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The Marine Fauna of New Zealand: Barnacles (Cirripedia: Thoracica)

by

BRIAN A. FOSTER



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A



B



C



D



E



F

FRONTISPIECE Species of *Balanus* found in New Zealand, showing the characteristic colouration of the opercular tissues: (A) *B. tintinnabulum*; (B) *B. decorus*; (C) *B. decorus* (right) and *B. campbelli* (left); (D) *B. trigonus*; (E) *B. amphitrite*; (F) *B. variegatus*. All these species are fouling barnacles in New Zealand waters. The commonest boat-fouling species in New Zealand is *Elminius modestus*, which has a white shell and white opercular tissues (see Plate 12).

NEW ZEALAND
DEPARTMENT OF SCIENTIFIC AND INDUSTRIAL RESEARCH

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CONTENTS

	<i>page</i>		
ABSTRACT	5	Suborder BALANOMORPHA	72
Introduction	6	Family Chthamalidae	72
Material studied and acknowledgments	6	Genus <i>Chamaesipho</i>	72
Historical survey	7	Family Pachylasmidae	76
Morphological and systematic characters . .	8	Genus <i>Pachylasma</i>	76
The shell plates	9	Genus <i>Hexelasma</i>	79
The mouthparts	10	Genus <i>Aptolasma</i>	83
The cirri	12	Family Tetraclitidae	86
The life-cycle	13	Genus <i>Epopella</i>	87
Systematics . .	14	Genus <i>Tesseropora</i>	90
Classification and list of species	14	Genus <i>Tetraclita</i>	91
Suborder LEPADOMORPHA	15	Genus <i>Tetraclitella</i>	93
Family Heteralepadidae	15	Family Balanidae	95
Genus <i>Heteralepas</i>	15	SUBFAMILY BALANINAE	95
Genus <i>Paralepas</i>	17	Genus <i>Elminius</i>	95
Family Iblidae	20	Genus <i>Balanus</i>	97
Genus <i>Ibla</i> . .	20	Genus <i>Creusia</i>	114
Family Oxynaspidae	22	SUBFAMILY CORONULINAE	115
Genus <i>Oxynaspis</i>	22	Genus <i>Coronula</i>	115
Family Poecilasmidae	24	Genus <i>Tubicinella</i>	116
Genus <i>Trilasmis</i>	24	Genus <i>Platylepas</i>	116
Genus <i>Megalasma</i>	26	Genus <i>Stomatolepas</i>	117
Family Lepadidae	29	Distribution of barnacles within the New Zealand region	118
Genus <i>Lepas</i>	29	Geographic affinities of the New Zealand barnacle fauna	120
Genus <i>Conchoderma</i>	35	Evolution of the Lepadomorpha	121
Genus <i>Alepas</i>	36	Evolution of the Balanomorpha	124
Family Scalpellidae	38	Zonation of barnacles . .	127
Genus <i>Calantica</i>	38	Evolution of barnacle zonation	128
Genus <i>Smilium</i>	49	Barnacle paleoecology	131
Genus <i>Arcoscalpellum</i> . .	51	REFERENCES . .	133
Suborder VERRUCOMORPHA	68	APPENDIX: Station details	136
Family Verrucidae	68	INDEXES	140
Genus <i>Verruca</i>	68	PLATES	144

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ABSTRACT

Barnacle specimens from the shore and shelf of New Zealand have been studied, and all known species from New Zealand waters are here systematically described and illustrated. The New Zealand barnacle fauna now comprises 61 species, of which 8 are described as new species, and 15 are recorded for the first time from New Zealand seas.

The material studied has revealed facts that have required changes in nomenclature for two well-known species. The endemic intertidal scalpellid long known as *Pollicipes spinosus* (Quoy & Gaimard) is placed in the genus *Calantica* since complementary males have been found in the interscutal niche in some specimens. The endemic intertidal balanomorph long known as *Elminius plicatus* (Gray) is placed in the genus *Epopella* of the family Tetraclitidae. The diagnosis of the characteristically subtidal balanomorph family Pachylasmidae is more clearly defined.

The New Zealand barnacle fauna is discussed in terms of its geographic distribution and affinities, and its bathymetric distribution (zonation). The isolation of certain morphologically primitive species—the calanticids *Calantica spinosa* and *C. villosa*, the tetraclitid *Epopella plicata*, and the balanids *Elminius modestus* and *Balanus vestitus*—is a notable feature, especially when it is considered that closely related species of these balanomorphs are isolated in temperate South American or Australasian seas.

The evolution of the Lepadomorpha is discussed in terms of their substrate requirements and the development or loss of capitular shell plates. The evolution of the Balanomorpha is discussed in terms of their shore zonation and the accompanying modifications of shell structure.

INTRODUCTION

Barnacles are familiar animals, commonly found on wharf piles, the bottoms of boats, and the rocks of the seashore. Although some species occur at high intertidal levels, where they are immersed in sea water for short and infrequent periods, and a few species extend their distribution into permanently brackish water, they are basically a marine group of animals. They feed by filtering plankton from the sea on the setose body appendages or cirri and, when mature, produce copious larvae which seek and colonise suitable substrates for the sessile adult existence.

Most species of barnacles have the body enclosed within protective shells which, on the animals' death, may be retained in marine sediments; this fossil record reveals a comparatively recent radiation of barnacles, from about the middle of the Carboniferous period. The series of jointed appendages and the various numbers, shapes, and arrangements of the shell plates in the external integument provide an unusually good array of morphological features. Consequently, the classification of barnacles has reached an agreeable level of sophistication.

The ascothoracican cirripedes, in contrast to the thoracican cirripedes or barnacles proper, have a less modified crustacean body plan, and are parasitic on echinoids and antipatharians on the sea floor. The basically sessile and hermaphroditic condition of the Thoracica may have resulted from parasitic origins, possibly via something like the Ascothoracica. Many modern stalked barnacles occur epizoically on benthic invertebrates—*Oxynaspis* on antipatharians, the poecilasmatids on crustaceans and echinoids, and *Paralepas* on

crustaceans. The lepads and heteralepads occur more indiscriminately on living, inorganic, floating, nektonic, or benthic objects. The scalpellids also have more catholic tastes for substrata, but are chiefly benthic in shallow and deep seas. The verrucosomorphs and balanomorphs seem to have been independently derived from scalpellid-like ancestors by the loss of the peduncle, probably in relation to not needing to elevate the body from the substratum on current- and wave-swept inshore surfaces. The Balanomorphs are essentially colonisers of hard, clean substrates, but some have assumed epizoic habits, with preferential selection of invertebrate and vertebrate hosts ranging from corals to whales. Barnacles have thus evolved to colonise a wide variety of surfaces in the sea.

This paper reviews the New Zealand barnacle fauna. Each species has been considered in as much detail as was permitted by the available material, to assess ontogenetic and environmental variation in the normally used taxonomic characters of the appendages and shell. The paper describes and illustrates each species systematically, and also considers ecological and zoogeographical implications to barnacle phylogeny and radiation.

Most of the species are illustrated in the 14 plates, and are arranged there in the same systematic order as in the text. The plates are grouped together, so that by a "flip through" the plates a barnacle can be positioned approximately in the taxonomic sequence. Detailed comparison with the photographs, and particularly with the text and accompanying line drawings, should enable specific identifications, unless of course the specimen in hand is new to the fauna.

MATERIAL STUDIED, AND ACKNOWLEDGMENTS

This study of the New Zealand barnacles was initiated by an invitation to work the extensive sorted collection of Cirripedia held by the New Zealand Oceanographic Institute. For this invitation, and for all their subsequent co-operation, I thank Mr E. W. Dawson and Dr Penelope Luckens of the Institute. The NZOI station data and the species identified or described for each station are listed in the Appendix.

Much other material has been examined. Many people have given specimens and information, and are collectively thanked here and noted in the relevant parts of the systematic treatment. Much of this material remains in my barnacle collection, which is now in the Zoology Department of the University of Auckland.

Several people have generously made available specimens in their charge. In particular I thank Dr E. J. Batham for the loan of some Otago shelf specimens and the use of facilities at the Portobello Marine Biological Station; Dr J. Yaldwyn for access to the barnacles in the National (formerly Dominion) Museum collection; and

the Directors of the Otago, Canterbury, and Auckland Museums for access to their respective collections.

Mr G. Batt has given invaluable assistance with the photography involved in the preparation of the manuscript.

Type specimens of material described as new in this work are deposited in the institutions designated in each case. Abbreviations of institutions and collections named in this paper are as follows:

Auck. Mus. – Auckland Museum;

Cant. Mus. – Canterbury Museum, Christchurch;

BAF – author's collection in Zoology Department, Auckland University;

Nat. Mus. – National Museum, Wellington;

NZOI – New Zealand Oceanographic Institute, Wellington;

PMBS – Portobello Marine Biological Station, University of Otago, Dunedin;

Otago Mus. – Otago Museum, Dunedin.

HISTORICAL SURVEY

New Zealand barnacles were probably included in the natural history collections of Cook's voyages, and some of the specimens may later have been the source of Darwin's New Zealand records. In 1827 the *Astrolabe* called at New Zealand; the barnacles collected during the voyage were described in the account of Quoy & Gaimard (1834), and included from New Zealand *Anatifa spinosa*, *A. elongata*, and *A. tubulosa*. The first of these is clearly what came to be known as *Pollicipes spinosus* and is herein referred to as *Calantica spinosa*. The second is herein recognised as *Lepas testudinata*, and *A. tubulosa* would seem to be what subsequently became known as *Heteralepas quadrata*.

In 1839 Dieffenbach visited New Zealand, and his collections, and those of others, were compiled by J. E. Gray into a "Fauna of New Zealand" as an appendix to Dieffenbach's "Travels in New Zealand" (1843). In this were listed 9 species of barnacles—those of Quoy & Gaimard, 2 whale barnacles now known as *Coronula diadema* and *Tubicinella major*, and 2 unidentified species of *Balanus*. Gray also recorded and named *Cortia depressa* (herein *Tetraclitella purpurascens*) and *Elminius plicatus* (herein *Epopella plicata*) in that list.

The foundations of modern barnacle studies were laid by the monographs of Darwin (1851, 1854), in which 146 species were systematically described, 59 of them as new species. Darwin specified New Zealand as a locality for 14 species—those of Quoy & Gaimard (except for *A. elongata*, which he found enigmatic), those of Gray (except for *Tubicinella major*), *Lepas australis*, *L. fascicularis*, *Pollicipes sertus* (now a synonym of *P. spinosus*), *Balanus decorus*, *B. trigonus*, *B. amphitrite*, *B. vestitus*, *Elminius modestus*, and *Chamaesipho columna*. Of these new records, only *L. fascicularis* and *C. columna* had already been named.

The barnacles held in the Otago Museum were listed by Hutton (1879), who described as new species *Pollicipes darwini*, *Elminius sinuatus*, and *Elminius rugosus*, none of which have since been upheld because they are clearly variants of the common intertidal species *Calantica spinosa*, *Elminius modestus*, and *Epopella plicata* respectively. Hutton was the first to record *Calantica villosa* and *Lepas pectinata* from the New Zealand coast.

The barnacles collected by the *Challenger* were described by Hoek (1883), and included the following five new species of scalpellids collected in New Zealand waters—*Scalpellum acutum*, *S. pedunculatum*, *S. elongatum* (= *Arcoscalpellum costellatum*), *S. novaezealandiae*, and *S. intermedium*. The first of these is now in the genus *Smilium*, the rest in *Arcoscalpellum*. Filhol (1885) reported on the barnacles collected by the *Venus* at Campbell Island, and described *Balanus campbelli*. The *Gazelle* collected only one new barnacle from off the New Zealand coast; this was described by Studer (1889) as *Chaetolepas segmentata*, but subsequently properly assigned to the genus *Ibla* by Broch (1922).

Weltner (1899), recorded ten species from shores at New Brighton, French Pass, and Chatham Island, including *Lepas pectinata* for the first time. Chilton (1909, 1911a) listed already known species of barnacles from the subantarctic islands and the Kermadec Islands, and in the former account, which was restricted to the stalked forms, listed for the first time in New Zealand *Lepas denticulata*. A new scalpellid from the New Zealand shelf was described as *Scalpellum spinosum* by Annandale (1911a), but is herein renamed *Calantica spinilatera*.

The New Zealand pedunculate barnacles were reviewed by Jennings (1915), who synonymised *Pollicipes sertus* and *P. darwini* with *P. spinosus*, and also drew attention to some specimens in New Zealand museums which, because they were either unlabelled or taken from ships' hulls while in New Zealand ports, could not be admitted to the New Zealand fauna. Jennings (1915) also recognised the existence of a distinct variety of *Lepas anatifera*, his "var. c", as well as the typical variety. This form was described by Borradaile (1916) as *Lepas affinis* from the collections from New Zealand waters by the *Terra Nova*, but both names are synonyms of *Lepas testudinata* of Aurivillius (1894). Borradaile also gave the first New Zealand record of *Conchoderma auritum*, and almost certainly his identification of *Chthamalus stellatus* refers to specimens of *Chamaesipho brunnea* described later by Moore (1944).

A fuller review of New Zealand barnacles by Jennings was published posthumously from manuscript notes by Dr Chilton (Jennings 1918). Two species in that list—*Balanus crenatus* and *B. porcatus*—were erroneous, as commented on later by Chilton (1920), Withers (1924), and in this paper. Two others, *Conchoderma virgatum* and *Balanus tintinnabulum*, were from a ship's hull and therefore not then admissible to the New Zealand fauna.

Dr Th. Mortensen's Pacific Expedition yielded a number of barnacles from Australasian seas, and from that collection Broch (1922) recorded a number of known species and described *Heteralepas dubia* and *Protomitella paradoxa* from the New Zealand coast, but these are herein held to be the same as *Heteralepas japonica* and *Calantica spinosa* respectively. Broch (1922) also described *Calantica mortenseni* as a new scalpellid from the northern New Zealand shelf, but this is the same as *Calantica studeri* collected by the *Gazelle* in 1874–6 from near the Three Kings Islands and described by Weltner (1922). Weltner's name is given priority by Utinomi (1968a).

Totton (1923) described *Oxynaspis terranova* from specimens collected on antipatharians by the *Terra Nova* to the north of New Zealand. Nilsson-Cantell (1927) reported on some barnacles in the British Museum, some of which were known species from New Zealand waters and included *Heteralepas japonica*, already recorded by Broch (1922) as *H. dubia*. A little later,

Nilsson-Cantell (1930b) listed three well-known species collected from Stewart Island.

Linzey (1942a) listed the rest of the barnacles from the Kermadec Islands not treated by Chilton (1909), and thereby included in the New Zealand fauna *Tetraclita rosea*, *Creusia spinulosa*, *Balanus tintinnabulum* (herein recognised as a new species), and a new species which he misidentified as *Elminius simplex*.

There followed a decade in which some common New Zealand barnacles received long-awaited full descriptions. Linzey (1942b) described the body appendages of *Balanus decorus*. Moore (1944) described the four common intertidal barnacles of New Zealand shores—*Elminius modestus*, what is herein called *Epopella plicata* but until recently was known as *Elminius plicatus*, *Chamaesipho columna*, and *C. brunnea*. Moore described and named the latter species for the first time, although it had previously been recognised on ecological grounds by Oliver (1923) and Cranwell & Moore (1938). The anatomy and development of the common intertidal scalpellid *Calantica spinosa* (= *Anatifa spinosa* Quoy & Gaimard) were described in detail in the classic studies of Batham (1945a, 1946). Dr Batham also described a new species of *Ibla*, *I. idiotica*, which she found on New Zealand shores (Batham 1945b).

Powell (1947) provided illustrations and brief notes on eight species of barnacles in the Auckland Museum. In that report, the example of *Mitella sertus* (herein *Calantica spinosa*) is correctly illustrated, but it is not from “deeper water off Mokohinau Islands”. This statement undoubtedly refers to specimens of *Calantica spinilatera* in the Museum but not illustrated by Powell. The specimens identified as *Calantica villosa* by Powell (1947) are in fact *Smilium zancleanum*, described herein from the same material.

Apart from mention in papers dealing with barnacles in the ecology of seashores, and the fouling of submarine surfaces, the New Zealand barnacle fauna received no further systematic attention until Foster (1967) dealt with intertidal balanomorphs, reporting no new species. Utinomi (1968a) described the barnacles collected by the Danish *Galathea* Expedition in New Zealand waters, including a problematical record of *Chthamalus stellatus* from a southern New Zealand shore. Recently, the *Eltanin* collected barnacles from the New Zealand shelf, and these were included in the report by Newman & Ross (1971) on the Antarctic Cirripedia. Their *Arcoscalpellum buccinum* from the Campbell Plateau is probably *A. costellatum*, collected by the *Challenger* a hundred years before. Newman & Ross (1971) also dealt with deep-sea balanomorphs, describing *Hexelasma fosteri* from a New Zealand shelf specimen herein assigned to *Aaptolasma*.

Withers (1913, 1924), reporting on fossil barnacles from New Zealand, described some fossil species and considered some of the Recent species. Subsequent descriptions of New Zealand fossil barnacle remains are given by Laws (1948), Withers (1953), Fleming (1959), Grant-Mackie (1965), and Beu (1971). It is beyond the scope of this paper to reconsider the fossil species in the systematics section, except for a little further information on the very large Miocene balanomorph *Hexelasma aucklandicum*.

This paper describes 8 new species and 1 new subspecies from the New Zealand region, and records a further 13 species for the first time from the region. With these records, the Recent New Zealand barnacle fauna now stands at 61 species.

MORPHOLOGICAL AND SYSTEMATIC CHARACTERS

All adult barnacles have the same basic plan. The prosoma, or appendage-bearing part of the body, is enveloped by a carapace arising from the anterior part of the body to form the capitulum. The “stalked” barnacles, the Lepadomorpha, have the capitulum held off the substratum by the often narrower and flexible peduncle (Fig. 1A). In the non-stalked species, the so-called “acorn” or “sessile” barnacles, the capitulum abuts directly onto the substratum, and the enclosing mantle and its shell plates are either laterally unsymmetrical, as in the Verrucomorpha, or symmetrical about the dorsoventral axis, as in the Balanomorpha (Fig. 1D).

In the adult barnacle the region, which in the larva is anterior to the mouth, is expanded and incorporated into the peduncle of lepadomorphs and the basis of others. The rest of the body is able to flex about within the mantle

cavity between the capitular walls, and the appendages are extended through the elongated orifice on the morphological ventral line. In the adult barnacle the conventional dorsal—ventral and anterior—posterior orientations of the body and capitulum become somewhat confused. For the capitulum and peduncle it is more convenient to refer to apical and basal orientation as respectively “away from” and “close to” the zone of attachment to the substrate. Transverse orientation is usually referred to the rostrocarinal axis, corresponding to the basic dorsoventral axis.

The integument of the capitulum may secrete calcareous shell plates, which become exposed on the wearing away of the external cuticle layer. The shape and arrangement of the various shell plates form a convenient means of describing barnacles and tracing phylogenetic changes.

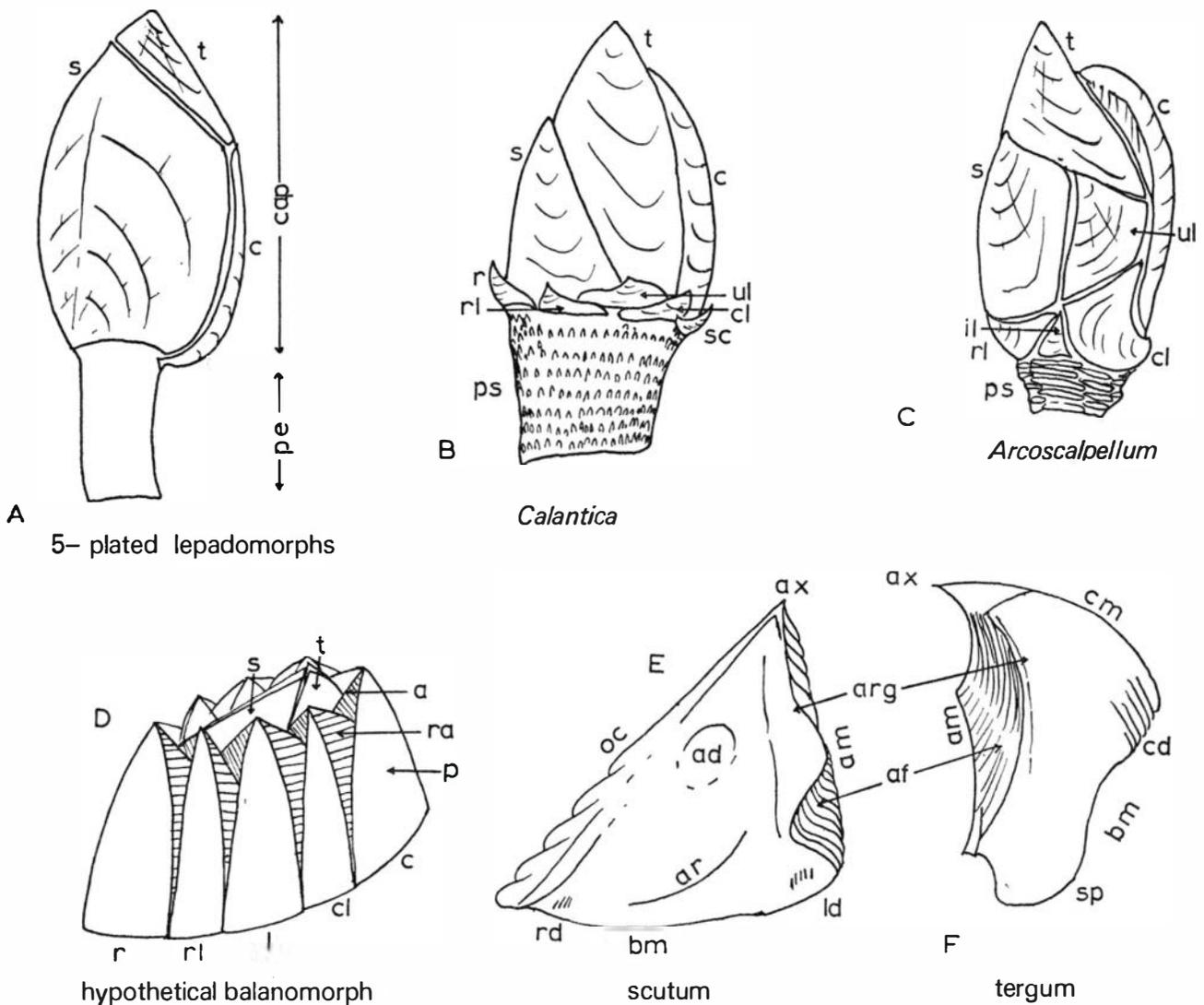


Fig. 1. External morphology of Thoracica: *A-C*, Lepadomorpha; *D*, a hypothetical balanomorph; *E, F*, inner views of balanomorph scutum and tergum — *a*, ala (pl. alae); *ad*, adductor muscle pit; *af*, articular furrow; *am*, articular margin; *ar*, adductor ridge; *arg*, articular ridge; *ax*, apex; *bm*, basal margin; *c*, carina; *cap*, capitulum; *cd*, crests of carinal depressor muscles; *cl*, carinolatus; *cm*, carinal margin; *il*, inframedian latus; *l*, latus (pl. latera); *ld*, crests of lateral depressor muscles; *oc*, occludent margin; *p*, paries (pl. parietes); *pe*, peduncle; *ps*, peduncular scales; *r*, rostrum; *ra*, radius (pl. radii); *rd*, crests of rostral depressor muscles; *rl*, rostral latus; *s*, scutum; *sc*, subcarina; *sp*, spur; *t*, tergum; *ul*, upper latus.

THE SHELL PLATES

The Heteralepadidae do not possess calcareous shell plates in the integument, and although there are often thickenings at the site of attachment of the transverse adductor muscle below the orifice, there is no evidence that calcareous plates were ever present in this group.

The Iblidae have 4 horny plates, a pair of terga dorsally and a pair of scuta ventrally, all with apical centres of growth (umbos). The apical position of the umbo is considered primitive. In some iblids the plates are weakly calcified.

In other barnacle families the plates are usually well calcified, or it is evident that any lack of shell plates is a secondary development. In the Oxynaspidae, Poecilasmataidae, and Lepadidae there are 5 plates, the paired terga and scuta, and the carina in the dorsal midline (Fig. 1A). In most living species the carina and scuta have subapical umbos, often quite basal, so the living representatives of these families do not retain primitive shell growth gradients.

In the Scalpellidae (Fig. 1B, C), some of the species do have entirely apical umbos, and the carina, terga, and scuta are always preceded in ontogeny by chitinous primordial plates, whereas other plates are not. Extra plates are added in whorls below the bases of the main five, the first whorl with a plate (the rostrum) in the ventral midline, and paired lateral plates (the upper latera) between the bases of the terga and scuta. The next whorl comprises a single subcarina in the dorsal midline, and paired lateral plates. The next whorl would appear to include a single subrostrum in the ventral midline, and more paired lateral plates. This tendency towards plate multiplication is perhaps best illustrated today in the ontogeny of *Pollicipes polymerus* (Plate 5A). As well as the new plates forming at the base of the capitulum and elevating those already formed and growing towards the apex, small calcareous scales are formed in this region, to be displaced onto the lengthening peduncle.

The production of capitular plates was evidently suppressed in the early calanticoids, so that relatively few identifiable plates constituted the lower whorl of plates on the capitulum, and to these specific names have been given (Fig. 1B). The changes in the relative positions of these plates, and sometimes the loss of some of them, coupled with alterations in the position of the umbo of the primary plates from the apical towards the basal position, has provided a convenient means of tracing scalpellid phylogeny. This is taken up further in the discussions in the systematics section.

Early in scalpellid evolution, probably involving ancestral *Pollicipes*, multi-plated forms dispensed with the peduncle and fixed the capitulum directly onto the substratum. The plates of the lower whorls plus the carina thus formed an encircling wall, each plate with an apical umbo (Fig. 1D). The non-stalked forms assumed a squatter, more rounded shape (an approach towards radial symmetry in sessile animals), and the terga and scuta became parallel to the lie of the prosoma and the substratum, together forming the opercular plates guarding the orifice. The outlines of subsequent balanomorph radiation are fairly well understood, and involve the loss and concrescence of parietal plates. Consequent on the need to enlarge the orifice at a rate greater than

that imposed by attrition and erosion by environmental factors, the upper parts of the primary plates or parietes develop, in addition, diametric growth gradients. The enlarging triangular area beneath an adjacent plate is termed an ala (pl. alae), and when an extra area develops over the ala it is termed the radius (pl. radii).

In balanomorphs, the opercular plates are the least influenced in shape by environmental factors such as substrate shape, crowding, etc. As they are movable relative to each other, and thus have a number of articular surfaces and muscle attachment sites, they are useful in taxonomy. The appropriate terminology of the opercular plates is shown in Fig. 1D, F.

Fundamentally the shell plates are solid, even though the calcite is laid down in layers. In some balanomorph genera the shell plates of the parietes and radii develop in a complex manner, so that the plates become permeated by chitinous material, or living tissue, or hollow tubes, in the direction of growth. These details are taken up further in the relevant parts of the systematic treatment.

In many species of balanomorphs, the basal tissues also secrete calcareous material onto the substrate. In membranous-based forms, fixation muscle fibres effect adhesion between the parietes and the substratum. The advantages of a calcareous base seem to be initially a separation of the tissues from some factors associated with the substratum, and that the base can interlock with ridges at the base of the parietes and make a more rigidly constructed shell. To this end, too, the edges of the radii (in those forms that have radii) interlock with the edges of the adjacent parietes.

The Verrucomorpha acquired a sessile habit independently of the Balanomorpha, evidently by resting on the side of the capitulum rather than on the base. This resulted in an asymmetrical arrangement of the plates, the terga and scuta of one side forming part of the parietal wall with the carina, rostrum, and (in fossil forms) some lateral plates of the other side. Only one tergum and scutum are movable as opercular valves. There is only one extant genus in the Verrucomorpha, and the terminology of its shell plates is given more fully in the systematics section.

THE MOUTHPARTS

The arrangement of the appendages of a barnacle is shown in Fig. 2. The antennules and antennae of the larvae (Fig. 2E, G) are incorporated into the base of the adult barnacle. The other head appendages form the mouthparts, and are arranged around the mouth on an elevated oral cone (Fig. 2A, B). The anterior mouth field is guarded by the labrum, which in lepadomorphs and some balanomorphs protrudes anteriorly (when it is termed “bullate”). The crest at the edge of the mouth

may be straight or concave, or have a deep, median notch. It may also bear chitinous teeth. Overlapping either side of the labrum are the mandibular palps, which help to guard the anterior ventral part of the mouth field.

The coxal endite of each mandible forms a toothed blade (Fig. 2C) directed towards its opposite number, and the term “mandible” is conveniently applied to the paired blades. The arrangement of the teeth on the

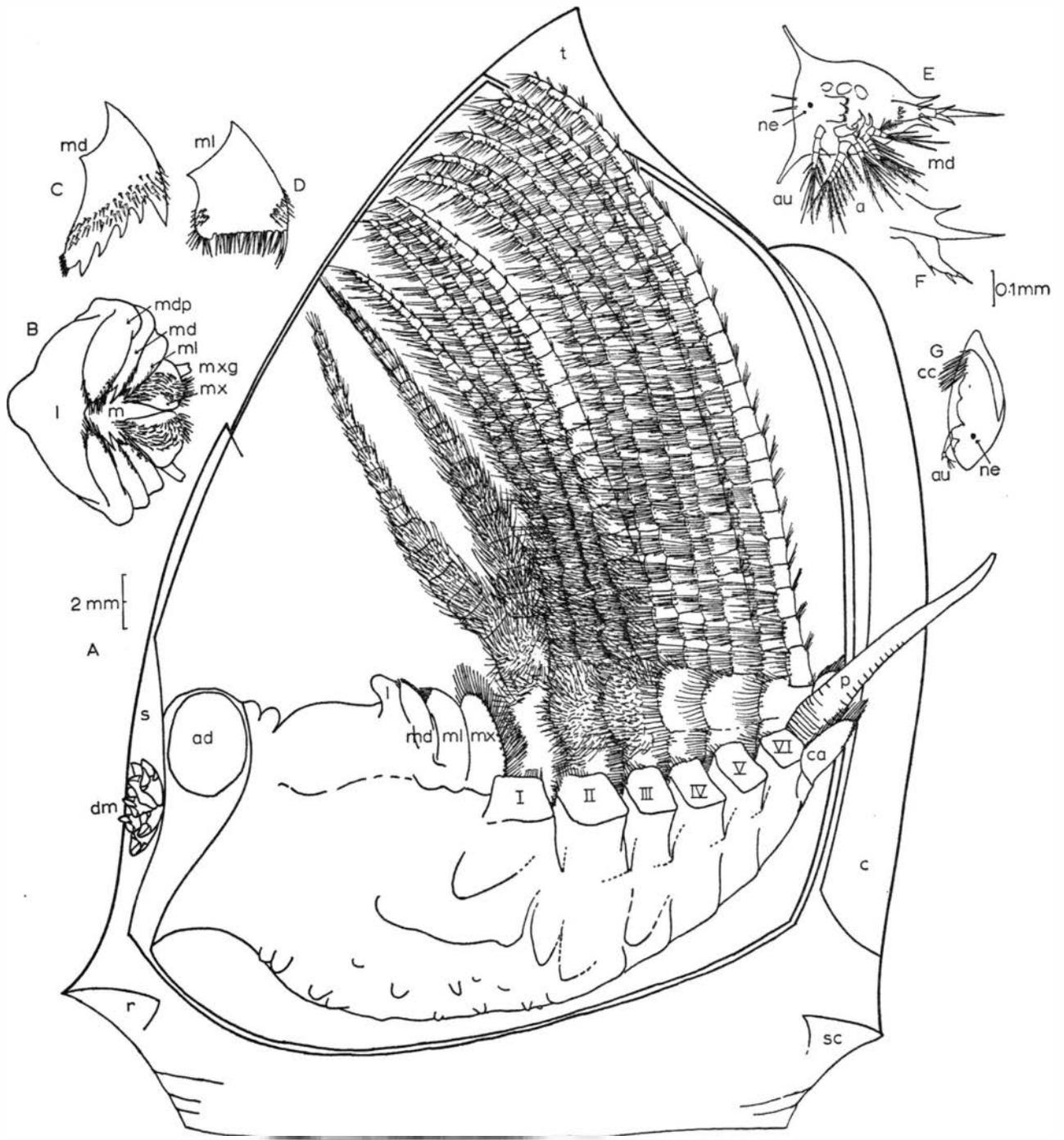


Fig. 2. Internal anatomy and larvae of Thoracica: *A*, adult *Calantica spinilatera*, capitular plates and cirri of right side removed; *B*, mouth field from above; *C*, mandible; *D*, maxillule; *E*, 4th nauplius, *Epopella plicata*, ventral view, left appendages removed; *F*, same, lateral view of posterior part; *G*, lateral view, cyprid, *Epopella plicata*—*a*, antenna; *ad*, adductor muscle; *au*, antennule; *c*, carina; *ca*, caudal appendage; *cc*, cyprid cirri; *dm*, dwarf males; *l*, labrum; *m*, mouth; *md*, mandible; *ml*, maxillule; *mx*, maxilla; *mxp*, maxillary gland opening; *mdp*, mandibular palp; *ne*, nauplius eye; *p*, penis; *r*, rostrum; *s*, scutum; *sc*, subcarina; *t*, tergum; *I–VI*, cirri.

mandible is of systematic value; in some forms there is a constant number during ontogeny, in others the number increases with growth. The lower angle of the mandible may bear a series of spines, or be molariform.

The maxillule is similarly blade-like (Fig. 2D), without a palp in the adult, and placed parallel to and behind the mandibles. The cutting edge may be straight, notched, or stepped, and is provided with groups of different-sized, spine-like setae.

The maxillae are triangular lobes that meet along their medial margins to form the posterior margin of the mouth field. The maxillary gland opens at the base of the maxilla, sometimes on a distinct papilla. As with the mandibles and maxillules, the maxillae bear groups of setae for directing and conveying food particles to the mouth.

THE CIRRI

The cirri, of which there are six, are biramous, stenopodial, thoracic limbs. Basally on each there is a two-segmented pedicel. The rami are the endopod and exopod. With the tendency towards lateral flattening and elongation of the prosoma the outermost exopod is placed anteriorly to the endopod, and reference is made to the anterior and posterior rami of each cirrus. The rami comprise segments which carry setae on some or all of their exposed faces. The setae vary greatly, and may be minute and simple, long and finely setuled or strongly barbed, or short, stout, and claw-like or tooth-like. A range of setal types is shown in Plate 1.

The anteriormost cirrus (cirrus I) is articulated with the prosoma close to the mouth cone. The oviduct opens at the base of the pedicel, and there are often filamentary processes on the pedicel and adjacent prosoma flanks. The rami have copious setae on the inner faces as well as fringing setae on the anterior and posterior edges of the segments. Cirrus I channels food particles from the more posterior cirri to the mouthparts, i.e., it functions as a maxilliped.

Cirri II and III also assist in the forward manipulation of food, in contrast to the catching or filtering function of the more posterior cirri. In lepadomorphs, the basal segments of the rami of cirri II and III have copious, medially directed setae on the inner faces; the more distal segments have sparser setae and no doubt function for food catching rather than manipulation, as with the posterior cirri. Generally in the lepadomorphs the cirri grade in size, increasing in length from I to VI. In balanids, the rami of cirri II and III can be as short as or shorter than those of cirrus I, and all much shorter than the rami of cirri IV–VI. All the segments of cirri II and

III have copious, medially directed setae. It is apparent that there is a progressive diminution of the food-catching role of cirri II and III in the evolution of the Balanomorphs, so that they come to have a purely maxilliped function.

In cirri IV–VI, the segments have the setae either in pairs along the length of the anterior edge, with smaller, intermediate setae at their bases and a group of a few setae at the posterior distal angle (ctenopod setation), or the setae are all grouped towards the distal margins of the segments (acanthopod setation). The lateral or outer faces of the segments of all the rami are usually devoid of prominent setae, but may bear scattered short cirri, or sometimes spines or stout teeth.

The numbers of segments of the cirri increase at each moult during ontogeny, and there is also a tendency in some species to increase the numbers of setae on the existing segments. In some species the number of setae on the segments of the posterior cirri is constant throughout ontogeny, and additional filtering capacity with growth is brought about by enlargement of existing setae and by the addition of extra segments at each moult. The use of segment and setal counts as specific characters needs to take account of such ontogenetic changes.

Caudal appendages are thought to be the remnants of further body segments, but they are not present in all barnacles. When present, they arise on either side of the anus at the bases of the pedicels of the sixth cirri. They may be small and of one segment with or without setae, or they may be ramiform, multiarticulated, and setose, and may reach up to half the length of the rami of cirrus VI.

THE LIFE-CYCLE

The male genital ducts evidently opened onto the abdominal somites of the ancestral thoracican, as they do in the Ascothoracica, but in the Thoracica the paired male ducts unite and are continued in the penis, which arises from between the bases of the sixth cirri, ventral to the anus. The penis is extensible, and in the withdrawn condition appears annulated. The surface of the penis may carry setae of various types.

The normal thoracican sex condition is hermaphroditic, the testes located in the prosoma and the ovaries in the basal or peduncular tissues. In some cases the "typical" form is a hermaphrodite which carries small individuals with reduced appendages and plates, or entirely without appendages or plates, but in either case with developed male gonads. In other cases the sexes are separate, the large "typical" form is without testes or a penis, and is thus a female, and complementary males are carried on the female and are essential for fertilisation. Sexual differentiation occurs in some of the Scalpellidae, in *Ibla*, and in one species of *Balanus*.

Fertilisation occurs in the mantle cavity or at the base of the oviduct, and the ova develop to the first-stage nauplius within the mantle cavity. In most species, the nauplii are hatched from the egg membranes and expelled from the mantle cavity by pumping movements of the body. The nauplii (Fig. 2E) then lead a planktonic existence, undergoing a further 5 moults (i.e., 6 nauplius stages) before moulting to the cyprid stage (Fig. 2G). Some species, mostly scalpellids, have non-feeding nauplius stages, releasing from the mantle cavity an ambulatory cyprid larva. The cyprid larva is a critical one in the life history, for its responses determine the ultimate site for fixation and metamorphosis to adult form. The development through the larval stages to the adult is a matter of progressive metamorphosis, the various larval stages being delineated by the moulting of the exoskeleton. During this metamorphosis, the occurrence and functions of the limb series are altered, as shown in Table 1. The larval stages should properly be incorporated into the descriptions of the species, but are still unknown for many of the New Zealand species.

Table 1. The somital arrangement and function of appendages in larval and adult stages of thoracican cirripedes (—, appendage not developed).

SOMITE NO.	NAUPLII I-VI		CYPRID		ADULT	
	APPENDAGE	FUNCTION	APPENDAGE	FUNCTION	APPENDAGE	FUNCTION
1	antennule	sensory	antennule	sensory 'walking' attachment	—	vestigial; incorporated into the basal tissues
2	antenna	sensory, swimming, feeding	—		rudimentary	
3	mandible		mandible	food manipulation		
4	—		maxillule			
5	—	maxilla				
6	—	progressively developed through the 6 stages, but rudimentary	cirrus I	swimming	cirrus I	food catching
7	—		cirrus II			
8	—		cirrus III			
9	—		cirrus IV			
10	—		cirrus V			
11	—		cirrus VI			
12	—		caudal furca	?sensory	caudal appendages	?sensory, when present

SYSTEMATICS

Classification and list of species

The classification of the Thoracica in this paper largely follows that of Newman *et al.* (1969), especially with regard to the families of the Lepadomorpha. Subsequent to the treatise account of Newman *et al.* (1969) the classification of the Balanomorpha received some attention, from which it became clear that the intertidal tetracitids and the deep-sea hexelasmids warrant familial status (Ross 1968, Utinomi 1968b, Newman & Ross 1971).

