1). Details of the mathematical derivations are given by Rao (1952:287).

Appendix E-1 (Continued).

E-1:1. Discriminant Function Coefficients of 15 Quantitative Characters for Closest Neighbor Pairs of Taxa of the *amphitrite*-complex

Pairs of taxa	Sample size (n)	spur width/ basal margin	spur length/ spur width	distance from angle/ spur width	distance from angle/ spur length	distance from angle/ basal margin	spur length/ basal margin	articular ridge/ tergal margin	articular ridge/ occludent margin	number of teeth on Labrum	number of spines on first maxilla	number of teeth on mandible	number of segments, cirrus I	number of segments, cirrus II	number of segments, cirrus III	number of paired setae, cirrus VI
B.a.amphitrite	272	-0.00037	-0.00473	-0.00220	-0.00325	-0.01012	-0.04470	-0.00774	0.00653	-0.00058	0.00036	-0.00302	-0.00008	0.00049	-0.00115	-0.00221
B.a. saltonensis	201															
B.subalbidus	95	0.21244	0.07048	-0.03265	-0.02988	0.51270	-0.50062	-0.01149	0.06810	0.00025	-0.00094	-0.00557	0.00031	0.00358	-0.00183	-0.00056
B.a.amphitrite	272															
B.eburneus	98	0.02083	0.02443	0.03106	-0.13044	0.56803	-0.25549	0.06736	0.34132	-0.00097	0.00248	0.06238	0.00133	0.00937	-0.00533	-0.00275
B.subalbidus	95															
B.improvisus	93	-0.26489	0.02316	-0.01314	0.04912	-0.75668	-0.10206	0.37695	-0.30896	0.00153	-0.01270	0.01240	-0.00854	-0.00372	0.01050	-0.00418
B.eburneus	98															
B.variegatus	61	-0.26407	0.03896	-0.06168	0.05327	-0.21090	-0.26067	-0.12848	-0.00036	0.00193	-0.00193	0.01044	0.00608	-0.00193	-0.00122	0.00501
B.reticulatus	108															
B.Kondakovi	60	0.53060	0.20898	-0.14995	-0.02199	0.59843	-0.71460	0.16902	0.11591	-0.00231	0.00904	0.02502	-0.00293	-0.00388	-0.00341	-0.00109
B.variegatus	61															
B.citerosum	90	0.15050	-0.00574	0.15236	0.61733	-2.75564	0.47773	-0.19729	0.01216	-0.01831	0.00563	0.03025	-0.00517	-0.00331	-0.00329	0.00532
B.subalbidus	41															
B.denticulatus	52	0.31411	-0.14456	0.77193	0.95638	-6.60729	2.21672	0.12932	-0.25302	-0.02471	-0.00739	0.27284	0.01010	-0.00625	0.00755	0.14062
B.subalbidus	41															
B.subalbidus	41	-0.23422	-0.00429	0.07979	-0.06925	-1.07839	0.15844	0.07254	-0.42638	0.01137	0.00554	0.00000	0.00987	0.00802	0.01558	0.01320
B.a.pacificus	71															
B.a.pacificus	71	0.15817	-0.03133	0.04229	0.09079	-0.21998	0.20269	-0.07395	0.07249	0.00236	0.00506	0.00000	0.00301	0.00443	0.00050	0.01089
B.a.mexicanus	104															
B.venustus	104	-0.15746	0.02025	-0.01491	0.01824	-0.23678	-0.07251	-0.01714	0.20829	-0.00049	-0.00527	0.01237	0.00225	0.00407	-0.00342	-0.01063
B.inexpectatus	151															
B.perrymans	87	-0.18090	-0.08175	-0.07629	-0.02175	0.13753	-0.06856	0.13515	-0.24002	0.00408	-0.00687	0.01242	-0.00045	-0.00411	-0.00432	-0.00264
B.inexpectatus	151															

E-2. Results and Test of Significance of Discriminant Function.

The resulting differences (Y) between "closest neighbor pairs" of taxa have been tested using the variance ratio test (Rao, 1948) with the null hypothesis that no difference in mean values of the discriminant function for any pair exists (E-2:1). The test consists of the computation of F-values with p and $n_1 + n_2 - 1 - p$ degrees of freedom such that:

$$F\ (p,\ n_1 + n_2 - 1 - p) = \frac{n_1 n_2 (n_1 + n_2 - p - 1)}{p(n_1 + n_2)\ (n_1 + n_2 - 2)} . D^2 \qquad (5)$$

where n_1 and n_2 are the sample sizes of populations 1 and 2, respectively, p is the number of characters, and D^2 is the variance between the population means as computed by the discriminant function. As all F-values are significant at the 5 percent level, the hypothesis of no differences in mean values is rejected; "closest neighbor pairs" are distinct taxa.

E-2:1. Results of Test of Significance of Discriminant Function Analysis of Closest Neighbor Pairs of Taxa

Pairs of taxa	sample size (n)	uncorrected D^2	corrected D^2	percent error of misclassification	mean Y	standard deviation of Y	critical Y (Y_0)	discriminant function F-value
B. a. amphitrite	272	5.14	5.01	13.14	-0.0639	0.0047	0.0694	F(15,457)
B. a. saltonensis	201				-0.0748	0.0050		38.42
B. subalbidus	95	16.53	16.32	2.17	0.0078	0.0139	0.0304	F(15,351)
B. a. amphitrite	272				0.0531	0.0100		74.62
B. eburneus	98	21.37	21,06	1.10	0.5818	0.0249	0.5259	F(15,177)
B. subalbidus	95				0.4700	0.0235		63.68
B. improvisus	93	30.30	29.98	0.31	-0.0284	0.0282	0.1086	F(15,175)
B. eburneus	98				-0.1887	0.0300		89.24
B. variegatus	61	6.08	5.70	11.70	-0.1740	0.0153	-0.1558	F(15,153)
B. reticulatus	108				-0.1376	0.0145		14.49
B. kondakovi	60	6.33	5.83	11.31	0.4371	0.0209	0.4638	F(15,105)
B. variegatus	61				0.4904	0.0214		11.26
B. citerosum	90	17.11	16.58	2.07	0.0720	0.0319	0.0057	F(15,115)
B. suturaltus	41				-0.0606	0.0325		28.64
B. dentivarians	52	95.60	94.94	<0.01	-3.4142	0.1224	-2.8890	F(15,77)
B. suturaltus	41				-2.3637	0.0846		123.63
B. suturaltus	41	15.70	15.17	2.56	-0.0617	0.0402	-0.1331	F(14,97)
B. c. pacificus	71				-0.2045	0.0334		25.71
B. c. pacificus	71	4.25	3.92	16.11	0.2015	0.0140	0.1892	F(14,160)
B. c. mexicanus	104				0.1769	0.0103		11.84
B. venustus	104	9.94	9.69	5.94	0.0172	0.0118	-0.0024	F(15,239)
B. inexpectatus	151				-0.0220	0.0129		38.54
B. peruvianus	87	14.16	13.89	3.07	0.2341	0.0149	0.2041	F(15,222)
B. inexpectatus	151				0.1741	0.0165		49.03

E-3. Classification of Individuals Known Only to Belong to a Given Species Pair: *B. variegatus* — *B. reticulatus.*

Use of the discriminant function to classify individuals requires definition of coefficients (λ_i) for each multiple character within reference populations. Classification of 45 individuals known only to belong to the species pair, *B. variegatus* — *B. reticulatus,* is based on character coefficients of the reference populations, *B. variegatus* — *B. reticulatus* (E-1:1), their mean Y values, and the critical Y value of the pair (E-2:1). Classification of unknown individuals is accomplished by application of the reference coefficients to the individual values of the respective multiple characters (E-3:1) for each specimen and calculating its Y value. The rule for classification of individuals into one of two populations (Rao, 1952:295) is:

$$Y_0 = \frac{\overline{Y}_1 + \overline{Y}_2}{2} \qquad (6)$$

where $\overline{Y}_1$ and $\overline{Y}_2$ are populations means estimated by the discriminant function for reference populations 1 and 2, respectively. Individuals from the unknown population with Y values greater than Y_0 are classified as belonging to the population with the larger Y; those individuals with Y values less than Y_0 are classified as belonging to the other population (E-3:2).

Appendix E-3 (Continued).

E-3-1. Values of Y for 45 Specimens of a Mixed Sample

$$Y = \lambda_1 x_1 + \lambda_2 x_2 + \ldots + \lambda_{15} x_{15}$$

where $\lambda_1, \lambda_2 \ldots \lambda_{15}$ are the coefficients of the reference populations, *B. variegatus* and *B. reticulatus*, and $x_1, x_2 \ldots x_{15}$ are the values of the characters.

