The barnacle fauna from the Northeastern Pacific has been summarized by PILSBRY (1916), CORNWALL (1951; 1955), NEWMAN (1982), ROSS (1962), NEWMAN & ABBOTT (1980) and YOUNG & ROSS (2000). However none of these authors recorded any verrucids, thus suggesting they are unknown in the Northeastern Pacific, although well known in other parts of the world. ZEVINA & GALKIN (1993) described the unique species Altiverruca beringiana occurring north of 30°N in the North Pacific. ZEVINA (1987) described A. galapagosa from the Galapagos Is. Not one species of Verrucidae has been reported from the eastern Pacific coast of Mexico, California and Oregon.

The verrucids from the Northeastern Pacific contained in the collections of the Scripps Institution of Oceanography and California Academy of Sciences are the focus of this study. Eight species of verrucids are recognized, of which six are new species. Therefore, the apparent lack of verrucids in this area appears to be related to the lack of studies of this taxon.

One of the most common verrucids found in the deep-sea is Altiverruca with more than 40 species described. Herein this genus is reevaluated and divided into three new taxa.

Suborder Verruco morpha PILSBRY, 1916
Family Verrucidae Darwin, 1854
Genus Altiverruca PILSBRY, 1916 s.l.


YOUNG (1998a) listed 43 described species and subspecies in Altiverruca s.l., 10 of which are considered synonyms. At the same moment, BUCKERIDGE (1997) described one more species of Altiverruca, enlarging the list to 44 species. In this study I revalidate six species previously considered to be synonyms of Altiverruca gibbosa, and describe five new species of this group bringing the total to 49 taxa, of which 45 are considered valid species.

The box-like shells of most verrucid genera appear to have evolved from erect shells such as Altiverruca s.l. (YOUNG, 1998a; NEWMAN, 2000). The generalized species of Altiverruca exhibit some plesiomorphic characters: (1) erect shell, (2) opercular plates with poorly developed ridges, (3) shell plates with simple sutures, (4) absence of radii-like structures, (5) absence of pits or ridges for insertion of the adductor muscle, and (6) having thin basal margins that are not inflected.

In reevaluating descriptions of the species of Altiverruca I recognized three groups, which can be characterized only by external characters. Many of these species are poorly described and figured, and most of them lack any description of the appendages. Certainly, with more accurate descriptions new characters should be used in the diagnoses of these genera or even in recognizing new groups of species. My reassessment of Altiverruca s.l. suggests it should be divided into Altiverruca s.s., and two new genera described below.

Altiverruca PILSBRY, 1916 s.s.

Verruca Section D: Altiverruca PILSBRY, 1916:40 (part).
Verruca (Altiverruca) – BROCH, 1931:45 (part);
FOSTER, 1978:68 (part).
Altiverruca – ZEVINA, 1987a:1813 (part);
BUCKERIDGE, 1994:92 (part); YOUNG, 1998a:77 (part).

Type species – Verruca hoeki PILSBRY, 1907, by original designation (PILSBRY, 1916: 40), Recent, Anegada Passage, Lesser Antilles, 18°30’N, 63°31’W, 907m.

Diagnosis – Shell small and erect, wall plates delicate. Rostrum nearly rectangular, shorter than carina, usually with a flat or ribbed surface between the uppermost articular ridge and the base of scutum. Rostrum and carina suture straight to undulated. Wall plates without longitudinal ribs, usually with outward projecting growth lines. Opercular plates erect, perpendicular to basis and almost parallel to fixed-scutum and tergum. Scutum and tergum with weak ridges, usually with one or two, and not more than three on each plate. Fixed
scutum without adductor ridge or myophore. Bases of wall plates not inflected.


Remarks – Altiverruca s.s. encompasses those delicate species with the erect shell, having the opercular plates perpendicular to the basis, without fully developed articular ridges and the sutures of the rostrum and carina feebly developed. This group of characters appears to be all simplesiomorphies from which evolved the more flattened shell and more elaborate shell and opercular plates of the other species of Verrucidae.

This genus includes many species with unfortunately brief descriptions and in many cases they are badly or not figured at all. Therefore, after examination of the type specimens some rearrangements may be necessary. Based on the original descriptions and figures of all species, I note that some of the species included in this genus do not conform with all of the diagnostics characters: A. plana is indifferently figured, not showing any ridge on the opercular plates and the suture between the rostrum and carina; the description of this species is possibly based on juveniles. A. inermis has the tergum figured with four conspicuous articular ridges. A. aves has the ridges on the opercular plates well developed. A. beringiana has the rostro-carinal suture undulated similar to those of Cristallinaverruca. For the present, these species are tentatively included in Altiverruca s.s. Altiverruca s.s. has a worldwide distribution with individuals occurring between 900 and 4950 meters. Figure 1 lists the type localities of all Altiverruca s.s. excluding the present synonyms.

Fig. 1- Type localities of all species included in Altiverruca s.s.

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<td>A. sculpturata</td>
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<td>A. laeviscuta</td>
<td>A. vertica</td>
<td>A. sansyoji sp. nov.</td>
<td>A. sala sp. nov.</td>
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Altiverruca beringiana Zevina & Galkin, 1993
(Figs.2-4)

Altiverruca beringiana Zevina & Galkin, 1992; 140:fig.2; 1993:62, fig.2 (translation of 1992); YOUNG, 1998a:77.

Material – Gulf of Alaska, Kodiak Seamount, 56º51.110’N, 149º15.830’W, 2051m, R/V Atlantis, Alvin dive 3440, P.Londsdale and L.Levin cols. 02 Aug 1999, 6 specimens, rc: 1.5-2.6mm, SIO-BIC C 10239, MNRJ 14333.

Supplementary description – The present specimens exhibit different stages of development (Fig.2). All of them are white and erect with the operculum very steep, almost parallel to the fixed scutum and tergum. The primordial valves are evident, even in the larger specimen. The number of articular ridges of the opercular plates and on the rostro-carinal suture changes during growth.

In smaller individuals, the tergum is quadrangular and has only the axial ridge, which is well marked at the carinal side (Fig.2a). During growth this ridge becomes to be conspicuous and well marked on both sides (Fig.2c). In the middle of the articular margin of the tergum another large, low ridge appears in the older specimens. The scutum has a conspicuous axial ridge and during growth, an articular ridge of the same width as the axial ridge also develops (Fig.2a-c). A scutal flat area appears above the articular ridge in the larger specimens.

The rostro-carinal suture (Fig.2a-c) is straight in young specimens and with the development of the rostrum and carina the ridges on the plates become indented.

Both rostral and carinal apexes are projected. Zevina and Galkin (1992) observed a constancy of a more projected carina, but the present specimens have all the states: rostrum more projected, carina more projected or both with the same projection. The fixed tergum and scutum (Fig.2d) are similar to those noted before.

Fig.2- Altiverruca beringiana Zevina & Galkin: (a-c) rostro-carinal view of three specimens in three distinct development stages; (d) fixed tergum and fixed scutum view of c; (e) tergum and scutum, internal view; (r) rostrum; (s) scutum; (t) tergum.
Labrum (Fig. 3a) with more than 80 sharp teeth along margin. Palp (Fig. 3a) small, elongated, with few simple setae. Mandible (Fig. 3b) with two large teeth and a wide denticulated lower margin; second tooth with denticle on upper margin. Maxilla I (Fig. 3c) with cutting border having lower third well projected; two large spines on upper margin followed by two median-size spines, lower margin with 4 large and median spines. Maxilla II (Fig. 3d) quadrangular, with few simple setae. Cirri with subequal rami, covered by simple setae (Fig. 4a, b). Length of median article of cirrus VI (Fig. 4c) about 2.5 times its width, with two pairs of setae on anterior margin, larger pair pinnate, and one or two simple setae on posterior angle; distal apical setae about 6 times width of article. Cirral counts in Table 1. Caudal appendage (Fig. 4d) multiarticulated, almost with same length of protopod.

Remarks – *Altiverruca beringiana* was originally found off Bering Is., 55°33.6’N, 167°19’E, 4000m. This new record at Kodiak Seamount, 56°51.110’N, 149°15.830’W, 2051m enhances its distribution.

The stability in number of articular ridges on the opercular valves has been discussed by some authors. FOSTER & BUCKERIDGE (1995a, b) observed variation in the number of ridges for some species. Others suppose this character is more stable for each species, but if there is variability in the number of ridges in a species it is largely because the specimens are in different stages of development (YOUNG, 1998a, b). The specimens of *Altiverruca beringiana* are a good example. The smaller ones have a smaller number of articular ridges with the number increasing during growth. But if the larger specimens are examined one can observe by the structure of the opercular plates that it also had an earlier stage with fewer articular ridges – easily observed by the absence of the median articular ridge of tergum along the first growth line. Another example is the change in the number of ridges on the plates of *Gibbosaverruca navicula* (Hoek, 1913), which depends upon its size. Therefore, changes in the number of ridges may occur during ontogeny.
In addition, I suspect there is little interspecific variation in the number of ridges, viz, specimens of the same size do not have a distinct number of ridges. When this is observed, there is probably more than one species involved.