On present reckoning the New Zealand barnacle fauna comprises 61 Recent species, distributed among 6 families of the Lepadomorpha, 1 of the Verrucomorpha, and 4 of the Balanomorpha, as follows (in the order with which they are dealt in this paper; familiar junior synonyms and suspected obsolete names [n.ob.] are given in brackets).

Suborder Lepadomorpha

Family HETERALEPADIDAE

- Heteralepas japonica* (Aurivillius) [*Heteralepas dubia* Broch]
Paralepas quadrata (Aurivillius) [*Anatifa tubulosa* Q. & G., n. ob.]
Paralepas minuta (Philippi)

Family IBLIDAE

- Ibla idiotica* Batham [*Chaetolepas segmentata* Studer n. ob.]

Family OXYNASPIDAE

- Oxynaspis indica* Annandale [*Oxynaspis celata novaezelandica* Broch]
Oxynaspis terranova Totton

Family POECILASMATIDAE

- Trilasmis (Poecilasma) kaempferi* (Darwin)
Megalasma carinatum (Hoek)
Megalasma striatum Hoek

Family LEPADIDAE

- Lepas anatifera* Linné
Lepas testudinata Aurivillius [*Anatifa elongata* Q. & G., n. ob.]
Lepas australis Darwin
Lepas pectinata Spengler
Lepas denticulata Gruvel
Lepas fascicularis Ellis & Solander
Conchoderma virgatum (Spengler)
Conchoderma auritum (Linné)
Alepas pacifica Pilsbry

Family SCALPELLIDAE

- Calantica spinosa* (Quoy & Gaimard) [*Pollicipes spinosus* Darwin]
Calantica spinilatera nom. nov. [*Scalpellum spinosum* Annandale]
Calantica villosa (Leach)
Calantica studeri (Weltner) [*Calantica mortenseni* Broch]
Calantica gemma (Aurivillius)
Smilium zanclearum (Seguenza)
Smilium acutum (Hoek)
Arcoscalpellum pedunculatum (Hoek)
Arcoscalpellum costellatum (Withers)
Arcoscalpellum vitreum (Hoek)
Arcoscalpellum trochelatum n. sp.
Arcoscalpellum affricatum n. sp.
Arcoscalpellum intermedium (Hoek)
Arcoscalpellum pertosum n. sp.
Arcoscalpellum novaezelandiae (Hoek)
Arcoscalpellum raccidium n. sp.

Suborder Verrucomorpha

Family VERRUCIDAE

- Verruca (Metaverruca) halothea* Pilsbry

Suborder Balanomorpha

Family CHTHAMALIDAE

- Chamaesipho columna* (Spengler)
Chamaesipho brunnea Moore

Family PACHYLASMIDAE

- Pachylasma scutistriata* Broch
Hexelasma alearum n. sp.
Aaptolasma fosteri (Newman & Ross)
Aaptolasma nolearia n. sp.

Family TETRACLITIDAE

- Epopella plicata* (Gray) [*Elminius plicatus* Darwin]
Epopella kermadeca n. sp.
Tesseropora rosea (Krauss)
Tetraclita aoranga n. sp.
Tetraclitella purpurascens (Wood) [*Tetraclita purpurascens* (Wood)]

Family BALANIDAE

Elminius modestus Darwin

Balanus (Austrobalanus) vestitus Darwin

Balanus (Solidobalanus) auricoma Hoek

Balanus (Megabalanus) tintinnabulum linzei n. ssp.

Balanus (Megabalanus) decorus Darwin

Balanus (Megabalanus) campbelli Filhol

Balanus (Balanus) amphitrite amphitrite Darwin

Balanus (Balanus) variegatus variegatus Darwin

Balanus (Balanus) trigonus Darwin

Creusia spinulosa Leach

Coronula diadema (Linné)

Coronula reginae Darwin

Tubicinella major Lamarck

Platylepas hexastylus (Fabricius)

Stomatolepas elegans (Costa)

Suborder LEPADOMORPHA Pilsbry, 1916

Thoracican cirripedes with body elongate and differentiated into capitulum and peduncle. Capitulum commonly protected by calcareous plates of specific form, but these may be vestigial or entirely absent. Capitulum forms mantle round prosoma. Peduncle contains testes in males; ovaries in females and hermaphrodites. Peduncle usually supplied with muscles which allow changes in orientation, and may or may not have calcareous scales in the integument.

Family HETERALEPADIDAE Nilsson-Cantell, 1921

Lepadomorpha without calcareous plates or scales on capitulum or peduncle, and with muscles of peduncle continued within integument of capitulum. Attachment sites of 'scutal' adductor muscles marked by small chitinous areas on each side below orifice. Segments of cirri have setae in tufts distally. Caudal appendages present, and are multiarticulate and spinose.

Genus *Heteralepas* Pilsbry, 1907

Heteralepadidae with posterior rami of cirri V and VI greatly reduced in length and width compared with anterior rami of cirri V and VI and with both rami of cirri II–IV. Segments of normal rami armed with 2 or 3 very long setae and a few minor setae at anterior distal angle, and a group of small setae at posterior distal angle.

Heteralepas japonica (Aurivillius) (Plate 2A, B; Fig. 3)

Alepas japonica Aurivillius, 1892: 125; Aurivillius 1894: 28.

Heteralepas (Heteralepas) dubia Broch, 1922: 288.

Heteralepas (Heteralepas) japonica. For synonymy see Nilsson-Cantell 1927: 755; Hiro 1933: 48.

MATERIAL EXAMINED: NZOI Stn F932 (1 specimen). Auck. Mus.: many, on pennatulid stalks from east of The Aldermen Is, 368–478 m *Valkyrie*. BAF: 4 specimens on craypot rope, Gt. Barrier I. (D. Hudson).

DISTRIBUTION: North-east New Zealand, 64–478m (Fig. 4); also Indomalaysia to Australasia.

DESCRIPTION: *Externals*: Variable external appearance, but usually with ventral margin protruding beyond orifice, which may be parallel or at an oblique angle to vertical axis of capitulum. Orifice crenulated, slightly protuberant, occupying $\frac{1}{3}$ – $\frac{1}{2}$ length of capitulum. Scutal attachment areas very small, particularly discernible in smaller specimens. Peduncle $\frac{1}{2}$ –4 × length of capitulum. Carinal margin of capitulum sometimes slightly elevated as a crest with warty protuberances, commonly 3 on capitulum and 1 on peduncle. Surface in some specimens wart-like. No differences detected in appendages of specimens showing these variable external appearances.

Mouthparts: Labrum with short row of blunt teeth. Mandibles with 4 teeth, shortest at lower angle, and with small denticles predominantly on upper surface of 2nd to 4th teeth, but sometimes a few on lower surfaces of 1st to 3rd teeth. Maxillules with 2 large and 1 small setae at upper angle, separated by wide notch from protuberant main cutting edge, which bears 2 rows of setae protruding as far as upper setae.

Cirri: Cirrus I with anterior ramus shorter than posterior ramus, and with segments twice as wide. One filamentary process at base of cirrus I. Both rami of cirri II–IV and outer rami of cirri V and VI with up to 80 segments, but difficult to determine because of extensive fusion of segments proximally; each segment bearing antero-distally a pair of very long, diverging setae. Posterior rami of cirri V and VI only about $\frac{1}{4}$ length of anterior rami, of up to 27 square segments much smaller than those of anterior rami. Caudal appendages with up to 8 elongate segments, extending as far as pedicel of cirrus VI. Penis annulated, sparsely hairy, with a bunch of setae near tip.

REMARKS: Nilsson-Cantell (1927) drew attention to the difficulties of using external characters, particularly peduncle length, in species diagnoses of heteralepads. *H. indica* Gravel has a longer peduncle than *H. japonica*,

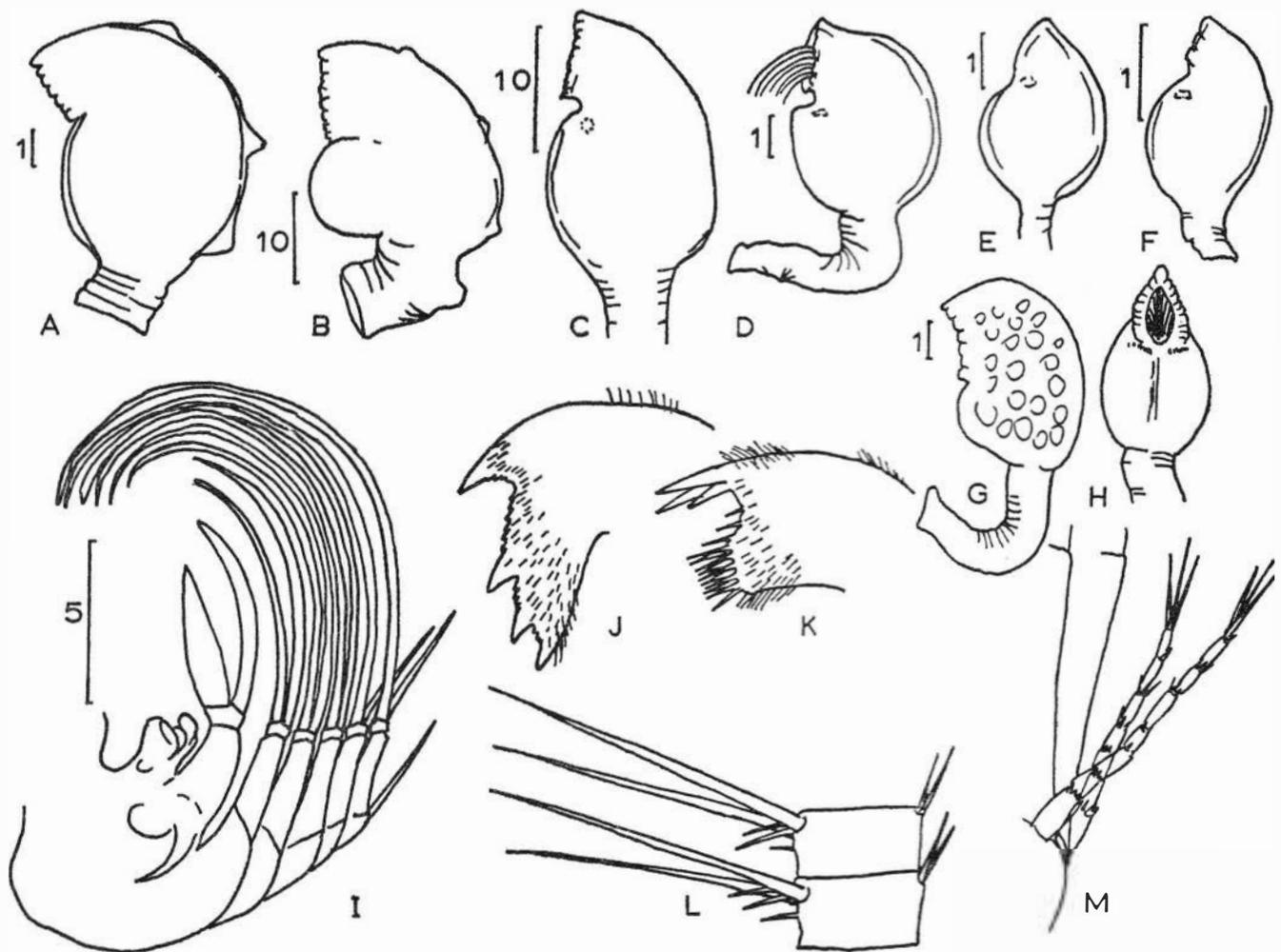


Fig. 3. *Heteralepas japonica* (Aurivillius): A–G, lateral views of specimens from — A, NZOI Stn F932, B, Great Barrier I, C–G The Aldermen Is; H, rostral view of specimen F; I, plan of prosoma, showing right-side appendages; J, mandible; K, maxillule; L, intermediate segments, cirrus VI; M, caudal appendages and posterior margins of pedicel, cirrus VI (scales in mm).

but this is suggested to be an ecological response to crowding, as in *Lepas* and *Balanus*, by Nilsson-Cantell (1927), who also questions the validity on external characters of *H. nicobarica* Annandale, *H. gigas* Annandale, and *H. cygnus* Pilsbry. The wart-like structures on the capitulum of some of the present specimens recall the condition of *H. utinomi*, described from Tasmania by Newman (1960), which is internally similar to *H. japonica*. The 3 carinal warts shown in Aurivillius' figure of *H. japonica* resemble the condition in *H. cornuta* Darwin, the description of which is not radically different from that of *H. japonica*. Also closely related is *H. lankestri* Gruvel, which Nilsson-Cantell (1927) regards as distinct from *H. japonica* mainly by the absence of external cuticular processes from all specimens of *H. japonica*. Even this is hard to justify, as it seems that they are not always present in *H. lankestri*, and the warts of

H. japonica are, after all, chitinous processes. A revision of the genus is called for. For the present, I have followed Nilsson-Cantell in recognising the Indomalayan species *H. japonica* as distinct from the Atlantic species-group.

Nilsson-Cantell (1927) recorded *H. japonica* from 128 m, 11 km east of North Cape, the specimens forming part of his synonymy of *japonica* and *indica*. Broch (1922) recorded *H. dubia* from Disaster Bay at 55–73 m, the distinctive feature of his specimens being the warty protuberances on the carinal edge. This, with the number of segments in the cirri and caudal appendages, and the "different small features" of the mouthparts which Broch considered important, is however encompassed in the variability of *H. japonica* tabulated by Nilsson-Cantell (1927) and reflected in the present suite of specimens.

Genus *Paralepas* (Pilsbry, 1907a)

Heteralepadidae with rami of cirri II–VI subequal, and composed of comparatively few square to elongate segments; each armed with semicircular brush of many setae on anterior face, and a group of setae at posterior distal angle.

Paralepas quadrata (Aurivillius) (Plate 2C; Fig. 5)

Alepes quadrata Aurivillius, 1894: 30.
Heteralepas (Heteralepas) quadrata. Nilsson-Cantell 1921: 248;
 Hiro 1937: 406; Hiro 1939: 248; Utinomi 1949: 20.
Anatifa tubulosa Quoy & Gaimard, 1834: 643.

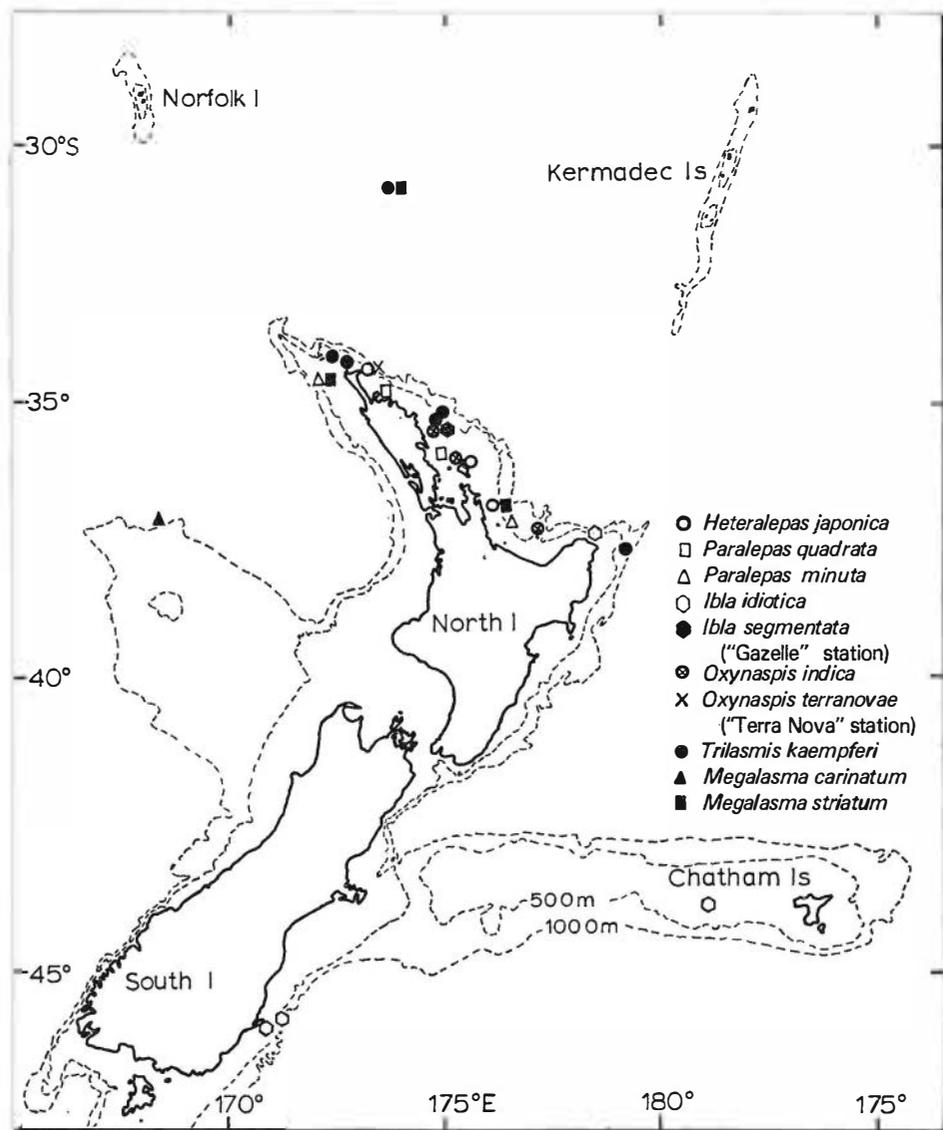
MATERIAL EXAMINED: Auck. Mus.: 1 specimen on *Jasus trauxi* (Milne-Edwards) Doubtless Bay (P. Shean).
 BAF: 18 specimens on pleopods of *Jasus*, Hen and Chickens Is (R. Sketchley).

DISTRIBUTION: North-eastern New Zealand (Fig. 4): also Java Sea, Formosa, Japan.

DESCRIPTION: *Externals*: Smooth capitulum only slightly laterally compressed, quadrate to ovoid in lateral view, with orifice set at 45° angle to vertical axis and back from rostral margin. Edge of orifice crenulated, sometimes extending as a short, tubular funnel. Scutal attachment areas obvious. Colour of Hen and Chickens specimens reported as “white with brown and mauve on capitulum”; that of Doubtless Bay specimens (preserved in glycerine) cream with mauve on capitulum. Peduncle about $\frac{1}{3}$ width and $\frac{1}{2}$ height of capitulum.

Mouthparts: Labrum with single row of prominent teeth. Mandible with 4 main teeth, small spines on lower side of each tooth and on lower angle. Maxillule with 1 large and 2 smaller setae at upper angle, separated by deep notch from protuberant main cutting edge, which bears a row of setae shorter than upper pair but reaching out as far.

Fig. 4. Records of Heteralepadidae, Iblidae, Oxynaspidae, and Poecilasmatidae in the New Zealand region.



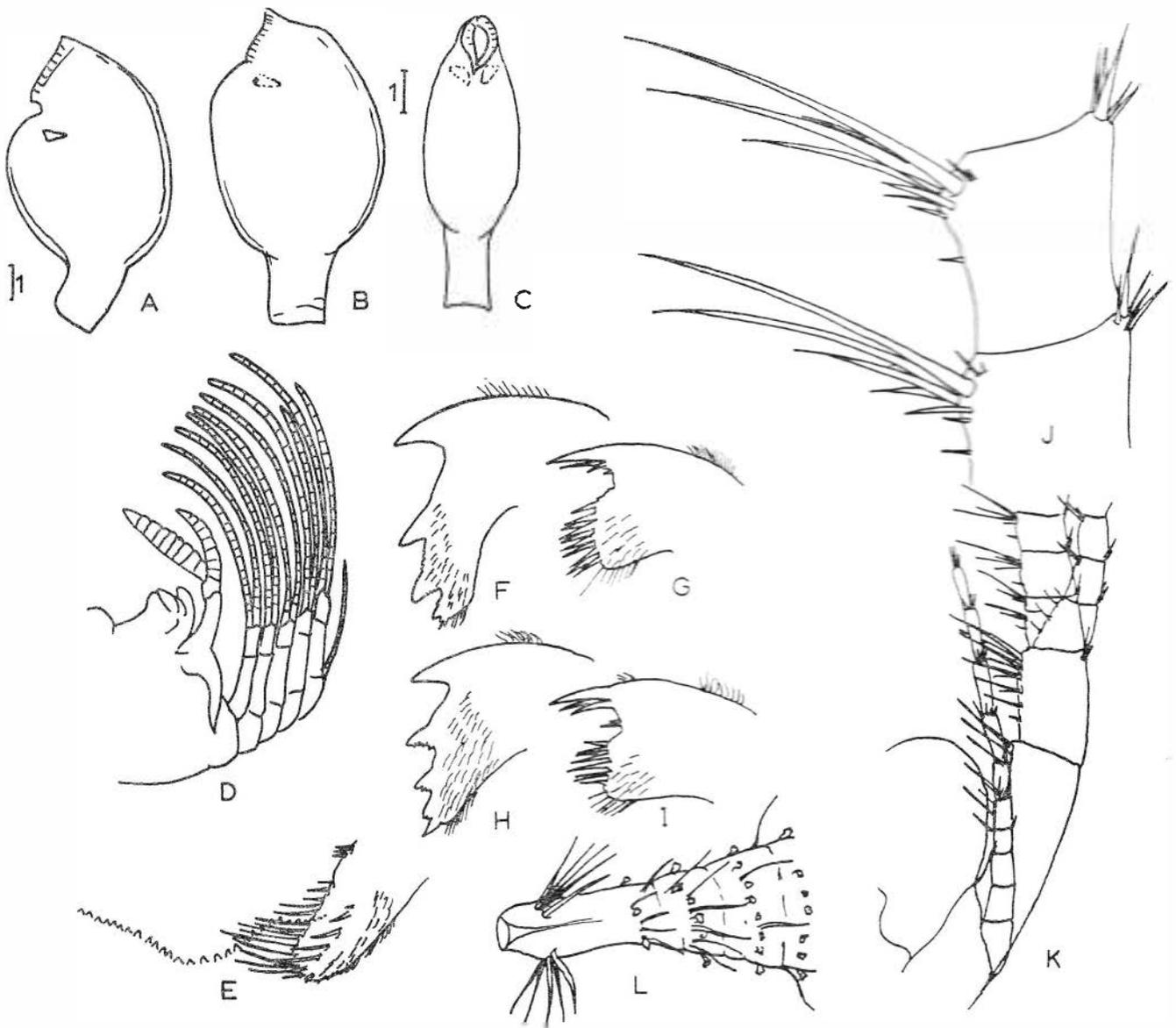


Fig. 5. *Paralepas quadrata* (Aurivillius): A, lateral view, specimen from Hen and Chicken Is; B, C, lateral and rostral view, specimen from Doubtless Bay; D, plan of prosoma, showing right-side appendages; E, labral crest and mandibular palp; F, G, mandible and maxillule, specimen A; H, I, same, specimen B; J, intermediate segment, posterior ramus, cirrus VI; K, pedicel and basal segments, rami, cirrus VI, with caudal appendage and base of penis; L, tip of penis (scales in mm).

Cirri: Anterior ramus of cirrus I longer by 2 or 3 segments and with broader segments than posterior ramus. Single filamentary process at base of first cirrus. Segments of anterior rami of cirri II–VI and posterior rami of cirri II–IV with 2 to 4 long setae and several smaller setae on anterior distal face. Posterior rami of cirri V and VI 1 to 5 segments shorter, with segments thinner, and reduced numbers and lengths of setae than corresponding anterior rami. Caudal appendages with up to 11 thin segments, reaching to basal 3 segments of rami of cirrus VI. Penis stout, $\frac{1}{2}$ length of cirrus VI, with annulations bearing a few setae and a circlet of peculiar, rivet-like appendages; tip abruptly tapering, smooth except for 2 tufts of long setae.

REMARKS: The peculiar setation of the penis resembles the condition in *Paralepas palinuri* (Newman 1960), *P. distincta* (Utinomi 1949), *P. lithotryae* (Hoek 1907), and *P. scyllarusi* (Utinomi 1967a), but *P. quadrata* is distinguishable from all these except *P. scyllarusi* by differences in the setation of the cirri. The chaetotaxy of the intermediate segments of the cirri approaches the *Heteralepas* condition, with the longest setae on the anterior edge, but there are setae arranged in transverse rows on the anterior and posterior edges at the distal part of each segment. Also, the shorter inner rami of cirri V and VI are intermediate between the very definite reduction in most species of *Heteralepas* and the sub-equal condition in most species of *Paralepas*,

including *P. scyllarusi*. Although Hoek (1907) regarded *P. quadrata* as being close to *P. lithotryae*, no later workers ranked the former in *Paralepas*. The distinction between *Heteralepas* and *Paralepas* is not as clear-cut as Newman (1960) would suppose. If the two genera are to be maintained, the affinities of *P. quadrata* with other recognised species of *Paralepas* are borne out by the bunched setae on the segments of the rami and the peculiar armature of the penis.

The record of *Anatifa tubulosa* Quoy & Gaimard from Tolaga Bay in New Zealand has long been problematic; the body of this nude lepadomorph was not described. Broch (1922) argued that the name should be dropped. Certain features of the original imperfect description of *A. tubulosa*, namely the habitat (attached to a palinurid), and the colour ("white with violet tints"), together with present knowledge indicate that Aurivillius redescribed Quoy & Gaimard's species. The illustration by Quoy & Gaimard (1834) does, however, show an orifice much more protuberant than in any of the present material. The antiquity of Quoy & Gaimard's name and

the loss of the specimens clearly render *A. tubulosa* a *nomen oblitum* under Art. 23b of the International Code of Zoological Nomenclature (1961).

Paralepas minuta (Philippi) (Plate 2D; Fig. 6)

Alepas minuta. Darwin 1851: 160. (see for earlier citations).
Heteralepas (Paralepas) minuta. Hiro 1933: 51.

MATERIAL EXAMINED: NZOI Stn E875 (3 specimens on echinoid spine). Nat. Mus.: 2, on echinoid spine, 37° 10'S 176° 24'E, 736 m, *Alert*.

DISTRIBUTION: Northern New Zealand: 485–736 m (Fig. 4); also Mediterranean, West Africa, Japan.

DESCRIPTION: *Externals*: Smooth, globose capitulum. Orifice about $\frac{1}{3}$ length of capitulum, inclined at 45° angle to its long axis; orifice lips crenulate but not protruding. Scutal attachment areas immediately below orifice, triangular in shape. Peduncle quite short, annulated in preserved specimens.

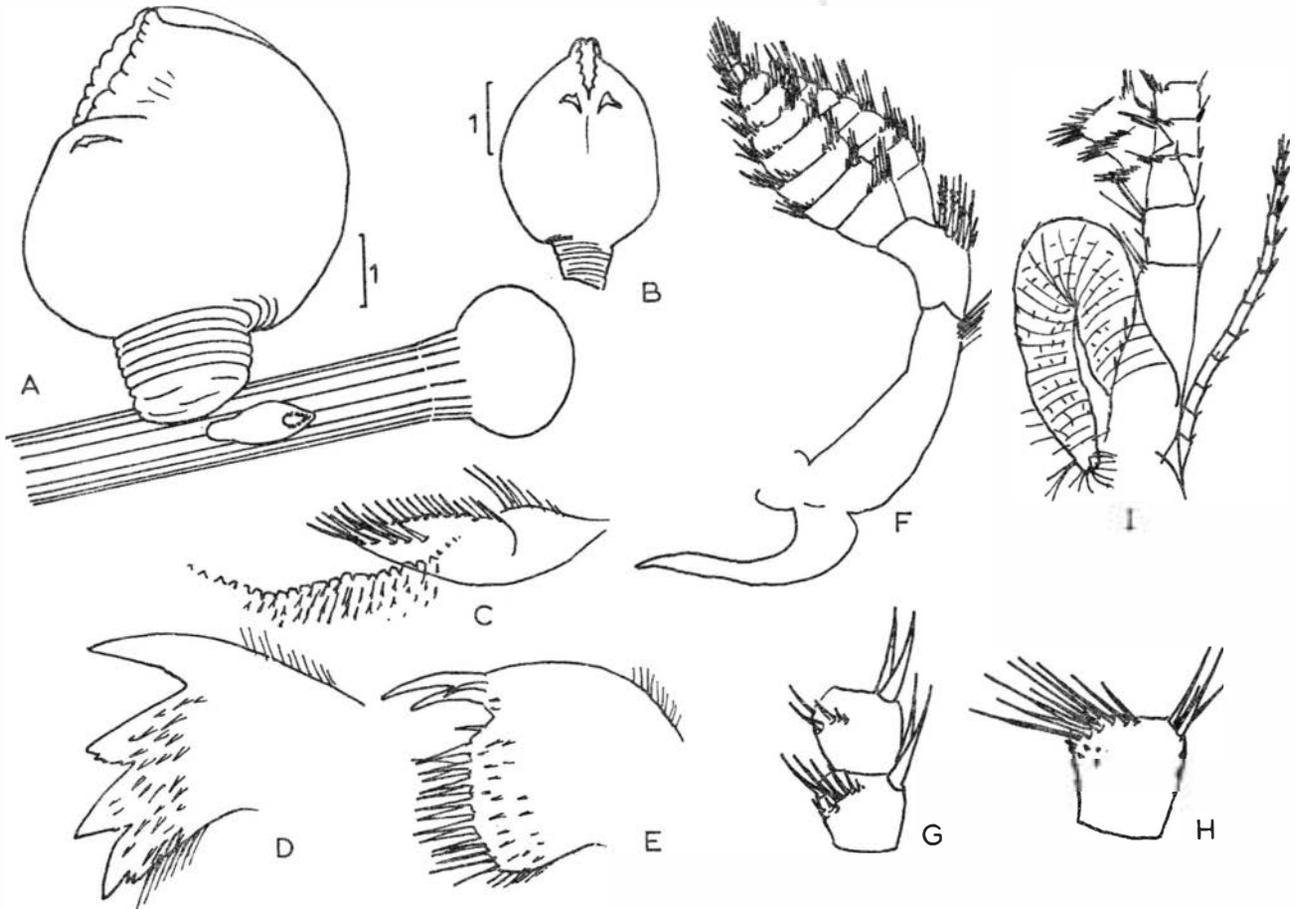


Fig. 6. *Paralepas minuta* (Philippi): A, B, specimens from NZOI Stn E875; C, labral crest and mandibular palp; D, mandible; E, maxillule; F, cirrus I, with filamentary process; G, distal segments, cirrus III; H, intermediate segment, cirrus VI; I, pedicel and basal segments of rami of cirrus VI, with caudal appendage and penis, specimen B (scales in mm).

Mouthparts: Labrum with row of pallsade-like teeth. Mandible with 4 major teeth, minor teeth on lower sides and at lower angle. Maxillule with 2 major and 1 small setae at upper angle, separated by small notch from slightly rounded main cutting edge, which bears 2 rows of setae reaching to setae at upper angle.

Cirri: Number of segments in rami of cirri and caudal appendages (c.a.) of a 4-mm-long specimen, anterior ramus 1st:

I	II	III	IV	V	VI	c.a.
9, 8	13, 13	12, 15	14, 13	14, 14	15, 12	10

Segments of rami of cirrus I very wide, single filamentary process at base of pedicel. Rami of cirri II–VI subequal; segments with setae extending distally around anterior and lateral faces, only slightly separated from a few stouter but, in basal segments, not longer setae at posterior distal angle. Stout posterior setae longer than reduced anterior setae distally in rami. Caudal appendages reach to 3rd segment of rami of cirrus VI. Penis stout, annulated, with short, backwardly-directed setae sparsely distributed over most of surface; a few longer setae towards tip.

REMARKS: This species probably has a cosmopolitan distribution in warmer seas. It differs from *Paralepas ovalis* (Hoek) only by the presence of the triangular scutal areas, and from *Paralepas nodulosa* Broch by not having “well defined, scanty, almost thornlike warts” (Broch 1922). As with *Heteralepas*, external appearances may not be reliable specific criteria for the identification of forms of *Paralepas*.

Family IBLIDAE Leach, 1825

Lepadomorpha with capitulum of female or hermaphrodite with 4 chitinous or weakly calcified plates; paired terga and scuta, with apical umbos. Peduncle not sharply demarcated from capitulum, clothed with chitinous spines. Dwarf males may occur in association with females or hermaphrodites.

Genus *Ibla* Leach, 1825

Characters as for the family.

DISCUSSION: Darwin (1851) recognised two species in this genus: *Ibla quadrivalvis* (Cuvier) has partial sexual differentiation, existing as hermaphrodites with complementary males; *I. cumingi* Darwin has complete sexual differentiation, existing as females with dwarf males. Hoek (1907) described *I. sibogae* from the Malay Archipelago, but this species has subsequently been regarded as synonymous with, or at best a subspecies of, *I. cumingi* (Annandale 1911b, 1916; Newman 1960). To date these species have been collected only intertidally, *I. cumingi* in tropical latitudes of the Indian Ocean,

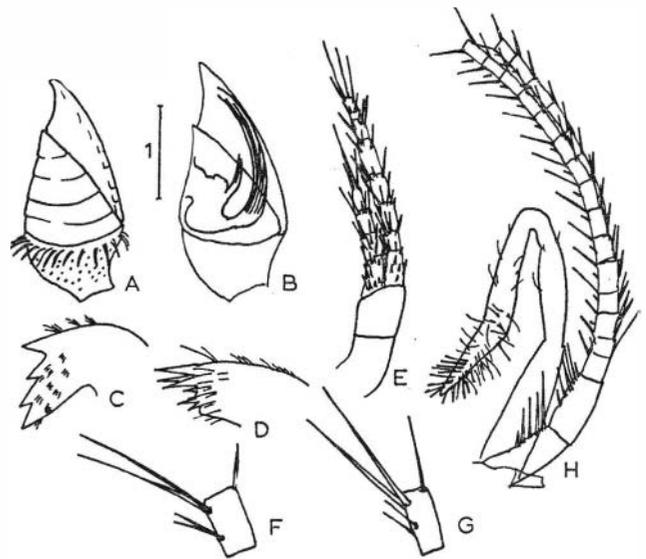


Fig. 7. *Ibla pygmaea* Broch: A, lateral view, 2.4-mm specimen; B, position of body in capitulum by transparency; C, mandible; D, maxillule; E, cirrus I; F, intermediate segment, cirrus III; G, same, cirrus VI; H, cirrus VI, with penis and base of caudal appendage (scale in mm).

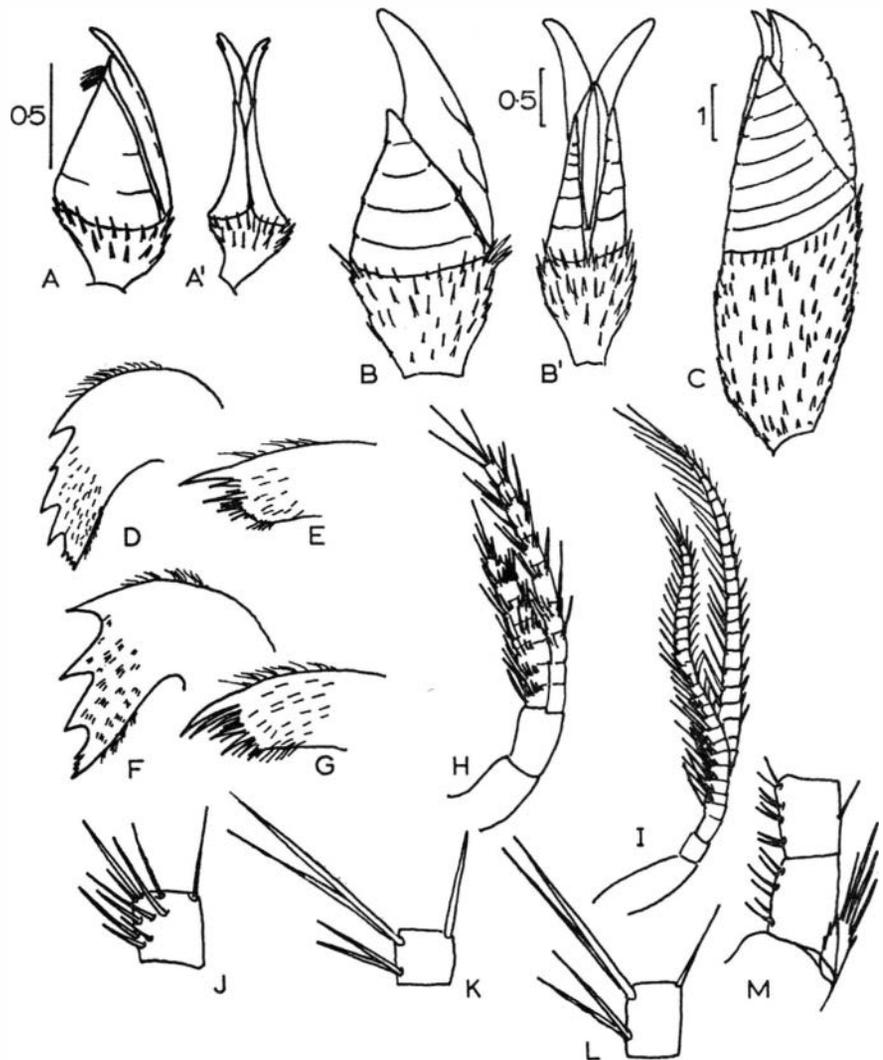
Malaysia, and Melanesia, and *I. quadrivalvis* from temperate Australian coasts. Gruvel (1902) also lists the East African coast and Fiji as localities for the latter species, but of these the latter at least is in doubt. Recent collecting (Foster 1974) has produced only *I. cumingi* in Fiji.

Broch (1922) named specimens collected by *Endeavour* from 184–294 m near Tasmania as *I. pygmaea*; these were hermaphrodites with multisegmented caudal appendages. Previously, Studer (1889) had very imperfectly described, as *Chaetolepas segmentata*, two specimens collected at the last station (about 55 km east of the Poor Knights Is) on the Brisbane-Auckland leg of the voyage of the *Gazelle*. Broch re-examined but did not dissect Studer's specimens, and on the strength of external similarities was satisfied of a synonymy. Broch (1922) amended his name *pygmaea* to *segmentata* before the publication of his account of Mortensen's cirripedes.

With the kind permission of Dr E. J. Batham I was able to examine a single specimen of the lot collected by *Endeavour* in 1914. Even though the specimen had dried out, the body was removed and the appendages mounted. The cirri had obviously been shortened in life, as the terminal segments of some were seta-less stubs. Drawings of this specimen are shown in Fig. 7; to the fairly full description of Broch (1922) may be added the details of cirral setation as shown.

Other species that have been described are *I. idiotica*, described from intertidal stations in New Zealand by Batham (1945b), and *I. atlantica*, described from 800 m in the Atlantic by Stubbings (1967). These are discussed further after the description of *I. idiotica* below.

Fig. 8. *Ibla idiotica* Batham: A, A', lateral and rostral views, 1-mm juvenile, NZOI Stn D90; B, B', same, 2.2-mm specimen, NZOI Stn E720; C, lateral view, 7.5-mm specimen, NZOI Stn D90; D, E, mandible and maxillule, specimen C; F-M from specimen B—F, G, mandible and maxillule; H, cirrus I; I, cirrus II; J, intermediate segment, cirrus II; K, same, cirrus III; L, same, cirrus VI; M, pedicel, cirrus VI, with caudal appendage (scales in mm).