Specimen Number	$-\lambda_1 x_1$	$+\lambda_2 x_2$	$-\lambda_3 x_3$	$+\lambda_4 x_4$	$-\lambda_5 x_5$	$-\lambda_6 x_6$	$-\lambda_7 x_7$	$-\lambda_8 x_8$	$+\lambda_9 x_9$	$-\lambda_{10} x_{10}$	$+\lambda_{11} x_{11}$	$+\lambda_{12} x_{12}$	$-\lambda_{13} x_{13}$	$-\lambda_{14} x_{14}$	$+\lambda_{15} x_{15}$	$-Y$
6488a	0.0555	0.0390	0.0814	0.0703	0.0591	0.0547	0.0938	0.0002	0.0077	0.0116	0.0522	0.0152	0.0019	0.0018	0.0200	0.1556
6488c	0.0713	0.0429	0.0586	0.0463	0.0527	0.0756	0.0899	0.0002	0.0077	0.0135	0.0522	0.0213	0.0029	0.0024	0.0200	0.1767
6488e	0.0687	0.0464	0.0648	0.0469	0.0569	0.0808	0.0925	0.0002	0.0145	0.0135	0.0522	0.0213	0.0019	0.0024	0.0263	0.1741
6489a	0.0687	0.0355	0.0481	0.0458	0.0443	0.0626	0.0951	0.0002	0.0077	0.0096	0.0522	0.0213	0.0029	0.0024	0.0200	0.1514
6489b	0.0660	0.0370	0.0444	0.0405	0.0380	0.0626	0.0951	0.0002	0.0077	0.0106	0.0626	0.0091	0.0019	0.0043	0.0200	0.1462
6489c	0.0660	0.0390	0.0500	0.0431	0.0422	0.0652	0.1015	0.0002	0.0077	0.0096	0.0522	0.0274	0.0010	0.0012	0.0200	0.1475
6489d	0.0581	0.0456	0.0685	0.0506	0.0527	0.0678	0.0938	0.0002	0.0077	0.0058	0.0522	0.0122	0.0029	0.0012	0.0175	0.1652
6489e	0.0475	0.0678	0.1036	0.0517	0.0633	0.0808	0.0835	0.0002	0.0077	0.0077	0.0522	0.0182	0.0039	0.0024	0.0200	0.1753
6489f	0.0607	0.0487	0.0709	0.0490	0.0569	0.0756	0.0887	0.0002	0.0068	0.0077	0.0522	0.0152	0.0019	0.0018	0.0200	0.1725
6489h	0.0687	0.0339	0.0592	0.0586	0.0527	0.0600	0.0887	0.0002	0.0077	0.0038	0.0522	0.0304	0.0029	0.0012	0.0200	0.1366
6489i	0.0687	0.0436	0.0592	0.0458	0.0506	0.0756	0.0912	0.0002	0.0077	0.0087	0.0522	0.0182	0.0029	0.0024	0.0200	0.1720
6489j	0.0528	0.0534	0.0845	0.0533	0.0569	0.0704	0.0797	0.0002	0.0077	0.0077	0.0522	0.0182	0.0039	0.0012	0.0200	0.1525
6489k	0.0555	0.0584	0.0771	0.0442	0.0569	0.0834	0.0835	0.0002	0.0077	0.0077	0.0522	0.0122	0.0019	0.0012	0.0200	0.1727
6489l	0.0475	0.0612	0.0925	0.0506	0.0591	0.0756	0.0925	0.0002	0.0077	0.0077	0.0522	0.0182	0.0029	0.0012	0.0200	0.1693
6489m	0.0607	0.0584	0.0759	0.0437	0.0612	0.0912	0.0874	0.0002	0.0077	0.0077	0.0522	0.0213	0.0019	0.0012	0.0250	0.1791
6491a	0.0871	0.0343	0.0432	0.0421	0.0485	0.0756	0.0887	0.0002	0.0068	0.0096	0.0522	0.0213	0.0029	0.0012	0.0200	0.1803
6491b	0.0581	0.0549	0.0580	0.0357	0.0443	0.0808	0.0861	0.0002	0.0077	0.0058	0.0522	0.0213	0.0039	0.0012	0.0200	0.1466
6491e	0.0687	0.0417	0.0555	0.0447	0.0506	0.0730	0.0874	0.0002	0.0077	0.0058	0.0522	0.0274	0.0039	0.0012	0.0200	0.1526
6492a	0.0660	0.0503	0.0685	0.0458	0.0591	0.0834	0.0809	0.0002	0.0077	0.0096	0.0522	0.0182	0.0039	0.0018	0.0200	0.1792
6492b	0.0475	0.0651	0.0987	0.0511	0.0591	0.0756	0.0899	0.0002	0.0077	0.0077	0.0522	0.0122	0.0029	0.0018	0.0200	0.1751
6493	0.0528	0.0534	0.0771	0.0485	0.0527	0.0730	0.0822	0.0002	0.0077	0.0048	0.0522	0.0152	0.0029	0.0024	0.0175	0.1536
6494	0.0449	0.0518	0.0771	0.0501	0.0464	0.0600	0.0835	0.0002	0.0077	0.0058	0.0522	0.0152	0.0019	0.0012	0.0175	0.1265
6495	0.0687	0.0444	0.0586	0.0442	0.0527	0.0782	0.0925	0.0002	0.0077	0.0096	0.0626	0.0243	0.0019	0.0012	0.0200	0.1604
6496a	0.0475	0.0623	0.0740	0.0400	0.0464	0.0756	0.0835	0.0002	0.0077	0.0048	0.0522	0.0122	0.0029	0.0006	0.0200	0.1411
6496b	0.0555	0.0487	0.0617	0.0426	0.0443	0.0678	0.0835	0.0002	0.0077	0.0048	0.0522	0.0152	0.0010	0.0012	0.0175	0.1361
6497	0.0502	0.0471	0.0882	0.0629	0.0591	0.0626	0.0874	0.0002	0.0087	0.0077	0.0522	0.0213	0.0010	0.0018	0.0200	0.1460
6498	0.0528	0.0429	0.0740	0.0581	0.0506	0.0573	0.0694	0.0001	0.0087	0.0039	0.0522	0.0122	0.0039	0.0018	0.0175	0.1222
6501	0.0581	0.0627	0.0752	0.0405	0.0569	0.0938	0.0887	0.0002	0.0077	0.0096	0.0626	0.0122	0.0039	0.0024	0.0225	0.1806
6502	0.0687	0.0436	0.0617	0.0474	0.0548	0.0756	0.0951	0.0002	0.0077	0.0096	0.0522	0.0304	0.0019	0.0024	0.0213	0.1674
6503	0.0502	0.0584	0.0771	0.0442	0.0485	0.0730	0.0822	0.0002	0.0077	0.0087	0.0522	0.0122	0.0019	0.0012	0.0200	0.1483
6504	0.0607	0.0491	0.0845	0.0575	0.0634	0.0756	0.0835	0.0002	0.0077	0.0096	0.0522	0.0243	0.0019	0.0024	0.0150	0.1780
6506	0.0475	0.0530	0.0956	0.0602	0.0569	0.0626	0.0835	0.0002	0.0077	0.0077	0.0574	0.0182	0.0029	0.0018	0.0200	0.1422
6507	0.0475	0.0682	0.0666	0.0330	0.0422	0.0834	0.1002	0.0002	0.0077	0.0058	0.0522	0.0152	0.0010	0.0006	0.0200	0.1512
6508	0.0766	0.0303	0.0438	0.0293	0.0422	0.0964	0.0758	0.0001	0.0077	0.0077	0.0522	0.0243	0.0029	0.0006	0.0200	0.1623
6509	0.0634	0.0518	0.0617	0.0400	0.0506	0.0808	0.0797	0.0001	0.0077	0.0039	0.0522	0.0152	0.0019	0.0018	0.0200	0.1570
6510	0.0607	0.0526	0.0617	0.0394	0.0485	0.0808	0.0874	0.0001	0.0077	0.0058	0.0522	0.0182	0.0019	0.0018	0.0200	0.1586
6511	0.0555	0.0503	0.0796	0.0533	0.0569	0.0704	0.0925	0.0002	0.0077	0.0039	0.0522	0.0213	0.0010	0.0018	0.0200	0.1570
6512	0.0607	0.0452	0.0814	0.0607	0.0633	0.0678	0.0797	0.0001	0.0077	0.0077	0.0522	0.0182	0.0019	0.0006	0.0200	0.1592
6513a	0.0528	0.0425	0.0839	0.0666	0.0569	0.0573	0.0758	0.0001	0.0077	0.0087	0.0522	0.0213	0.0029	0.0012	0.0175	0.1318
6513b	0.0766	0.0273	0.0456	0.0359	0.0464	0.0547	0.0887	0.0002	0.0068	0.0077	0.0626	0.0243	0.0019	0.0012	0.0200	0.1261
6514	0.0713	0.0390	0.0666	0.0575	0.0612	0.0704	0.0784	0.0002	0.0087	0.0096	0.0626	0.0243	0.0019	0.0012	0.0200	0.1487
6515	0.0528	0.0573	0.0820	0.0485	0.0569	0.0756	0.0874	0.0002	0.0077	0.0058	0.0626	0.0213	0.0039	0.0018	0.0175	0.1515
6516	0.0449	0.0623	0.0864	0.0463	0.0506	0.0730	0.0719	0.0001	0.0077	0.0096	0.0626	0.0182	0.0019	0.0012	0.0200	0.1247
6517	0.0739	0.0464	0.0567	0.0410	0.0548	0.0886	0.0822	0.0001	0.0077	0.0096	0.0574	0.0182	0.0019	0.0024	0.0200	0.1795
6518	0.0502	0.0557	0.0746	0.0453	0.0485	0.0704	0.0925	0.0002	0.0077	0.0058	0.0522	0.0152	0.0010	0.0012	0.0200	0.1483

Appendix E-3 (Continued).

E-3:2. Mixed Sample of 45 Specimens Classified with Discriminant Function

$$Y_0 = \frac{-0.1740 + -0.1376}{2} = -0.1558$$

Where -0.1740 and -0.1376 are mean values of Y for reference populations, *B. variegatus* and *B. reticulatus*.

B. variegatus				*B. reticulatus*			
Specimen number	Y value	Specimen number	Y value	Specimen number	Y value	Specimen number	Y value
6501	-0.1806	6489f	-0.1725	6488a	-0.1556	6491b	-0.1466
6491a	-0.1803	6489i	-0.1720	6493	-0.1536	6489b	-0.1462
6517	-0.1795	6489l	-0.1693	6491e	-0.1526	6497	-0.1460
6492a	-0.1792	6502	-0.1674	6489j	-0.1525	6506	-0.1422
6489m	-0.1791	6489d	-0.1652	6515	-0.1515	6496a	-0.1411
6504	-0.1780	6508	-0.1623	6489a	-0.1514	6489h	-0.1366
6488c	-0.1767	6495	-0.1604	6507	-0.1512	6496b	-0.1361
6489e	-0.1753	6512	-0.1592	6514	-0.1487	6513a	-0.1318
6492b	-0.1751	6510	-0.1586	6518	-0.1483	6494	-0.1265
6488e	-0.1741	6511	-0.1570	6503	-0.1483	6513b	-0.1261
6489h	-0.1727	6509	-0.1570	6489c	-0.1475	6516	-0.1247
						6498	-0.1222

E-4. Test for Discriminatory Significance of Characters.

The discriminant function coefficients (λ_i) indicate the relative discriminatory efficacy of the characters (E-1:1); therefore, the characters may be reordered for each of the "closest neighbor pairs" according to their discriminatory power (E-4:1). To determine the significance of individual characters, the null hypothesis, D^2 does not increase in going from a discriminant function using p number of characters to one using $p + q$ characters, was tested by the following F-test:

$$F = \frac{n_1 + n_2 - p - q - 1}{q} \quad (R - 1) \qquad (7)$$

with q and $(n_1 + n_2 - p - q\ 1)$ degrees of freedom; where n_1 and n_2 are the sample sizes from populations 1 and 2, respectively, and R is defined as:

$$R = \frac{1 + \frac{n_1 n_2}{(n_1+n_2)\ (n_1+n_2-2)} D^2_{p+q}}{1 + \frac{n_1 n_2}{(n_1+n_2)\ (n_1+n_2-2)} D^2_{p}} \qquad (8)$$

where D^2_{p+q} is the D^2 value computed by the discriminant function using $p + q$ characters and D^2_p is the D^2 value computed using p characters (Rao, 1952:253). In this test $p + q$ was defined as the total number of characters; p was the reduced number of characters and q was the difference between them. In each successive F-test, p was reduced by 1 until the 5 percent level of significance was reached (E-4:2).

Appendix E-4 (Continued).

E-4:1. Quantitative Characters Ranked According to Contribution to D^2 of Closest Neighbor Pairs of Taxa and Results of Test of Significance

		spur width/ basal margin	spur length/ spur width	distance from angle/ spur width	distance from angle/ spur length	distance from angle/ basal margin	spur length/ basal margin	articular ridge/ tergal margin	articular ridge/ occludent margin	number of teeth on labrum	number of spines on first maxilla	number of teeth on mandible	number of segments, cirrus I	number of segments, cirrus II	number of segments, cirrus III	number of paired setae, cirrus VI
B.a.amphitrite	272	*13	5	9	6	2	1	3	4	11	*14	7	*15	*12	10	8
B.a.saltonensis	201															
B.subalbidus	95	3	4	6	7	1	2	8	5	*15	*12	9	*14	10	11	*13
B.a.amphitrite	272															
B.eburneus	98	9	8	7	4	1	3	5	2	*15	*13	6	*14	10	11	*12
B.subalbidus	95															
B.improvisus	93	4	7	8	6	1	5	2	3	15	9	10	12	14	11	13
B.eburneus	98															
B.variegatus	61	1	7	5	6	3	2	4	*15	*11	*12	8	9	*13	*14	*10
B.reticulatus	108															
B.kondakovi	60	3	4	6	9	2	1	5	7	*14	10	8	*13	*11	*12	*15
B.variegatus	61															
B.citerosum	90	6	10	5	2	1	3	4	9	8	11	7	*13	*14	*15	12
B.suturaltus	41															
B.dentivarians	52	5	8	4	3	1	2	*10	7	*11	*14	6	*12	*15	*13	9
B.suturaltus	41															
B.suturaltus	41	3	*14	5	7	1	4	7	2	10	*13	**	11	*12	8	9
B.c.pacificus	71															
B.c.pacificus	71	3	8	7	4	1	2	5	6	*13	10	**	*12	11	*14	9
B.c.mexicanus	104															
B.venustus	104	3	5	8	6	1	4	7	2	*15	11	9	14	12	13	10
B.inexpectatus	151															
B.peruvianus	87	2	5	6	8	3	7	4	1	*13	10	9	*15	12	11	*14
B.inexpectatus	151															

* Indicates no significant contribution to D^2.

** Constant for both members of pair, therefore, omitted from test.

Appendix E-4 (Continued).

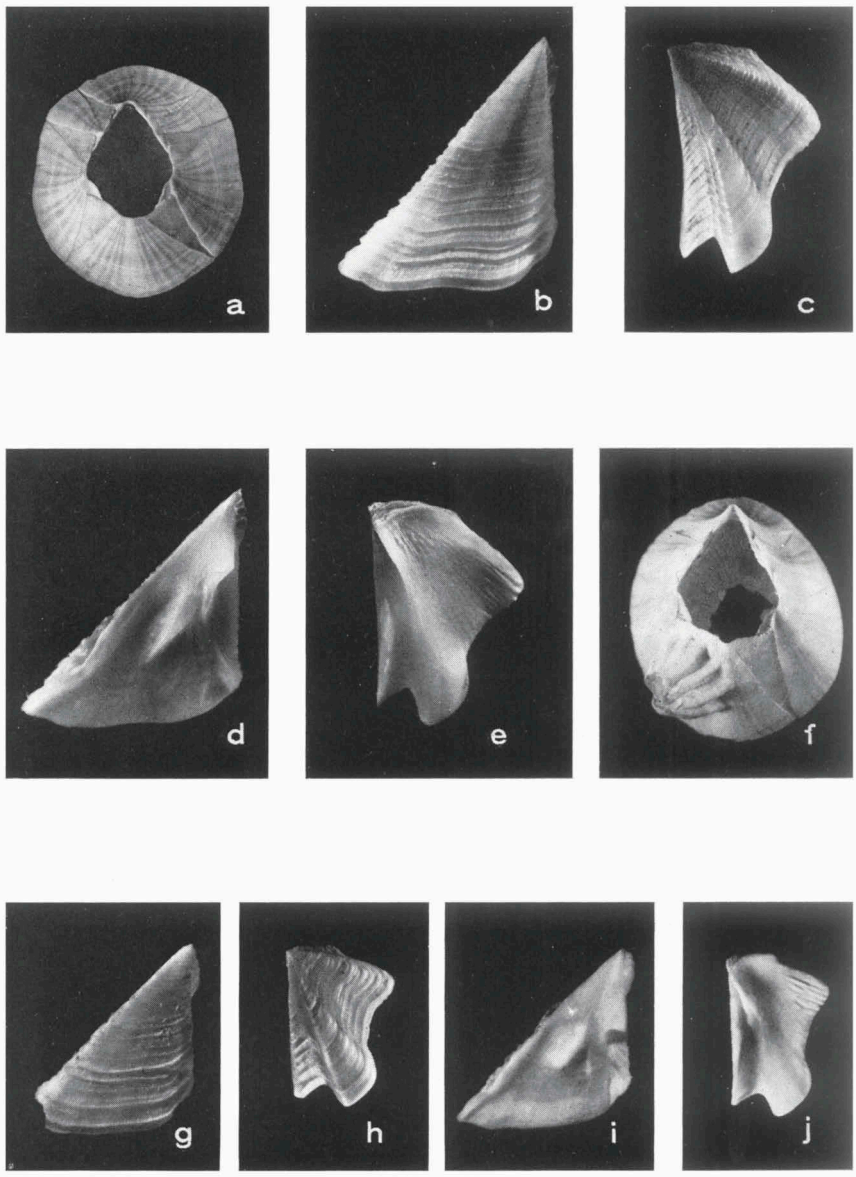
E-4:2. Summary of Tests of Significance of Corrected D^2 for Reduced Number of Characters

