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ZOOLOGISCHE VERHANDELINGEN

UITGEGEVEN DOOR HET RIJKSMUSEUM VAN
NATUURLIJKE HISTORIE TE LEIDEN

(MINISTERIE VAN WELZIJN, VOLKSGEZONDHEID EN CULTUUR)

No. 235

**THE RECENT SPECIES OF *MEGABALANUS* (CIRRIPEDIA:
BALANOMORPHA) WITH SPECIAL EMPHASIS ON *BALANUS*
TINTINNABULUM (LINNAEUS) SENSU LATO**

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**THE RECENT SPECIES OF MEGABALANUS (CIRRIPIEDIA:
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Henry, Dora P. & Patsy A. McLaughlin: The Recent species of *Megabalanus* (Cirripedia: Balanomorpha) with special emphasis on *Balanus tintinnabulum* (Linnaeus) sensu lato.

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Since Darwin's (1854) description of 11 varieties of *Megabalanus tintinnabulum* (Linnaeus) [as *Balanus tintinnabulum*], 26 Recent taxa have been assigned to the genus. In this review, two taxa confounded by Darwin are reestablished [i.e., *M. crispatus* (Schröter) and *M. dorbignii* (Chenu)]. *M. antillensis* (Pilsbry) and *M. intermedius* (Darwin) are placed in synonymy with *M. tintinnabulum* sensu stricto. *M. galapaganus* (Pilsbry) is synonymized with *M. peninsularis* (Pilsbry) and *M. xishaensis* Xianqui & Liu is considered a synonym of *M. occator*. Diagnoses and an illustrated key to the species are presented. Lectotypes are designated for *M. tintinnabulum*, *M. crispatus*, *M. dorbignii*, *M. coccopoma* (Darwin), *M. spinosus* (Chenu), *M. validus* (Darwin), and *M. ajax* (Darwin).

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INTRODUCTION

“Mega-balanus” was the name proposed by Hoek (1913) for Darwin’s (1854) first subdivision of the genus *Balanus*, because this section “. . . contains the largest forms of existing Balani.” Until recently, most members of this group were considered subspecies (and/or varieties) of *Balanus* (*Megabalanus*) *tintinnabulum* (Linnaeus). Although the accepted formal original description of *Megabalanus tintinnabulum* is that of Linnaeus (1758), it is unclear whether he actually examined specimens of this taxon. It appears that his description was based primarily on the works of Rumphius (1705), Lang (1722), Gualtierus (1742), and Dezallier d’Argenville (1742). Among post-linnaean carcinologists, several (Ellis, 1758; Chemnitz, 1785; Bruguière, 1789; Spengler, 1790; W. Wood, 1815; Chenu, 1843) described and/or figured *M. tintinnabulum* sensu lato, but it was Darwin (1854) who undertook a detailed investigation of this taxon. His study led him to conclude that *B. tintinnabulum* was a highly variable species best considered as only a series of varieties. His diagnoses of these varieties were brief and his illustrations insufficient. Consequently, subsequent carcinologists have found it very difficult to correctly assign specimens to Darwin’s taxa. Until recently the only known source of darwinian material was the British Museum (Natural History), London. However, a review of the early “Day Book” accessions of the Universitetets Zoologisk Museum, Copenhagen (R. Manning, personal communication) revealed that representatives of several of Darwin’s recognized varieties had been deposited there, perhaps in an exchange arranged by H. Krøyer, the

curator (T. Wolff, personal communication). In addition to studying the darwinian collection, we have been able to examine Spengler's (1790) collections also housed in the Zoologisk Museum (ZMC); representatives of the Darwin (1854) collection in the British Museum (Natural History) (BMNH); types of the varieties and/or subspecies subsequently described by Hoek (1913) [Zoological Museum, Amsterdam (ZMA)]; Pilsbry (1916, 1928) [Academy of Natural Sciences, Philadelphia (ANSP), National Museum of Natural History, Smithsonian Institution (USNM)]; Zullo (1969) [California Academy of Sciences (CAS)]; and Foster (1978) [National Museum of New Zealand (NMNZ)], as well as relevant material from the general collections of the National Museum of Natural History, the Academy of Natural Sciences, Scripps Institution of Oceanography (SIO) and the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH). A list of the material examined is presented in the Appendix.

HISTORICAL ACCOUNT

In his monograph of sessile barnacles, Darwin (1854) divided the genus *Balanus* into six sections on the basis of shell structure. Section A was defined as having parietes, basis, and radii permeated by pores. To this section, Darwin assigned *Balanus tintinnabulum* (Linnaeus), *B. tulipiformis* Ellis, *B. psittacus* (Molina), *B. capensis* Ellis, *B. nigrescens* Lamarck, *B. decorus* Darwin, *B. vinaceus* Darwin, and *B. ajax* Darwin. Darwin started his systematic account of *B. tintinnabulum* and its 11 varieties with the remark: "This, the first species of *Balanus*, is, perhaps with the exception of *B. amphitrite*, the most difficult and variable in the genus." From his "Siboga" material of Megabalanus, Hoek (1913) briefly described two new varieties of *B. tintinnabulum*. Pilsbry (1916) gave subgeneric rank to *Megabalanus* and elevated Darwin's (1854) varieties of *B. tintinnabulum* to subspecific rank. Pilsbry (1916) also redescribed six of Darwin's varieties and described seven new subspecies for this taxon. In his key to the species of the subgenus *Megabalanus*, he included, in addition to the members of Darwin's (1854) Section A, *B. campbelli* Filhol and the new species *B. algicola* Pilsbry. Although Darwin had cited Ellis (1758) as the author of *B. tulipiformis* and *B. capensis*, in his discussion of the former species (footnote, p. 204), he noted that Ellis had not followed the linnaean system of nomenclature. He also pointed out that the only other name proposed for *B. tulipiformis* was preoccupied. Stebbing (1910), recognizing that Ellis' name for *B. capensis* was invalid, suggested that Darwin should be cited as the author. Pilsbry (1916: 53) correctly credited Darwin

with authorship of *B. tulipiformis*; however, he proposed (1916: 77) the next presumably available name, *B. maxillaris* Gronovius, for Ellis' (1758) *B. capensis*. Subsequently, Holthuis & Sivertsen (1967) pointed out that Gronovius' (1781) work had been suppressed by an Opinion of the International Commission on Zoological Nomenclature (1925, Opinion 89) and therefore, the valid name for this taxon is *Lepas cylindrica* Gmelin.

In the years that followed Pilsbry's (1916) monographic review of the genus *Balanus*, three additional new species were referred to the subgenus *Megabalanus*, i.e., *B. (M.) krakatauensis* Nilsson-Cantell, 1934; *B. (M.) squillae* Daniel & Ghosh, 1963; and *B. (M.) isolde* Holthuis & Sivertsen, 1967. In addition, *Balanus stultus* Darwin, which Darwin (1854) regretfully placed in his Section B because he thought the radii lacked tubes, was assigned to *Megabalanus* by Ross (1968) who discovered that tubes, though not readily observable, were present in the radii. Three new taxa of *B. tintinnabulum* also were described (i.e., *B. tintinnabulum* forma *maroccana* Broch, 1927; *B. tintinnabulum tanagrae* Pilsbry, 1928; and *B. tintinnabulum clippertonensis* Zullo, 1969. However, Beach (1972) demonstrated that the characters of *B. tintinnabulum* forma *maroccana* were not consistent with those of *Megabalanus* and transferred this taxon to the subgenus *Balanus*.

In a major revision of the balanomorph hierarchy, Newman & Ross (1976) elevated *Megabalanus* to generic rank. They gave specific rank to the 22 taxa previously referred to *M. tintinnabulum* and listed 12 additional Recent species in the genus. However, *B. squillae*, which had been assigned to the subgenus *Megabalanus* by Daniel & Ghosh (1963), was overlooked. Subsequently, Foster (1978) described a new subspecies of *B. tintinnabulum* and Xianqui & Liu (1978) a new species of *Balanus*, both assigned to the subgenus *Megabalanus*. Newman (1979), in a more extensive revision of *Megabalanus*, proposed the subfamily Megabalaninae for those species having radii with transverse tubes between denticulate septa, type *Megabalanus* Hoek. Further, he restricted *Megabalanus* to those species having regular secondary denticles on both upper and lower sides of the primary denticles of the septa. For those species with irregular secondary denticles only on the lower side of the primary denticles, Newman erected new genera, *Austromegabalanus* (five species, one new) and *Notomegabalanus* (three Recent species). Again Daniel & Ghosh's (1963) species was not considered. Although the septa of the radii of *B. (M.) squillae*, a very small species, are distinctly dentate on one side only, the tergum lacks a beak and the spur furrow is closed, characters of *Notomegabalanus* and *Austromegabalanus*, respectively. We questionably have assigned *B. squillae* to *Notomegabalanus* as the scutum is broad like that of *N. algicola*, and Pilsbry (1916) described the spur furrow of *N. algicola* as

being "more or less open". Subsequently, Buckeridge (1983) reduced *Notomegabalanus* to subgeneric rank under *Austromegabalanus*.

Because of the wide range of intraspecific variation among species formerly adjudged to be varieties or subspecies of *M. tintinnabulum*, subsequent

Megabalanus tintinnabulum Group

tintinnabulum (Linnaeus, 1758) (as var. *communis* Darwin, 1854)
antillensis (Pilsbry, 1916) = *M. tintinnabulum*
azoricus (Pilsbry, 1916)
californicus (Pilsbry, 1916)
clippertonensis (Zullo, 1969)
coccopoma (Darwin, 1854)
concinus (Darwin, 1854)
costatus (Hoek, 1913) incertae sedis
crispatus (Schröter, 1786)
dorbignii (Chenu, 1843)
galapaganus (Pilsbry, 1916) = *M. peninsularis*
intermedius (Darwin, 1854) = *M. tintinnabulum*
linzei (Foster, 1978)
occtor (Darwin, 1854)
peninsularis (Pilsbry, 1916)
plicatus (Hoek, 1913) incertae sedis
rosa (Pilsbry, 1916)
spinus (Bruguière, 1789)
tanagrae (Pilsbry, 1928)
validus (Darwin, 1854)
vesiculosus (Darwin, 1854)
volcano (Pilsbry, 1916)
zebra (Pilsbry, 1916)

Remaining *Megabalanus*

ajax (Darwin, 1854).
echinata (Spengler, 1790) = *M. spinus*
krakatauensis (Nilsson-Cantell, 1934)
stultus (Darwin, 1854)
tulipiformis (Darwin, 1854)
vinaceus (Darwin, 1854)
xishaensis (Xianqui & Liu, 1978) = *M. occtor*

Austromegabalanus (*Austromegabalanus*)

cylindricus (Gmelin, 1790)
isolde (Holthuis & Sivertsen, 1967)
nigrescens (Lamarck, 1818)
psittacus (Molina, 1782)
zulloi Newman, 1979

Austromegabalanus (*Notomegabalanus*)

algicola (Pilsbry, 1916)
campbelli (Filhol, 1886)
decorus (Darwin, 1854)
?squillae (Daniel & Ghosh, 1963)

Table 1. Recent species of *Megabalanus* sensu lato.

workers found it difficult to recognize many of these taxa, particularly Darwin's. Our examination of the 23 reported taxa of *B. tintinnabulum* (table 1) indicates that Darwin (1854) confounded some taxa and unjustifiably separated others. For example, Darwin described the scuta of var. *crispatus* Schröter with the external surface either with or without ornamentation. Pilsbry (1916) believed his new taxon *B. tintinnabulum volcano* agreed with those specimens of var. *crispatus* sensu Darwin having ornamented scuta. The specimen of var. *crispatus* we examined is one with "plain" scuta (Darwin, 1854: 196) and, while Schröter (1786) did not describe the opercular valves, his description and figure of the shell agree with the darwinian specimen. Therefore, Darwin's var. *crispatus* included both Schröter's taxon and *M. volcano*. Furthermore, it is clear that Darwin confounded representatives of two taxa under the name *d'Orbignii*. By selection of Chenu's (1843, pl. 6 fig. 10) figured specimen as the lectotype, *M. dorbignii* is herein restricted. Darwin's (1854) remarks and his figure (pl. 1 fig. 1) of the shell of var. *d'Orbignii*, with its strongly oblique radii, do not agree with the specimens of this taxon remaining in the collections of the British Museum (Natural History) and Zoologisk Museum, all of which were identified by Darwin himself. Darwin's figure of the shell does agree with the representative of Spengler's (1790) *Balanus tintinnabulum* var. b remaining in the collection of the Zoologisk Museum and with one of the paratypes of *M. ajax* (see discussion under *M. ajax*, p. 50). These shells not only lack tubes in the radii but also in the parietes and are herein referred to *Chirona amaryllis* (Darwin).

Darwin's var. *intermedius* (fig. 5k, l) exhibits characters well within the range of variation of *M. tintinnabulum*, as surmised by Pilsbry (1916). Darwin (1854) implied that his var. *vesiculosus*, which he distinguished solely by the longitudinally grooved and pitted scuta, might be the juvenile form of *M. tintinnabulum*. Among representatives of this latter taxon, we have observed a few small individuals with apically furrowed and pitted scuta. Similarly, we have observed specimens of *M. vesiculosus* that lack scutal pits. However, as pointed out by McLaughlin & Lacombe (1979), several other characters distinguish these two species.

Hoek's (1913) *B. tintinnabulum* varieties *costatus* and *plicatus* that were described on one and two small individuals, respectively, have not been reported again. We have examined a pair of opercular valves of each of these taxa. The differences stated by Hoek to distinguish *costatus* from *plicatus* are minor in view of the variation common to species of the *tintinnabulum* group. Although Hoek indicated that the radii had tubes, he did not describe the positions of the secondary denticles. It is probable that these varieties represent a single taxon in either the subgenus *Austromegabalanus* or

Notomegabalanus but, until supplemental material is found, both taxa must be considered incertae sedis.

Pilsbry's (1916) subspecies *galapaganus* was based on a clump of small individuals. In his description he differentiated it from *B. t. concinnus*, *B. t. coccopoma*, and *B. t. tintinnabulum*. However, he did not contrast it with his new taxon *B. t. peninsularis*, known at that time from only one locality in Baja California, Mexico. Our examination of several hundred specimens of *M. peninsularis* from the Gulf of California to Ecuador, including the Galapagos Islands, has convinced us that *M. galapaganus* is synonymous with *M. peninsularis*. Pilsbry (1953) found that specimens of *B. t. antillensis* from Florida closely resemble *B. t. tintinnabulum*. Although he did not synonymize the two taxa, he stated that recognition of his "Antillean" form appeared of "doubtful utility". Having examined Atlantic specimens agreeing with the descriptions of both *M. tintinnabulum* and *M. antillensis*, as well as Indo-Pacific specimens assignable to the former species, and finding no character or suite of characters by which the two can be separated, we have concluded that *M. antillensis* is not a distinct species and should be put in synonymy with *M. tintinnabulum*.

Xianqui & Liu (1978) differentiated their new species, *M. xishaensis*, from *M. occator* and all other species of *Megabalanus* by the toothed inner surface of the spur. Although we have not examined representatives of this taxon, we have observed similar projections on the inner surface of the spur in other species of *Megabalanus*. The authors acknowledged the close similarity of their species to *M. occator*, and nothing in their description would otherwise separate the two taxa. Thus we must conclude that *M. xishaensis* is a junior synonym of *M. occator*.

TAXONOMIC ACCOUNT

Megabalaninae Newman, 1979

Balanidae with tubiferous parietes, tubiferous or solid basis and well developed radii with transverse tubes between denticulate septa. Littoral, approximately 53 species. Type genus *Megabalanus* Hoek, 1913.

Megabalanus Hoek, 1913

Megabalaninae with primary denticles of sutural edges of radii with regular secondary denticles on both upper and lower sides; basis usually tubiferous;

tergum usually without beak, spur furrow open or closed; labrum usually with few well developed teeth on each side of notch. Oligocene to Recent; approximately 42 species, 23 Recent; warm and tropical seas. Type species: *Megabalanus tintinnabulum* (Linnaeus, 1758), by monotypy.

In the key that follows, characters most subject to changes with growth and to extremes in intraspecific variability have been avoided as much as possible; however, some do remain. For example, the spur furrow is typically open in young individuals, but in species of *Megabalanus* an open spur furrow in adults is diagnostic for one cluster of species. Longitudinal striae frequently do not develop until the animal matures; however, adults of a number of species can be distinguished by the presence or absence of longitudinal striae on the scuta and terga. The tergal segment of the scutum is defined as the tergal portion of the scutum delineated by a hypothetical line drawn from the apex to the point on the basal margin at which the margin ascends to the basitergal angle (cf. McLaughlin, 1980, fig. 19G). All other terminology follows that of Henry & McLaughlin (1975). The description of the type species, *M. tintinnabulum* includes, for completeness, characters that have proved to be of limited diagnostic value. These characters will not be repeated in the diagnoses of the remaining species unless they differ from the type. Synonymies are limited to those authors who illustrated the species or provided range extensions.

KEY TO THE RECENT SPECIES OF *MEGABALANUS*

1. Scutum with basal margin (exclusive of tergal segment) sinuous and strongly protuberant medially [parietes white or faintly tinged with purple; usually attached to and often encrusted by *Millepora* (fig. 4m)] *M. stultus*
- Scutum with basal margin (exclusive of tergal segment) straight or only slightly sinuous, not strongly protuberant medially (fig. 1a) 2
2. Exterior of scutum with growth ridges not well developed (fig. 1b) . 3
- Exterior of scutum with growth ridges prominent (figs. 1a, c, d) . . . 4
3. Longitudinal striae on exterior of scutum distinct; [parietes dark purplish brown; inner lamina of parietes cancellated; radii horizontal (fig. 4o)] *M. vinaceus*
- Longitudinal striae on exterior of scutum not distinct; [parietes reddish to deep purple; summits of radii oblique (fig. 4n)] . . . *M. tulipiformis*
4. Exterior of scutum deeply concave medially, with occludent side noticeably elevated, frequently with deep pits between growth ridges, at

- least apically [parietes ribbed, usually with spine-like projections, bluish or pinkish purple, with white ribs, spines and longitudinal striations (fig. 4g)] *M. vesiculosus*
- Exterior of scutum not as above 5
5. Scutum clearly marked by longitudinal striae (figs. 1a, d, e) 6
- Scutum not clearly marked by longitudinal striae (fig. 1f) 15
6. Spur furrow of tergum open (in adults) (fig. 1g) 7
- Spur furrow of tergum closed or nearly so (fig. 1h) 8
7. Adductor ridge of scutum present [parietes ribbed, with numerous well developed spines, whitish, tinged with red or purple or reddish purple with white striae (fig. 4d)] *M. spinosus*
- Adductor ridge of scutum absent [parietes pinkish, ribbed, ribs often with pale purple to cream, spinose projections (fig. 3n, o)] *M. occator*
8. Tergal segment of scutum very broad [parietes smooth to weakly plicate, with longitudinal and transverse striae of purple and violet on white surface, giving speckled appearance (fig. 3i)] *M. concinnus*
- Tergal segment of scutum narrow to moderately broad (figs. 1b, d, f; 2a) 9
9. Adductor ridge of scutum prominent (fig. 2b) 10
- Adductor ridge of scutum weak or absent (fig. 2c) 13
10. Parietes prominently ribbed, at least apically 11
- Parietes smooth, roughened, or plicate, not prominently ribbed .. 12
11. Tergum with crests for depressor muscle strongly developed [parietes reddish purple to dark blue-purple with white ribs; sheath madder brown (fig. 4j, k)] *M. zebra*
- Tergum with crests for depressor muscle weakly developed [parietes blue-violet to purple and white; sheath pale violaceous (fig. 3d, e)] *M. azoricus*
12. Growth ridges of scutum strongly scalloped by longitudinal striae; parietes usually with spines or spinose projections [parietes purplish red to deep slate violet, fading to smoke-gray when worn (fig. 4h, i) *M. volcano*
- Growth ridges of scutum not scalloped by longitudinal striae; parietes without spines or spinose projections [parietes smooth to roughened, occasionally weakly plicate; reddish purple, purplish pink to blackish purple, often with darker or lighter longitudinal striae (fig. 3a, b, c)] *M. tintinnabulum*
13. Spur three of four times own width from basiscutal angle [parietes red or reddish purple; sheath dark purplish brown (fig. 4f)] *M. validus*
- Spur own width or less from basiscutal angle (fig. 2d, e) 14