***Ibla idiotica* Batham**

(Plate 2E; Fig. 8)

Ibla idiotica Batham, 1945b: 347.

?*Chaetolepas segmentata* Studer, 1889: 270.

not *Ibla segmentata*. Broch 1922.

MATERIAL EXAMINED: NZOI: Stn D90 (3 specimens on worm tube), E720 (7 on *Calantica studeri*). PMBS: 3 specimens on shell of gastropod (*Fusitriton laudandus*) occupied by a hermit crab (*vide* E. J. Batham), Saunders canyon, 423–920 m. BAF: 1 specimen on *Calantica villosa*, intertidally, Little Papanui.

DISTRIBUTION: New Zealand, from low intertidal to 920 m (Fig. 4).

DESCRIPTION: Externals: Sexes separate. Females with triangular and chitinous terga and scuta, apices of terga beak-like and diverging; parts of terga may be calcified in larger specimens. Peduncle sparsely clothed with chitinous hairs for all its length.

Mouthparts: Labrum without teeth. Mandible with 3 or 4 teeth and pectinated lower angle. Maxillule bears 1 or 2 stout setae at upper angle, and below a receding cutting edge with a number of thinner and shorter setae.

Cirri: Cirrus I widely spaced from cirrus II, anterior ramus shorter than posterior ramus. Numbers of segments in rami of 2 specimens as follows, anterior ramus 1st:

Cap. length	I	II	III	IV	V	VI
2.2 mm	6, 9	10, 10	12, 12	16, 21	22, 22	24, 24
7.5 mm	10, 14	25, 26	29, 29	34, 34	34, 35	37, 38

Segments of cirri II–VI more elongate posteriorly; those of cirrus II square with a number of setae on anterior and medial faces, particularly in basal part of rami. Segments of cirri III–VI bear 2 pairs of setae on anterior edge, more distal pair twice as long as more proximal pair. One seta at posterior distal angle of each segment. Caudal appendages leaf-like, with a few longer

setae distally and smaller setae laterally, and not quite half the length of basal segments of pedicels of cirrus VI. No penis. Males (*vide* Batham 1945b) triangular, lie free in mantle cavity of adult, have 2 large frontolateral horns, and lack peduncle, mantle, plates, and all appendages except antennules.

REMARKS: Batham (1945b) described this species from intertidal specimens of length range 1.3–3.5 mm. The present deep-water specimens are 1.0–7.5 mm long with the plates occupying about three-quarters of the total length in the smallest to less than half in the largest. The species has previously been found only intertidally, in low tidal and desiccation-protected habitats, e.g., amongst the peduncles of larger lepadomorphs. The intertidal occurrence is therefore interpreted as being the fringe of a more characteristic sublittoral habitat.

I. idiotica can be distinguished from the Australian specimens described by Broch (1922) as *I. pygmaea* by a number of characters, including the more complete coverage of the peduncle by chitinous hairs. Despite other inadequacies of the description of *Chaetolepas segmentata* by Studer (1889), his illustration depicts a complete coverage of the peduncle by hairs, and therefore that specimen, from New Zealand waters, is more likely to be the same as *I. idiotica*. This synonymy is not yet proven, but nor is the identity of *I. pygmaea* certainly the same as *I. segmentata*. A decision should not be made until Studer's type is re-examined, particularly with respect to the development or not of the penis and caudal appendages. In any case Studer's name must be regarded as a *nomen oblitum*, and Batham's name will stand.

The sexual condition of *I. idiotica* is like that of tropical *I. cumingi* whereas that of *I. pygmaea* is like that of *I. quadrivalvis*, which occurs on Australian shores near the *Endeavour* station. *I. quadrivalvis* has not yet been identified from a sublittoral habitat.

I. atlantica Stubbings resembles *I. idiotica* in having uni-articulate caudal appendages, the sexes differentiated, the peduncle clothed for all its length with chitinous hairs, and in occurring sublittorally. Apart from its geographic separation, it can be distinguished from *I. idiotica* by the unbeaked tergum, the greater numbers of segments in the cirri, and the demarcated capitulum and peduncle of the male.

Family OXYNASPIDAE Pilsbry, 1907

Lepadomorpha with capitulum of 5 approximate or variously reduced plates; scuta with umbo subcentral but not basal, terga have an apical umbo, and carinal umbo varies from subapical to sub-basal. Apex of carina extends up between terga. Caudal appendages minute, if present at all. Usually attached to antipatharians.

Characters as for the family.

Oxynaspis indica Annandale (Plate 2F; Fig. 9)

Oxynaspis celata indica Annandale, 1910: 69; Broch 1931: 34.
Oxynaspis celata. Broch 1922: 275 (with 'forms' *japonica* and *novazelandica*).
Oxynaspis indica. Totton 1940: 474; Withers 1953: 21.

MATERIAL EXAMINED: Nat. Mus.: on *Aphanipathes* sp., *ikatere*, off Little Barrier I; 25 specimens on antipatharian, off White I, 110 m. BAF: 14 specimens on *Antipathes aperta*, off Poor Knight's Is, 50–60 m.

DISTRIBUTION: Indian Ocean (Annandale), Japan, and Australasia (Broch). In New Zealand from north-eastern waters (Fig. 4).

DESCRIPTION: *Externals and shell plates:* Plates nearly approximate and covered by horny bark, in part contiguous with coenosarc of antipatharian host. Occludent margin of capitulum sinuous. Scuta and terga white and radially striated externally. Scuta have bluntly serrate tergal and basal margins, umbo $\frac{1}{2}$ – $\frac{3}{4}$ distance down from apex on occludent margin, basal margin rounded and confluent with carinal margin. Rostral angle of scuta often slightly produced, and internally bears an articular groove. Carina deeply concave, rectangularly bent at umbo; the part above umbo tinted red, and 2–3.5 × as long as lower part; umbo generally more basally situated in larger specimens.

Mouthparts: Labrum very prominent and without teeth. Mandible has 4 or 5 teeth plus the lower angle. Maxillule has a wide notch occupying about $\frac{1}{2}$ cutting edge and separating protuberant lower part of cutting edge from large setae at upper angle.

Cirri: Number of segments in rami of cirri of 2 specimens as follows, anterior ramus 1st:

cap. length	I	II	III	IV	V	VI
8.2 mm	7, 10	12, 13	14, 14	15, 14	15, 15	15, 15
14.9 mm	7, 11	11, 11	15, 16	16, 16	15, 17	16, 17

Cirrus I not very distant from cirrus II but shorter, and with anterior ramus shorter and thicker than posterior ramus. Segments of rami of cirrus II square in side view and bear medial setae. Segments of cirri III–VI become more elongate posteriorly, so that with only slightly more segments rami of cirrus VI are longer than those of cirrus III. Segments of cirri III–VI bear usually 5, rarely 4 or 6, pairs of setae on anterior edge, with a single, minute seta between bases of major pairs. A few slender setae clustered at posterior distal angle. Anterior faces of pedicels of cirri II–VI protuberant and spinose. Penis in larger specimens almost as long as cirrus VI, and has sparse, fine setae. Caudal appendages and prosomal filaments absent.

REMARKS: These specimens are identical with those taken by *Endeavour* on antipatharians near Tasmania, and referred to as *O. celata* forma *novazelandica* by Broch (1922). The *Terra Nova* collected material from a depth

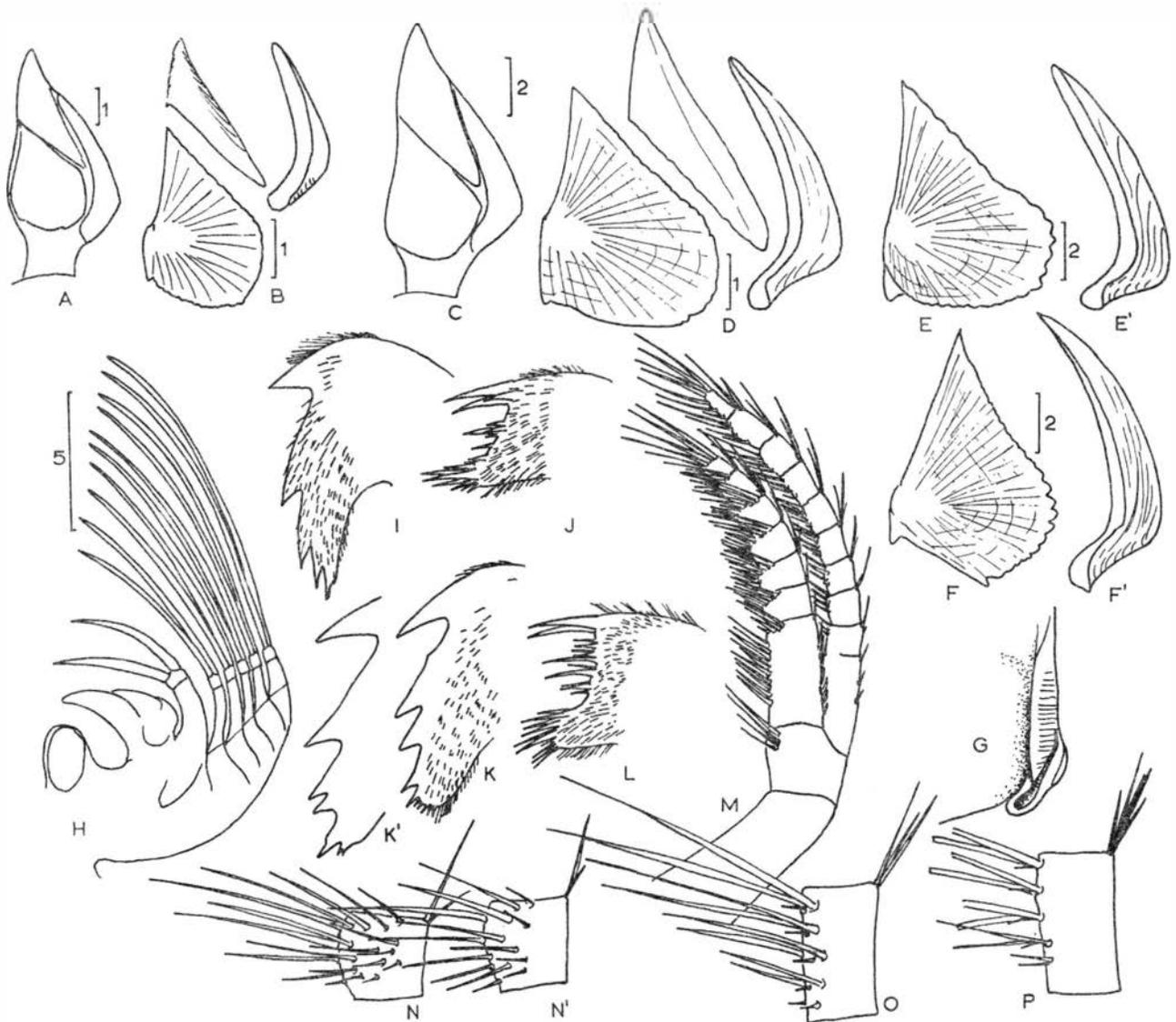


Fig. 9. *Oxynaspis indica* Annandale: A, lateral view, plate plan in 4.9-mm capitulum-length specimen; B, plates, specimen A; C, lateral view, plate plan of 8.2-mm cap. length specimen; D, plates, specimen C; E, E', scutum and carina of 13.5-mm capitulum length specimens F, F', same, 17.0-mm capitulum length specimen; G, inner view, umbo of scutum F; H, plan of prosoma, specimen E, right hand appendages shown only; I, J, mandible and maxillule, specimen C; K, K', L, same, specimen E; M, cirrus I, specimen C; N, N', intermediate segments, anterior and posterior rami of cirrus II, specimen C; O, same of anterior ramus of cirrus III, specimen C; P, same of cirrus VI, specimen E (scales in mm).

of 189 m at a station 11 km east of North Cape, from which Totton (1923) described 5 new species of antipatharians. A photograph (Totton 1923, pl. 2, fig. 2) of *Antipathes aperta* shows two attached oxynaspids. These look similar to the facies presented by the present specimens. Although Totton described *O. terranova* off *Antipathes lilliei* from the same station and in the same paper, there is no more than a passing mention of the existence of oxynaspids on *A. aperta*, nor are they referred to in a later report (Totton 1940) describing various oxynaspids in the British Museum. However, in that paper Totton distinguished *O. celata* Darwin of the Atlantic from *O. indica* Annandale of the Indian

Ocean. Broch (1922) recognised the near relationship of Indian Ocean and western Pacific specimens, but followed Annandale's specific designation as *O. celata*. The two species are undoubtedly closely related. Nilsson-Cantell (1921) put *O. indica* in synonymy with *O. celata*, and thereby extended the geographical range to Japan and Western Australia. Stubbings (1936) commented on the geographical distribution of the species of *Oxynaspis*, and merely took the specific designation given by previous workers, leading to his suggested Atlantic, Indian, and western Pacific distribution for *O. celata*, and an Indian Ocean to western Pacific distribution for *O. indica*. There is still some confusion, but it may be re-

solved in the future by proving the synonymy of the two species. In the meantime the Indian Ocean-western Pacific species is regarded as *O. indica*. Future revision may well need to take into account antipatharian host species.

Oxynaspis terranovae Totton (Fig. 10)

Oxynaspis terranovae Totton, 1923: 116.

ORIGINAL DESCRIPTION: "Valves partly separated, a distinct interspace between middle lobe of scutum and basal part of tergum, and between scutum and upper (tergal) limb of carina. Tergum with basal (scuto-carinal) angle rounded. Scutum trilobed; rostral angle produced into a short spur, which forms the basal lobe; middle lobe largest, rounded, undivided, reaching lower (scutal) limb of carina; umbo slightly above middle of occludent margin; part above the umbo narrowed to form upper (tergal) lobe, which meets the tergum for a quarter of the length of its scutal margin; a furrow extending from the umbo to a notch which separates the rostral angle (basal lobe) from the middle lobe. Carina with umbo well below middle, distal (tergal) limb being $2\frac{1}{2}$ or more times the length of basal limb. Peduncle about the same length of the capitulum, finely corrugated, springing from flared opening of tubular sheath, formed on chitinous axis of branchlet of *Antipathes lilliei*. Capitulum and peduncle overgrown by antipatharian tissue, which covers the cirripede with a thin chitinous membrane bearing spines.

Caudal appendages vestigial, each with 2 setae. Filamentary appendages: dorsal absent, one pair at base of first pair of cirri. Mandible with 4 teeth and an acute, serrated proximal angle. Maxillule with inner edge hardly emarginate, with group of strong spines distally, and with very prominent spinose proximate angle. Cirri with long setae on protuberances on basal segments except on basal parts of those of first pair, where they are reduced to short spinules. Two small conical bosses covered with short spinules present between bases of first cirri. Ovigerous frena finger-shaped, provided with a row of processes."

ORIGINAL MATERIAL: 2 specimens on *Antipathes lilliei*, 189 m, 11 km east of North Cape, New Zealand.

REMARKS: This species has not been re-encountered, but it clearly differs from *O. indica* not only in having different host species but in the morphological details of shape of scutum, the filamentary processes at the base of cirrus I, and the peculiar, spined boss on the pedicel of cirrus I.

Family POECILASMATIDAE Annandale, 1910

Lepadomorpha with up to 5 plates on the capitulum, including a carina, and paired terga and scuta. Scuta in some species split into 2 (resulting in 7 plates). Some or all of plates may be degenerate or absent. Umbos of terga apical, those of carina and scuta fundamentally basal. Peduncle without calcareous scales. Maxillule not stepped. Cirrus I widely separated from more posterior cirri, and much shorter. Caudal appendages uniarticulate and spinose.

Genus *Trilasmis* Hinds, 1844

Poecilasmatae with approximate capitular plates. Carina lacks an internal transverse shelf. Terga absent in some species (subgenus *Trilasmis*). When terga present, scuta either split into 2 parts (subgenus *Temnaspis*) or entire (subgenus *Poecilasma*). Apex of carina abuts onto truncated angle of terga. Filamentary processes absent.

Trilasmis (*Poecilasma*) *kaempferi* (Darwin) (Plate 3A; Fig. 11)

Poecilasma kaempferi Darwin, 1851: 102; Pilsbry 1907a: 183; Annandale 1910: 90; Broch 1922: 270; Nilsson-Cantell 1927: 761; Barnard 1926: 51.
Poecilasma (*Poecilasma*) *kaempferi*. Nilsson-Cantell 1921: 254 (full synonymy, including, *P. aurantium* Darwin, *P. dubium* Hoek, *P. inaequilaterale* Pilsbry); Stubbings 1936: 5.
Trilasmis (*Poecilasma*) *kaempferi*. Utinomi 1949: 21; Stubbings 1965: 879.

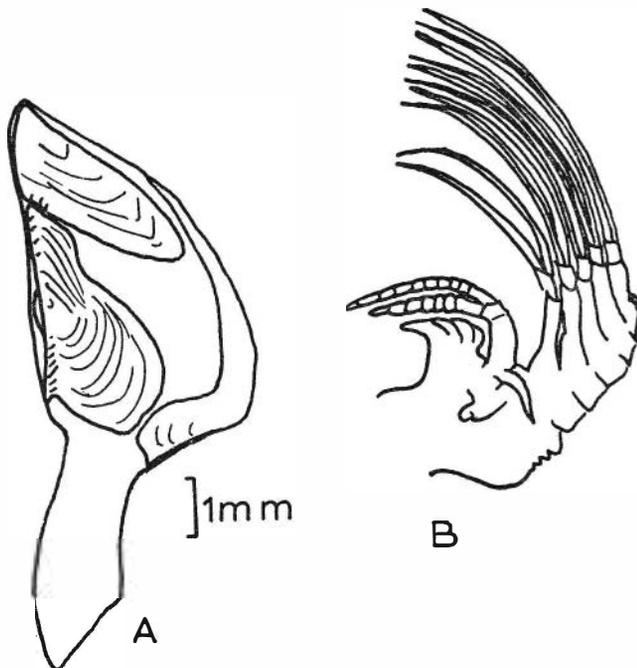


Fig. 10. *Oxynaspis terranovae* Totton: A, lateral view of whole animal; B, plan of prosoma (after Totton 1923).



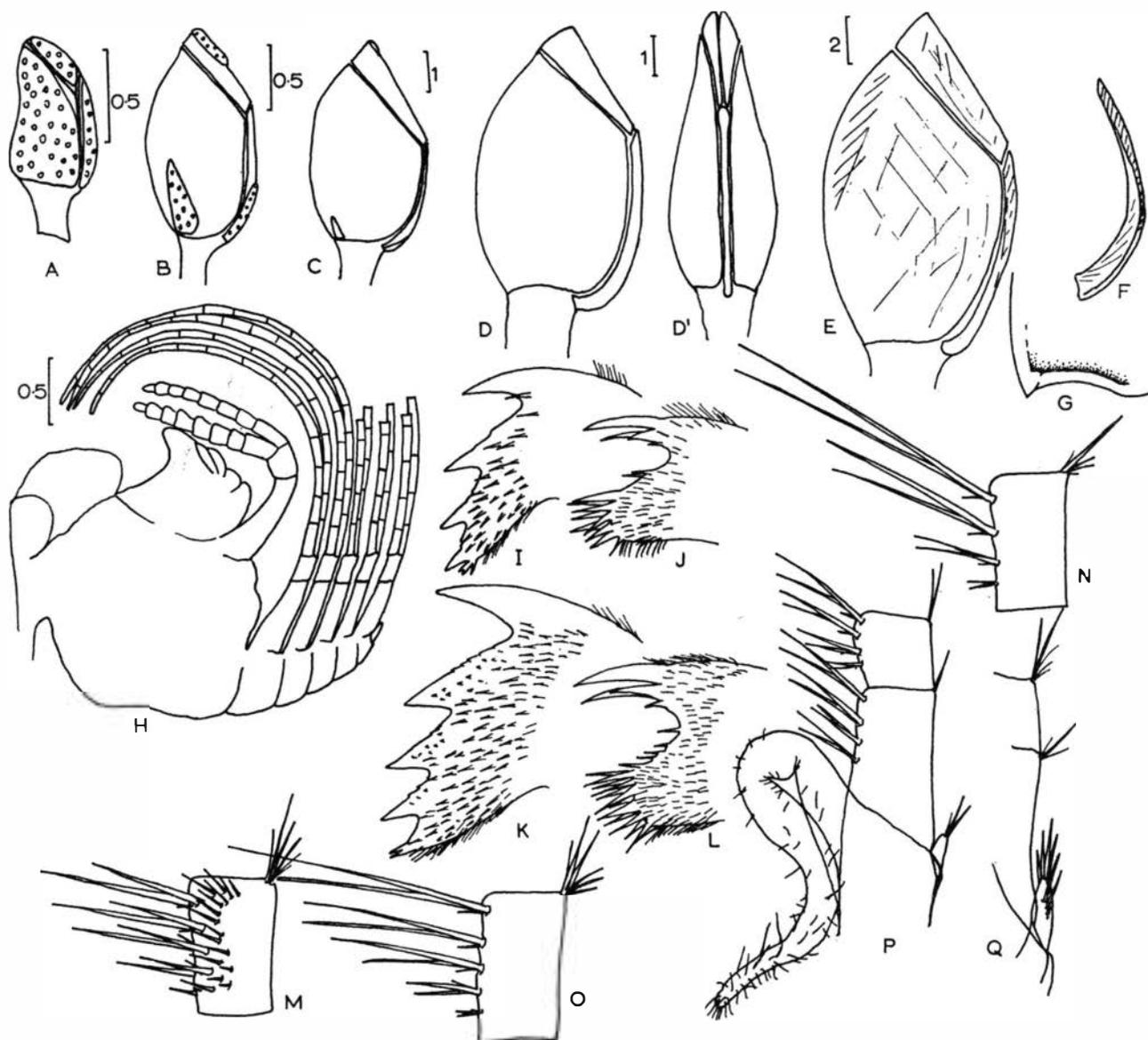


Fig. 11. *Trilasmis kaempferi* (Darwin): A-E, series of specimens of increasing size, capitulum lengths 0.8, 1.6, 5.4, 7.4 and 14.7 mm respectively, showing primordial plates in smaller specimens, carinal view in D', faint shell sculpturing in E; F, carina; G, inner view, umbonal angle of scutum; H, plan of prosoma of a 4-mm specimen showing right hand appendages; I, J, mandible and maxillule of a 4-mm specimen; K, L, same, 14.7-mm specimen; M, intermediate segments, ramus of cirrus II, 14.7-mm specimen; N, same, cirrus VI of 4-mm specimen; O, same, 14.7-mm specimen; P, pedicel of cirrus VI with caudal appendage and penis, 4-mm specimen; Q, posterior edge, pedicel of cirrus VI and caudal appendage, 7.8-mm specimen (scales in mm).

MATERIAL EXAMINED: NZOI: Stn F868 (1 specimen), F921 (6), F924 (13). Nat. Mus.: on *Nephrops challengeri*, Marine Dept. Prawn Survey, 36 km NE of Poor Knights Is, 507–544 m.

BAF: 4 specimens on *N. challengeri*, *Ikaterere*, out of Auckland; 1 specimen on *Megalasma striatum*, *Tui*, 30°45'S 173°51'E, 540–680 m; 30 specimens on ♂ *N. challengeri*, Marine Dept., around 35°7'S 174°50'E, (P. M. Hine).

DISTRIBUTION: Cosmopolitan in tropical and warm-temperate seas, 185–2000+ m; In New Zealand in north

and north-eastern waters, 315–924 m (Fig. 4).

DESCRIPTION: *Externals and shell plates:* Capitulum oval with the 2 sides symmetrical in typical forms, but with varying degrees of asymmetry described in other specimens (e.g., Pilsbry's *Poecilasma inaequilaterale*). Plates approximate with faint radial striations and concentric growth lines. Terga with truncated carinal angle forming a short margin almost parallel to occludent margin. Dorsal and scutal margins of terga straight. Scuta entire and largest plates of capitulum longer than broad, and have apico-basal ridge near occludent margin.

Umbonal tooth and basal ledge internally on each scutum. Carina arched, of nearly equal dimensions throughout its length, abuts onto terga apically, truncated basally.

Mouthparts: Mandibles have 4 teeth and sharp lower angle which is frequently bifurcate. Maxillules have 3 stout setae at upper angle, below which the protuberant cutting edge carries setae which increase in number with increase in size of the individual.

Cirri: The number of segments in the rami increase slightly with ontogeny as follows, anterior ramus 1st:

cap. length	I	II	III	IV	V	VI
4.4 mm	8, 8	13, 13	13, 15	14, 14	15, 15	15, 15
7.4 mm	8, 9	15, 16	17, 18	18, 18	18, 18	19, 19
14.7 mm	8, 10	16, 19	20, 21	20, 20	21, 19	21, 22

Intermediate segments of anterior ramus of cirrus I slightly wider than those of posterior ramus. Segments of cirri II–VI similar, and carry 4 or 5 pairs of setae on anterior edge with a small seta between bases of pairs, and a group of setae at posterior distal angle. Basal segments of cirrus II develop setae on anterior part of medial face, more abundantly in larger specimens. Caudal appendages about $\frac{1}{2}$ length of basal segment of pedicel of cirrus VI, and carry marginal setae of which distal ones longest.

REMARKS: These specimens are the typical form which has been described from Japanese and South Pacific localities. Broch (1922) and Nilsson-Cantell (1927) record specimens from Tasmanian waters, but the present records are the first for New Zealand seas. *T. kaempferi* is frequently found attached to decapod crustaceans, and has also been recorded on echinoid spines (Annandale 1910). Of the present material, where a substrate is identifiable, most lots were associated with decapods, but the *Tui* specimen was removed from the capitulum of the barnacle *Megalasma striatum*. Mr P. M. Hine (pers. comm.) reports that, of several thousand *Nephrops challengeri* collected from all around New Zealand, barnacles were found only on large males off the Poor Knights Is.

Genus *Megalasma* Hoek, 1883

Poecilasmatae with 5 entire and approximate plates on capitulum. Carina progressively larger towards base, at least in side view, has an internal transverse shelf, and abuts onto terga apically. Dorsal filamentary processes may be present on prosoma.

DISCUSSION: The species of *Megalasma* have been subdivided into two subgenera; those in which the basal margin of the scutum forms a distinct angle at the umbo with the occludent margin (*Glyptelasma*), and those in which the two are confluent (*Megalasma sensu stricto*). However, the distinctions between the two subgenera, and indeed between some species of *Megalasma* and some of *Poecilasma*, are not well demarcated.

Megalasma carinatum (Hoek) (Plate 3B; Fig. 12)

Poecilasma carinatum Hoek, 1883: 44; Hoek 1907: 5.

Poecilasma (Glyptelasma) carinatum. Nilsson-Cantell 1921: 258.

Megalasma (Glyptelasma) carinatum. Calman 1918a: 401; Calman 1919: 370.

Megalasma carinatum. Barnard 1926: 54.

Glyptelasma carinatum. Broch 1931: 32.

MATERIAL EXAMINED: Nat. Mus.: 3 specimens off cable, *Recorder*, 640 km NW of Wellington, 1104 m, (W. Foster).

DISTRIBUTION: Cosmopolitan, 138–1633 m. In New Zealand, on Challenger Plateau (Fig. 4).

DESCRIPTION: *Externals and shell plates:* Capitular plates smooth, with very faint radial striations and growth lines, partially covered with integument. Terga quadrangular in side view, with truncated basal margin about $\frac{1}{2}$ as long as occludent margin. Carina curved, spatulate apically, with dorsal flat part narrowing basally as lateral parts widen, an internal ledge not far above basal margin, and to each side of shelf a rounded tooth. Scuta bowl-shaped in lower part, have a faint occludent ridge which ends in a small, projecting tooth at umbo, basal margin forms a short, curved flange below the umbo before curving sharply into carinal margin in conformity with lateral margins of carina. Scuta without basal rims, and basal margins of scuta and carina together form a straight line distinct from occludent scuta! margin.

Mouthparts: Labrum with a row of very small teeth on its crest. Mandibles of one specimen with irregular dentition, and pectinate lower angle. Maxillules bear a number of stout setae on a rounded upper angle, and similar-length setae on wider, rounded, main cutting edge.

Cirri: Cirrus I set apart from other cirri; its segments shorter than those of more posterior cirri, and those of both rami about same thickness. Basal parts of rami long, and counting these as one segment, each ramus of cirrus I has 10 or 11 segments. Cirri II–VI alike, with from 18 segments in rami of more anterior cirri to 25 in more posterior cirri. Segments elongate, and carry 5–7 pairs of long setae on anterior edge, with a single, small seta at and between bases of larger pairs. Caudal appendages about $\frac{1}{2}$ length of basal segment of pedicel of cirrus VI, truncated, and bear long setae apically. Penis with long, fine setae distally. Prosoma bears a small pair of dorsal filamentary processes.

Remarks: This species belongs to the subgenus *Glyptelasma*. The present specimens are quite large, nearly 30 mm in capitular length, and this may account for the irregular dentition of the mandible, which approaches the condition described for *M. gigas* by Annandale (1916). *M. carinatum* has been recorded from a variety of substrata, including other barnacles, but it has not so far been recorded from decapod Crustacea, the preferred habitat of *Trilasmis*, to which it bears a superficial resemblance.

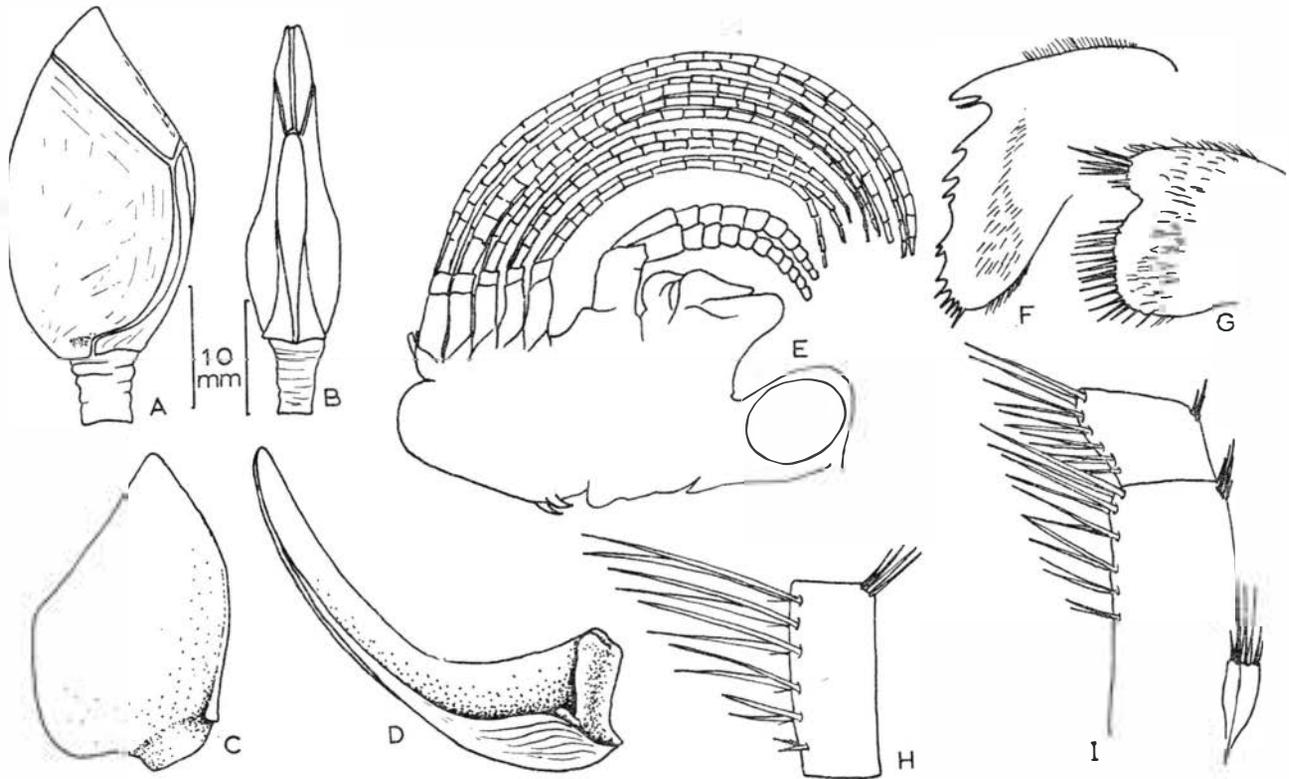


Fig. 12. *Megalasma carinatum* (Hoek): A, B, lateral and carinal views, 28-mm capitulum length specimen; C, inner view, scutum; D, oblique view, carina; E, plan of prosoma; F, mandible; G, maxillule; H, intermediate segment, cirrus VI; I, caudal appendage and pedicel, cirrus VI.

***Megalasma striatum* Hoek** (Plate 3C; Fig. 13)

Megalasma striatum Hoek, 1883: 51; Hoek 1907: 31; Broch 1922: 270; Broch 1931: 33; Nilsson-Cantell 1938: 29; Utinomi 1958: 292.

MATERIAL EXAMINED: NZOI: Stn E875 (8 specimens). Auck. Mus.: 1 specimen, "sector east of Alderman Is". BAF: 36 specimens, *Tui*, 30°45'S, 173°51'E, 540–680 m.

DISTRIBUTION: Indian Ocean and western Pacific, Japan to New Zealand, 180–984 m. In New Zealand: north and north-eastern waters, 368–680 m (Fig. 4).

DESCRIPTION: *Externals and shell plates*: Capitular plates heavily calcified and markedly sculptured with radial striations between grooves of growth lines. Tergum triangular in lateral view, with dorsal ledge which abuts onto apex of carina. Carina with dorsal roof widening apically on either side of a midline groove. Laterally and at 90° to roof, carina widens towards base, and internally a ledge occurs between a tooth on each side. Scuta have basal margin rotated, so that it is in line below umbo with curvature of occludent margin above umbo. Scuta with internal umbonal teeth, and external arc of more prominent portions of growth zones extends as beads from umbo to carinal-tergal angle. A similar arc extends from basal margin below umbo of scuta to carinal margin, and is continued

externally on carina to umbo of carina. This lower ridge especially developed in larger specimens, but is not always apparent.

Mouthparts: Mandibles have 4 teeth and a sharp lower angle. Maxillules with 3 stout setae at upper angle separated by a wide notch, bearing a few short setae, from a protuberant cutting edge, which carries numerous stout setae.

Cirri: Intermediate segments of anterior ramus of cirrus I almost twice as wide as those of posterior ramus. Numbers of segments in the rami of 2 specimens are as follows, anterior ramus 1st:

cap. length	I	II	III	IV	V	VI
8.8 mm	9, 10	14, 17	15, 14	14, 15	16, 16	16, 15
13.5 mm	9, 11	15, 16	16, 17	18, 17	17, 17	17, 17

Intermediate segments of rami of cirrus II shorter than those of more posterior cirri, carry a few setae on anterior part of medial face, 4 or 5 pairs of major setae on anterior face, and a bunch of setae at posterior distal angle. Caudal appendage about 1/3 length of basal segment of pedicel of cirrus VI, and carries marginal, plumose setae. Posterior margins of basal segment of pedicel serrated with minute, upwardly directed spines. Penis has long, fine setae distally. Prosoma carries a pair of filamentary processes on dorsal surface.

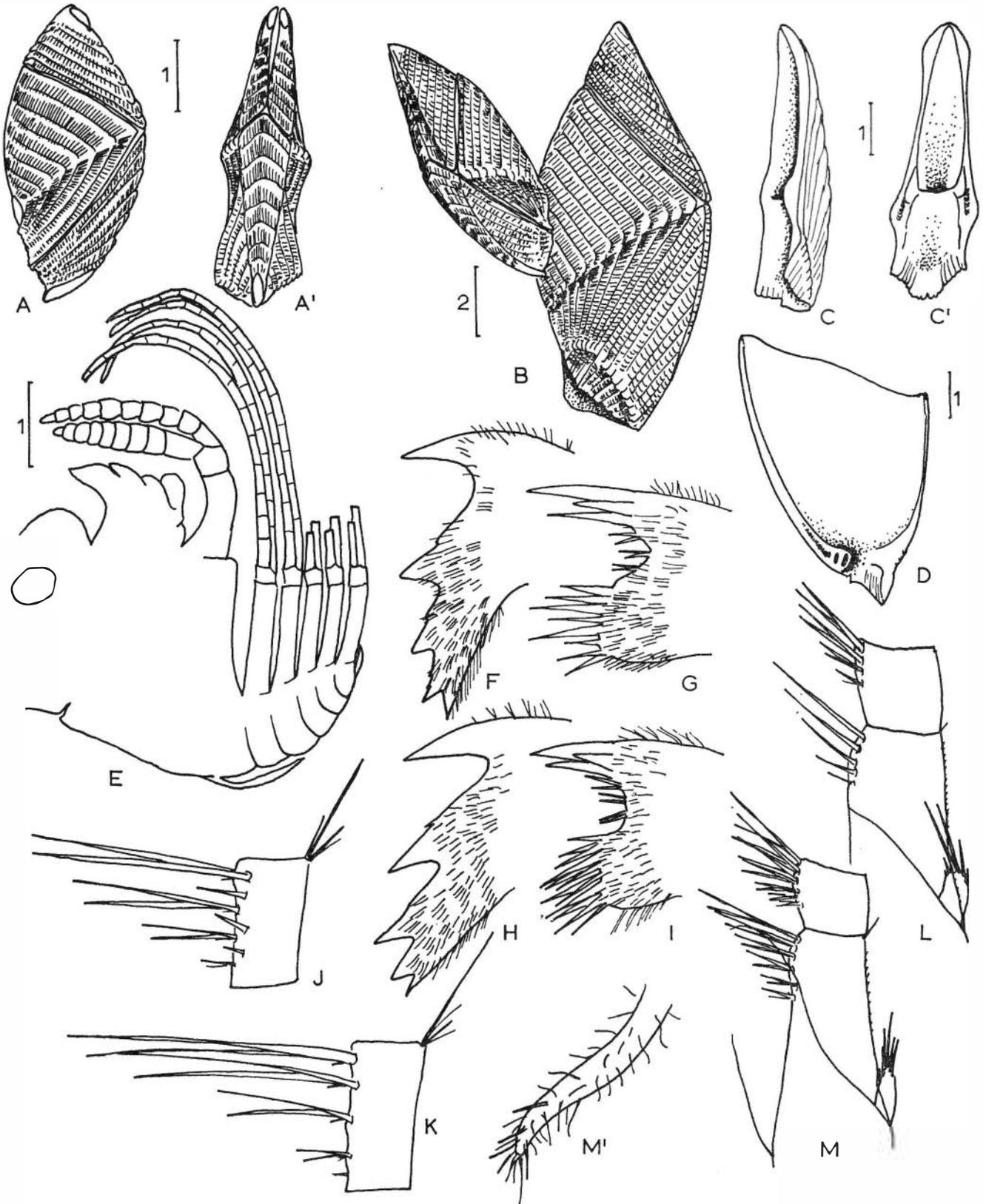


Fig. 13. *Megalasma striatum* (Hoek): A, A', lateral and carinal views, 4.3-mm long specimen; B, further specimens, the largest 13-mm long; C, C', oblique-lateral and inner view of carina; D, inner view, scutum; E, plan of prosoma, 8.8-mm specimen showing right appendages; F, G, mandible and maxillule, 8.8-mm specimen; H, I, same, 13.5-mm specimen; J, inner view, intermediate segment of ramus, cirrus II of 8.8-mm specimen; K, same, cirrus VI of 8.8-mm specimen; L, pedicel of cirrus VI and caudal appendage, 8.8-mm specimen; M, same, 13.5-mm specimen, tip of penis shown in M' (scales in mm).