Pairs of taxa	p characters *	corrected D^2	percent error of misclassification	p + q characters	corrected D^2	percent error of misclassification
B. a. amphitrite - *B. a. saltonensis*	11	4.97	13.35	15	5.01	13.14
B. subalbidus - *B. a. amphitrite*	11	16.01	2.28	15	16.32	2.17
B. eburneus - *B. subalbidus*	11	20.14	1.25	15	21.06	1.10
B. improvisus - *B. eburneus*	..	.....	....	15	29.98	0.31
B. variegatus - *B. reticulatus*	9	5.32	12.51	15	5.70	11.70
B. kondakovi - *B. variegatus*	10	5.40	12.30	15	5.83	11.31
B. citerosum - *B. suturaltus*	12	15.73	2.39	15	16.58	2.07
B. dentivarians - *B. suturaltus*	9	86.27	<0.01	15	94.94	<0.01
B. suturaltus - *B. c. pacificus*	11	14.10	3.01	14†	15.16	2.56
B. c. pacificus - *B. c. mexicanus*	11	3.73	16.60	14†	3.92	16.11
B. venustus - *B. inexpectatus*	14	9.71	5.94	15	9.69	5.94
B. peruvianus - *B. inexpectatus*	12	13.34	3.36	15	13.89	3.07

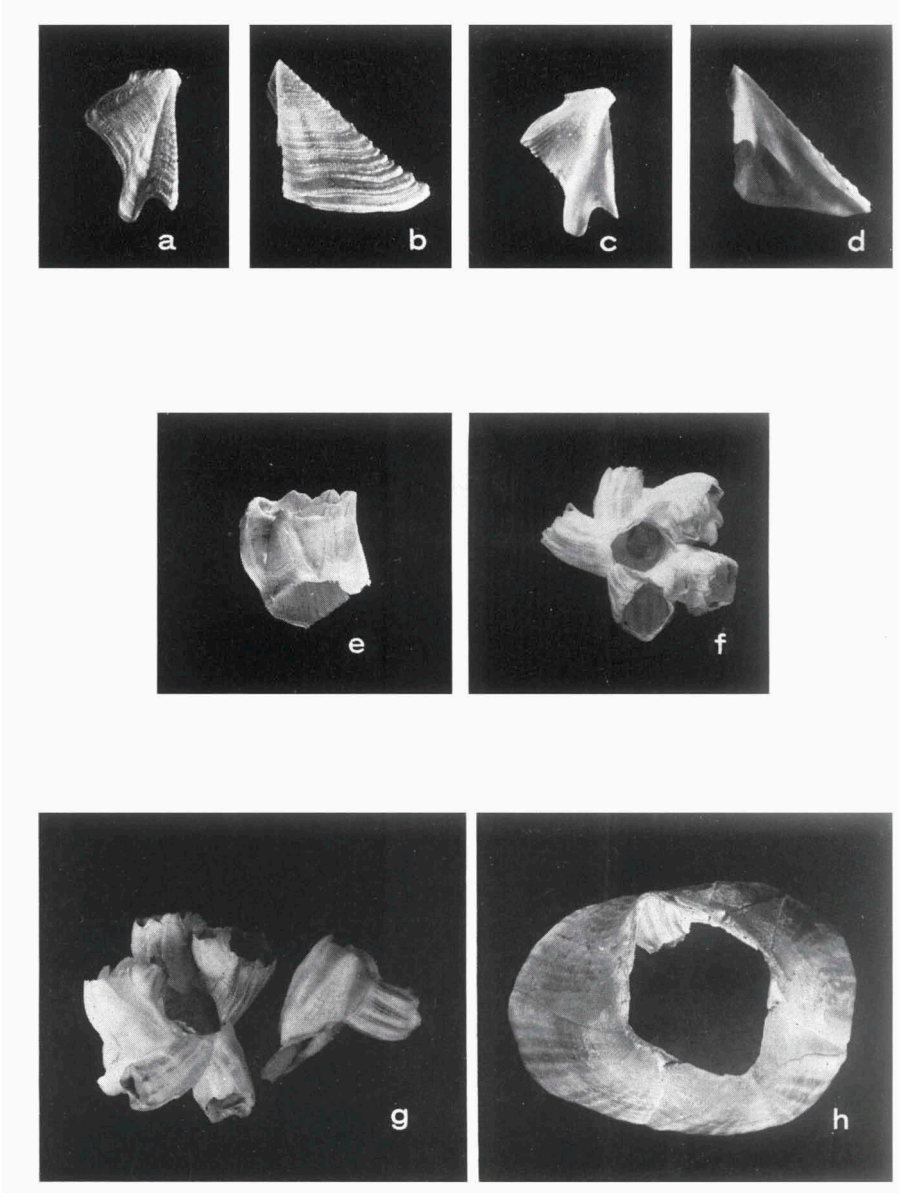
* Significant at 5 percent level.

† One character, constant for both members, not included.

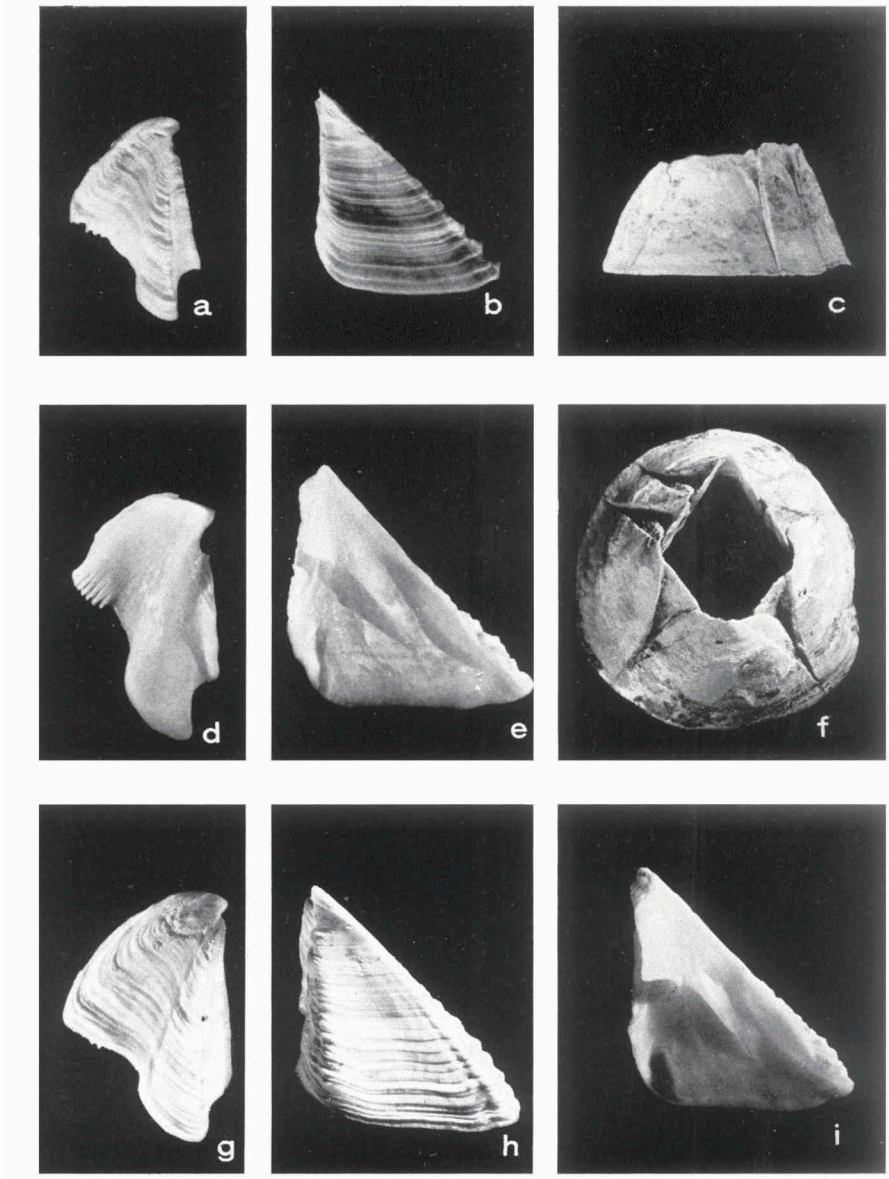
PLATES



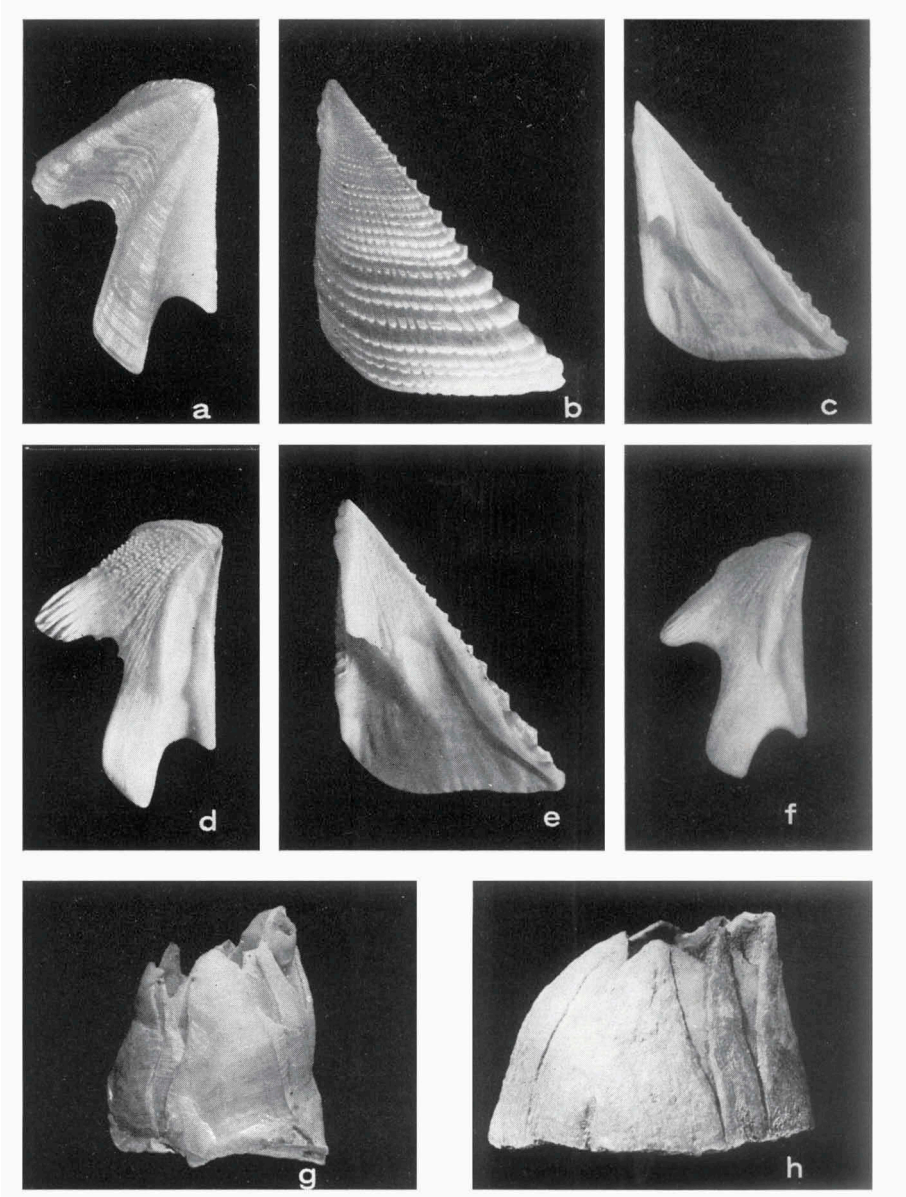
Balanus amphitrite amphitrite Darwin. a, apical view of shell; b-e, external and internal views of opercular valves (Honolulu); f, apical view of shell, with *B. glandula* Darwin on rostrum; g-j, external and internal views of opercular valves (Newport Bay, California). a, f × 2; b-e, g-j × 5.