**TABLE 1**

<table>
<thead>
<tr>
<th>Number of articles on cirri I-VI, and caudal appendage of <em>Altiverruca beringiana</em> Zevina &amp; Galkin</th>
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Tergum (Fig.5a, c) quadrangular, with three articular ridges; axial ridge prominent, intermediate ridge as wide as axial ridge; upper ridge thin and marginal to occludent margin, with a conspicuous depression between upper and intermediate ridges; carinal area smooth. Internally, smooth and flat; scutal margin undulated with a median protuberance. Scutum (Fig.5a, d) smaller than tergum; with two articular ridges; axial ridge conspicuous, thin; second ridge as wide as axial ridge, and a flat upper triangular projection at scutal margin; rostral area smooth. Internally, with a long concavity along articular margin, its upper portion for insertion of adductor muscle; tergal margin straight, except for a notch at medio-basal portion.

Labrum (Fig.6a) with a series of about 25 simple sharp teeth. Palp (Fig.6b) short, acuminate, with few simple setae on inner margin and distal region. Mandible (Fig.6c, d) with three teeth, distance between first and second two times distance between second and third, second and third tooth denticulated on the upper margin; lower angle denticulated. Maxilla I (Fig.6e) with notch and lower part strongly projected; 2 large spines at upper border, 3 median spines on notch and 2 large and 2 median spines on lower projected border. Maxilla II (Fig.6f) triangular, anterior margin with conspicuous concavity medially; covered by long simple setae, except on the concavity.

Cirrus I (Fig.7a) with equal rami, both rami covered with several, long simple setae. Cirrus II (Fig.7b) with unequal rami, anterior ramus about 2/3 length.
of posterior; both rami covered by numerous long, simple setae, distal articles of anterior ramus also with finely pinnate setae. Rami of cirrus III subequal and of cirri IV-VI equal in length. Intermediate articles of cirrus VI (Fig. 7c) having their width about 1/2 their length; three pairs of setae on anterior margin, large antero-distal pair finely pinnate; one or two fine simple setae and multifid setae on posterior angle. Caudal appendage (Fig. 7d) with 7 articles, slightly longer than protopodite; long simple setae on distal margins of articles. Penis short, distally clothed with thin setulae. Number of articles of cirri I-VI and caudal appendage is presented in table 2.

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<td>16/15+</td>
<td>16+/7+</td>
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Earliest juvenile with primordial valves conspicuous (Fig. 5e). Carina asymmetrical, slightly displaced toward right side; slightly higher than wide, extending up short distance between terga. Tergum large, symmetrical on each side, scutal margin somewhat concave.

Fig. 6- *Altiverruca galapagosa* Zevina: (a) labrum; (b) palp; (c-d) mandibles; (e) maxilla I; (f) maxilla II. a, d, from one specimen and others from another specimen figured in figs. 7 and 9.
Scutum larger than tergum, almost symmetrical on each side, only distinct at basal margin, superimposing over the terga as a large extension of the articular margin.

Remarks – The specimens available agree with the original description and figures of ZEVINA (1987a: 1814, fig.1). Altiverruca galapagosa was described from 5°13.6' S, 107°31.7'W, between 3830-3850m.

The present record (1°22.20'S, 89°49.20'W), at 354m differs somewhat from its original geographical and depth range. BUCKERIDGE (1994: 95) also recorded this species from New Caledonia, from 570-3680m, but further study may indicate we are dealing with two species.

NEWMAN (2000: 80) compared the primordial plates of the earliest juvenile stages of the Neoverrucidae, X-juvenile, Verrucidae and others. The Verrucidae was typified by the development of Verruca stroemia (Müller, 1776) (RÜNNSTROM, 1927). He noted that juveniles had the carina about as wide as high, shorter than the terga, displaced to one side, not extending up between the terga, and the terga and scuta were distinctly asymmetrical on each side. Verruca stroemia represents a highly derived species whereas species of Altiverruca s.l. encompass the most primitive genus of the family.

Altiverruca sala sp.nov.
(Figs.8-10)

Material – Holotype: Green Seamount, AD1639, 20°48’N, 109°16’W, 1850m, P. Londsdale & L. Levin cols. Sept. 1985, 1 specimen, rc: 3.2mm, SIO-BIC C 10309. Paratype, same locality, 1875m, 1 specimen, rc: 3.6mm, MNRJ 14340.

Diagnosis – Shell with growth lines prominent on all plates. Tergum with only an axial ridge. Scutum with two articular ridges, both having the same width. Cirrus I with equal rami; cirrus II with anterior ramus about 2/3 length of posterior.

Fig.7- Altiverruca galapagosa Zevina: (a) cirrus I; (b) cirrus II; (c) intermediate article of cirrus VI; (d) caudal appendage, protopodite and penis. (CI-CVI) cirri I to VI; (a.) anterior ramus; (c.a.) caudal appendage; (p.) posterior ramus; (pe.) penis.
Intermediate articles of cirrus VI with two pairs of setae on anterior margin. Caudal appendage 3 times length of protopodite.

Description – Shell (Fig. 8a, b) white, opercular valves oblique to base of wall, with growth lines prominent on all plates; wall plates without longitudinal ridges; basal margin not thickened. Cuticle persistent on shell and opercular valves with rows of bristles along the growth lines. Rostrum (Fig. 8a, b) and carina similar in size, with slightly undulated rostro-carinal articulation, not forming articular ridges; rostrum and fixed scutum articulation without large radius-like projection, apex slightly projected, straight. Carina (Fig. 8a, b) without large radius-like projection toward fixed tergum; apex projected and recurved. Fixed tergum (Fig. 8b) slightly higher than fixed scutum, both sides with well-developed alar-like projections; apex straight. Fixed scutum (Fig. 8b) with wide alar-like process directed toward rostrum and a poorly defined radius-like process directed toward fixed tergum, apex curved toward fixed tergum; internally, without pit or ridge for adductor muscle. Tergum (Fig. 8a, c) nearly quadrangular, with only a prominent axial ridge, having only growth lines besides the axial ridge with a notch on their projected surface; carinal area smooth. Internally flat, and with a large concavity on most of its surface; scutal margin straight except for a small protuberance on upper portion. Scutum (Fig. 8a, c) straight, slightly smaller than tergum; with two articular ridges; axial ridge projected, with both borders conspicuous, thin; second ridge with same width as axial ridge, without flat upper triangular projection at scutal margin; rostral area smooth; apex acute. Internally, with a large concavity parallel to occludent margin, which on upper portion adductor muscle attaches; tergal margin straight, except for a small notch at upper portion.

Fig. 8 - *Altiverruca sala* sp. nov. Holotype: (a) rostro-carinal view; (b) fixed tergum and fixed scutum view; (c) tergum and scutum, internal view; (c) carina; (fs) fixed-scutum; (ft) fixed-tergum; (r) rostrum; (s) scutum; (t) tergum.
Labrum (Fig.9a) with a series of 43 simple sharp teeth and multifid scales on the inner border but large scales covering the outer border. Palp (Fig.9a) short, acuminate, with few simple setae on inner margin and distal region. Mandible (Fig.9b) with three teeth, distance between first and second a slightly more than distance between second and third, third tooth tri-cuspid; lower angle denticulated. Maxilla I (Fig.9c) with lower part projecting strongly; 2 large and 3 short spines at upper border, 3 median spines on lower projected border. Maxilla II (Fig.9d) triangular, anterior margin with shallow concavity medially; covered by long simple setae, except on the shallow concavity.

Cirrus I (Fig.10a) with equal rami, both rami covered with several long simple setae. Cirrus II (Fig.10b) with unequal rami, anterior ramus about 2/3 length of posterior, articles more protuberant; both rami covered by numerous long, simple setae. Rami of cirri III-VI equal in length. Intermediate articles of cirrus VI (Fig.10c) with width about 1/2 length; two pairs of setae on anterior margin, longer pair finely pinnate, smaller pair simple; one or two fine simple setae and multifid setae on posterior angle. Caudal appendage (Fig.10d) with 16/17 articles, 3 times length of protopodite. Penis smaller than coxopodite, clothed with thin setulae. Number of articles of cirri I-VI and caudal appendage is presented in table 3.

Etymology – from the Latin salum (the open sea).