REMARKS: This species belongs to the subgenus *Megalasma*. Zullo & Newman (1964) recognise two series of *Megalasma* (s. str.), which differ in the proportions and details of the articulation of the plates. *M. striatum* and *Megalasma elegans* Newman make up the first series. *M. elegans* was collected from a south-east Pacific station, and is said to differ from *M. striatum* by the absence of the ridged arc across the bases of the scuta and carina (Zullo & Newman 1964); in the present material some of the specimens, particularly the smaller ones, lack traces of this arc. The other differences enumerated by Zullo & Newman (1964) concern body structures, but in the light of examination of the present material these appear insignificant. The setae on the caudal appendages of *M. striatum* are pinnate; the omission of the setules in the figures by Utinomi (1958) and in Fig. 13L, M is because of the disparities between scale and detail. In the present material the posterior margin of the pedicel of the cirri bears only one series of minute spines, in contrast to the two rows figured by Utinomi (1958). There can be no doubt that *M. striatum* and *M. elegans* are very closely related, and the New Zealand records help to bridge the geographical gap between them.

Family LEPADIDAE Darwin, 1851

Lepadomorpha with a capitulum with up to 5 calcareous plates or their rudiments, including a carina and paired

terga and scuta. Peduncle without scales. Mandible with 5 teeth and a pectinate lower angle, smallest tooth nearest the lower angle. Maxillule with a step-like cutting edge. Caudal appendages, when present, non-setose and never multiarticulated.

Genus *Lepas* Linné, 1758

Lepadidae with 5 plates covering most of capitulum. Carina extends between terga. Scutal umbos basal.

Lepas anatifera Linné (Plate 4A, B, D; Fig. 14)

Lepas anatifera. Darwin 1851: 73 (see for earlier citations); Chilton 1911a: 571 (in part); Jennings 1915: 285, 288; Powell 1947: 40; Utinomi 1968a: 165; Newman & Ross 1971: 31.

MATERIAL EXAMINED: NZOI: Stns D595, D720, D891, E161, F932, Z553, Z554, Z1025, Z1026. Nat. Mus.: specimens from Mayor I, Sunday I (E. B. Davidson), McCauley I (J. C. Yaldwyn), and Raoul I (N. S. Kirton) in the Kermadecs; Norfolk Is; from Mayor I (P. J. Castle) and Omaio Bay (R. K. Dell) in the Bay of Plenty; and from Muriwai (on the carapace of *Aretmochelys imbricata*), Opunake, Paekakariki (G. A. Rutland), Paraparaumu (W. J. Phillips & C. J. Lindsay), Lyall Bay (R. K. Dell), and New Brighton Beach (W. R. B. Oliver). BAF: specimens from White Beach, Bethells Beach, Leigh.

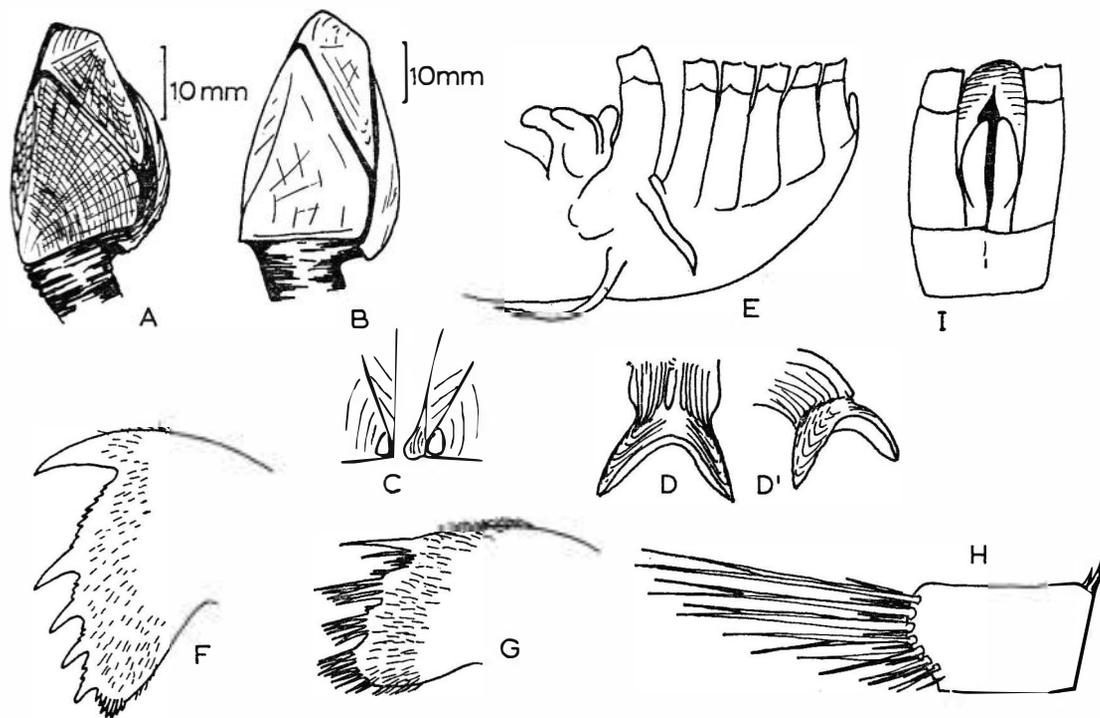


Fig. 14. *Lepas anatifera* Linné: A, B, lateral views, capitulum and upper peduncle of striated and smooth plated forms; C, external view, umbos of the scuta; D, D', views, fork of the carina; E, plan of the prosoma; F, mandible; G, maxillule; H, intermediate segment, cirrus VI; I, posterior view, caudal appendages and pedicels, cirrus VI.

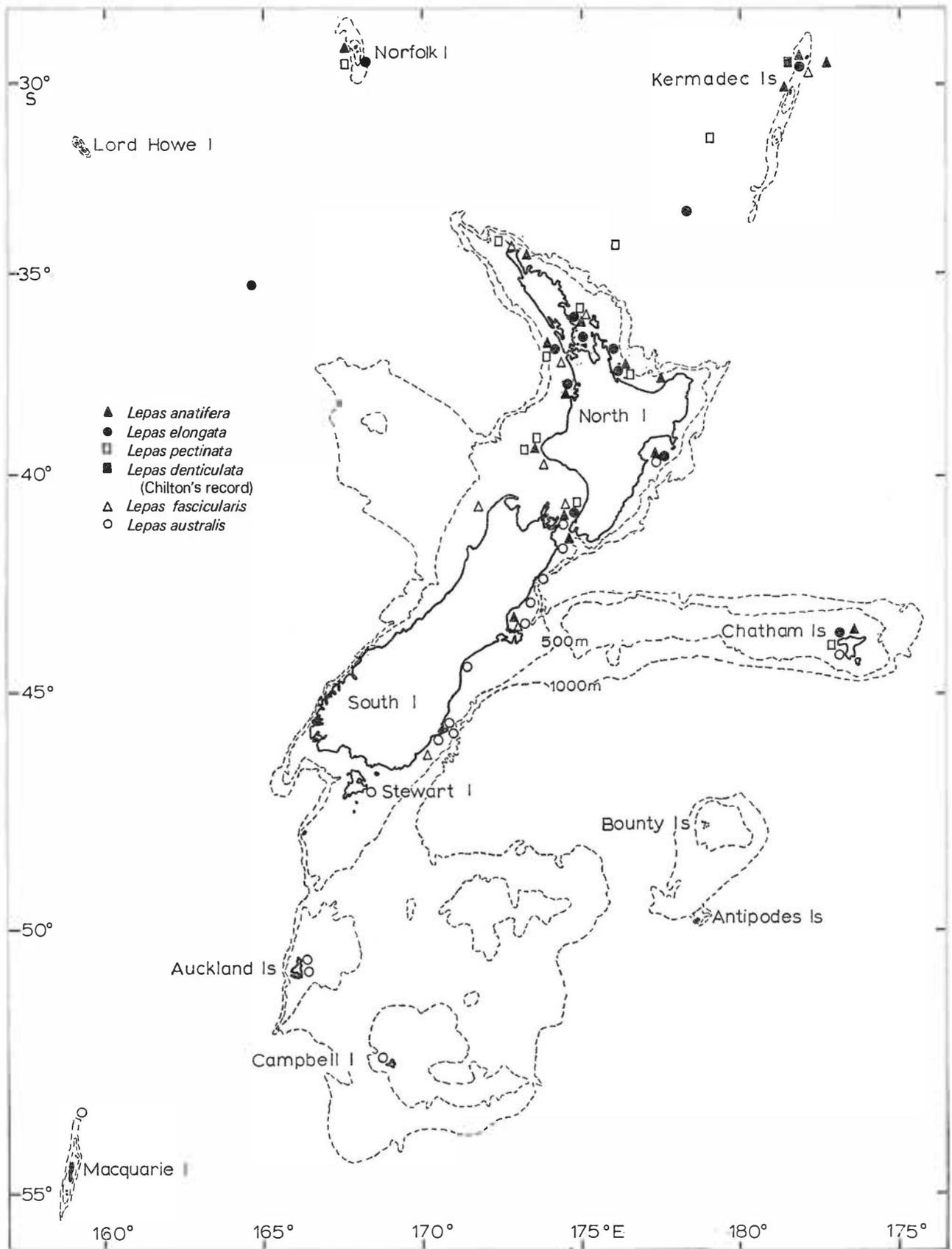


Fig. 15. Records of *Lepas* in the New Zealand region. Individual stations around the Auckland, Wellington, Hawke's Bay, and Pegasus Bay areas are numerous and not all are represented.

For *Lepas elongata* read *Lepas testudinata*.

DISTRIBUTION: Cosmopolitan in tropical and temperate seas, generally attached to floating objects. In New Zealand, northern (Fig. 15).

DESCRIPTION: *Externals and shell plates:* Approximate or nearly approximate plates, externally smooth or delicately striated. Carina forked below umbo and with embedded prongs. Right scutum (but not left) has an internal umbonal tooth.

Prosoma: 2 filamentary processes on each side, 1 at base of peduncle of cirrus I and a longer 1 on flank of prosoma below. Caudal appendages more than $\frac{1}{2}$ height of basal segment of pedicel of cirrus VI. Intermediate segments of rami of cirrus VI with 6 or 7 pairs of setae on anterior edge, with smaller setae between bases of these pairs, and without lateral setae.

***Lepas testudinata* Aurivillius (Plate 40; Fig. 16)**

Anatifa elongata Quoy & Gaimard, 1834: 635; Darwin 1851: 374; Hutton 1879: 336.

Lepas elongata. Filhol 1885: 485.

Lepas hilli. Hutton 1879: 329; Filhol 1885: 485; ?Young 1929: 158; (not Darwin 1851; not Jennings 1915).

Lepas testudinata Aurivillius 1892: 128; Aurivillius 1894: 7; Gruvel 1905: 109; Borradaile 1916: 131.

Lepas anatifera. Chilton 1911a: 571 (in part).

Lepas anatifera var. "c" Jennings, 1915: 285; Jennings 1918: 57.

Lepas affinis Borradaile, 1916: 131.

Lepas anatifera var. *testudinata*. Nilsson-Cantell 1928a: 12.

MATERIAL EXAMINED: NZOI: Stns Z360, Z365, Z398, Z543, Z544, Z545, Z546, Z547, Z548, Z549, Z550, Z552, Z553, Z554, Z555, Z1025, Z1026, Z1028, Z1236, Z1238. Nat. Mus.: specimens from Sunday I (R. S. Bell) in the Kermadecs; Norfolk I (H. Marwick); Waiheke I, Mayor I (P. J. Castle), Waipapakauri (R. K. Dell), Otaki (R. K. Dell), Raglan (W. R. B. Oliver), and Chatham Is (W. R. B. Oliver). BAF: Mangawhai, Pakiri, Leigh, Whangamata (C. Hatton), Piha; *Tui*, 33°13'S, 178°24'E.

DISTRIBUTION: Southern hemisphere in temperate seas, generally attached to floating objects. In New Zealand, northern (Fig. 15).

DESCRIPTION: *Externals and shell plates:* Apex of carina standing away from basal corner of tergum, all plates smooth externally and separated by conspicuous areas of integument. Carina bifurcate below umbo with short, rounded prongs not deeply embedded. Scuta without internal umbonal teeth.

Prosoma: 2 filamentary processes on each side, 1 at base of peduncle of cirrus I and a longer 1 on flank of prosoma below. Caudal appendages less than $\frac{1}{2}$ height of basal segment of pedicel of cirrus VI. Intermediate segments of rami of cirrus VI have 6 pairs of setae on anterior edge, shorter setae between bases of pairs, and a few short setae laterally near base of upper pair. The

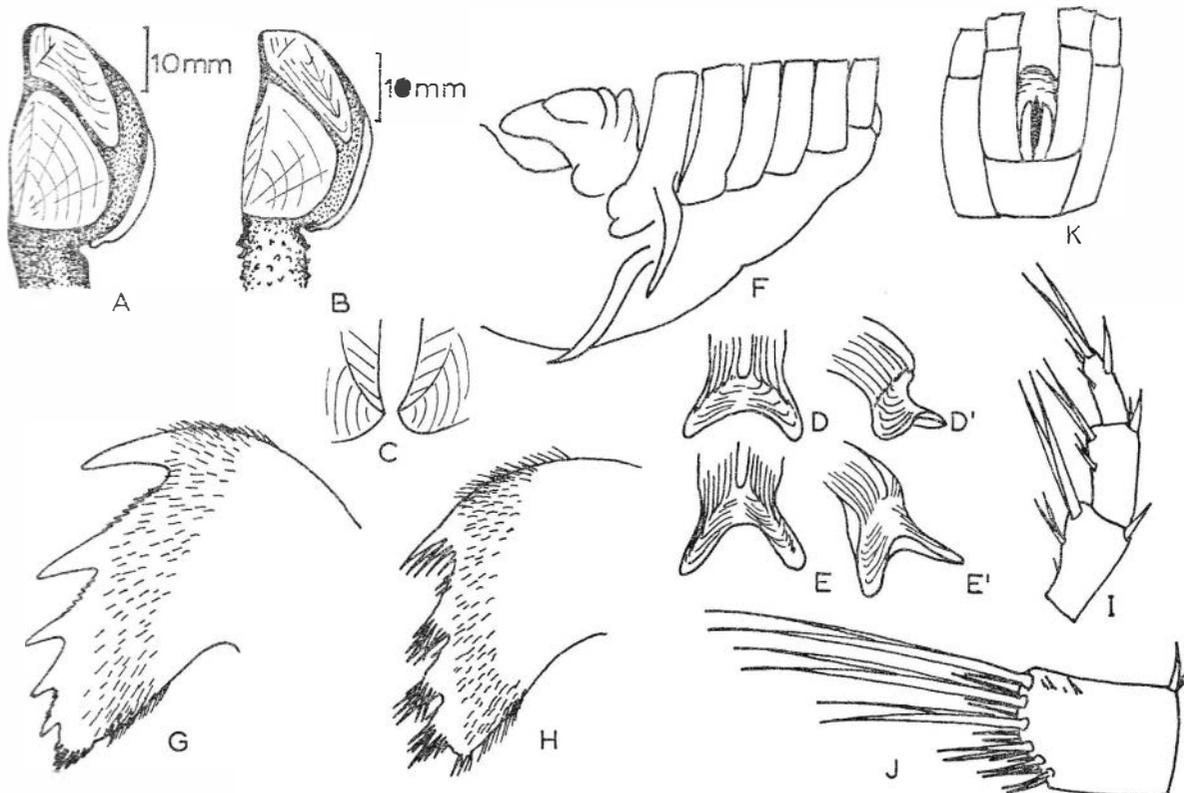


Fig. 16. *Lepas testudinata* Aurivillius: A, B, lateral views, capitulum and upper peduncle, smooth and spined peduncle forms; C, external view, umbos of the scuta; D, D', views, fork of the carina; E, E', same, another specimen; F, plan of the prosoma; G, mandible; H, maxillule; I, distal segments, ramus of cirrus V; J, intermediate segment, ramus of cirrus VI; K, posterior view, caudal appendages and pedicels, cirrus VI.

peduncle may be quite smooth externally, but often bears cuticular spines.

REMARKS: Darwin (1851) was unsure of the classification of *Anatifa elongata* collected by the *Astrolabe* from the Bay of Islands, but suspected it to be *Poecilasma*. It is clear from the original figure (Quoy & Gaimard 1834, pl. 93, fig. 6) that the carina extends beyond the bases of the terga, and the species is therefore in the genus *Lepas*. Although the carina is not very widely spaced from the other capitular plates, the tuberculated peduncle is clearly shown, and indicates the identity with some of the present material. The coincidence of geographic localities reinforces the identity with *Lepas elongata*. However, as Quoy & Gaimard's name has remained unused in the literature for more than 50 years it must be considered a *nomen oblitum* according to the 1961 International Code of Zoological Nomenclature.

The forms with a tuberculated peduncle differ in no important way from smooth-skinned forms referable to *Lepas testudinata* Aurivillius. Nilsson-Cantell (1928a) ranked Aurivillius' species as a variety of *L. anatifera*, largely because in both there are but two filamentary processes on each side. Whereas *L. hilli* has 3, and *L. anserifera* has 5 or 6 processes on each side, *L. australis* also has only 2 filamentary processes, and is clearly distinguishable from any of the above-named species. By combination of characters, *L. testudinata* is as valid a species as *L. australis*. In the wealth of *Lepas* material examined for this study from New Zealand, there has been no difficulty in distinguishing *L. testudinata* from *L. anatifera* and *L. australis*.

L. testudinata may, however, be confused on external appearances with *L. hilli* because of the separation of the plates, but in the latter species the carina extends upwards well past the bases of the terga, and bends towards them. The resemblance evidently led to a misidentification by Hutton (1879). As stated by Jennings (1915, p. 287), Hutton's specimens are beyond examination for internal characters, but his specimens now in the Otago Museum do not differ externally from smooth-peduncled forms in the present material. Filhol (1885) placed *L. hilli* in the New Zealand list on the basis of Hutton's record. The specimens found attached to driftwood on the beaches of the Chatham Is were probably *Lepas testudinata*. There is no certain evidence that *L. hilli* occurs naturally in New Zealand waters, although the specimens taken from the hull of the *Terra Nova* and identified by Jennings (1915) as *L. hilli* do have 5 filamentary processes on each side. As these possibly settled in New Zealand seas, *L. hilli* can be expected to occur in the New Zealand region.

There is no record of *Lepas anserifera* from New Zealand.

Lepas australis Darwin

(Plate 4D, F; Fig. 17)

Lepas australis Darwin, 1851: 89; Hutton 1879: 329; Filhol 1885: 485; Weltner 1899: 442; Jennings 1915: 289; Jennings 1918: 58; Nilsson-Cantell 1930b: 210; Utinomi 1968a: 166; Newman & Ross 1971: 31 (for further citations).

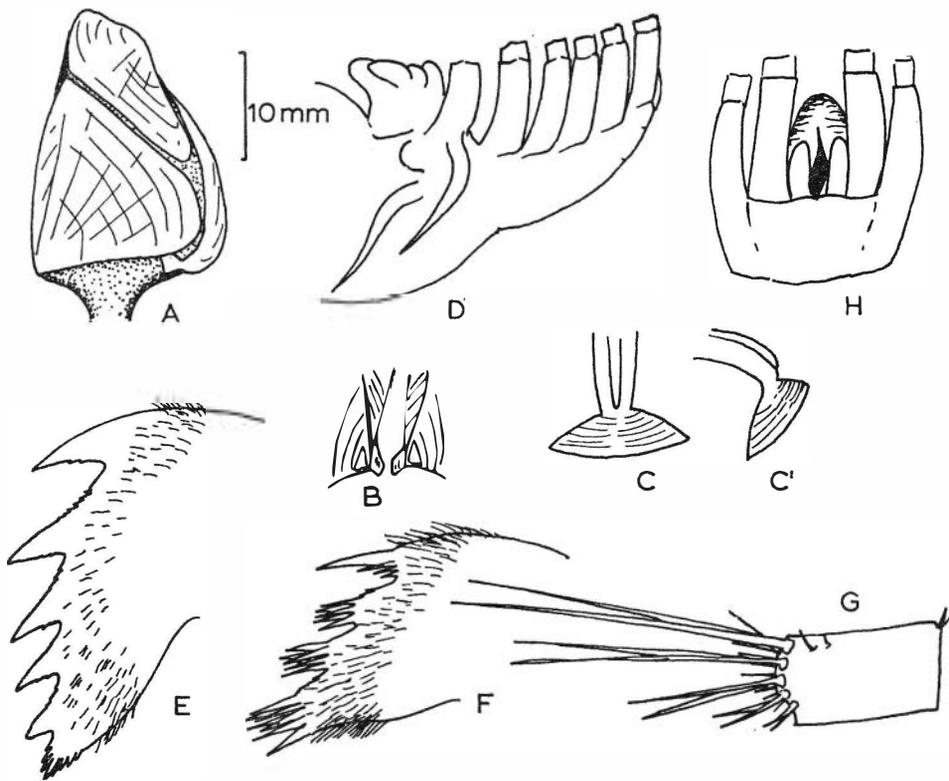


Fig. 17. *Lepas australis* Darwin: A, lateral view, capitulum and upper peduncle; B, external view, umbos of scuta; C, C', views, fork of the carina; D, plan of the prosoma; E, mandible; F, maxillule; G, intermediate segment, ramus of cirrus VI; H, posterior view, caudal appendage and pedicels, cirri V and VI.

MATERIAL EXAMINED: NZOI: Stns C675, C729, C735, Z540, Z541, Z542, Z544, Z545, Z547, Z555, Z556, Z557, Z558, Z559, Z1025, Z1026, Z1027, Z2114. Nat. Mus.: specimens from Waikanae (T. Deveraii), Lyall Bay (R. K. Dell; including one lot from feet and tail feathers of a Fiordland crested penguin), Chatham Is, Auckland Is (J. C. Yaldwyn), and Campbell I (J. H. Sorenson; from a sea leopard). PMBS: St. Clair Beach. Canterbury University, Zoology Department: Auckland Is, on elephant seal (P. M. Johns). BAF: on floating *Macrocystis* off Otago Peninsula.

DISTRIBUTION: Southern Hemisphere in antarctic to cold temperate seas; in New Zealand, southern (Fig. 15).

DESCRIPTION: *Externals and shell plates:* Plates nearly approximate, thin, and externally smooth. Below umbo of carina a wide triangular plate not deeply embedded. Scuta have internal umbonal teeth.

Prosoma: 2 filamentary processes on each side, 1 on posterior margin of basal segment of peduncle of cirrus I, other on flank of prosoma below. Caudal appendages less than $\frac{1}{2}$ height of basal segment of peduncle of cirrus VI. Intermediate segments of rami of cirrus VI with 5 pairs of setae on anterior edge, with sparse, shorter setae between bases of pairs, and a few very short setae laterally near base of distal pair. Peduncle smooth and constricted close under capitulum.

Lepas pectinata Spengler

(Plate 4E; Fig. 18)

Lepas pectinata. Darwin 1851: 85 (see for earlier citations); Hoek 1883: 40; Weltner 1899: 442; Chilton 1911a: 571; Jennings 1915: 286; Jennings 1918: 57; Broch 1922: 266; Borradaile 1916: 131; Utinomi 1968a: 166.

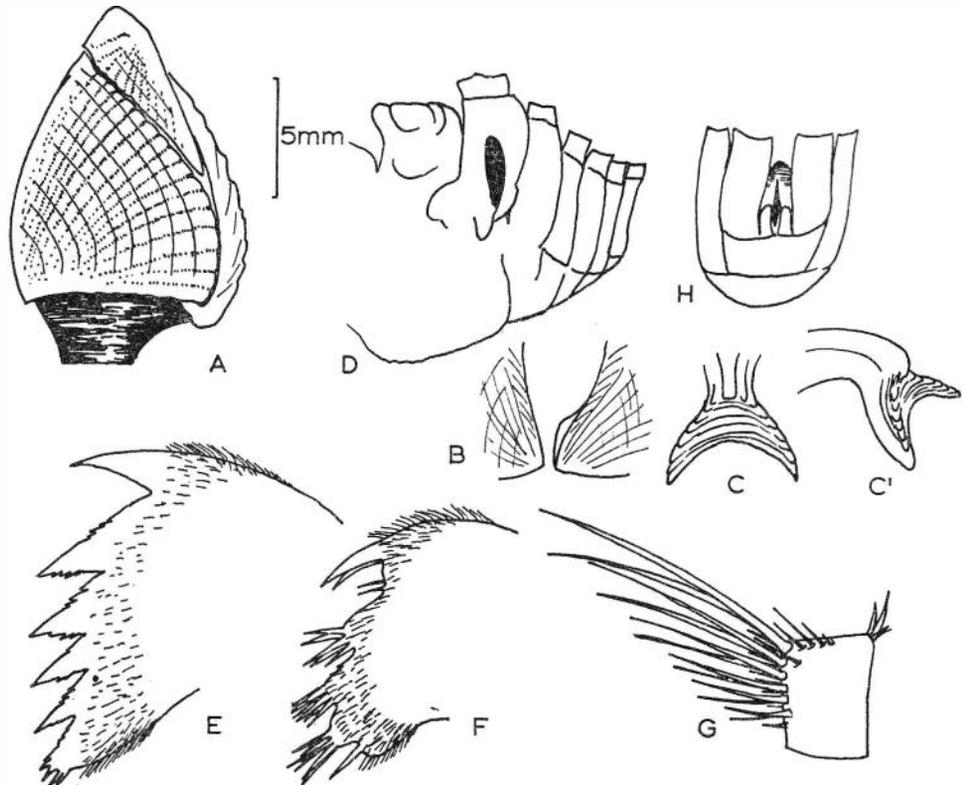
MATERIAL EXAMINED: NZOI: Stns Z1024, Z1913. Nat. Mus.: specimens from Norfolk I (H. Marwick), Mayor I (P. J. Castle), Opunake (M. A. Crozier), and Waiterere Beach near Levin. BAF: specimens from Mangawhai, Leigh, and Piha; *Tui*, 34°15'S, 176°15'E and 31°24'S 179°00'E.

DISTRIBUTION: Cosmopolitan in tropical to subtropical seas. In New Zealand, northern (Fig. 15).

DESCRIPTION: *Externals and shell plates:* Approximate, radially ridged plates often profusely spinose. Carina has below umbo diverging prongs embedded in integument. Tergum has a notch which receives apex of scutum. Scuta with apicobasal ridge very close to occludent margin, and with variously developed internal umbonal teeth, one on right often larger.

Prosoma: Filamentary processes absent, or just one short, obtuse projection on posterior of base of 1st segment of pedicel of cirrus I. Caudal appendages about $\frac{1}{4}$ height of basal segment of pedicel of cirrus VI. Intermediate segments of cirrus VI have 6 pairs of setae on anterior face, with sparse shorter setae between bases of

Fig. 18. *Lepas pectinata* Spengler: A, lateral view, capitulum and peduncle; B, external view, umbos of scuta; C, C', views, fork of the carina; D, plan of the prosoma; E, mandible; F, maxillule; G, intermediate segments, ramus of cirrus VI; H, posterior view, caudal appendages and pedicels, cirri V and VI.



pairs, and with a group of quite long setae on lateral distal margin and at base of distal pair of setae. Peduncle smooth, usually shorter than capitulum.

Lepas denticulata Gruvel (Plate 4C)

Lepas denticulata Gruvel, 1905: 106; Chilton 1911a: 571; Jennings 1915: 286; Jennings 1918: 58

MATERIAL EXAMINED: Cant. Mus.: AQ. 3188, 4 specimens from Sunday I (Chilton 1911a).

DESCRIPTION: Approximate plates. Scuta radially ridged and with an apico-umbonal ridge situated apart from occludent margin, and with slight internal umbonal teeth. Carina dorsally crested and toothed, with short, embedded, and diverging prongs below umbo. Filamentary processes absent. Peduncle short.

REMARKS: These specimens agree well with the figure given by Gruvel (1905) for specimens from the Philippine Is. No further material has been located in Kermadec Is collections.

Lepas fascicularis Ellis & Solander (Plate 4H; Fig. 19)

Lepas fascicularis. Darwin 1851: 92 (see for earlier citations); Hutton 1879: 329; Hoek 1883: 41; Weltner 1899: 442; Chilton 1911a: 572; Jennings 1915: 286; Jennings, 1918: 58;

Young 1929: 157; Utinomi 1968a: 167; Newman & Ross 1971: 33.

MATERIAL EXAMINED: PMBS: specimens coll. by *Galathea* from west of Nelson. Nat. Mus.: specimens from Sunday I in the Kermadecs (W. R. B. Oliver), Hawera, mouth of Manawatu River (F. E. Wilson), Waitarere Beach (T. Eastern), and *Galathea* specimens from off Nelson. Otago Mus.: specimens from The Nuggets, mus. no. A.99.82. BAF: Leigh, Mangawhai, Manukau Heads, Waiuku coast (latter two localities-N. Douglas).

DISTRIBUTION: Cosmopolitan in tropical and temperate seas. In New Zealand, as shown in Fig. 15.

DESCRIPTION: *Externals and shell plates*: Inflated capitulum with plates smooth, thin, transparent, and separated by chitinous interspaces. Carina prominently and angularly bent at umbo, with lower part a wide truncated disc. Scuta have no internal umbonal teeth, but have basal margin reflexed to form a rim.

Prosoma: 5 filamentary processes on each side, of which 4 arise from basal part of first segment of pedicel of cirrus I, and other from flank of prosoma below. Caudal appendages about $\frac{1}{2}$ height of basal segments of cirrus VI. Segments of posterior cirri of larger specimens have a dense anterodistal brush of setae. (This acanthopod condition contrasts with ctenopod condition of previous species.) Peduncle smooth and short, and secretes from its base a rounded flotation device.

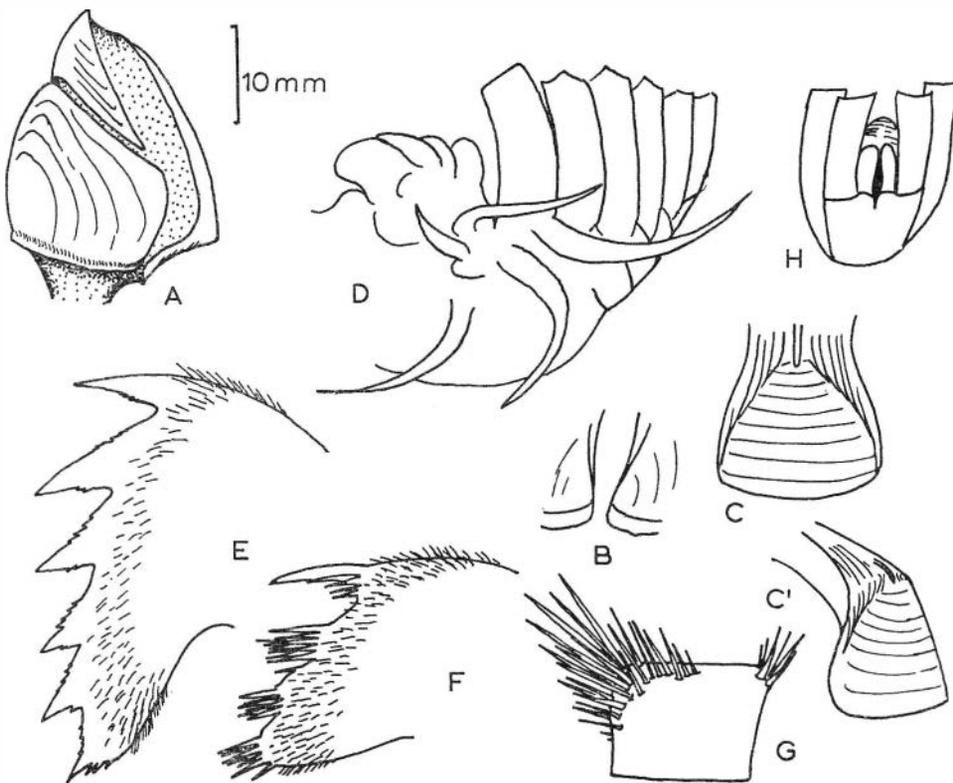


Fig. 19. *Lepas fascicularis* Ellis and Solander: A, lateral view, capitulum and upper peduncle; B, external view, umbos of the scuta; C, C', views, base of the carina; D, plan of the prosoma; E, mandible; F, maxillule; G, intermediate segment, ramus of cirrus VI; H, posterior view, caudal appendages and pedicels, cirri V and VI.



Lepadidae with 5 or 2 reduced and remote capitular plates. Scuta lie close to base of orifice and have medial umbones. Cirri with stout, claw-like setae on distal segments.

Conchoderma virgatum Spengler (Plate 3D; Fig. 20)

Conchoderma virgatum. Darwin 1851: 146 (see for earlier citations); Jennings 1918: 59; Hiro 1937: 402; Powell 1947: 41; Newman & Ross 1971: 35.

MATERIAL EXAMINED: NZOI: Stns Z1060, Z1238. Nat. Mus.: specimens taken from jaw of hapuka, (*Polyprion oxygeneios*) SSE of Alderman Is at 127–274 m; specimens from the claspers of a shark (*Carcharodon carcharias*), Tory Channel. Auck. Mus.: specimens on a hawksbill turtle stranded on Piha beach; and unlabelled specimens on a parasitic copepod (*Penella*). BAF: on drifting buoy off Leigh (B. Russell).

DISTRIBUTION: Cosmopolitan on floating and nektonic objects.

DESCRIPTION: *Externals and shell plates*: Capitulum with 5 reduced plates, of which carina is without a basal

fork or knob, tergum concave internally and has apices curved inwards, and scutum 3-lobed. Two or three longitudinal purple bands on each side that extend onto peduncle.

Prosoma: 6 filamentary processes on each side, 2 on posterior margin of base of cirrus I, 1 on flank of prosoma below articulation of cirrus I, and 1 on base of each of pedicels of cirri III–V. Processes on posterior cirri quite short. Caudal appendages less than $\frac{1}{2}$ height of basal segment of pedicle of cirrus VI. Segments of rami of more anterior of cirri II–VI bear numerous setae on lateral and anterior faces, particularly in anterior ramus of cirrus II. Intermediate segments of cirrus VI have 5 pairs of setae on anterior face, with short setae between bases of pairs and laterally near bases of distal pair.

REMARKS: Previous records of *C. virgatum* from New Zealand waters were based on ship-fouling specimens (see Jennings, 1915). Skerman (1960) has also recorded the transport of the species to New Zealand by ships. These latter records are unsatisfactory for inclusion in the New Zealand list, but the present records confirm the existence of breeding populations of this distinctive species in New Zealand seas.

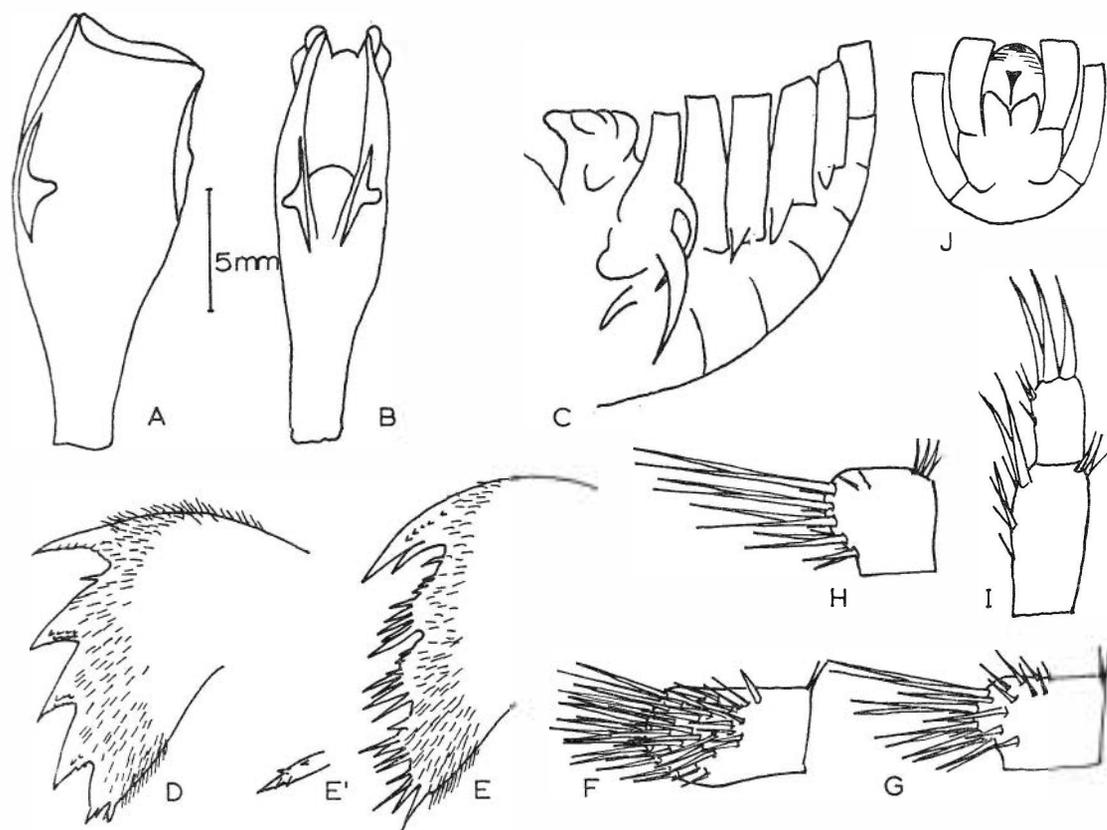


Fig. 20. *Conchoderma virgatum* (Spengler): A, B, lateral and rostral views, 18-mm specimen; C, plan of prosoma; D, mandible; E, maxillule; E', detail, large seta; F, intermediate segment, anterior ramus of cirrus II; G, same, posterior ramus of cirrus II; H, same, anterior ramus of cirrus VI; I, distal segments, ramus of cirrus VI; J, posterior view, caudal appendages and pedicels, cirri V and VI.