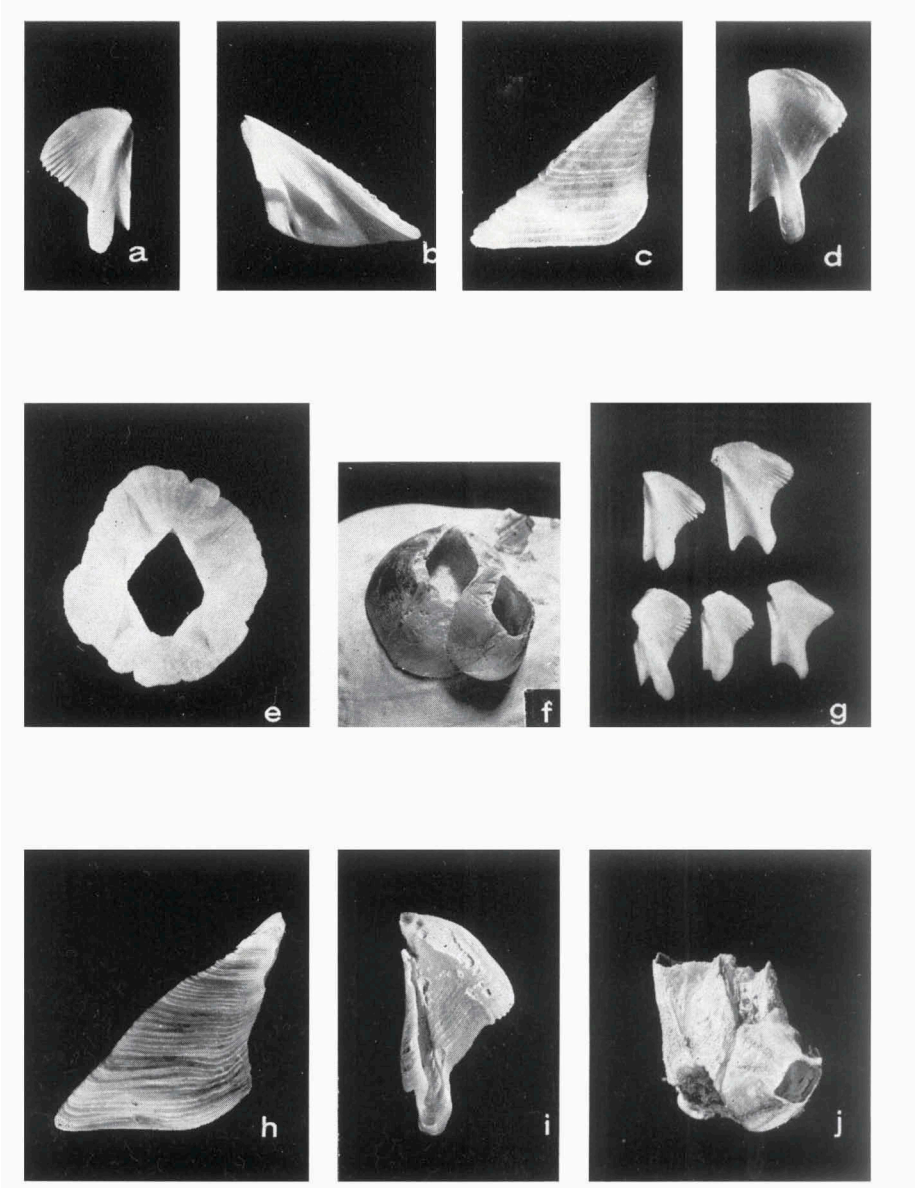
Balanus amphitrite saltonensis Rogers. a-d, external and internal views of opercular valves; e, lateral view of shell (Wilmington Harbor, California); f, g, three groups of superimposed shells (Salton Sea, 2/55); h, apical view of shell with small specimen on sheath of carina (Fish Springs). a-d × 5; e-h × 2.



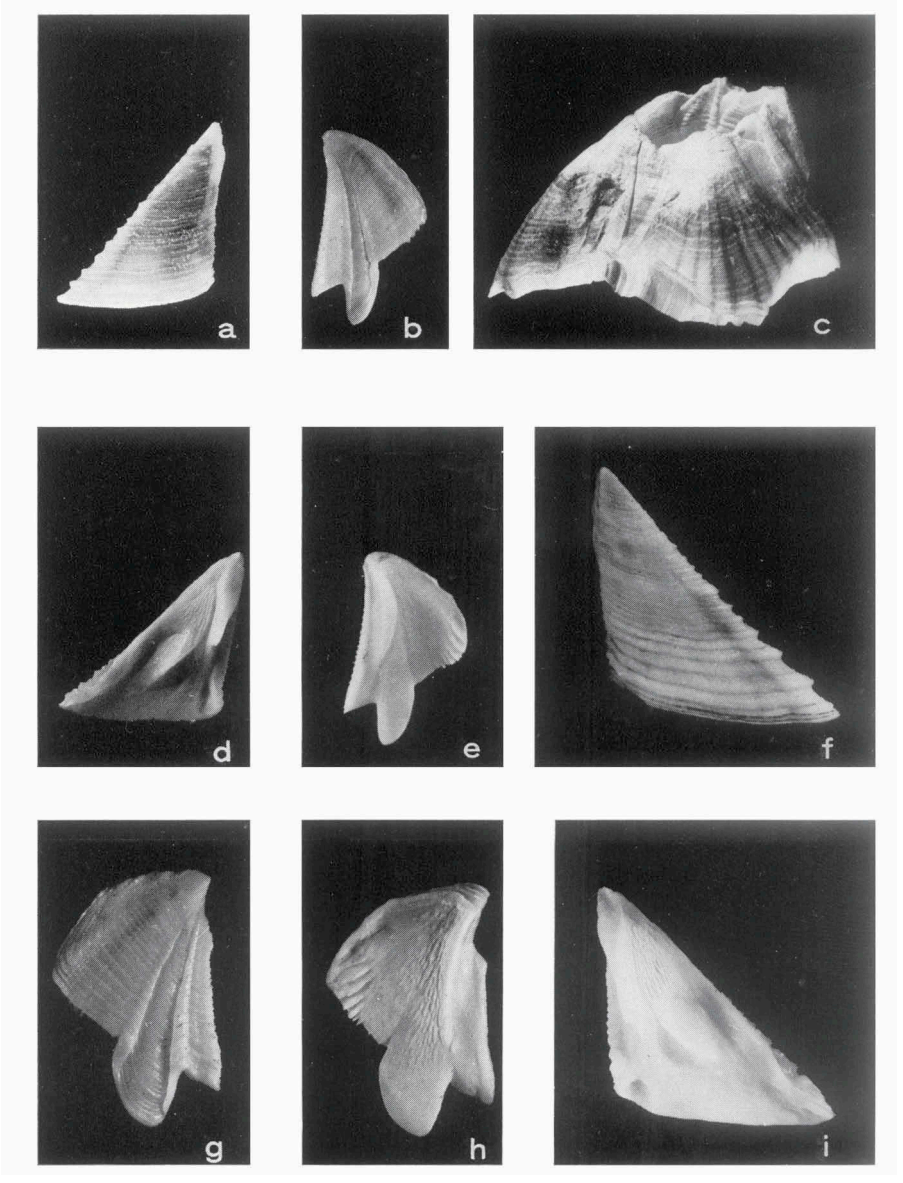
Balanus subalbidus Henry. a, b, external views of tergum and scutum (paratype); c, lateral view of shell; d, e, internal views of tergum and scutum (holotype); f, apical view of shell; g, h, external views of tergum and scutum; internal view of scutum (Pass Christian, Mississippi). a, b, d, e, g-i × 5; c, f × 2. (after Henry, 1974).



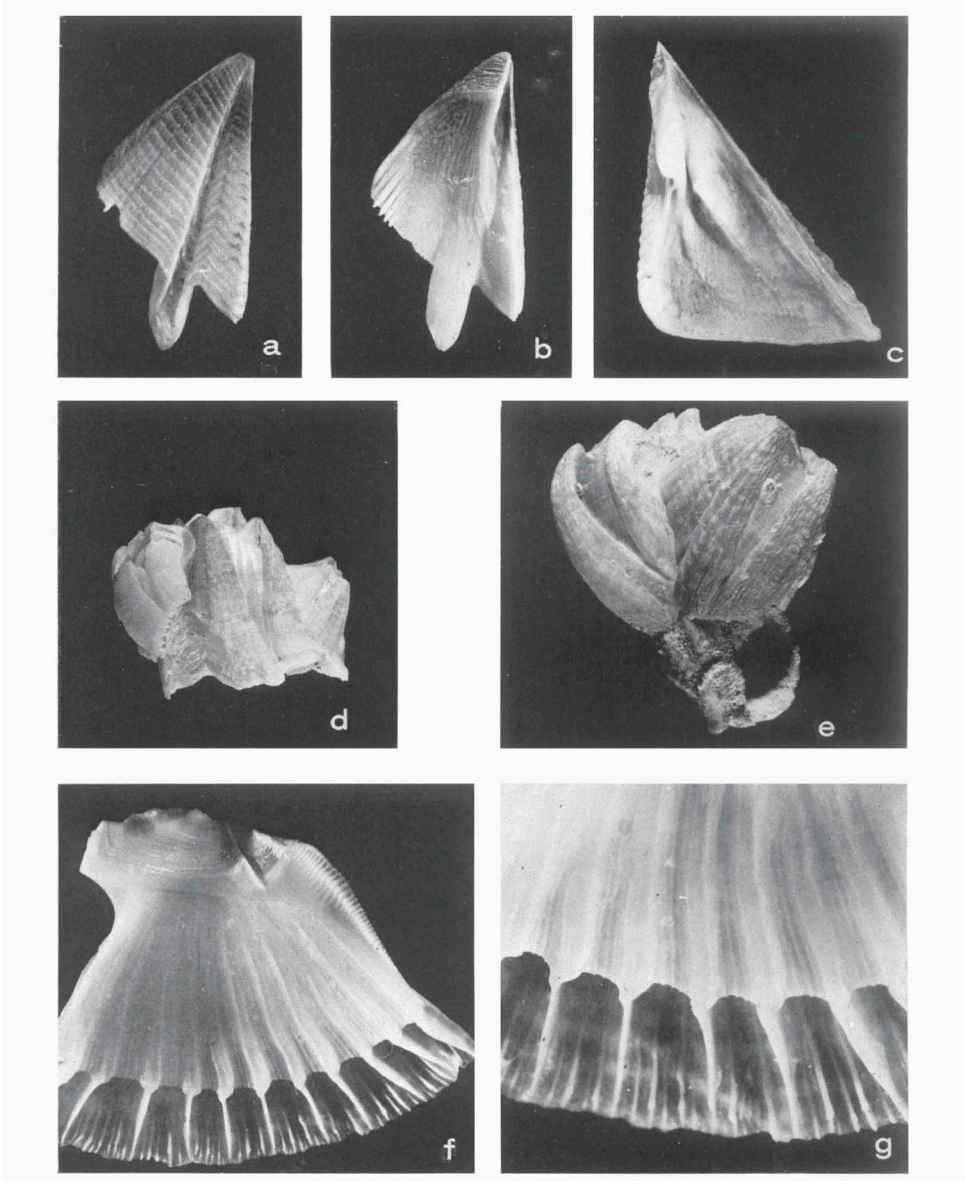
Balanus eburneus Gould. a, b, d, e, external and internal views of opercular valves; h, lateral view of shell (Saint Marks, Florida); c, f, internal views of scutum and tergum; g, lateral view of shell (Tampa Bay, Florida). a-f × 5; g, h × 2. (c-h, after Henry, 1959).



