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BREDIN-ARCHBOLD-SMITHSONIAN BIOLOGICAL SURVEY OF DOMINICA¹

8. The Intertidal Balanomorph Cirripedia

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The present study on the intertidal balanomorph barnacles of Dominica is based on incidental collections made during April and May of 1966 by Dr. Ernst Kirsteuer of the American Museum of Natural History and by Dr. Klaus Rützler of the Smithsonian Institution. These collections are of considerable value largely because there have been no previous studies or mention of the Cirripedia of Dominica. Represented in the collections are: Chthamalus angustitergum Pilsbry, 1916; Tetraclita (Tetraclita) stalactifera (Lamarck), 1818; Tetraclita (Tetraclitella) divisa Nilsson-Cantell, 1921; and Balanus (Megabalanus) stultus Darwin, 1854. That this list does not embrace all the barnacles inhabiting this region is recognized, but it probably includes the more common species.

All the Dominica species have been reported previously from other regions in the Caribbean and western Atlantic with the exception

¹See list at end of paper.

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of *T. divisa*; however, these barnacles remain poorly known because earlier workers failed to provide detailed descriptions and illustrations of their distinctive features, especially of the mouth field and cirral appendages. The addition of such information, provided herein for the Dominica fauna, should aid materially in an understanding of the morphological and biological characters of other populations of the same species as well as closely related species in the Caribbean and elsewhere.

The dissected specimens, which have been figured, are deposited in the collections of the American Museum of Natural History (AMNH). Representative samples of all the species have been placed in the collections of the American Museum and the U.S. National Museum (USNM).

The author is indebted to Drs. Ernst Kirsteuer and Klaus Rützler, who made these collections available for study. Dr. William K. Emerson of the American Museum kindly read a manuscript draft of this paper and offered several suggestions for improvement. Dr. William A. Newman, Scripps Institution of Oceanography, first brought to the writer's attention the fact that *Balanus stultus* was a megabalanid. The writer should also like to thank Dr. Newman for many informative discussions on the systematics, evolution, and phylogeny of the Cirripedia.

Family CHTHAMALIDAE Darwin, 1854

Genus Chthamalus Ranzani, 1817

Chthamalus angustitergum Pilsbry

FIGURE 1

Chthamalus stellatus angustitergum Pilsbry, 1916, p. 305, text-figs. 85, 86, pl. 71, figs. 5, 5a, 5b; 1927, p. 37, fig. 1.—Nilsson-Cantell, 1933, p. 506.—Kolosváry, 1939, p. 161, figs. 6–1, 6–2; 1941, p. 68, fig. 1sa.—Stephensen and Stephensen, 1950, p. 389; 1954, p. 80.—Henry, 1954, p. 444.—Wells, 1966, p. 92.

Chthamalus stellatus.—Smith, Williams, and Davis, 1950, p. 134.—Marshall, 1953, p. 435.—Voss and Voss, 1960, p. 102.—Werner, 1967, p. 70.

Chthamalus angustitergum.—Newell, Imbrie, Purdy, and Thurber, 1959, p. 209.

Material.—Western side of Panto Hole Bay, east of town of Marigot, approximately 15°32′21″N, 61°17′31″W; intertidal, on Tetraclita (Tetraclita) stalactifera; May 1–10, 1966; about 100 specimens.

DIAGNOSIS.—Articular ridge of scutum straight to slightly convex, basal end of which evenly rounded and not projecting beyond the basitergal angle. Tergum narrow, about twice as high as broad, and nearly twice as thick as scutum. Mandible quadridentoid, with basal

comb containing 22-28 teeth. Maxilla I with subapical notch, below which spines divided into two distinct clusters.

Supplementary description.—In the majority of the specimens examined, prominent radial ribs or their remnants ornament the parietes. The shell is pale grey as is the outer surface of the operculum. Internally, near the apices, the opercular plates are tinted pale pink.

Measurements (in mm) of the five specimens dissected are as follows:

		shell		operculo	ır plates
specimen	carino-rostral diameter 5.8	lateral diameter	height 2.7	scutum height	tergum height
$\frac{1}{2}$	6. 1	5. 6 6. 0	$\frac{2.7}{2.7}$	1. 5 1. 8	1.6 1.9
3	8.0	8.0	3. 1	1. 5	1.6
4 5	5. 3 5. 1	4. 9 5. 4	2. 0 3. 1	1. 2 1. 1	1.3 1.2

The height of the scutum is about one-half its width. The articular ridge extends about three-fifths the length of the tergal margin. It is straight, and the basal margin is evenly rounded and does not project. There is no adductor ridge; the adductor muscle depression is very small and deep. Situated on the basitergal angle, which projects beyond the tergal margin, is the pit for the depressor muscle.

The tergum is about one-half as wide as it is high, and the plate is exceedingly thick. There is a small, narrow, and clearly delimited spur. Crests for the tergal depressor muscle number five to seven.

The multidenticulate labrum has a shallow, medial, saddle-like depression, on each side of which are 11-14 teeth. Short setae are dispersed between the teeth along the crest of the labrum (fig. 1f). A large elongate-oval patch of downward-directed spines extends obliquely from each side of the superolateral margins toward the basimedial portion of the labrum.

The superior margin of the palp is straight and free of setae (fig. 1c). The basal margin is covered with short setae, but those on the superodistal margin are extremely long; all of the setae are clothed with spinules.