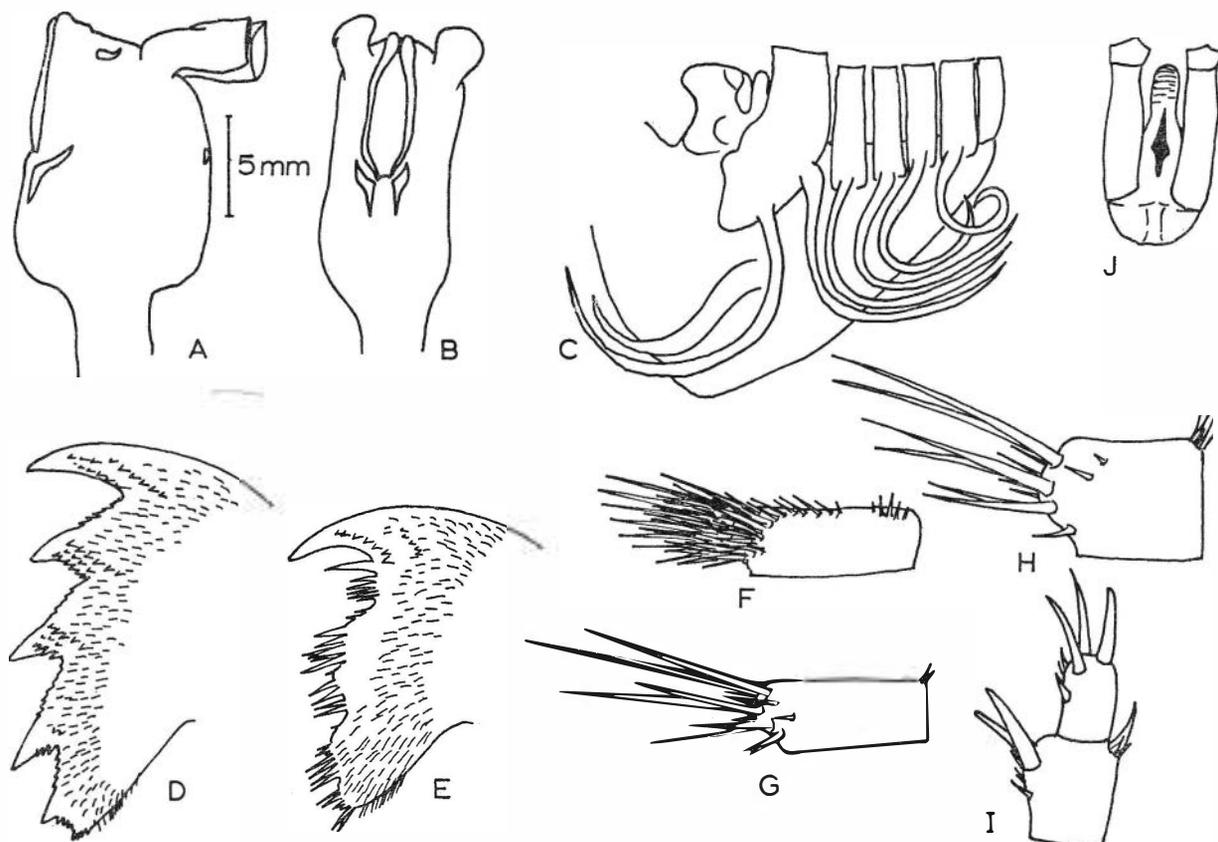


Fig. 21. *Conchoderma auritum* (Linné): A, B, lateral and rostral views, capitulum and upper peduncle; C, plan of prosoma; D, mandible; E, maxillule; F, basal segment, posterior ramus of cirrus I; G, same, posterior ramus of cirrus III; H, intermediate segment, anterior ramus of cirrus VI; I, distal segments, anterior ramus of cirrus VI; J, posterior view, prosoma and pedicels of cirrus VI.

Conchoderma auritum Linné (Plate 3F; Fig. 21)

Conchoderma auritum. Darwin 1851: 141 (see for earlier citations); Jennings 1915: 287; Jennings 1918: 58; Borradaile 1916: 132; Nilsson-Cantell 1921: 240; Hiro 1937: 401; Powell 1947: 41.

MATERIAL EXAMINED: NZOI: Stn Z1060 (off ships). Nat. Mus.: numerous specimens on *Coronula* from humpback whales, and also on claspers of *Carcharodon carcharias* (a shark) from Tory Channel. Auck. Mus.: numerous specimens in association with *Coronula diadema* from whales, some of which were flensed at Whangamumu, G. Barrier I.

DISTRIBUTION: Cosmopolitan in all seas, attached to floating, nektonic, and usually living objects.

DESCRIPTION: *Externals and shell plates:* Five rudimentary plates in smaller specimens, 2 in older ones. Scuta bilobed, carina and terga often absent in larger specimens. Capitulum bears 2 ear-like, tubular processes behind positions of terga.

Prosoma: 7 long and tapering filamentary processes on each side, 2 on posterior margin of base of pedicel of cirrus I, 1 on flank of prosoma below articulation of cirrus I, and 1 on base of pedicel of cirri II–V respectively.

Caudal appendages absent. Segments of rami of cirrus I and anterior ramus of cirrus II have dense setae on protuberant anterior part. In posterior rami, intermediate segments have 4 pairs of setae on anterior edge, with intermediate short setae between bases of pairs, and with a few short setae laterally near base of distal pair of setae.

REMARKS: Borradaile (1916) gave the first authentic record of this distinctive species in New Zealand, on whales in the Bay of Islands and off Cape Brett. Specimens in the Auckland, National, Canterbury, and Otago Museums are also from whales in the New Zealand region. On whales, *C. auritum* is usually associated with the balanid *Coronula diadema*.

Genus Alepas Rang, 1829

Lepadidae with a capitulum with thin integument, without internal muscular layer, and with pair of small, lobed and imperfectly calcified scuta with medial umbos situated at base of orifice. Terga of carina absent.

Alepas pacifica Pilsbry

(Plate 3F; Fig. 22)

Alepas pacifica Pilsbry, 1907a: 105; Nilsson-Cantell 1921: 243; Hiro 1937: 404; Tubb 1946: 383.

MATERIAL EXAMINED: BAF: numerous specimens attached to a scyphomedusan, collected by *Ikatere* out of Auckland (no other data).

DISTRIBUTION: Malaysia, Pacific Ocean from Japan and California to Tasmania; South Atlantic; attached to large jellyfish.

DESCRIPTION: Externals: Integument externally smooth, with scuta chitinous, indistinct, and irregularly lobed.

Prosoma: 6 filamentary processes on each side, 2 on posterior margin of bases of pedicel of cirrus I, 1 on

flank of prosoma below articulation of cirrus I, and 1 associated with base of pedicel of cirri III–V respectively. Number of segments in rami of cirri increase slightly with increasing size, as follows, anterior ramus 1st:

cap. length	I	II	III	IV	V	VI
2.3 mm	6, 5	6, 6	6, 6	7, 7	7, 7	7, 7
8.3 mm	6, 6	8, 8	9, 9	9, 9	10, 10	10, 10
11.8 mm	7, 7	9, 10	10, 10	10, 11	11, 11	11, 11
16.2 mm	—	9, 10	10, 11	10, 11	10, 11	11, 11

Setation of segments acanthopod, i.e., setae largely restricted to distal margin and extend onto sides as well as anterior and posterior edges. Number of setae increases with increasing size of specimens. Setae on distal segment not claw-like. Caudal appendages minute, about $\frac{1}{4}$ length of pedicel of cirrus VI.

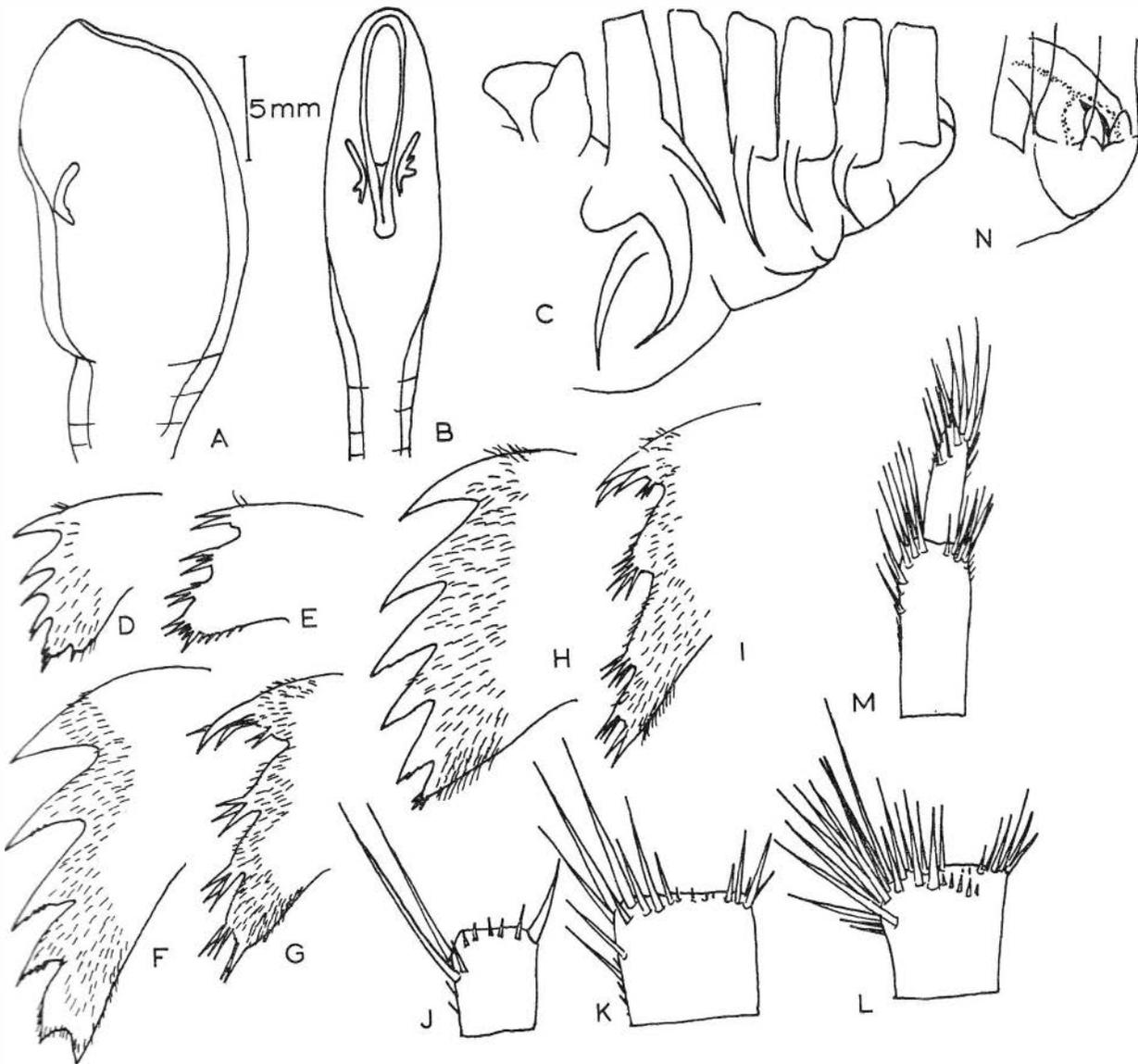


Fig. 22. *Alepas pacifica* Pilsbry: A, B, lateral and rostral views, capitulum and upper peduncle; C, plan of prosoma; D, E, mandible and maxillule, 2.3-mm specimen; F, G, same, 11.8-mm specimen; H, I, same, 16.2-mm specimen; J, intermediate segment, ramus of cirrus VI, 2.3-mm specimen; K, same, 8.3-mm specimen; L, same, 16.2-mm specimen; M, distal segments to L; N, oblique view, caudal appendages and pedicels, cirri V and VI.



REMARKS: These specimens are undoubtedly the Pacific form of *Alepas*, recorded as far south as Tasmania (Tubb 1946). It is problematical whether *A. univalvis* (Quoy & Gaimard) (= *A. parasita*) and *A. pellucida* Aurivillius, both from the North Atlantic, and *A. navigator* Pilsbry and *A. spectrum* Pilsbry, both from the Philippine Is, are specifically distinct, because all of these differ from *A. pacifica* largely in being relatively poorly described. *Alepas* is the only cirripede associated with large, pelagic medusae, which habitat "leads us to anticipate a wide dispersion" (Pilsbry 1907a) and probable synonymy.

Family SCALPELLIDAE Pilsbry, 1907

Lepadomorpha with capitulum of at least 6 calcareous plates or their rudiments, including a carina, a rostrum, and paired terga and scuta, and various other plates. Peduncle usually with rows of uniform-sized calcareous scales. Caudal appendages setose, and may be multi-articulated. Mandible with 3 teeth and a pectinate lower angle, but sometimes has smaller extra teeth below upper tooth. Maxillule lacks a step-like cutting edge. Small males may be facultatively or obligatorily associated with larger hermaphrodites or females.

Genus *Calantica* Gray, 1825

Scalpellidae in which hermaphrodites develop in addition to 6 primary plates, a subcarina, sometimes a subrostrum, and a number of paired latera. Plates generally triangular, with apical umbos. Upper latus without a distinct carinal margin. Filamentary processes absent. Caudal appendages uniaarticulate and setose. Small males may be attached to integument between scuta, below adductor muscle.

DISCUSSION: It is generally held that scalpellid evolution has involved reduction in plate numbers from a multi-plated and completely armoured capitulum. In some cases this has been accompanied by reduction in the extent of calcification of some of the plates, so that areas of integument are unprotected. In other cases there is subsequent secondary covering of the integument by more extensive calcification from the reduced condition, involving changes in the position of the umbos from the primitive apical position. *Pollicipes*, *Calantica*, and *Lithotrya* have the capitular plates with apical umbos.

In *Pollicipes pollicipes*, *P. polymerus* (Plate 5A), and *P. elegans* the capitulum is enclosed by numerous, regularly formed whorls of plates. These species of *Pollicipes* stand apart from other scalpellids in having filamentary processes on the prosoma, and in the structure of the maxillule, in which respects they are more closely related to the condition of 5-plated

lepadids. There can be no doubt that *Pollicipes* (= *Mitella*) as defined by Darwin (1851) is heterogeneous, and it would seem prudent to rank the above three species in a separate family.

In *Pollicipes polymerus* there appears to be a two-way calcite-forming zone at the base of the capitulum, producing plates onto the capitulum and scales onto the peduncle. By repression of the tendency to form large numbers of plates on the capitulum, the scalpellid condition is reached; and by the loss of the peduncle the balanomorph condition of *Catophragmus* could be derived. A polliciped ancestor may have given rise to the scalpellids and the balanomorphs, but separately.

The tendency to form extra plates on the capitulum occurs in *Pollicipes spinosus* (sensu Darwin), and also in recognised calanticoid species such as *Calantica quinquelatera* (see Hiro 1932), *C. kampeni* (see Withers 1953) and *C. spinilatera* (see below). That *P. spinosus* should be regarded as a primitive calanticoid is strongly justified by the discovery of complementary males in this species. Complementary males have not to date been reported in other species assigned to *Pollicipes*.

The structure of the appendages of the calanticoid complementary male is comparable to that of similar-sized but more free-living juveniles of the same species, except that the male reproductive apparatus is developed. These small males invariably have the primary 6 capitular plates, but sometimes further small latera occur, when the males resemble even more the free-living juveniles which, during ontogeny and after the 6 primary plates are formed, add an upper latus and then the other latera and the subcarina. In the calanticoids, small males seem purely facultative; they are not invariably present, and the large forms are hermaphrodites. It appears that the ordinary development of cyprids that settle within the confines of the scuta of an adult is arrested.

The inclusion of Quoy & Gaimard's *Anatifa spinosa* in *Calantica* (see below) does not really strengthen the definition of *Calantica*. A number of developments are encompassed in this primitive group which, like *Pollicipes*, is represented today by scattered remnant species. *Calantica spinosa* can have a large complement of capitular plates, but various ones of these may be absent in other species. A stable 13-plated condition is the minimum number attained, where the subcarina, upper latera, carinolatera, and rostralatera are situated below the primary plates. The genus *Smilium* is also of this 13-plated condition, but differs from *Calantica* in that the upper latus is well elevated between the carina and scuta, and has a distinct carinal margin. The genus *Euscalpellum*, which is not represented in the New Zealand fauna, has 15 plates on the capitulum, including an inframedian latus; *Euscalpellum* may represent an earlier line from the calanticoid stock than *Smilium*. These three genera—*Calantica*, *Smilium*, and *Euscalpellum*—have a subcarina, and may carry complementary males on the integument between the scuta near the adductor muscle; these features set them apart from other scalpellids.

Calantica spinosa (Quoy & Gaimard)
(Plate 5B, C; Fig. 23)

Anatifa spinosa Quoy & Gaimard, 1834: 629.
Pollicipes spinosus. Darwin 1851: 324; Hutton 1879: 329; Filhol 1885: 486; Jennings 1915: 286; Jennings 1918: 60; Batham 1945a: 359; Batham 1946: 405.
Pollicipes sertus Darwin, 1851: 327; Filhol 1885: 486; Weltner 1899: 443; Jennings 1915: 286.
Pollicipes darwini Hutton, 1879: 329; Filhol 1885: 486; Jennings 1915: 286.
Protomitella paradoxa Broch, 1922: 246.
Mitella sertus. Broch 1922: 260; Powell 1947: 41.

MATERIAL EXAMINED: NZOI: Stns D140, E767, E809. Nat. Mus.: Intertidal specimens from Great King I (F. M. Climo), Spirits Bay (R. K. Dell), Hen I and Little Barrier I (W. R. B. Oliver), White I (M. A. Crozier), Castlepoint (F. M. Climo), Stephen I (R. K. Dell), Queen Charlotte Sound (M. A. Crozier), and Stewart I. Type specimens of *Protomitella paradoxa* Broch. BAF: numerous specimens from intertidal sites in the north of New Zealand, and Otago Peninsula.

DISTRIBUTION: New Zealand; intertidal, from the Three Kings Is to The Snares, but evidently absent from the Chatham Is and the subantarctic islands (Fig. 46). The Chatham Is record of Young (1929) is doubtful.

DESCRIPTION: *Externals and shell plates:* Hermaphrodites with capitular plates embedded in smooth, thick integument, apical parts emergent and eroded in older specimens. Plates include primary 6 and, as well, a subcarina, an upper latus, usually a subrostrum, and a variable number of other small latera which vary in shape from broadly triangular to elongate spines. Plates have faint external growth lines. Tergum with a faint broad apicobasal ridge. Peduncle with minute embedded spines. Complemental males occasionally present, and have at least 6 primary plates sometimes more.

Mouthparts: Labrum bullate with a row of minute teeth on crest. Mandibles have 3 teeth in very small specimens, including males, but otherwise bear 1–3 extra teeth below upper tooth. Maxillules bear 1 or 2 prominent setae at upper angle, a few small setae on a prominence at lower angle, and in between a number of intermediate-sized setae which are more abundant in bigger specimens.

Cirri (see Plate 1A–D): Number of segments in the cirri increase with age, as follows, the anterior ramus 1st:

cap. length	I	II	III	IV	V	VI
1.0 mm (♂)	4, 4	5, 4	5, 5	5, 5	5, 5	5, 5
2.1 mm	6, 6	8, 9	10, 11	10, 10	11, 11	12, 12
4.8 mm	7, 7	10, 10	11, 11	12, 12	12, 12	12, 12
9.6 mm	11, 10	13, 14	14, 14	16, 16	17, 17	17, 17

Basal segments of each ramus of cirri II and III thicker and slightly protuberant, and bear 4 stout, plumose setae anterolaterally, longest distally, and have a cluster of setae which become less dense distally in rami. Many of clustered setae stout and serrated (Plate 1D). Distal segments of cirri II and III have 3 anterior setae plus a few setae in anterodistal region (Plate 1B). Segments of

cirri IV–VI thinner than basal ones of cirri II and III, and bear 3 or 4 pairs of setae on anterior face (Plate 1C), outer seta of outer ramus and inner seta of inner ramus longer than its partner, especially basally. This inequality of setal length more pronounced in anterior cirri. Penis proportionately shorter in juvenile specimens, but in males sometimes longer than pedicel of cirrus VI.

REMARKS: The statement by Powell (1947) that this species can be found in deep water is a mistake, and probably originates from data attached to *C. spinilatera* in the Auckland Museum. *C. spinosus* is characteristically intertidal in occurrence. The detailed studies of adult anatomy and larval development by Batham (1945a, 1946) complement the description by Darwin (1851), such that no other scalpellid is so well described.

The variation in external appearance, which to some extent is due to the intertidal habitat, has led to the naming of a number of species, but with large numbers of specimens for study there is no doubt that there is but one species (Jennings 1918). Although plate shape may be influenced by weathering and crowding, the variability in the number of capitular plates is due to other reasons. In a sample of 33 specimens, the numbers of capitular plates varied from 11 to 52, with up to 22 pairs of latera, not always the same on both sides, and in a few cases with the subrostrum missing. Nine of the specimens had 18 or fewer plates. Traditionally, *Pollicipes* has been separated from other scalpellids by having more than 18 plates.

The enigmatic *Protomitella paradoxa* described by Broch (1922) from New Zealand shores was regarded by Broch to link *Pollicipes* (*spinosus* group) and *Calantica* towards the former. Batham (1945a) was unable to find the species again, even in the type locality, and considered the structure of the lower latera within the range of variation of *Pollicipes spinosus*. Broch himself was cautious of distinguishing his specimens from *Pollicipes darwini*, but felt compelled to do so because of the presence of complemental males in one of the specimens. It was not unduly surprising to find a few specimens of *Calantica spinosa* which carried males between the scuta, and which approached the appearance of Broch's *Protomitella*. The 3 figured (Fig. 23) were found by searching 100 specimens. The males differ from the one figured by Broch only by their lack of any trace of latera. The male studied by Broch had not only a lateral plate, but also extra teeth on the mandible, and more central setae on the cutting edge of the maxillule than in the males of the present study. It would thus seem to be more developed. Comparison of the anatomy of juvenile and male specimens indicates the relative underdevelopment of the latter, except for the proportionately larger penis.

Even with synonymy of *Protomitella paradoxa* with *Pollicipes spinosus*, the species can still be regarded as intermediate between more stable-plated calanticoids that more frequently bear complemental males, and the multiplated, purely hermaphrodite condition of *Pollicipes polymerus*. Indeed, Darwin (1851, p. 331) and Withers

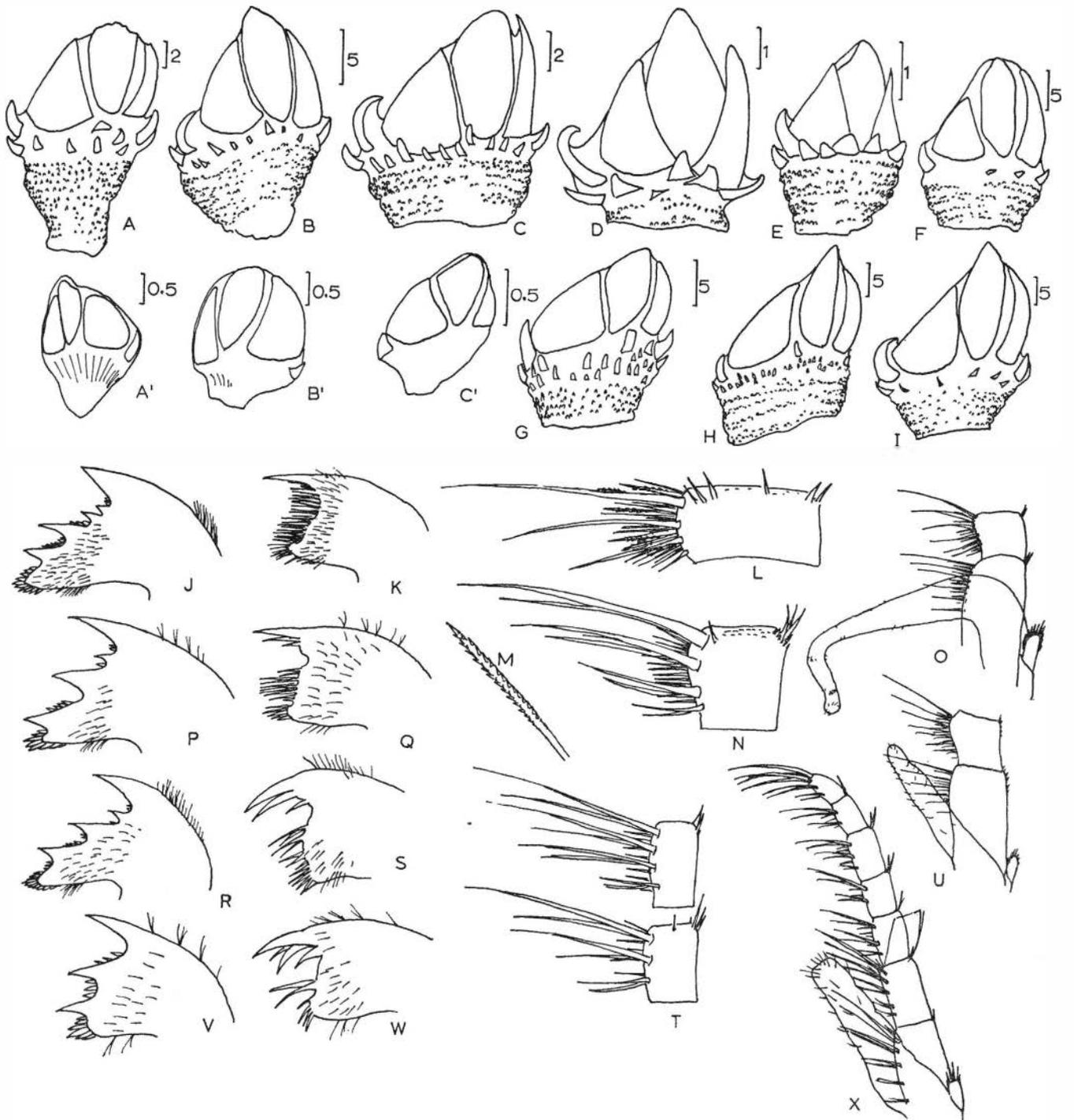


Fig. 23. *Calantica spinosa* Quoy and Gaimard: *A, B, C*, hermaphrodites with respective males *A', B', C'*; *D-I*, hermaphrodites showing variable plate arrangement; *J-O* from specimen *A* of 9.6-mm capitulum length — *J*, mandible; *K*, maxillule; *L*, outer side, intermediate segment of cirrus II; *M*, serrated seta from same; *N*, outer view, intermediate segment of cirrus VI; *O*, caudal appendage, penis, and pedicel of cirrus VI; *P, Q*, mandible and maxillule, specimen *D*, 4.8-mm capitulum length; *R-U* from specimen *E*, 2.1-mm capitulum length — *R*, mandible; *S*, maxillule; *T*, intermediate segments, cirrus VI; *U*, caudal appendage, penis, and pedicel of cirrus VI; *V-X* from male *A'*, 1-mm capitulum length—*V*, mandible; *W*, maxillule; *X*, caudal appendage, penis, pedicel, and one ramus of cirrus VI (scales in mm).

(1935, p. 21) have regarded *P. spinosus* as being nearly related to *Calantica*, and it seems good sense to remove the species from *Pollicipes*, which should be retained for *P. polymerus*, *P. elegans*, and *P. pollicipes*. Further, the multiarticulated caudal appendages and the strongly sculptured plates of *Pollicipes mitella* would warrant its separate generic recognition, for which Withers (1928, p. 32) has suggested the resurrection of the name *Capitulum*. But *P. spinosus* is clearly a calantid, and pending a revision of *Calantica* is here assigned to this large genus.

Contrary to the interpretation of Broch (1922), the possession of complementary males seems to be a more advanced feature than their absence, as in *Pollicipes*, and the rare occurrence of males seems not so much "proof of the male being about to disappear in the genus" as perhaps indicative of the establishment of the male condition in scalpellids. Indeed, the association appears purely facultative, because in *C. spinosa* the interscutal niche sometimes harbours small mussels of the genera *Perna* and *Xenostrobus*, which are part of the associated intertidal fauna. In deeper sea habitats, the possession of complementary males would have more advantages because of the fewer and more restricted settlement sites. Only in some acroscaepellids of the deep sea is the possession of males obligatory for sexual reproduction.

Calantica spinosa, then, seems to satisfy requirements for a primitive calantid, and thus a primitive scalpellid. The restricted intertidal habit of species of *Pollicipes* and *C. spinosa* is suggestive of an ancient intertidal origin of scalpellids.

***Calantica spinilatera* nom. nov.**

(Plate 5D; Figs. 2A–D, 24)

Scalpellum (Smilium) spinosum Annandale, 1911a: 164; Jennings 1915: 286.

Scalpellum spinosum. Chilton 1911b: 311; Jennings 1918: 59.

Smilium spinosum. Borradaile 1916: 128.

MATERIAL EXAMINED: NZOI: Stns A901 (2 specimens), C175 (1), C363 (scutum only), D121 (12 large and numerous juveniles), Z2366 (3), Z2368 (6). Nat. Mus.: specimens collected by *Ikatere* off Little Barrier I, on *Aphanipathes*, and at 37°30'S, 176°32'E at 220–258 m; other specimens from off Mahia at 156 m, and off Napier (A. G. Clark). Auck. Mus.: specimens from off Moko-hinau Is. PMBS: specimens from off Elizabeth I, Doubtful Sound, 55 m. Cant. Mus.: specimens from *Nora Niven* Expedition 1907, Foveaux Strait (Chilton 1911b).

DISTRIBUTION: New Zealand, 50–258 m (Fig. 25).

DESCRIPTION: *Externals and shell plates:* Capitular plates of hermaphrodite externally smooth and shallowly embedded in a minutely hirsute integument. In older specimens apex of tergum recurved towards carina and occludent margins with those of scuta, to form a nearly vertical straight line. Carina deeply concave, and apical umbo comes to stand apart from terga by

development of side walls (parietes). Lower plates small, triangular, and in older specimens widely spaced, with apices protruding spine-like or even curved downwards. Subrostrum absent. Usually 4 sometimes 5 pairs of latera developed. Free-living specimens show full plate complement at about 3-mm capitulum length. After 6 primary plates, upper latus appears first, then rostrolatus, carinolatus and subcarina, and finally a central latus probably identifiable as inframedian latus.

Mouthparts (Fig. 2B–D): Labrum bullate, crest bears a row of blunt teeth, particularly obvious in juvenile specimens. With increase in size, mandibles develop up to 4 extra teeth below upper one, but denticles of upper edges of teeth become less obvious. Maxillules also show an increase in extent of double series of setae on cutting edge between groups at upper angle and slightly prominent lower angle.

Cirri (Fig. 2A): Rami subequal. Number of segments in rami increase with size of individual as follows, anterior ramus 1st:

cap. length	I	II	III	IV	V	VI
1.0 mm (♂)	3, 3	5, 5	6, 6	6, 6	5, 5	7, 7
1.2 mm	4, 4	4, 6	6, 6	6, 6	6, 6	7, 7
9.5 mm	14, 17	20, 21	22, 22	23, 22	21, 22	19, 20
38.0 mm	16, 20	21, 22	24, 26	26, 28	28, 27	26, 27

Basal segments of cirri II and III brush-like. Distal segments of these cirri and all segments of cirri IV–VI have 3 or 4 pairs of setae on anterior face, with sometimes a minor 5th pair proximally, with small, medial setae between bases of larger pairs. Longest seta of posterior distal tuft as long as succeeding segment. Caudal appendages have marginal setae, longest and most distal reaches as far as distal end of basal segment of pedicel of cirrus VI. Appendages of a complementary male similar to those of a free-living juvenile except for presence of a stout penis.

REMARKS: Annandale (1911a) classified this species in the subgenus *Smilium*, but did not then recognise the distinction between *Calantica* and *Smilium*, and favoured the latter by priority. Now that both groups are recognised as genera, some of Annandale's species require reassignment. The present species is put in *Calantica* because of the triangular shape of the scutum and upper latus. The tergum does not completely occupy the space between the scuta and carina, but neither does the upper latus. The distinction between *Calantica* and *Smilium* is tenuous, and is not helped by existing rather vague diagnoses. The main characters for the latter genus are given and discussed below.

The placing of *Anatifa spinosa* of Quoy & Gaimard in the genus *Calantica* renders Annandale's name invalid, and in the absence of synonyms a substitute name is suggested to signify the same meaning, namely the spiny nature of the latera of larger individuals.

The specimens with 5 pairs of latera may represent a recapitulation of an ancient, multiplated condition, even though a subrostrum has not been found. *Calantica spinilatera* is closely related to *C. pollicipedoides* (Hoek) and *C. kampeni* (Annandale) of Malaysian seas. Hoek



(1907, p. 63) draws attention to 2 extra plates on one side of 1 of his 6 specimens of *C. pollicipedoides*, and Broch (1931) comments on the reduction of the inframedian latus in some specimens of *C. kampeni* which leads to a superficial resemblance to some 13-plated calanticoids like *C. studeri* (see below). In *C. spinilatera* and *C. kampeni*, removal of the inframedian latus would give the 13-plated condition of *C. scorpio* (Aurivillius) (= *Scalpellum sexcornutum* Pilsbry). The 15-plated condition of *C. spinilatera* is essentially that of the genus

Euscalpellum, and by loss of the subcarina it is a short step to the capitular arrangement of *Scalpellum* (sensu stricto) and *Arcoscalpellum*. In *C. spinosa*, *C. pollicipedoides*, *C. kampeni*, *C. spinilatera*, and *C. quinquilatera*, not only is there a tendency to increase the number of latera of the lower whorl, but the dentition of the mandible increases with age. This group would seem to represent a primitive one, intermediate between *Pollicipes* and other scalpellids.

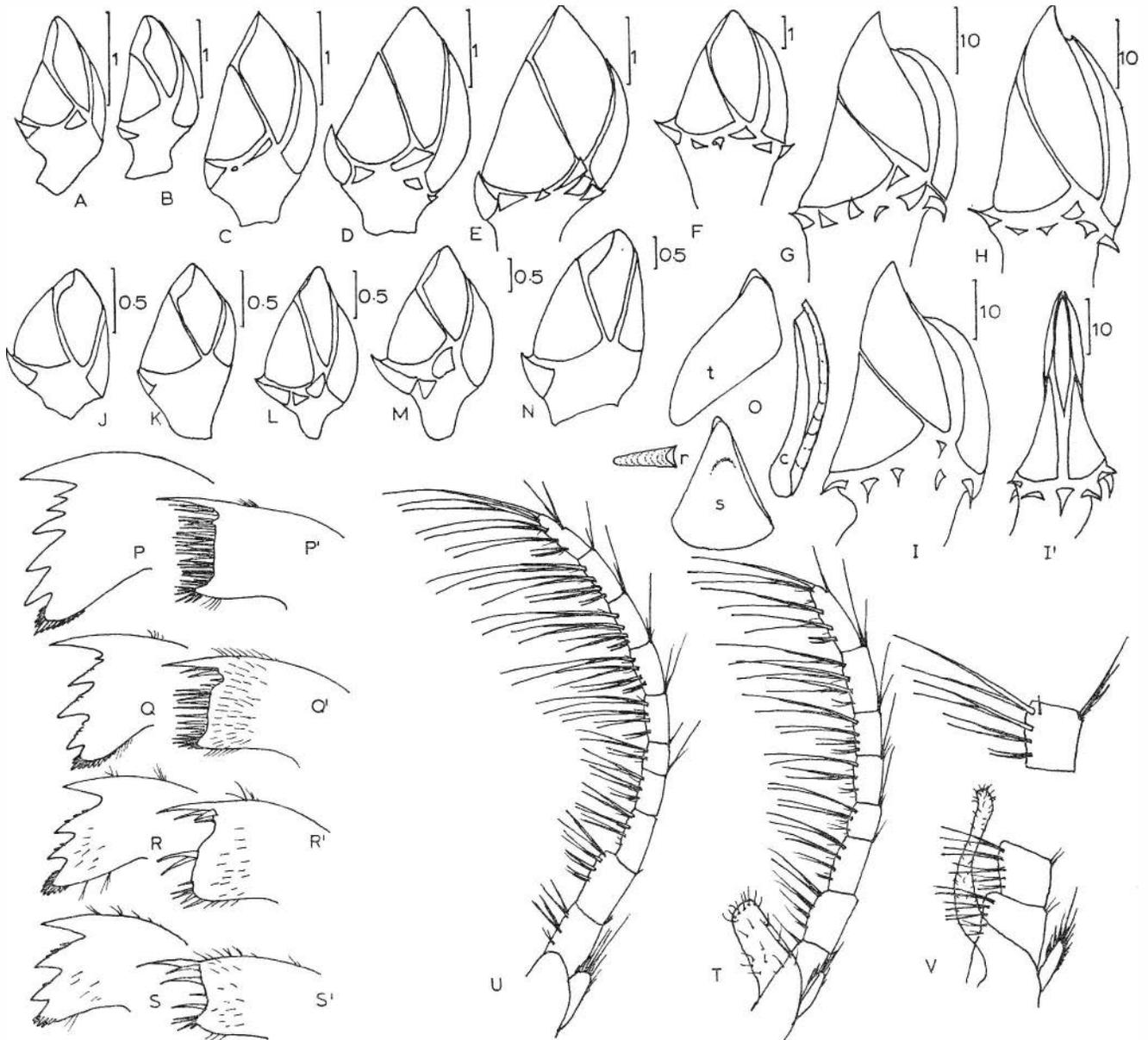


Fig. 24. *Calantica spinilatera* nom. nov.: A-I, free-living specimens arranged in order of increasing capitulum length, from 1.2 mm (A) to 9.5 mm (I) (specimen G from *Nora Niven* station 5); I', rostral view, specimen I; J-N, males in order of increasing size; O, inner views, tergum (t), scutum (s), carina (c), and rostrum (r); P, P', mandible and maxillule from specimen I, 38-mm capitulum length; Q, Q', R, R', S, S', same from specimens F, R, and male J; T, caudal appendage, penis, pedicel, and one ramus of cirrus VI, male J; U, same of specimen A; V, pedicel, and an intermediate segment of cirrus VI, penis and caudal appendage, specimen F (scales in mm).

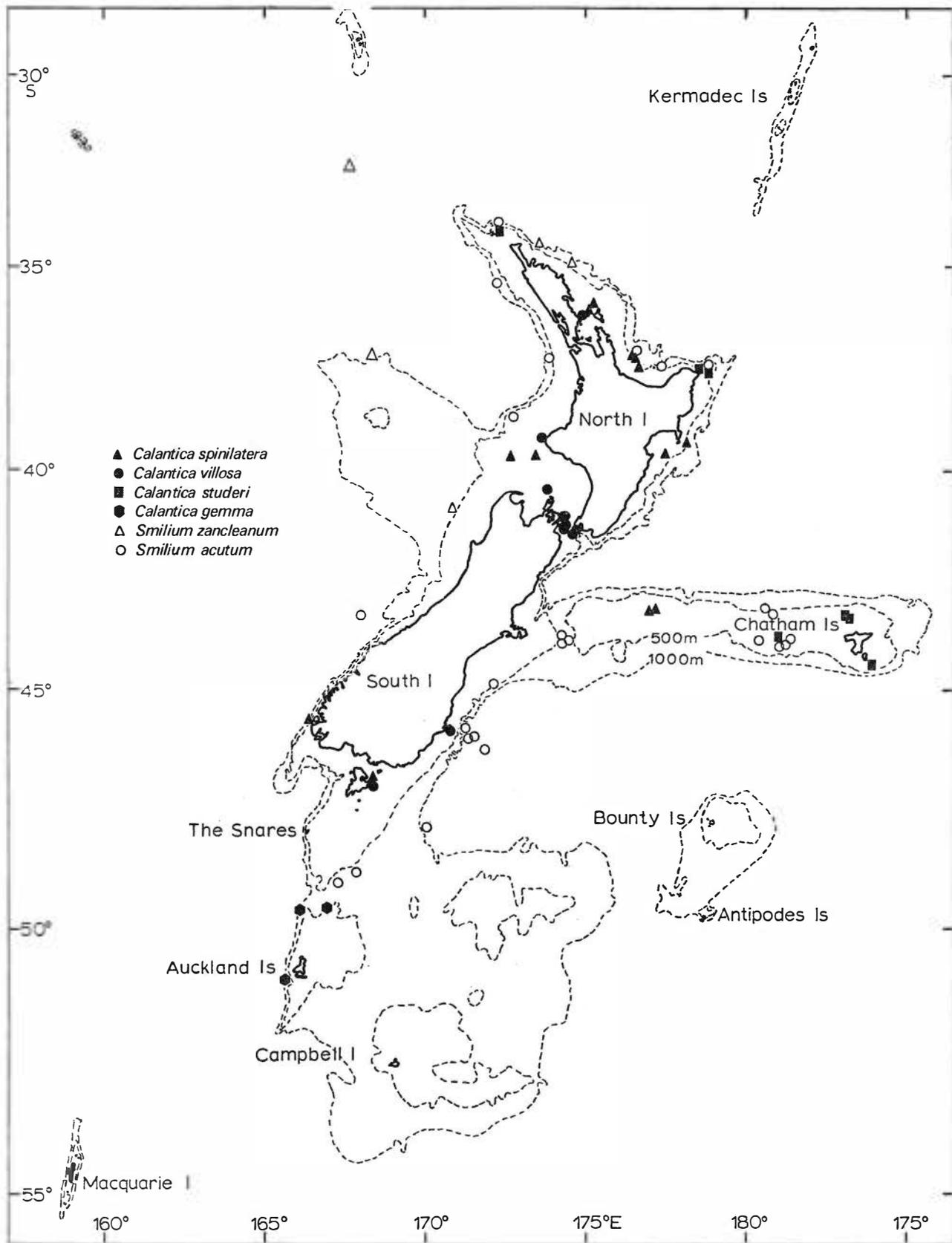


Fig. 25. Records of *Calantica* and *Smilium* in the New Zealand region. *Calantica spinosa* is not shown here, but has been collected from numerous shore localities from the Three Kings Is to Stewart I, but not in the Chatham Is or subantarctic islands (see Fig. 46).