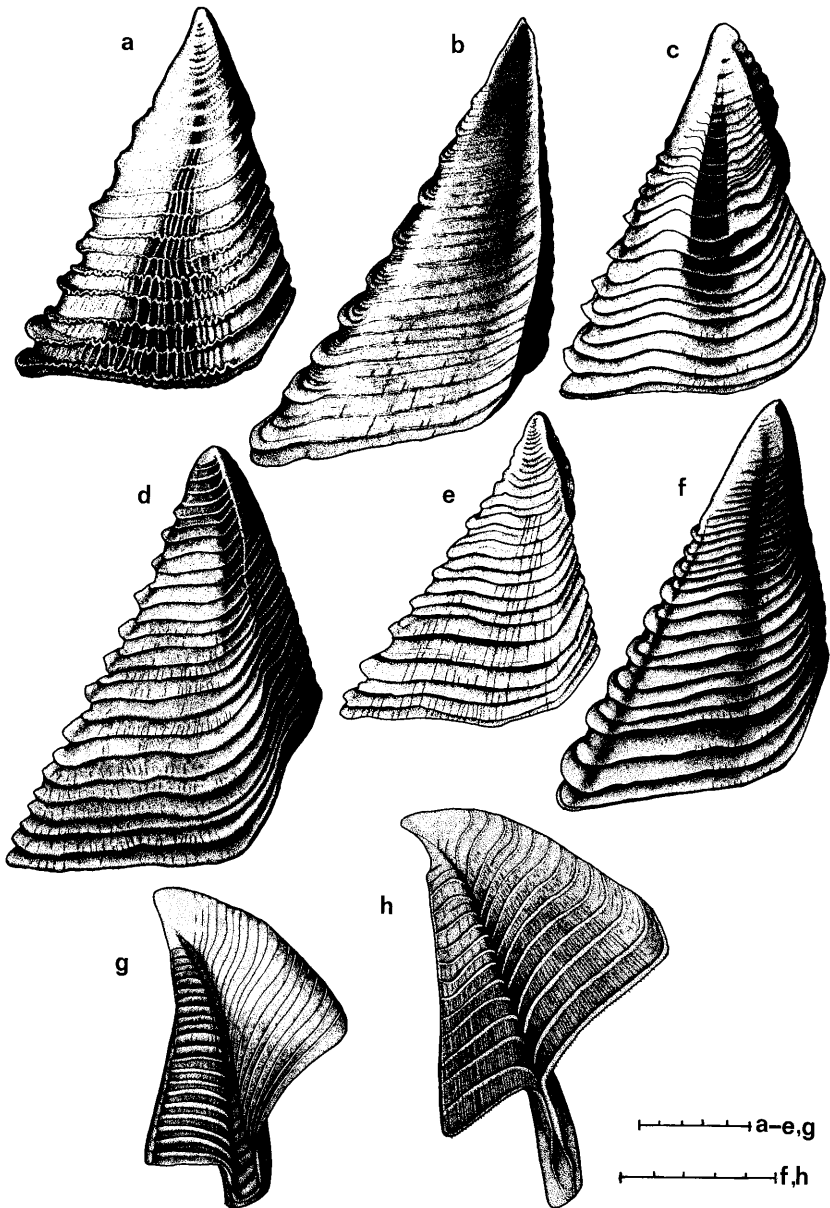


Fig. 1a-f. Exterior views of scuta: a, *Megabalanus azoricus* (USNM 48126); b, *Megabalanus tulipiformis* (USNM 170617); c, *Megabalanus vesiculosus* (Baia de Guanabara, Brazil); d, *Megabalanus californicus* (USNM 9434a); e, *Megabalanus tintinnabulum* (Baia de Guanabara, Brazil); f, *Megabalanus peninsularis* (USNM 63487). g-h, external views of terga: g, *Megabalanus tanagrae* (Oahu, Hawaii); h, *Megabalanus peninsularis* (Punta Carnero, Ecuador). Scales equal 5 mm.

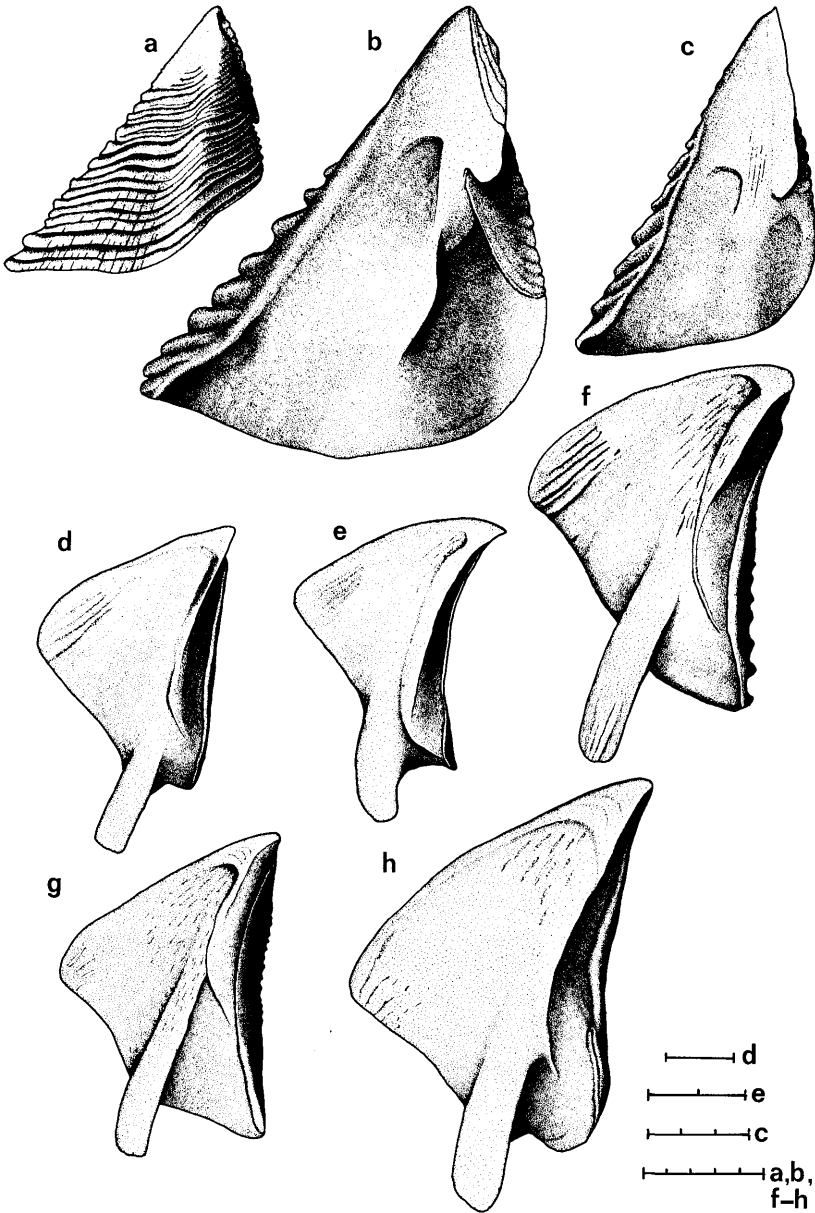


Fig. 2a-c. Scuta: a, external view, *Megabalanus tintinnabulum* (Baia de Guanabara, Brazil); b-c, internal views: b, *Megabalanus peninsularis* (Acapulco, Mexico); c, *Megabalanus dorbignii* (ZMC). d-h, internal views of terga: d, *Megabalanus occator* (RMNH 397c); e, *Megabalanus dorbignii* (BMNH); f, *Megabalanus zebra* (Indonesia); g, *Megabalanus tintinnabulum* (Baia de Guanabara, Brazil); h, *Megabalanus tintinnabulum* (off Galveston, Texas). Scales equal 1 mm, d; 2 mm, e; 3 mm, c; 5 mm a-b, f-h.

Fig. 3. Shells of *Megabalanus* species

a, *M. tintinnabulum*
[(0.57 ×) Spengler collection,
ZMC]



b, *M. tintinnabulum*
[(1.14 ×) Darwinian collection,
BMNH]



c, *M. tintinnabulum* [(0.5 ×)
Ft. Pierce, FL, ANSP 6662]



d, *M. azoricus* [(0.38 ×)
type series, USNM 4.126]



e, *M. azoricus* [(0.5 ×) St.
Helena I., RMNH]



f, *M. californicus* [(0.38 ×)
type series, USNM 9434a]



g, *M. clippertonensis*
[(1.14 ×) paratype, CAS
029823]



h, *M. coccopoma* [(0.76 ×)
lectotype, Darwinian collection,
BMNH]



i, *M. concinnus* [(0.76 ×)
Darwinian collection,
BMNH]



j, *M. crispatus* [(0.5 ×) Dar-
winian collection, BMNH]



k, *M. dorbignii* [(1.5 ×)
Darwinian collection,
BMNH]



l, *M. dorbignii* [(0.57 ×)
Darwinian collection, ZMC]



m, *M. linzei* [(0.57 ×)
paratype, NMNZ]



n, *M. occator* [(1.14 ×)
Philippine Is., USNM
52116]



o, *M. occator* [(1.5 ×) ship,
RMNH 397]

Fig. 4. Shells of *Megabalanus* species (cont.)a, *M. peninsularis* [(0.57×)
Bahia de Acapulco, Mexico]b, *M. peninsularis* [(0.76×)
Malpelo Island, Colombia]c, *M. rosa* [(0.76×) type,
USNM 43494]d, *M. spinosus* on *Lepas* sp.
[(1×) Darwinian collection,
BMNH]e, *M. tanagrae* [(0.57×)
Hookena, Hawaii]f, *M. validus* [(0.38×) lec-
totype, Darwinian collec-
tion, ZMC]g, *M. vesiculosus* [(1.5×)
Baia de Guanabara, Brazil]h, *M. volcano* [(0.38×)
type, USNM 43488]i, *M. volcano* [(0.5×)
Japan, USNM 177932]j, *M. zebra* [(1.14×) Darwi-
nian collection, BMNH]k, *M. zebra* [(0.76×) Darwi-
nian collection, ZMC]l, *M. ajax* [(0.38×) lec-
totype, Darwinian collec-
tion, BMNH]m, *M. stultus* [(0.76×)
Galeta, Panama]n, *M. tulipiformis* [(0.57×)
off El Hank, Casablanca,
USNM 170617]o, *M. vinaceus* [(1.14×)
Playas, Ecuador]

14. Exterior of tergum with faint longitudinal striae [parietes red with white longitudinal striae (fig. 3f)] *M. californicus*
 – Exterior of tergum with strong longitudinal striae, at least on scutal side of spur [shell often elongated in rostrocarinal axis, parietes pale pink, smooth (fig. 4l)] *M. ajax*
15. Spur furrow of tergum open (in adults) (fig. 1g) 16
 – Spur furrow of tergum closed or nearly so (fig. 1h) 18
16. Adductor ridge of scutum absent [parietes pinkish red to grayish red-purple with indistinct darker longitudinal striae (fig. 3g)]
 *M. clippertonensis*
 – Adductor ridge of scutum present (fig. 2b) 17
17. Tergum with crests for depressor muscle prominent [parietes ribbed, ribs often with numerous spinose projections; bluish or pinkish purple; orifice slightly toothed (fig. 3k, l)] *M. dorbignii*
 – Tergum with crests for depressor muscle weak or absent [parietes weakly plicate, often minutely spinose, whitish, pink or pale purple (fig. 4e)]
 *M. tanagrae*
18. Scutum with very broad tergal segment [parietes red, reddish purple or purplish blue, rarely with light colored longitudinal transverse lines (fig. 3h)] *M. coccopoma*
 – Scutum with narrow to moderately broad tergal segment (fig. 1b, d, e, f) 19
19. Spur less than own width from basiscutal angle [parietes white or dull rose with red longitudinal lines] *M. krakatauensis*
 – Spur own width or greater than own width from basiscutal angle (fig. 2f, g, h) 20
20. Tergum with crest for depressor muscle prominent [parietes strongly ribbed, at least apically, blackish or pinkish purple (fig. 3m)] . *M. linzei*
 – Tergum with crests for depressor muscle weak or absent (fig. 2g)
 21
21. Adductor ridge of scutum confluent with articular ridge [parietes smooth, pink, rose or white; radii reddish purple or white (fig. 4c)] .. *M. rosa*
 – Adductor ridge of scutum not confluent with articular ridge (fig. 2b) 22
22. Tergal segment of scutum flat or slightly inflected; exterior of tergum with strong longitudinal striae, at least on scutal side of spur [parietes rugose or ribbed; reddish, pinkish or bluish purple, pink or white, often with white longitudinal striae or riblets, frequently with minute spines (fig. 4a, b)] *M. peninsularis*

- Tergal segment of scutum obtusely inflected; exterior of tergum with only faint longitudinal striae [parietes bluish purple, with minute spine-like processes; radii darker (fig. 3j)] *M. crispatus*

Megabalanus tintinnabulum (Linnaeus, 1758)

(figs. 1e, 2a, g, h, 3a-c, 5a-l)

- Balani* Rumphius, 1705: 121, pl. 41 figs. A,C,D.
Balanus tintinnabuliformis laevis Lang, 1722: 4.
Balanus cylindraceus unicum thalamum efformans, magis ventricosus Gualtierus, 1742: unnumbered page, pl. 106 fig. H.
 Glands de mer de la grande espèce: Dezallier d'Argenville, 1742: 364, pl. 30 fig A; 1757: 364, pl. 26 fig. A.
Lepas Tintinnabulum Linnaeus, 1758: 668. — Chemnitz, 1785 (in part): pl. 97 figs. 830, 831, not figs. 828, 829 (see remarks).
Lepas calyciformis orientalis Ellis, 1758: 845, pl. 34 figs. 8, 9.
Balanus tintinnabulum: Bruguière, 1789 (in part): 165 (see remarks). — Holthuis & Heerebout, 1972: 24, pl. 1.
Lepas tintinnabulum: Wood, 1815: 38, pl. 6 figs. 1, 2.
Lepas spinosa: Wood, 1815 (in part): pl. 7 fig. 4 (large shell only; small shells = *M. spinosus*).
Balanus tintinnabulum var. *communis* Darwin, 1854: 105, pl. 1 figs. a, b, f supra, pl. 2 figs. 1a, c, d, e, i, k. — Hoek, 1883: 147, pl. 12 figs. 18, 19. — Sundra Raj, 1927: 112, pl. 14 figs. A1-A5.
Balanus tintinnabulum tintinnabulum: Pilsbry, 1916: 55, pl. 10 figs. 1-1e. — Hiro, 1939: 258, figs. 7a-b. — Daniel, 1956: 17, pl. 4 figs. 1-6. — Davadie, 1963: 26, pl. 2 fig. 4, pl. 6 figs. 1a-2b. — Zevina & Tarasov, 1963: 87, fig. 8. — Stubbings, 1964b: 335, fig. 3; 1967: 263. — Karande & Palekar, 1966: 142, figs. 1, 2, pl. 1 fig. 1, pl. 3 row 1.
Balanus tintinnabulum antillensis Pilsbry, 1916: 63, pl. 13 figs. 1-2e. — 1953: 24, pl. 2 figs. 4-4c. — Oliveira, 1941: 14, pl. 3 fig. 2.
Balanus tintinnabulum var. *tintinnabulum*: Oliveira, 1941: 11, text fig. 1, pl. 2 figs. 1, 2, pl. 4 fig. 1, pl. 5 fig. 3, pl. 8 fig. 6.
Megabalanus antillensis: Newman & Ross, 1976: 67.
Megabalanus tintinnabulum: Newman & Ross, 1976: 68. — Lacombe & Rangel, 1978: 3, fig. 4.
Balanus (Megabalanus) tintinnabulum tintinnabulum: Xianqui & Liu, 1978: 121, text fig. 1, pl. 1 figs. 1-5.
 not *Lepas Tintinnabulum*: Spengler, 1790: 180 (= *Megabalanus occator*).
 not *Lepas Tintinnabulum* var. a: Spengler, 1790: 181 (incertae sedis).
 not *Lepas Tintinnabulum* var. b: Spengler, 1790: 182 (= *Chirona amaryllis*).
 not *Balanus tintinnabulum*: Chenu, 1843, pl. 2 fig. 8, pl. 3 fig. 5 (See *Megabalanus ajax* and *M. tulipiformis*).
 not *Balanus tintinnabulum* var. *communis*: Krüger, 1911: 46, pl. 3 figs. 31a₁-b₂ (= ? *Megabalanus volcano*).
 ? not *Balanus (Megabalanus) tintinnabulum*: Withers, 1924: 24, pl. 6 figs. 4-7 (? = *Megabalanus linzei*).
 not *Balanus tintinnabulum antillensis*: Pilsbry, 1927: 38, fig. 3a-c (= *Megabalanus stultus*).
 not *Balanus tintinnabulum tintinnabulum*: Linzey: 1942: 279 (= *Megabalanus linzei*).
 not *Balanus tintinnabulum*: Foster, 1967: 81, fig. 2a, b (= *Megabalanus linzei*).

Type. — Lectotype herein designated: specimen figured in Rumphius, 1705, pl. 41 fig. A (specimen with cirri extended).

Type locality. — Amboina, Indonesia.

Distribution. — Worldwide.

Diagnosis. — Shell cylindrical, cylindroconic or conic, basis often lengthened; parietes smooth, plicated or roughened; radii wide, usually horizontally striated, summits horizontal; summits of alae oblique; orifice moderately small to large, $1/3$ to $2/3$ basal diameter, subcircular to subtriangular. Scutum with narrow to moderately broad tergal segment, usually flat or slightly inflected in cylindrical specimens, obtusely inflected in cylindroconic and conic specimens; external surface occasionally with shallow median depression, rarely also with few shallow pits in very small individuals; basal margin straight or slightly sinuous; occludent margin toothed; growth ridges prominent; longitudinal striae well developed, at least basally; articular ridge reflexed, $1/2$ to $2/3$ length of tergal margin; adductor ridge rounded or acute, confluent with articular ridge; pit for adductor ridge shallow to moderately deep; pit for lateral depressor muscle shallow to moderately well developed, sometimes with longitudinal crests. Tergum frequently wider than scutum, with spur furrow closed; spur moderately long, narrow to moderately wide, separated from basiscutal angle by $1\frac{1}{2}$ to 4 times own width; basal margin straight or slightly sloping to spur on both sides; scutal margin denticulate; growth ridges prominent at least in basal half; longitudinal striae fine, sometimes absent; articular ridge approximately $2/3$ length of scutal margin; crests for depressor muscle weakly to moderately well developed.

Color. — Parietes reddish or bluish purple to brownish red, usually with longitudinal striations, often also with narrow or wide transverse bands, both either darker or lighter than parietes; radii dark reddish or bluish purple, occasionally white, tinged with yellow, pink or purple. Sheath dirty white, usually with dull pink or purple splotches. Scutum externally pink to light or dark reddish or bluish purple in basal $1/3$ to $1/2$, white apically, less frequently also with 1 or 2 white or yellow longitudinal stripes, internally white or white tinged with purple; tergum white or white with tinges of purple or pink.

Remarks. — Of the prelinnaean carcinologists, Rumphius (1705) presented three figures of *Balanus tintinnabulum* (cf. Holthuis, 1959), a group of three, the animal removed from the shell and the opercular valves, and a general account including color and habitat. We have selected as the lectotype of this species the middle specimen in Rumphius' figure A.