Remarks – *Altiverruca* s.s. can be separated into two groups of species: one encompassing those species with a rostrum having a smooth or ribbed surface above the upper articular ridge and directed toward the scutum basis and the other in which the species have the upper margin directly connected with the articulation with the carina. The first group contains 12 species of *Altiverruca* s.s. and the second, including *A. sala*, has 11 species. The latter is represented by: *A. obliqua* (Hoek), *A. quadrangularis* (Hoek), *A. inermis* (Aurivillius), *A. plana* (Gruvel), *A. spongicola* (Gruvel), *A. angustiterga* Zevina, *A. sculpturata* Zevina, *A. sublima* Zevina, *A. gira* (Zevina), *A. tchesunovi* Zevina, *A. beringiana* Zevina & Galkin and *A. vertica* Foster & Buckeridge (= *A. obliqua*).
Altiverruca sala sp.nov. has a characteristic straight scutum with two ridges: the axial and another on the tergal margin. Only A. obliqua and A. quadrangularis have similar opercular valves with the same number of articular ridges. But both species do not have projected growth lines, the tergum has a wide ridge above the axial ridge in the former and the latter species has a more elaborated carino-rostral articulation. Furthermore, both species were described from the Atlantic Ocean, but A. quadrangularis was also recorded from the Philippines and Reunion Is. (ROSELL, 1989: 24; FOSTER & BUCKERIDGE, 1995b: 367). A. sala sp.nov. is based on only two specimens collected together with Newmaniverruca digitiformis sp.nov. on Green Seamount, off Puerto Vallarta, Mexico, from 1850m.

Altiverruca vansyoci sp.nov. (Figs.11-14)

Material – Holotype: Off Oregon coast, 44°4.90’N, 125°24.50’W, 2938m, R/V Yaquina coll., 15 Jun 1972, rc: 5.3mm, on octocoral stem, CASIZ 138571. Paratypes: Same locality, 8 specimen, rc: 2.6-5.6mm, CASIZ 115100; MNRJ 14335.

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**TABLE 3**

Number of articles on cirri I-VI, and caudal appendage of *Altiverruca sala* sp.nov.

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[Ci-VI] cirri I to VI; (CA) caudal appendage; (RC) right cirri; (LC) left cirri.

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Fig.10- *Altiverruca sala* sp.nov: (a) cirrus I; (b) cirrus II; (c) intermediate article of cirrus VI; (d) caudal appendage and protopodite, (Ci-CVI) cirri I to VI; (a.) anterior ramus; (c.a.) caudal appendage; (p.) posterior ramus.
Diagnosis – Shell with growth lines not prominent on all plates. Rostrum with undulated rostro-carinal articulation, forming one upper articular ridge and with a large surface above articular ridge varying from smooth to with low ridges turned toward scutum. Fixed tergum much higher than fixed scutum with apex curved toward fixed scutum. Tergum with only poorly developed axial ridge. Scutum axial ridge slightly projected and a second ridge slightly discernable beside axial ridge. Cirri I and II with anterior rami slightly longer than posterior. Intermediate articles of cirrus VI with two pairs of setae on anterior margin. Caudal appendage two times length of protopodite.

Description – Shell (Fig.11a, b) white, opercular valves perpendicular to base of wall, with growth lines not prominent on all plates; shell plates without longitudinal ridges; basal margin not thickened. Cuticle not persistent on shell and opercular valves. Rostrum (Fig.11a) rectangular, with an undulated rostro-carinal articulation, forming one upper articular ridge and sometimes a tooth below (Figs.11a, 12), with a large surface above articular ridge varying from smooth to with low ridges turned toward scutum; rostrum and fixed scutum articulation without large radius-like projection, apex usually marginal, but sometimes displaced anteriorly from margin, slightly projected, straight. Carina (Fig.11a) without radius-like projection toward fixed tergum; apex slightly projected and straight. Fixed tergum (Fig.11b) much higher than fixed scutum, both sides with well-developed alar-like projections; apex curved toward fixed scutum. Fixed scutum (Fig.11b) with wide alar-like process directed toward rostrum and a poorly defined radii-like process directed toward fixed tergum, apex straight; internally, without pit or adductor ridge.

Tergum (Fig.11a, c) nearly quadrangular, with only axial ridge, slightly prominent; carinal area smooth.

Fig.11- *Altierverruca vansjoci* sp.nov. Holotype: (a) rostro-carinal view; (b) fixed tergum and fixed scutum view; (c) tergum and scutum, internal view; (e) carina; (fs) fixed-scutum; (ft) fixed-tergum; (r) rostrum; (s) scutum; (t) tergum.
Internally, flat; scutal margin nearly straight. Scutum (Fig. 11a, c) smaller than tergum; axial ridge slightly projected sloping gradually at scutal side, thin; a second ridge slightly discernable beside axial ridge, and a small, straight flat upper projection at scutal margin; rostral area smooth. Internally, with a large concavity for adductor muscle conspicuous at occcludent margin; tergal margin nearly straight.

Labrum (Fig. 13a) with a series of approximately 70 simple sharp teeth becoming two rows laterally and some scattered teeth on the median area; large scales covering the outer border. Palp (Fig. 13a) short, triangular, with few simple setae on outer margin. Mandible (Fig. 13b) with three teeth, distance between first and second a slightly more than distance between second and third, second and third teeth with upper margin denticulated; lower angle denticulated. Maxilla I (Fig. 13c) with lower part projected; 2 large and 3 short spines at upper border, 4 median spines on lower projected border. Maxilla II (Fig. 13d) rounded, anterior margin with shallow concavity medially; covered by long simple setae, except on the shallow concavity.

Cirrus I (Fig. 14a) with anterior rami a few segments longer than posterior, both rami covered with several long simple setae. Cirrus II (Fig. 14b) with posterior ramus a few segments longer than anterior, articles more protuberant on anterior ramus; both rami covered by numerous long, simple setae. Rami of cirri III-VI equal in length. Intermediate articles of cirrus VI (Fig. 14c) with width 1/2 length; two pairs of setae on anterior margin, longer pair finely pinnate and smaller pair simple; one or two fine simple setae on posterior angle. Caudal appendage (Fig. 14d) with 9-10 articles, two times length of protopodite; long simple setae on distal margins of articles. Penis (Fig. 14d) smaller than coxopodite, clothed with thin setulae. Number of articles of cirri I-VI and caudal appendage is presented in table 4.

![Fig. 12 - *Altiverruca vansyoci* sp. nov.: Rostro-carinal suture of several specimens. Note the variation in the development of the tooth below the large articular ridge of rostrum; the variation on the apex position, from marginal to displaced; (c) carina; (r) rostrum.](image-url)
Etymology – Named in honor of Dr. Robert J. Van Syoc, cirripedologist who was largely responsible for making the California Academy of Science specimens available for this study.

Remarks – *Altiverruca vansyoci* sp.nov. is included in the *Altiverruca* group in which the species have a rostrum with a flat or ribbed surface above the upper articular ridge and directed toward the base of the scutum (see remarks under *A. sala* sp.nov.). This group contains 12 species: *A. incerta* (Hoek), *A. erecta* (Gruvel), *A. longicarinata* (Gruvel), *A. hoeki* (Pilsbry), *A. joubini* (Gruvel), *A. casula* (Hoek), *A. ornata* Nilsson-Cantell, *A. aves* (Zevina), *A. galapagosa* Zevina, *A. longa* Zevina, *A. vitrea* Zevina, *A. galkini* Zevina. Of these, five species have very distinct opercular plates, with the terga with two conspicuous ridges (*A. aves, A. galapagosa, A. incerta, A. longa and A. vitrea*).

Of the remaining species, *A. erecta, A. galkini, A. joubini* and *A. ornata* have the rostro-carinal suture straight or undulated without an upper articular ridge on the rostrum as seen in *A. vansyoci* sp.nov. Therefore three species of *Altiverruca s.s.* have similar opercular valves and rostro-carinal sutures: *A. longicarinata, A. hoeki* and *A. casula. Altiverruca longicarinata* was described from the Sargasso Sea (GRUVEL, 1900: 242; 1902: 91) and subsequently recorded from the Guiana Basin and Mid-Atlantic Ridge (ZEVINA, 1987b: 1305; YOUNG, 1998c:113). In this species the rostrum has a smooth surface above the articular ridge; the apexes of rostrum and carina are more projected; the mandible has the 2nd and 3rd teeth with smooth upper margin (based on Zevina’s specimens). *Altiverruca hoeki* was described from Anegada Passage, Lesser Antilles (PILSBRY, 1907) and subsequently recorded from the Grenada Basin (ZEVINA, 1975). It has the terga squared, the rostro-carinal suture is less undulated with the upper ridge less pronounced, the apexes of rostrum and carina are more projected, the apex of the fixed tergum is straight; and the fixed scutum with narrow radii-like process directed toward the fixed tergum.
restricted to the lower part. *Altiverruca casula* was described from the Ceram Sea, Indonesia (HOEK, 1913). It has a scutum with two conspicuous ridges, the rostrum with a smooth surface above the articular ridge; fixed tergum with a large rounded projection directed toward the fixed-rostrum. *Altiverruca vansyoci*, besides the differences described above, was collected off the coast of Oregon, 44°4.90'N, 125°24.50'W, far from the localities of the related species.