The cutting edge of the mandible is armed with five teeth including the inferior angle (fig. 1a). The distance between the second and third teeth is one-half that between the first and second teeth. The fourth tooth is bifid. The inferior angle bears three to four spines, above which is the typically developed comb, containing about 22–28 spinules.

Maxilla I has a somewhat trilobed cutting edge. There is a prominent subapical, V-shaped notch, and on some specimens there is a suprabasal notch. The spination along the edge is readily separable into three zones, the apical consisting of both long and short, stout

spines; the medial, below the subapical notch, containing long, slender spines; and the basal, which may or may not be set off from the medial by a slight notch, containing only short, slender spines (fig. 1b).

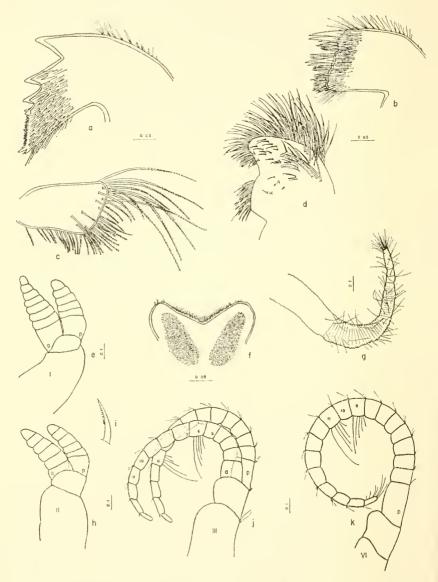


FIGURE 1.—Chthamalus angustitergum Pilsbry, 1916, AMNH 12458, Panto Hole Bay, Dominica: a, mandible; b, maxilla I; c, palp; d, maxilla II; e, cirrus I; f, labrum; g, distal end of penis; h, cirrus II; i, comb seta from cirrus II; j, cirrus III; k, cirrus VI. (Setae omitted on cirri I and II; on numbered segments of cirri III and VI, only one set of setae shown; a = anterior ramus; p = posterior ramus; scale in millimeters.)

Maxilla II has a distinctly bilobed anterior margin. The appendage is broad, but the height is somewhat greater.

The anterior ramus of cirrus I is slightly longer than the posterior ramus, and all of the articles of both rami are broader than they are high. The terminal article of the posterior ramus bears a few comb setae. The same relationships as found in cirrus I hold for cirrus II except that comb setae are found on the terminal articles of both rami. The comb setae on both cirri lack basal guards. Cirrus III is not modified. Cirri III–VI are essentially equal in length with equal rami. At each articulation along the posterior curvature of the intermediate articles of cirri III–VI there are 1–3 long, slender setae and 1–3 short, slender setae. There are no bristles or teeth arrayed along the lateral faces of the posterior cirri. Pigment spots occur at each articulation along the posterior border of the cirri and along the whole length of the anterior border of the cirri. Chaetotaxis of the anterior border of the intermediate articles of cirri IV–VI is typically ctenopod, there being 5 pairs.

A count of the segments of specimen number 1, illustrated in figure 1, is as follows:

,		I	II	111	1V	V	VI
	anterior	8	6	14	17	19	19
right	posterior	6	6	15	17	19	19
left	anterior	7	7	13	18	19	19
	posterior	6	7	15	XX	19	19

Data on the cirral counts of the five specimens dissected are presented below. The range (R) and mean (\bar{x}) values for the number of segments in the anterior (a) and posterior (p) rami of the right side are as follows:

		I	I	I	1	OI.	1.	V	1	-	V	I
	(1	7)	a	n	a	n	a	p	a	7)		7)
		P		P		P		1'		1'	w	P'
\mathbf{n}	5	5	5	5	5	5	5	5	5	5	5	5
\mathbf{R}	6-8	5-6	6-9	5-7	14-15	14-16	13-17	15-17	16-19	16 - 19	17 - 19	17-19
\bar{Z}	7.0	6.0	7.4	6.0	14.5	15.0	15.4	16.0	17.4	16.8	18.0	17.6

The penis is annulated throughout its length, and it is covered with long bristles. The distal extremity is densely clothed with bristles. There is no basidorsal point.

Remarks.—The nominal subspecies Chthamalus stellatus angustitergum is readily separable from C. stellatus stellatus (Poli, 1791) on taxonomic as well as geographic and reproductive grounds. Although apparently alike superficially, differences exist that clearly warrant the recognition of this Caribbean barnacle at the specific level. Although there are notable differences in the coloration of these two species, by far the greatest number of distinguishing characters are found in the opercular plates. The scutum of the Caribbean species is about one-half as tall as it is wide, whereas in *C. stellatus* it is about two-thirds. In the latter species the adductor muscle pit is exceedingly large and the basal end of the articular ridge is acute, extending out to the basitergal angle; the opposite conditions exist in *C. angustitergum*. In *C. angustitergum*, furthermore, the tergum is narrow—hence, the name—the width being about one-half the height and the spur being well set off from the basiscutal angle, but in *C. stellatus* the spur is virtually confluent with the basiscutal angle and the height of the plate exceeds the width by one-fourth or less. Crests for the tergal depressor muscles, of which there are four in *C. stellatus*, are low and feebly developed. In *C. angustitergum* there are five crests, which are both high and strongly developed.