Spengler (1790) briefly described "*Lepas tintinnabulum* Lin." and in his synonymy referred to both Rumphius' (1705) and DeZallier d'Argenville's [(1757, pl. 26) 2nd edition] figures. However, the opercular valves of this

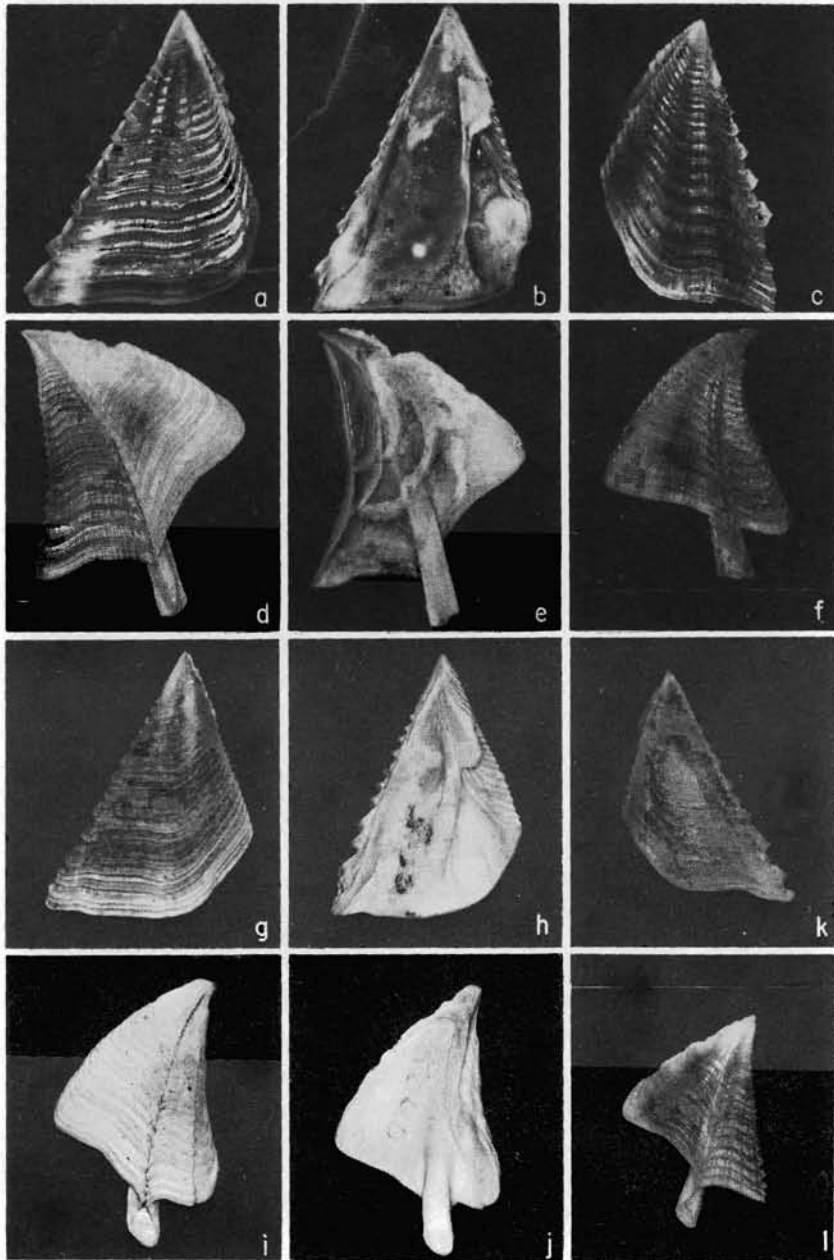


Fig. 5. *Megabalanus tintinnabulum* (Linnaeus). a-b, d-e external and internal views of opercular valves; c, f external views of scutum and tergum of second specimen, Darwinian collection, BMNH); g-j, external and internal views of opercular valves (off Galveston, Texas); k-l, external views of scutum and tergum of "var. *intermedius*" (Darwinian collection, BMNH). a-b, d-e $\times 6.2$; c, f $\times 5.3$; g-j $\times 2.3$; k-l $\times 4.4$.

specimen, still retained in the Spengler collection, are those of *M. occator*. Variety "a" (Spengler, 1790: 181) can no longer be identified in the collection; thus its identity must remain uncertain. As previously indicated, Spengler's var. "b" is not a megabalanid and has been assigned to *Chirona amaryllis*.

Chemnitz's (1785) pl. 97 figs. 828, 829 show animals with prominently beaked terga. This character, attributed to *Austromegabalanus* by Newman (1979), and the colorations depicted for the shells suggest that these individuals should be referred to *A. nigrescens*.

Bruguière (1789: 165) cited *Balanus tintinnabulum* (Linnaeus), not *Balanus tulipa* Bruguière as stated by Darwin (1854: 105). However, Bruguière did include *Lepas tulipa* Müller and *Lepas tulipa alba* Chemnitz (1785, pl. 98 fig. 832) in his synonymy. Both were subsequently referred by Darwin (1854) to *Balanus hameri* Ascanius.

The large specimen in Wood's figure (1815, pl. 7, fig. 4) clearly is *M. tintinnabulum*, whereas the smaller specimens are *M. spinosus*.

There are no specimens remaining in the darwinian collection labeled by Darwin as var. *communis*; however, it is presumed that those specimens that Darwin identified simply as "*Balanus tintinnabulum*" represent his var. *communis* (G. Boxshall, personal communication). We have examined one so identified lot of four specimens. Two are identifiable with Darwin's and subsequent descriptions of *M. tintinnabulum* sensu stricto (e.g., Pilsbry, 1916); the other two agree in all respects with Pilsbry's description of *M. antillensis*. In his description of *B. t. antillensis* Pilsbry remarked that the opercular valves were substantially like those of *B. t. tintinnabulum*. He figured the type and paratype group (ANSP 2083), a set of opercular valves (1916: pl. 13 figs. 1, 1a-c, e) and another tergum (fig. 1d), as well as two shells, a tergum and scuta (pl. 13 figs. 2, 2a-e) from a specimen removed from a Cape Cod whaling vessel (USNM 48005). However, figure 1d is actually the internal view of the other tergum from the Cape Cod whaler specimen (fig. 2c). These specimens from the whaler are unquestionably *M. tintinnabulum*. After examining numerous specimens of *M. antillensis* from the western Atlantic, including Pilsbry's type material, we have concluded that some of the purported differences between the opercular valves of the two taxa are a function of shell morphology. In specimens attributable to *M. tintinnabulum*, the shells are usually cylindrical, with wide orifices; the tergal segments of the scuta are flat or only slightly inflected. In contrast, specimens attributable to *M. antillensis* are conic or cylindroconic, with orifices less than 1/2 the width of the bases. In these specimens the tergal segments of the scuta are broader and obliquely inflected. The differences in the length-width relationships of the tergal spurs and their distances from the basiscutal angle are highly variable,

as they are in other species of the genus. Although the "typical" *M. tintinnabulum* has been described as having the spur medial in position, it varies from twice to four or times its own width from the basiscutal angle. Specimens usually referred to *M. antillensis* commonly have the spur slightly closer to the basiscutal angle. However, when all characters of the shell and opercular valves are considered, no specific distinctions can be made between the two taxa. Consequently, we must consider *M. antillensis* synonymous with *M. tintinnabulum*.

Darwin (1854) considered pitted scuta one of the characters of young individuals, which is possibly why he thought that his specimens of var. *vesiculosus* were young. We have observed a few very small specimens of *M. tintinnabulum* in which the scutum has a very shallow median depression and a few shallow pits; however, this condition has not been observed in any but the smallest individuals of this species. In contrast, in small specimens of *M. vesiculosus*, the characteristic median furrow and accompanying pits frequently are not present. There is no question that *M. tintinnabulum* is distinct from *M. vesiculosus*.

When the type lot of *M. antillensis* was reexamined, it was found to contain two clumps of barnacles, both bearing the same museum number. One clump was identifiable as *Austromegabalanus psittacus* (Molina). As it is clear from Pilsbry's remarks (1916: 63) that only one cluster of barnacles represented the type series, the *A. psittacus* clump must have been added after his study.

Megabalanus azoricus (Pilsbry, 1916)

(figs. 1a, 3d,e, 6a-d)

Balanus tintinnabulum azoricus Pilsbry, 1916: 62, figs. 8, 11c, pl. 12 figs. 2-2b.

Megabalanus azoricus: Newman & Ross, 1976: 67.

Type. — USNM 48126, containing 17 individuals.

Type locality. — Crace, Terciera, Azores on *Patella coerulea*.

Distribution. — Azores to St. Helena Island.

Diagnosis. — Shell cylindrical; parietes finely ribbed or roughened by irregular riblets; radii wide, summits horizontal; orifice moderately wide, ovate to trigonal, greater than 1/2 basal diameter. Scutum moderately narrow, with extremely narrow tergal segment slightly inflected; growth ridges prominent, usually strongly crenulate, longitudinal striae usually prominent in intervals; articular ridge strongly reflected, 1/2 to 2/3 length of tergal margin; adductor ridge strong, acute, confluent with articular ridge; adductor muscle pit well

defined, shallow to moderately deep; lateral depressor muscle pit shallow. Tergum broad, with acute apex; spur furrow closed or nearly so; spur moderately short, separated from basiscutal angle by at least twice own width; basal margin straight on scutal side of spur, sloping on carinal side; growth ridges prominent, especially on scutal side of spur furrow, longitudinal striae weak to strongly developed in intervals; articular ridge approximately 3/4 length of scutal margin; depressor muscle crests weakly developed.

Color. — Parietes reddish or bluish purple, radii whitish or pinkish purple; sheath white or faintly pink. Scuta externally white to pink or pinkish purple, internally white or white with purple centrally. Tergum externally white or yellowish, sometimes with faint pinkish purple on scutal side of spur; internally white.

Remarks. — In addition to the type series we have examined two lots from St. Helena Island (RMNH, USNM). Most of these specimens differ from those from the Azores in having broader terga with shorter spurs. In small individuals (cr diameter 17-20 mm) the prominent longitudinal striae characteristic of the scuta of this species have not yet developed. Specimens from Ruperts Bay were on a buoy or a cable. Two specimens that were removed by a diver from the R/V Geronimo while the vessel was in port at Monrovia, Liberia, also had broad terga. This vessel had been cruising off West Africa.

Megabalanus californicus (Pilsbry, 1916)

(figs. 1d, 3f, 6e-h)

Balanus tintinnabulum californicus Pilsbry, 1916: 65, pl. 14 figs. 1-3, pl. 15 fig. 4. — Henry, 1942: 118, fig. 2a-d, pl. 4 figs. 10-12; 1960: 138. — Cornwall, 1951: 324, pl. 3 figs. D-E. — Zullo, 1968: 1, figs. 1, 2.

Megabalanus californicus: Newman & Ross, 1976: 68.

Type. — USNM 9434a, 5 individuals.

Type locality. — San Diego, California.

Distribution. — Northern California to northwest coast of Baja California, and Gulf of California.

Diagnosis. — Shell conic or cylindrical; parietes finely striate; radii moderately wide, summits horizontal; orifice large (usually greater than half basal diameter), subtriangular. Scutum with shallow longitudinal depression medially and narrow tergal segment acutely inflected; occludent margin acutely toothed; growth ridges strong, closely set; longitudinal striae clearly discernible; articular ridge approximately 4/5 length of tergal margin; adductor

ridge weak, usually confluent with articular ridge; adductor muscle pit moderately deep; lateral depressor muscle pit deep. Tergum moderately broad, with spur furrow closed or nearly so, except on spur; spur moderately short or short, separated from basiscutal angle by own width or less; basal margin straight on scutal side of spur, straight or sloping on carinal side; growth ridges moderately strong, with faint longitudinal striae in intervals; articular ridge approximately $5/6$ length of scutal margin; crests for depressor muscle weakly or moderately well developed.

Color. — Parietes red or reddish purple, striae white; radii white or pinkish, often with splotches of red or dark pink. Scutum externally pink or red, often darker marginally; internally white or pinkish, particularly near basal margin. Tergum externally pink or pinkish white, usually darker marginally and at edges of furrow; internally white or pinkish.

Remarks. — Associated with the type series of *M. peninsularis* (USNM 43486) is a small specimen with a pink shell ornamented with white ribs. This specimen, not mentioned by Pilsbry (1916) in his description of *M. peninsularis*, was subsequently identified as *M. californicus* (identifier unknown). However, the scutum resembles that of *M. coccopoma* in having a broad tergal segment, toothed occludent margin, strong and long articular ridge and acute adductor ridge. The spur furrow of the tergum is open, the scutal margin toothed, spur less than own width from basiscutal angle and the articular ridge high and very long. It is probable that the identifier placed more emphasis on the ribbed shell in assigning this specimen to *M. californicus* than to the configuration of the opercular valves. Although *M. coccopoma* is not typically ribbed, we have observed some individuals whose shells have approached the ribbed condition of this specimen.

Megabalanus clippertonensis (Zullo, 1969)

(figs. 3g, 6i-l)

Balanus tintinnabulum clippertonensis Zullo, 1969: 502, figs. 1-26.

Megabalanus clippertonensis: Newman & Ross, 1976: 68.

Type. — University of California Museum of Paleontology (UCMP) 10184; paratype: California Academy of Sciences (CAS 13584), 1 individual plus 1 empty shell.

Type locality. — Clipperton Island.

Distribution. — Known only from type locality.

Diagnosis. — Shell globuloconic, thick; parietes irregularly roughened;

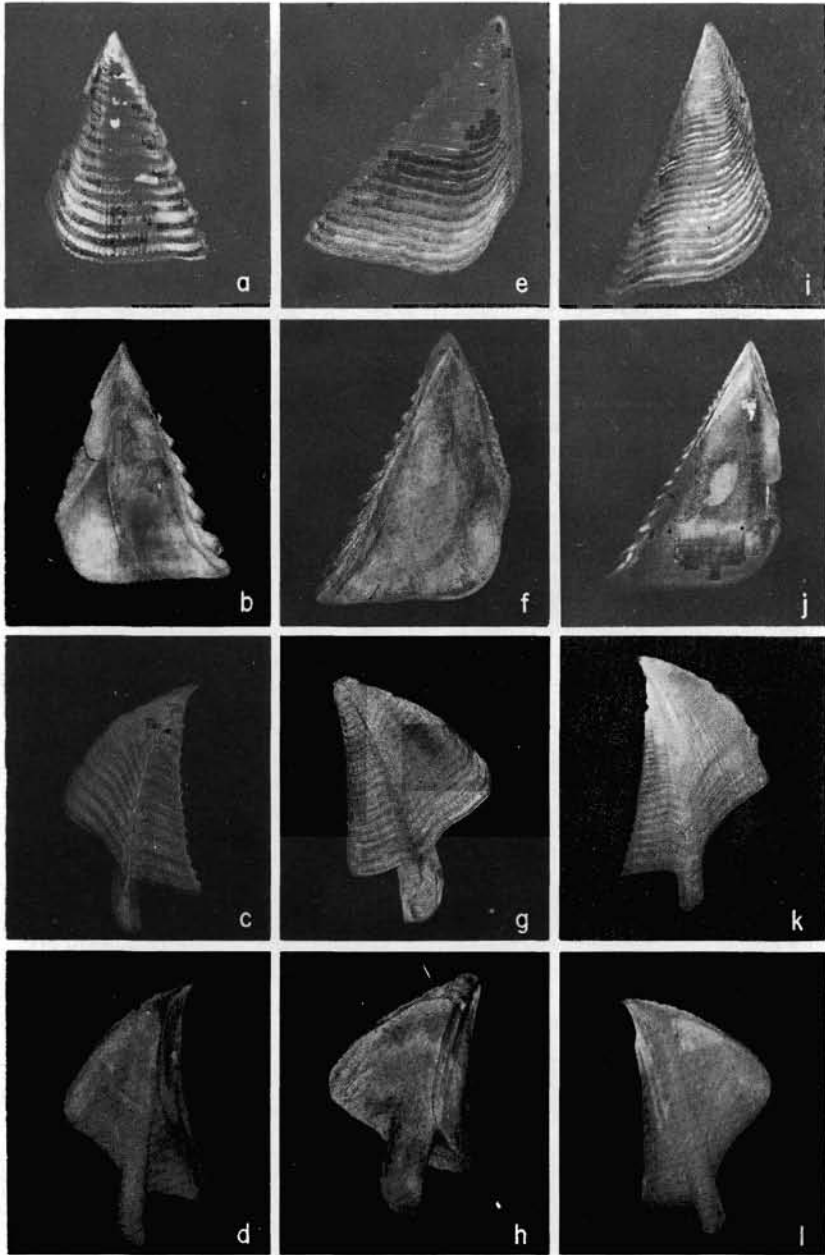


Fig. 6. *Megabalanus azoricus* (Pilsbry). a-d, external and internal views of opercular valves of syntype (USNM 48126). — *Megabalanus californicus* (Pilsbry). e-h, external and internal views of opercular valves of syntype (USNM 9434a). — *Megabalanus clippertonensis* (Zullo). i-l, external and internal views of paratype (CAS 029823). a-h \times 2.0; i-l \times 6.1.

radii moderately wide, summits horizontal; orifice approximately half basal diameter, subtriangular. Scutum concave medially, with tergal segment ill-defined, not inflected; occludent margin toothed; growth ridges strong, closely-set; longitudinal striae not distinct; articular ridge $2/3$ to $3/4$ length of tergal margin; adductor ridge absent; adductor muscle pit clearly defined, moderately deep; lateral depressor muscle pit small, deep. Tergum moderately broad, with spur furrow open; spur short, moderately narrow, separated by approximately twice own width from basiscutal angle; basal margin straight on scutal side, strongly sloping to spur on carinal side; growth ridges strong on scutal side of spur, longitudinal striae fine; articular ridge approximately $4/5$ length of tergal margin, moderately strong above, weak below; crests for depressor muscle indistinct.

Color. — Shell pinkish red to grayish red-purple, radii light to dark purple. Scutum pale pink with white articular ridge. Tergum white.

Megabalanus coccopoma (Darwin, 1854)
(figs. 3h, 7a-f)

Balanus tintinnabulum var. *coccopoma* Darwin, 1854: (? in part) 196, pl. 1 fig. d, pl. 2 figs. 1f, 1l, 1o (see remarks).

Balanus tintinnabulum coccopoma: Pilsbry, 1916: 68, pl. 16 figs. 1, 1a, 2, 2a. — Henry, 1942: 120, figs. 3a, b. — Davadie, 1963: 26, pl. 2 fig. 1. — Lacombe & Monteiro, 1974: 613, figs. 2, 3.

Megabalanus coccopoma: Newman & Ross, 1976: 67.

Type. — Lectotype herein selected, BMNH.

Type locality. — Panama.

Distribution. — Pacific Ocean: Southwest coast of Mexico to Peru and Galapagos Islands; Atlantic Ocean: vicinity of Rio de Janeiro, Brazil.

Diagnosis. — Shell globuloconic; parietes smooth, rugose or occasionally finely ribbed; radii moderately wide, summits horizontal; orifice moderately small, subovate, usually less than $1/2$ basal diameter. Scutum with very broad, obtusely inflected tergal segment; occludent margin strongly toothed; growth ridges closely set, longitudinal striae faint or absent; articular ridge approximately $4/5$ length of tergal margin; adductor ridge strong, well separated from articular ridge; adductor muscle pit shallow; lateral depressor muscle pit deep. Tergum moderately narrow, with spur furrow closed or nearly so; spur moderately long, usually separated by own width or less from basiscutal angle; basal margin usually sloping to spur on both sides, occasionally straight on one or both sides, protuberant near carinal margin; growth ridges faint to

moderately strong; longitudinal striae faint; articular ridge approximately 4/5 length of scutal margin; crests for depressor muscle moderately well developed.

Color. — Shell usually deep red, occasionally with fine white longitudinal lines or stripes; radii deep purple or reddish purple. Scutum externally purple or reddish purple with white tergal segment; internally white above, purple below. Tergum white.

Remarks. — Darwin (1854) mentioned that he had seen specimens from Mexico and California with bluish-purple rugged shells, but opercular valves exactly like those of his variety *coccopoma*. Pilsbry (1916) remarked that he had not observed this variation; however, some of our specimens of *M. coccopoma* from Ecuador agree with Darwin's description.