**Gibbosaverruca** gen.nov.

(Fig.15)


Type species – *Verruca gibbosa* Hoek, 1883, Recent, Challenger Expedition, Argentine Basin, sta. 317, 48°37'S, 55°17'W, 1035 fathoms [1892m].

**Etymology** – from the Latin *gibbosus* (protuberant) and *verruca* (wart); feminine gender.

**Diagnosis** – Shell large and inclined, wall plates massive. Rostrum triangular, same height of carina, usually without a flat or ribbed surface between the uppermost articular ridge and the base of scutum. Rostrum and carina united by strong ridges, the uppermost on rostrum being the largest. Shell plates varying from smooth to strongly ornamented. Operculum oblique to basis inclined more than 45° and also oblique to fixed-scutum and tergum. Scutum and tergum with more than two conspicuous ridges on each valve. Fixed scutum without adductor ridge or myophore. Bases of wall plates not inflected.

Remarks – Most of the species included in this genus were considered synonyms of *G. gibbosa* (NILSSON-CANTELL, 1928; 1938; 1955; TARASOV & ZEVINA, 1957; ZEVINA, 1976; FOSTER & BUCKERIDGE, 1995a) but others suggested it was a species complex (NEWMAN & ROSS, 1971; YOUNG, 1998a).

HOEK (1883), based on the Challenger Expedition samples, described *Gibbosaverruca gibbosa* from the southern Atlantic, and it has been recorded several times from different oceans. Five described species and one subspecies were considered synonyms of *G. gibbosa* including *Verruca sulcata* Hoek, 1883, described from the South Fiji Basin; *V. mitra* Hoek, 1907, from off Antarctic Peninsula; *V. bicornuta* Pilsbry, 1916 from East of Nantucket, Massachusetts; *V. darwini* Pilsbry, 1907, from Cape May, New Jersey; *V. rathbuniana* Pilsbry, 1916, from Southeast of Cape Cod, Massachusetts; and *V. gibbosa somaliensis* Nilsson-Cantell, 1929 from the coast of Somalia (NILSSON-CANTELL, 1928: 25; TARASOV & ZEVINA, 1957: 154). When the descriptions and figures of these species are examined in detail, there are two conclusions: either *Gibbosaverruca gibbosa* is a very plastic species having an exceptional morphological variation, or it actually represents a complex of species.

Based on the series of characters listed in table 5, I propose that *Gibbosaverruca gibbosa* is a group of species and all of the previously described species have to be reevaluated. In the *G. gibbosa* complex, considered herein as *Gibbosaverruca* gen.nov., 6 species should be included: *G. nitida* (Hoek, 1883), *G. navicula* (Hoek, 1913), *G. costata* (Aurivillius, 1898), and the three new species described below. These species are relatively large with the shell having pronounced growth lines and well-developed articular ridges on the opercular plates, rostrum and carina. *G. gibbosa somaliensis* is elevated to species status; *G. darwini* is tentatively included in this genus, but it does not have the upper articular ridge of the rostrum much larger than the one on the carina. Figure 15 presents the type localities of all species of *Gibbosaverruca* gen.nov. excluding the previous synonyms.

Fig.15- Type localities of all species included in *Gibbosaverruca* s.s.
<table>
<thead>
<tr>
<th>species characters</th>
<th>G. gibbosa</th>
<th>G. sulcata</th>
<th>G. mitra</th>
<th>G. darwini</th>
<th>G. rathbuniana</th>
<th>G. somalensis</th>
<th>G. monterey sp.nov.</th>
<th>G. robusta sp.nov.</th>
<th>G. mateoi sp.nov.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scutum: articular ridges (No)</td>
<td>3</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Scutum: marginal articular ridge</td>
<td>Vestigial, marginal</td>
<td>Vestigial, marginal</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
</tr>
<tr>
<td>Scutum: intermediate articular ridge</td>
<td>Protuberant, curved, near and with same width of axial ridge</td>
<td>Protuberant, curved, near and with same width of axial ridge</td>
<td>Protuberant, curved, near and with same width of axial ridge</td>
<td>Protuberant, curved, near and with two times wider than axial ridge</td>
<td>Protuberant, curved, near and wider than axial ridge</td>
<td>Protuberant, curved, near and wider than axial ridge</td>
<td>Protuberant, curved, as wide as axial ridge</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Scutum: accessory articular ridge</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
</tr>
<tr>
<td>Scutum: axial ridge</td>
<td>Conspicuous, with both sides well marked</td>
<td>Conspicuous, with both sides well marked</td>
<td>Conspicuous, with only tergal side well marked</td>
<td>Conspicuous, with both sides well marked</td>
<td>Conspicuous, with both sides well marked</td>
<td>Conspicuous, with only tergal side well marked</td>
<td>Conspicuous, with both sides well marked</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tergum: articular ridges (No)</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Tergum: marginal articular ridge</td>
<td>Marginal, thin</td>
<td>Marginal, wide</td>
<td>Marginal, wide</td>
<td>Marginal, thin</td>
<td>Marginal, thin</td>
<td>Marginal, wide</td>
<td>Marginal, thin</td>
<td>Marginal, thin</td>
<td></td>
</tr>
<tr>
<td>Tergum: intermediate articular ridge</td>
<td>Protuberant, curved, near and with same width of axial ridge</td>
<td>Slightly protuberant, curved, medial, with same width of axial ridge</td>
<td>Slightly protuberant, curved, medial, with two times wider than axial ridge</td>
<td>Slightly protuberant, curved, medial, wider than axial ridge</td>
<td>Slightly protuberant, curved, medial, wider than axial ridge</td>
<td>Slightly protuberant, curved, straight, with same width of axial ridge</td>
<td>Protuberant, curved, as wide as axial ridge</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tergum: accessory articular ridge</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Protuberant, curved, near and with same width of axial ridge</td>
<td></td>
</tr>
<tr>
<td>Scutum/tergum basis length ratio</td>
<td>1/2</td>
<td>2/5</td>
<td>2/3</td>
<td>2/3</td>
<td>2/3</td>
<td>4/5</td>
<td>3/4</td>
<td>1/2</td>
<td>2/3</td>
</tr>
<tr>
<td>Rostrum: No and development of articular ridges</td>
<td>3, decreasing in width from apex to basis</td>
<td>4, of same width</td>
<td>2, of same width</td>
<td>3, 1st smaller, 2nd largest</td>
<td>3, 1st smaller, 2nd largest</td>
<td>3, decreasing in width from apex to basis</td>
<td>5, uppermost smaller, 2nd larger and decreasing in width to basis</td>
<td>3, medial wider</td>
<td>3, decreasing in width from apex to basis continue...</td>
</tr>
<tr>
<td>species</td>
<td>G. gibbosa</td>
<td>G. sulcata</td>
<td>G. mitra</td>
<td>G. darwini</td>
<td>G. rathbuniana</td>
<td>G. somaliensis</td>
<td>G. monterey</td>
<td>G. robusta</td>
<td>G. mateoi</td>
</tr>
<tr>
<td>----------------------------</td>
<td>------------</td>
<td>------------</td>
<td>----------</td>
<td>------------</td>
<td>---------------</td>
<td>----------------</td>
<td>-------------</td>
<td>------------</td>
<td>----------</td>
</tr>
<tr>
<td>Carina: No and development of articular ridges</td>
<td>3, decreasing in width from apex to basis</td>
<td>3, 1st largest, 2nd and 3rd equal in width</td>
<td>3, decreasing in width from apex to basis</td>
<td>3, decreasing in width from apex to basis</td>
<td>4, decreasing in width from apex to basis</td>
<td>5, uppermost smaller, 2nd larger and decreasing in width to basis</td>
<td>3, medial wider</td>
<td>3, decreasing in width from apex to basis</td>
<td></td>
</tr>
<tr>
<td>Length of fixed-Tergum</td>
<td>Higher than fixed scutum</td>
<td>Higher than fixed scutum</td>
<td>Higher than fixed scutum</td>
<td>As high as scutum</td>
<td>Higher than fixed scutum</td>
<td>Higher than fixed scutum</td>
<td>Higher than fixed scutum</td>
<td>Higher than fixed scutum</td>
<td>Higher than fixed scutum</td>
</tr>
<tr>
<td>Rostrum: flatter surface directed to scutum</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Present, well developed</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
<td>Present, well developed, with ridge</td>
</tr>
<tr>
<td>Fixed-scutum: Alar-/radii-like processes width ratio</td>
<td>2 times</td>
<td>1/2</td>
<td>3 times</td>
<td>2 times</td>
<td>2 times</td>
<td>2 times</td>
<td>2 times</td>
<td>3 times</td>
<td>2 times</td>
</tr>
<tr>
<td>Fixed-tergum: carinal/fixed-scutum alar-like processes width ratio</td>
<td>1/2</td>
<td>Not visible in figure</td>
<td>1/2</td>
<td>Equal</td>
<td>1/2</td>
<td>Equal</td>
<td>Equal</td>
<td>Equal</td>
<td>1/2</td>
</tr>
<tr>
<td>Rostrum: apex</td>
<td>Incurved</td>
<td>Incurved</td>
<td>Straight</td>
<td>Incurved</td>
<td>Straight</td>
<td>Straight</td>
<td>Straight</td>
<td>Recurved</td>
<td>Straight</td>
</tr>
<tr>
<td>Carina: apex</td>
<td>Recurved</td>
<td>Recurved</td>
<td>Recurved</td>
<td>Straight</td>
<td>Recurved</td>
<td>Recurved</td>
<td>Recurved</td>
<td>Recurved</td>
<td>Recurved</td>
</tr>
<tr>
<td>Cirrus I: anterior and posterior rami length</td>
<td>Equal</td>
<td>-</td>
<td>-</td>
<td>Subequal</td>
<td>Subequal</td>
<td>Unequal</td>
<td>Equal</td>
<td>Subequal</td>
<td>Subequal</td>
</tr>
<tr>
<td>Cirrus II: anterior and posterior rami length</td>
<td>1/2</td>
<td>-</td>
<td>-</td>
<td>2/3</td>
<td>4/5</td>
<td>1/2 to 1/3</td>
<td>2/3</td>
<td>2/3</td>
<td>1/2</td>
</tr>
<tr>
<td>Cirrus II: anterior and posterior rami length</td>
<td>Subequal</td>
<td>-</td>
<td>-</td>
<td>Subequal</td>
<td>Subequal</td>
<td>Equal</td>
<td>Equal</td>
<td>Equal</td>
<td>Equal</td>
</tr>
<tr>
<td>Cirrus VI: No of pairs of setae on anterior margin of articles</td>
<td>3</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>3</td>
<td>2</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Caudal appendage: No of articles</td>
<td>11</td>
<td>-</td>
<td>-</td>
<td>11</td>
<td>-</td>
<td>18</td>
<td>20</td>
<td>17</td>
<td>9</td>
</tr>
<tr>
<td>Caudal appendage /protopodite of cirrus VI length</td>
<td>1 1/2 times</td>
<td>-</td>
<td>-</td>
<td>1 1/3 times</td>
<td>-</td>
<td>Larger than protopod</td>
<td>2 times</td>
<td>2 times</td>
<td>Little longer</td>
</tr>
</tbody>
</table>
*Gibbosaverruca montereyi* sp.nov.  
(Figs.16-18)