Complemental males were invariably present in the specimens from NZOI Stn D121, with up to 16 crowded between the scuta of the larger hermaphrodites. Males were found in the specimens from C175 and the larger one from A901, but they were not found in any other material, nor did Annandale find any in the type specimen. The males ranged in size from 1.0 to 3.2 mm capitulum length, and usually had the 6 primary plates. Some, however, showed two pairs of accessory latera in the positions of the upper latus and rostrolatus.

Calantica villosa (Leach) (Plate 5E; Fig. 26)

Scalpellum villosum. Darwin 1851: 274 (see for earlier citations); Hutton 1879: 329; Weltner 1899: 442; Jennings 1915: 286; Jennings 1918: 59.

Calantica villosa. Broch 1922: 227.

not *Calantica villosa*. Powell 1947: 41.

MATERIAL EXAMINED: NZOI: Stns A444 (1 specimen), E767 (9), E768 (2). Nat. Mus.: intertidal specimens from Omaio Bay (R. K. Dell), Kau Point in Wellington Harbour (R. K. Dell and M. A. Crozier), Lyall Bay (W. S. Cobham), Long I in Queen Charlotte Sound (M. A. Crozier), and Paterson Inlet at Stewart I; also specimens from off Stephens I at 201 m (*Alert*), and in Cloudy Bay at 55 m (F. Abernethy). BAF: Shore collections from Auckland, Cape Egmont, and Otago.

DISTRIBUTION: New Zealand: intertidal from Auckland to Stewart I (Jennings 1918); also subtidal to 276 m (Fig. 25). NOTE: Darwin (1851) quoted "Eastern Seas" as the locality for this species. Many subsequent studies on the Oriental and Malaysian cirripedes do not re-identify the species in spite of its intertidal habitat. As other localities quoted by Darwin are doubtful, the

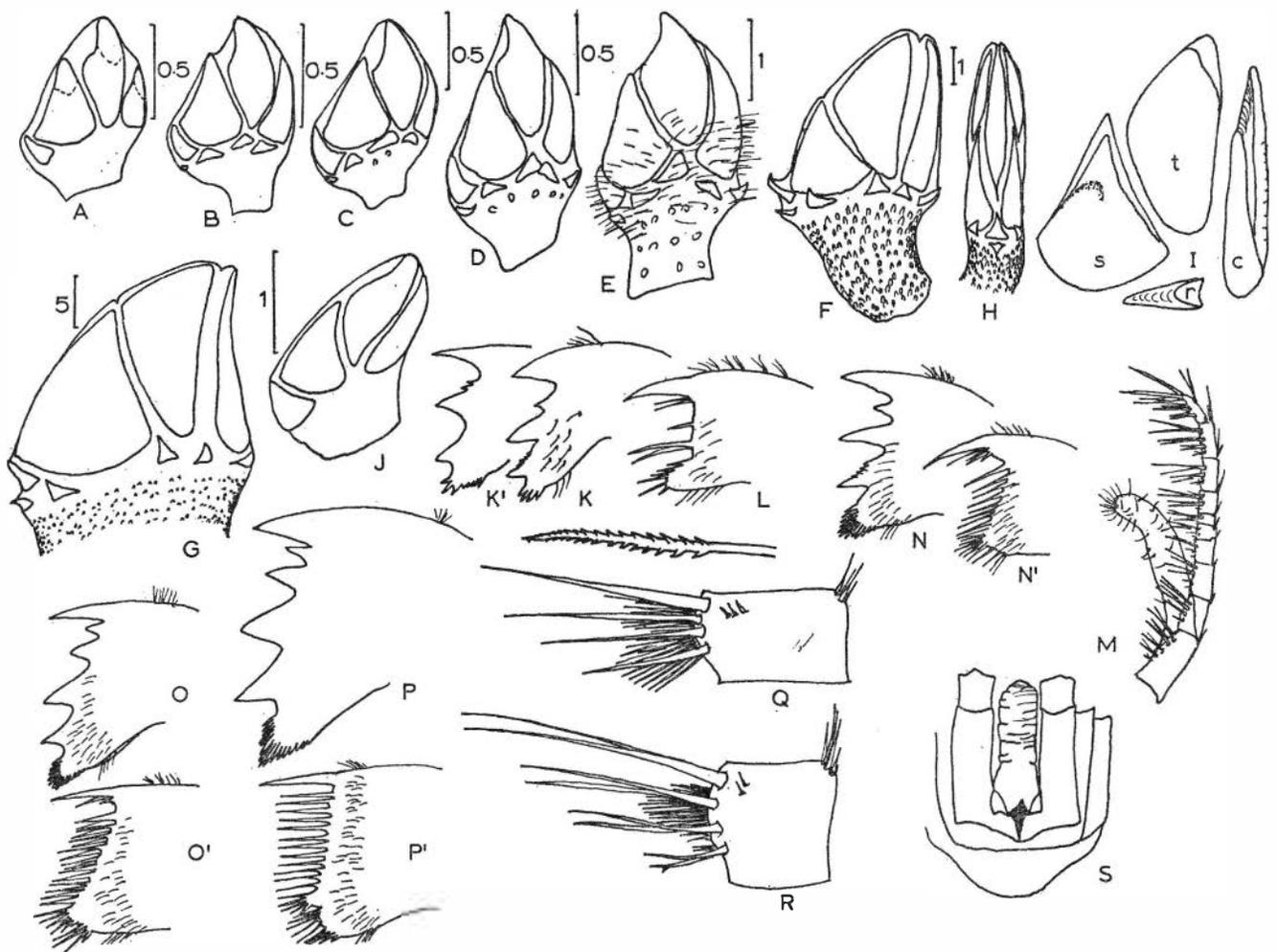


Fig. 26. *Calantica villosa* (Leach): A-G, lateral views, hermaphrodites in order of increasing size; H, rostral view, specimen F (hirsute integument not shown in F and G); I, inner views, tergum (t), scutum (s), carina (c), and rostrum (r); J, male from a hermaphrodite of 20-mm capitulum length; K, K', mandibles; L, maxillule; M, penis, pedicel, and a ramus of cirrus VI, male J; N, N', O, O', P, P', mandibles and maxillules of hermaphrodites of 6.3, 16.8 and 26.3-mm capitulum length respectively; Q, outer face, intermediate segment of cirrus II, specimen G, with medial serrated seta shown separately; R, same, cirrus VI of specimen G; S, posterior view of prosoma to show rudimentary caudal appendages (scales in mm).

occurrence of this species outside New Zealand is not established.

DESCRIPTION: *Externals and shell plates:* Hermaphrodite with 14 capitular plates covered in larger specimens by a thickly hirsute integument. In adults; occludent margin of capitulum arched; carina straight; tergum does not extend above umbo of carina, and occupies all space between carina and scutum. Lower plates small and widely separated in larger specimens, and include a subcarina, subrostrum, and 3 pairs of latera. Peduncle provided with small spindle-shaped scales embedded in integument. Hirsute integument can, in larger specimens, mask all plate features, and have a felt-like texture.

Complemental males with 6 capitular plates have been found in a few hermaphrodites (7 out of 72 in one collection from Little Papanui).

Mouthparts: Mandibles have one or two extra, smaller teeth beneath upper tooth in older specimens. Maxillules have a slight prominence set above lower angle. Number of setae on cutting edge of maxillule increase with size of specimens.

Cirri: Rami subequal; the numbers of segments per ramus increasing with size of specimen as follows, anterior ramus 1st:

cap. length	I	II	III	IV	V	VI
1.0 mm (♂)	5, 5	5, 5	6, 6	6, 6	6, 6	7, 7
6.3 mm	10, 10	14, 15	14, 16	19, 18	18, 18	17, 20
16.8 mm	13, 13	16, 16	16, 17	16, 16	19, 18	20, 20
26.3 mm	13, 12	17, 17	17, 20	19, 20	21, 22	19, 20

Basal segments of cirri II and III slightly protuberant medially; and bear copious setae, coarsely serrated in larger specimens. Distal segments of cirri II and III, and all segments of posterior cirri have 3 or 4 pairs of setae on anterior edge, with a few shorter, intermediate setae, sparse in juveniles but collected into prominent tufts in larger specimens. Segments of cirri bear medial, transverse bands of pigment, which emphasise segmental nature of cirri. Caudal appendages best represented by small, triangular swellings on either side of anus. Penis relatively more developed in males, being longer than pedicel of cirrus VI, than it is in hermaphrodites up to 6 mm capitular length, in which it is as long as pedicel.

REMARKS: This, the type-species for *Calantica*, is characterised by the felt-like integument, the tergum not extending above the straight carina, the possession of a subrostrum, and the stable capitular plate arrangement. *C. villosa* stands apart from other calanticids in the lack of caudal appendages, which are apparently secondarily lost. The subrostrum allies *C. villosa* with *C. spinosa*. Both species are unusual among the scalpellids in that they occur intertidally, apparently only in New Zealand. *C. spinosa* is exclusively intertidal, and *C. villosa* occurs there in desiccation-protected habitats (Batham 1945b). Both species develop coarsely serrated spines on the anterior cirri, and have tufts of small setae between the paired major spines of the posterior cirri. This recalls the

condition in *Pollicipes* and some balanomorphs found intertidally on wave exposed coasts, e.g., *Chamaesipho*, other chthamalids (Pope 1965), and tetracitids. These facts are perhaps indicative of shallow-water origins of scalpellids and balanomorphs, as further discussed below.

Calantica studeri (Weltner) (Plate 6A; Fig. 27)

Scalpellum (*Calantica*) *studeri* Weltner, 1922: 100.
Calantica mortenseni Broch, 1922: 228.
Calantica studeri. Utinomi 1968a: 161.

MATERIAL EXAMINED: NZOI: Stns C814 (2 specimens plus numerous plates), D876 (8), D878 (4), D906 (2), D907 (1), E140 (2), E323 (1), E720 (c. 200).

DISTRIBUTION: North-west Australian coast and New Zealand. In New Zealand, north-east to Chatham Is shelf, 60–248 m (Fig. 25).

DESCRIPTION: *Externals and shell plates:* Hermaphrodite with 13 capitular plates covered by a thin, sparsely hirsute integument. Terga extend above carina for about $\frac{1}{4}$ of their length, in older specimens apex may become worn and rounded. When not worn, occludent edge of terga stands at a distinct angle to that of scuta. Carina slightly bowed towards terga, and develops parietes in upper part. Lower plates include a subcarina and 3 pairs of latera, and together with rostrum occupy all space at base of capitulum. Rostrolatus and carinolatus have their apices directed towards rostrum and carina respectively, and both overlap base of upper latus. Peduncle with rows of blunt scales embedded in integument. Some of larger specimens examined carried complemental males. Of 31 specimens from NZOI Stn E720, 3 had 1 male, 2 had 2, 2 had 3, and 24 had none. Males usually have a capitulum with 6 primary plates, but of 13 examined, 4 had accessory plates; 1 with an upper latus on one side only, another had an upper latus on both sides and a rostrolatus on one side only, another had an upper latus and rostrolatus on one side only, and one somewhat larger specimen (2.7-mm capitular length) had a capitular skeleton like free-living juveniles. Of small specimens that occurred on outside of older specimens, complete 13-plate arrangement developed by time capitulum reached 1.4 mm in length.

Mouthparts: Mandible initially with 3 teeth, but up to 3 extra teeth may develop below upper 1. Cutting edge of maxillule lengthens with ontogeny, and can carry up to 10 pairs of setae between upper major seta or setae and slightly protuberant lower angle.

Cirri: Rami subequal with 5–13 segments in cirrus I and 9–20 in posterior cirri, lower numbers being found in males and juveniles. Basal segments of anterior rami of cirri II and III somewhat thicker than those of posterior rami, and carry more medial setae. Brush-like basal segments develop, particularly in larger specimens. Distal segments of cirri II and III and all segments of posterior cirri have 3–6 pairs of setae on anterior edge, higher numbers attained with greater size of specimen.



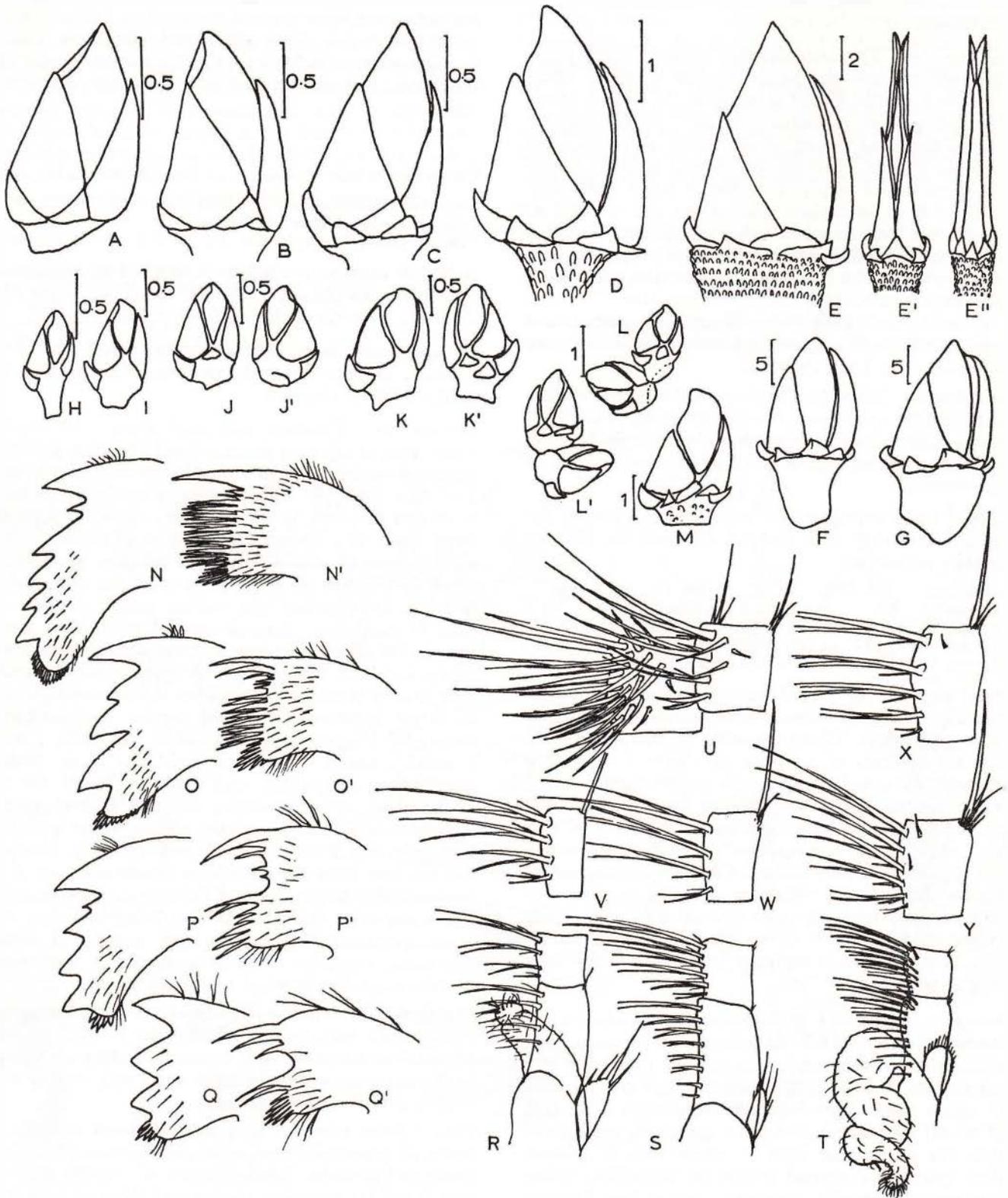


Fig. 27. *Calantica studeri* (Weltner): A-G, hermaphrodites in order of increasing size; E, E', E'', rostral and carinal views, specimen E; H-M, males arranged approximately in order of increasing size, with J, K, L, the other sides of specimens J, K, L, and M from same bunch of males as specimen L; N-Q', mandibles and maxillules of specimens with capitulum lengths 14.6 mm (N), 8.0 mm (O), 2.1 mm (P) and a male of 1.0 mm (Q); R-T, pedicel of cirrus VI, caudal appendage, and penis of specimens of 1.0 mm (male) (R), 2.1 mm (S), and 14.6 mm (T); U, inner aspect, basal segments of anterior (left) and posterior (right) of cirrus II, 8.0-mm specimen; V-Y, outer aspects, intermediate segments of cirrus VI of specimens of 1.0 mm (male) (V), 2.1 mm (W), 8.0 mm (X), and 14.6 mm (Y) (scales in mm).

One of 2 short setae occur between base of each pair of major setae. Longest setae of posterior distal tuft longer than succeeding segment. Caudal appendages unarticulated, leaflike, and less than $\frac{1}{2}$ length of proximal segment of pedicel of cirrus VI. In larger specimens, fringe of setae of caudal appendage may be very short or absent. Penis in hermaphrodites up to about $\frac{1}{3}$ length of cirrus VI, and provided with tufts of fine setae distally. Appendages of males very similar to those of free-living juveniles, except penis relatively longer.

REMARKS: This species is closely related to *C. trispinosa* (Hoek) from the Philippines, *C. eos* (Pilsbry) from Japan, and *C. krugeri* Hiro, also from Japan. Hiro (1932) pointed out that the differences between these species largely depended on the dubious value of the shape of the primary capitular plates. The material examined by Weltner (1922) for the description of *C. studeri* included a lot from the north-west Australian coast, a lot from off the Three Kings Is in New Zealand, and two lots from Japan. Utinomi (1958) thought that Weltner's Japanese material was referable to *C. eos*. The figure of Weltner (1922, pl. 3, fig. 13) of the west Australian specimen is certainly not outside the range of variation seen in the present material. It is not altogether certain that Weltner's Japanese specimens are of a different species.

Broch's account of Mortensen's Pacific cirripedes appeared in the same year as Weltner's account, even though the latter's manuscript was finished in 1917. Utinomi (1968a) gave Weltner's name priority.

Broch (1922) described a single hermaphrodite and the two complemental males it bore. One of the males had 3 pairs of latera. Broch took this to be a standard condition for the species, and because the condition of males with more than 6 plates was not then known for other species, he regarded *C. studeri* as being a rather primitive form, standing "comparatively near the ancestors of the entire group, which in all probability have had separate sexes with equally highly developed males and females" (Broch 1922, p. 231). The weight of evidence is for the interpretation that the hermaphrodite condition is basic in the Thoracica, and from the ontogenetic evidence presented for this and other species in this paper it appears that the males develop from normal cyprids which, except for the male reproductive system, are arrested in growth by some factor of the interscutal habitat.

The structure of the hermaphrodites of *C. studeri* points to their derivation from a more multiplied condition. They differ from those of previously described species in this paper, all of which have, or can have, more numerous capitular plates, in that neither a subrostrum nor an inframedian latus is present. Further, the plates of the lower whorl cover all the space below the upper plates, and the rami of cirri II and III are unequal in their modification of the basal segments. In these features *C. studeri* resembles *C. gemma*, described below.

***Calantica gemma* (Aurivillius) (Plate 6B, C; Fig. 28)**

Scalpellum gemma Aurivillius, 1892: 126; Aurivillius 1894: 41.

MATERIAL EXAMINED: NZOI: Stns D160 (7 disarticulated specimens and separate old plates), D171 (plates), F81 (1 specimen).

DISTRIBUTION: North Atlantic and New Zealand. In New Zealand, on the Auckland Is Plateau, 401–722 m (Fig. 25).

DESCRIPTION: *Externals and shell plates:* Capitulum of hermaphrodite develops 13 well-calcified plates, externally sculptured with longitudinal striations and faint growth lines and not covered by integument. Apices of latera stand out from capitulum, and recurved towards and over bases of primary plates. Terga and scuta have wide apicobasal ridges and thick occludent margins. Carina slightly bowed, but may stand apart from terga apically, with strong, rounded medial and lateral ribs. Rostrum has an apicobasal rib. Upper latera and carinolatera, but not rostrilatera or subcarina, have submedial longitudinal ribs or folds. Peduncle covered with emergent, triangular scales.

Mouthparts: Labrum bullate and devoid of teeth. No accessory teeth present on mandibles. Maxillules have a wide notch occupying about $\frac{1}{2}$ cutting edge.

Cirri: Number of segments in cirri of one specimen were as follows, anterior ramus 1st:

I	II	III	IV	V	VI
15,15	19,20	20,21	21,21	24,22	24,22

Cirrus I set only slightly apart from rest of cirri. Basal segments of anterior ramus of cirri II and III wider than those of cirrus I, and nearly twice as wide as posterior rami of same cirri. Basal segments of rami of cirri II and III have medial and anterior setae, but medial setae diminish in numbers distally in rami to become restricted to anteriodistal corner. Segments of rami of cirri IV–VI alike; medially in ramus with 4 anterior pairs of setae, distally with 3 pairs. Caudal appendages unarticulate, with a few distal setae. Penis has sparse, fine setae; in preserved state reaches as far as 5th segment of cirrus VI.

REMARKS: The above description is based on specimens with capitular lengths of 30–35 mm. No small individuals or males were present. The specimens from station D160 were very poorly preserved; the plates had largely disarticulated, and the chitinous parts of the body were separated from the shells. The illustration in Fig. 28A is from a specimen that was partly cohesive.

These specimens belong to the supposed subgenus *Scillaelepas*, which is distinguished from *Calantica* (sensu stricto) in that the plates and scales protrude apically and overlap to completely enclose the animal. Previously, *Scillaelepas* has been found only in the North Atlantic, but there are widespread localities for fossil forms, including New Zealand. There are 7 described extant species, and not many more known specimens. Some possess a subrostrum, and only *C. gemma*, *C. grimaldi* (Aurivillius) and *C. superba* Pilsbry have 13

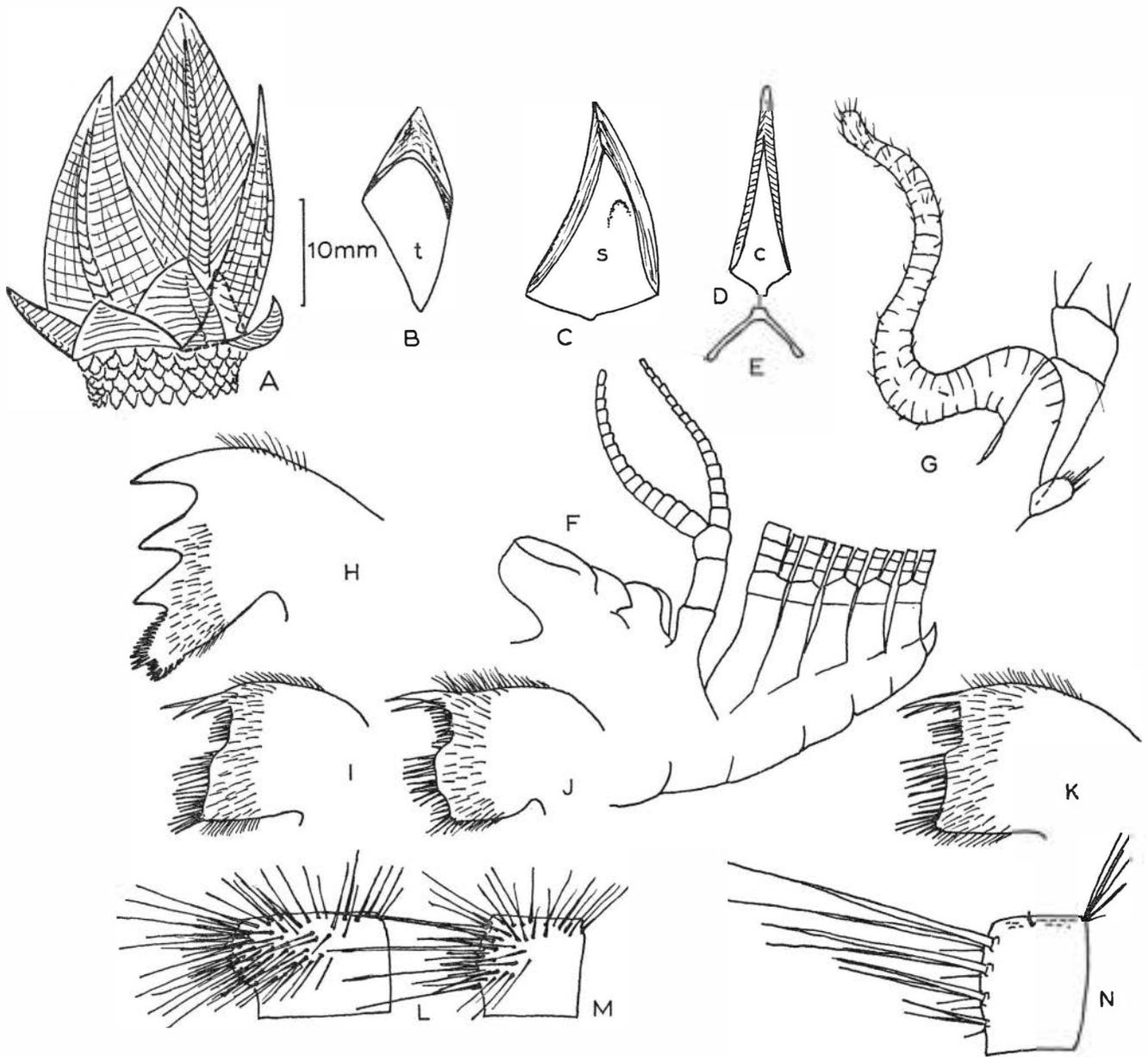


Fig. 28. *Calantica gemma* (Aurivillius): *A*, lateral view, almost complete adult (33.8-mm capitulum length), position of the carinolatus indicated; *B*, *C*, *D*, inner views of tergum, scutum, and carina respectively; *E*, cross section of carina; *F*, side plan of prosoma; *G*, caudal appendage, penis, and pedicel of cirrus VI; *H*, mandible; *I*–*K*, maxillules of 3 separate specimens; *L*, *M*, 9th segments, anterior and posterior rami of cirrus II, inner view; *N*, 9th segment of anterior ramus of cirrus VI, inner view.

plates arranged as in the present material. The shape of the lower latera favours identity with *C. gemma* collected from 1800 m off Greenland. The specimen described and figured by Aurivillius is slightly more squat, and the apex of the tergum is reflexed towards the carina more than in any of the present material, but it is probable that the direction of the protruding apices of the capitular plates is variable. Of the fossil forms, *C. arguta*, described by Withers (1924, 1953) from the lower Oligocene of Greymouth, New Zealand, is very close to the present species.

There have been attempts (Aurivillius 1894, Newman *et al.* 1969) to compare the plate arrangement of calantico scalpellids, especially *Scillaelepas* in which the latera overlap, with that of the basic parietal arrangement in balanomorphs. With the loss of the peduncle and the subcarina, the plates in *C. gemma* resemble the arrangement in *Octomeris* except for one major obstacle: the base of the upper latus is overlapped by that of the carinolatus, rather than the other way round as in the balanomorphs. It is probable that the upper latus is not homologous with the lateral parietal

plate of acorn barnacles, but the inframedian latus could qualify if the loss of the upper latus is postulated. This would point beyond the base of the scillaelepad stock for the origins of the chthamalids. *Scillaelepas* may not be the ancient scalpellid stock, as Withers (1953) supposed. The resemblance to the intertidal *Pollicipes mitella* (sensu Darwin) is striking.

Genus *Smilium* Leach, 1825

Scalpellidae in which hermaphrodites develop, as well 6 primary capitular plates, a subcarina, and 3 pairs of latera; upper latus situated between scuta and carina and has a distinct carinal margin. Umbos of carina, scuta, and upper latus may be subapical. Otherwise as for *Calantica*.

DISCUSSION: Many species have been assigned to *Smilium*, only to be subsequently removed to *Calantica*. Past diagnoses for *Smilium* emphasise the presence of the upper latus in the space between the scuta and carina, in contrast to the traditional diagnosis for *Calantica*, which states that the tergum occupies all the space between the carina and scuta (Pilsbry 1907a, 1908; Withers 1953; Newman *et al.* 1969). However there are species of *Calantica*, viz., *C. pollicipedoides*, *C. spinilatera*, and *C. kampeni*, which have an elevated upper latus occupying some of the space between the normal-shaped scuta and carina. Clearly, a more definite character is required, and it is here taken that *Smilium* includes those scalpellids with a subcarina in which the upper latus has a carinal margin, and is thus quadrangular in shape rather than triangular, and in which the scutum has a near-90° bend in the basal margin, acquiring rostral and upperlateral margins on either side of the apicobasal ridge. On both of these criteria, *S. scorpio* Aurivillius (= *S. sexcornutum* Pilsbry) should be assigned to *Calantica*, and on the basis of the structure of the scutum, the fossil forms *Scalpellum subplanum* Withers, *Calantica sulci* Withers, and *Scalpellum zancleanum* Seguenza are in the genus *Smilium*. Even though this may strengthen the recognition of *Smilium*, there is little else in the anatomy that will distinguish it from *Calantica*. In the species of *Smilium* of which the appendages have been described, these differ from those of *Calantica* in that the first cirrus is set further apart from the rest, and has unequal rami. If *Smilium* is to be maintained as a distinct genus, then a revision of *Calantica* will no doubt identify groups as distinct from each other as from *Smilium*.

Smilium zancleanum (Seguenza) (Plate 6D, E; Fig. 29)

Scalpellum (*Smilium*) *nudipes* Annandale, 1916: 287; Calman 1918b: 99.

Calantica villosa. Powell 1947: 41 (not *C. villosa* of Darwin, 1851).

Calantica (*Calantica*) *zancleana*. Withers 1953: 143 (for synonymy).

MATERIAL EXAMINED: NZOI: Stn E862, 127 m (1 rostrum). Nat. Mus.: 7 specimens, *Recorder*, 640 km NW of Wellington, 1104 m, (W. Foster). Auck. Mus.: 14 specimens, *Iris*, 34°30'S, 173°38'E, 950 m, (T. A. Vickers); 34 specimens, *Iris*, east of Doubtless Bay, 960 m, (W. Foster); 3 specimens plus 4♂, *Recorder*, 41°01'S, 171°01'E, 890 m, (W. Foster); unlabelled group of 30 specimens.

DISTRIBUTION: Recent: Java Sea, 239-920 m; New Zealand, 127-1104 m (Fig. 25). Pliocene of Sicily.

DESCRIPTION: *Externals and shell plates*: Hermaphrodite capitulum ovoid, often massive, with nearly approximate, smooth plates with basal margins embedded in smooth integument. Carina has an apical umbo, arched transversely and has very narrow, inflected parietes. Upper latus wider than high. Rostrum largest of lower plates, strongly concave transversely and has a slight median keel. Peduncle embedded, with spindle-shaped scales inconspicuous in larger specimens.

Largest specimen was in unlabelled group from the Auckland Museum, and has a capitulum length of 68 mm and a peduncle 128 mm long; with a carinal length of 54 mm, this specimen approaches size of fossil plates quoted by Withers (1953, p. 144). Largest of labelled specimens, *Recorder* specimens, had a capitular length of 66 mm; this was only specimen in which 4 complementary males found in expected place (Plate 6E). Males ranged in capitulum length from 3 mm to 5.8 mm, and thus exceeded in size many free-living juveniles attached to peduncles of larger specimens. Largest male had a small, independently growing plate at base of carina on one side, but this clearly arose after fragmentation of base of carina. Another specimen had on one side an upper latus neatly interposed between carina and scutum. Otherwise males 6-plated.

Mouthparts: Dentition of mandibles increases with size of specimens, largest having 7 teeth. Likewise, number of setae on cutting edge of maxillule increases with size.

Cirri: Cirrus I slightly removed from rest of cirri, with anterior ramus slightly shorter than posterior ramus. Number of segments in rami increases with size, as follows, anterior ramus 1st:

cap. length	I	II	III	IV	V	VI
2.3 mm	3, 3	5, 6	6, 6	6, 6	7, 7	7, 7
3.3 mm (♂)	6, 7	10, 10	10, 10	11, 11	11, 11	12, 13
4.4 mm (♂)	8, 9	11, 13	13, 13	13, 14	14, 15	14, 15
20.0 mm	16, 21	24, 24	26, 28	26, 26	24, 25	27, 27
58.0 mm	22, 25	25, 25	28, 28	28, 28	29, 29	28, 28

Segments of rami of cirri II and III bear medial setae, more pronounced in basal segments of anterior ramus of cirrus II and larger specimens. Basal segments of

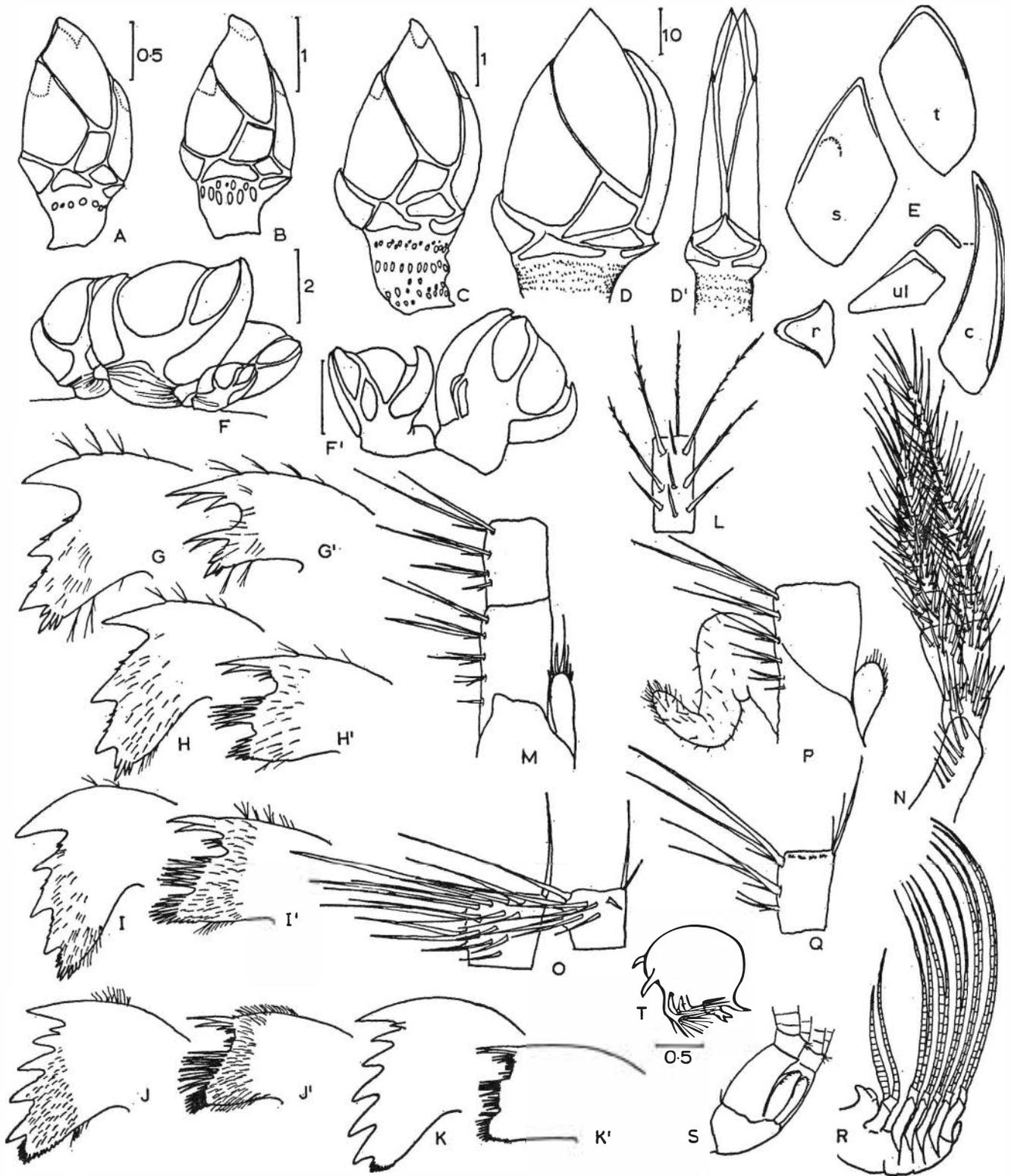


Fig. 29. *Smilium zancleanum* (Seguenza): A–D, lateral views, juvenile to fully mature hermaphrodite; D', rostral view, specimen D; E, inner views, some of the capitular plates, key in Fig. 1; F, group of males from a large hermaphrodite; F', reverse view, two of F, to show an extra latus in one male, split carina in the other; G–K, mandibles and maxillule from specimens with capitulum lengths 2.3 mm (G), 3.3 mm, male (H), 4.4 mm (male) (I), 20.0 mm (J), and 58.0 mm (K); L, anterior view, intermediate segment of cirrus VI, 6.3-mm cap. length specimen; M, caudal appendage and pedicel, cirrus VI of a 2.3-mm specimen; N, cirrus I of a male of 4.4-mm cap. length; O, inner aspects, basal segments of anterior (left) and posterior (right) rami, cirrus II of 4.4-mm cap. length male; P, caudal appendage, penis, and basal segment of pedicel, 3.3-mm cap. length male; Q, outer aspect, intermediate segment of cirrus VI 4.4-mm cap. length male; R, plan of prosoma and cirri of 58-mm cap. length hermaphrodite; S, caudal appendages and bases, cirrus VI of 58-mm cap. length hermaphrodite; T, nauplius larva from mantle cavity of a mature hermaphrodite (scales in mm).

anterior ramus of cirri II and III slightly thicker than corresponding segments in posterior rami. Distal segments of these cirri, and segments of rami of cirri IV–VI, have 2–4 pairs of setae on anterior face, with a single, small seta interposed between bases of pairs. Longest of setae at posterior distal angle of each segment exceeds length of next segment. Caudal appendages leaf-like; in smaller specimens about same length as basal segment of pedicel of cirrus VI and have long, terminal setae reaching to distal margin of that segment; but in larger specimens about $\frac{1}{2}$ length of segment and with minute setae around entire edge. Penis retracted to about $\frac{1}{2}$ length of cirrus VI in larger specimens, not developed in free-living juveniles, but exceeds length of the pedicel of cirrus VI in males.

REMARKS: This handsome and large species was described by Annandale (1916) and Calman (1918b) from specimens from the same sample collected in the Java Sea. The specimen examined by Calman was figured by Withers (1953, pl. 44), and on this specimen he founded synonymy with Pliocene fossils. Because “the carina is still of the *Calantica* type”, Withers placed the species in *Calantica* (*Calantica*) despite Calman’s recognition of the quadrangular form of the upper latus and its inter-position “as clearly as possible” between the carina and scuta. Withers presumably meant that the carina of *Smilium* develops wide parietes, but this is not universally so in *Smilium*, nor is the converse true in *Calantica*. Such features of the appendages as the inequality of the segment size and setation of the rami of cirri II and III do, however, indicate a relationship between *Smilium* and the 13-plated calanticoids.