Pilsbry considered it quite possible that Darwin (1854) had confounded *M. coccopoma* with *M. rosa*, as he believed that *M. coccopoma* was restricted to the Panamic Faunal Province. The differences, cited by Darwin, for his China specimens are not of diagnostic significance; consequently these specimens cannot be assigned to any taxon. Xianqui & Liu (1978) recently have reported *M. rosa* from China.

Megabalanus concinnus (Darwin, 1854)

(figs. 3i, 7g-l)

Balanus tintinnabulum var. *concinnus* Darwin, 1854: 196, pl. 1 fig. e, pl. 2 fig. e. — Gruvel, 1903: 126.

Balanus tintinnabulum: Pilsbry, 1909: 65, pl. 16 fig. 3, pl. 18 figs. 5-8 [not *Balanus tintinnabulum* (Linnaeus)].

Balanus tintinnabulum concinnus: Pilsbry, 1916: 69, pl. 15 fig. 3, pl. 16 fig. 3, pl. 17 figs. 5-8.

Megabalanus concinnus: Newman & Ross, 1976: 67.

not *Balanus tintinnabulum* var. *concinnus*: Jennings, 1918: 60. (= *Megabalanus linzei*).

not *Balanus tintinnabulum concinnus*: Cranwell & Moore, 1938: 400 (= *Megabalanus linzei*).

Type. — BMNH.

Type locality. — West coast of South America.

Distribution. — Peru to Straits of Magellan.

Diagnosis. — Shell conic or globuloconic; parietes finely ribbed or weakly rugose; radii wide, summits horizontal; orifice moderately small, usually less than 1/2 basal diameter, subtriangular to subovate. Scutum with tergal segment very broad, obtusely inflected; occludent margin strongly toothed in noncorroded specimens; growth ridges strong, moderately well separated; longitudinal striae prominent; articular ridge approximately 2/3 length of tergal margin; adductor ridge long, strong, not confluent with articular ridge;

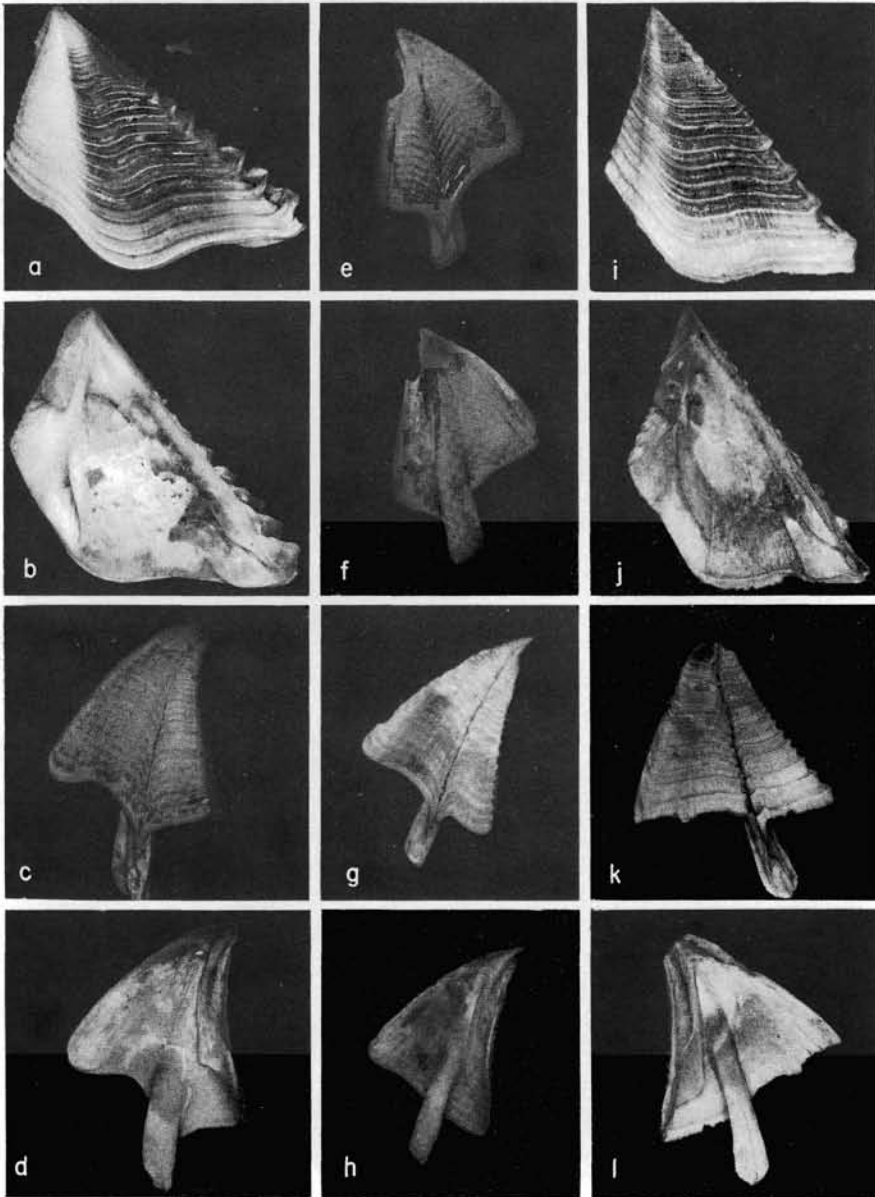


Fig. 7. *Megabalanus coccopoma* (Darwin). a-d, external and internal views of opercular valves of lectotype (Darwinian collection, BMNH); e-f, external and internal views of terga (Punta Carnero, Ecuador). — *Megabalanus concinnus* (Darwin). g-h, external and internal views of terga (Salaverry, Peru). i-l, external and internal views of opercular valves (Darwinian collection, BMNH). a-d $\times 4.3$; e-f $\times 2.8$; g-h $\times 3.1$; i-l $\times 4.0$.

adductor muscle pit well defined; lateral depressor muscle pit shallow to moderately deep; plate for rostral depressor muscle sometimes protruding below basal margin. Tergum moderately broad, with spur furrow closed or nearly so; spur long, narrow, separated by more than twice own width from basiscutal angle; basal margin straight on both sides of spur, finely denticulate; growth ridges strong; longitudinal striae prominent; articular ridge approximately 9/10 length of scutal margin; crests for depressor muscle moderately strong.

Color. — Shell reddish or bluish purple mottled with white giving a speckled appearance; radii reddish purple; sheath faintly pink. Scutum externally pinkish purple with white tergal segment, internally dull purple or white. Tergum white, occasionally pink at apex.

Remarks. — Pilsbry (1909: 65, pl. 16 fig. 3, pl. 18 figs. 5-8) referred specimens from Peru to *Balanus tintinnabulum*, remarking that they belonged to the variety referred to by Darwin (1854) as *communis*. In his subsequent monograph, Pilsbry (1916) included these same specimens in his description of *B. tintinnabulum concinnus* and reproduced his 1909 plate 18 (1916, pl. 17) of the opercular valves of this species and of *B. psittacus*. His earlier figure of the shell (Pilsbry, 1909, pl. 16 fig. 3) is not representative of *M. concinnus* and apparently for this reason Pilsbry (1916, pl. 16 fig. 3) chose to refigure the shell; however, he did include the earlier figure in his synonymy of the species.

The specimens recorded by Jennings (1918) as *B. tintinnabulum concinnus* were reexamined by Foster (1978) and found to be comparable with *Megabalanus linzei* (Foster). Although the specimens from Poor Knights Islands, New Zealand, assigned to *B. tintinnabulum* by Cranwell & Moore (1938) were not available for reexamination, Foster (1978) found that subsequent collections from that locality included only *M. linzei*; thus he concluded that all reports of *M. concinnus* from New Zealand waters and at least some of those of *M. tintinnabulum* referred to *M. linzei*.

***Megabalanus crispatus* (Schröter, 1786)**
(figs. 3j, 8a-d)

Lepas crispata Schröter, 1786: 534, pl. 9 fig. 21.

? *Lepas crispata*: Wood, 1815: 51, pl. 8 figs. 1-4 (see remarks).

Balanus tintinnabulum var. *crispatus*: Darwin, 1854 (in part): 195; not pl. 1 fig. h (= *M. volcano*).

Megabalanus crispatus: Newman & Ross, 1976: 67.

Type. — Lectotype herein designated: specimen figured by Schröter (1786) on pl. 9 fig. 21.

Type locality. — Unknown.

Distribution. — Unknown.

Diagnosis. — Shell conic; parietes roughened, with numerous spine-like projections; radii wide, summits horizontal; orifice moderately wide, approximately $1/2$ basal diameter. Scutum with moderately broad tergal segment obtusely inflected; growth ridges moderately well developed; longitudinal striae faint; articular ridge slightly more than $1/2$ length of tergal margin; adductor ridge moderately strong, not confluent with articular ridge; adductor muscle pit indistinct; lateral depressor muscle pit shallow. Tergum broad; spur furrow closed, except on spur; spur short, more than twice own width from basiscutal angle; basal margin sloping to spur on carinal side, almost straight on scutal side; growth ridges moderately well developed; longitudinal striae faint; articular ridge slightly more than $1/2$ length of scutal margin; crests for depressor muscle indistinct.

Color. — Shell bluish purple, radii bluish and white; sheath pale purple, darker on rostral half. Scutum faintly colored, tergum white.

Remarks. — Wood (1815) referred to Schröter and Bruguière in his report of *Lepas crispata*. His figures (pl. 8, figs. 1-4) do resemble the specimen of *M. crispatus* that we examined, but as the opercular valves apparently were not present, Wood's taxon can only be questionably assigned to this species.

As previously indicated, Darwin (1854) confounded two taxa under the name var. *crispatus*. Pilsbry (1916) pointed out that the specimens Darwin described with scuta having "radiating lines formed of hood-like projecting points" are probably referable to *M. volcano* and the "specimens with 'plain' scuta (that is with growth-ridges only) belong to another race". The one remaining specimen of var. *crispatus* in the British Museum's darwinian collection has "plain" scuta and does not agree with *M. volcano* in certain diagnostic characters, i.e., the external surface of the scutum of *M. crispatus* lacks prominent ornamentation, and the adductor ridge is not confluent with the articular ridge. The shell of *M. crispatus* is much more profusely spinose than the larger specimens of *M. volcano* in the type series; however, this character, as well as the breadth and inflection of the tergal segment of the scutum are strongly influenced by size.

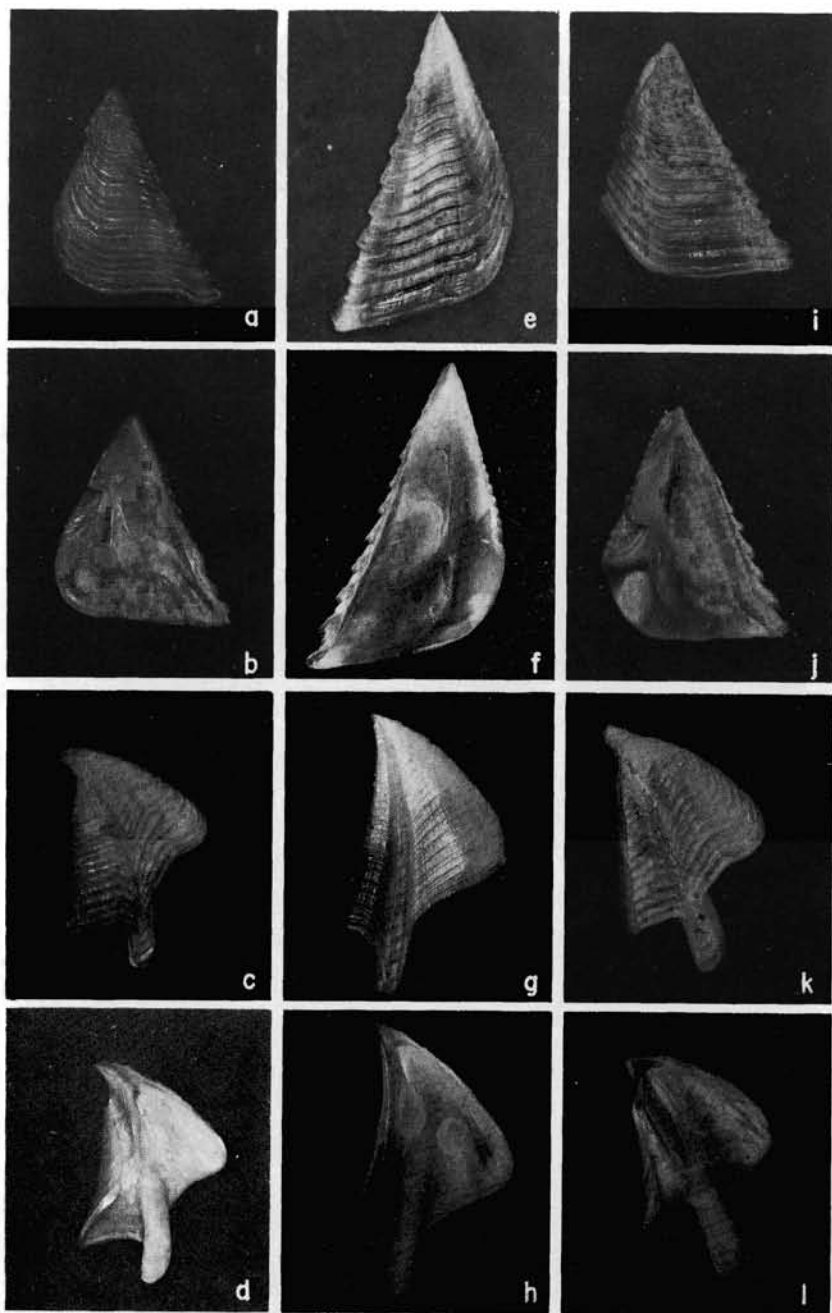


Fig. 8. *Megabalanus crispatus* (Schröter). a-d, external and internal views of opercular valves of [Darwinian collection, BMNH]. — *Megabalanus dorbignii* (Chenu). e-h, external and internal views of opercular valves (Darwinian collection, ZMC). — *Megabalanus linzei* (Foster). i-l, external and internal views of opercular valves of paratype (NMNZ Z Cr 1964). a-d, i-l $\times 2.2$; e-h $\times 4.4$.

Megabalanus dorbignii (Chenu, 1843)

(figs. 2c,e, 3k,l, 8e-h)

Balanus d'Orbignii Chenu, 1843 (in part): pl. 6 fig. 10; not pl. 4 fig. 15 (see remarks).

Balanus tintinnabulum var. *d'Orbignii*: Darwin, 1854 (in part): 196, pl. 2 figs. m, n; not pl. 1 fig. 1 (see remarks).

Balanus tintinnabulum dorbignyi: Pilsbry, 1916: 67.

Balanus tintinnabulum var. *dorbignyii*: Pilsbry, 1916: 71.

Megabalanus dorbignii: Newman & Ross, 1976: 68.

Type. — Lectotype herein designated: specimen figured by Chenu (1843) on pl. 6 fig. 10.

Type locality. — Unknown.

Distribution. — Unknown.

Diagnosis. — Shell conic, parietes ribbed, ribs often with spine-like processes; radii moderately wide, summits slightly oblique; orifice subcircular, less than 1/2 basal diameter, slightly toothed. Scutum with very narrow tergal segment acutely inflected; apex reflexed; growth ridges well separated; longitudinal striae few, faint; articular ridge long, approximately 4/5 length of tergal margin; adductor ridge weak; pit for adductor muscle clearly delineated; pit for lateral depressor muscle shallow to moderately deep. Tergum with spur furrow open, moderately deep; spur moderately short, separated from basiscutal angle by own width or less; basal margin sloping to spur on both sides, very abruptly adjacent to spur on scutal side; growth ridges low; longitudinal striae lacking; articular ridge acute, approximately 9/10 length of scutal margin; crests for depressor muscle moderately to strongly developed.

Color. — Shell bluish purple basally, white in upper third, radii white or white with longitudinal band of dark purple; sheath white or white with patches of bluish purple. Scutum dark bluish purple with apex and articular ridge white; tergum white with scutal margin externally and scutal side of spur internally deep purple.

Remarks. — Chenu (1843) cited two figures as *B. d'Orbignii*, i.e., plate 4 figure 15 and plate 6 figure 10. We, like Darwin (1854), do not believe that plate 4 figure 15 (cited by Darwin as fig. 13) represented *M. dorbignii*. However, neither Darwin's brief description of var. (11) *d'Orbignii* nor his figure of the shell (pl. 1 fig. 1) agree with either of Chenu's (1843) figures nor with the specimens remaining in the darwinian collections of the British Museum or the Zoologisk Museum. We have examined these specimens and have found that the shells do agree with Chenu's (1843) plate 6 figure 10. The terga of these specimens also agree with Darwin's (1854) figures of the tergum of var. *d'Orbignii* (pl. 2 figs. m, n). Additionally, we have found, in the

Spengler collection, several specimens that correspond in shell morphology and color with Darwin's (1854) description and figure (pl. 1 fig. 1) of var. *d'Orbignii*. As previously stated, these specimens have been referred to *Chirona amaryllis*. Thus it would appear that while Darwin identified and figured the tergum of *M. dorbignii* sensu stricto, he described and, in part, figured specimens of another species.

Megabalanus linzei (Foster, 1978)

(figs. 3m, 8i-l)

Balanus tintinnabulum var. *concinus*: Jennings, 1918: 60 (not *Balanus tintinnabulum* var. *concinus* Darwin).

? *Balanus* (*Megabalanus*) *tintinnabulum*: Withers, 1924: 24, pl. 6 figs. 4-7 [? not *Balanus tintinnabulum* (Linnaeus)].

Balanus tintinnabulum concinns: Cranwell & Moore, 1938: 400 (not *Balanus tintinnabulum concinns* Darwin).

Balanus tintinnabulum tintinnabulum: Linzey, 1942: 279 [not *Balanus tintinnabulum* (Linnaeus)].

Balanus tintinnabulum: Foster, 1967: 81, fig. 2a, b [not *Balanus tintinnabulum* (Linnaeus)].

Balanus (*Megabalanus*) *tintinnabulum linzei* Foster, 1978: 102, fig. 61, pl. 13A, B.

Type. — National Museum of New Zealand Z. Cr. 1964.

Type locality. — Cape Karikari, Poor Knights Islands, New Zealand.

Distribution. — Northeast waters of North Island, New Zealand and Norfolk and Kermadec islands.

Diagnosis. — Shell conic to globuloconic; parietes strongly ribbed, only apically in old specimens; radii moderately wide to wide; summits slightly oblique; orifice rhomboidal, greater than 1/2 basal diameter. Scutum with moderately broad tergal segment obtusely inflected; growth ridges strong; longitudinal striae few, faint; articular ridge approximately 3/4 length of tergal margin; adductor ridge weak or absent; pit for adductor muscle clearly delineated; pit for lateral depressor muscle very deep. Tergum broad, with spur furrow deep, nearly closed; spur moderately long, separated from basiscutal angle by slightly more than own width; basal margin straight on scutal side of spur, sloping on carinal side; growth ridges strong; longitudinal striae faint on scutal side; articular ridge acute, approximately 7/8 length of scutal margin; crests for depressor muscle strongly developed.

Color. — Parietes blackish purple, sometimes pink, with ribs often white or lighter pink. Radii dark pinkish purple; sheath dark bluish purple. Scutum externally reddish purple with longitudinal band of white marking tergal segment and occludent margin; internally faintly tinged with reddish purple, ar-

ticular ridge white. Tergum faint purple, at least in upper half both externally and internally.

Remarks. — As previously indicated, Foster (1978) reexamined the specimens recorded by Jennings (1918) as *Balanus tintinnabulum concinnus* and found them to actually represent *M. linzei*. Similarly, specimens collected from Poor Knights Island also were *M. linzei*; thus Foster (1978) concluded that the specimens from this locality assigned to *Balanus tintinnabulum concinnus* by Cranwell & Moore (1938) were *M. linzei*. Specimens reported by Withers (1924) as *Balanus (Megabalanus) tintinnabulum*, Foster (1978) referred, without comment, to *M. linzei*. Since Withers' (1924) specimens all lacked opercular valves, it would be impossible, as Withers himself stated, to correctly identify the "variety" to which they belonged; however, because of their occurrence in the New Zealand region, and because Withers included the Jennings' (1918) citation in his synonymy it is probable that they represent *M. linzei*. It is not clear from his remarks whether Foster actually examined specimens of Linzey's (1942) *Balanus tintinnabulum tintinnabulum*, but the collections upon which the description of *M. linzei* are based came from the same locality and exhibited the same differences from Pilsbry's (1916) description of *B. t. tintinnabulum* that were cited by Linzey.