Material – Holotype, Monterey Submarine Canyon, Monterey, California, 36º46'28.7"N, 121º59'27.5"W, 750m, J. Barry coll. 17 Aug 1992, rc: 13.0, SIO-BIC C 9890; Paratypes: same locality, 2 specimens, rc: 12.9 and 3.9mm, SIO-BIC C 10304; MNRJ 14336.

Diagnosis – Shell with growth lines prominent on all plates. Rostrum with five flat articular ridges, uppermost very small, second largest, decreasing in size toward basis. Tergum quadrangular, with three articular ridges; axial ridge well prominent; intermediate ridge wide. Scutum with two articular ridges; axial ridge thin; second ridge twice width of axial ridge. Cirrus I with equal rami. Cirrus II with anterior ramus about 2/3 length of posterior. Intermediate articles of cirrus VI with three pairs of simple setae on anterior margin. Caudal appendage two times length of protopodite.

Description – Shell (Fig.16a, b) white, opercular valves oblique to base of wall, with growth lines well prominent on all plates; rostrum and carina undulated, forming large and low longitudinal ridges, fixed tergum and scutum without longitudinal ridges; basal margin not thickened. Cuticle yellowish, smooth, persistent on shell and opercular valves. Rostrum (Fig.16a) and carina similar in size, former with five flat articular ridges, with shallow grooves between them on the rostro-carinal articulation, uppermost very small, second largest, decreasing in size toward basis; rostrum and fixed scutum articulation with large radius-like projection, apex projected. Carina (Fig.16a) with five articular ridges directed toward scutum, uppermost very small, others of similar width or with second larger, with shallow grooves between them, with large radius-like projection toward fixed tergum; apex curved and projected. Fixed tergum (Fig.16b) higher than fixed scutum, both sides with well-developed alar-like projections; apex straight.

![Figure 16](image-url)

**Fig.16** *Gibbosaverruca montereyi* sp.nov.: (a) rostro-carinal view; (b) fixed tergum and fixed scutum view; (c) tergum and scutum, internal view.
Fixed scutum (Fig.16b) with wide alar-like process directed toward rostrum twice width of radii-like process directed toward fixed tergum; internally, with a pit for adductor muscle and a narrow projected adductor ridge.

Tergum (Fig.16a, c) quadrangular, with three articular ridges; axial ridge prominent, narrower than intermediate ridge; intermediate ridge wide, upper ridge thin and marginal to occludent margin, with a large conspicuous depression between upper and intermediate ridges; carinal area smooth. Internally, smooth and flat; scutal margin straight except for protuberance on upper portion. Scutum (Fig.16a, c) smaller than tergum; with two articular ridges; axial ridge somewhat triangular in shape with scutal border conspicuous and sloping gradually to rostral surface, thin; second ridge twice width of axial ridge, and a flat upper triangular projection at scutal margin; rostral area smooth. Internally, with a large concavity on upper portion for adductor muscle; tergal margin straight, except for notch at upper portion.

Labrum (Fig.17a) with a series of simple sharp teeth, rarely bifid or multifid. Palp (Fig.17a) short, acuminate, with simple setae on inner margin and distal region. Mandible (Fig.17b) with three teeth, distance between first and second twice distance between second and third, upper margin of third tooth with accessory denticule; lower angle denticulated. Maxilla I (Fig.17c) with lower part slightly projected and with a shallow concavity in middle; two large and one median spines at upper angle, 10 small spines in the concavity, and lower projected part, with two large spines medially positioned, five median-size spines on upper portion and seven small spines on lower portion. Maxilla II (Fig.17d) triangular, anterior margin with shallow concavity medially; covered by long simple setae, except on the shallow concavity.

Cirrus I (Fig.18a) with equal rami, both rami with wide basal articles tapering toward distal portion, covered with several long simple setae. Cirrus II (Fig.18b) with unequal rami, anterior ramus about 2/3 length of posterior, articles more protuberant; both rami covered by numerous long, simple setae.

Fig.17- Gibbosaverruca montereyi sp.nov.: (a) labrum and palp; (b) mandible; (c) maxilla I; (d) maxilla II.
Rami of cirri III-VI equal in length. Intermediate articles of cirrus VI (Fig.18c) with width equal to length; three pairs of simple setae on anterior margin; none to two fine simple setae on posterior angle, multifid scales at distal margin. Caudal appendage (Fig.18d, e) with 20 articles, two times length of protopodite; long simple setae on distal margins of articles. Penis smaller than coxopodite, clothed with thin setulae. Number of articles of cirri I-VI and caudal appendage is presented in table 6.

Etymology – From Monterey, California, the locality where it was collected.

Remarks – *Gibbosaverruca montereyi* sp.nov. and *G. robusta* sp.nov. were collected at the same locality, off Monterey, and both are large verrucids having rostro-carinal diameters reaching more than 10mm. At first, I thought they were variants of the same species, but *G. montereyi* is easily distinguished by the presence of two articular ridges on the scutum and three on the tergum instead of respectively, three and four in *G. robusta*. The differential characters of these new species and that species of the *Gibbosaverruca gibbosa* group are listed in table 5.

**TABLE 6**

<table>
<thead>
<tr>
<th></th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>V</th>
<th>VI</th>
<th>CA</th>
</tr>
</thead>
<tbody>
<tr>
<td>RC</td>
<td>27/24</td>
<td>16/26</td>
<td>31/34</td>
<td>36/37</td>
<td>37+/42</td>
<td>36+/42</td>
<td>15+</td>
</tr>
<tr>
<td>LC</td>
<td>27/25</td>
<td>18/26</td>
<td>29/33</td>
<td>35/37</td>
<td>40/42</td>
<td>41/41</td>
<td>20</td>
</tr>
</tbody>
</table>

Table 6: Number of articles on cirri I-VI, and caudal appendage of *Gibbosaverruca montereyi* sp.nov.