Insular populations of *C. angustitergum* in the Caribbean are obviously isolated geographically from the Asia Minor, Mediterranean, and eastern Atlantic populations of *C. stellatus*—indeed, there is no indication of recruitment of *C. stellatus* in the Caribbean; consequently, the populations of these two species are reproductively isolated and more than likely have been for a significantly long period. Such isolation, both reproductive and spatial, speaks in favor of eliminating the antequated subspecific label attached to

C. angustiteraum.

There are at least three other species of Chthamalus in the Caribbean and western Atlantic: C. fragilis Darwin, 1854; C. stellatus thompsoni Henry, 1958; and C. rhizophorae de Oliveira, 1940. There should be little confusion regarding the identity and distinction among these species. Chthamalus fragilis is confined for the most part to the Atlantic coast of the United States, although it has been reported in the Caribbean and on the west African coast (Stubbings, 1967, p. 262). Bermuda is apparently the only locality where C. stellatus thompsoni occurs (Henry, 1958, p. 220). The euraphian, C. rhizophorae, has been collected by the present writer at several localities in the Bahamas, although previously it was known only from Brazil (Oliveira, 1940b, p. 379; Stubbings, 1967, p. 257).

Family Tetraclitidae Nilsson-Cantell, new status

Tetraclitinae Nilsson-Cantell, 1921, p. 357.

At the present time, students of balanomorph systematics favor inclusion of the tetraclitids in the family Balanidae. Although Nilsson-Cantell (1921) took the first and only bold step when he segregated the two dozen or so species of this complex into a distinct subfamily,

there apparently has been no further attempt to reevaluate the systematic position of these barnacles. Assignment of the tetraclitids as a subfamily of the Balanidae seems untenable at this time because they obviously represent a different and distinct lineage that in many respects parallels closely that of the Chthamalidae.

The tetraclitids are compounded of forms with a shell consisting of only four tubiferous plates, the number of tubes ranging from one row in *Tesseropora* to several rows in *Tetraclita* and *Tetraclitala*. In the latter group the radii are also tubiferous, and only in this group are the radii as well developed as they are in the Balanidae. The basis with few exceptions is membraneous, and where calcareous, it is neither tubiferous nor does it possess complex ridges marginally that interdigitate with the basal margin of the wall.

One of the salient structures of primary importance in the classification of the Balanomorpha is the state of development of the labrum. In the Chthamalidae there is no notch in the labrum, and it is effectively bullate, whereas in the Balanidae the labrum is distinctly notched and not bullate. In the tetraclitids this structure is clearly not bullate, nor is it notched, but rather it holds an intermediate position since it is thin, as in the balanids, and the crest has a saddle-like groove, as in *Chthamalus*. The presence of a bullate or simple un-notched labrum indicates a primitive evolutionary state, which is readily recognizable in the chthamalids and, of the other Thoracica, in the verrucomorphs and lepadomorphs. On the basis of the foregoing evidence alone it is not likely that an un-notched labrum could have evolved from a notched labrum; hence, the tetraclitids could not have evolved from the balanids.

Modifications in tetraclitid mandibular structure closely parallel that found in the chthamalids, wherein there are groups with either a comblike or serrate inferior margin. The inferior margin is never molariform as is frequently the case in the Balanidae.

The first three pairs of cirri in the Balanidae are highly modified and effectively serve as mouth appendages. In *Chthamalus* and related genera only the first two pairs of cirri are so modified. In the tetraclitids, cirrus III is modified as a mouth appendage but significantly less so than in the Balanidae. In the Balanidae the third cirrus is never antenniform, but it commonly is in the Chthamalidae and rarely in tetraclitids of the *Tetraclita squamosa* complex.

Other features that argue for exclusion of the tetraclitids from the Balanidae are the absence of a basidorsal point on the intromittant organ and the presence of comb setae on the anterior cirri. Caudal appendages, present in many of the chthamalids, are lacking in the tetraclitids as well as the balanids.

In all likelihood the tetraclitids and chthamalids shared a common ancestry, but unlike the chthamalids the tetraclitids probably evolved and deployed far more rapidly. The balanids, on the other hand, probably evolved from the chthamalid lineage, but at a much later time. Unfortunately, the fossil evidence documenting these evolutionary steps remains to be discovered.

Inclusion of the tetraclitids in the Balanidae would clearly appear to be precluded on the basis of the foregoing. By the same token their inclusion in the Chthamalidae would serve only to weaken the definition of this group also. Because no intergrades or transitionary forms are known to occur between the Balanidae and tetraclitids, separation of these two groups at the familial level is clearly warranted.

Genus Tetraclita Schumacher, 1817

Tetraclita (Tetraclita) stalactifera (Lamarck)

FIGURE 2

Balanus ponderosus [Lightfoot, 1786,] p. 89.—Dillwyn, 1823, p. 23. Balanus stalactiferus Lamarck, 1818, p. 394.—Lamy and André, 1932, p. 222. Balanus latus Lamarck, 1818, p. 397.—Lamy and André, 1932, p. 222.

C[onia] stalactifera.—Chenu, 1843, pl. 4, figs. 6-8.

Tetraclita porosa var. communis Darwin, 1854, in part, p. 329, pl. 10, fig. 1a, 1i (?), 1k (?).

Tetraclita porosa.—Verrill, 1901, p. 22.—Bigelow, 1901, p. 180.

