The Barnacles of Fiji, with Observations on the Ecology of Barnacles on Tropical Shores[1]

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ABSTRACT: Twenty species of barnacles are now known from Fiji as a result of recent collecting. The barnacle fauna has Malaysian affinities, but there are no endemic species. Brief descriptions and notes on habitats are given. The effects of erosion on the shell are described for the common intertidal species.

The distribution patterns of the common intertidal species, except for those of the coral-boring barnacles, are described; and from these the influence of environmental factors on barnacle distribution is inferred. By determining upper lethal temperatures, recording a few environmental temperatures, and comparing these with similar information on temperate barnacles and shores, I have concluded that high temperatures could be a deterrent to the existence of large numbers of barnacles on sun-exposed surfaces of tropical shores. In shaded conditions barnacles can, however, occupy most of the available surface.

THE BARNACLES on many temperate shores are well known and form conspicuous zones that vary in extent with the ecological conditions on the shore. Ecological information about barnacles on tropical shores is sparse. In the Pacific Ocean, the sessile barnacle faunas of the western and eastern seaboards are distinct (Zullo 1966), but there is still need for more information on the habitats and ranges of intertidal barnacles in the islands of the tropical Pacific.

Some progress has been made toward an understanding of the causes of barnacle zonation in terms of environmental factors (Foster 1971*b*). It has been established, for example, that desiccation resulting from emersion stresses sets the upper limits of the zones, but most of this type of work has been confined to temperate shores. On tropical shores one of the emersion stresses —high temperatures—must be more severe than it is in temperate waters and may be reflected in more restricted intertidal distribution patterns of barnacles on tropical shores, and in their greater temperature tolerance.

This paper describes the species of barnacles found on the shores of Viti Levu during 3 weeks' stay at the University of the South Pacific in May and June 1972. The ecological distribution patterns of the common shore species are described, and, with some observations on the temperature responses of the species, are used to discuss the effects of tropical shore climates on shore biotic zoning.

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SYSTEMATIC PART

The known cirripedes of Fiji now number 20 species in 12 genera as listed below. Although the intertidal shore barnacles of Viti Levu were fairly well sampled, this list does

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not pretend to be complete insofar as the whole island group is concerned. Only a few of the coral-associated barnacles were collected, as they were not deliberately pursued during the stay. Deep water, pelagic, and epizoic species are barely represented.

Lepadomorpha

Lithotrya valentiana (Gray)
Ibla cumingi Darwin
Lepas anatifera Linné (recorded by Borradaile 1900)
Lepas anserifera Linné
Trilasmis amygdalum (Aurivillius)

Balanomorpha

Octomeris brunnea Darwin
Chthamalus intertextus Darwin
Chthamalus caudatus Pilsbry
Chthamalus malayensis Pilsbry
Tetraclita squamosa viridis Darwin
Tesseropora pacifica Pilsbry
Tetraclitella divisa (Nilsson-Cantell)
Tetraclitella multicostata (Nilsson-Cantell)
Balanus (Megabalanus) tintinnabulum occator Darwin
Balanus (Balanus) amphitrite amphitrite Darwin
Balanus (Balanus) amphitrite malayensis Hoek
Balanus (Conopea) cymbiformis Darwin
Creusia spinulosa euspinulosa Broch
Creusia spinulosa acuta Hiro
Pyrgoma milleporae Darwin

SUBORDER LEPADOMORPHA

FAMILY SCALPELLIDAE

Lithotrya valentiana (Gray)

Fig. 1 *C–D*

This barnacle lives in oval holes up to 10 × 7 mm in diameter in coral boulders at the edge of the reef. From above, and when the animal is withdrawn into the hole, the deep locking fold between the terga and scuta can be seen (Fig. 1 *D*). The capitulum has five prominent calcareous plates, the carina and paired terga and scuta, which become eroded apically. The latera and rostrum are absent but sometimes the scales of the upper whorl of peduncle scales are elongated between the bases of the terga and scuta and between the bases of the scuta. The truncate appearance of the plates is due to their apical erosion. The movements of the plates against the rock whilst the animal is feeding wear the plates and effect the burrowing (Otter 1937).

Borradaile (1900) recorded *Lithotrya pacifica* (=*L. dorsalis* according to Sewell 1926) from Funafuti, and this species is distinguished from *L. valentiana* by the presence of prominent lateral plates on the capitulum.

FAMILY IBLIDAE

Ibla cumingi Darwin

Fig. 1 *A–B*

Two specimens were found in crevice habitats at about midtide level on the breakwater at Laucala Bay. The genus is unmistakable because of the four fingernail-like plates, the terga and scuta, rising from the chitinous, hair-covered peduncle, the whole a golden brown in color.

Nilsson-Cantell (1921) recorded *Ibla quadrivalvis* from Fiji. Annandale (1911) cautioned on the identification of *Ibla* species, citing one case of misidentification of the sexually differentiated *I. cumingi* for the hermaphrodite *I. quadrivalvis*. Hiro (1936) accepted Nilsson-Cantell's identification of Fijian *Ibla* when considering the geographic distribution of the genus. In view of more recent ecological accounts of Australian shores (e.g., Endean, Kenny, and Stephenson 1956), which reveal that *I. quadrivalvis* occurs on cool temperate New South Wales shores and that *I. cumingi* occurs on the tropical Queensland shores with no overlap of the species, the existence of the former species in Fiji seemed doubtful.

To check on the Fijian record, I searched

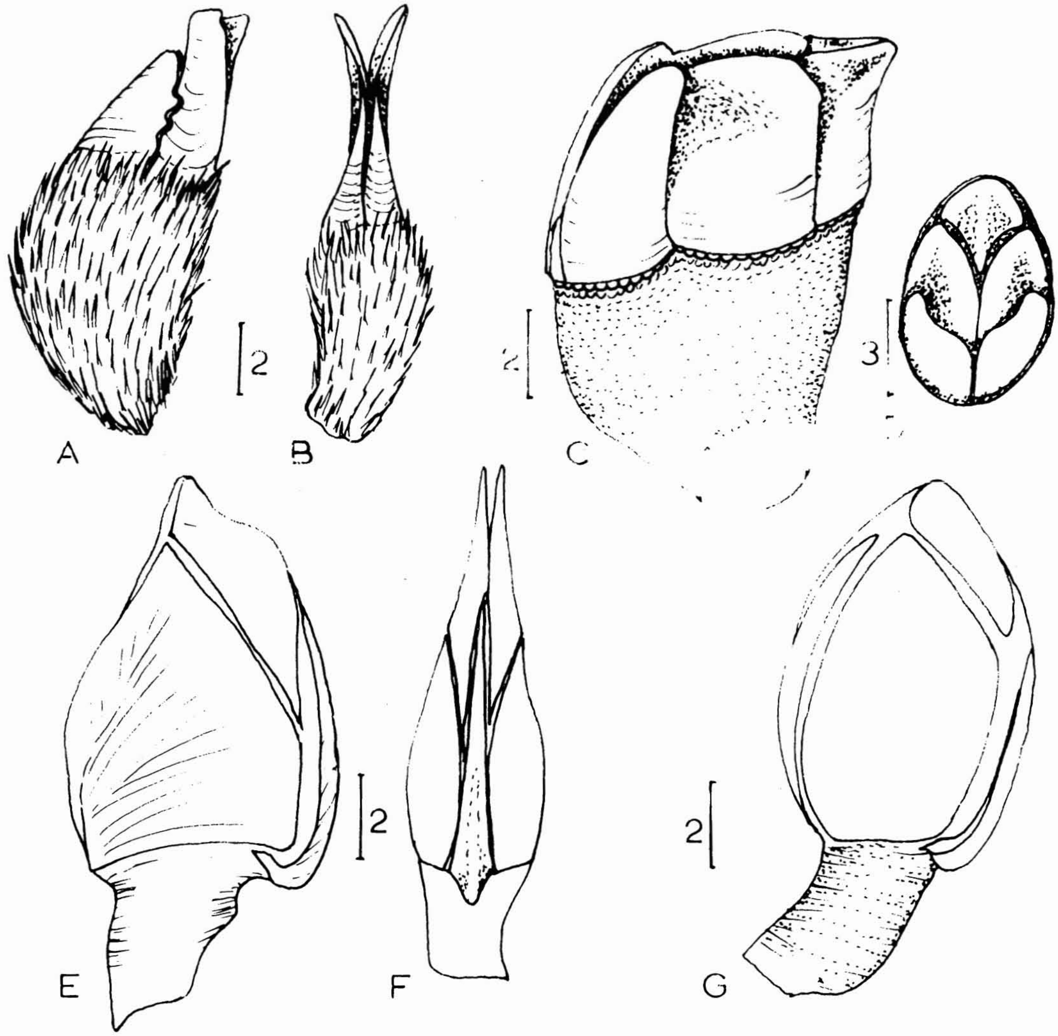

FIG. 1. Lepadomorpha: *A–B*, lateral and rostral views of *Ibla cumingi; C–D*, lateral and apical views of *Lithotrya valentiana; E–F*, lateral and carinal views of *Lepas anserifera; G*, lateral view of *Temnaspis amygadalum*. Scales in millimeters.

likely habitats for *Ibla*. Only two specimens were found, both without a penis and with caudal appendages only a little longer than the protopod of the sixth cirrus. The available data indicate that it is zoogeographically more plausible for only *I. cumingi* to occur in Fiji.

FAMILY LEPADIDAE

Lepas anserifera Linné

Fig. 1 *E–F*

Numerous specimens were found stranded in Laucala Bay attached to driftwood. *Lepas anserifera* is not easily distinguished by external features from *L. anatifera*, which was also recorded from Fiji by Borradaile (1900), but can be identified by the number of filamentary processes on the protopod of the first cirrus and on the side of the prosoma. In *L. anserifera* there are five such processes, but in *L. anatifera* there are only two on each side. Other species of *Lepas* probably also occur in Fijian waters.