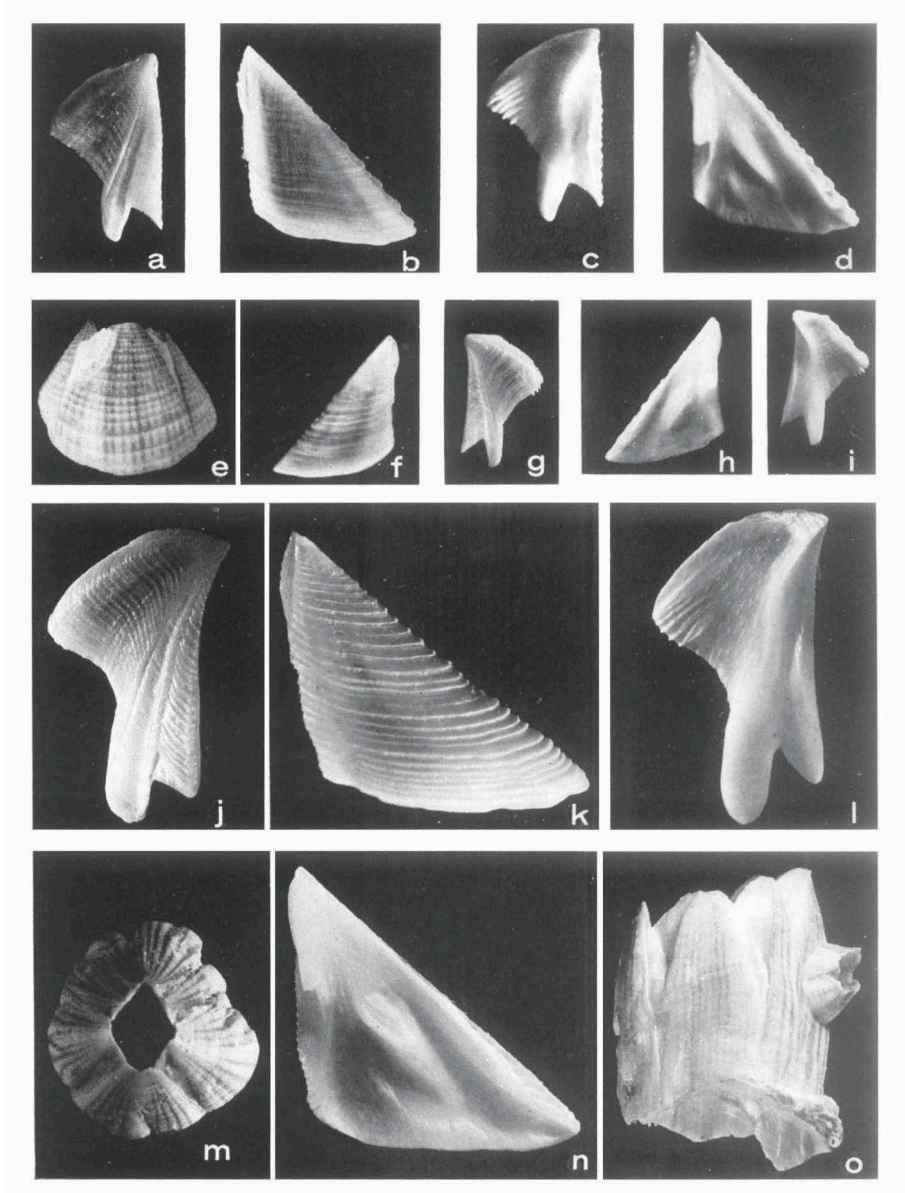
Balanus improvisus Darwin. a, b, internal views of tergum and scutum (Coles Point Bar, Maryland); c, d, external views of scutum and tergum; e, apical view of shell (Playas, Ecuador); f, apical view of shell, with *B. subalbidus* on lateral [terga, fig. g, lower row, left and middle] (Lake Ponchartrain, Louisiana); g, internal views of terga of young specimens: upper row, left, *B. venustus,* right, *B. a. amphitrite* (Tampa Bay, Florida); lower row, left, *B. improvisus,* middle, *B. subalbidus* (shells, fig. f), right, *B. eburneus* (Tampa Bay, Florida); h, i, external views of scutum and tergum; j, lateral view of corroded shell, with uncorroded specimen rostrolaterally (Patuxent River, Maryland). a-d, g, h, i × 5; e, f, j × 2. (a, b, f-j, after Henry, 1959).



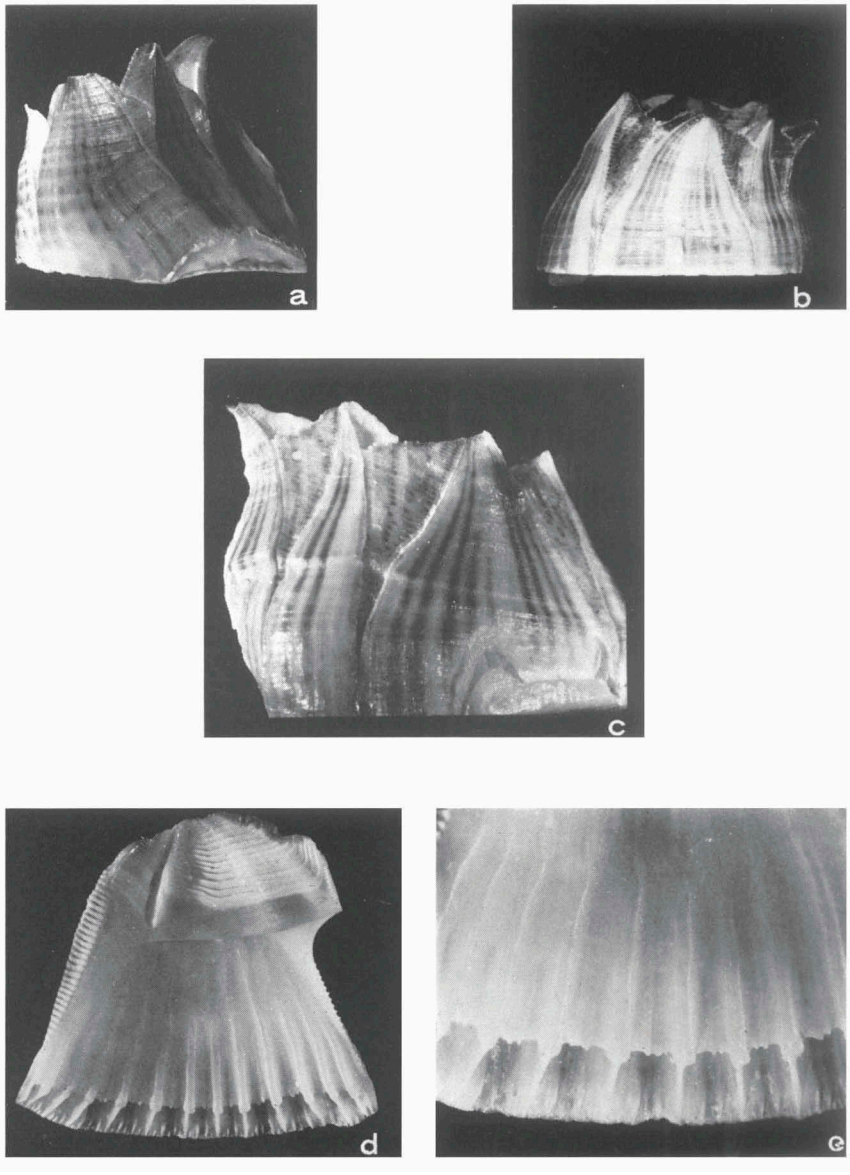
Balanus variegatus Darwin. a, b, d, e, external and internal views of opercular valves [shell, pl. 7 fig. d] (Benkoelen, Sumatra); c, lateral view of shell; f-i, external and internal views of opercular valves (Benkoelen, Sumatra). a, b, d, e, f-i × 5; c × 2.



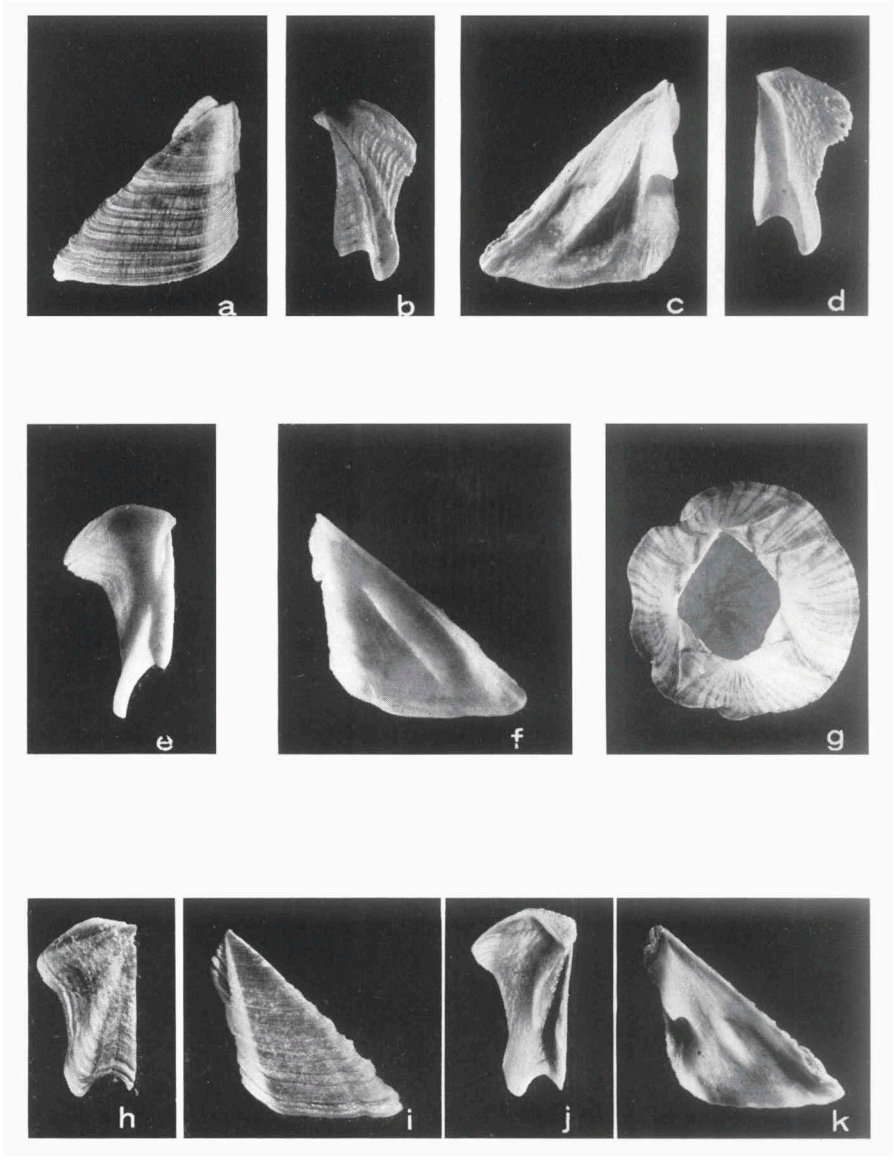
Balanus variegatus Darwin. a, external view of tergum; b, c, internal views of tergum and scutum; e, lateral view of shell, with darker colored shell carinolaterally (Singapore); d, rostrolateral view of shell, with smaller specimen on lateral and *B. reticulatus* on rostrum [opercular valves, pl. 6 figs. a, b, d, e] (Benkoelen, Sumatra); f, g, internal views of lateral and basal part of lateral, respectively, showing striae and few denticles on inner lamina basally between ribs (Bombay, Indian Union). a-c, f × 5; d, e × 2; g × 10.



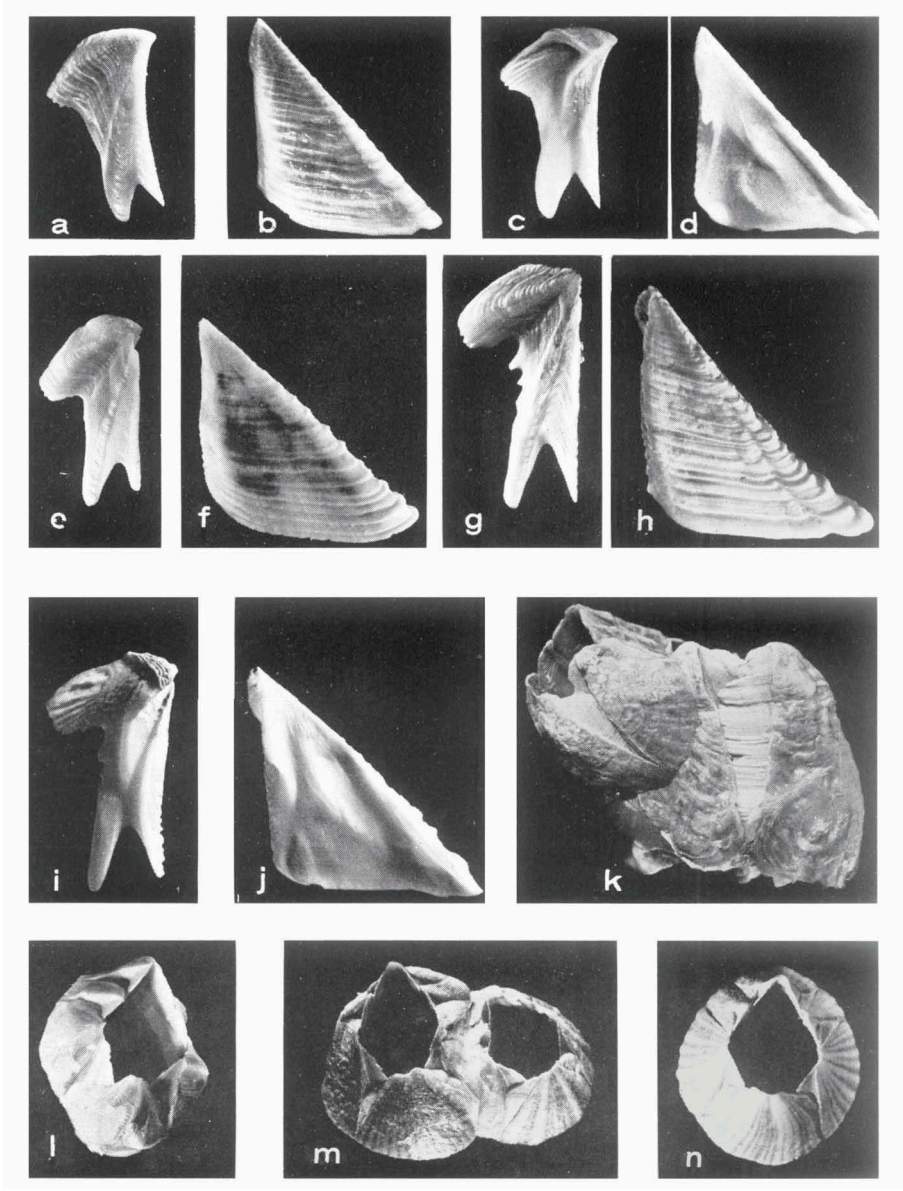
Balanus reticulatus Utinomi. a-d, external and internal views of opercular valves; e, lateral view of shell (Oahu, BPBM 268); f-i, external and internal views of opercular valves; m, apical view of shell (Oahu, BPBM 314); j-l, n, external and internal views of opercular valves; o, lateral view of shell, with smaller specimen on carina (Langsuan, Thailand). a-d, f-i, j-l, n × 5; e, m, o × 2.