Tetraclita squamosa stalactifera.—Pilsbry, 1916, p. 254, pl. 59, figs. 1, 1a, 1b.—Oliveira, 1940a, p. 138; 1941, p. 7, pl. 1, figs. 1, 2, pl. 2 (fig. 4), pl. 10 (figs. 1, 3, 6); 1947, p. 715.—Stephensen and Stephensen, 1950, p. 388; 1952, p. 8.—Henry, 1954, p. 444; 1958, p. 224, pl. 1, fig. b, pl. 5, figs. a, b.—Newell, Imbrie, Purdy, and Thurber, 1959, p. 209.—Voss and Voss, 1960, p. 102, 106.—Ross, 1962, p. 31.—Rehder, 1967, p. 16.

Tetraclita stalactifera.—Pilsbry, 1927, p. 38.

Tetraclita porosa stalactifera.—Nilsson-Cantell, 1933, p. 508; 1939, p. 5.

Tetraclita squamosa.—Smith, Williams, and Davis, 1950, p. 134.—Marshall, 1953, p. 435.—Werner, 1967, p. 70.—Multer and Milliman, 1967, p. 260, fig. 2.

MATERIAL.—Scotts Head Bay, at southern end of Soufriere Bay, approximately 15°12′40″ N, 61°22′40″ W; 0.5 meters; May 17–28, 1966; about 150 specimens. Middle Bay, adjacent to town of Marigot, approximately 15°32′21″ N, 61°17′28″ W; intertidal, on basaltic rocks; April 15–30, 1966; 4 specimens; same locality as that cited by Kirsteuer (1967). Western end of Panto Hole Bay, approximately 15°32′21″ N, 61°17′31″ W; intertidal, on basaltic rocks; May 1–10, 1966; about 125 specimens.

Diagnosis.—Sheath of shell tinted plumbeous black and opercular plates violet black or raisin black with whitish or paler borders and ridges. Parietes relatively thin; tubes large, commonly in 3–5 rows. Radii very poorly developed or obsolete. Labrum with slight notch

and 4 teeth on each side of notch. Mandible with 6 teeth including inferior angle; second and third teeth bifid; fifth tooth rudimentary; inferior angle strongly pectinate. Maxilla I with 2 spines above

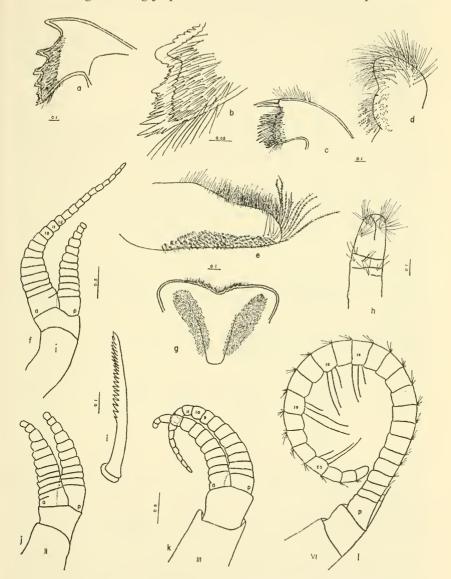


FIGURE 2.—Tetraclita stalactifera (Lamarck), 1818, AMNH 12459, Scotts Head Bay, Dominica: a, mandible; b, enlarged view of fourth tooth and inferior angle of mandible shown in a; c, maxilla I; d, maxilla II; e, palp; f, cirrus I; g, labrum; h, distal end of penis; i, comb seta from cirrus II; j, cirrus II; k, cirrus III; l, cirrus VI. (Setae omitted on cirri I-III; on numbered segments of cirrus VI, only one set of setae shown; a = anterior ramus; p=posterior ramus; scale in millimeters.)

subapical notch, and 18-24 spines beneath, unequally divided into 2 clusters. Anterior ramus of cirrus I longer than rami of cirri II and III. Comb setae of cirri II and III lacking basal guards.

Supplementary description.—The shell is typically conic, spreading, commonly eroded externally, and tinted various shades of white with deep purple. The radii are extremely narrow or obsolete, and often external demarcation of the four parietal plates is virtually impossible to recognize. The surface of the body cavity wall is smooth or slightly irregular but never ribbed or ridged.

Externally, the surface of the scutum is eroded, as is the tergum. The adductor ridge of the scutum extends nearly the whole length of the valve. It is long, low, deeply undercut, and the ridge moderately thin. The articular ridge occupies about two-thirds the length of the tergal margin, and it is evenly and broadly rounded distally. Prominent ridges exist for the insertion of the lateral and rostral depressor muscles. Dentition of the occludent margin is limited to 4–6 strong, oblique teeth. The number and development of these teeth, however, is no doubt contingent upon the age and degree of corrosion of the specimen.

The apex of the tergum is produced into a slight but noticeable beak. The articular ridge is high, and its thickness varies. There are 6–8 strong, well-spaced, inclined crests for the insertion of the depressor muscles.