FAMILY POECILASMATIDAE

Trilasmis (Temnaspis) amygadalum (Aurivillius)

Fig. 1 *G*

Numerous specimens were found on the mouthparts of a palinurid lobster taken at a depth of 20 feet off Bulia, Kadavu, and they are now in the collections of the University of the South Pacific. The specimens range in size from about 1 to 9 mm capitulum length. Three small specimens were also found on the mouthparts of the lobster *Palinurus versicolor* taken off Nasese Point, Suva.

Some species of *Trilasmis,* namely those of the subgenus *Poecilasma,* are externally similar to *Lepas,* but details of their appendages as well as of their habit—living attached to benthic invertebrates—distinguish them from the pelagic lepadids. In the subgenus *Temnaspis* the scutum is secondarily split, giving a total of seven capitular plates. *T. amygadalum* has been recorded on palinurid decapods from Madagascar through Malaysia to Hawaii (Pilsbry 1927, Nilsson-Cantell 1938).

SUBORDER BALANOMORPHA

Balanomorph barnacles are particularly characteristic of intertidal surfaces. They are prone to desiccation and erosion, although these environmental stresses are somewhat mitigated by the growth of the shell plates. Shell erosion results in a variety of external appearances that makes it difficult to use external shape, color, or sculpture as infallible specific criteria. Balanomorph barnacles can be placed into genera on the basis of the shell plate arrangement. The basic condition is that represented by *Octomeris* (Fig. 2*A–B*) which has eight shell plates enclosing the body and surrounding and supporting the paired opercular valves, the terga and scuta. The shell plates generally overlap or are overlapped by adjacent plates. There is generally an extension of the adjacent plate beneath or internally (the ala) and sometimes an extension (the radius) over the ala of the adjacent plate as well. As the barnacle grows and enlarges, the orifice through which the cirri are protruded needs also to enlarge, and this is primarily effected by attrition of the older apical parts of each plate, including the upper margins of the alae and radii. Some barnacles, particularly those of sublittoral habitats, also enlarge the orifice by the diametric growth of the alae and/or radii.

The individual shell plates are identifiable. In *Octomeris,* the lateral plate is the largest and the carinolaterals and rostrolaterals are placed between the laterals and the unpaired carina and rostrum. In *Chthamalus* there are but six parietal plates, and the arrangement is broadly comparable to *Octomeris* except for the lack of the carinolaterals. Thus in *Chthamalus* the smaller of the lateral plates is situated next to the rostrum and overlies the alae of both the laterals and the rostrum. The possession of a distinct rostrolateral plate characterizes the intertidal Chthamalidae.

In the Balanidae, *Balanus* also has six shell plates, resulting from the fusion of the rostrum and rostrolaterals. The smallest plate is the carinolateral which overlaps the alae of the carina but is itself overlapped by the radius of the lateral. In many species of *Balanus* the shell plates have longitudinal tubes which arise by the folding of the internal plate surface. In *Creusia* the carinolaterals are not developed, and the shell has four plates. In *Pyrgoma,* the shell plates are concrescent as solid shell. *Creusia* and *Pyrgoma* are both coral symbionts.

The Tetraclitidae all have four plates, and are distinguished from balanids on the basis of internal appendages. Most tetraclitids have porous wall plates and the tubes develop toward the outer shell surface. In *Tesseropora,* there is one primary row of tubes which extend from the inner to the outer shell laminae even though secondary tubes may develop peripherally. The radii are poorly developed, and orifice enlargement is by apical attrition. *Tetraclita* also has poorly developed radii, but there are many rows of tubes in the shell plates. *Tetraclitella* also has many rows of tubes in the shell plates, but orifice enlargement is brought about by diametric growth of alae and radii.

KEY TO THE GENERA OF FIJIAN BALANOMORPHS

1.	Shell plates 8 in number	*Octomeris*
	Shell plates 6 in number	2
	Shell plates 4 in number	3
	Shell plates fused into a cylinder	6
2.	The rostrum is overlapped by the rostrolaterals; plates are solid; carinolaterals absent	*Chthamalus*
	The rostral plate overlaps the latera; plates porous; carinolaterals present	*Balanus*
3.	Barnacles embedded in coral	*Creusia*
	Barnacles with exposed shell plates	4
4.	Shell plates without radii and separated by a narrow fissure	5
	Shell plates with wide radii	*Tetraclitella*
5.	Shell plates permeated by one complete row of large tubes	*Tesseropora*
	Shell plates permeated by numerous rows of small tubes	*Tetraclita*
6.	Barnacles embedded in coral	*Pyrgoma*
	Barnacles with exposed shell plates	7
7.	Shell plates with longitudinal tubes	5
	Shell plates solid	*Chthamalus*

The opercular valves are the terga and scuta. These have internally various ridges, crests, and pits by which the valves articulate with each other or to which muscles are attached. Because the internal sculpture is less subject to environmental alteration, the opercular valves provide good taxonomic characters.

FAMILY CHTHAMALIDAE

Octomeris brunnea Darwin

Fig. 2 *A–D*

The shell is generally a depressed conical shape. In uneroded and juvenile specimens the color is gray-brown, the plates are ribbed, and the crenated margins of the plates diverge from the orifice, like spokes on a wheel. Toward the base, the plates abut in crenate sutures. The persistent brown epidermis bears tiny spines along the horizontal growth lines on the ribs. Eroded specimens are grayish with black areas and streaks where chitinous laminae in the shell are exposed. The apices of the plates are worn so that there is a smooth, wide orifice. The zigzag sutures between the plates extend from the orifice to the base and are more or less obvious. The articulating edges of the scuta and terga are initially straight when viewed from the exterior, but with erosion the ends of the articular ridges become obvious, producing the wavy, dovetailed sculpture characteristic of eroded chthamalids.

Octomeris brunnea has been well described anatomically by Darwin (1854), Hiro (1939), and Pope (1965) from southern Japan through Malaysia to the Coral Sea (Pope 1965). It also occurs on the mainland of Queensland, in the New Hebrides Islands, and in the Santa Cruz Islands.

Chthamalus intertextus Darwin

Fig. 3 *A–E*

This species is the highest intertidal barnacle on Fijian shores, and is readily recognized by a unique set of shell characters. As in all chthamalids, appearance varies with the degree of erosion of the shell.

The shell is generally much depressed. In young and uneroded specimens the plates

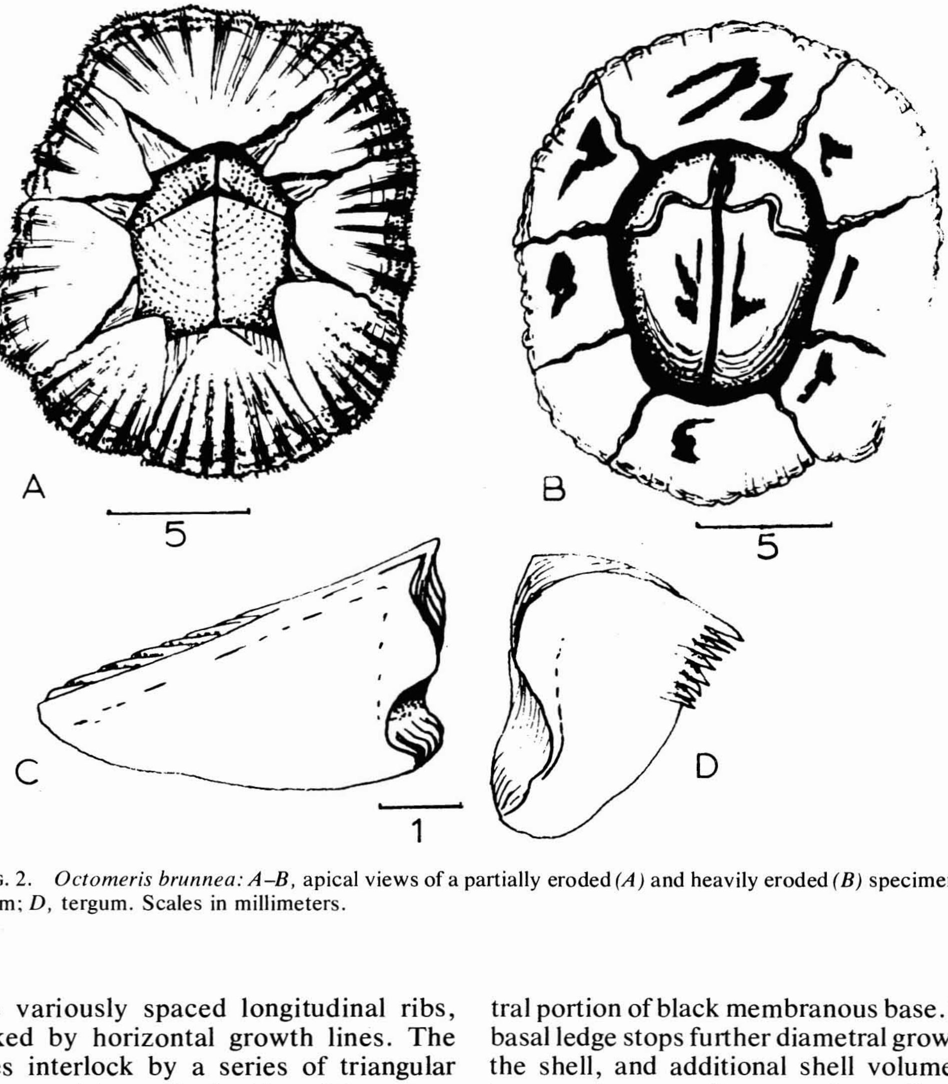

FIG. 2. *Octomeris brunnea: A–B,* apical views of a partially eroded *(A)* and heavily eroded *(B)* specimens; *C,* scutum; *D,* tergum. Scales in millimeters.

have variously spaced longitudinal ribs, marked by horizontal growth lines. The plates interlock by a series of triangular laminae, arising on both sides of the suture and external to the alae, and producing pronounced zigzag sutures. With increasing erosion these sutures become wavy, then straight, and in larger specimens are obliterated altogether. In older eroded specimens the surface of the shell is finely granular and is of a white to pale violet color. Internally, the shell plates are violet colored; the coloration is particularly intense near the sutures and may show up externally along the lines of the sutures. In larger specimens the base is partially calcareous; a peripheral shelf of shell is firmly calcified to the inner basal shelf of the wall plates, leaving a central portion of black membranous base. This basal ledge stops further diametral growth of the shell, and additional shell volume enlargement apparently occurs by vertical elevation of the basal ledge, resulting in a curious columnar form to the shell (Fig. 3*D*).