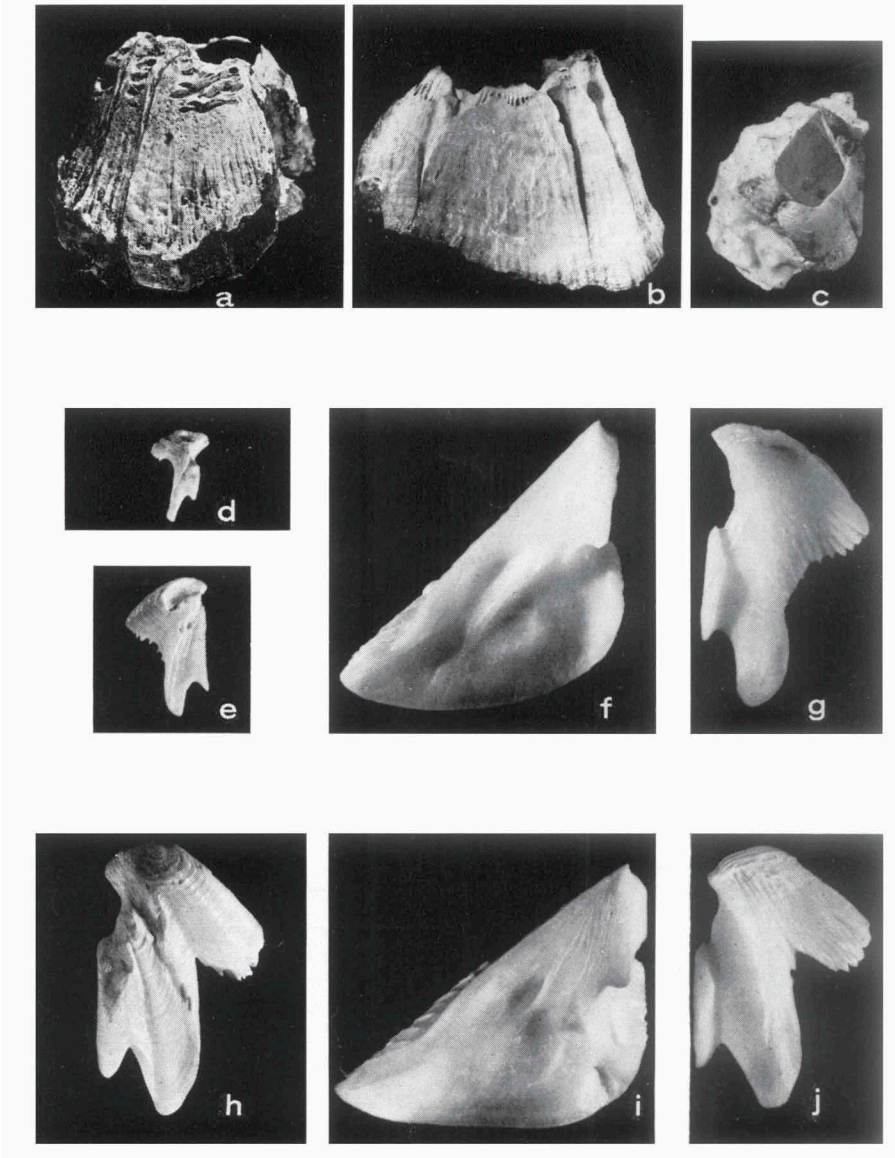
Balanus reticulatus Utinomi. a, shell viewed from right side; d, e, inner views of lateral and basal part of rostrum, showing denticles and few striae on inner lamina basally between ribs (Bombay, Indian Union). — *Balanus amphitrite amphitrite* Darwin. b, c, shell viewed from right and left sides, respectively (Ago Bay, Japan). a, b × 4; c, d × 5; e × 10.



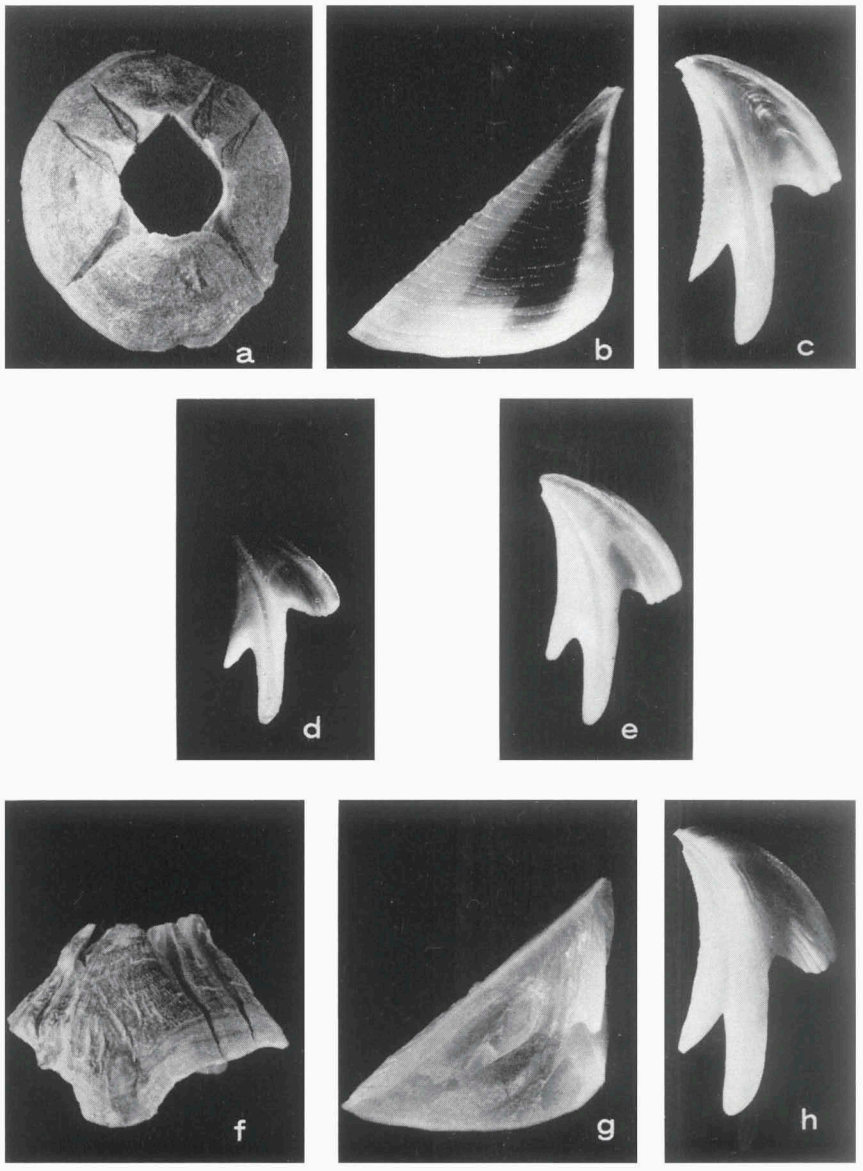
Balanus pallidus Darwin. a-d, external and internal views of opercular valves; g, apical view of shell (Sicily); e, f, internal views of tergum and scutum (French Guiana). — *Balanus albicostatus* Pilsbry, h-k, external and internal views of opercular valves [shell, pl. 11 fig. n] (Minhow, China). a-f, h-k × 5; g × 2.



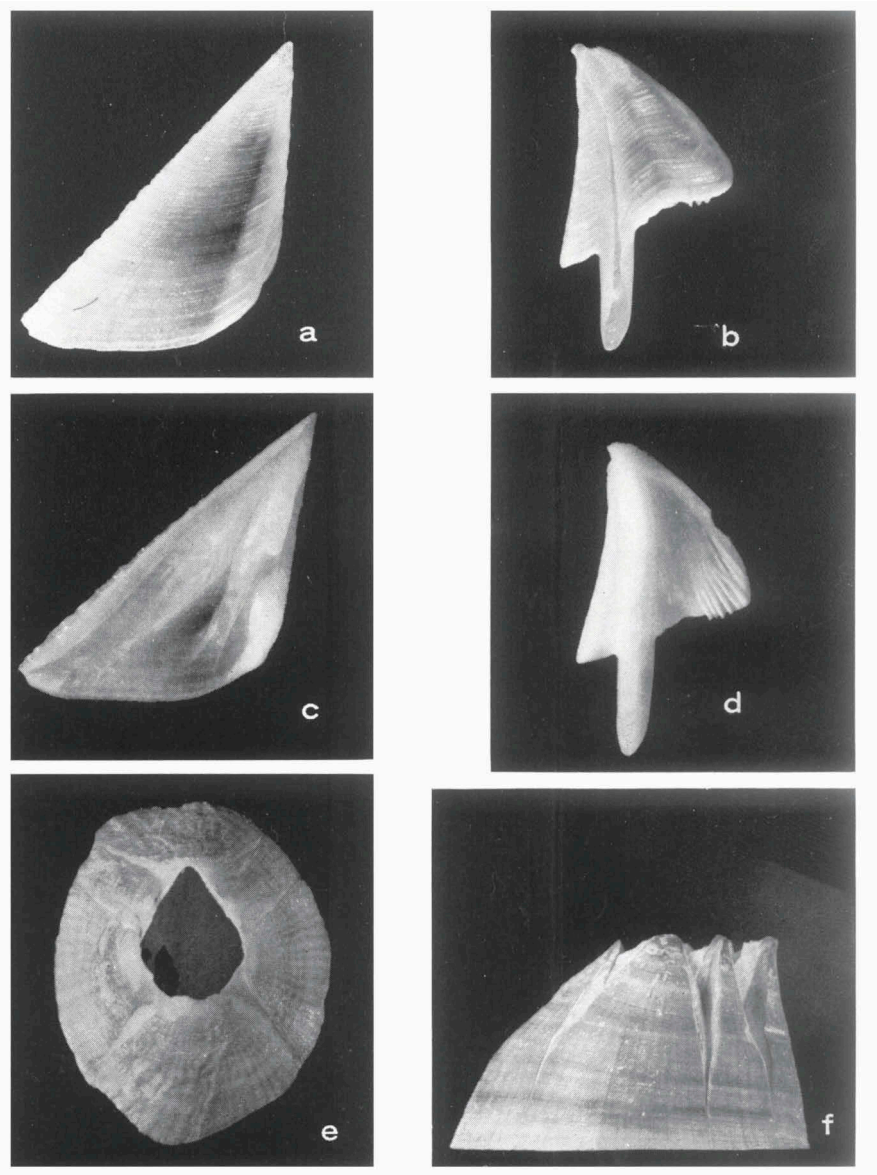
Balanus kondakovi Tarasov & Zevina. a-d, external and internal views of opercular valves; 1, subapical view of shell (Samut Prahan, Thailand); e, f, external view of tergum and scutum; g-j, external and internal views of opercular valves (Benkoelen, Sumatra); k, rostrolateral and lateral views of two shells (China); m, apical view of shell, with *B. albicostatus* on lateral (Shinagawa Bay, Japan). — n, *Balanus albicostatus* Pilsbry apical view of shell [opercular valves, pl. 10 fig. h-k] (Minhow, China). a-j × 5; k-n × 2.