Parameters of the shell and opercular plates of the five dissected specimens (in mm) are as follows:

		shell		opercul	ar plates
specimen	carino-rostral diameter	lateral diameter	height	scutum height	tergum height
1	19.5	17.2	13.4	5.1	6.0
2	18.7	17.6	12.1	5.4	6.5
3	20.6	18.6	12.9	6.1	7.0
4	30.8	27.2	16.2	7.8	8.6
5	11.9	17.6	4.7	2.9	2.8

On both sides of the shallow, saddle-like groove in the crest of the labrum there are four short teeth, although in one specimen dissected there were four teeth on one side and only three on the other. Interspersed among the teeth in the notch and extending laterally along the rim of the labrum are short, slender bristles (fig. 2g). Two elongate-oval patches of spines extend obliquely from the superolateral margin on each side of the crest toward the basicentral portion of the labrum.

The palps are long, high, and free of setae along their basal margins; however, the basal portion of the appendage is uniformly covered with ctenoid scales (fig. 2e). The setae on the distal extremity are long and setulose whereas those on the superior margin are shorter and not covered with setules.

Along the cutting edge of the mandible there are six teeth including the inferior angle (fig. 2a). The distance between teeth decreases by about one-half, proceeding from the first tooth to the fifth. Both the second and third teeth have subsidiary cusps. Along the superior slope of the third and fourth teeth there are serrations. Similarly, the inferior angle is serrate, but very coarsely.

Maxilla I has a deep subapical notch (fig. 2c). Above the notch there are two long, stout spines and one or two shorter, slender spines. Below the notch 11–16 long, slender spines and 8–14 shorter, slender spines are present. On larger and older specimens there may be little distinction between these two spine clusters.

Maxilla II is taller than broad and distinctly bilobed. The setae on the basal lobe are setulated.

The rami of cirrus I are grossly unequal in length, the posterior ramus being about one-half the length of the anterior ramus (fig. 2f). The rami of cirrus II are essentially equal in length while the posterior ramus of cirrus III is slightly longer than the anterior ramus. The intermediate and basal articles of the anterior three pairs of cirri are squat, not appreciably protuberant. Both rami of cirrus II and III are clothed with long comb setae, which lack basal guards. Cirri IV-VI are essentially equal in length with equal rami. At each articulation along the posterior curvature of the intermediate articles of cirri IV-VI there is one short, stout seta, 2-4 long, slender setae, and 1-2 short, slender setae. On the lateral face of both rami of cirri IV-VI immediately below each articulation of the intermediate articles, there is a single row of short spines. Chaetotaxis of the intermediate articles of the posterior three pairs of cirri, along the anterior curvature, is ctenopod, there being three pairs of setae. Between or at the bases of the distal one or two pairs of setae there are one or two short slender setae.

A count of the segments of the cirri of specimen 1 above, illustrated in figure 2, is as follows:

right	anterior ramus	$\frac{1}{22}$ 12	11 11 11	$\frac{111}{13}$	IV 19 22	$\frac{\frac{V}{21}}{25}$	$ \begin{array}{r} \text{VI} \\ 23 \\ \hline 26 \end{array} $
left	anterior ramus	$\frac{23}{12}$	11	$\frac{12}{18}$	$\frac{18}{21}$	$\frac{22}{24}$	$\frac{21}{21}$

Counts of the cirral segments are summarized below for the five specimens dissected. The range (R) and mean (\bar{x}) values for the number of segments in the anterior (a) and posterior (p) rami of the cirri of the right side are as follows:

	I		I.	I	1	11	I	V	V		V.	
	а	p	a	p	а	p	а	p	a	p	а	p
n	5	5	5	5	5	5	5	5	5	5	5	5
\mathbf{R}	15 - 26	8-17	9-14	8-13	8-14	11-20	16-21	16-22	18-24	18-26	19 - 26	19 - 26
$\bar{\mathbf{Z}}$	20.4	11.8	10.8	10.8	11.4	17.2	18.8	20.6	21.0	23.0	22.4	23.4

The intromittant organ is distinctly annulated throughout its length. It is sparsely hirsute except for the tip where there are two or three distinct clusters of setae. There is no basidorsal point.

REMARKS.—In a recent study Rehder (1967) listed the valid zoological names from an anonymously authored auction catalogue of the Portland Museum collections. Of the names cited in this catalogue, which is purported to have been authored by the Reverend John Lightfoot, only one, Balanus ponderosus, is of concern here. In listing this name, Lightfoot referred to a published figure of Lister's (1770, pl. 442, fig. 284). The species represented by that figure most closely resembles Tetraclita stalactifera of all the presently known Caribbean barnacles. Although this illustration of a specimen from Barbados is poorly executed, Rehder (1967, p. 17) stated that, "The form, sculpture, and locality cited under Lister's figure seem to point to this tropical Western Atlantic barnacle but because Lightfoot's name has never been used for this subspecies, it should be considered a nomen oblitum." In concurring with Rehder, it need only be added that Lamarck's species should be conserved because of its widespread and common usage for 150 years, whereas Lightfoot's name, as noted by Rehder, has never appeared in the primary literature.

Passing mention should be made of the species Balanus latus Lamarck (1818, p. 397). This name was also based on the same figure as that of B. ponderosus. Under these circumstances it is obviously not amiss to include this name in the synonymy of T. stalactifera.

Tetraclita stalactifera ranges from South Carolina, through the Caribbean to southern Brazil (Stephensen and Stephensen, 1952; Pilsbry, 1916). It also has been reported from Bermuda (Verrill, 1901; Henry, 1958). Its range in the eastern Pacific is from the Gulf of California to Acapulco, Mexico.