In uneroded specimens the scuta show growth lines and there is a faint indication of the wavy articular line with the terga, but in eroded older specimens the externally featureless opercular valves are firmly calcified.

Chthamalus intertextus has been recorded from a number of Pacific localities ranging from Malaysia to Hawaii through Melanesia and Micronesia. It was previously recorded from Fiji by Pope (1965).

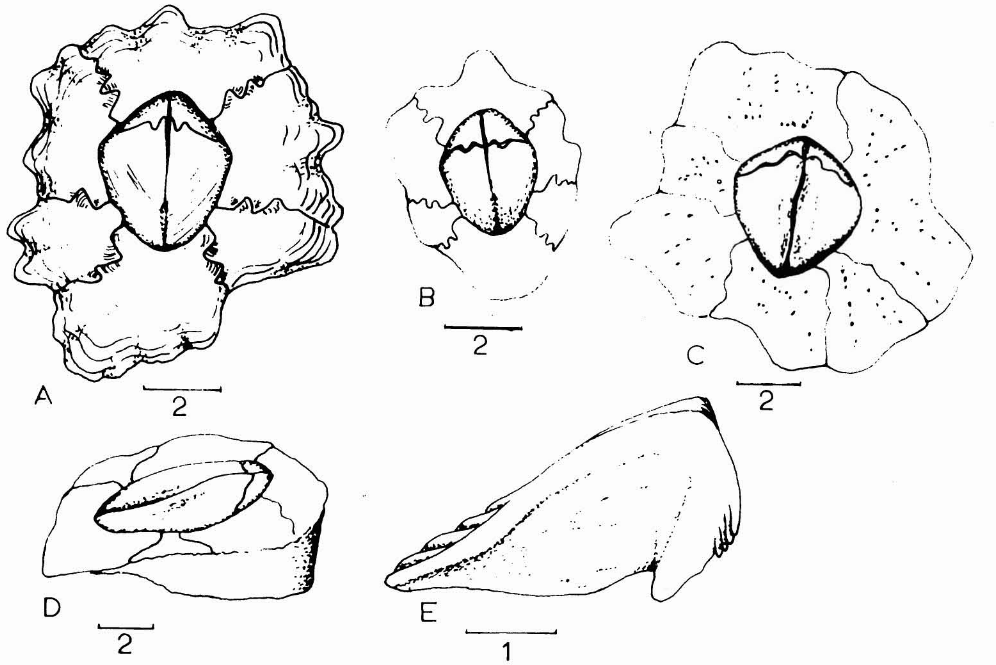

FIG. 3. *Chthamalus intertextus: A–C*, apical views of progressively more eroded specimens; *D*, lateral view of specimen with vertical basal wall; *E*, inner view of fused scutum and tergum. Scales in millimeters.

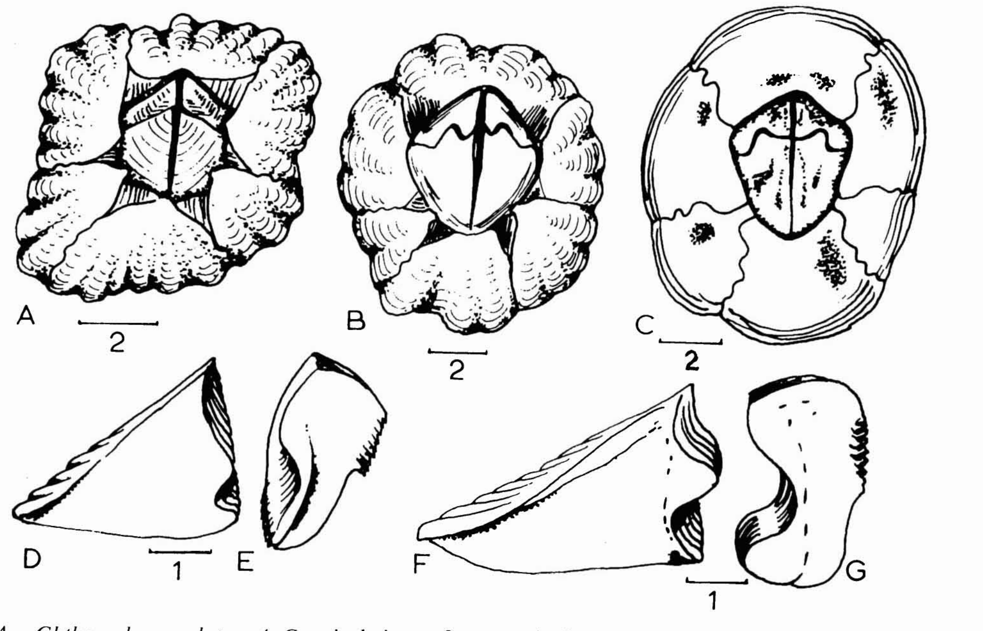

FIG. 4. *Chthamalus caudatus: A–C*, apical views of progressively more eroded specimens; *D–E*, scutum and tergum of an uneroded juvenile specimen; *F–G*, scutum and tergum of a large and eroded specimen. Scales in millimeters.

Chthamalus caudatus Pilsbry

Fig. 4 *A–G*

This species occurs commonly on and under intertidal rock or stonework. The most characteristic features are the long caudal appendages arising on either side of the anus at the bases of the protopods of the sixth cirri. The original description has been amplified by Pope (1965). The shell is conical but depressed; in juveniles and uneroded specimens it is covered by brown integument. The shell plates have two to four broad ribs, and the orifice is toothed by the projecting apices of the lateral and rostrolateral plates. In eroded specimens the shell is generally a light gray color with darker areas or lines showing through as shell laminae are eroded. In juveniles and uneroded specimens the shell plates meet below the exposed part of the alae in a straight line, but with erosion of surface shell layers the sutures become wavy, especially toward the base. In eroded specimens, the opercular valves also lose their external sculpturing and show a dovetailed suture between terga and scuta. The base is membranous and when ruptured reveals red ovarian masses within.

C. caudatus is found throughout the Malaysian Archipelago, the Philippines, South China Sea, Palau Islands to the Queensland coast, south to a lattitude of about 25° S.

Chthamalus malayensis Pilsbry

Fig. 5 *A–G*

This species is remarkably versatile with respect to its substratum requirements and tolerance of shore environmental factors, and consequently exhibits a variety of shell

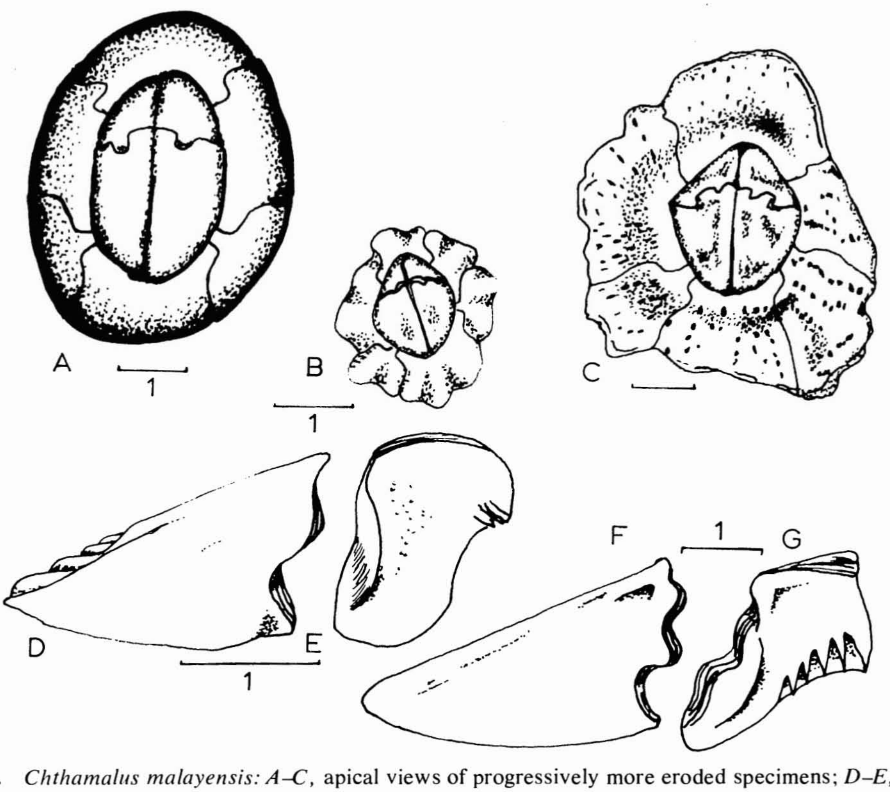

FIG. 5. *Chthamalus malayensis: A–C*, apical views of progressively more eroded specimens; *D–E*, scutum and tergum of an uneroded juvenile specimen; *F–G*, scutum and tergum of a large and eroded specimen. Scales in millimeters.

forms. Pope (1965) has resolved many of the problems surrounding the identity of this species. Young and uneroded specimens (Fig. 5 *A*) retain a persistent dark brown integument, and the shell plates may be quite smooth or with a few broad ribs. Young, eroded specimens, such as those typical of reef crest boulders (Fig. 5 *B*) are devoid of epidermis, are of a whitish color and usually have markedly ribbed shell plates. In shaded habitats the species may reach quite large sizes (15 mm diameter) and be very eroded, with longitudinal rows of black bosses on the shell plates (Fig. 5 *C*). The suture between the terga and scuta is dovetailed and wavy and becomes more pronounced with erosion. The sutures between the shell plates are, however, always simple. The base is membranous, and the underlying ovarian tissue is a creamy yellow color.