***Smilium acutum* (Hoek) (Plate 6F; Fig. 30)**

Scalpellum acutum Hoek, 1883: 80; Hoek 1907: 64.
Smilium acutum. Broch 1922: 234; Newman & Ross 1971: 38 (for other citations).

MATERIAL EXAMINED: NZOI: Stns C636 (1 specimen), D119 (2), D904 (8), D905 (2), E399 (2), E400 (2), E433 (3), E784 (2), E840 (1), E880 (1), E893 (1), F91 (1), F95 (6), F868 (2), F878 (5), G305 (6), G342 (10), G403 (29), G651 (3), G652 (60), G667 (1), G700 (45), H55 (2). Nat. Mus.: 5 specimens, *Alert*, 37°10'S, 176°24'E, 736 m. PBMS: Mu 67–61 (1 specimen), Mu 68–27 (1), Mu 67–43 (7), Mu 69–43 (6), Mu 71–266 (1).

DISTRIBUTION: Cosmopolitan, 61–2480 m. In New Zealand, throughout, 391–1220 m (Fig. 25).

DESCRIPTION: *Externals and shell plates:* *Smilium* with hermaphrodite capitulum elongate, with occludent margin parallel to vertical axis. Plates approximate, with faint growth lines, and covered by a thin, hairless integument. Carina simply bowed, with slightly developed parietes and an apical umbo. Upper latus has an elongate basiscutal angle. Carinal latus quadrangular. Peduncle usually about $\frac{1}{2}$ height of capitulum and has closely set and overlapping rounded scales.

Complemental males, found in usual place, minute, with a short peduncle and 6 plates, tergum does not extend fully between scutum and carina; rostrum bigger than carina.

Mouthparts: Mandible with only 3 teeth.

Cirri: Cirrus I separated from cirrus II by a gap as wide as space occupied by rest of cirri together. Anterior ramus of cirrus I longer than posterior ramus. Cirri II–VI with subequal rami, with up to 18 segments per ramus in larger specimens. Segments of posterior rami have 3–5, commonly 4, pairs of setae on anterior edge, most proximal usually minute. Single small seta between bases of each of major setae. Basal segments of rami of cirri II and III have scattered setae on inner faces, and always more setae on anterior ramus than in corresponding posterior ramus. Caudal appendages about $\frac{1}{2}$ height of basal segments of pedicel of cirrus VI, and have a fringe of setae, of which longest at tip overlaps 2nd segment of pedicel. Penis with sparse setae, and in preserved older specimens reaches almost as far as second segment of rami of cirrus VI. Appendages of males like very juvenile free-living individuals, except for a very stout penis almost as long as whole of cirrus VI.

REMARKS: The original description of *S. acutum* was based on *Challenger* material from stations in the Atlantic and near the Kermadec Is. The species has since been taken from New Zealand waters by *Eltanin* on the Campbell Plateau (Newman & Ross 1971). The NZOI Collection confirms its occurrence throughout New Zealand waters.

S. acutum differs from other species of *Smilium* in the nature of the armature of the peduncle. Whereas in other species the small, embedded scales are like those of the subgenus *Calantica* of *Calantica*, in *S. acutum* the plates completely cover the peduncle.

Newman & Ross (1971) assert that the complemental male is 7-plated, recognising 2 rostralateral plates but no rostrum. In the present suite of specimens, all undamaged specimens show a complete rostrum, which is often the largest plate in the capitulum. Lateral pressure on the scuta of the hermaphrodite could longitudinally crack the rather thin, transversely placed rostrum of the male. None of the males of the present suite of specimens had more than 6 plates.

Genus *Arcoscalpellum* Hoek, 1907

Scalpellidae in which hermaphrodite or female has a capitulum with up to 14 fully or partially calcified plates identifiable as paired terga, scuta, upper latera, rostralatera, inframedian latera and carinolatera, a carina, and a small, inconspicuous rostrum. Umbos of terga and scuta apical, but may not be so in other plates, when subepidermal secondary flanges of shell develop. Subcarina absent, carinolatera occlude below carina.





Fig. 30. *Smilium acutum* (Hoek): A-E, free-living specimens in order of increasing size—A, B, with primordial plates; F, inner views, some of the capitular plates of the mature hermaphrodite E, key in Fig. 1; G-H, males; H', rostral view of H; I-K, mandibles and maxillules of specimens with cap. lengths 0.6 mm (male) (I), 1.9 mm (J), and 9.4 mm (K); L, cirrus I of male G; M, caudal appendage, penis and cirrus VI, male G; N, caudal appendage and pedicel of cirrus VI, 1.9-mm cap. length hermaphrodite; O, plan of prosoma and cirri of hermaphrodite; P, cirrus I of 9.0-mm hermaphrodite; Q, caudal appendage, penis, and pedicel, cirrus VI of 9.0-mm hermaphrodite; R, R', inner views, 4th segment of anterior and posterior rami, cirrus II of a mature hermaphrodite; S, outer view, intermediate segment of cirrus VI, mature hermaphrodite (scales in mm).

Cirrus I much shorter than others and separated from them, usually with anterior ramus shorter than posterior, and with median segments wider and more protuberant than corresponding ones in posterior ramus. Cirri II–VI similar, but with number of setae on medial faces of segments decreasing apically, posteriorly, and in younger specimens. Caudal appendages articulated, often multiarticulated. Small males are sac-like, with or without 4 rudimentary plates around an orifice, and lodged in a pouch inside occludent margin near umbo of scuta.

DISCUSSION: *Arcoscalpellum* contains a large number of named species, most of them not completely described. Newman & Ross (1971) elevated Pilsbry's section *Neoscalpellum* and Hoek's section *Mesoscalpellum* to generic rank, and named 4 other genera distinct from *Arcoscalpellum*. Of the present material, only one species, *A. intermedium*, would fall into any of their new genera. However, *A. intermedium* shows in its young stages and in certain details of its appendages setation affinities with forms that do not have reduced calcification in the capitular plates. The morphological distinctions between the 7 genera proposed by Newman & Ross (1971) are not at all clear.

A more clearly defined group would be one containing forms like *A. pedunculatum*, in which the capitular plate armature is intact, the basal whorl of plates is small compared with the upper plates, the peduncle is longer than the capitulum, and the small males are accessory to the hermaphrodite. Other species have relatively longer lower whorl plates, a short peduncle, and the sexes separate. In these respects the *A. pedunculatum* group approaches the calanticids, and is probably more primitive than other arcoscalpellids. Subsequent lines might involve such characters as the marked hypolasiopod condition of the setation of the posterior cirri, the interarticular setation of the posterior edge of the segments of the posterior cirri, the nature of the incompleteness of the capitular skeleton, and the subsequent way in which secondary, apically directed plated growth-areas occur. It is apparent that, until the ontogenetic development of these features is described for many of the named species, there is little point in attempting a subdivision of *Arcoscalpellum*.

After studying the arcoscalpellid material available, 9 species are now recognised from New Zealand waters.

***Arcoscalpellum pedunculatum* (Hoek) (Plate 7A; Fig. 31)**

Scalpellum pedunculatum Hoek, 1883: 99.

MATERIAL EXAMINED: NZOI: Stns C166 (4 specimens), C642 (1), D220 (5), D245 (c. 200), Z2374 (1). Auck. Mus.: 2 specimens, *Valkyrie*, east of Aldermen Is, 368–478 m. Nat. Mus.: 5 specimens, 40°17'S, 172°14'E, 202 m.

DISTRIBUTION: New Zealand, 202–478 m (Fig. 32).

DESCRIPTION: *Externals and shell plates:* Capitular plates of hermaphrodite covered by a very thin and sparsely hirsute integument. Lower plates less than $\frac{1}{10}$ height of capitulum. Carina with sides almost at 90° to roof, and apex stands well above level of that of scuta. No internal apical pit on scuta for males. Rostrum and inframedian latera triangular, and interposed neatly between other lower latera. Carinolatera have umbo subspiral, and initially at base of sides of carina, but stand clear of capitulum in larger specimens. Lower parts of carinolatera meet without interdigitating below base of carina. Upper latera and inframedian latera develop in larger specimens subepidermal apical flanges. Peduncle often longer than capitulum, and has 11 rows of transversely lengthened scales covered by integument more hirsute than that over capitulum. Males globulo-cyprid-shaped, and their integument has minute, external spines directed towards a lateral orifice bordered by 4 minute, rudimentary plates.

Mouthparts: Mandible with 3 teeth.

Cirri: Intermediate segments of anterior ramus of cirrus I more than $2 \times$ width of those of posterior ramus. Anterior ramus of cirrus II only slightly wider than posterior ramus. Amount of setation on inner faces of segments of posterior cirri decrease posteriorly distally, and in smaller specimens. In larger specimens posterior interarticular edge of segments of anterior ramus of cirrus II bears strong setae, but other rami devoid of such setae. Medial segments of cirrus VI usually have 4 pairs of setae on anterior edge, sometimes with a small, basal, 5th pair, and have a few short setae at bases of larger pairs; setae of anterior ramus a little longer than those of posterior ramus. Caudal appendage in small specimens barely length of pedicel of cirrus VI, composed of about 6 segments; but in large specimens (approx. 47-mm capitulum length) attains up to 37 segments and is then about $\frac{1}{2}$ length of cirrus VI, which has about same number of segments per ramus. Penis of larger specimens tapers, about $\frac{1}{2}$ length of cirrus VI.

REMARKS: The *Challenger* collected one specimen of this species at 39°32'S, 171°48'E at 276 m; this station practically coincides with the location of most of the NZOI specimens examined here. None of the NZOI specimens, which range in size up to 30-mm capitulum length, have the carinolatus projecting beyond the carina to the same extent as shown in Hoek's figure, but even that is exceeded by the larger specimens collected by *Valkyrie* from near the Aldermen Is and those in the National Museum. The largest specimen (47-mm capitulum length) has a peduncle three times as long.

With growth, the plates of the lower whorl undergo negative allometry, but there is an increase in the numbers of segments of the cirri and caudal appendages, and in the number of setae on the appendage segments and the cutting edge of the maxillule. The number of teeth on the mandible, however, remains constant.

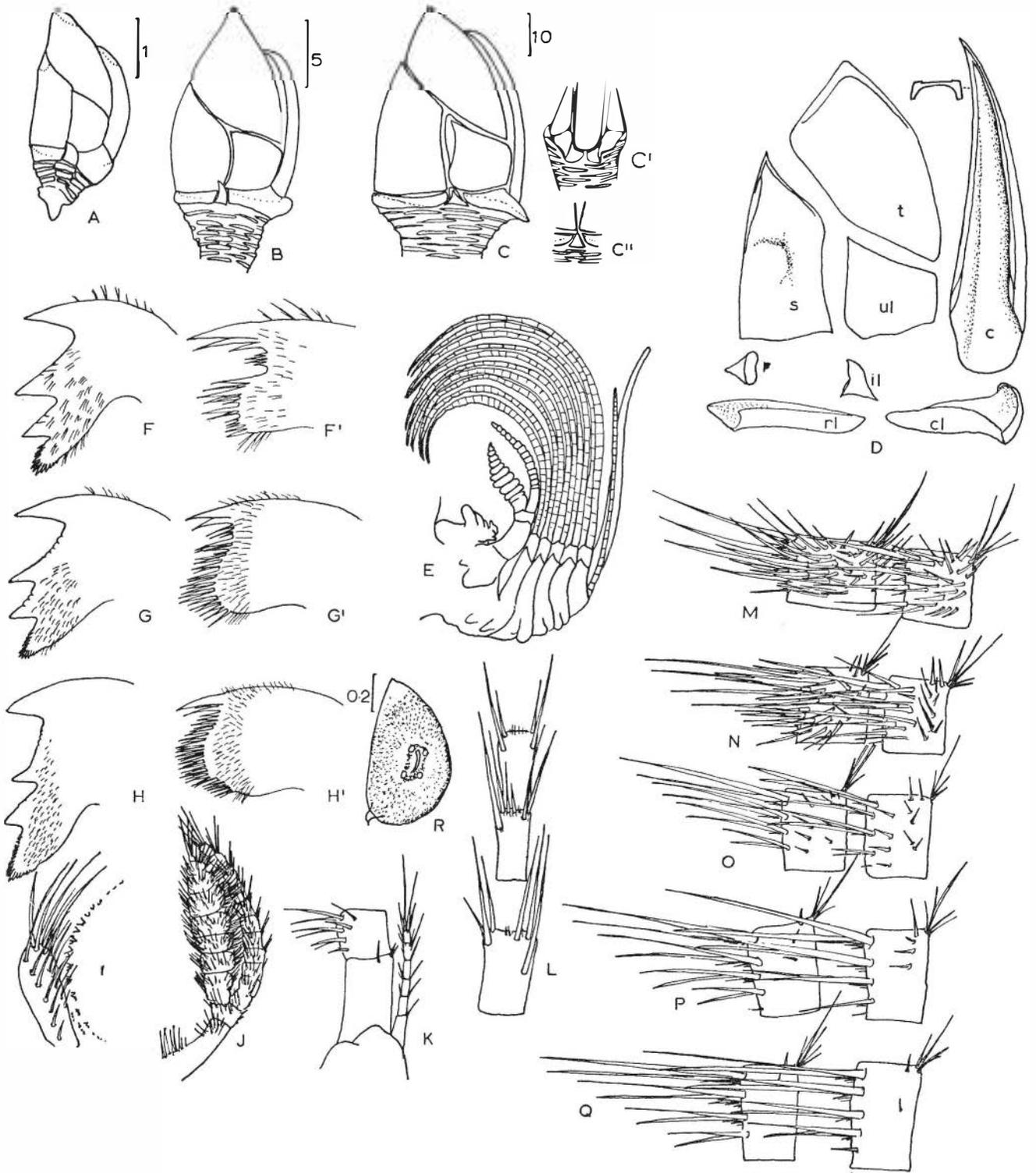


Fig. 31. *Arcoscalpellum pedunculatum* (Hoek): A–C, lateral views, hermaphrodites in order of increasing size; C', lower carinal part of capitulum; C'', lower rostral part of capitulum; D, inner views of the capitular plates, key in Fig. 1; E, plan of prosoma and cirri; F–H, mandibles and maxillules, specimens of capitulum lengths 4.5 mm (F), 15.5 mm (G), and 48 mm (H); I, labral teeth and mandibular palp, 4.5-mm cap. length specimen; J, inner view of cirrus I, 4.5-mm cap. length specimen; K, caudal appendage and pedicel, cirrus VI of a 4.5-mm cap. length specimen; L, a basal (lower) and two intermediate segments, caudal appendage of 15.5-mm capitulum length specimen; M–Q, inner views, intermediate segments of the anterior (left) and posterior (right) rami of cirri II (M), III (N), IV (O), V (P), and VI (Q), 15.5-mm capitulum length specimen (scales in mm).

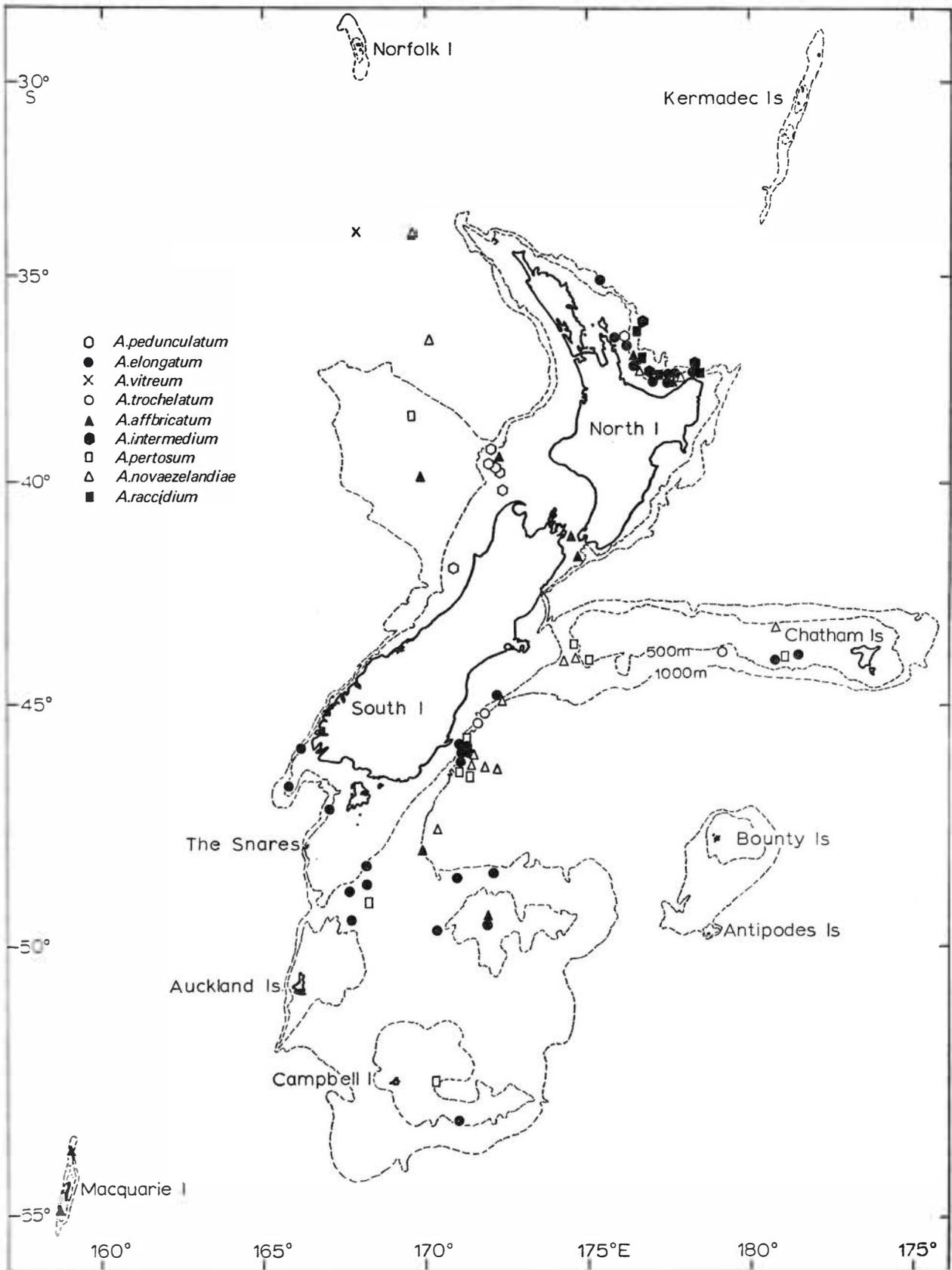


Fig. 32. Records of *Arcoscalpellum* taken at benthic stations in the New Zealand region.

For *A. elongatum* read *A. costellatum*.

A. pedunculatum is related to deep-water forms which attain large sizes even though the plates of the lower whorl remain proportionately small, e.g., *A. michelottianum*, *A. gigas*, and *A. darwinii* (see Newman & Ross 1971, p. 60). The shallower habitat of *A. pedunculatum* was remarked on by Hoek (1883). Pilsbry (1907a) compared *A. portoricanum* from shallow seas off Porto Rico with *A. pedunculatum*, but the former species has a carinolatus as high as or higher than it is wide, and in this respect resembles the rest of the species of *Arcoscalpellum* dealt with in this paper.

***Arcoscalpellum costellatum* (Withers)**

(Plate 7B, C; Fig.33)

Scalpellum elongatum Hoek, 1883: 93; Nilsson-Cantell 1928a: 8. not *Scalpellum (Arcoscalpellum) costellatum* (Steenstrup 1837)
Scalpellum (Arcoscalpellum) costellatum Withers, 1935: 279
Scalpellum (Scalpellum) elongatum. Stubbings 1936: 25.
Arcoscalpellum buccinum Newman & Ross, 1971: 55.

MATERIAL EXAMINED: NZOI: Stns D85 (1 specimen), D210 (1), D904 (2), D905 (5), E400 (1), E 803 (1), E822 (2), E830 (4), F90 (8), F91 (17), F94 (3), F95 (2), F104 (5), F107 (7), F144 (2), F870 (11), F875 (3), F876 (4), F883 (3), F884 (1), F909 (1), G667 (3), G688 (1). PMBS: Mu 67–142, 735 m, (2 specimens); Mu 67–43, 625–650 m, (1); Mu 71–250, 480 m, (2). Auck. Mus.: 53 specimens, east of Aldermen Is, 370–478 m. Nat. Mus.: 3 specimens, *Alert*, 37°10'S, 176°24'E, 736 m. Marine Dept. Prawn Survey: between Aldermen Is and Red Mercury I.

DISTRIBUTION: South Atlantic, South Pacific, and Indian Oceans, 110–2013 m. In New Zealand, throughout, 260–1020 m (Fig. 32).

DESCRIPTION: *Externals and shell plates*: Female: capitulum triangular, with approximate plates ornamented with radial ridges and covered by a sparsely hirsute integument. Carina with roof deeply grooved because of strong lateral ridges, wide in lower part, and has ribbed parietes in upper part. Scutum with apex overlapping tergum, and internally a pit for complementary males above a shallow pit for adductor muscle. Upper latus has straight sides, sometimes with scutal margin slightly concave, and apex fits snugly between tergum and scutum. Carinolatera as high as wide, and interdigitate below base of carina. Inframedian latus triangular, has an apical umbo, and occupies all space between carina and rostrilatera in specimens less than about 6-mm capitulum length, and only about ¼ of height in specimens longer than 14 mm. Rostrum sagittate, and appears externally as an inverted triangle in smaller specimens; in larger specimens, encroaching rostrilatera reduce visible portion to a narrowly oval slip between occludent edges of latera. Peduncle has 6 rows of wide, alternately placed scales which do not overlap, so that cuticle is visible between them.

Males borne in scutal pouches, and have external striations and minute spines, but lack traces of plates.

Mouthparts: Mandible has 3 teeth throughout ontogeny. Maxillules have a notch or gap between 2 or 3 stout setae at an upper angle and a group of more slender setae on cutting edge.

Cirri: Number of segments in rami of the cirri increase slightly with growth, as follows, anterior ramus 1st:

cap. length	I	II	III	IV	V	VI
3.6 mm	7, 7	8, 11	11, 11	13, 13	13, 13	13, 13
6.0 mm	8, 10	14, 14	13, 14	15, 16	16, 16	17, 18
8.3 mm	8, 10	15, 15	16, 15	17, 16	18, 18	17, 18
12.2 mm	8, 10	15, 14	15, 15	18, 16	17, 18	18, 18
16.5 mm	8, 10	17, 17	19, 19	20, 20	27, 20	21, 21
15.3 mm*	8, 10	15, 16	20, 20	20, 21	22, 31	25, 24
25 mm**	9, 11	20, 21	24, 26	27, 28	–, 29	–, 29

*after Newman & Ross (1971)

**after Nilsson-Cantell (1928a)

Anterior ramus of cirrus I slightly shorter than posterior ramus, and has intermediate segments about 2 × as wide. Anterior ramus of cirrus II has segments slightly thicker than those of posterior ramus, more setose, even bearing setae on posterior edge between articulations, but this occurs very rarely in posterior ramus or in those of more posterior cirri. Intermediate segments of cirrus VI have 4 major pairs of setae on anterior edge, with 1 or 2 short setae between bases of pairs, except for those of distal pair of setae on anterior ramus, which are longer. Caudal appendages uniaarticulate, and only about ¼ length of basal segment of pedicel of cirrus VI.

REMARKS: This species was described from specimens from 3 *Challenger* stations, 1 off Tristan da Cunha, 1 off Sydney, and 1 off East Cape in New Zealand. It is not clear from which station the type was taken. Withers (1935) pointed out that *Scalpellum elongatum* (Steenstrup 1837), a fossil arcoscalpellid, has priority of name over Hoek's species. Withers renamed the Recent species *S. (A.) costellatum*. The species has subsequently been identified from the Indian Ocean (Nilsson-Cantell 1928a, Stubbings 1936). Nilsson-Cantell's specimen shows a wide interspace between the carina and terga, in contrast to the ribbed parietes of the carina occupying this space in the generally smaller specimens studied here, otherwise the descriptions are not at variance. Newman & Ross (1971) described *Arcoscalpellum buccinum* from specimens collected by *Eltanin* from the Campbell Plateau. These specimens were evidently distinguished from *A. costellatum*, because in Hoek's drawing the carinal latera appear not to interdigitate. Nilsson-Cantell (1928a) re-examined the type specimen before identifying the Indian Ocean material, and showed that the carinal latera do interdigitate in the fashion shown by Newman & Ross for *A. buccinum*, and as seen in the present material. Comparison of the shape of the disarticulated rostrum with its *in situ* appearance in other species seems an erroneous procedure. As the NZOI collections range over the Campbell Plateau, and the distribution of the present species encompasses the



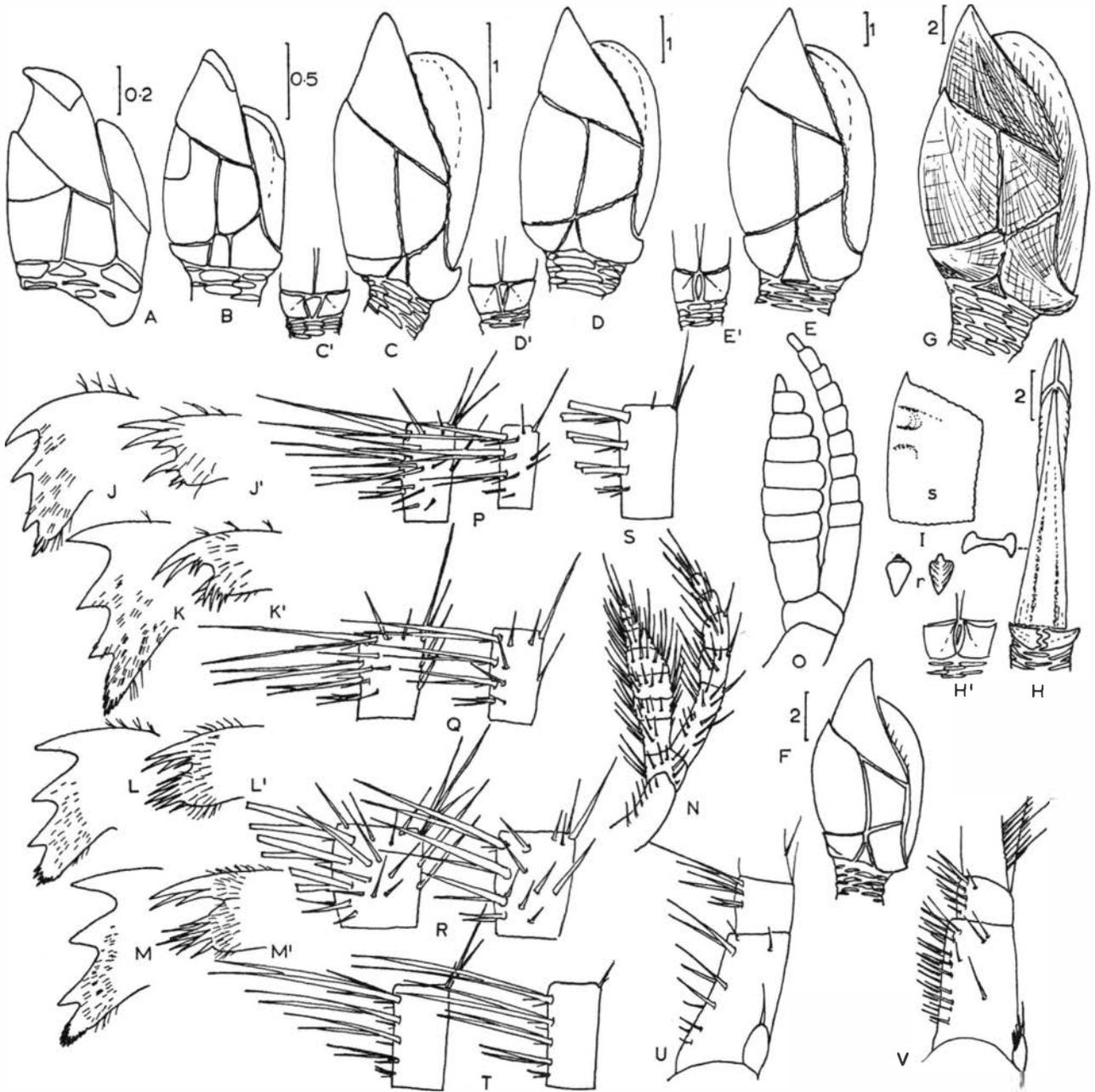


Fig. 33. *Arcoscalpellum costellatum* (Withers): A–G, lateral views, females in order of increasing size, of capitulum lengths 0.9 mm (A), 1.6 mm (B), 3.4 mm (C), 6.0 mm (D), 8.5 mm (E), 9.0 mm (F), and 16.5 mm (G), and rostral views of lower capitulum in C', D', E', H, H', carinal and rostral views, capitulum of 12.2-mm cap. length female; I, inner view of scutum (s), inner and outer views of rostrum (r), specimen H; J–M, mandibles and maxillule of specimens, cap. lengths 3.6 mm (J, J'), 6.0 mm (K, K'), 12.2 mm (L, L'), and 1.65 mm (M, M'); N, O, cirrus I, specimens of capitulum lengths 3.6 mm and 8.3 mm; P, Q, R, inner view, intermediate segment, anterior and posterior rami of cirrus II, specimens of 6.0 mm (P), 8.3 mm (Q), and 12.1 mm (R); S, intermediate segment, anterior ramus of cirrus VI, 6.0-mm cap. length specimen; T, intermediate segments, anterior and posterior rami, cirrus VI of 16.5-mm cap. length specimen; U, V, caudal appendage and pedicel, cirrus VI of 3.6-mm and 12.2-mm cap. length specimens (scales in mm).

Plateau and one of the type localities for *A. costellatum*, *A. buccinum* is held to be the same species as taken by Challenger. There are two features of the appendages not so far mentioned in the descriptions, firstly the presence of setae on the interarticular posterior edge

of the segments of particularly the anterior ramus of cirrus II, and the hypolasiopod condition of the distal setae of the segments of the anterior rami of the posterior cirri. In these features *A. costellatum* approaches *A. vitreum*, taken in the north of New Zealand.

Arcoscalpellum vitreum (Hoek) (Plate 7D; Fig. 34)

Scalpellum vitreum Hoek, 1883: 115.

not *S. vitreum*. Utinomi 1958: 283.

not *Arcoscalpellum vitreum*. Newman & Ross 1971: 87.

Scalpellum formosum Hoek, 1907: 110; Nilsson-Cantell 1921: 187.

not *S. formosum*. Pilsbry 1907a: 58.

? not *Arcoscalpellum formosum*. Newman & Ross 1971: 60.

MATERIAL EXAMINED: NZOI Stn E869 (1 specimen).

DISTRIBUTION: Western Pacific, Japan through Malaysia to New Zealand, 600 – 3450m. In New Zealand, the one station in the north at 1685 m (Fig. 32).

DESCRIPTION: Of the one New Zealand specimen, 19-mm capitulum length: *Externals and shell plates*: Female: capitulum elongate, wider centrally than basally. Plates approximate, with radial ridges, covered by a very thin, hairless integument. Roof of carina flat, with slight lateral ridges. Scutum with apex just overlapping tergum, and has internally a shallow pit for complementary males. Upper latus with straight sides, apex fits snugly between tergum and scutum. Carinolatera wider than high, and interdigitate below carina. Inframedian latus narrowly triangular with an apical umbo, extending part-way between carina and rostralatera in larger specimens. Rostrolatera higher than wide. Rostrum visible externally as a narrow slip between occludent edges of rostralatera. Peduncle has 7 rows of wide, non-overlapping scales.

Males borne in scutal pouches, and have external striations and minute spines, but no traces of plates.

Mouthparts: Mandible has 3 teeth. Maxillule with a notch below stout setae at upper angle.

Cirri: Number of segments in rami as follows, anterior ramus 1st:

I	II	III	IV	V	VI
13,15	22,21	22,25	30,29	27,25	24+,29

Intermediate segments of anterior ramus of cirrus I more than $2 \times$ width of those of posterior ramus, and all segments bear numerous anterior, medial, and posterior setae. Segments of posterior cirri generally not much longer than wide, and may bear setae on posterior interarticular edge, particularly in anterior rami of other cirri, but in at least some of segments of all rami. Segments generally bear 3 pairs of anterior setae and a minute 4th pair, occasionally 4 strong pairs and an extra small pair, and have a few short spines between bases of major pairs, except that these are longer between distal pair of setae in each segment of anterior rami. Caudal appendage unarticulated and short, about $\frac{1}{4}$ length of basal segment of pedicel of cirrus VI.

REMARKS: This specimen belongs, with *Arcoscalpellum costellatum*, to a group of species which have in common the striations of the capitular plates, the straight-sided upper latus with the apex fitting snugly into the angle between the terga and scuta, and the triangular inframedian latus which initially extends fully between the rostro- and carinolatera in juvenile females but becomes relatively shorter in older specimens. This specimen agrees with the figures and descriptions of external form given by Hoek for both *S. vitreum* from off Japan and *S. formosum* from Malaysia. These two named forms were distinguished by Hoek on the apparent absence of a rostrum in the former, but it is now apparent that in this group of arcoscalpellids the rostrum, like the inframedian latus, is practically vestigial, and becomes more so with growth. Its external appearance in an intact specimen provides an unreliable character for specific distinction.

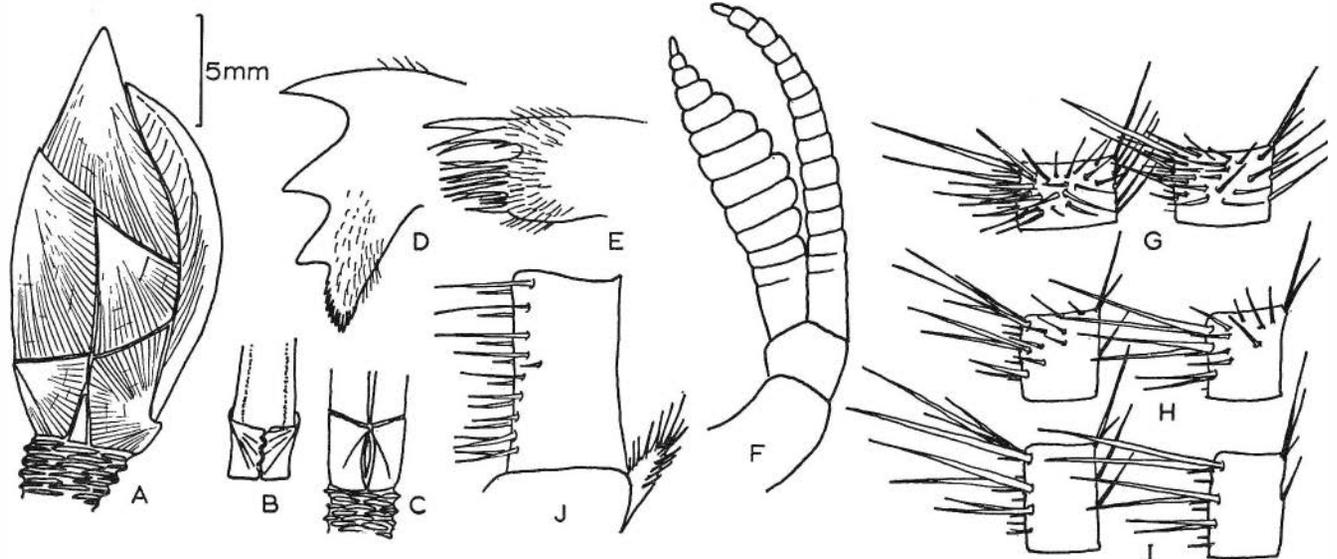


Fig. 34. *Arcoscalpellum vitreum* (Hoek): A, lateral view of 19.0-mm capitulum length female; B, C, carinal and rostral views, lower part of capitulum, specimen A; D, mandible; E, maxillule; F, plan of cirrus I; G, inner view, intermediate segments of anterior and posterior rami, cirrus II; H, same of cirrus IV; I, same of cirrus VI; J, caudal appendage and basal segment, pedicel of cirrus VI.

The *S. vitreum* of Utinomi (1958) looks quite distinct from Hoek's figures, and it seems right for Newman & Ross (1971, p. 86) to have renamed these Japanese specimens, as *A. utinomii*.

North Atlantic specimens of this group were first described as *S. talismani* by Gruvel (1902). This (*vide* Broch, 1953) is the senior synonym for *S. bellum*, which is the replacement name for *S. formosum* of Pilsbry (1907a). Newman & Ross (1971) put Atlantic and south-eastern Pacific material into the same synonymy, and further, because they could not recognise any external differences between some of these specimens and the description of *S. vitreum*, put all in synonymy with *S. vitreum*. However, no description of the appendages of *S. vitreum* from western Pacific material existed. The present specimen, which more resembles Hoek's figures than any of those of Atlantic material, differs from the description given by Newman & Ross in the shape of the segments and their setation. It has a wide anterior ramus to cirrus I, it has hypolasiopod setation in the posterior cirri, and it has prevalent setae on the posterior interarticular edges of the segments. In these

characters it approaches *A. costellatum*, but can be distinguished by the proportionately longer lower latera and the consequent changes in the shape of the capitulum. It would seem prudent at this stage to separate the western Pacific species, as *A. vitreum* (Hoek), from the Atlantic *A. talismani* (Gruvel).

***Arcoscalpellum trochelatum* n.sp.** (Plate 8A; Fig. 35)

MATERIAL EXAMINED: NZOI: Stns C607 (2 specimens), E413 (2), G675 (1).

DISTRIBUTION: New Zealand, 426–792 m (Fig. 32).

DESCRIPTION: *Externals and shell plates*: Female capitulum triangular in lateral view, and has approximate plates with radial ridges and covered by a thin, hirsute integument. Roof of carina deeply grooved because of strong lateral ridges, and ribbed parietes well developed in upper part of carina. Scutum just overlaps tergum, and has a small point at tergo-lateral angle.