The presence of this species in the eastern Pacific, although over a considerably restricted range, indicates it is a relatively old species, probably ranging as far back as the Miocene. It is readily separable from all other forms of *Tetraclita* on the basis of its geologic history, distribution, color, shell and trophic morphology, and cirral counts;

consequently, it is regarded herein as a full species and cited accordingly.

Subgenus Tetraclitella Hiro, 1939

Tetraclita (Tetraclitella) divisa Nilsson-Cantell

Tetraclita divisa Nilsson-Cantell, 1921, pp. 93, 362, text-figs. 8, 83, pl. 3 (fig. 11).— Visscher, 1927, p. 201, fig. 68.—Hiro, 1939, p. 275, fig. 15.—Zevina and Tarasov, 1963, p. 96, fig. 13.—Stubbings, 1967, p. 291, fig. 21.

Tetraclita (Tetraclitella) divisa subquadrata Ross, 1961, p. 210, pl. 4, fig. 1–5. Tetraclita costata.—Pilsbry, 1928, p. 316.

Material.—Western side of Panto Hole Bay, east of town of Marigot, approximately 15°32′21″ N, 61°17′31″ W; intertidal, on *Tetraclita stalactifera*; May 1–10, 1966; 2 specimens.

Diagnosis.—Shell covered by persistent, hirsute, chitinous membrane; parietes furnished with prominent, radial ribs. Radii with horizontal summits parallel to base; external surface covered with horizontal ridges scored at regular, close-spaced intervals. Scutum broader than high; adductor ridge of variable degrees of prominence, and apically fused with articular ridge to effectively form roof. Tergum only slightly higher than wide; both terga form about one-third of bulk of operculum; spur extremely broad and separated from basiscutal angle by less than one-half its own width. Few low denticles on both sides of shallow, saddle-shaped groove in labrum. Cutting edge of mandible armed with 5 teeth including strongly serrate inferior angle, not furnished with comb.

Supplementary description.—The small size, peltate form, regularity of shell ornamentation and outline, and the pale purple or whitish-purple shell of this species should serve as readily recognizable features for field identification.

Measurements (in mm) of the two specimens in the present collections are as follows:

		shcll		opercular plates			
specimen.	carino-rostral diameter	lateral diameter	height	scutum height	tergum height		
1	11.1	11.1	3.9	4.2	4.0		
2	8.2	7.6	2.6	3.7	3.0		

In view of the excellent available descriptions of this species by Nilsson-Cantell (1921), Hiro (1939), Zevina and Tarasov (1963), and Stubbings (1967), nothing more need be added at this time; however, the specimens were dissected, and cirral counts are given below for each of them:

	right	anterior posterior	1 9 - 5	$\frac{11}{6}$	$\frac{6}{5}$	$\frac{10}{11}$	$\frac{V}{15}$	$\frac{15}{15}$
specimen 1	left	anterior posterior	$\frac{7}{5}$	6 - 5	5 - 4	$\frac{11}{13}$	$\frac{14}{14}$	$\frac{15}{15}$
	right	anterior posterior	$\frac{x}{5}$	6 - 5	$\frac{6}{5}$	$\frac{12}{12}$	$\frac{14}{14}$	$\frac{15}{15}$
specimen 2	left	anterior posterior	$\frac{9}{5}$	$\frac{7}{6}$	5 - 4	$\frac{11}{13}$	$\frac{13}{14}$	$\frac{15}{15}$

In the larger of the two dissected specimens there were about 45 embryos. In the smaller specimen there were 32 cyprids. The latter have been figured by Nilsson-Cantell (1921, text-fig. 8).

Remarks.—Based on specimens collected by A. E. Verrill in the Hawaiian Islands the present writer described *T. divisa subquadrata* (Ross, 1961, p. 210). After critical reexamination of the type specimens the author has concluded that this subspecies does not warrant recognition, and should be considered a synonym of the nominate species.

Nilsson-Cantell (1921, p. 364) described *T. divisa* from specimens collected in Sumatra. Subsequent workers have reported it from Formosa (Hiro, 1939, p. 275), the South China Sea (Zevina and Tarasov, 1963, p. 97), and Ghana on the west coast of Africa (Stubbings, 1967, p. 293). The presence of this species in the Caribbean and the Hawaiian Islands extends greatly its known distribution. The fact that it has virtually a circumtropical distribution tends to confirm the long history of members of the Tetraclitidae.

Family BALANIDAE Leach, 1817

Genus Balanus DaCosta, 1778

Subgenus Megabalanus Hoek, 1913

Balanus (Megabalanus) stultus Darwin

FIGURE 3

Balanus stultus Darwin, 1854, p. 216, pl. 3, figs. 2a–2d.—Weltner, 1897, p. 262.—Gruvel, 1905, p. 221, fig. 243.—Pilsbry, 1916, p. 235.—Nilsson-Cantell, 1929, p. 1, figs. 1c, 1d, 2; 1939, p. 5.—Pilsbry, 1953, p. 25, pl. 2 (figs. 1–3).—Henry, 1954, p. 443.

Tetraclita radiata.—Pilsbry, 1927, p. 38.

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

MATERIAL.—Scotts Head Bay, at southern end of Soufriere Bay; approximately 15°12′40″ N, 61°22′40″ W; 0.5 meters; May 17–28, 1966; 5 living and 2 dead specimens on *Millepora complanata* Lamarck; locality no. 2 of Kier (1966).