Chthamalus malayensis ranges from the Persian Gulf and Western Australia to Formosa, the Philippines, New Caledonia, Palau Islands, and south on the Queensland coast to a latitude of about 25° S (Pope 1965).

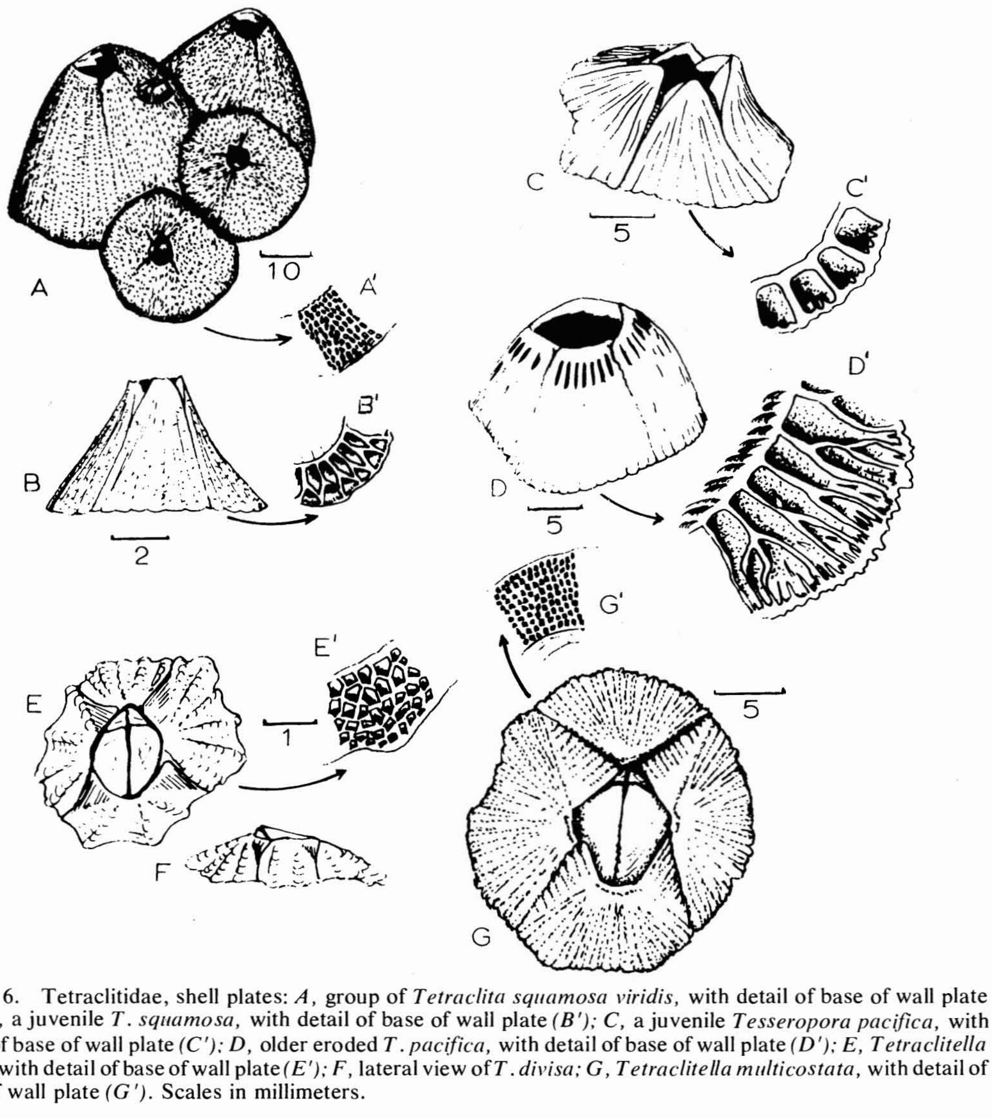

FIG. 6. Tetraclitidae, shell plates: *A*, group of *Tetraclita squamosa viridis*, with detail of base of wall plate *(A')*; *B*, a juvenile *T. squamosa*, with detail of base of wall plate *(B')*; *C*, a juvenile *Tesseropora pacifica*, with detail of base of wall plate *(C')*; *D*, older eroded *T. pacifica*, with detail of base of wall plate *(D')*; *E*, *Tetraclitella divisa*, with detail of base of wall plate *(E')*; *F*, lateral view of *T. divisa*; *G*, *Tetraclitella multicostata*, with detail of base of wall plate *(G')*. Scales in millimeters.

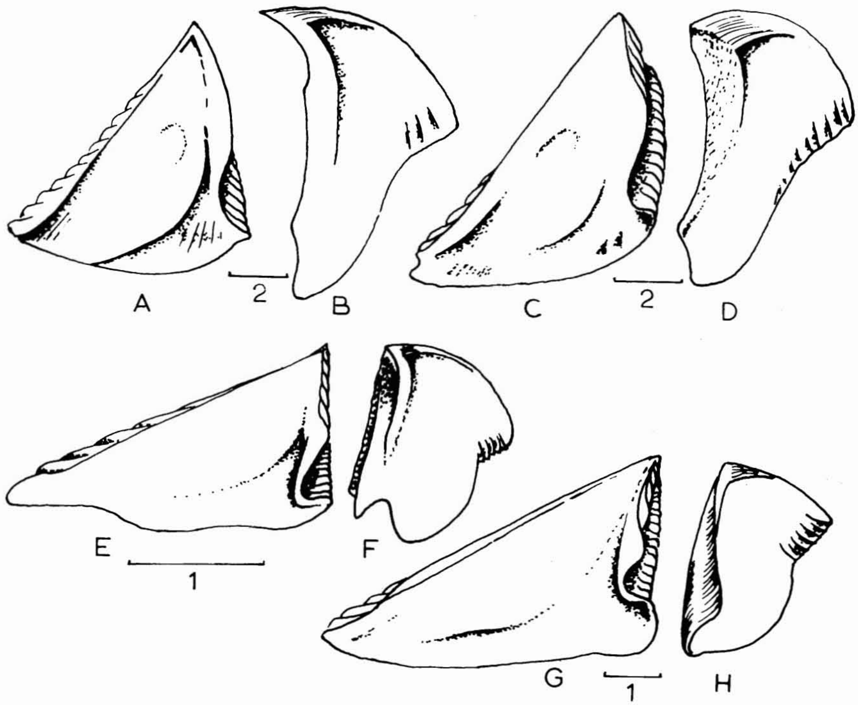

FIG. 7. Tetraclitidae, opercular valves: *A–B*, scutum and tergum of *Tetraclita squamosa viridis*; *C–D*, same of *Tesseropora pacifica*; *E–F*, same of *Tetraclitella divisa*; *G–H*, same of *Tetraclitella multicostata*. Scales in millimeters.

FAMILY TETRACLITIDAE

Tesseropora pacifica (Pilsbry)

Figs. 6 *C–D*, 7 *C–D*.

This species occurs commonly on emergent boulders on the reef flat, particularly where there is likelihood of considerable water movement. The shell shape varies from depressed to steeply conical or truncated-conical, with a rhomboidal orifice from ⅓ to ½ the basal diameter. In juvenile and uneroded specimens the outside of the shell plates is longitudinally and finely ribbed and of a faint pinkish color. In older eroded specimens the ribs are more prominent, especially on the upper part where they are pink or purplish and form the upstanding secondarily filled tubes of the plates. There is but one complete row of tubes, although in large specimens the intertube laminae branch peripherally and somewhat irregularly once, twice, or three times, producing extra rows of secondary and tertiary tubes. The primary tubes, however, reach the outer shell lamina. Short plates and sharp curved spines depend from the outer lamina into the tubes. The radii are narrow and when not obliterated by erosion show denticulate sutural edges. The sutures between the plates become obscure with erosion. In older specimens there is a thick nonporous calcareous base. Internally, the sheath is reddish brown.

Tesseropora pacifica is characterized by the presence of calcareous spines in the parietal tubes and by the inconspicuous scutal adductor ridge. It has been recorded from Wake and Necker islands (Pilsbry 1927) and from the Marshall Islands (Henry 1957). I have also examined specimens from New Caledonia. The species has not been recorded from the Australian mainland and is not represented in collections examined from the Solomon Islands. *Tetraclita vitiata*, however, occurs in both Queensland

and the Solomons, and a related species, *Tesseropora wireni,* is also present in the Solomons. Henry (1957) has remarked that the tendency to form secondary rows of tubes in older specimens renders the distinction between *Tesseropora* and *Tetraclita* invalid. On the basis of there being only one complete row of tubes Zullo (1968) and Ross (1969) have confined the present species to *Tesseropora*. In relatively large specimens of *Tetraclita vitiata* (22 mm basal diameter) examined from the Solomon Islands, some of the tubes extend from inner to outer laminae. *T. vitiata* would seem, therefore, more properly assigned to *Tesseropora* if both genera are to be recognized.