M. linzei resembles *M. zebra* in the color of the parietes and in the darkly colored sheath. However, the prominent white ribs of *M. zebra* usually will easily distinguish this species from *M. linzei*. Although Foster (1978) only described the adductor ridge of the scutum of *M. linzei* as parallel to the articular ridge, our examination of paratypic material suggests that the adductor ridge is weak in this species. In *M. zebra* the adductor ridge is moderately strong and sometimes acute.

Megabalanus occator (Darwin, 1854)

(figs. 2d, 3n-o, 9a-d)

Balanus tintinnabulum: Spengler, 1790: 180 [not *Balanus tintinnabulum* (Linnaeus)].

Balanus tintinnabulum var. *occator* Darwin, 1854: 196, pl. 1 fig. k, pl. 2 fig. 1b.

Balanus tintinnabulum occator: Pilsbry, 1916: 59, pl. 11 figs. 1-1e. — Hiro, 1939: 260. — Kolosváry, 1950: 290, fig. 1, pl. 11 figs. a-s, pl. 12 figs. a-i, pl. 13 fig. a. — Utinomi, 1954: 22.

Megabalanus occator: Newman & Ross, 1976: 68.

Balanus (Megabalanus) xishaensis Xianqui & Liu, 1978: 123, 191, text fig. 2, pl. 2 figs. 1-9. not *Balanus tintinnabulum occator*: Zevina & Tarasov, 1963: 88, fig. 9a, b, v (= *Megabalanus volcano*).

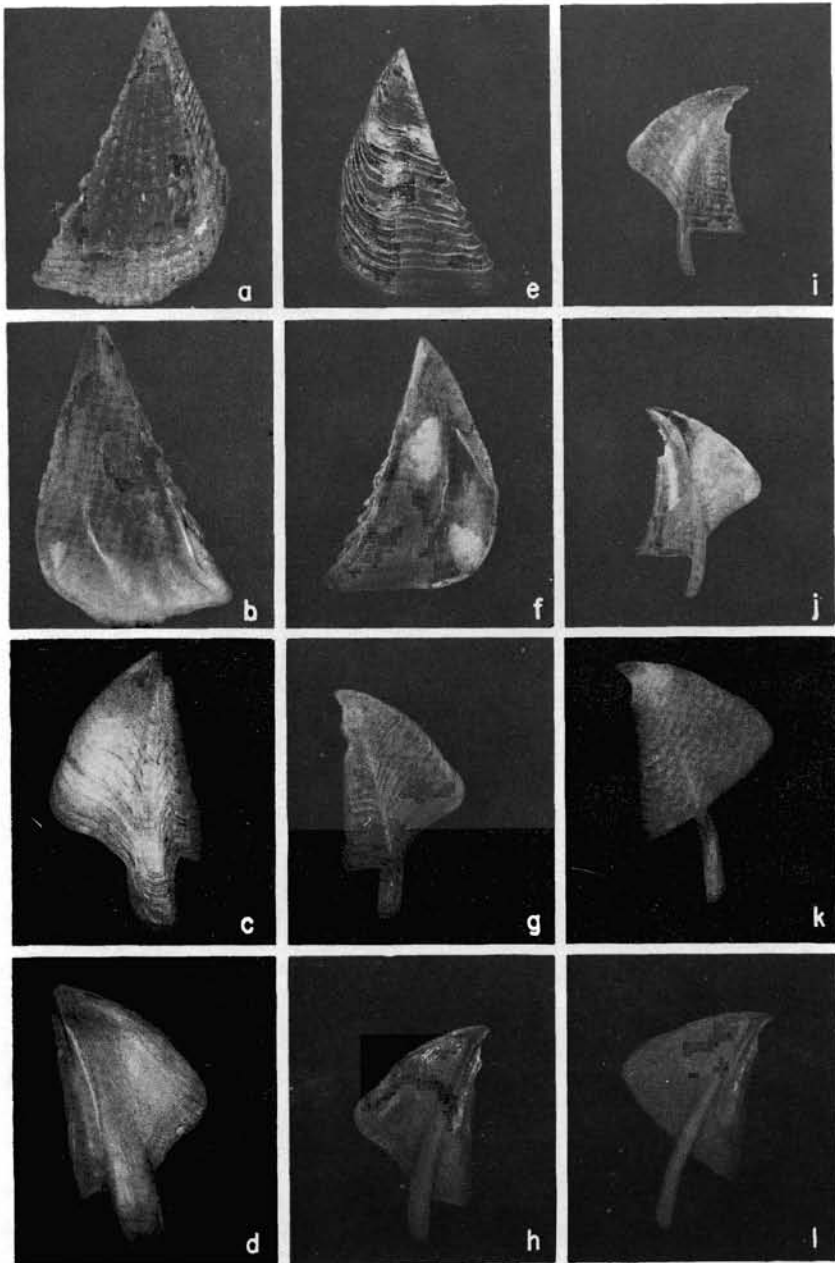


Fig. 9. *Megabalanus occator* (Darwin). a-d, external and internal views of opercular valves (Philippine Islands, USNM 52116). — *Megabalanus peninsularis* (Pilsbry). e-h, external and internal views of opercular valves of paratype (USNM 43487); i-j, external and internal view of tergum of type of "*Balanus tintinnabulum galapaganus*" Pilsbry (USNM 48003); k-l, external and internal views of tergum (Punta Carnero, Ecuador). a-d $\times 3.9$; e-h $\times 1.9$; i-j $\times 5.9$; k-l $\times 3.1$.

Type series. — Apparently no longer extant.

Type locality. — "South Seas".

Distribution. — Coasts of East China Sea, Taiwan, Mindanao (Philippines), Bonin and Fiji islands.

Diagnosis. — Shell conic or cylindroconic; parietes usually strongly ribbed, ribs often with spine-like projections; radii wide, summits usually oblique, occasionally only slightly oblique; orifice subtriangular, less than 1/2 basal diameter. Scutum with narrow tergal segment acutely inflected; occludent margin toothed; basal margin weakly crenulate, particularly in small individuals; growth ridges strong; longitudinal striae well developed, usually forming hood-like projections at intersections with growth ridges, except on tergal segments or in very small individuals; articular ridge approximately 2/3 length of tergal margin; adductor ridge absent; pit for adductor muscle shallow to moderately deep; pit for lateral depressor muscle moderately shallow. Tergum narrow to moderately broad, with spur furrow open; spur moderately long, usually narrow, separated from basiscutal angle by less than own width; basal margin straight on scutal side of spur, straight or slightly sloping on carinal side; growth ridges moderately well developed, stronger on scutal side of spur; longitudinal striae absent; articular ridge 5/6 to 7/8 length of scutal margin; crests for depressor muscle weakly developed.

Color. — Parietes pale pink or pinkish-white with longitudinal stripes of bluish or pinkish purple; radii dark bluish purple or purple; sheath bluish purple, fainter on carinal half. Scutum purplish; tergum white.

Remarks. — Although the shell of the specimen that Spengler (1790) referred to *Balanus tintinnabulum* (Linnaeus) is no longer identifiable among his collections in the Zoologisk Museum, the opercular valves were carefully stored in a hand-made wooden box. Our examination of these valves has shown that the specimen should be referred to *Megabalanus occator*.

As previously indicated, Xianqui & Liu (1978) distinguished their new species, *Balanus xishaensis*, from *M. occator* and all other species of *Megabalanus* by the presence in the former species of several teeth on the tergal spur. Although a toothed spur was not observed in the specimens of *M. occator* examined during this study, we have observed this condition in other species of *Megabalanus*, e.g., *M. tintinnabulum*, *M. rosa* and *M. zebra*, and therefore do not believe that this character is valid in differentiating species. In all other characters, *B. (M.) xishaensis* falls within the range of variation observed in *M. occator*.

Zevina & Tarasov's (1963) description and figure of *Balanus tintinnabulum occator* are clearly not of this species. Xianqui & Liu (1978) correctly assigned this taxon to *Megabalanus volcano*.

Megabalanus peninsularis (Pilsbry, 1916)
(figs. 1f,h, 2b, 4a-b, 9e-l)

Balanus tintinnabulum peninsularis Pilsbry, 1916: 66, pl. 15 figs. 1-2d. — Henry, 1941: 102, pl. 13 figs. 6-9; 1942: 120, fig. 3a, b. — Kolosváry, 1939: 92, fig. 1 (see remarks).

Balanus tintinnabulum galapaganus Pilsbry, 1916: 70, pl. 12 figs. 1, 1a, 1b.

Megabalanus galapaganus: Newman & Ross, 1976: 68.

Megabalanus peninsularis: Newman & Ross, 1976: 68.

not *Balanus tintinnabulum peninsularis*: Nilsson-Cantell, 1927: 783, fig. 18a, b (= *Megabalanus volcano*).

Holotype. — USNM 43486; paratypes: 2 clumps, 45 + individuals.

Type locality. — Cape St. Lucas, Lower California.

Distribution. — Northwest Mexico to Ecuador, Malpelo and Galapagos islands.

Diagnosis. — Shell conic to cylindrical; parietes rugose to strongly ribbed, frequently with spines or spine-like projections; radii moderately wide, summits horizontal; orifice small and oval to moderately large and subtriangular. Scutum with narrow tergal segment slightly inflected; growth ridges prominent; longitudinal striae usually lacking, occasionally faint; articular ridge 1/2 to 2/3 length of tergal margin; adductor ridge well developed, not confluent with articular ridge; pit for adductor muscle shallow to moderately deep; pit for lateral depressor muscle very shallow or absent. Tergum moderately wide, with spur furrow closed; spur moderately short to very long, usually narrow, sometimes extremely so, separated from basiscutal angle by 2 to 4 times spur width; basal margin generally straight on both sides of spur; growth ridges strong, moderately closely spaced; longitudinal striae frequently well developed, particularly on scutal side; articular ridge 1/2 to 2/3 length of scutal margin; crests for depressor muscle usually lacking, occasionally weakly developed in large individuals.

Color. — Parietes usually reddish to bluish purple, sometimes pinkish or red in small individuals; radii purplish white to dark purple; sheath white, sometimes tinged with purple. Scutum reddish or bluish purple, articular ridge white; tergum white.

Remarks. — Pilsbry (1916) described *B. t. peninsularis* from a series of specimens from a single locality off Baja California, Mexico. In the same publication, he described the subspecies *B. t. galapaganus* from a single locality off the Galapagos Islands. We have examined the two paratypic clusters of *M. peninsularis* and the type series of *M. galapaganus*. The *M. peninsularis* material consists of approximately 45 specimens with shells between 15 and 22 mm in diameter, generally cylindrical and dull bluish or reddish purple. Although there are over sixty individuals in the type series of *M. galapaganus*,

none exceed 15 mm in diameter and most lack opercular valves. As previously stated, Pilsbry compared the Galapagos taxon with the nominal subspecies, *tintinnabulum*, and with the subspecies, *concinus* and *coccpoma*, but not with *M. peninsularis*. We have examined several hundred lots of *M. peninsularis* over its entire geographic range and have found it to be highly variable. The shell color varies from red or pink in very small individuals to reddish or bluish purple in larger individuals. Local populations exhibit striking differences from the type series; however, a continuum in morphological characters has been observed. *M. galapaganus* falls well within this range, and we have not been able to find any characters by which this taxon can be distinguished from *M. peninsularis*. Therefore we must conclude that *M. galapaganus* is not a distinct species.

Kolosváry's (1939) specimens were reputed to be from the South Pacific Ocean, a locality which is doubtful for this species.

Megabalanus rosa (Pilsbry, 1916)

(figs. 4c, 10a-d)

Balanus tintinnabulum rosa Pilsbry, 1916: 61. — Hiro, 1932: 549, fig. 3a, b; 1937: 431, fig. 19b.

— Nilsson-Cantell, 1932: 16, text fig. 6, pl. 1 fig. 3.

Balanus (Megabalanus) tintinnabulum rosa: Tarasov & Zevina, 1957: 164, frontispiece B, figs. 55, 56. — Utinomi, 1970: 349, pl. 18 fig. 7.

Balanus (Megabalanus) rosa: Yamaguchi, 1973: 130, fig. 10, pl. 6 figs. 1a-j, 3, 6, 7, pl. 7 figs. 3a, 4b, pl. 8 figs. 1-2b. — Xianqui & Liu, 1978: 127, text-fig. 4, pl. 1 figs. 17-21.

Megabalanus rosa: Newman & Ross, 1976: 68.

Type series. — USNM 43494, 25 individuals, all lacking opercular valves.

Type locality. — Azabu, Japan.

Distribution. — Japan to China and Taiwan.

Diagnosis. — Shell conic; parietes smooth; radii moderately wide, summits horizontal; orifice usually greater than 1/2 basal diameter. Scutum with narrow tergal segment acutely inflected; occludent margin toothed; basal margin slightly sinuous; growth ridges strongly developed, rather widely separated; longitudinal striae usually lacking, occasionally faint; articular ridge 2/3 to 3/4 length of tergal margin; adductor ridge blunt or acute, confluent with articular ridge, often extending nearly to basal margin; pit for adductor muscle shallow; pit for lateral depressor muscle moderately deep, sometimes with moderately well developed crests. Tergum moderately broad with spur furrow closed or nearly so; spur short, moderately broad, separated from basiscutal angle by own width or more; basal margin straight or slightly sloping on both

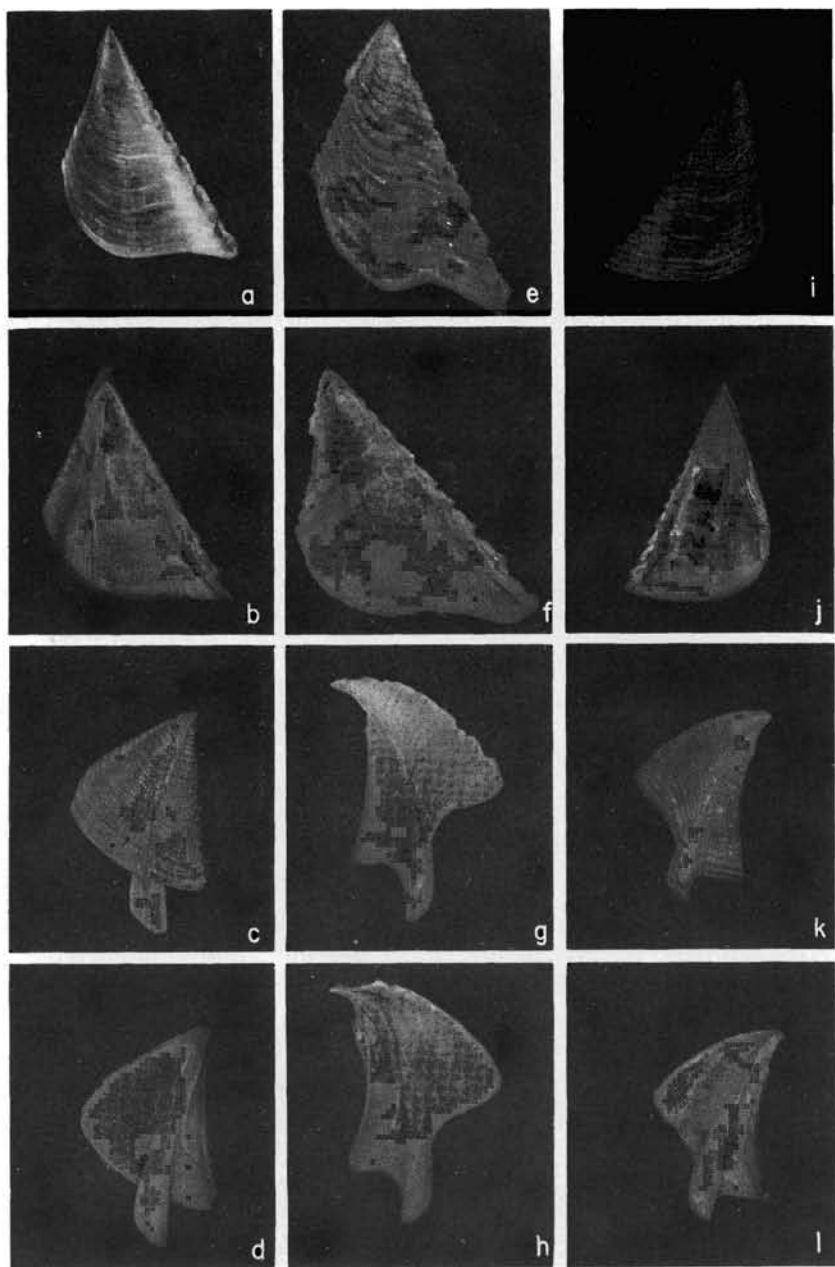


Fig. 10. *Megabalanus rosa* (Pilsbry). a-d, external and internal views of opercular valves (Japan, USNM 177932). — *Megabalanus spinosus* (Bruguière). e-h, external and internal views of opercular valves (Darwinian collection, BMNH). — *Megabalanus tanagrae* (Pilsbry). i-l, external and internal views of opercular valves (Hookena, Hawaii). a-d $\times 3.9$; e-h $\times 1.9$; i-j $\times 5.9$; k-l $\times 3.1$.

sides of spur; growth ridges strong, widely separated; longitudinal striae very faint or absent; articular ridge $3/4$ to $4/5$ length of scutal margin; crests for depressor muscle weakly developed.

Color. — Parietes pinkish red to reddish purple, occasionally entirely white; radii slightly darker than parietes except in white individuals; sheath reddish, pinkish purple or white. Scutum pinkish purple and white; tergum pinkish purple to white.

Remarks. — The type series of *Megabalanus rosa* all lacked opercular valves; consequently, Pilsbry (1916) briefly described, but did not figure, the opercular valves from a series of small individuals from another locality in Japan. In his description, he called attention to the short spur of the tergum. However, in his diagnosis of *M. rosa*, Yamaguchi (1973) stated that the spur was wide and in his description, referred to it as long. In the moderately large specimens that we have examined, the spur appeared short in relation to its breadth.

***Megabalanus spinosus* (Bruguière, 1789)**

(figs. 4d, 10e-h)

Lepas spinosa, echinata, tubulis et spinis circumstipata Chemnitz, 1785: 317, pl. 98 fig. 840, pl. 99 fig. 841.

Balanus spinosus Bruguière, 1789: 167.

Lepas echinata Spengler, 1790: 177.

Lepas echinata var. a: Spengler, 1790: 179.

Lepas spinosa: Gmelin, 1791: 3213.

Lepas spinosa: Wood, 1815 (in part): pl. 7 figs. 4, 5 (not large shell shown on figure 4) (see remarks under *M. tintinnabulum*).

Balanus tintinnabulum var. *spinosus*: Darwin, 1854: 196, pl. 1 fig. i. — Hoek, 1883: 148.

Balanus tintinnabulum spinosus: Pilsbry, 1916: 58, fig. 10. — Stubbings, 1961: 184, figs. 2, 3.

Megabalanus spinosus: Newman & Ross, 1976: 68.

not *Balanus tintinnabulum spinosus*: Lacombe & Monteiro, 1975: 635, 641 (= *Megabalanus vesiculosus*).

Type. — Lectotype herein designated: the specimen figured by Chemnitz (1785) on pl. 98 fig. 840.

Type locality. — Unknown.

Distribution. — Principe, São Tomé and Annobon islands; Gulf of Guinea.