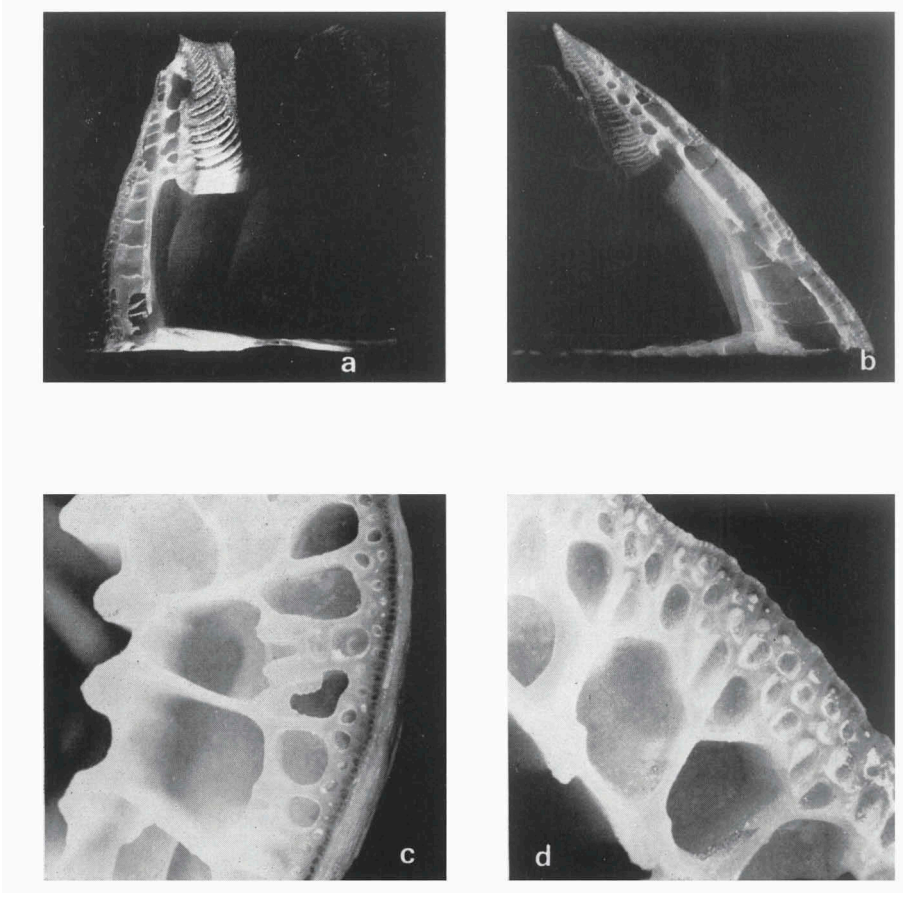
Balanus citerosum Henry. a, lateral view of shell, with exposed vesicular sheath and parietal tubes (paratype); b, lateral view of shell; f, g, internal views of scutum and tergum (holotype); c, apical view of shell with basis of another specimen on lateral; d, e, external views of terga of small specimens (Rio Baguassù); h, external view of tergum; i, j, internal views of scutum and tergum (another paratype). a-c × 5; d-j × 2. (after Henry, 1974).



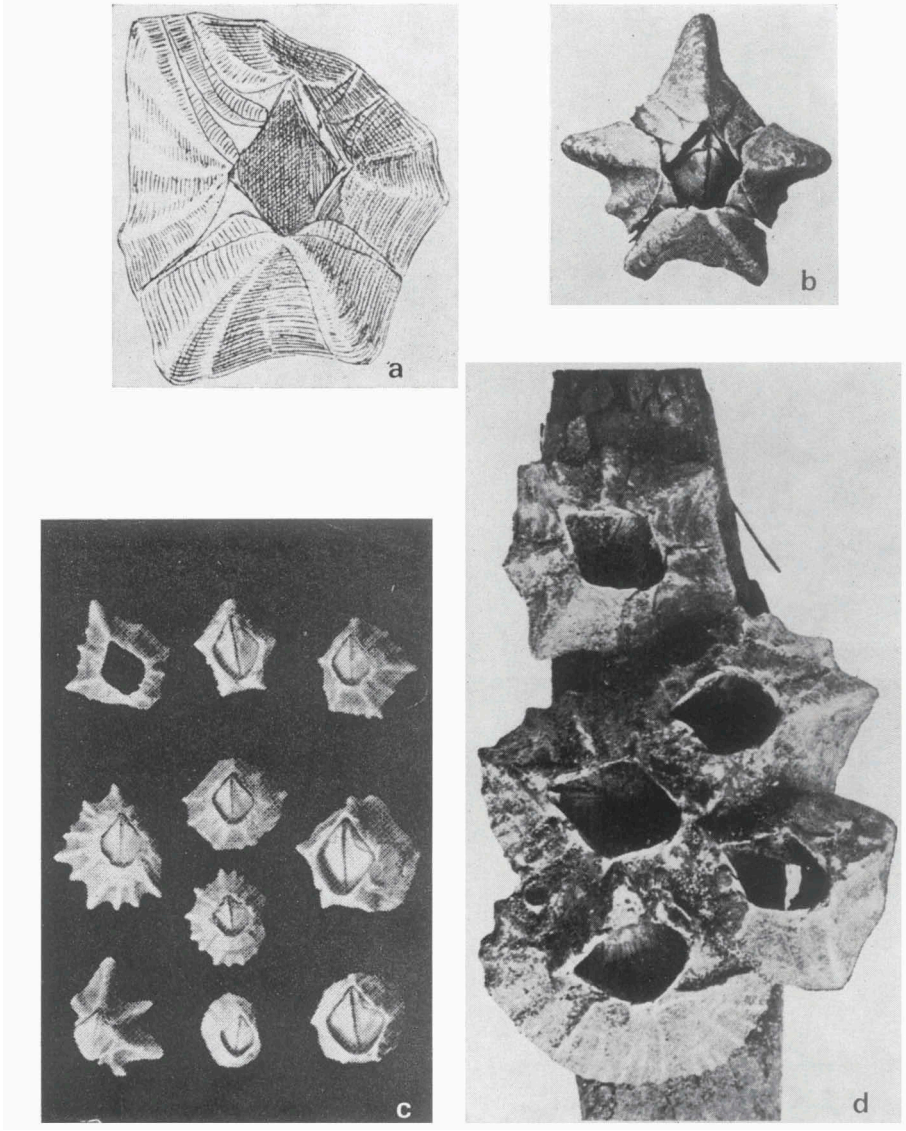
Balanus suturaltus Henry. a, apical view of shell; b, c, g, h, external and internal views of opercular valves (holotype); d, e, external views of terga (paratypes); f, lateral view of shell (another paratype). b-e, g, h × 5; a, f × 2. (after Henry, 1974).



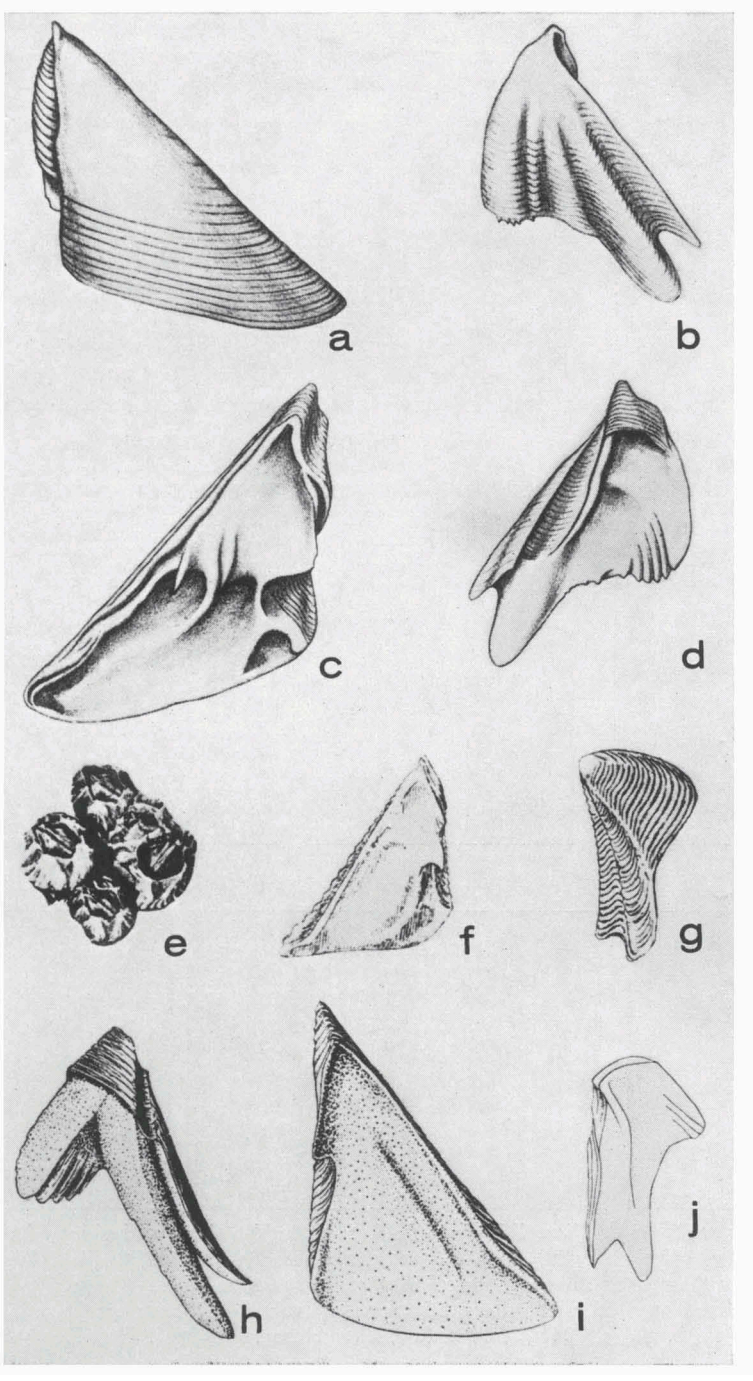
Balanus dentivarians Henry. a-d, external and internal views of opercular valves; e, apical view of shell (holotype); f, lateral view of shell (Guayaquil, Ecuador). a-d × 5; e × 2; f × 1.5. (after Henry, 1974).



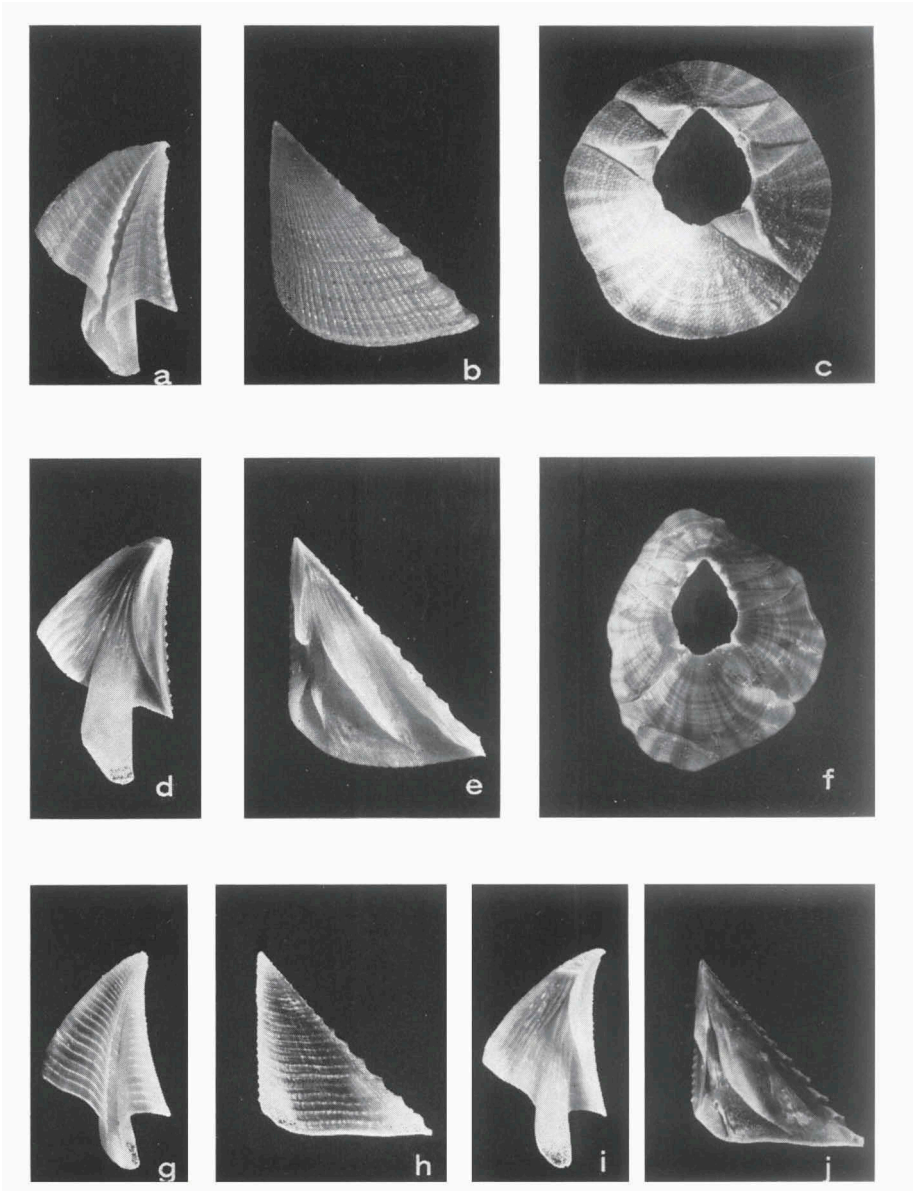
Longitudinal and transverse sections of parietes. a, b, longitudinal section through carina and rostrum, respectively, showing vesicular sheath and primary and subsidiary parietal tubes (*Balanus dentivarians*); c, d, basal views, showing inner lamina (left), primary and subsidiary parietal tubes, and outer lamina (right) (c, *B. suturaltus*; d, *B. dentivarians*). a, b × 2; c, d × 10. (after Henry, 1974).