Tetraclita squamosa viridis Darwin

Figs. 6 *A–B*, 7 *A–B*

This subspecies, like *Tesseropora pacifica,* occurs commonly on emergent boulders on the reef flat where there is likelihood of considerable water movement. The shell shape varies from depressed conical to steeply conical, and is characterized by the relatively small orifice, craterlike at the top of the cone. In juvenile uneroded specimens (Fig. 6 *B*) the four shell plates are distinct and longitudinally ribbed with an intact integument. The ribs correspond to the outer row of longitudinal tubes within the plates. Very young specimens have a single row of tubes, each of which in cross section is elongated along the radius of the whole shell (Fig. 6 *B′*). As the animal grows, the septae between the primary row of tubes repeatedly bifurcate, yielding numerous honeycomblike tubes externally and basal to the primary ones. In their upper part the tubes become solidly filled up with a hard purplish black substance. The radii are narrow.

As the outer and upper parts of the shell become eroded, the solid tube filling is exposed as longitudinal ridges that are usually finely beaded. With considerable erosion, the sutures between the plates become obscure. In older specimens a solid calcareous base is laid down. The shell varies externally in color from light gray to purplish black. Internally, the sheath and the inner surfaces of the opercular valves are of a greenish hue.

This subspecies has been well described by Darwin (1854) as *Tetraclita porosa viridis,* by Pilsbry (1916) as *T. squamosa squamosa,* and by Nilsson-Cantell (1921) as *T. porosa viridis*. Although the nominate species has a circumtropical distribution, the subspecies *viridis* has an Indo-Malay-Pacific distribution. It occurs as far east as in the Gulf of Panama (Broch 1932) but not in the West Indies as quoted by Nilsson-Cantell (1938). The nearest to Fiji it has been recorded is Rotuma Island (Borradaile 1900). The subspecies occurs on the Queensland coast south to a latitude of about 25° S (Endean, Kenny, and Stephenson 1956).

Tetraclitella divisa (Nilsson-Cantell)

Figs. 6 *E–F*, 7 *E–F*

This species is a member of the "hypobion" or understone fauna of the shore. The shell is depressed and, when uneroded, pale purplish in color and covered by a hirsute chitinous integument. The orifice is about one-quarter the basal diameter and is diamond shaped. The shell plates have more or less prominent radiating ribs and are internally composed of up to five rows of four- to six-sided tubes. Radii occupy the whole of the space between adjacent shell plates. The radii are porous, the tubes running parallel to the base of the shell. Externally on the radii there are lines of growth paralleling the suture of the adjacent plate.

There is a complete nonporous calcareous base in larger specimens, but it is only peripherally perfect in smaller specimens.

T. divisa is somewhat atypical among balanomorph barnacles in that the embryos are brooded in the mantle cavity to the cypris larval stage, whereas most other species release the first stage nauplius (Nilsson-Cantell 1921, Hiro 1939). The species is circumtropic in distribution and has been recorded from Malaysia, the South China Sea and Formosa, Hawaii, Ghana, and the

Caribbean Sea (Ross 1968). I have also examined specimens from Aldabra Island, Indian Ocean.

Tetraclitella multicostata (Nilsson-Cantell)

Figs. 6 *G*, 7 *G–H*

Two specimens, one intact and one empty shell, were collected from sun-exposed low tidal surfaces amongst breakwater boulders in Laucala Bay. It is certainly not a common species as more specimens deliberately were sought on other low tides. The specimens are identified as being of the same species as the single specimen described from Misool Archipelago as *Tetraclita purpurascens multicostata* by Nilsson-Cantell (1930). This form has not been redescribed; therefore, a fairly full description is given here.

The shell is depressed-conical, with a rhomboidal orifice about one-third the width of the base. The shell plates are externally finely ribbed longitudinally and contain numerous small tubes which are honeycomblike in end view. The radii are well developed and have summits parallel to the base of the shell. The external surface of the radii is ribbed transversely in the same fashion as the longitudinal ribs on the parietes. Internally, the radii are superficially porous in the direction of growth, but deeper in the tubes run longitudinally, parallel to those of the main part of the shell plates. The apices of the radii of the lateral plates stand above the apex of the carina.

There is a thin calcareous base. The scuta are transversely elongated, with a nearly straight basal margin and a very faint adductor ridge. The terga are triangular, with a wide articular furrow, and the basal margin curves convexly from the crests of the depressor muscle to the basiscutal angle.

Although the opercular valves resemble those of *Tetraclitella purpurascens*, the specimens cannot be referred to this latter species because of differences in the shell plates. The pores are much smaller and more numerous than in equivalent sized *T. purpurascens* from New Zealand. The radii have external ribbing like those of the parietes, in contrast to the smoother radii of *T. purpurascens;* and, contrary to the condition in the latter species, there is a thin calcareous base. The elevated apices of the radii of the lateral plates resemble the condition in *Tetraclitella darwini* (Pilsbry) from Japan, which species, however, does not have an elongated scutum. Contrary to the sentiments of Nilsson-Cantell (1930), I regard the points concerning the parietal plates important differences from *T. purpurascens,* and must regard *multicostata* as a separate species.

T. purpurascens is recorded as occurring on the plates of the pedunculate barnacle *Pollicipes mitella,* and, therefore, as being of a tropical west Pacific distribution (Nilsson-Cantell 1921, 1930). The opercular valves of *T. purpurascens* figured by Nilsson-Cantell (1921) are somewhat different from New Zealand material in that the spur of the tergum is indistinguishable from the basiscutal angle and that the scutum is not as elongated. *T. purpurascens* occurs commonly on temperate Australian and New Zealand shores, but it does not occur on the Queensland coast north of a latitude of about 25° S (Endean, Kenny, and Stephenson 1956). It is, therefore, possible that the extra-Australasian records of *T. purpurascens,* except for those of the forms *chinensis* and *nipponenses* (which are now regarded as a separate species, *T. chinensis*), may refer to *T. multicostata,* which would then have a Malaysia-West Pacific distribution.

FAMILY BALANIDAE

Balanus tintinnabulum occator Darwin

Fig. 8 *K–M*

Specimens were found on the lower levels of a large coral boulder on the reef edge of Laucala Bay. The shells are steeply conical and with close-set longitudinal ribs, the lower half of which bear erect, upwardly curved, calcareous spines. The plates, when not encrusted, are white or tinged a light drab purple. There is a calcareous base. The radii have striations parallel to the base of

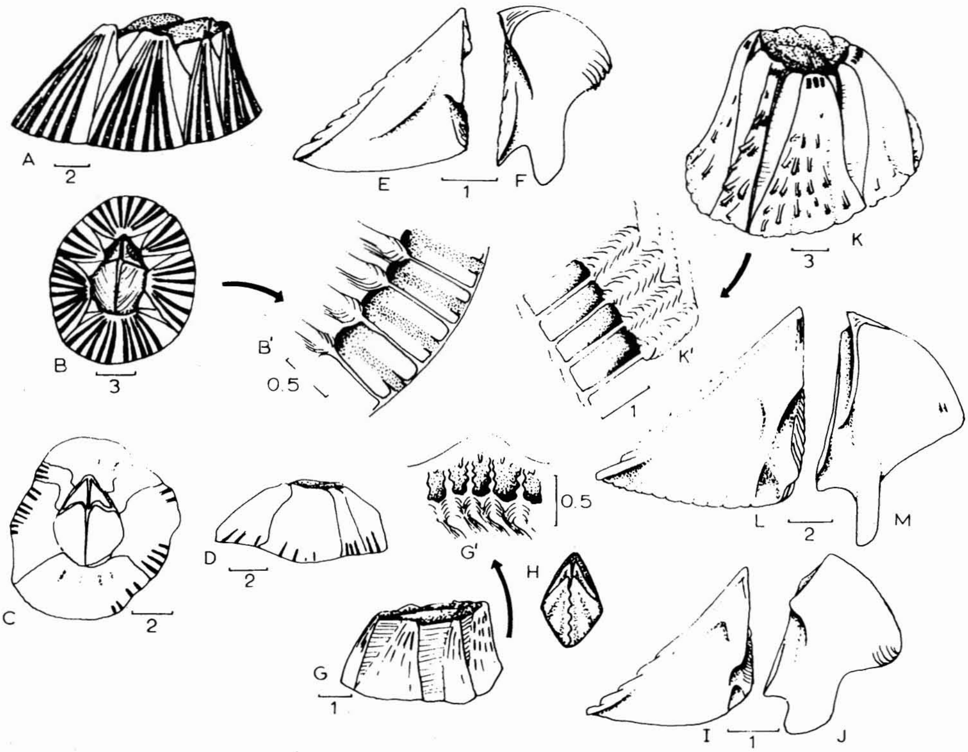

FIG. 8. Balanidae, free-living *Balanus: A–B*, lateral and apical views of *Balanus amphitrite amphitrite*, with detail of base of wall plate *(B'); C–D*, apical and lateral views of eroded *B. a. amphitrite; E–F*, scutum and tergum of *B. a. amphitrite; G*, lateral view of *Balanus amphitrite malayensis*, with detail of base of wall plate *(G'); H*, apical view of opercular valves of *B. a. malayensis; I–J*, scutum and tergum of *B. a. malayensis; K*, lateral view of *Balanus tintinnabulm occator*, with detail of base of wall plate *(K'); L–M*, scutum and tergum of *B. t. occator*. Scales in millimeters.

the shell and, like the shell plates, contain a single row of tubes. The tubes may be open apically in eroded specimens, revealing horizontal partitions in each tube.