DIAGNOSIS.—Basis, radii, and parieties tubiferous. Basal margin of scutum sinuous and strongly protuberant medially; growth ridges of plate straight and narrow at lateral extremities, but flexed basally in medial third. Labrum with 3 teeth on each side of medial notch. Mandible with 5 teeth including inferior angle; second tooth bifid. Cutting edge of maxilla I straight. Living strictly on milleporine corals.

Supplementary description.—This barnacle is readily recognized by its habitat, although the shell is commonly overgrown by the milleporine. In all of the present specimens the shell is high, conical, the parietes slightly to strongly ribbed, and the basis flat. The radii are moderately broad with summits parallel to the basis. The sutural surface of the radii and opposed sutural surfaces possess septa on which both the superior and inferior margins are denticulate.

Shell and opercular dimensions (in mm) of four dissected specimens are as follows:

io as rom	3W5.	shell		opercul	ar plates
specimen	carino-rostral diameter	lateral diameter	height	height scutum	height tergum
1	23.8	18.9	14. 0	5. 9	6. 9
2	19. 1	15.0	13. 2	5.2	6. 1
3	20.7	18.7	16. 1	6. 2	7.3
4	23.4	15.9	16. 7	6.8	7. 1

Both the scutum and tergum are tinted apically, either pink or pale purplish blue. The articular ridge of the scutum is about two-thirds the length of the articular margin, and it terminates in an acute point. In young stages the adductor ridge is prominent, acute, and it extends nearly to the midpoint of the basal margin, but in older specimens it is less prominent and less broadly rounded. The adductor muscle depression is deep, and its outline varies from elongate-oval to oval, to nearly circular.

The tergum is broad, triangular, and thinner than the scutum. The spur is separated by about its own width from the basiscutal angle. Externally, the longitudinal furrow is commonly closed but sometimes open. Crests for the attachment of the tergal depressor muscles are weakly developed, and few in number.

On each side of the deeply notched crest of the labrum there are three teeth (fig. 3d). Interspersed among the teeth and extending laterally the complete length of the crest, there are short, soft setae. Extending obliquely from the superolateral margin on each side of the crest toward the basicentral portion of the labrum, there are

large, elongate-oval patches of spines directed downward toward the esophagus.

The palps are long, high, and spatulate. Along the superior margin the setae are moderately long and densely concentrated, whereas

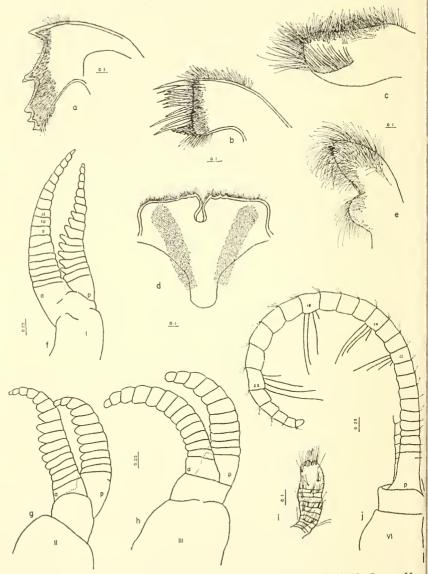


FIGURE 3.—Balanus (Megabalanus) stultus Darwin, 1854, AMNH 12460, Scotts Head Bay, Dominica: a, mandible; b, maxilla I; c, palp; d, labrum; e, maxilla II; f, cirrus I g, cirrus II; h, cirrus III; i, distal end of penis; j, cirrus VI. (Setae omitted on cirri I-III on numbered segments of cirrus VI, only one set of setae shown; a=anterior ramus p=posterior ramus; scale in millimeters.)

at the distal extremity they are significantly longer and more sparsely concentrated. A single row of long setae occurs on the outer lateral face, above and oblique to the basal margin of the appendage.

Five teeth, including the inferior angle, occur along the cutting edge of the mandible (fig. 3a). The distance between the teeth decreases by about one-half proceeding from the first tooth to the inferior angle. The inferior angle is simple, not molariform, and does not project forward beyond the fourth tooth. The second and occasionally the third tooth is bifid, or it bears subsidiary cusps.

Maxilla I has a straight cutting edge, although on one specimen dissected there appears to be a minute notch above the center. The spines are separable into three poorly defined groups, the apical consisting of two long, stout spines, a central group of 10–14 spines of varying lengths and diameters, and a basal cluster of about 7–12 short, very slender spines.

Maxilla II is tall, slender, and the anterior edge distinctly bilobed (fig. 3e). At the juncture of the two lobes there is a large patch of short, stiff bristles.

The anterior ramus of cirrus I is slightly longer than the posterior ramus, the intermediate articles of which are strongly protuberant, whereas those of the anterior ramus are less so (fig. 3f). The anterior ramus of cirri II and III are longer than the posterior. The intermediate articles of both rami of cirrus II are strongly protuberant, but less so in cirrus III (figs. 3g, h). Cirri IV-VI are essentially equal in length, with rami of more or less similar lengths. At each articulation along the greater curvature of the intermediate articles of cirri IV-VI there are two to three short, slender bristles, one short, stout bristle, and one to two very short, fine bristles. Immediately below each articulation of the inner lateral faces of both rami of the posterior three pair of cirri there is a row of short, triangular spines. Chaetotaxis along the anterior curvature of intermediate articles of cirri IV-VI is ctenopod, there being four pairs of setae on each article.