Diagnosis. — Shell conic or globuloconic; parietes thin, ribbed, usually with spine-like projections or strong, upturned spines; radii wide, summits horizontal; orifice circular to subtriangular. Scutum with moderately broad tergal segment obliquely inflected; basal margin slightly sinuous; growth ridges moderately strong, widely spaced; longitudinal striae fine; articular

ridge approximately $3/4$ length of tergal margin; adductor ridge acute, reaching nearly to basal margin, confluent with articular ridge; pits for adductor muscle and lateral depressor muscle moderately shallow. Tergum narrower than scutum, apex protuberant; spur furrow open; spur moderately short, slightly more than own width from basiscutal angle; basal margin strongly sloping to spur on scutal side, straight or slightly concave on carinal side; growth ridges moderately strong, usually widely separated; longitudinal striae faint; articular ridge approximately $3/4$ length of scutal margin; crests for depressor muscle indistinct or lacking.

Color. — Shell whitish to reddish or bluish purple, with white to purple ribs and spines; radii white or tinged with reddish purple. Scutum dull purple to light pink; tergum opaque or white.

Remarks. — Both Bruguière (1789: 167) and Gmelin (1791: 3213) referred to the figures of Chemnitz's (1785, pl. 98 fig. 840, pl. 99 fig. 841) *Lepas spinosa*, *echinata*, *tubulis et spinis circumstipata* in their descriptions of *M. spinosus*. Darwin (1854: 195) cited *Lepas spinosa* Gmelin, but not *Balanus spinosus* Bruguière, thus crediting Gmelin (1791) with authorship of this species. However, in his synonymy of *Balanus perforatus* Bruguière, Darwin (1854: 231) cited both Bruguière's ("1789, pl. 164 fig. 12 *infra*") *Balanus perforatus* and Gmelin's ("1879") *Lepas angusta* in his synonymy of the species. Darwin (1854) remarked that while he had no means of ascertaining the priority of the two publications "within the same year", he was selecting Bruguière's name as the better known. In view of Darwin's reference only to Bruguière's figure of *B. perforatus*, it would appear that he had not seen Bruguière's (1789) text. Bruguière's description of *B. perforatus* appears on the same page as his description of *M. spinosus* (P. 167). Bruguière's contribution to the "Encyclopédie méthodique" was published in two parts, with part 1 appearing in 1789 (pp. 1-344) and part 2 in 1792 (pp. 345-758); therefore, it is clear that Bruguière must be credited with authorship of both species.

Megabalanus spinosus, because of its usually spinose parietes and generally striking appearance, was recognized and figured by several early naturalists, but surprisingly few specimens have actually been examined. Stubbings (1963) gave the first description of the animal. The specimens identified as *B. tintinnabulum spinosus* by Lacombe & Monteiro (1975) were subsequently shown by McLaughlin & Lacombe (1979) to represent *Megabalanus vesiculosus*. The latter authors compared not only the characters of the shells and opercular valves but the animals of the two species and cited numerous characters which separate them; however, their comparisons were based on descriptions of *M. spinosus* from the literature. Now, having examined the darwinian collections

of *M. spinosus* from the British Museum and the Zoologisk Museum, it is possible to compare the two species more accurately. The exterior of the scutum of *M. spinosus* was described by Darwin (1854) as smooth; the growth ridges are not as strongly developed and are more widely separated than those of *M. vesiculosus*. Although the slightly sinuous basal margin of the scutum of *M. spinosus* gives the appearance of an external longitudinal groove being present, a groove such as is seen in the scutum of *M. vesiculosus*, is not developed. The tergum is much narrower than the tergum of *M. vesiculosus*.

Megabalanus tanagrae (Pilsbry, 1928)

(figs. 1g, 4e, 10i-l)

Balanus tintinnabulum tanagrae Pilsbry, 1928: 311, pl. 25 figs. 5-8. — Zullo, 1969: 509.

Megabalanus tanagrae: Newman & Ross, 1976: 68.

Type. — Bernice P. Bishop Museum (BPBM) 500.

Type locality. — Necker Island, Hawaiian Islands.

Distribution. — Hawaii to Marshall islands.

Diagnosis. — Shell conic; parietes roughened or finely ribbed, occasionally with spinose projections; radii moderately wide, summits horizontal; orifice moderately small, usually less than 1/2 basal diameter. Scutum with very narrow tergal segment slightly inflected; growth ridges prominent; longitudinal striae faint or absent; articular ridge 3/4 to 5/6 length of tergal margin; adductor ridge low, confluent with articular ridge; pit for adductor muscle moderately deep; pit for lateral depressor muscle large, usually shallow. Tergum approximately as wide as scutum, with spur furrow open, shallow; spur short, separated from basiscutal angle by own width to twice own width; basal margin straight on scutal side of spur, sloping on carinal side; growth ridges strong, at least on scutal side; longitudinal striae absent or occasionally faint; articular ridge 3/4 to 4/5 length of scutal margin; crests for depressor muscle weakly developed.

Color. — Parietes pinkish to bluish purple, ribs and spines similarly colored, radii darker; sheath white, tinged with purple in carinal half. Scutum light to dark bluish purple or white; tergum white.

Remarks. — *M. tanagrae* removed from seawater lines (6 inch PVC) at Kewalo Marine Laboratory, Honolulu, reached 40 mm in carinorostral diameter. The shells are thin and fragile; the lavender parietes are finely ribbed and/or finely spinose, except near the apex.

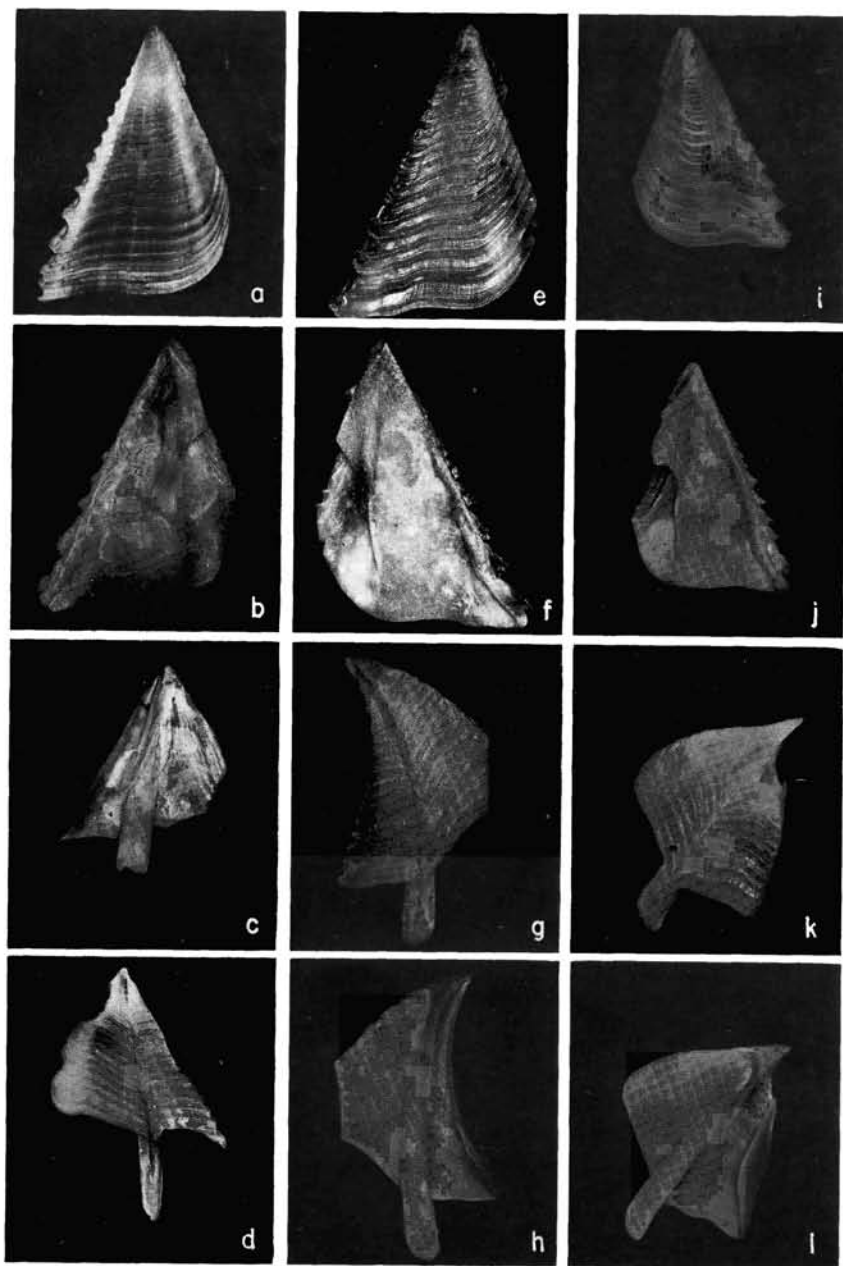


Fig. 11. *Megabalanus validus* (Darwin). a-c, external and internal views of opercular valves of lectotype (Darwinian collection ZMC); d, external view of tergum of paralectotype (Darwinian collection, ZMC); e-h, external and internal views of scutum and tergum (Hoek's Siboga material, ZMA). — *Megabalanus vesiculosus* (Darwin). i-l, external and internal views of opercular valves (Baia de Guanabara, Brazil). a-d $\times 2.1$; e-h $\times 4.2$; i-l $\times 4.4$.

Megabalanus validus (Darwin, 1854)
(figs. 4f, 11a-h)

Balanus tintinnabulum var. *validus* Darwin, 1854: 195, pl. 1 figs. c, f infra. — Hoek, 1913: 164, pl. 13 figs. 16-18, pl. 14 figs. 1-4.

Megabalanus validus: Newman & Ross, 1976: 69.

Type. — Lectotype herein selected: Zoologisk Museum, Copenhagen.

Type locality. — Unknown.

Distribution. — Malay Archipelago.

Diagnosis. — Shell tubuloconic to cylindrical; parietes rugose or coarsely ribbed, ribs flexuous; radii wide, summits horizontal; orifice subtriangular, less than 1/2 or 1/2 basal diameter. Scutum with moderately broad tergal segment obtusely inflected; growth ridges prominent on lower half, sometimes becoming obsolete apically; longitudinal striae well developed; articular ridge approximately 1/2 length of tergal margin; adductor ridge weak, usually represented by thickening of middle part of valve; pit for adductor muscle moderately deep; pit for lateral depressor muscle shallow to moderately deep. Tergum moderately broad with spur furrow closed; spur long, narrow, separated from basiscutal angle by 3 to 4 times spur width; basal margin straight or sloping on either side of spur; growth ridges low, not prominent; longitudinal striae lacking; articular ridge 3/4 to 4/5 length of scutal margin; crests for depressor muscle moderately well developed.

Color. — Parietes pinkish red, reddish purple or light to dark chocolate-purple, with irregular white longitudinal stripes or ribs, sometimes also with red longitudinal lines; radii dark bluish purple or purple; sheath dark purple basally. Scutum externally reddish purple at least basally, white above and on occludent margin and usually 1 or 2 darker purple stripes; internally dull white with splotches of purple; tergum externally reddish purple except for white spur, internally dull purple except for white spur.

Remarks. — No specimens of *M. validus* remain in the darwinian collection of the British Museum (G. Boxshall, personal communication). However, three specimens, each bearing the label "var. *validus*" in Darwin's handwriting, are in the collection of the Zoologisk Museum. Since it is obvious from his remarks that he examined several specimens of this species (Darwin, 1854: 201), it is reasonable to assume that the specimens in the Zoologisk Museum darwinian collection were among those upon which he based his description of this taxon. None of these specimens has a complete set of opercular valves; however, the lectotype selected has a pair of scuta and one tergum. One paralectotype has one tergum completely intact, but is missing

the scuta; the other has a pair of scuta and a broken tergum. We have also identified several shells, without opercular valves, from the Spengler collection.

Hoek's (1913) report of var. *validus* was devoted primarily to a description of the animal and thus could not be compared with Darwin's diagnosis. We have been able to examine a pair of opercular valves from Hoek's specimen and have confirmed the identity of this individual as *Megabalanus validus*.

***Megabalanus vesiculosus* (Darwin, 1854)**

(figs. 1c, 4g, 11i-l)

Balanus tintinnabulum var. *vesiculosus* Darwin, 1854: 195, pl. 2 fig. 1h.

Balanus tintinnabulum var. 3: Lacombe & Monteiro, 1975: 635, fig. 1.

Balanus tintinnabulum spinosus: Lacombe & Monteiro, 1975: 635, 641 [not *Balanus tintinnabulum spinosus* (Bruguère)].

Megabalanus vesiculosus: Newman & Ross, 1976: 69. — Mc Laughlin & Lacombe, 1979: 37, figs. 1-15.

Type. — Apparently no longer extant.

Type locality. — Unknown.

Distribution. — Brazil.

Diagnosis. — Shell conic, globuloconic or subcylindric; parietes ribbed, ribs usually with spine-like projections; radii moderately wide to wide, summits subhorizontal; orifice moderately small, usually less than 1/2 basal diameter. Scutum usually with median, broad, deep, pitted longitudinal groove; tergal segment narrow, obtusely inflected; basal margin slightly sinuous; occludent margin toothed; growth ridges strong; longitudinal striae faint or lacking; articular ridge usually greater than 1/2 tergal margin; adductor ridge acute, confluent with articular ridge, extending nearly to or to basal margin; pit for adductor muscle shallow; pit for lateral depressor muscle moderately well delineated. Tergum broad, with spur furrow closed or nearly so; spur moderately short, separated from basiscutal angle by approximately 4 times spur width; basal margin sloping to spur on both sides; growth ridges moderately well developed; longitudinal striae present; articular ridge 3/4 to 4/5 length of scutal margin; crests for depressor muscle moderately weak.

Color. — Shell bluish or pinkish purple, at least in lower half, sometimes with white longitudinal striations; ribs and spines generally white; radii usually purple, occasionally white tinged with purple; sheath white or faintly colored. Scutum pink to purple; tergum white with purplish splotches.

Remarks. — As previously indicated, Darwin (1854) thought that

Megabalanus vesiculosus was probably the juvenile form of *M. tintinnabulum*. However, several characters clearly separate this species from *M. tintinnabulum*. In particular, the pitted scutum is not a juvenile character in *M. vesiculosus*; it is best developed in older, larger individuals. The parietes of *M. tintinnabulum* frequently are slightly roughened or weakly plicated in small and medium-sized individuals, but spinose ribs are not developed. *M. tintinnabulum* reaches a very large size, whereas *M. vesiculosus* appears never to reach a comparable size, and the parietes of the largest specimens examined have spinose ribs. The characters that distinguish *M. vesiculosus* from *M. spinosus* have been discussed under the latter species.

Megabalanus volcano (Pilsbry, 1916)
(figs. 4h-i, 12a-d)

- Balanus tintinnabulum* var. *crispatus*: Darwin, 1854: 195 (in part; not *Lepas crispatus* Schröter; see remarks under *M. crispatus*, p. 29).
 ? *Balanus tintinnabulum* var. *communis*: Krüger, 1911: 46, pl. 3 figs. 31a₁-b₂ (not *Balanus tintinnabulum* var. *communis* Darwin) (see remarks).
Balanus tintinnabulum volcano Pilsbry, 1916: 60, pl. 11 figs. 2-2c. — Nilsson-Cantell, 1932: 19, figs. 7a-e. — Hiro, 1937: 430, fig. 19a.
Balanus tintinnabulum peninsularis: Nilsson-Cantell, 1927: 783, fig. 18a, b (not *Balanus tintinnabulum peninsularis* Pilsbry).
Balanus (Megabalanus) tintinnabulum volcano: Tarasov & Zevina, 1957: 165. — Utinomi, 1970: 350, pl. 18 fig. 6.
Balanus tintinnabulum occator: Zevina & Tarasov, 1963: 89, fig. 9 (not *Balanus tintinnabulum occator* Darwin).
 ? *Balanus (Megabalanus) volcano*: Yamaguchi, 1973: 133, text-fig. 11, pl. 6 figs. 2a-j, 4, 5, pl. 7 figs. 1a-2b, pl. 8 figs. 1-2b (see remarks).
Megabalanus volcano: Newman & Ross, 1976: 69.
Balanus (Megabalanus) volcano: Xianqui & Liu, 1978: 125, text-fig. 3, pl. 1 figs. 6-16.

Type. — USNM 43488.

Type locality. — Japan.

Distribution. — Japan and China.

Diagnosis. — Shell conic; parietes roughened, frequently with numerous small spines or spine-like projections; radii moderately wide, summits horizontal; orifice rhomboidal or subtriangular, less than 1/2 basal diameter. Scutum with narrow tergal segment slightly inflected in small to medium sized individuals, moderately broad and obtusely inflected in large individuals; growth ridges prominent, strongly scalloped by well developed longitudinal striae; articular ridge approximately 2/3 to 3/4 length of tergal margin; adductor ridge prominent, often acute, confluent with articular ridge; pits for adductor and lateral depressor muscles shallow. Tergum moderately broad,

with spur furrow closed; spur moderately long and narrow, separated from basiscutal angle by own width to twice own width; basal margin usually straight on scutal side of spur, slightly sloping on carinal side; growth ridges prominent, at least on scutal side; longitudinal striae fine; articular ridge 3/4 to 4/5 length of scutal margin; crests for depressor muscle moderately well developed.

Color.— Parietes dull reddish or bluish purple or grayish purple; radii similar in color. Scutum pink or pinkish to bluish purple externally, white tinged with purple internally; tergum white.

Remarks. — The type material of *M. volcano* (USNM 43488) has two sets of opercular valves, in addition to the shell (Pilsbry, 1916, pl. 11 fig. 2d). Representatives of both sets (pl. 11 figs. 2, 2b and 2a, 2c, 2e, respectively) were figured by Pilsbry. The scutum of the larger pair (fig. 2b) has a moderately broad tergal segment obtusely inflected, whereas the tergal segment of the single scutum of the smaller set (fig. 2a) is narrow and only slightly inflected. Our figure of the external view of the larger scutum (fig. 12a) clearly shows the obtusely inflected, moderately broad tergal segment. The scuta of the paratype (USNM 52117), also a large specimen, similarly have moderately broad and obtusely inflected tergal segments. It would appear that Pilsbry's (1916: 60) description of a "flat" scutum in *M. volcano* was based on the scutum of the smaller set accompanying the type. We have examined both sets of valves carefully and are confident that the larger set belongs to the type shell.

As previously remarked, Krüger's (1911) *Balanus tintinnabulum* var. *communis* is not Darwin's (1854) taxon. Hiro (1932) referred it to *Balanus tintinnabulum* *rosa*, but remarked that *B. t. volcano* was closer to "var. *communis*". Subsequently he (Utinomi, 1958) cited Krüger's (1911) taxon in the synonymy of *B. t. volcano*. Krüger did not describe his specimens, and his illustrations are diagrammatic. Although the short spur figured resembles *M. rosa* and *M. crispatus*, the presence of apparent crests for the depressor muscle of the tergum and the general shape of the scutum suggest the referral to *M. volcano*.

Nilsson-Cantell (1927) assigned specimens from Japan to *M. peninsularis* because the shells bore spines similar to those described by Pilsbry (1916) for *M. peninsularis*. As this species is endemic to the western coast of Central and South America (including the Galapagos Islands), it is most improbable that Nilsson-Cantell correctly identified these specimens. The figures of the opercular valves presented by Nilsson-Cantell (1927) strongly suggest that he actually had specimens of *M. volcano*.

Zevina & Tarasov (1963) illustrated but only very briefly described the oper-

cular valves of the specimens that they referred to *M. occator*. Their illustration of the exterior of the scutum (fig. 9a) shows a moderately broad tergal segment, obtusely inflected; the tergal segment of *M. occator* is narrow and acutely inflected. Although they did not describe nor illustrate the spur furrow, (open in *M. occator*, closed in *M. volcano*), their figure of the tergum (fig. 9v) clearly is not that of *M. occator*. Therefore, we concur with Xianqui & Liu (1978) that this specimen should be referred to *M. volcano*.