Balanus tintinnabulum (sensu lato) is cosmopolitan. The specimens to which Darwin gave the subspecific name *occator* were from the "South Seas." Borradaile (1900) recorded the more definite location of Fiji. Pilsbry (1916) doubted the authenticity of the Fiji habitat because most specimens of *Balanus tintinnabulum* in collections were taken off ships, and, from his evidence, he cited the distribution as being Indo-Pacific. Hiro (1939) recorded the species from Formosa.

The species may or may not have been introduced by shipping, but the habitat that this subspecies occupies in Fiji is comparable to that occupied by another subspecies on northern New Zealand shores. Both are established members of the surf-exposed low tidal faunas.

Balanus amphitrite amphitrite Darwin

Fig. 8 *A–F*

Specimens of this typical form of *Balanus amphitrite* were found at low tidal levels on the breakwater at Laucala Bay, at higher levels in desiccation-protected habitats within the boulder piles, and also on a permanently submerged surface of a floating pontoon in Laucala Bay. The shell shape is usually truncated-conical, sometimes with a concave carina. The external surface is without ribs, but there are continuous longitudinal stripes of purplish red which on the rostral plate may be in two groups on either side of a median, wide, white band. In eroded specimens, the stripes remain only toward the base, and the sutures between the shell plates are linear. The shell plates, except for the radii, have a single row of tubes, each elongated in the radial axis of the shell. There is a calcareous base in which there are radiating tubes.

Balanus amphitrite amphitrite is a cosmopolitan, tropical to warm temperate water barnacle, and has variously been recorded from a number of localities as any of the varieties *"communis," "hawaiensis,"* or *"denticulata"* (Stubbings 1967). It is a fouling species and appears to be restricted to the quieter waters of harbors and lagoons.

Balanus amphitrite malayensis Hoek

Fig. 8 *G–J*

This subspecies was found on dead coral on the reef flat at Korotoga. It is of a low truncated conical shape, and the plates are externally smooth and colored white with discontinuous pink vertical stripes. The shell plates contain small rounded longitudinal tubes. The radii are broad and solid. The base is calcareous with a few small radiating tubes.

These specimens belong to the "Philippine forms of *amphitrite* in which the adductor ridge of the scutum is very much reduced" (Pilsbry 1916). Pilsbry promised to illustrate these forms later, but the relevant report evidently did not appear. The descriptions and figures of Hoek's var. 10 for *B. amphitrite* (Hoek 1913), which he called *malayensis,* are fairly close to the present material. Forms of *B. amphitrite* without an adductor ridge on the scutum have been described so far from Malaysian and Philippine localities.

Balanid barnacles associated with and boring into coelenterate hosts were not deliberately sought. The following were encountered and are listed and illustrated for completeness: *Balanus (Conopea) cymbiformis* Darwin (Fig. 9 *A–C*), on red and yellow gorgonian in the collections of the University of the South Pacific but without data. This species has a tropical Indo-West-Pacific distribution and has been re-

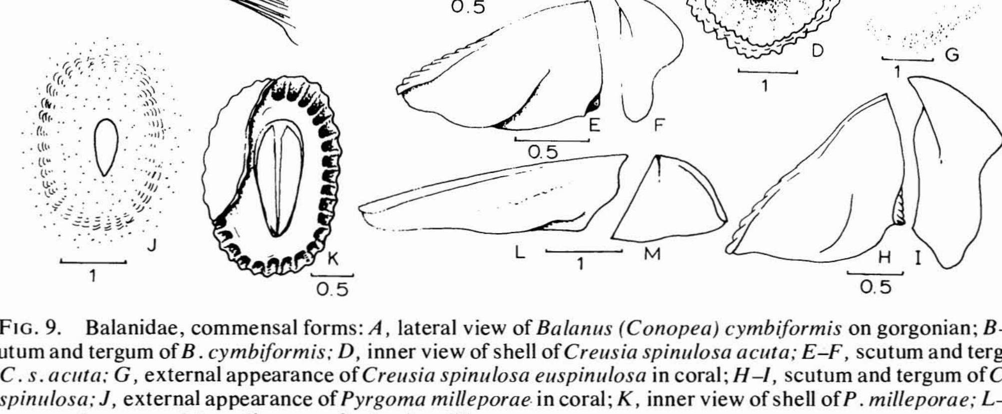

FIG. 9. Balanidae, commensal forms: *A*, lateral view of *Balanus (Conopea) cymbiformis* on gorgonian; *B–C*, scutum and tergum of *B. cymbiformis; D,* inner view of shell of *Creusia spinulosa acuta; E–F,* scutum and tergum of *C. s. acuta; G,* external appearance of *Creusia spinulosa euspinulosa* in coral; *H–I,* scutum and tergum of *C. s. euspinulosa; J,* external appearance of *Pyrgoma milleporae* in coral; *K,* inner view of shell of *P. milleporae; L–M,* scutum and tergum of *P. milleporae*. Scales in millimeters.

corded from Fiji ("südöstlich von Mbau, auf *Melitodes* in der Ebbregion") (Nilsson-Cantrell 1921); *Creusia spinulosa euspinulosa* Broch (Fig. 9 *G–I*), in coral; *Creusia spinulosa acuta* Hiro (Fig 9 *D–F*), in coral; and *Pyrgoma milleporae* Darwin (Fig. 9 *J–M*), in millipore coral.

ZOOGEOGRAPHY

The barnacle fauna of Fiji is tropical, without any endemic species. None of the species are known from cool temperate seas, and only two (*Lepas anatifera* and *Balanus amphitrite amphitrite*) are known from warm temperate waters to the south in New Zealand. These two species, and *Lepas anserifera, Tetraclitella divisa, Pyrgoma milleporae,* and *Creusia spinulosa* are, at any rate, cosmopolitan. Their powers of dispersal apparently have overcome marine geographic barriers.

The rest of the species would seem to represent a Malaysian-derived fauna, with *Ibla cumingi, Temnaspis amygadalum, Chthamalus malayensis, Tetraclita squamosa viridis, Balanus cymbiformis,* and possibly *Balanus tintinnabulum occator* known from the Indian Ocean and extending eastward into the Pacific Ocean. *Lithotrya valentiana, Octomeris brunnea,* and *Chthamalus caudatus* have a distribution from Malaysia to Queensland, whilst *Chthamalus intertextus, Tetraclitella multicostata,* and *Balanus amphitrite malayensis* (so far as is known for the latter two) do not reach Australia but occur in Malaysia and the Philippine Archipelago. Only one species, *Tesseropora pacifica,* is known only from tropical West Pacific islands.

This fauna shows a derivation distinct from that of tropical northern Australia, where species such as *Tetraclita vitiata, T. coerulescens,* and *Chthamalus withersi,* which are not found in Fiji, occur. Of the barnacles of the Kermadec Islands to the south of Fiji, only *Lepas anatifera* and *Creusia spinulosa* are also in the Fijian fauna, and they are cosmopolitan. The others show Australasian affinities. Unfortunately too little is known of the barnacles of other Polynesian islands to gauge the extent of the Malaysian influence eastward in the Pacific Basin.

THE DISTRIBUTION OF THE SPECIES ON FIJIAN SHORES

Lepas spp. are associated with floating and drifting objects, *Temnaspis amygadalum* and *Balanus cymbiformis* are associated with subtidal invertebrate hosts, *Creusia* and *Pyrgoma* are associated with corals, and *Ibla* was found in the expected intertidal crevice habitat. The other species are all colonizers of available space on intertidal substrata, and the following account describes for these species the distribution patterns with respect to tidal height, shading from insolation and exposure to surf, strong water currents, or prevailing winds.

Figures 10 and 11 show information gathered from three localities on Viti Levu: Laucala Bay near Suva, the reef area near Korotoga on the "coral coast," and the northeastern part of the island.

In Laucala Bay (Fig. 10), visits were made to the foreshore, the man-made breakwater extending out into the bay, and the boulders at the reef edge. The foreshore is silted and unsuitable for barnacle attachment except where there are branches and roots of mangroves and where man-made jetties or seawalls have been constructed. The breakwater provides hard, massive boulders within the intertidal zone and, also, has seaward and landward aspects (Fig. 10 *B–C*). The dominant foci in the zonation on these hard surfaces are a rock oyster and a small black mussel. Barnacles are not very conspicuous on exposed boulder surfaces but are more noticeable on vertical surfaces and underneath boulders. *Chthamalus intertextus* is the highest occurring species but is found only on the seaward side which is also exposed to the prevailing wind. It tends to be patchy in distribution, occurring in densities up to 10/dm² and reaching a size of 15 mm shell diameter. It ranges over about one-third of a meter at the mean high water neaps level, above the oysters.

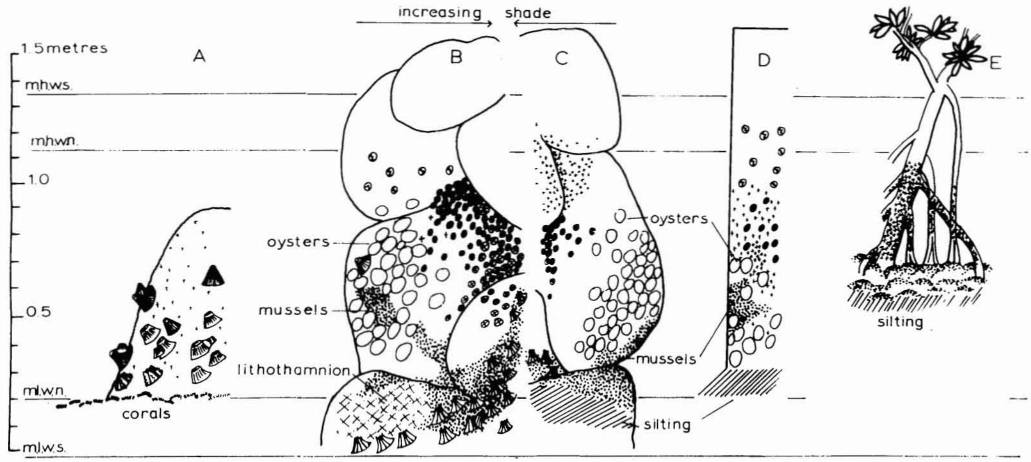

FIG. 10. The intertidal distribution of barnacles on surfaces in Laucala Bay: *A*, on coral boulder toward the reef edge; *B*, seaward side of breakwater; and *C*, landward side of breakwater; *D*, seawall at Suva Point; *E*, mangrove tree toward upper beach. See Fig. 11 for key to the species of barnacles. Tidal information from Admiralty Tide Tables.