A count of the segments for specimen 1 above (fig. 3) is as follows:

		I	11	111	IV	V	VI
	anterior	19	16	14	25	26	29
right	posterior	17	12	12	31	31	28
left	anterior	19	15	15	23	27	31
-010	posterior	15	14	13	31	32	32

A summary of the data on the cirri of the four specimens dissected are summarized below. Range (R) and mean (\bar{x}) values for the number of segments in the anterior (a) and posterior (p) rami of the cirri of the right side are as follows:

	I				II	Ι	17	7	\	7	V	I
n	а 4	$_{4}^{p}$	$egin{array}{c} a \ 4 \end{array}$	$_{4}^{p}$	a 4	*,	a 4	$_{4}^{p}$	a 4	$p \\ 3$	$\frac{a}{2}$	р 4
R	17-21	13-18	13-16	10-13	12-15	11-14	25-29	29-31	26-32	31-35	29-32	28-34
Ž	19.5	13.2	14.7	11.5	13.2	12.2	28.2	30.0	29.2	32.6	30. 5	31.2

The penis is annulated throughout its length, but it is sparsely hirsute except for the distal extremity (fig. 3i). The basidorsal point is small, bluntly rounded, and sparsely covered with short, stiff bristles

Remarks.—Balanus stultus is herein assigned to the subgenus Megabalanus. Darwin (1854, p. 216), however, obviously could not reconcile the morphological evidence with the sectional (=subgenus) diagnosis he proposed for other megabalanids, and, consequently, he was forced to assign B. stultus to a different section of Balanus, subsequently regarded as the subgenus Conopea. Pilsbry (1953, p. 27) also could not accept the fact that B. stultus is a megabalanid; he stated:

In Florida when I first saw these barnacles I thought they were a species of *Megabalanus* (the *B. tintinnabulum* group), but the absence of pores in the radii was against this view. Later, upon identifying them as *B. stultus*, I was amused to find that Darwin had been similarly embarrassed by the structure of this barnacle.

The failure of earlier workers to note the obvious affinities of *B. stultus* stems from the fact that the tubes of the radii are not readily observed unless the radius is broken away from the parietes. Particularly significant, in regard to facies similarity, are the form and topography of the opercular valves and the structure of the trophic as well as the cirral appendages. It should be pointed out at this time, however, that there are at least two recognizable species groups in the megabalanids that are based in part on certain elements of the mouth field and on certain shell and opercular characters. Some semblance of these two groups may be seen in the key to the species of *Megabalanus* presented by Pilsbry (1916, p. 53). Of these groups, *B. stultus* perhaps is allied most closely to the *B. tintinnabulum* group.

The specimens that Pilsbry (1927, p. 38) reported as *Tetraclita radiata* were subsequently reexamined by Nilsson-Cantell (1939, p. 5), who found them to be specimens of *B. stultus*. It would also appear that the specimen Pilsbry cites and illustrates in the same paper as *B. tintinnabulum antillensis*, growing on *Millepora alcicornis*, may also prove, on closer scrutiny, to be a specimen of the present species.

In a recent paper, Kolosváry (1966) reported the occurrence of what he believed to be a new subspecies of *B. stultus* from Cuba, which he called *morycowae*. The cardinal differences between *morycowae* and the nominate subspecies is that, in the former the adductor

muscle pit of the scutum is circular in outline and the spur faciole of the tergum is extremely narrow and apparently closed. To judge from the studies of earlier workers and from specimens on hand, it appears that the degree and length of closure of the longitudinal furrow of the tergum is highly variable and of little diagnostic value in this species. In regard to the outline of the adductor muscle depression, this too appears to be quite variable and no doubt dependent on the age of the specimen, among other things. Consequently, the author unhesitantly considers Kolosváry's taxon a junior synonym of *B. stultus* and not worthy of recognition.

Although Darwin (1854, p. 216) reported *B. stultus* from Singapore as well as from the West Indies, the western Pacific record obviously is an error.

DISTRIBUTION.—Balanus stultus ranges from the Dry Tortugas (Nilsson-Cantell, 1929) and Florida (Pilsbry, 1953) to Cuba (Kolosváry, 1966) and Curação (Pilsbry, 1927; Nilsson-Cantell, 1939). Pilsbry (1927) reported it growing on Millepora alcicornis Linnaeus, and Weltner (1897) found it to be living on M. complanata.

Summary

Four species of intertidal cirripeds, reported for the first time from the island of Dominica, West Indies, are described and illustrated. Chthamalus angustitergum and Tetraclita stalactifera are elevated to the rank of species. Tetraclita divisa is shown to be of circumtropical distribution, and T. divisa subquadrata is accordingly placed in synonymy with the nominate subspecies. Balanus stultus is removed from the subgenus Conopea and assigned to Megabalanus on the basis of facies similarity and the presence of tubes in the radii. The subfamily Tetraclitinae is elevated to the rank of family.

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1	Kier	Echinoids	1966	121	3577
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3	Kirsteuer	Marine archiannelids	1967	123	3610
4	Allen	Hymenoptera: Tiphiidae	1967	123	3617
5	James	Diptera: Stratiomyidae	1967	123	3622
6	Jones and Schwartz	Bats of genus Ardops	1967	124	3634
7	Schwartz and Jones	Bats of genus Monophyllus	1967	124	3635