Yamaguchi's (1973) description of the scutum of *M. volcano* is difficult to understand. Although he described the surface as smooth with faint growth ridges and very weak longitudinal striations, he adds "Folding of the projecting portions of ridges develops at each intersection between faint growth ridges and longitudinal striations." The latter statement might be his way of saying "ribs prominent on growth ridges, which are deeply scalloped by them" (Pilsbry, 1916: 60). However, his figures of the scuta (pl. 6 figs. 2c, 2e) do not show the prominent growth ridges and longitudinal striations characteristic of *M. volcano*. They resemble *M. crispatus* in this character, but differ from that species in the adductor ridge being confluent with the articular ridge. The tergal spur in small specimens of *M. volcano* is longer and narrower than in large specimens; thus the terga illustrated by Yamaguchi [pl. 6 figs. 2g-j (cited as scuta in the figure legend)] are within the expected range of variation for this species.

Megabalanus zebra (Darwin, 1854)
(figs. 2f, 4j-k, 12e-l)

Balanus tintinnabulum var. *zebra* Darwin, 1854: 195, pl. 1 fig. g. — Karande & Palekar, 1966: 143, pl. 1 fig. 2.

Balanus tintinnabulum zebra: Pilsbry, 1916: 57, pl. 10 figs. 2-3. — Hiro, 1939: 259. — Davadie, 1963: 26, pl. 2 fig. 6. — Stubbings, 1967: 264.

Megabalanus zebra: Newman & Ross, 1976: 69.

Type series. — BMNH.

Type locality. — Unknown.

Distribution. — Atlantic Ocean: west coast of Africa; Indian Ocean: Bombay, Thailand.

Diagnosis. — Shell conic or tubuloconic; parietes with well developed ribs, acute in small individuals, often obsolescent in large individuals; radii wide, summits horizontal; orifice 1/3 to 2/3 basal diameter. Scutum with narrow tergal segment slightly inflected; growth ridges moderately prominent to prominent; longitudinal striae well developed, at least on basal half; articular

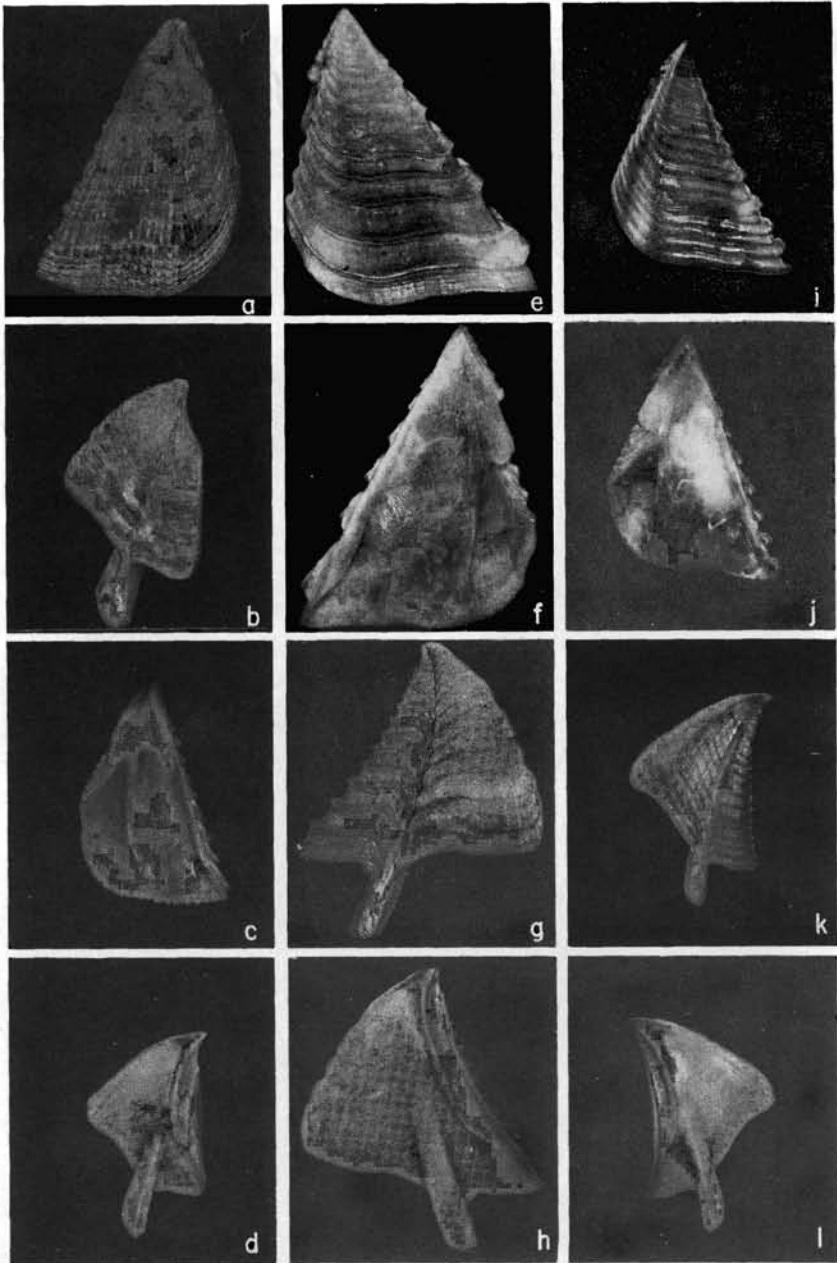


Fig. 12. *Megabalanus volcano* (Pilsbry). a-b, external views of scutum and tergum of type (USNM 43488); c-d, internal views of scutum and tergum of paratype (USNM 43488) [opposing views of opercular valves figured by Pilsbry (1916, pl. 11 figs. 2, 2b, 2a, 2c)]. — *Megabalanus zebra* (Darwin). e-h, external and internal view of opercular valves (Darwinian collection, BMNH); i-l, external and internal views of opercular valves (Darwinian collection, ZMC). a-d $\times 1.4$; e-h $\times 5.6$; i-l $\times 3.0$.

ridge strong, approximately $2/3$ length of tergal margin; adductor ridge sometimes acute, often thickened, not confluent with articular ridge; pit for adductor muscle shallow; pit for lateral depressor muscle moderately deep, often with longitudinal crests. Tergum approximately as wide as scutum; spur furrow closed or nearly so; spur moderately long, separated from basiscutal angle by $1\ 3/4$ to twice own width; basal margin relatively straight on scutal side of spur, sloping on carinal side; growth ridges prominent, particularly on scutal side; longitudinal striae fine; articular ridge $3/4$ to $4/5$ length of scutal margin; crest for depressor muscle prominent.

Color. — Parietes reddish or bluish purple with white ribs, frequently also with fine white transverse striae; radii and sheath dark purple to "madder" brown. Scutum externally yellowish white to pink or purple, sometimes with 1 or 2 darker longitudinal stripes near tergal segment, occasionally with white tergal segment; internally white tinged with pink or purple; tergum white, externally sometimes tinged with pink or purple, particularly on scutal margin.

Remarks. — Among the specimens included under USNM catalog number 43489 is a small specimen of *M. zebra* with the accompanying notation "pl. 10 fig. 3a". This figure is also cited at the bottom of the legend for plate 10 (Pilsbry, 1916: 340); however, figure 3a was not included on this plate.

Pilsbry's description of specimens of *Megabalanus zebra* was brief. He did not figure the opercular valves, but stated that they resembled those of *M. tintinnabulum*. The principal character by which he differentiated *M. zebra* from all other species (as subspecies) of the *tintinnabulum* group was the color of the sheath, which he described as rich "madder" brown. As Pilsbry had not seen representatives of *M. validus*, he was unaware that this species also has a dark colored (purple to brown) sheath. Not only in sheath coloring, but in the ribbed shell, *M. validus* closely resembles *M. zebra*. However, several characters, e.g., the inflection of the tergal segment of the scutum and the position of the spur, readily differentiate the two species.

***Megabalanus ajax* (Darwin, 1854)**

(figs. 4l, 13a-d)

Balanus tintinnabulum: Chenu, 1843 (in part): pl. 2 fig. 8 [not *Balanus tintinnabulum* (Linnaeus)].

Balanus ajax Darwin, 1854 (in part): 214, pl. 3 figs. 1a-d (see remarks). — Pilsbry, 1916: 74. — Nilsson-Cantell, 1938: 34, fig. 6.

Megabalanus ajax: Newman & Ross, 1976: 67.

Type. — Lectotype herein selected: BMNH.

Type locality. — Philippine Archipelago, attached to *Millepora complanata* Lamarck, 1816.

Distribution. — Indian Ocean: Maldive, Seychelles and Chagos islands; Pacific Ocean: Philippines, Solomon Islands, New Caledonia and Japan.

Diagnosis. — Shell globuloconvex, extremely massive and heavy, sometimes elongated in carinorostal axis; parietes smooth; radii moderately wide, summits horizontal; orifice oval, relatively small. Scutum with moderately narrow tergal segment obtusely inflected; occludent margin acutely toothed; basal margin deeply scalloped on both faces; growth ridges strong; longitudinal striae prominent, often forming hood-like projections at intersections with growth ridges, except on tergal segment; articular ridge approximately $4/5$ length of tergal margin; adductor ridge represented by slight ridge bordering shallow lateral depressor muscle pit; adductor muscle pit moderately shallow. Tergum with spur furrow closed or nearly so; spur moderately long, narrow, separated from basiscutal angle by $1/2$ own width to own width; basal margin sloping to spur on both sides, on carinal side from median concavity; growth ridges strong, with hood-like projections on scutal side of spur, sometimes also in 1 to 3 rows close to furrow on carinal side; articular ridge not prominent; depressor muscle crests absent.

Color. — Parietes pale pink with purple traces; radii either like parietes or chestnut-brown; sheath purplish chestnut-brown. Scutum pinkish; tergum white.

Remarks. — We have examined three specimens of *M. ajax* from the type series in the British Museum's darwinian collection. One of the larger shells is most certainly that figured by Darwin (1854: pl. 3 fig. 1a) and is herein selected as the lectotype. The two larger specimens agree well with Darwin's description, with one exception. He stated that the spur was ". . . placed at twice its own width from the basiscutal angle."; however, neither his figure (pl. 3 fig. 1c) nor the single tergum accompanying the shells have the spur placed more than its own width from the basiscutal angle. The third, much smaller specimen, has one scutum and a pair of terga still intact, but it is clearly not a megabalanid. The radii are very narrow and have markedly oblique summits; they lack tubes as do the parietes. This specimen agrees in all details of the shell and opercular valves with Spengler's (1790) *Balanus tintinnabulum* var. b, which we believe represents *Chirona amaryllis* Darwin, 1854.

Megabalanus krakatauensis (Nilsson-Cantell, 1934)

Balanus krakatauensis Nilsson-Cantell, 1934: 53, figs. 10, 11.

Megabalanus krakatauensis: Newman & Ross, 1976: 68.

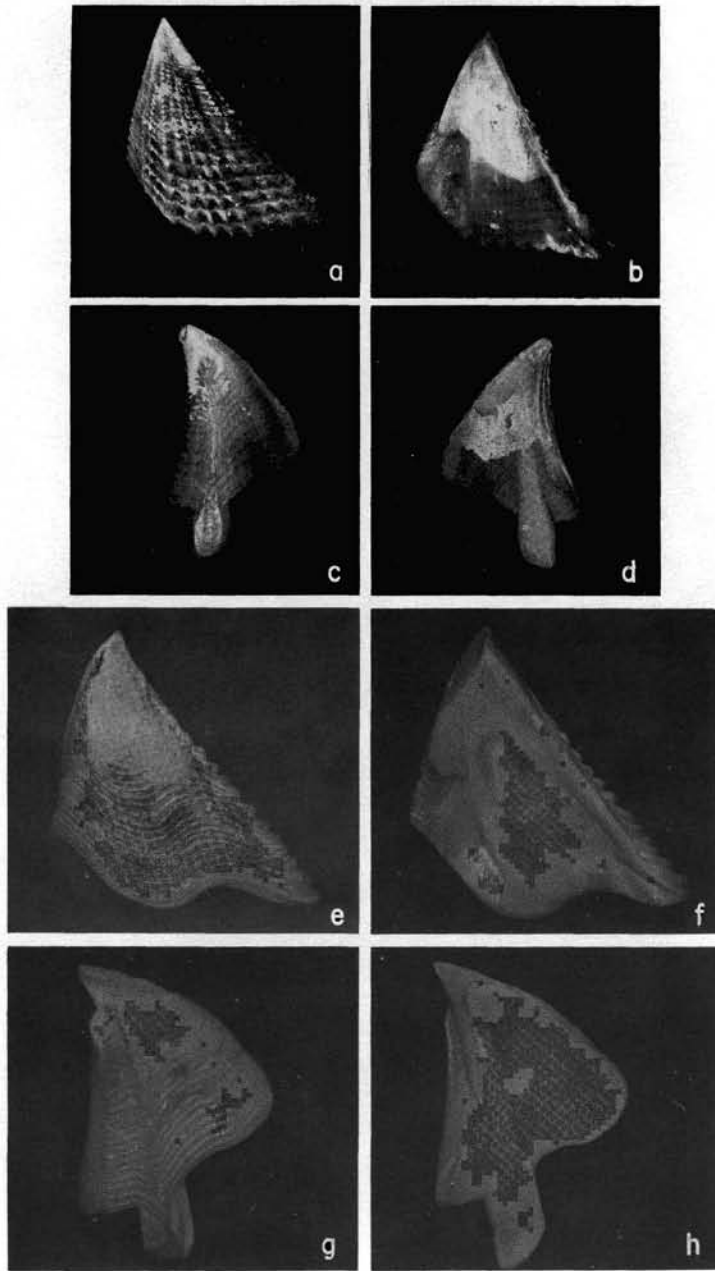


Fig. 13. *Megabalanus ajax* (Darwin). a-d, external and internal views of opercular valves of lectotype (Darwinian collection, BMNH). — *Megabalanus stultus* (Darwin). e-h, external and internal views of opercular valves (Galeta, Panama). a-d $\times 2.5$; e-h $\times 5.1$.

Type. — Zoological Museum, Amsterdam.

Type Locality. — Krakatau, Sunda Strait, Malay Archipelago.

Distribution. — Known only from type locality.

Diagnosis. — Shell conic to cylindric; radii wide, summits horizontal; orifice rhomboid. Scutum with narrow tergal segment acutely inflected; growth ridges prominent, widely spaced; longitudinal striae lacking; articular ridge nearly equaling length of tergal margin; adductor ridge absent; pits for adductor and lateral depressor muscles shallow. Tergum moderately broad, with spur furrow more or less closed; spur moderately short, separated from basiscutal angle by half own width; basal margin hollowed out on scutal side, straight on carinal side; articular ridge not prominent; depressor muscle crests indistinct.

Color. — Parietes white or dull rose with red longitudinal lines; radii nearly white.

Remarks. — Nilsson-Cantell (1934) related this species most closely to *Austromegabalanus algicola*, apparently because of the general similarity of the terga of the two species and their small size. However, the radii are described as denticulate on both sides, thereby differing from those of *A. algicola*. We have not examined this species.

Megabalanus stultus (Darwin, 1854)

(figs. 4m, 13e-h)

Balanus stultus Darwin, 1854: 216, pl. 3 fig. 2a-d. — Nilsson-Cantell, 1929: 1, figs. 1c, 2. — Pilsbry, 1953: 25, pl. 2 figs. 1-3. — Lacombe & Rangel, 1978: 4, fig. 12.

Balanus tintinnabulum antillensis: Pilsbry, 1927: 38, figs. 3a-c [not *Balanus tintinnabulum antillensis* (= *M. tintinnabulum*)].

Tetraclita radiata: Pilsbry, 1927: 38 (not *Balanus radiata* Bruguière).

Balanus stultus morycowae Kolosváry, 1966: 69, pls. 1, 2.

Balanus (Megabalanus) stultus: Ross, 1968: 14, fig. 3.

Megabalanus stultus: Newman & Ross, 1976: 68.

Type. — BMNH.

Type locality. — West Indies.

Distribution. — Florida to Rio de Janeiro, Brazil.

Diagnosis. — Shell conic, more or less elongated in carinorostral axis; parietes slightly to strongly ribbed; radii moderately wide, summits horizontal; orifice moderately small, oval, pointed at carinal end. Scutum externally convex, with broad tergal segment obtusely inflected; basal margin markedly sinuous, strongly protuberant medially; growth ridges prominent, flexed in median third; longitudinal striae faint or absent; articular ridge 2/3 to 4/5

length of tergal margin; adductor ridge acute in young to blunt, less prominent in old specimens, close to but not confluent with articular ridge, extending nearly to basal margin; pits for adductor and lateral depressor muscles deep. Tergum broad, with spur furrow usually closed, except on spur; spur moderately long, usually wide, sometimes narrow; separated from basiscutal angle by own width or slightly less; basal margin straight on scutal side of spur, straight or sloping on carinal side; growth ridges strong; longitudinal striae weak or absent; articular ridge long, approximately $5/6$ length of scutal margin; depressor muscle crests weakly developed.

Color. — Parietes dirty white, often tinged with purple; sheath pale purplish blue. Scutum and tergum tinted apically pink or pale purplish blue, sometimes entirely chalky white.

Remarks. The specimen of *B. t. antillensis* figured by Pilsbry (1927: fig. 3) could not be located. However, the figure of the tergum and the description of the scutum indicates that the specimen on *Millepora*, at least, should be referred to *M. stultus*, as suspected by Ross (1968).

Megabalanus tulipiformis (Darwin, 1854)
(figs. 1b, 4n, 14a-d)

Balanus tulipiformis ex corallio rubro Ellis, 1758: pl. 30 fig. 10.

Lepas tulipa Poli, 1791: pl. 5 figs. 1, 6.

Balanus tintinnabulum: Chenu, 1843 (in part): pl. 3 fig. 5 [not *Balanus tintinnabulum* (Linnaeus)].

Balanus tulipiformis Darwin, 1854: 204, pl. 2 figs. 2a-2d. — Nilsson-Cantell, 1921: 308, fig. 63a-c. — Southward & Crisp, 1963: 28, fig. 12. — Stubbings, 1964a: 108; 1967: 266.

Balanus (Megabalanus) tulipiformis: Utinomi, 1959: 282.

Balanus tulipiformis tulipiformis: Davadie, 1963: 30, pl. 2 figs. 3, 3a, pl. 7 figs. 1a, 1b.

Megabalanus tulipiformis: Newman & Ross, 1976: 69.

Type series. — BMNH.

Type locality. — Unknown.

Distribution. — Eastern Atlantic: Bay of Biscay to Mediterranean; Madeira, Canary and Cape Verde islands; west coast of Africa to Angola.

Diagnosis. — Shell tubuloconic or conic; parietes moderately smooth; radii moderately wide, summits oblique; orifice wide, nearly equaling basal diameter. Scutum with extremely narrow tergal segment acutely inflected; epicutical persistent; growth ridges weak; longitudinal striae, if present, faint; articular ridge not reflexed, approximately $2/3$ length of tergal margin; adductor ridge absent; pit for adductor muscle shallow; pit for lateral depressor muscle small, variable in depth. Tergum moderately narrow, with spur furrow

closed; spur short to moderately long, narrow, separated from basiscutal angle by approximately own width; basal margin usually straight on both sides of spur; growth ridges weak; longitudinal striae absent; articular ridge approximately 7/8 length of scutal margin; crests for depressor muscle very well developed.

Color. — Parietes yellowish red, rose or red, with tinge of purple, occasionally entirely purple, sometimes also with fine dark, longitudinal striae; radii nearly as dark or darker than parietes, sheath generally white or tinged with purple. Scutum purple to light pink, usually with thick, persistent yellow epicuticle; tergum pale pink or purple, spur often white.

Megabalanus vinaceus (Darwin, 1854)

(pl. 2 fig. o, pl. 12 figs. e-h)

Balanus vinaceus Darwin, 1854: 213, pl. 2 figs. 7a-7d. — Henry & McLaughlin, 1975: 70, 181.
Megabalanus vinaceus: Newman & Ross, 1976: 69. — Newman, 1979: 288, pl. 2 figs. 3, 4.
 ? not *Balanus vinaceus*: Kolosváry, 1943: 122 (see remarks).

Type. — BMNH.

Type locality. — West coast of South America.

Distribution. — West coast of Costa Rica to Ecuador.