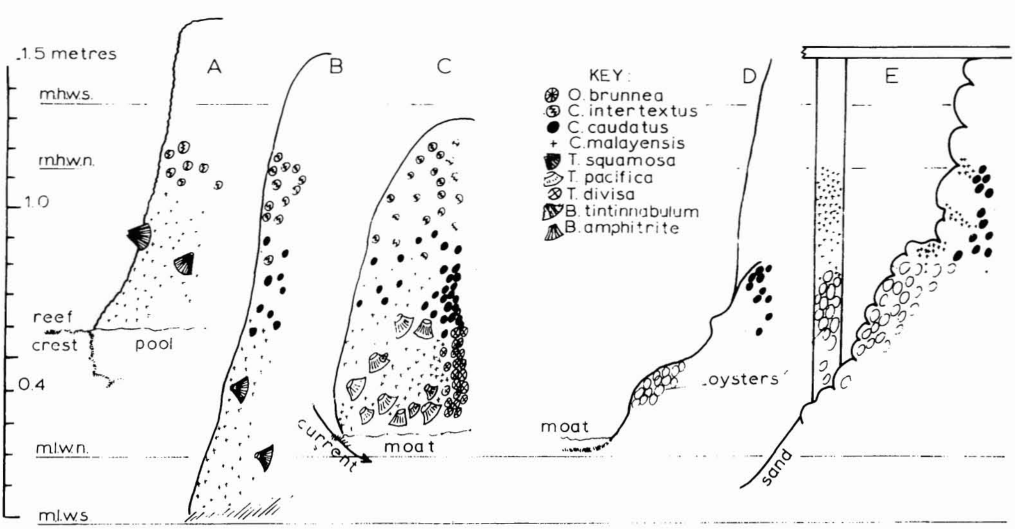

FIG. 11. The intertidal distribution of barnacles on surfaces at Korotoga *(A–C)* and northeast Viti Levu *(D–E)*: *A*, coral boulder on reef crest; *B*, basalt boulder in lower level drainage area associated with the Korotoga Stream; *C*, basalt boulder on the edge of the raised reef flat, showing a crevice to the lower right; *D*, basalt shore at Uthuinathauthau Point, with the horizontal scale considerably shortened; *E*, beneath the wharf at Ellington Wharf. Tidal information from Admiralty Tide Tables.

Amongst the oysters and only on the seaward side is an occasional large *Tetraclita squamosa*, about one solitary individual every 3 meters along the breakwater. At low tidal levels, mean high water neaps to mean low water springs, encrusting lithothamnion and mussles dominate, on the latter of which specimens of *Balanus amphitrite* occur.

Further into shaded conditions *Chthamalus caudatus* dominates the rock surface from about midtide level to mean low water neaps, reaching maximum sizes of about 10 mm shell diameter and averaging densities of about 40/dm^2, although the species was denser on the seaward side and in more shaded and higher places. Amongst the outermost *C. caudatus* on the seaward side, occasional large specimens of *Chthamalus malayensis* are found. Densities of *C. malayensis* on the lee side occur up to 3,000/dm^2, but all specimens are small (2 mm shell diameter). Occasional specimens of *Octomeris brunnea* are also intermingled with the densest aggregations of *Chthamalus caudatus*.

In even more shaded conditions, as in places where one had to crawl in amongst the boulders, the rock surface from about mean low water neaps to just above midtidal level is dominated by *Tetraclitella divisa*, a species which there frequently covers 100 percent of the rock surface. Below the *T. divisa*, and intermingled with them to about midtidal level, *Balanus amphitrite* occurs in densities up to 200/dm^2, frequently on mats of mussels.

On the east side at the shore end of the breakwater, where it traverses a sandy beach and where the rocks receive glancing wave action, *Chthamalus intertextus* is rare at high tidal levels, and *C. malayensis* occurs abundantly on shaded surfaces of the boulders. No other barnacles were found. On the west side, where wind and wave conditions are minimal, the only barnacle present is *C. malayensis*, which is abundant above the dense mats of mussels to about mean high water neaps, particularly on shaded surfaces. Fig. 10*E* shows the stems and roots of a small mangrove tree in this locality, which carry a 100 percent cover of *C. malayensis* 5 mm in diameter.

On the west-facing side of a concrete wall to the west of the breakwater, sheltered from prevailing winds but experiencing some wave action through the entrance to the breakwater-protected part of Laucala Bay, narrow zones of scattered individuals of *C. intertextus* and *C. caudatus* occur above the oysters. Here also, *C. malayensis* occurs scattered amongst the oysters and *C. caudatus*, but is nowhere more abundant than 300/dm^2 and is very small. A floating pontoon moored at the end of this wall carries dense populations of *Balanus amphitrite* on its submerged parts.

On the vertical seawall at Suva Point, (Fig. 10 *D*), which is not protected by the breakwater and which faces due south, the bands of *C. intertextus*, *C. caudatus*, and *C. malayensis* are as at the jetty wall in Laucala Bay, but the specimens are more dense and the zones more obvious.

All of the sites so far mentioned are protected from severe surf action by the offshore barrier coral reef. The strength of the surf is such that intertidal surfaces above the reef flat at the reef edge are absent. There are occasional coral boulders set back on or beyond the reef crest which must be exposed to considerable water turbulence when the tide is in. On these boulders (Fig. 10 *A*), if they are high enough, is a narrow zone of *C. intertextus* at mean high water neaps to mean high water springs, and below this to the moat level the large barnacles *Tetraclita squamosa* and *Tesseropora pacifica* occur, often growing on each other. *B. tintinnabulum* was found here at the lowest levels. Also, below the *Chthamalus intertextus* is a scattering of *C. malayensis*, and, burrowing into the rock, *Lithotrya valentiana*.

At Korotoga (Fig. 11 *A–C*), there are a number of basalt boulders on the reef flat, which would not be subject to such turbulent conditions as occur near the reef crest. Nevertheless, there is for much of the tide a steady current flow past some of these boulders as the sea water drains off the reef flats into lower level drainage areas associated with the Korotoga stream. Basalt boulders here have a band of *Chthamalus intertextus* at high levels and an underlying zone of *C. caudatus*, both species being more dense in crevices or under overhangs. Below the *C. caudatus* is a scattering of *C. malayensis* and variable numbers of the large tetraclitids *Tetraclita squamosa* and *T. pacifica*. One boulder (Fig. 11*C*) has a deep fissure on its lower part, and in the depths of this is *T. divisa*. Oysters and mussels were not noted on any of these boulders.

At Uthuinathauthau Point on the northeast of Vitu Levu (Fig. 11*D*), a small inshore reef is situated close to a gently sloping, rocky shore. A narrow band of oysters is present, and the only other noticeable sessile animal above the corals is *Chthamalus caudatus,* this species living in local aggregations in shaded sides of boulders and ridges at slightly higher levels. This is a shore of high insolation and minimal wave action, the former because of the gentle slope, the latter because of the accumulation of coral particles (but not silt) between the rocks. In nearby Viti Levu Bay (at Naiserelangi), where there are mangroves in extremely sheltered parts, stones and rocks on the beach under the shade of overhanging trees are covered by aggregations of small *C. malayensis* and *C. caudatus*.

At Ellington Wharf (Fig. 11*E*), the basalt boulders of the roadway to the wharf are devoid of barnacles, but under the superstructure and on the piles of the wharf *C. malayensis* and *C. caudatus* occur. On the inner pilings, *C. malayensis* occurs in densities up to $3{,}000/dm^2$.

The northeast Viti Levu situations are not exposed to the prevailing trade winds as are the Laucala Bay and Korotoga regions. The lack of wave action is likely to be expressed by the absence of the high tidal splash zone and surf-dependent reef crest barnacles, such as *C. intertextus* and *T. squamosa* respectively.

ENVIRONMENTAL FACTORS THAT INFLUENCE THE DISTRIBUTION OF FIJIAN BARNACLES

The importance of various environmental factors are inferred below from the distribution patterns. The inferences are at least consistent with the facts and with what is known about barnacle zonation on temperate shores (Foster 1969, 1971*a, b*).

Water turbulence is apparently a requirement of *Tetraclita squamosa* and *Tesseropora pacifica;* specimens reach their largest size and greatest densities near the reef crest. *Chthamalus intertextus* also evidently requires some degree of wave turbulence at high tidal levels. The significance of the hazardous conditions of the emersion environment is indicated by the erosion of the older shells and by the paucity of barnacles on rock surfaces that would be likely to receive prolonged emersion and insolation, particularly over the midday periods. At the relatively low tidal levels that *Tesseropora squamosa* and *T. pacifica* occupy, the adults obviously survive these conditions if only because of their large size (reduced permeability compared with juveniles, see Foster 1971*a*). Evidently enough individuals also survive through postsettlement stages to maintain viable adult populations; chances of survival are no doubt greatly enhanced by the short emersion periods and proximity to wave turbulence. Similar chance factors must operate for the establishment of *Chthamalus intertextus* at high tidal levels, but this species must be better equipped to withstand emersion conditions.