Fig.18- *Gibbosaverruca montereyi* sp.nov.: (a) cirrus I; (b) cirrus II; (c) intermediate article of cirrus VI; (d) caudal appendage and protopodite; (e) intermediate article of caudal appendage; (CI-CVI) cirri I to VI; (a.) anterior ramus; (c.a.) caudal appendage; (p.) posterior ramus.
**Gibbosaverruca robusta** sp.nov.  
(Figs.19-21)

Material – Holotype: Monterey Submarine Canyon, Monterey, California, 36°46’28.7"N, 121°59’27.5"W, 750m, J. Barry coll. 17 Aug 1992, rc: 12.4mm, SIO-BIC C 10239. Paratypes: same locality, 2 specimens, one specimen lacking rostrum, one specimen only with carina, opercular plates and body, SIO-BIC C 10304, MNRJ 14337.

Diagnosis – Shell with growth lines prominent on all plates. Rostrum with three articular ridges, intermediate widest. Tergum with four articular ridges; axial ridge prominent with another similar ridge beside it, intermediate ridge wider than axial ridge. Scutum with three articular ridges; axial ridge thin; second ridge twice width of axial ridge. Cirrus I with anterior ramus slightly smaller than posterior. Cirrus II with anterior ramus about 2/3 length of posterior. Intermediate articles of cirrus VI with two pairs of setae. Caudal appendage two times length of protopodite.

Description – Shell (Fig.19a, b) white, opercular valves oblique to base of wall, with growth lines prominent on all plates; rostrum and carina undulated, forming large and low longitudinal ridges, fixed tergum and scutum without longitudinal ridges; basal margin not thickened. Cuticle smooth, persistent on shell and opercular valves. Rostrum (Fig.19a) and carina similar in size, former with three articular ridges, with shallow grooves between them on the rostro-carinal articulation, intermediate largest; rostrum and fixed scutum articulation without radius-like projection, apex straight, projected.

---

**Fig.19-** *Gibbosaverruca robusta* sp.nov.: (a) rostro-carinal view; (b) fixed tergum and fixed scutum view; (c) tergum and scutum, internal view.
Carina (Fig. 19a) with four articular ridges directed toward scutum, second largest, others small, with shallow grooves between them, with large radius-like projection toward fixed tergum; apex curved and projected. Fixed tergum (Fig. 19b) higher than fixed scutum, both sides with well-developed alar-like projections; apex straight. Fixed scutum (Fig. 19b) with wide alar-like process directed toward rostrum three times width of radii-like process directed toward fixed tergum; internally, with a pit for adductor muscle and a small projected adductor ridge.

Tergum (Fig. 19a, c) quadrangular, with four articular ridges; axial ridge prominent with another similar ridge beside it, intermediate ridge wider than axial ridge; upper ridge thin and marginal to occludent margin, with a large conspicuous depression between upper and intermediate ridges; carinal area smooth. Internally, smooth and flat; scutal margin straight except for protuberance on upper portion. Scutum (Fig. 19a, c) smaller than tergum; with three articular ridges; axial ridge somewhat triangular in shape with scutal border conspicuous and sloping gradually to rostral surface, thin; second ridge twice width of axial ridge, third ridge thin, and a flat upper triangular projection at scutal margin; rostral area smooth. Internally, with a large concavity on upper portion for adductor muscle; tergal margin straight, except for notch at upper portion.

Labrum (Fig. 20a) with a series of simple sharp teeth, rarely bifid or multifid. Palp (Fig. 20a) short, acuminate, with simple setae on inner margin and distal region. Mandible (Fig. 20b) with three teeth, distance between first and second three times distance between second and third; lower angle denticulated. Maxilla I (Fig. 20c) with lower part slightly projected; 2 large spines at upper angle, 19 small spines in the middle followed by 4 large spines medially positioned and 10 small spines on basal projection. Maxilla II (Fig. 20d) triangular, anterior margin with concavity medially; covered by long simple setae, except on the shallow concavity. Papillae of maxillary gland small, rounded.

Fig. 20 - Gibbosaverruca robusta sp. nov.: (a) labrum and palp; (b) mandible; (c) maxilla I; (d) maxilla II.

Cirrus I (Fig. 21a) with subequal rami, anterior a little smaller than posterior, both rami with wide basal articles tapering to distal portion, covered with several long simple setae. Cirrus II (Fig. 21b) with unequal rami, anterior ramus about 2/3 length of posterior; both rami covered by numerous long, simple setae. Rami of cirri III-VI equal in length. Intermediate articles of cirrus VI (Fig. 21c) with width equal to length; 2 pairs of long simple setae and 1 simple setulae on anterior margin; 2 or 3 simple setae on posterior angle, multifid scales at distal margin. Caudal appendage (Fig. 21d, e) with 17 articles, two times length of protopodite; long simple setae on distal margins of articles. Penis smaller than coxopodite, clothed with thin setulae. Number of articles of cirri I-VI and caudal appendage is presented in table 7.

Etymology – From the Latin robustus, massive, referring to the large size of this species.

Remarks – The comparison of this species with others of the G. gibbosa group is presented in table 5. G. robusta is easily characterized by its large size, with the growth lines very prominent on all plates and the rostrum having three and tergum four articular ridges. None of other species of these group have this large number of ridges on the scutum and tergum.

TABLE 7

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(CI-CVI) cirri I to VI; (CA) caudal appendage; (RC) right cirri; (LC) left cirri; (+) broken ramus.

Fig. 21- *Gibbosaverruca robusta* sp.nov.: (a) cirrus I; (b) cirrus II; (c) intermediate article of cirrus VI; (d) caudal appendage and protopodite; (e) intermediate article of caudal appendage; (CI-CVI) cirri I to VI; (a.) anterior ramus; (c.a.) caudal appendage; (p.) posterior ramus.
Gibbosaverruca mateoi sp.nov.  
(Figs.22-24)

Material – Holotype: California, San Mateo County, Off San Mateo Point, 9.6 miles, 768-823m, G.D.Hanna col., “N.B. Scofield”, 23 Jan 1953, on Hyalonema spicule, one specimen, rc: 5.3mm, CASIZ 061442.

Diagnosis – Shell with growth lines prominent on all plates. Rostrum with three articular ridges and one small turned toward scutum. Tergum with three articular ridges. Scutum with two articular ridges. Cirrus I with anterior ramus a little smaller than posterior. Cirrus II anterior ramus about 1/2 length of posterior. Intermediate articles of cirrus VI with three pairs of setae on anterior margin. Caudal appendage a little longer than protopodite.

Description – Shell (Fig.22a, b) white, opercular valves oblique to base of wall, with growth lines prominent on all plates, without longitudinal ridges; basal margin not thickened. Cuticle not persistent on shell and opercular valves. Rostrum (Fig.22a, b) and carina with similar size, former with three articular ridges and one small turned toward scutum, with shallow grooves between them on the rostro-carinal articulation, upper ridge largest; rostrum and fixed scutum articulation with small radius-like projection, apex incurred, projected. Carina (Fig.22a, b) with three articular ridges directed toward scutum, first and second of similar size, with shallow grooves between them; with large radius-like projection toward fixed tergum; apex recurved and projected. Fixed tergum (Fig.22a) higher than fixed scutum, both sides with well-developed alar-like projections;

Fig.22- Gibbosaverruca mateoi sp.nov.: (a) rostro-carinal view; (b) fixed tergum and fixed scutum view; (c) tergum, internal view; (d) scutum, internal view.
apex curved toward fixed scutum. Fixed scutum (Fig.22a) with wide alar-like process directed toward rostrum two times width of radii-like process directed toward fixed tergum, apex curved to fixed tergum; internally, with an apical pit for adductor muscle. Tergum (Fig.22a, c) quadrangular, with three articular ridges; axial ridge well prominent, curved, intermediate ridge as wide as axial ridge; upper ridge thin and marginal to occludent margin, with a large conspicuous depression between ridges; carinal area smooth. Internally, smooth and flat; scutal margin undulated. Scutum (Fig.22a, c) smaller than tergum; with two articular ridges; axial ridge prominent, thin; second ridge as wide as axial ridge; and a flat upper triangular projection at scutal margin; rostral area smooth. Internally, with a large concavity on upper portion for adductor muscle; tergal margin nearly straight, except by a medio-basal projection of second ridge.

Labrum (Fig.23a) with a series of 41 simple sharp teeth. Palp (Fig.23a) acuminated, with simple setae on margins. Mandible (Fig.23b) with three teeth, third tooth with a small denticule on upper margin, distance between first and second 1.5 distance between second and third; lower angle denticulated. Maxilla I (Fig.23c) with lower part projecting; two large and one median-size spine at upper angle, two small, strong spines in the middle followed by nine medium to large spines on lower portion of basal projection. Maxilla II (Fig.23d) triangular, anterior margin with shallow concavity medially; covered by long simple setae, except in the shallow concavity. Cirrus I (Fig.24a) with subequal rami, anterior a little smaller than posterior, both rami with wide basal articles tapering to distal portion, covered with several long simple setae. Cirrus II (Fig.24b) with unequal rami, anterior ramus about 1/2 length of posterior; both rami covered by numerous long,
simple setae and distal articles of anterior ramus also with pinnate setae. Rami of cirri III-VI equal in length. Intermediate articles of cirrus VI (Fig.24c) with width 1/2 the length; three pairs of simple setae on anterior margin; one or two simple setae on posterior angle. Caudal appendage (Fig.24d) with 9 articles, a little longer than protopodite; long simple setae on distal margins of articles. Penis (Fig.24d) longer than protopodite, apically clothed with thin setulae. Number of articles of cirri I-VI and caudal appendage is presented in table 8.