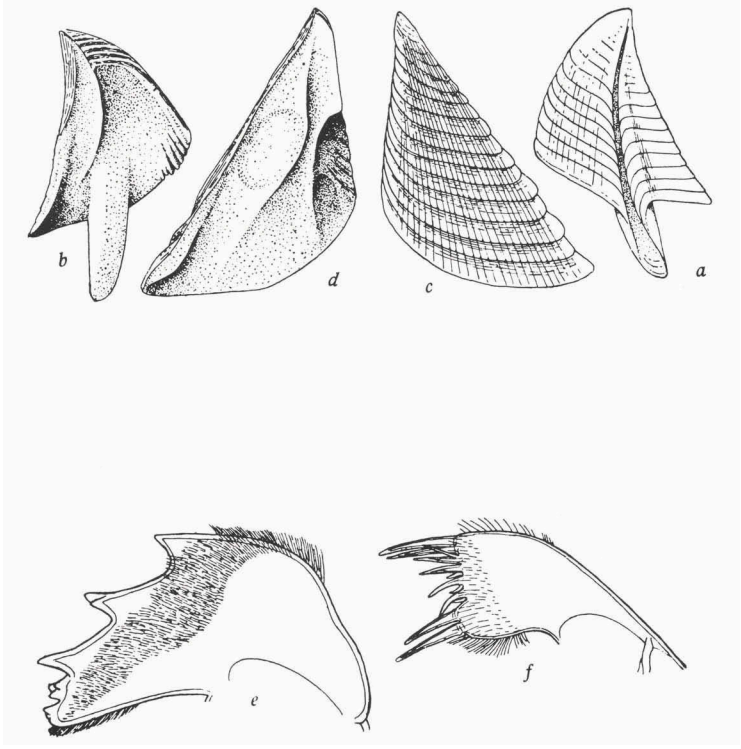
Balanus patelliformis Bruguière. a, apical view of shell (after Darwin, 1854); b, d, apical views of shells (after Nilsson-Cantell, 1938); c, apical views of shells (after Utinomi, 1968). b × ca. 3; d × ca. 1.5.



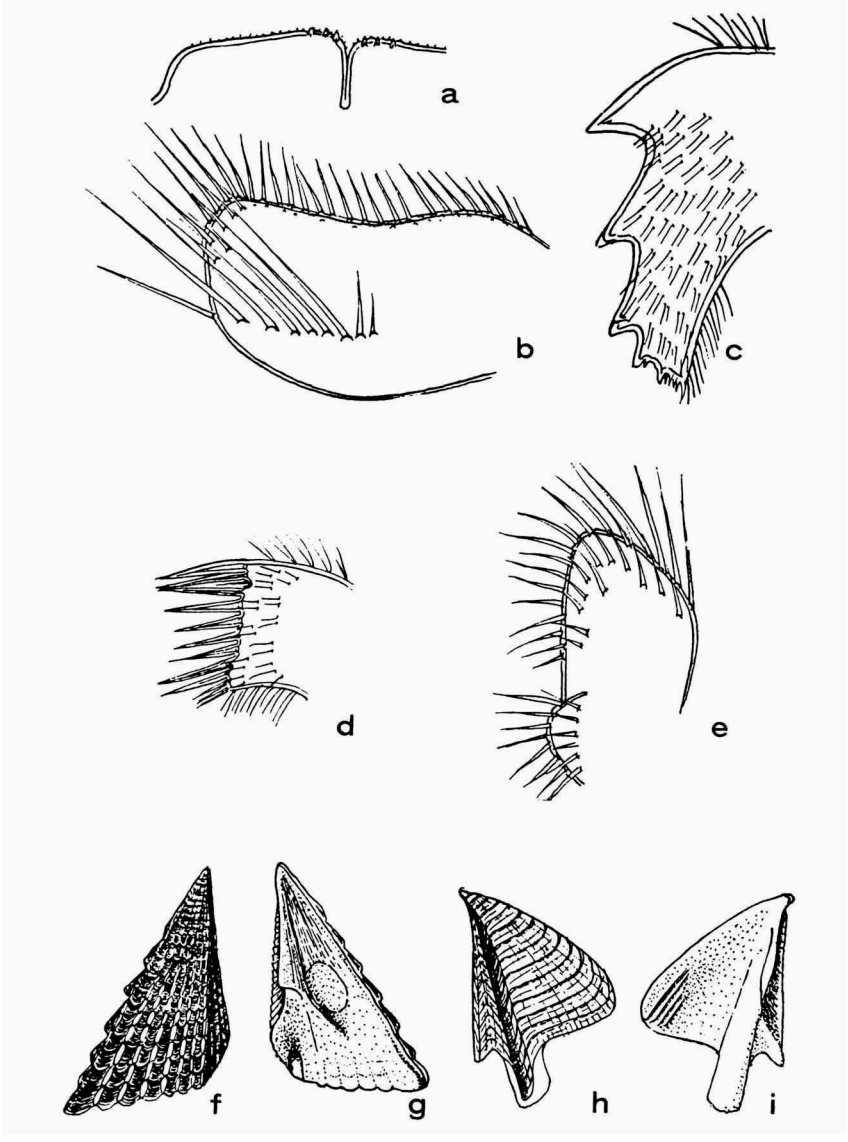
Balanus abeli Lamy & André. a-d, external and internal views of opercular valves; e, apical view of shells (after Gruvel, 1903c). — *Balanus patelliformis* Bruguière. f, internal view of scutum; g, external view of tergum (after Darwin, 1854); h, i, internal views of tergum and scutum (after Nilsson-Cantell, 1929); j, internal view of tergum (after Utinomi, 1968).



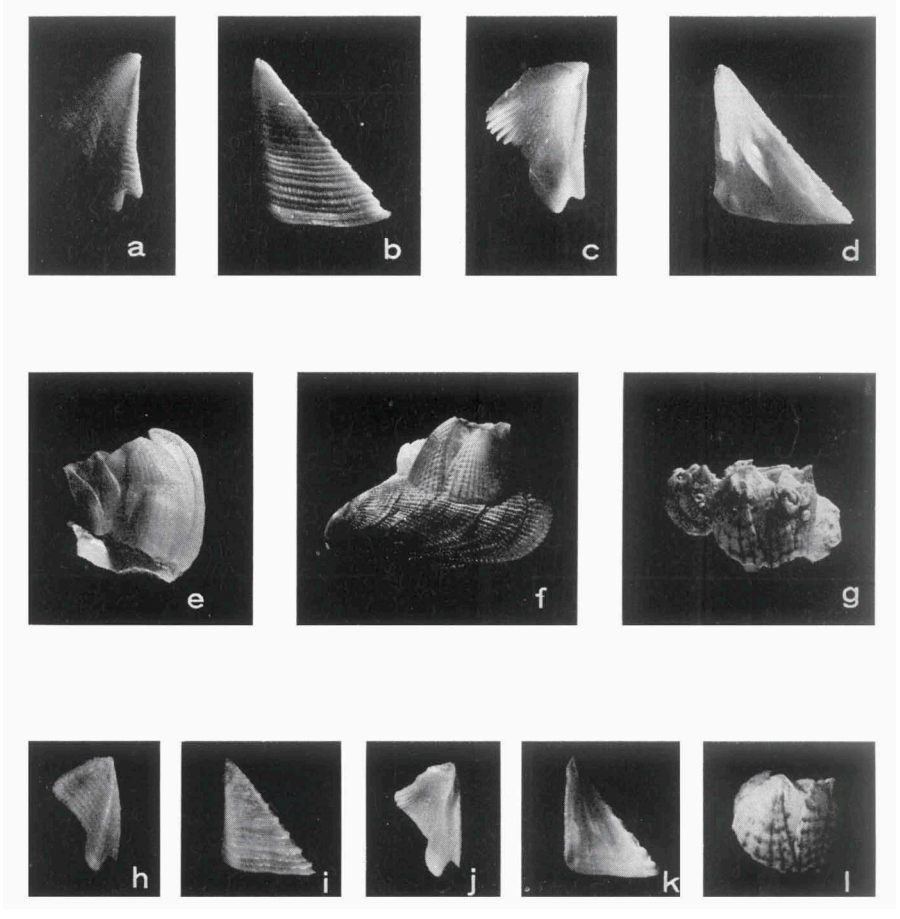
Balanus concavus pacificus Pilsbry. a, b, d, e, external and internal views of opercular valves; c, apical view of shell (Santa Maria Beach, Baja California). — *Balanus concavus mexicanus* Henry. f, apical view of rare striped shell (Guaymas, Mexico); g-j, external and internal views of opercular valves (another specimen, Guaymas, Mexico). a, b, c, e, g-j × 5; f × 2. (a-e, after Henry, 1959; g-j, after Henry, 1960).



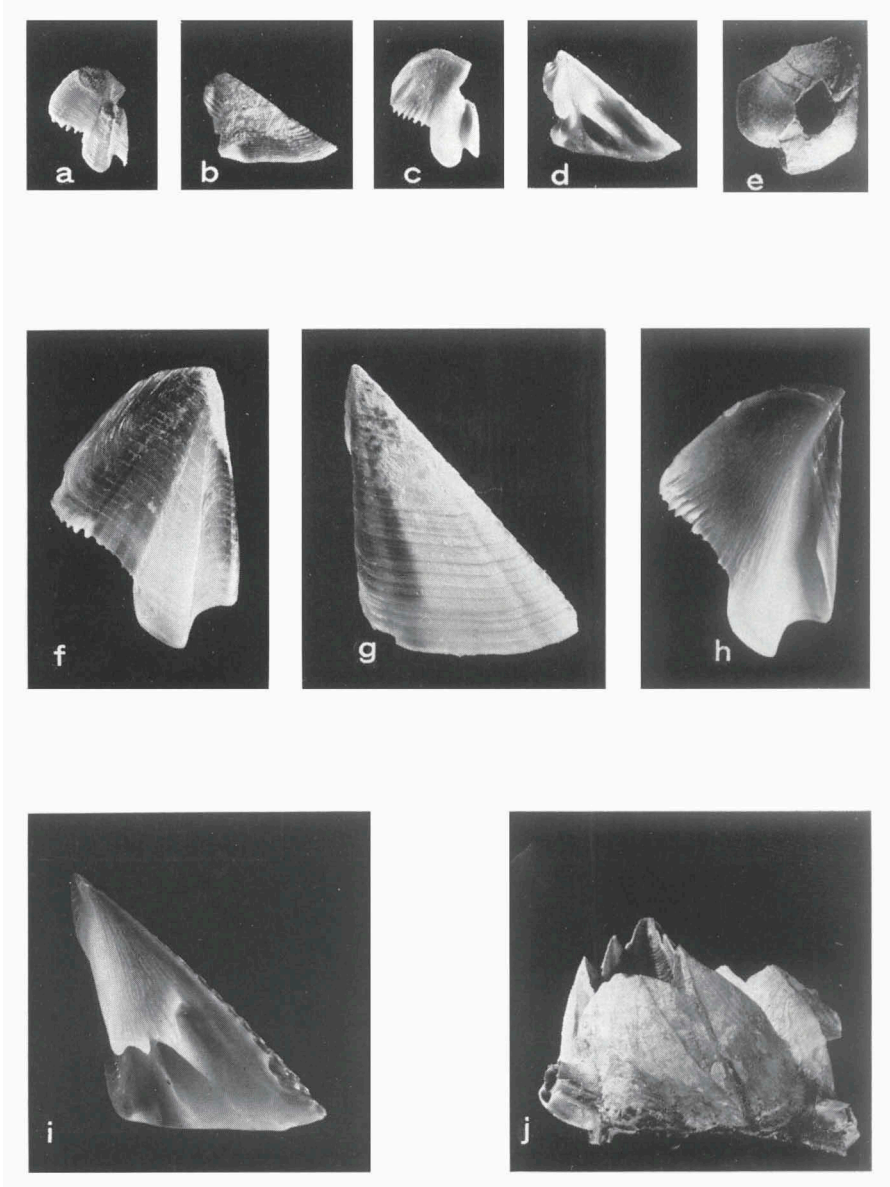
Balanus concavus sinensis Broch. a, b, external and internal views of tergum; c, d, external and internal views of scutum; e, mandible; f, 1st maxilla (after Broch, 1931). a-d × 6; e, f × 35.



Balanus concavus indicus Nilsson-Cantell. a, labrum; b, palpus; c, mandible; d, e, 1st and 2nd maxillae; f, g, external and internal views of scutum; h, i, external and internal views of tergum (after Nilsson-Cantell, 1932d).



Balanus venustus Darwin. a-d, external and internal views of opercular valves; e, lateral view of shell (Tampa Bay, Florida); f, lateral view of shell, showing replication of substratum (Alligator Harbor, Florida). — *Balanus poecilotheca* Krüger. g, lateral view of shell with smaller specimens on lateral and carina; h-k, external and internal views of opercular valves (shell in fig. 1); l, lateral view of shell (off Sulada Island). a-d, h-k × 5; e-g, l × 2.



Balanus inexpectatus Pilsbry. a-d, external and internal views of opercular valves; e, apical view of shell (Puna Island, Ecuador). — *Balanus peruvianus* Pilsbry. f-i, external and internal views of opercular valves; j, rostrolateral view of shell (San Lucas Island, Costa Rica). a-d, f-i × 5; e, j × 2.