Other species are characteristically "hypobiotic": *Chthamalus caudatus, Octomeris brunnea,* and, especially, *Tetraclitella divisa* can only establish themselves in habitats not too exposed to drying, i.e., at lower levels than *Chthamalus intertextus* and in shaded positions. Presumably the upper limit of distribution of these species is set by desiccating conditions acting on the juvenile stages. The lower limits may be set by biotic factors associated with the immersion environment, such as predation or competition for space.

In contrast, *Balanus amphitrite* is a sublittoral species, utilizing what space it can and extending into the intertidal to progressively higher levels with increasing shade. It settles on mussels and does not necessarily compete for rock space with them. It is an "opportunist" in the sense that the species rapidly colonizes available space as long as the physical factors permit. It is a fouling species.

In the same sense, *Chthamalus malayensis* is also an opportunist, but this species is restricted to intertidal levels. It is not a sublittoral fouling barnacle. Compared with

Balanus malayensis, it evidently has a greater tolerance to emersion conditions and has less ability to compete with or otherwise meet the space demands of lower shore and sublittoral encrusting life. *Chthamalus malayensis* occurs over most of the shore irrespective of wave conditions, but it reaches greater sizes and densities in shaded conditions. Like *Balanus amphitrite,* it beats its cirri through the water and will hold its cirri erect in passive filter feeding. Probably because shore shading is more prevalent on the wind and wave sheltered inshore regions, *Chthamalus malayensis* is more characteristic of the calmer regions.

Balanus tintinnabulum apparently is a species not adapted to prolonged emersion and requires reasonably strongly turbulent conditions. It is restricted to wave-exposed low tidal levels.

Sun-exposed rock surfaces in wave-sheltered conditions are inhospitable to the survival of barnacles. Because much of the actual shoreline space is wave protected by wave-mitigating coral reefs and platforms, it is not surprising that, compared with temperate shores, tropical shores seem somewhat depauperate of barnacles. Only when shaded habitats or boulders in regions of strong water movement are examined do barnacles become obvious. Thus, as the emersion climate on tropical shores must be more severe than that on temperate shores, the barnacle species may not necessarily be correspondingly more tolerant than temperate species. An attempt to assess the physiological adaptation of tropical shore barnacles is described in the next section.

THE TEMPERATURE TOLERANCE OF FIJIAN BARNACLES

A determination of the tolerance of a species to all the factors of the emersion environment would require control of such factors as temperature, humidity, and wind velocity, as well as a consideration of the size and shape of the animals. Some progress has been made toward these goals on European species (Foster 1969, 1971*b*).

High tidal species appear to tolerate higher temperatures than do low tidal species. The assessment of temperature tolerance is a lengthy procedure if tolerance is defined with respect to age, acclimation, duration of exposure, etc. However, the upper lethal temperature (LT_{50}; that temperature which will cause 50-percent death in a population sample when the temperature is raised at a constant and specified rate) seems little affected by age or acclimation. Time-temperature-survival curves that define the 50-percent survival limit when temperatures lower than the LT_{50} are maintained also tend to have the same shape for several species. Assuming the universality of these findings, at least among barnacles, LT_{50}s were determined for some of the Fijian species, and from curves fitted to these values the temperatures required to kill half the populations after certain times were also assessed.

Barnacles were collected on Laucala Bay shores, brought into the laboratory, and immersed in fresh and aerated seawater, the temperature of which was slowly raised (0.2 C°/minute). The activity of the barnacles was observed. Particular note was made of the temperatures at which the valves no longer responded to touch (coma) and of the temperatures at which the specimens failed to recover on being returned to normal temperatures in fresh seawater. This latter characteristic was determined by removing samples of the specimens at various temperatures, allowing time for recovery (6 hours), and testing for a positive and full withdrawal of the opercular valves when the latter were touched. The upper lethal temperature was that at which 50 percent of the sample failed to recover in this way.

The data are given in Table 1. It is clear that the species can be ranked in order of their intertidal zonation, the highest occurring species, *Chthamalus intertextus,* being the most tolerant of high temperatures. The low tidal to sublittoral species *Balanus amphitrite* was least tolerant of high temperatures.

The highest temperatures experienced by these barnacles would occur when the animals are exposed to the insolation effects of

TABLE 1

TEMPERATURE TOLERANCES (IN °C) OF BARNACLES FROM FIJI*

SPECIES	HEAT COMA AT:	HEAT DEATH AT:	DEATH AFTER 3 HOURS WHEN MAINTAINED AT:	DEATH AFTER 6 HOURS WHEN MAINTAINED AT:
Chthamalus intertextus	46	52.0	47.3	45.4
Chthamalus caudatus	46	51.5	46.9	45.0
Tetraclita squamosa	–	51.4	46.6	44.7
Chthamalus malayensis	44	49.7	45.1	43.2
Tesseropora pacifica	44	49.2	41.7	42.5
Balanus amphitrite	43	45.4	41.7	38.9

NOTE: Specimens were raised from ambient temperature at a rate of 0.2 Centigrade degrees per minute.

the sun when the tide is out. Information on temperatures on tropical shores is practically lacking, but some field temperatures were recorded on the sunniest day during the stay in Suva. A thermistor mounted in the end of a fine probe was used to measure temperatures in animal tissues and on the rock surface, and the temperatures were then recorded on a strip chart. Maximum temperatures are given in Table 2. On the other days, with hazy cloud conditions, rock surfaces at right angles to the sun reached temperatures of between 35° C and 40° C, and the temperatures of tissues of oysters and barnacles were a few degrees below.

TABLE 2

TEMPERATURES RECORDED BY THERMISTOR PROBE THERMOMETER IN THE FIELD, LEE OF BREAKWATER, LAUCALA BAY 26 MAY 1972

Max temp on rock surface in sun at top of barnacles (maintained for 45 min, at least)	45° C
Max temp of oyster tissues, in sun	40.5° C
Max temp of tissues of *Chthamalus intertextus*, in sun	42.5° C
Max temp of tissues of *Chthamalus caudatus*, in shade	28.0° C

The temperatures given in Table 2 do not represent the highest possible. However, rock surface temperatures of 45° C could be expected and would be instantaneously lethal to *B. amphitrite*, and, if held for a few hours, would be lethal to *Tesseropora pacifica* and *Chthamalus malayensis*. It is these species that occur either low on the shore where they are emersed but for short periods or in shaded midtidal habitats. The more heat-tolerant species, too, would experience temperatures not far below those that are lethal if they occurred on the exposed rock surfaces. High temperatures may be a significant factor in limiting zonation of barnacles on tropical shores, keeping sun-exposed surfaces clear of barnacles, particularly at the higher levels. At and after settlement, higher temperatures would accelerate water loss from juveniles with larger surface area to volume ratios and poorer integumental permeability. Then the effect may be dehydration as much as heat death.

The temperature tolerances of Fijian barnacles are compared in Table 3 with those of species of barnacles from the shores of North Wales and northern New Zealand. The differences between the temperature tolerances of high tidal species from these shores is less than that between high and low tidal species of any one of these shores. From this it may be inferred that microclimatic gradients are more severe across a shore than between the same levels of these cool-temperate to tropical shores.

The upper shore barnacles of Fiji are not markedly more tolerant of high temperatures than are those of the temperate shores. With the higher environmental temperatures, the result, in zonation terms, is that

TABLE 3

COMPARISON OF THE INSTANTANEOUS LETHAL TEMPERATURES (°C) OF INTERTIDAL BARNACLES FROM WALES, NEW ZEALAND, AND FIJI.

POSITION	MENAI BRIDGE, NORTH WALES		AUCKLAND, NEW ZEALAND		SUVA, FIJI	
High Tidal	*Chthamalus stellatus*	49.7	*Chamaesipho brunnea*	51.6	*Chthamalus intertextus*	52.0
Mid Tidal	*Balanus balanoides*	42.2	*Chamaesipho columna*	48.1	*Chthamalus caudatus*	51.5
	Elminius modestus	44.2	*Elminius modestus*	44.5	*Chthamalus malayensis*	49.7
			Elminius plicatus	46.9	*Tetraclita squamosa*	51.4
					Tesseropora pacifica	49.2
Low Tidal	*Balanus crenatus*	36.8	*Balanus amphitrite*	46.7	*Balanus amphitrite*	45.4
	Balanus balanus	36.5				

the zones on Fijian shores are not so much depressed tidally as driven into shaded conditions. But shaded intertidal surfaces suitable for barnacle settlement are not common; inshore there are beaches or silted conditions, and near the reef edge strong surf prevents an accumulation of boulders. It is not surprising, therefore, that many of the surfaces studied and described for this paper are man-made ones. The piled boulders of the breakwater in particular provide a range of habitats across gradients of the factors associated with exposure to wind, waves, and sun; deep within the shade of the breakwater, conditions are apparently favorable for 100-percent barnacle cover at midtidal levels.

The paucity of barnacle biomass on tropical West Pacific shores has been commented on by Newman (1960). To account for this paucity Stephenson and Searles (1960), Newman (1960), and Stephenson (1961) maintain that fish browsing is a chief cause. Grazing by herbivorous fish and by large chitons keeps the low tidal surfaces clear of algae and also probably accelerates the rate of coral erosion. Such activities may indeed contribute to set the lower limits of barnacle zones, but are not necessarily the cause of overall low barnacle biomass. From further field observations, Stephenson (1968) had doubts about the fish-grazing hypothesis, noting varying rates of settlement and mortality due to unknown causes among populations of *Tetraclita vitiata* at Heron Island. His earlier experiments with caged samples of this species (Stephenson, 1961) could be explained on climatic causes; caged barnacles will be shaded microclimatically to some degree and could be expected to survive the occasional severe conditions better than could uncaged ones.

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