Remarks – *Gibbosaverruca mateoi* sp.nov. is not a very large species like the other two described above: about 5 mm or rostro-carinal length. It has two articular ridges on scutum and three on tergum. Therefore, its number of ridges on the opercular plates are equal to those of *G. mitra*, *G. darwini*, *G. rathbuniana*, *G. somaliensis*, and *G. montereyi*. But *G. mateoi* presents the rostrum with a surface above the upper articular ridge with one small ridge turned toward scutum that distinguishes it from all other *Gibbosaverruca*.

The comparison of this species with others of the *G. gibbosa* group is presented in table 5.

**TABLE 8**

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<td>3+/20</td>
<td>21/12+</td>
<td>24/23</td>
<td>27/26</td>
<td>9</td>
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</table>

Fig.24- *Gibbosaverruca mateoi* sp.nov.; (a) cirrus I; (b) cirrus II; (c) intermediate article of cirrus VI; (d) caudal appendage, penis and protopodite; (CI-CVI) cirri I to VI; (a.) anterior ramus; (c.a.) caudal appendage; (p.) posterior ramus; (pe.) penis.
Cristallinaverruca gen.nov.  
(Fig.25)

Verruca (Altiverruca) – BROCH, 1931:45 (part);  
FOSTER, 1978:68 (part).

Altiverruca – ZEVINA, 1987a:1813 (part);  
BUCKERIDGE, 1994:92 (part); YOUNG, 1998a:  
77 (part).

Type species – Verruca cristallina Gruvel, 1907,  
Recent, R/V Investigator, Andaman Islands, Cap  
Bluff, 768m and Andaman Islands, Cinque  
Island, 785m.

Etymology – from the Latin cristallu (limpid) and  
verruca (wart); feminine gender.

Diagnosis – Shell moderate in size and inclined, wall  
plates massive. Rostrum nearly rectangular to  
triangular, same height of carina, rarely with a flat  
or ribbed surface between the uppermost articular  
ridge and the base of scutum. Rostrum and carina  
sutural area formed by several imbricating ridges  
similar in size. Shell plates usually smooth except  
for articular ridges. Operculum oblique to basis  
inclined more than 45° and also oblique to fixed-  
scutum and tergum. Scutum and tergum with  
conspicuous two to five ridges, usually ornamented.  
Fixed scutum without adductor ridge or myophore.  
Bases of wall plates not inflected.

Species – C. cristallina (Gruvel, 1907), C. crenata  
(Aurivillius, 1898), C. cassis (Hoek, 1913) (= C.  
cristallina), C. bicornuta (Pilsbry, 1916), C. cristallina  
laevis (Broch, 1922) (= C. cristallina), C. regularis  
(Nilsson-Cantell, 1929), C. cristallina typica (Broch,  
1931) (= C. cristallina), C. allisoni (Rao and Newman,  
1972), C. mollae (Zevina, 1990), ? C. jonesae  
(Buckeridge, 1997).

Remarks – Cristallinaverruca gen.nov. encompasses  
species of moderate size that have fully developed  
articular ridges on the opercular plates, rostrum  
and carina. The ridges on the rostral and carinal  
suture are similar in size, making a characteristic  
imbricating pattern. All of the species agree with  
the proposed diagnosis, except for C. jonesae, which  
has an ornamented shell. In figure 25 the type  
localities of all the species of Cristallinaverruca  
gen.nov. are shown excluding the previous synonyms.  
None of the species included in the genus were  
studied herein.

Fig.25- Type localities of all species included in Cristallinaverruca s.s.
Genus *Newmaniverruca* Young, 1998

*Newmaniverruca digitiformis* sp.nov.

(Figs.26-28)

Material – Holotype: Green Seamount at 21°N on the East Pacific Rise, off Mexico, 20°48’N, 109°16’W, 1875m, P.Lonsdale and L.Levin cols., Sept. 1985, rc: 6.2mm, SIO-BIC C 10224. Paratypes, same locality, 28 specimens and fragments, rc: 3.4-10.0mm, SIO-BIC C 10307, MNRJ 14338. Green Seamount, AD1639, 1821m, 6 specimens, rc: 2.0 to 6.5mm, SIO-BIC C 10306; AD1639-7, 1821m, 2 specimens, rc: 1.9-5.0mm, SIO-BIC C 10305; AD1639-9, 1871m, 5 specimens, rc: 1.5 to 5.7mm, SIO-BIC C 10308.

Diagnosis – Shell box-like, articular ridges forming digitiform projections. Rostrum with one small ridge directed to axial ridge of scutum. Scutum and tergum with three articular ridges.

Description – Shell (Fig.26a, b) white, box-like, opercular valves parallel to base of wall, with crenulated growth lines projecting on all plates, more developed on the rostro-carinal articular ridges, forming digitiform projections; parietal plates of shell corrugated, forming rough longitudinal ridges; basal margin not thickened. Cuticle yellowish, smooth, persistent on shell and opercular valves. Rostrum (Fig.26a, b) and carina similar in size, former with about six well developed articular ridges and deep grooves between them on the rostro-carinal articulation, better developed on the distal margin, and one smaller ridge going to axial ridge of scutum; parietal plate with large irregular longitudinal ridges; rostrum and fixed scutum articulation with a small radius-like projection, apex curved and slightly projected. Carina (Fig.26a, b) with about five articular ridges and deep grooves between them, directed toward scutum, more developed distally, and one wide flat ridge on distal margin, with small radius-like projection toward fixed tergum; parietal plate with irregular longitudinal ridges; apex projected. Fixed tergum (Fig.26b) with the same size of fixed scutum,

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Fig.26- *Newmaniverruca digitiformis* sp.nov.: (a) rostro-carinal view; (b) fixed tergum and fixed scutum view; (c) tergum and scutum, internal view.
both sides with well-developed alar-like projections; apex projecting slightly backwards. Fixed scutum (Fig.26b) with wide alar-like projection directed toward rostrum, small radii-like projection to fixed tergum; internally, with only a deep scar for adductor muscle, without myophore.

Tergum (Fig.26a, c) quadrangular, with three articular ridges; axial ridge prominent, but narrower than intermediate ridge; intermediate ridge large, with the growth lines crenulated, upper ridge thin and marginal to occludent margin, with a large conspicuous depression between upper and intermediate ridges; carinal area smooth. Internally, smooth; scutal margin nearly straight except for notch on upper portion. Scutum (Fig.26a, c) smaller than tergum; with three articular ridges; axial ridge conspicuous, thin, both sides well marked, intermediate ridge twice width of axial ridge, upper ridge separated from intermediate ridge by wide groove; rostral area smooth. Internally, smooth; tergal margin nearly straight, except for protuberance at upper part.

Labrum (Fig.27a) with a series of teeth, each having three to five acicular cusps, multifid spinules on the inner surface and scales on the outer surface. Palp (Fig.27a) acuminate, with few simple setae on inner margin and distal region. Mandible (Fig.27b) with three teeth, distance between first and second twice distance between second and third, upper margin of second and third teeth denticulated; lower angle denticulated. Maxilla I (Fig.27c) with lower part projecting; two large spines at upper angle, 4-6 small spines between upper large spines and lower projected part, and 6-7 unpaired spines on basal portion. Maxilla II (Fig.27d) triangular, anterior margin with shallow concavity medially; covered by long simple setae, except on the shallow concavity. Cirrus I (Fig.28a) with unequal rami, anterior ramus 2/3 length of posterior, covered with several long simple setae. Cirrus II (Fig.28b) with anterior ramus about 1/2 length of posterior, articles more protuberant; both rami covered by numerous long, simple setae, anterior ramus also with finely

![Diagram](image-url)

Fig.27- *Newmaniverruca digitiformis* sp.nov.: (a) labrum and palp; (b) mandible; (c) maxilla I; (d) maxilla II.
bipectinate setae at distal article (Fig. 28c). Rami of cirri III–VI equal in length. Intermediate articles of cirrus VI (Fig. 28d) with width 1/2 length; two pairs of setae on anterior margin, longer setae finely pinnate; none to two fine simple setae on posterior angle, multifid scales at distal margin. Caudal appendage (Fig. 28e, f) with 23 articles, three times length of protopodite; long simple setae on distal margins of articles. Penis twice length of protopodite, clothed with thin setulae. Number of articles of cirri I–VI and caudal appendage is presented in table 9.