Diagnosis. — Shell conic; parietes smooth, with fine longitudinal striae; inner lamina with several rows of secondary longitudinal tubes; radii moderately wide, summits horizontal; orifice large, rhomboidal. Scutum nearly flat, apex acute, reflexed; occludent margin with widely-spaced acute teeth; growth ridges not prominent; longitudinal striae fine, extremely numerous; articular ridge approximately 2/3 length of tergal margin, only slightly reflexed; adductor ridge lacking; pits for adductor and lateral depressor muscles very shallow. Tergum with spur furrow open, shallow; spur moderately long, separated from basiscutal angle by about own width; basal margin sloping to spur on both sides, almost to tip on scutal side; growth ridges weak; longitudinal striae absent; articular ridge about 2/3 length of scutal margin; crests for depressor muscle lacking.

Color. — Parietes and radii dark purplish brown; sheath nearly colorless. Scutum externally brownish or reddish purple, usually with one or two white bands on occludent margin, internally dull purple with white articular ridge; tergum brownish or reddish purple on carinal side of spur, sometimes also on scutal side externally and internally; spur and spur furrow white.

Remarks. — Kolosváry's (1943) report of *B. vinaceus* from South Africa,

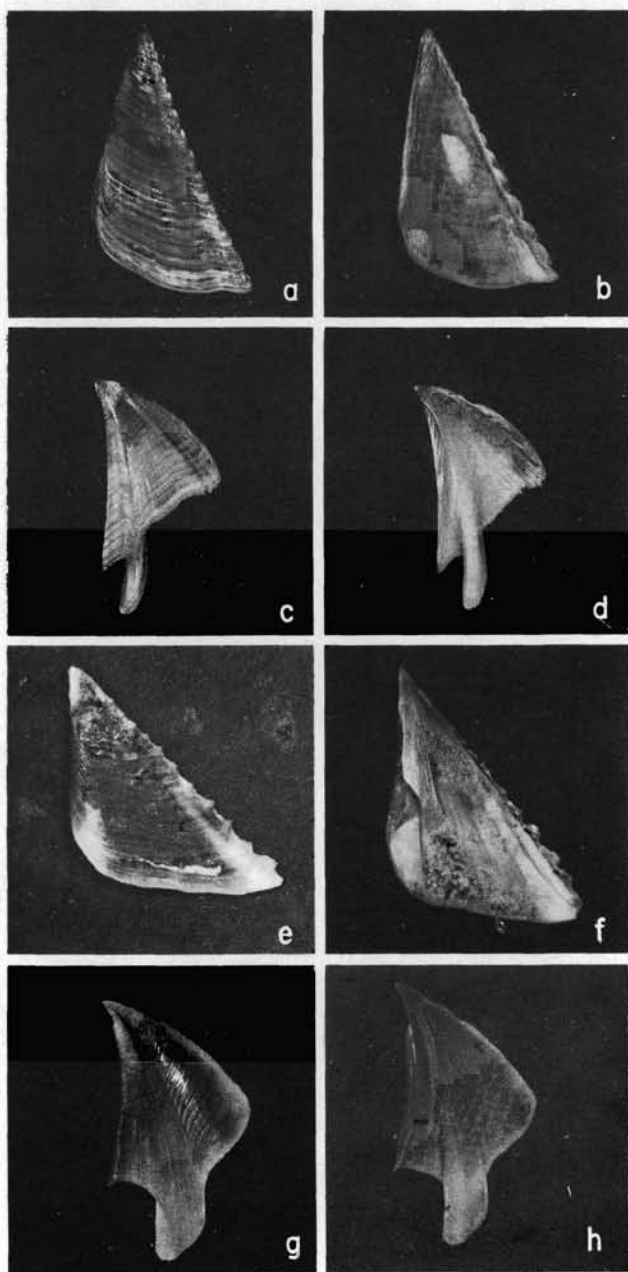


Fig. 14. *Megabalanus tulipiformis* (Darwin). a-d, external and internal views of opercular valves (off El Hank, Casablanca USNM 170617). — *Megabalanus vinaceus* (Darwin). e-h, external and internal views of opercular valves (Playas, Ecuador). a-d $\times 1.6$; e-h $\times 5.0$.

associated with *B. maxillaris* Gronovius (= *Austromegabalanus cylindricus*) and *A. algicola*, is doubtful. All other records of *M. vinaceus* are from the west coasts of Central and South America. In the same paper Kolosváry recorded the two South African species, also in the Hamburg Museum material, from California and Peru.

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APPENDIX: MATERIAL EXAMINED

Source	Locality	Remarks	Deposition
<i>Megabalanus tintinnabulum</i> (Linnaeus, 1758)			
BMNH	—	darwinian collection 4 with valves	Returned
ZMC	—	? darwinian collection, 1 with valves	Returned
ZMC	—	Spengler collection, 1 with valves, 1 without valves	Returned
EASTERN ATLANTIC			
ANSP 5405	Boynton Beach, FL	2 with valves	Returned
ANSP 6662	Ft. Pierce, FL	5 shells with numerous loose valves	Returned
ANSP 6664	Ft. Pierce, FL	4 shells with valves	Returned
McLaughlin	Oil rig off Galveston, TX	5 with valves & animals, 4 without valves	USNM
Henry	Portete, Costa Rica	1 with valves	USNM
Henry	Galeta, Panama	2 with valves	USNM
ANSP 2060	Havana, Cuba	3 with valves	Returned
ANSP 2083	St. Thomas, Virgin Islands	Type lot, <i>B. t.</i> <i>antillensis</i>	Returned
RMNH 1446	Aruba	1 without valves	Returned
RMNH 1447	Curaçao	2 with valves	Returned
RMNH 1443	Bonaire	1 without valves	Returned
RMNH 1445	Bonaire	2 without valves	Returned
Henry	Bonaire	1 with valves & animal	USNM
RMNH 1444	Centinela, Venezuela	3 with valves & animals	Returned
Lacombe	Rio de Janeiro, Brazil	12 with valves & animals, 3 without valves	SIO
ANSP 2354	Rio de la Plata, Uru- guay	2 with valves	Returned
INDOPACIFIC			
Henry	Bombay, India	1 with valves & animal	USNM
USNM 51656	Indonesia	3 with valves	Returned
USNM 51680	Australia	2 with valves	Returned
From Ships			
RMNH, 150, 397, —		24 without valves, 10 with valves	Returned
411, 608, 933		1 each without valves	Returned
RMNH 935-943	—	11 with valves	Returned
USNM 51630	—	7 without valves	Returned
USNM 51437	—	2, 1 with valves	Returned
USNM 48005	—	12 with valves	USNM
Henry	—	1 without valves	Returned
ZMC			

APPENDIX (*continued*)

Source	Locality	Remarks	Deposition
<i>Megabalanus azoricus</i> (Pilsbry, 1916)			
EASTERN ATLANTIC			
USNM 48126	Crace, Terciera, Azores	type lot	Returned
USNM 22150	Ruperts Bay, St. Helena	32 with valves & animals	Returned
RMNH	St. Helena	8 with valves	Returned
From Ship			
Henry	—	2 with valves & animals	USNM
<i>Megabalanus californicus</i> (Pilsbry, 1916)			
EASTERN PACIFIC			
California			
Henry	Goleta	1 with valves & animal	USNM
Henry	Port Hueneme	2 with valves & animals	USNM
Henry	Santa Cruz I.	10 with valves & animals	RMNH
Henry	Anacapa I.	2 without valves	USNM
Henry	Point Mugu	23 with valves & animals	USNM
Henry	Long Beach	2 with valves & animals	USNM
Henry	Huntington Beach	5 with valves	USNM
Henry	Corona del Mar	8 with valves & animals	RMNH
Henry	San Clemente	45 most with valves & animals	USNM
USNM 9434a	San Diego	type lot	Returned
Mexico			
Henry	Baja California	7 with valves & animals	USNM
<i>Megabalanus clippertonensis</i> (Zullo, 1969)			
CAS 029823	Clipperton Island	paratype with valves	Returned
<i>Megabalanus coccopoma</i> (Darwin, 1854)			
BMNH	—	darwinian collection, 2, 1 with valves	Returned
ZMC	—	darwinian collection, 2 without valves	Returned
ZMC	—	1 without valves	
Henry	Humpback whale	1 without valves	USNM

APPENDIX (continued)

Source	Locality	Remarks	Depositor
EASTERN PACIFIC			
Henry	Mazatlan, Mexico	20 without valves	USNM
Henry	San Blas, Mex.	2 without valves	USNM
Henry	Puerto Vallarta, Mex.	4 with valves & animals	USNM
Henry	Zihuantanejo, Mex.	1 with valves & animal	USNM
Henry	Canal de Boca Chica, Mex. (off Roqueta I.)	7 with valves & animals	USNM
Henry	Canal de Boca Chica, Mex. (off mainland)	15 with valves & animals	RMNH
Henry	Bahia de Acapulco, Mex. (off Malecon)	14 with valves & animals	USNM
Henry	Bahia de Acapulco (off Playa Hornos)	6 with valves & animal	USNM
Henry	Bahia de Acapulco (off Playa Icacos)	30 with valves & animals	RMNH
Henry	Bahia de Acapulco (off Playuela)	6 with valves & animals	USNM
Henry	San Jose, Guatemala	140 most with valves & animals	USNM
Henry	Acajutla, El Salvador	120 most with valves & animals	USNM
Henry	Bahia del Coco, Costa Rica	5 with valves & animals	RMNH
Henry	Cedro I., C.R.	65 most with valves & animals	USNM
Henry	Jesusita I., C.R.	45 most with valves & animals	RMNH
Henry	Puntarenas, C.R.	170 most with valves & animals	USNM
Henry	Boca de Barranca, C.R.	125 most with valves & animals	USNM
Henry	San Francisco Beach, Panama	24 without valves	USNM
Henry	Palo Seco Beach, Pan.	4 without valves	USNM
Henry	Taboguilla I., Pan.	1 with valves & animal	USNM
Henry	Malpelo I., Colombia	59 with valves & animals	USNM
USNM 93322	Salinas, Ecuador	8 without valves	Returned
Henry	Salinas, Ec.	180 with valves & animals	USNM
Henry	Punta San Lorenzo, Ec.	6 with valves & animals	USNM
McLaughlin	La Libertad, Ec.	6 without valves	USNM
Henry	Punta Carnero, Ec.	52 with valves & animals	RMNH
Henry	Playas, Ec.	7 with valves & animals	USNM
McLaughlin	Posorya, Ec.	5 with valves & animals	RMNH
USNM 93322	Paita, Peru	120 most with valves & animals	Returned

APPENDIX (continued)

Source	Locality	Remarks	Deposition
Galapagos Islands			
McLaughlin	Baltra I.	10 with valves & animals	USNM
McLaughlin	Santa Cruz Island	2 without valves	USNM
WESTERN ATLANTIC			
Lacombe	Rio de Janeiro, Brazil	8 with valves	SIO
Henry	Punta Sernambetiba, Br.	14 with valves & animals	USNM
From Ship			
Henry	—	9 without valves	USNM
<i>Megabalanus concinnus</i> (Darwin, 1854)			
BMNH		darwinian collection, 1 with valves	Returned
EASTERN PACIFIC			
Peru			
ANSP 1813	Bay of Sechura	valves only	Returned
ANSP 6533	—	1 with valves	Returned
ANSP 6537	Pacasmayo	1 with valves	Returned
USNM 93322	Paita	105 with valves & animals	Returned
USNM 93322	Salaverry	22 with valves & animals	USNM
Henry	Chimbote	8 without valves	USNM
McLaughlin	Macabi Is.	10 with valves & animals	RMNH
<i>Megabalanus crispatus</i> (Schröter, 1786)			
BMNH	—	darwinian collection, 1 with valves	Returned
<i>Megabalanus dorbignii</i> (Chenu, 1843)			
BMNH	—	darwinian collection, 2, 1 with valves	Returned
ZMC	—	darwinian collection, 5, 2 with valves	Returned

APPENDIX (continued)

Source	Locality	Remarks	Deposition
<i>Megabalanus linzei</i> (Foster, 1978)			
NMNZ	Kermadec Is., New Zealand	paratypes, 2 with valves & animals	Returned
<i>Megabalanus occator</i> (Darwin, 1854)			
ZMC	—	Spengler collection, valves only, as <i>M. tintinnabulum</i>	Returned
USNM	—	3 with valves	Returned
USNM 52116	Philippine Islands	1 with valves	Returned
From Ship			
RMNH 397	—	5 with valves & animals	Returned
RMNH 608	—	1 with valves & animals	Returned
<i>Megabalanus peninsularis</i> (Pilsbry, 1916)			
EASTERN PACIFIC			
USNM 11332	—	20 with valves & animals	Returned
USNM 43486	Cabo San Lucas, Baja California, Mexico	paratype lot	Returned
Henry	Mazatlan, Mex.	1 without valves	USNM
Henry	Puerto Vallarta, Mex.	12 with valves & animals	USNM
Henry	Manzanillo, Mex.	60 most with valves & animals	USNM
Henry	Zihuantanejo, Mex.	50 most with valves & animals	RMNH
Henry	Canal de Boca Chica, Mex. (near Roqueta I.)	125 most with valves & animals	RMNH
Henry	Canal de Boca Chica, Mex. (near mainland)	25 most with valves & animals	USNM
Henry	Bahia de Acapulco, Mex. (off Ensenada de los Precos)	200 most with valves & animals	USNM
Henry	Bahia de Acapulco (off Malecon)	25 with valves & animals	USNM, RMNH
Henry	Bahia de Acapulco (off Playas Hornos)	6 with valves & animals	USNM
Henry	Bahia de Acapulco (off Playas Icacos)	50 most with valves & animals	USNM
Henry	Bahia de Acapulco (off Playuela)	40 with valves & animals	RMNH
Henry	Bahia de Acapulco (off Ensenada Verde)	50 most with valves & animals	USNM
Henry	Bahia de Acapulco (off Punta Rocosa)	25 most with valves & animals	USNM

APPENDIX (continued)

Source	Locality	Remarks	Deposition
Henry	Bahia de Acapulco (off Puerto Marques north)	15 most with valves & animals	USNM
Henry	Bahia de Acapulco (off Puerto Marques south)	100 most with valves & animals	USNM
Henry	Puerto Escondido, Mex.	8 without valves	USNM
Henry	Bahia del Coco, Costa Rica	19 with valves & animals	USNM
Henry	Punta Gorda, C.R.	1 with valves & animals	USNM
USNM 131571	Golfo de Chiriqui, Islas Secas, Panama	2 with valves & animals	Returned
Henry	Bahia de Panama, Chorrero Beach, Pan.	3 without valves	USNM
Henry	Malpelo Island, Colombia	9 with valves & animals	USNM
Henry	Punta Carnero, Ecuador	24 most with valves & animals	USNM
Galapagos Islands			
USNM 48003	Hood I.	type lot of <i>M. galapaganus</i>	Returned
McLaughlin	Academy Bay, Santa Cruz I.	20 with valves & animals	RMNH
McLaughlin	Off Punta Astrada, Santa Cruz I.	65 most with valves & animals	USNM
USNM 128938	Tagus Cove, Isabela I.	1 with valves & animal	Returned
McLaughlin	Tagus Cove, Isabela I.	28 most with valves & animals	RMNH
McLaughlin	Fernandina I.	50 most with valves & animals	USNM
USNM 131571	Marchena I.	2 with valves & animals	Returned
From Ships			
USNM 163527	—	13 with animal & valves	Returned
USNM 177937	—	10 with valves & animals	Returned
Henry	—	14 most with valves	RMNH
BPBM 341	—	17 with valves & animals	Returned
BPBM	—	14 most with valves	Returned
Henry	—	9 without valves	USNM
<i>Megabalanus rosa</i> (Pilsbry, 1916)			
Henry	On glass float	11 without valves	USNM

APPENDIX (continued)

Source	Locality	Remarks	Deposition
WESTERN PACIFIC			
Japan			
USNM 177932	—	35 most with valves & animals	Returned
USNM 43494	Azabu	type series	Returned
USNM 43493	Wakanoura	type series	Returned
Henry	Tateyama Bay	3 without valves	USNM
From Ship			
Henry	—	2 with valves	RMNH
<i>Megabalanus spinosus</i> (Bruguière, 1789)			
BMNH	—	darwinian collection, 2, 1 with valves	Returned
ZMC	—	darwinian collection, 3, without valves	Returned
ZMC	—	Spengler collection, 59 some with valves	Returned
ANSP 6674	—	1 without valves	Returned
From Ships			
RMNH 943	—	1 without valves	Returned
ZMC	—	2 with valves	Returned
<i>Megabalanus tanagrae</i> (Pilsbry, 1928)			
CENTRAL PACIFIC			
Henry	Kure Atoll, Leeward Is.	23 most with valves	USNM
BPBM 303	Midway I.	2 with valves & animals	Returned
BPBM 273	Waimanalo, Oahu, HI	1 without valves	Returned
Henry	Honolulu, Oahu	16 without valves	USNM
Henry	Hookena, HI	2 with valves	RMNH
Henry	Rongelap Atoll, Marshall Islands	5 without valves	USNM
<i>Megabalanus validus</i> (Darwin, 1854)			
ZMA	Malay Archipelago	pair of valves only	Returned
ZMC	—	darwinian collection, 3 with some valves	Returned
ZMC	—	5 without valves	Returned
ZMC	—	2 with valves	Returned

APPENDIX (continued)

Source	Locality	Remarks	Deposition
<i>Megabalanus vesiculosus</i> (Darwin, 1854)			
WESTERN ATLANTIC			
Brazil			
ANSP 2369	São Paulo	8 with some loose valves	Returned
ANSP 2371	Bertioza Santos	1 with valves	Returned
Lacombe	Baia de Guanabara	11 with valves	UNSM, RMNH
<i>Megabalanus volcano</i> (Pilsbry, 1916)			
WESTERN PACIFIC			
USNM 43488	Japan	type	Returned
USNM 52117	Japan	paratype	Returned
USNM 77932	—	1 with valves	Returned
From Ships			
USNM 14563	—	2 with valves & animals	Returned
Henry	—	6 with valves	USNM, RMNH
<i>Megabalanus zebra</i> (Darwin, 1854)			
BMNH	—	darwinian collection, 7, 2 with valves	Returned
ZMC	—	darwinian collection, 1 with valves	Returned
USNM 12386	—	25, also loose valves	Returned
USNM 52089	(? Dublin Bay)	1 without valves	Returned
WESTERN PACIFIC			
RMNH 423	Japan	1 without valves	Returned
INDOPACIFIC			
USNM 43489	Zamboanga, Philippine Is.	9 with loose valves	Returned
RMNH 420	Indonesia	1 without valves	Returned
RMNH 422	Amboina, Indonesia	1 without valves	Returned
RMNH 425	Sumatra	5 with valves	Returned
RMNH 424	New Caledonia	3 without valves	Returned
RMNH 421	Australia	1 without valves	Returned
From Ships			
USNM 9287	—	1 without valves	Returned
Henry	—	7 with valves	USNM, RMNH

APPENDIX (*continued*)

Source	Locality	Remarks	Deposition
<i>Megabalanus ajax</i> (Darwin, 1854)			
BMNH	Philippine Islands	2 cotypes	Returned
<i>Megabalanus krakatauensis</i> (Nilsson-Cantell, 1934)			
None examined			
<i>Megabalanus stultus</i> (Darwin, 1854)			
WESTERN ATLANTIC			
USNM 54232	Biscayne Bay, FL	5 with valves	Returned
USNM 182974	Rincon, Puerto Rico	4 with valves & animals	Returned
Henry	Galeta, Panama	2 with valves & animals	RMNH
<i>Megabalanus tulipiformis</i> (Darwin, 1854)			
USNM 170617	Off El Hank, Casablanca	17 most with valves & animals	Returned
<i>Megabalanus vinaceus</i> (Darwin, 1854)			
EASTERN PACIFIC			
Henry	Puntarenas, Costa Rica	13 with valves & animals	USNM
Henry	Playas, Ecuador	10 with valves & animals (removed from boat when beached)	USNM, RMNH
Henry	Posorja, Ec.	2 without valves	USNM