Etymology – from the Latin *digitus* (finger) and *forma* (shape).

**TABLE 9**

<table>
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<th>CI-VI</th>
<th>(CA) cirri I to VI; (RC) right cirri; (LC) left cirri.</th>
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Remarks – Most species of *Newmaniverruca* have a smooth shell without radial ridges on the plates. Only two species, *N. multicostata* (Gruvel, 1907) and *N. albatrossiana* (Pilsbry, 1912), have the shell ornamented with conspicuous radial ridges, but...
none with the growth lines so pronounced and forming digitiform projections. Furthermore, N. multicostata differs from N. digitiformis sp.nov. by having five articular ridges on the scutum, and the tergum and rostrum do not have the upper ridge turning toward the axial ridge of scutum. On the other hand, N. albatrossiana has a scutum with narrow articular ridges and its rostral area has longitudinal ridges; the tergum has five articular ridges and the carinal area has longitudinal ridges; the rostrum has a very wide upper triangular portion, which is conspicuously observed in apical view. The specimens do not exhibit variation in the number of ridges on the scutum and tergum despite the large range of size available. Only one specimen, from 1821m, has its opercular valves in a more angular position (45°) relative to the base of the wall.

In a recent revision of Verrucidae (YOUNG, 1998a), Costatoverruca was separated from Neumaniverruca and Metaverruca by the rostrum of the former having radial ridges directed toward the scutum whereas the latter two genera do not have these ridges. This new species is intermediate between the latter two genera and Costatoverruca: it has a small apical ridge on the rostrum, which is not articular, and it is directed toward the axial ridge of the scutum. This appears to be an intermediate stage before the development of the series of upper ridges in Costatoverruca. I have maintained it in Neumaniverruca because this ridge is not well developed when compared with the series of upper ridges directed toward the scutum in the species of Costatoverruca.

KEY TO THE GENERA OF THE FAMILY VERRUCIDAE
(modified from YOUNG, 1998a)

1a. Shell erect; opercular plates perpendicular to base, more than 45° to base; without adductor ridge or myophore on fixed-scutum ............................... 2
1b. Shell not erect; opercular plates at no more than 45° to base; with or without adductor ridge or myophore on fixed-scutum ........................................ 4

2a. Shell small and erect, wall plates delicate; rostrum and carina suture linear to undulated, usually without but rarely with weak articular ridges, opercular plates erect, perpendicular to basis and almost parallel to fixed-scutum and tergum ....... Altiverruca Pilsbr, 1916 s.s. 3
2b. Shell moderate to large and inclined, wall plates massive; rostrum and carina very undulated, united by strong articular ridges; operculum oblique to basis inclined more than 45° and also oblique to fixed-scutum and tergum ........................................ 3

3a. Large size; rostrum and carina united by strong ridges, the uppermost on rostrum being the largest ........................................ Gibbosaverruca gen.nov.
3b. Moderate size; rostrum and carina sutural area formed by several imbricating ridges similar in size ........................................ Cristallinaverruca gen.nov.

4a. Fixed tergum and rostrum medially expanded, forming internal partitioned cavities; opercular plates 45° to base; with adductor ridge on movable scutum ........................................ Costatoverruca Pilsbr, 1916
4b. Fixed tergum and rostrum not medially expanded, without internal cavities; opercular plates less than 45° to base; without adductor ridge on movable scutum ........................................... 5

5a. Shell box-like; opercular plates proportionally large, their width one half or more the width of shell; with or without myophore ........................................ 6
5b. Shell flattened; opercular plates proportionally small, their width less than one half the width of shell; with a large myophore ......... Verruca Schumacher, 1817
5c. Rostrum without secondary ridges directed toward scutal base; without myophore; basal margin of shell not thickened .............. Neumaniverruca Young, 1998
5d. Rostrum with secondary ridges; with or without myophore; basal margin of shell not thickened ............................................. Costatoverruca Young, 1916
5e. Rostrum without secondary ridges directed toward tergal base; with myophore; basal margin of shell thickened ..................... Metaverruca Pilsbr, 1916

6a. Umbo of rostrum and carina marginal ........................................ 7
6b. Umbo of rostrum not marginal, of carina marginal or displaced from margin ........................................ 8
6c. Rostrum without secondary ridges directed toward tergal base; without myophore; basal margin of shell thickened .......... Metaverruca Young, 1916
6d. Umbo of rostrum displaced from margin ........................................... Rostratoverruca Broch, 1922
6e. Umbo of rostrum and carina displaced from margin ........................................... Brochiverruca Zevina, 1993

THE VERTICAL DISTRIBUTION OF VERRUCID GENERA DISCUSSION

The Verrucidae has a wide bathymetric range from the intertidal zone to 5700m. In figure 29, the depth range of all the species of Verrucidae is presented. Due to certain problems in the identification of verrucid species I accepted all the names published, but did not consider whether or not any of them are synonyms. Therefore, the Verrucidae contains 117 recent species/subspecies distributed in 10 genera: Verruca (6), Rostratoverruca (11), Costatoverruca (13), Neumaniverruca (10), Cameraverruca (2), Brochiverruca (4), Cristallinaverruca gen.nov. (10), Metaveruca (22), Gibbosaverruca gen.nov. (13) and Altiverruca (26). The greatest number of species occurs between 300 and 1500m. Above 300m the number of species decreases significantly, with the occurrences of the balanomorphs at the shallower depth.

Otherwise, the pedunculates are abundant below 1000m, where they dominate. There is a substitution from balanomorphs to verrucomorphs and from verrucomorphs to pedunculates along a depth gradient.

Organizing the depth distribution by genera another pattern of substitution can be observed (Fig.30). Most of the genera have different patterns of distribution. *Verruca* s.s. predominates in shallow water (0-100m), followed by *Costatoverruca* (250-500m), *Metaverruca* (1000-2000m), *Gibbosaverruca* (2000-3000m) and *Altiverruca* (4000-5000m). The apparent dominance of *Cristallinaverruca* at 5000-6000m is because there is only one species recorded for this depth. The genera considered more derived are found in shallower waters (*Verruca*, *Rostratoverruca*, *Brochiverruca* and *Costatoverruca*) and that the ones considered more plesiomorphic occur the greatest depth (*Altiverruca*).
ACKNOWLEDGEMENTS

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ABSTRACT

The genus *Altiverruca* is divided into three genera: *Altiverruca* s.s., *Gibbosaverruca* gen.nov. and *Cristallinaverruca* gen.nov. These are distinguished mostly by the size of the shell, structure of the rostrocinal articulation, shape of the rostrum and the development of articular ridges on the opercular plates. A key for the genera of *Verrucidae* is provided. The verrucid fauna of the Northeastern Pacific is analyzed. *Altiverruca beringiana*, *A. galapagosa* and six new species: *Altiverruca sala* sp.nov., *A. vansyoci* sp.nov., *Gibbosaverruca montereyi* sp.nov., *G. robusta* sp.nov., *G. mateoi* sp.nov. and *Newmaniverruca digitiformis* sp.nov. occur within this region and are described herein.

The depth distribution of the Verrucidae and the predominant genera at selected intervals are graphically portrayed. The Verrucidae most commonly occur between 300 and 1500m and there are pronounced changes in the distribution of genera along a depth gradient.

Key words: Crustacea, Cirripedia, Pacific Ocean, Verrucidae, new genera, taxonomy.

RESUMO

VERRUCIDAE DA COSTA OESTE DA AMÉRICA DO NORTE, COM REVISÃO DO GÊNERO ALTIVERRUCA

O gênero Altiverruca é dividido em três gêneros: Altiverruca s.s., Gibbosaverruca gen.nov. e Cristallinaverruca gen.nov. Estes são diferenciados basicamente pelo tamanho da carapaça, estrutura da sutura rostro-carenal, forma do rostro e desenvolvimento das cristas articulares da placa opercular. Uma chave para a identificação dos gêneros de Verrucidae é apresentada.

A fauna de verrucídeos do nordeste do Pacífico é analisada. Altiverruca beringiana, A. galapagosa e seis espécies novas: Altiverruca sala sp.nov., A. vangsoyi sp.nov., Gibbosaverruca montereyi sp.nov., G. robusta sp.nov., G. mateoi sp.nov. e Neumaniverruca digitiformis sp.nov. ocorrem nesta região e são descritas neste estudo.

A distribuição batimétrica de Verrucidae e dos gêneros predominantes em intervalos selecionados é apresentada graficamente. Verrucidae ocorre mais comumente entre 300 e 1500m e foi observada uma mudança acentuada na distribuição dos gêneros ao longo de um gradiente de profundidade.

Palavras-chave: Crustacea, Cirripedia, Ocean Pacífico, Verrucidae, géneros novos, taxonomia.

LITERATURE CITED