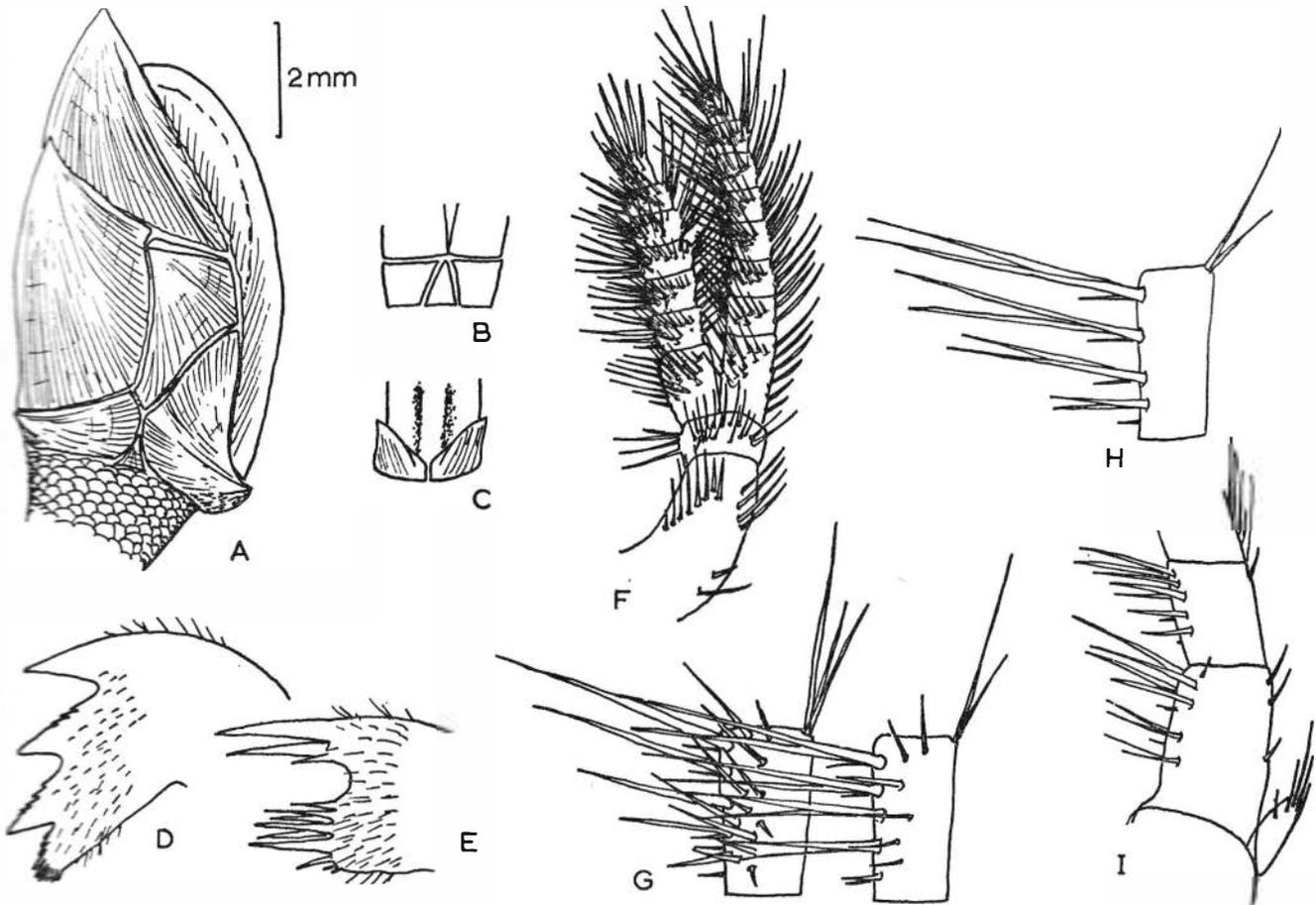


Fig. 35. *Arcoscalpellum trochelatum* n.sp.: A, lateral view of 8.5-mm capitulum length female; B, C, rostral and carinal views, lower part of capitulum; D, mandible; E, maxillule; F, inner view of cirrus I; G, inner view, intermediate segments of anterior (left) and posterior (right) cirrus II; H, same, anterior ramus of cirrus VI; I, caudal appendage and pedicel, cirrus VI.

Upper latus with apex situated below tergo-lateral point of scutum, a secondary flange which develops towards tergum, a convex scutal margin, and a produced basal arm forming a short but distinct margin with rostrolaterus. Carinolatera almost as high as wide, and meet without interdigitating below carina. Inframedian latus triangular with an apical umbo extending, in specimens examined, about $\frac{1}{2}$ way between lateral margins of rostrolatera and carinolatera. Rostrolatera wider than high, and do not cover rostrum. Rostrum visible externally as an erect, triangular plate as high as adjacent edges of rostrolatera. Peduncle provided with numerous, close-packed, and overlapping scales.

Complemental males borne in scutal pouches, and have external striations and very minute spines, but lack traces of plates.

Mouthparts: Mandible with 3 teeth. Maxillule has a notch between stout setae at upper angle and more slender setae on cutting edge.

Cirri: Number of segments in rami of 2 specimens as follows, anterior ramus 1st:

cap. length	I	II	III	IV	V	VI
8.5 mm	7, 8	11, 11	12, 12	13, 13	13, 14	13, 14
9.1 mm	7, 8	11, 11	13, 13	14, 13	14, 14	14, 14

Anterior ramus of cirrus I not much shorter than posterior ramus, and segments hardly wider. Rami of posterior segments subequal, generally with more medial setae on segments of anterior ramus than corresponding posterior ramus, and decreasing in abundance posteriorly. Intermediate segments of cirrus VI alike in anterior and posterior rami, bearing 4 or 5 pairs of setae on anterior edge, with small spines between bases of major pairs. Longest setae of those at posterior distal angle generally equal or exceed length of next segment. Setae absent on interarticular posterior edge of any of segments of cirri II–VI. Caudal appendage uniaarticulate, about $\frac{1}{3}$ height of basal segment of pedicel of cirrus VI, and apical setae extending for an equivalent length.

HOLOTYPE: NZOI 201, the larger of the specimens from station E413 (Plate 8A, left).

REMARKS: This species bears a superficial resemblance to *A. costellatum*, but can be distinguished by the shape of the upper latus and the nature of the peduncular scales. The distinction is confirmed by differences in the setation of the cirri.

***Arcoscappellum affricatum* n. sp.** (Plate 7E, F; Fig. 36)

Scappellum aff. *imbricatum* Broch, 1922: 344, fig. 77.

MATERIAL EXAMINED: NZOI: Stns A426 (1 specimen), C627 (2), C734 (1), D210 (1), D227 (1), E234 (2), F875 (1), H55 (1), Z2368 (1). Auck. Mus.: 1 specimen, *Recorder*, on cable in Cook Strait, 130–147m. Nat. Mus.: 1 specimen, *Alert*, 37° 20'S, 176° 21'E, 497 m.

DISTRIBUTION: New Zealand, 130–752 m (Fig. 32).

DESCRIPTION: Externals and shell plates: Female capitular plates covered by hairless integument, smooth, and initially nearly approximate but come to stand apart from each other in larger specimens. Carina has a flat roof with very low lateral ridges, and narrow parietes occupying upper $\frac{1}{2}$ of plate. Tergum with apex generally recurved towards carina, and a distinct notch on carinal margin for reception of apex of carina. Scuta just overlap terga, without a tergo-lateral arm, and internally with a moderately deep pit for complemental males. Upper latus has apex pointed and curved, and in larger specimens develops a small, rounded, subepidermal flange. Carinolatera higher than wide, not interdigitating below carina. Rostrolatera wider than high. Inframedian latus somewhat variable, generally triangular with an apical umbo, and in smaller specimens extending all the way between latera, but it may be narrow and slip-like, and be undercut by rostrolatera, with apex standing out from capitulum only part of way between latera. Rostrum has an apical umbo, externally visible in larger specimens as an erect, triangular plate full height of occludent edges of rostrolatera. Peduncle has 8 rows of wide scales separated by continuous areas of integument.

Males borne in scutal pouches, and have external striations, minute spines, and 4 small, calcified plates around orifice.

Mouthparts: Mandible has 3 teeth throughout ontogeny. Maxillule has a more-or-less pronounced notch below group of 3 or 4 setae at upper angle.

Cirri: Anterior ramus of cirrus I shorter than posterior one, and intermediate segments $2\times$ as wide. Intermediate segments of cirrus II have setae on interarticular posterior edge as well as minute, upwardly directed spines which increase in number with increasing size of specimen. They also occur on anterior ramus of cirrus III, in larger specimens on anterior ramus of cirrus IV, very occasionally on other rami. Number of segments increases with size, as follows, anterior ramus 1st:

cap. length	I	II	III	IV	V	VI	c.a.
6.4 mm	7, 8	10, 10	11, 11	11, 12	11, 11	12, 13	1/1
10.5 mm	7, 9	13, 13	14, 15	16, 15	15, 16	17, 17	1/1
11.5 mm	8, 10	14, 14	16, 16	16, 16	16, 16	17, 17	2/2
14.7 mm	7, 8	13, 15	14, 15	16, 16	16, 16	15, 17	1/2

Intermediate segments of posterior cirri have 4 or 5 pairs of setae on anterior edge, with short setae between bases of major pairs; those between distal pair of anterior ramus only a little longer than those in posterior ramus. Caudal appendage shorter than basal segment of pedicel of cirrus VI, and has 1 or 2 segments with distal setae reaching to limit of basal pedicel segment.

HOLOTYPE: NZOI 202, the specimen from station C734 (Plate 7E).

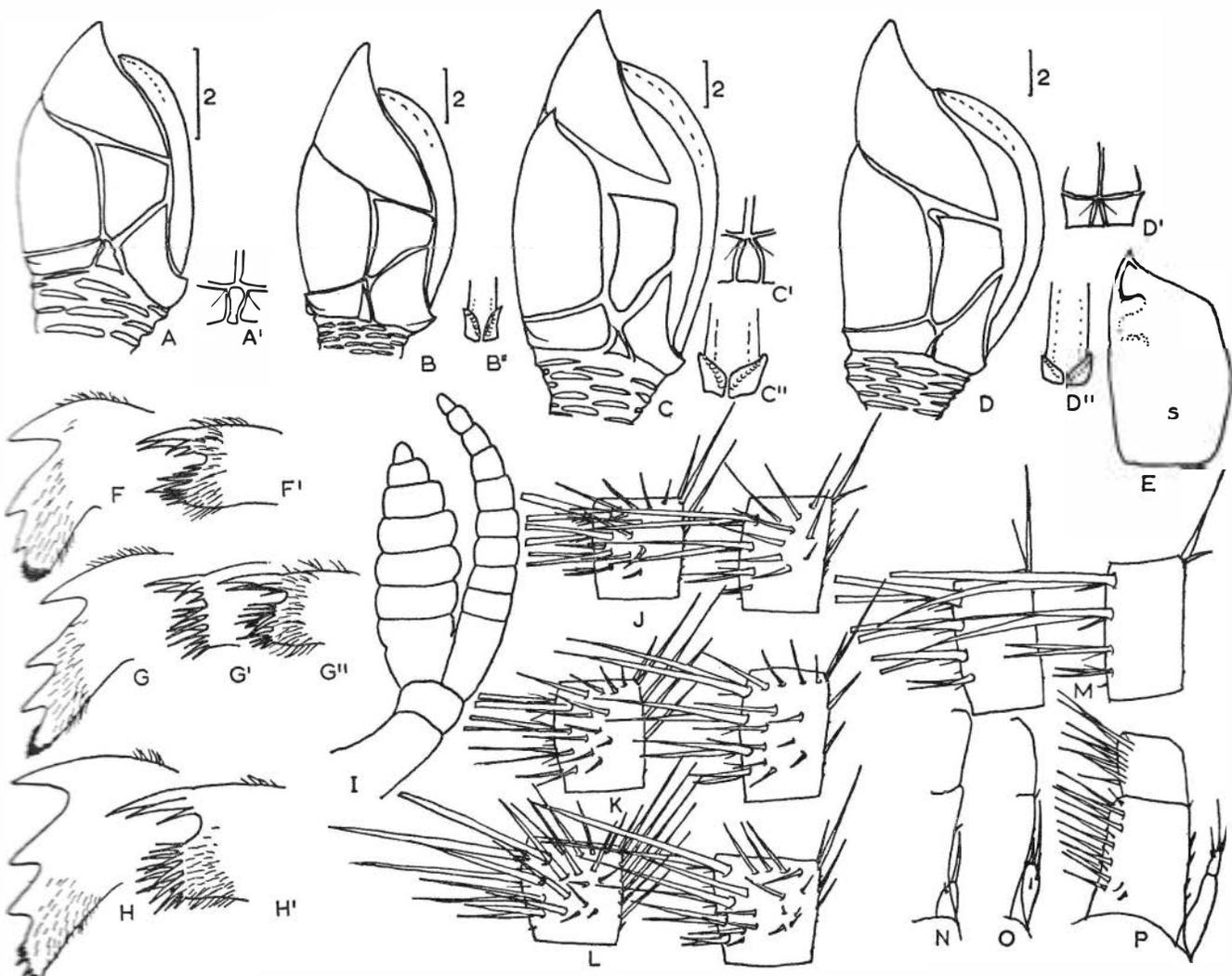


Fig. 36. *Arcoscalpellum affbricatum* n.sp.: A–D, lateral views, females in order of increasing size and of capitulum lengths 6.4 mm (A), 10.5 mm (B), 14.7 mm (C), and 14.3 mm (D), with appropriate rostral and carinal views of lower part of capitulum; E, inner view of scutum; F, F', mandibles and maxillules, 6.4-mm cap. length specimen; G, G', G'', same, 11.5 mm specimen; H, H', same, 14.7 mm specimen; I, plan of cirrus I, 11.5-mm specimen; J, inner view, intermediate segments of the anterior (left) and posterior (right) rami, cirrus II of 6.4-mm specimen; K, same, 10.5 mm specimen; L, same, 14.7 mm specimen; M, same, cirrus VI of a 10.5-mm specimen; N, caudal appendage in relation to pedicel of cirrus VI, of 6.4 mm specimen; O, same, 10.5 mm specimen; P, same, 11.5 mm specimen (scales in mm).

REMARKS: These specimens are undoubtedly the same species as taken by a New Zealand Government Trawling Expedition and subsequently described but not named by Broch (1922). They differ from *Scalpellum imbricatum* Hoek from Malaysian seas in that the roof of the carina lacks a deep, longitudinal furrow, and the peduncle is not covered by small, rounded and overlapping scales. *A. affricatum* more closely resembles *A. antillarum* (Pilsbry) from the Gulf of Mexico, but differs in that, in Pilsbry's specimens of 10-mm capitulum length, the plates stand more apart, and the tergo-lateral flange of the upper latus is more pronounced than even in specimens of around 15-mm length in the present material. The appendages of *A. antillarum* have not been described, preventing a full comparison.

Arcoscalpellum intermedium (Hoek) (Plate 8B; Fig. 37)

Scalpellum intermedium Hoek, 1883: 70; Nilsson-Cantell 1921: 208.

Scalpellum nipponense Pilsbry, 1907a: 73; Broch 1931: 24; Hiro 1933: 25.

Litoscalpellum nipponense. Newman & Ross 1971: 112.

MATERIAL EXAMINED: NZOI: Stns F873 (1 specimen), F884 (4), F900 (1).

DISTRIBUTION: Japan, east Australia, and New Zealand. In New Zealand, in the north-east, 211–1288 m (Fig. 32).

DESCRIPTION: *Externals and shell plates:* Capitulum of female with smooth plates covered by a sparsely hirsute integument, approximate in younger specimens, but in older specimens those of upper part particularly stand apart from each other. Carina with narrow parietes and a flat roof with slight lateral ridges in young specimens. Tergum develops an indented basal margin, pointed carinal arm longer than truncated occludent arm. Scutum has a short tergo-lateral arm, and becomes quite narrow in upper part with increasing size. Scutum internally with a long pit for accommodation of up to 3 complementary males. Upper latus has a pointed apex directed beneath tergo-lateral arm of scutum, and stands away from scutum in larger specimens, in which it develops a secondary apical flange. Upper latus with basal margin slightly concave in larger specimens. Carinolatera as wide as high, and meet without interdigitating below carina. Rostrolatus a little wider than high in side view, umbo at occludent scutal angle supporting umbo of rostrum. Bulk of rostrum covered by rostralatera. Inframedian latus triangular, retains an apical umbo, and separates carinolatera and rostralatera. Peduncle has 7 rows of wide scales, not overlapping.

Males borne in scutal pouches, and have external striations, minute spines, and 4 rudimentary plates around orifice.

Mouthparts: Mandible has 3 teeth throughout ontogeny. Maxillule has a group of 4 setae at upper angle separated by a gap from lower part of cutting edge, which bears up to 7 setae of various lengths.

Cirri: Number of segments in rami of cirri increases through ontogeny, as follows, anterior ramus 1st:

cap. length	I	II	III	IV	V	VI	c.a.
3.3 mm	6, 8	11, 11	13, 11	13, 13	13, 13	13, 13	1/1
5.4 mm	7, 8	12, 13	14, 15	16, 16	17, 17	19, 18	3/4
11.0 mm	8, 11	11, 17	18, 18	21, 22	21, 21	22, 23	4/4

Intermediate segments of anterior ramus of cirrus I slightly wider than those of posterior ramus. Segments of cirri II–VI have medial setae decreasing in abundance distally and posteriorly, and more abundant in older specimens. Setae on posterior interarticular edge likewise more abundant in anterior rami than corresponding posterior rami, and in anterior cirri and older specimens. Intermediate segments of posterior cirri with 4 pairs of setae, those of anterior rami, particularly, unequal in length. Between anterior pairs a single, short seta, except for distal-most pair on segments of anterior rami, which has a group of longer setae. Interarticular posterior-edge setae and seta at upper posterior angle short and spine-like in older specimens. Caudal appendages of 1–4 segments with long setae, which in larger specimens reach base of rami of cirrus VI. Penis absent.

REMARKS: This species was first described from material taken by *Challenger* in Australian and New Zealand seas, the latter from off East Cape. Hoek's largest specimen had a capitulum length of 9 mm. There is no doubt about the specific identity of the present material, which has provided further information about the arthro-dial structures and ontogenetic development. Pilsbry (1907a) described *Scalpellum nipponense* from a Japanese specimen with a capitular length of 15 mm, larger than any of the specimens to hand, and in which the plates stand further apart and a concavity of the upper margin of the carinal latus is developed. However, these are ontogenetic developments that might be expected in larger specimens of *A. intermedium*. Nilsson-Cantell (1921) examined further Japanese material of 5 and 10 mm, and regarded *S. nipponense* as a synonym of *S. intermedium*. Broch (1931) described a 13-mm specimen from Japanese seas, identifying it as *S. nipponense*, and regarded Nilsson-Cantell's specimens as *S. intermedium* in which the maxillule is un-notched and both rami of the posterior cirri have interarticular spines on the posterior edge of the segments, whereas *S. nipponense* has this feature only on the inner rami of posterior cirri. Newman & Ross (1971) provided details of the arthro-dial structures of the holotype of *S. nipponense*, made no point about any difference between the posterior setation of the posterior cirri, but showed that the maxillule is not notched in the holotype and pointed out the hypolasiopod condition of the posterior cirri. In view of the ontogenetic development of the setation of the appendages and the shape of the capitular plates, there are no morphological grounds for distinguishing Japanese and Australasian specimens.

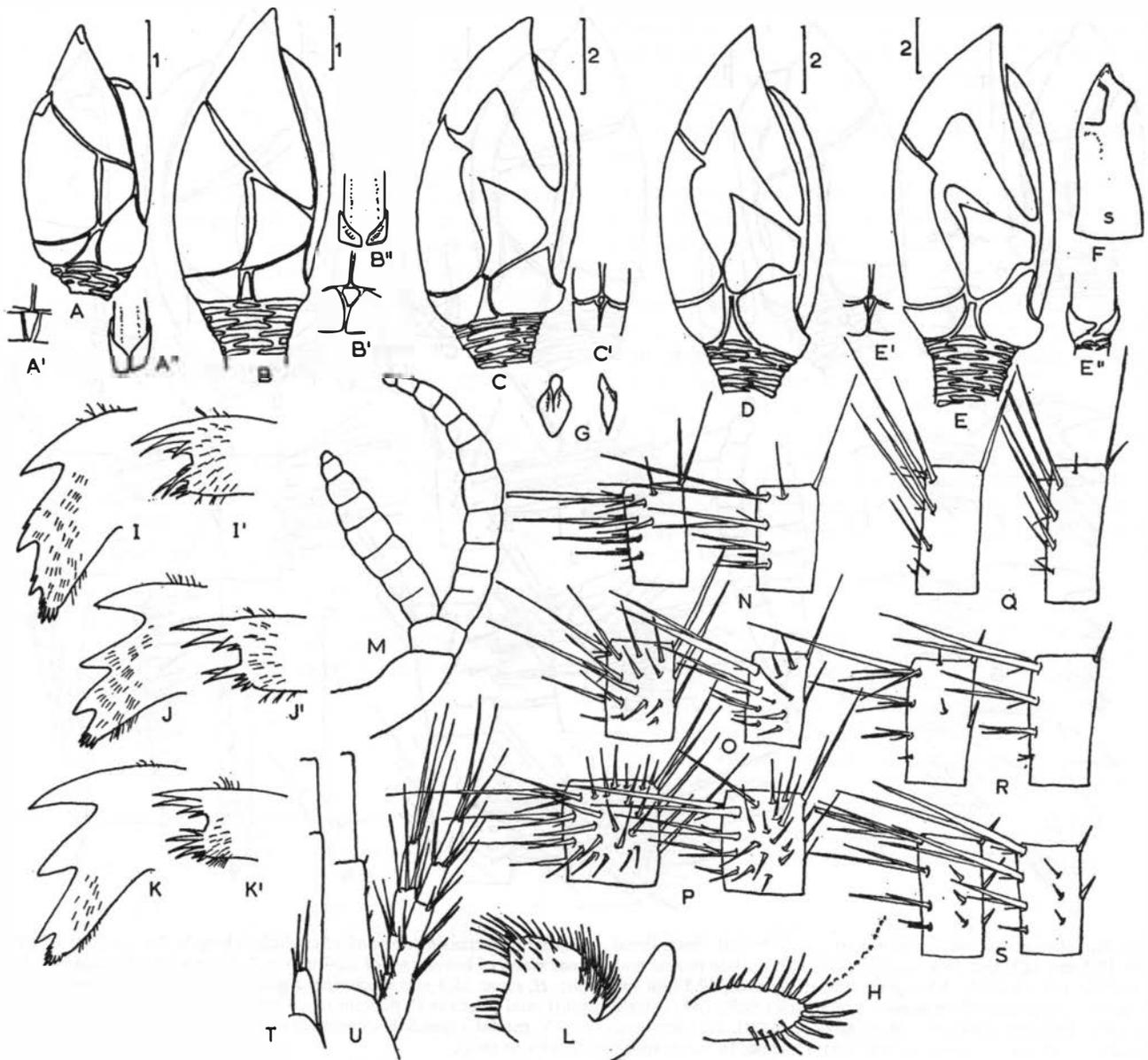


Fig. 37. *Arcoscappellum intermedium* (Hoek): A-E, lateral views, females in order of increasing size and of capitulum lengths 3.3 mm (A), 5.4 mm (B), 8.0 mm (C), 10.2 mm (D), and 11.0 mm (E), with appropriate rostral and carinal views of lower part of capitulum; F, inner view, scutum of E; G, outer (left) and side views of rostrum; H, a few labral teeth and mandibular palp of 11.0-mm specimen; I, I', mandibles and maxillule of 3.3 mm specimen; J, same, 5.4 mm specimen; K, same, 11.0-mm specimen; L, maxilla of 11.0-mm specimen; M, plan of cirrus I, 11.0-mm specimen; N, inner view, intermediate segments of anterior (left) and posterior (right) rami, cirrus II of 3.3-mm specimen; O, same, 5.4-mm specimen; P, same, 11.0 mm specimen; Q, same, cirrus VI of 3.3 mm specimen; R, same, 5.4 mm specimen; S, same, 11.0 mm specimen; T, caudal appendage in relation to the pedicel of cirrus VI, 3.3-mm specimen; U, same, 11.0-mm specimen (scales in mm).

***Arcoscappellum pertosum* n. sp. (Plate 8C; Fig. 38)**

MATERIAL EXAMINED: NZOI: Stns D904 (2 specimens), E421 (4), E433 (11), F95 (1), F143 (3), G688 (2), G700 (3), J35 (2). PMBS: 6 specimens, Mu 67-43, 625-650 m. Nat. Mus.: 37 specimens, Stn B.S. 300, 41°30'S 174° 54'E, 644-662m.

DISTRIBUTION: New Zealand, 380-1116 m (Fig. 32).

DESCRIPTION: *Externals and shell plates:* Female capitular plates smooth, nearly approximate, and covered by a sparsely hirsute integument. Carina with flat roof with slight lateral ridges. Tergum slightly notched on carinal margin for reception of apex of

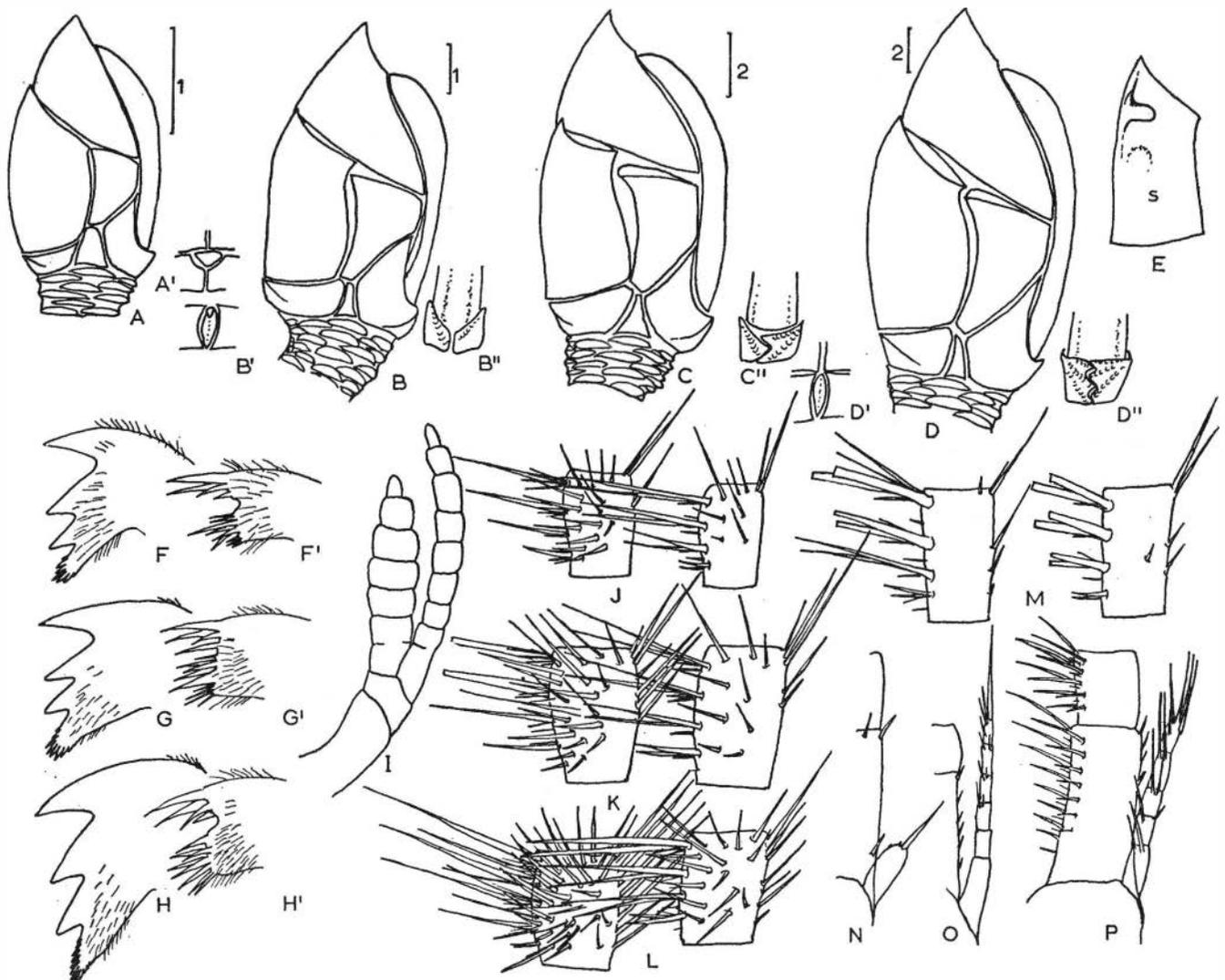


Fig. 38. *Arcoscaldpellum pertosum* n.sp.: A–D, lateral views, females in order of increasing size and of capitulum lengths 2.4 mm (A), 6.5 mm (B), 10.5 mm (C), and 16.3 mm (D), with appropriate rostral and carinal views of lower part of capitulum; E, inner view of scutum; F, F', mandible and maxillule, 6.5-mm specimen; G, same, 10.5-mm specimen; H, same, 16.3-mm specimen; I, plan of cirrus I, 6.5-mm specimen; J, inner view, intermediate segments of anterior (left) and posterior (right) rami of cirrus II, 6.5 mm specimen; K, same, 10.5 mm specimen; L, same, 16.3-mm specimen; M, same of cirrus VI, 16.3-mm specimen; N, caudal appendage in relation to the pedicel of cirrus VI, 2.4-mm specimen; O, same, 16.5-mm specimen; P, same, 16.7-mm specimen (scales in mm).

carina. Scutum just overlaps tergum, has a tergo-lateral arm, a sinuous lateral margin; in larger specimens a secondary flange develops on tergal margin, internally a deep pit for males. Upper latus has a curved apex lying below tergo-lateral arm of scuta, and in older specimens develops a secondary flange on tergal border. Carinolatera not much higher than wide, meet below carina simply at first, but with increasing size by a number of interdigitations. Rostrolatera become almost as high as wide, supporting between their umbo umbo of rostrum which, with growth, appears externally as a narrowly oval plate between occludent edges of rostrilatera. Inframedian latus triangular, and extends fully between rostrilatera and carinolatera,

with apex permanently apical and often curved towards rostral side. Peduncle has about 8 rows of wide scales which almost overlap. Males borne in scutal pouches, have external striations, minute spines, and 4 rudimentary plates.

Mouthparts: Mandible has 3 teeth throughout ontogeny. Maxillule has a more-or-less pronounced notch below a group of 4 setae at upper angle.

Cirri: Anterior ramus of cirrus I a little shorter than posterior ramus, and with shorter and wider intermediate segments. Number of segments in rami of

cirri increases with size, as follows, anterior ramus Ist:

cap. length	I	II	III	IV	V	VI	c.a.
2.4 mm	5, 6	7, 7	9, 9	9, 9	9, 9	9, 9	1/1
6.5 mm	7, 9	11, 11	14, 14	15, 15	14, 14	malformed	
10.5 mm	7, 9	11, 11	13, 14	14, 14	15, 15	15, 14	6/5
16.3 mm	9, 11	17, 19	22, 22	25, 25	24, 26	26, 28	6/6

Some intermediate segments of cirri II-VI bear inter-articular setae on posterior edge, particularly in more anterior cirri and in older specimens. Intermediate segments of posterior cirri bear 4 pairs of setae on anterior edge, with small setae between bases of major pairs, except that those between distal setae of segments of anterior ramus of considerable length. Caudal appendages of 6 segments in larger specimens, with distal setae reaching to base of rami of cirrus VI.

HOLOTYPE: NZOI 203, the largest of the specimens from station G700 (Plate 8C).

REMARKS: This species can be distinguished from *A. affricatum*, to which it bears some external similarity, by the way in which the plate increments occur between the terga and the upper latera and scuta, in contrast to the meagre apical flange of the upper latus in *A. affricatum*. *A. pertosum* is very closely related to *A. aurivilli* (Pilsbry) from the North Atlantic, but differs in that the scuta and upper latus are relatively longer and the rostral latus is relatively lower, and in the less pronounced asymmetry of the anterior setae on the segments of the posterior cirri.

***Arcoscalpellum novaezelandiae* (Hoek) (Plate 8D; Fig. 39)**

Scalpellum novae-zelandiae Hoek, 1883: 124; Gruvel 1902: 54; Annandale 1908: pl. 5, fig. 7; Annandale 1913: 231.

MATERIAL EXAMINED: NZOI: Stns E399 (3 specimens), E406 (3), E871 (1), F878 (27), G305 (5), G651 (12), G652 (6), G666 (2), G700 (7), G702 (1), G703 (5), J45 (2).

DISTRIBUTION: Atlantic, 2400–2500 m; Indian Ocean, 900–2800 m; New Zealand, 455–2146 m (Fig. 32).

DESCRIPTION: *Externals and shell plates:* Female capitulum becomes very elongate with growth, with nearly approximate plates covered by a very thin, hairless integument. Carina with flat roof, and narrow parietes in upper part. Tergum with apex of larger specimens recurved towards carina, and a distinct notch on carinal margin for reception of carina. Scutum with apex overlapping lower occludent angle of tergum. Occludent margin of scutum sinuous, convex in upper part and concave in lower part. Apex of upper latus in older specimens lies below tergal lateral angle of scuta, and a subepidermal flange develops towards tergum. Rostrolatus as wide as high. Carinolatus almost 2× as high as wide in larger specimens, with umbo nearly basal and standing slightly out from carina. Inframedian latus narrowly quadrate, initially with an apical umbo, but this becomes displaced from apex at about 3-mm capitulum length to become almost basal in specimens larger than 12 mm.

Rostrum minute and horn-shaped, with umbo apical, elevated between upper occludent angles of rostrilatera. Peduncle shorter than capitulum, with 7 longitudinal rows of wide and not overlapping scales.

Males borne in scutal pouches, and have numerous, minute, external spines but no traces of plates or their rudiments.

Mouthparts: Mandible has 3 teeth. Maxillule has a notch beneath a group of stout setae at upper angle, and about 6 setae on lower part of cutting edge.

Cirri: Intermediate segments of anterior ramus of cirrus I 2× as wide as those of longer posterior ramus. Setae on medial faces of segments decrease in abundance from cirrus II posteriorly, as well as distally, in each ramus. Intermediate segments of posterior cirri bear 4 pairs of setae on anterior edge, sometimes with an extra, minute, basal pair and a single small seta between bases of each of major pairs. Anterior and posterior rami similar. Longest setae at posterior distal angle about ½ length of next segment. Posterior edges of segments of cirri II–VI otherwise devoid of setae. Caudal appendages have up to 6 segments, and may be as long as, but not longer than, pedicel of cirrus VI. Penis absent.

REMARKS: This species was originally described from a specimen collected by *Challenger* in New Zealand waters (37°34'S, 179°22'E, 1300 m), and has subsequently been taken from near the Azores (Gruvel 1902) and in the northern part of the Indian Ocean (Annandale 1913). *A. novaezelandiae* is closely related to *A. flavum* (Hoek), from the south-west Indian Ocean; *A. gracilius* (Pilsbry) and *A. albatrossianum* (Pilsbry), both from the North Atlantic Ocean; and less clearly to other species in the group of *Scalpellum idioplax* of Pilsbry (1907a).

***Arcoscalpellum raccidium* n. sp. (Plate 8E; Fig. 40)**

MATERIAL EXAMINED: NZOI: Stns F872 (2 specimens), F883 (1), F900 (2). Nat. Mus.: 5 specimens, *Alert*, 37°10'S, 176°24'E, 736 m.

DISTRIBUTION: North-east New Zealand, 725–855 m (Fig. 32).

DESCRIPTION: *Externals and shell plates:* Female capitulum ovoid with nearly approximate plates covered by a thin, hairless integument. Carina with roof grooved because of lateral ridges, and wide parietes developed in upper part. Tergum with apex recurved towards carina. Scutum with apex overlapping tergum, its occludent margin continuously convexly arched, and tergolateral angle produced into a point. In older specimens, shell added secondarily on tergal margin of scutum. Apex of upper latus lies just below scutal point, and in older specimens subepidermal flanges added to upper latus on tergal and scutal margins. Rostrolatus as wide as high. Carinolatus less than 2× as high as wide, and retains its proportions in ontogeny. Inframedian latus initially triangular with an apical umbo

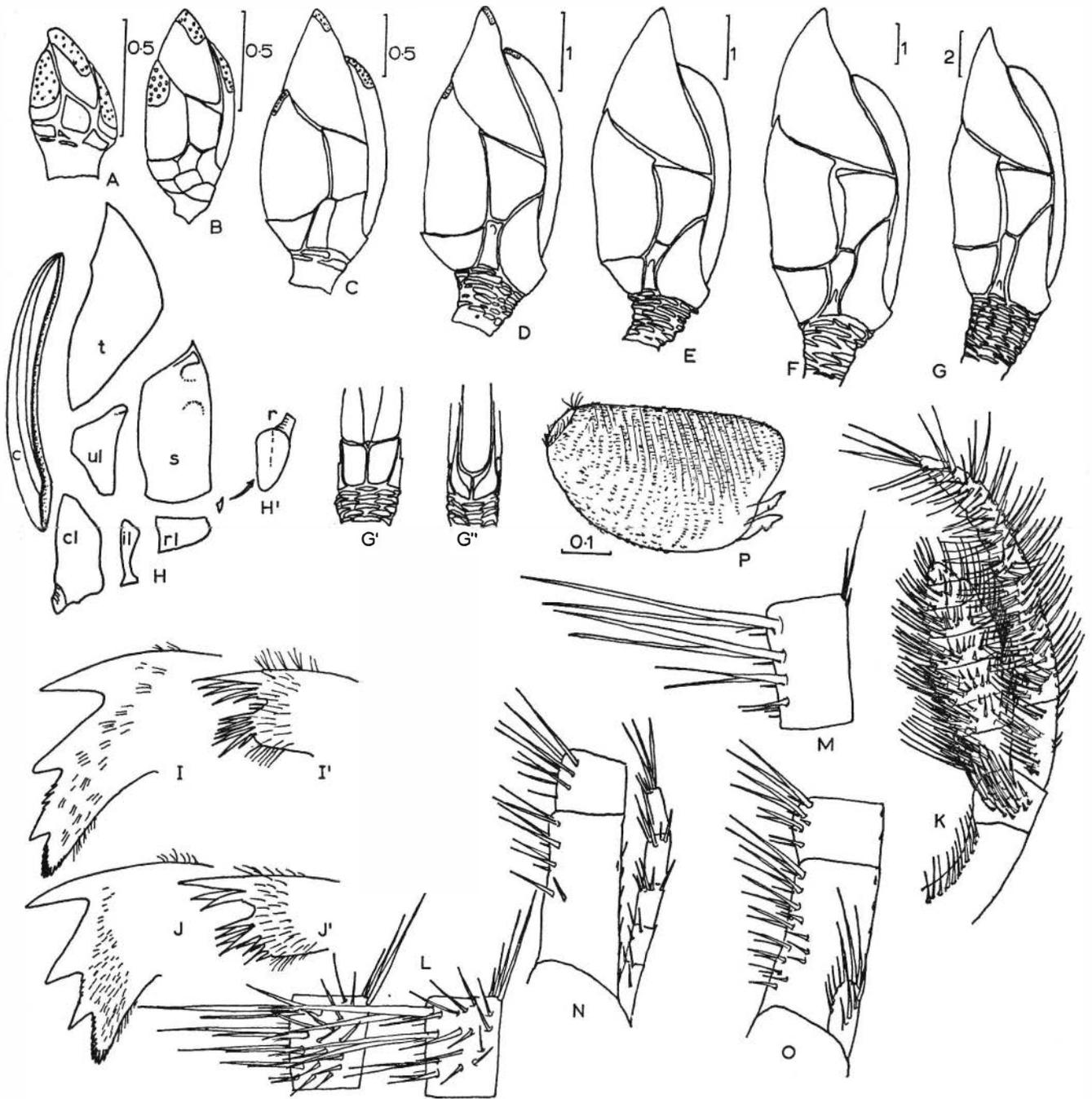


Fig. 39. *Arcoscalpellum novaehollandiae* (Hoek): A–G, lateral views, females in order of increasing size and of capitulum lengths 0.5 mm (A), 0.9 mm (B), 1.9 mm (C), 3.4 mm (D), 4.5 mm (E), 8.8 mm (F), and 12.3 mm (G), with appropriate rostral and carinal views in G', G''; H, inner views, capitular plates, with H' enlarged rostrum—keys as in Fig. 1; I, I', mandible and maxillule, 8.8-mm specimen; J, J', same, 12.5-mm specimen; K, cirrus I, 12.3-mm specimen; L, intermediate segments of anterior (left) and posterior (right) rami of cirrus II, 8.8-mm specimen; M, intermediate segment, anterior ramus of cirrus VI, 12.3-mm specimen; N, caudal appendage and pedicel of cirrus VI, 8.8-mm specimen; O, same, 12.3-mm specimen; P, dwarf male from specimen G (scale in mm).

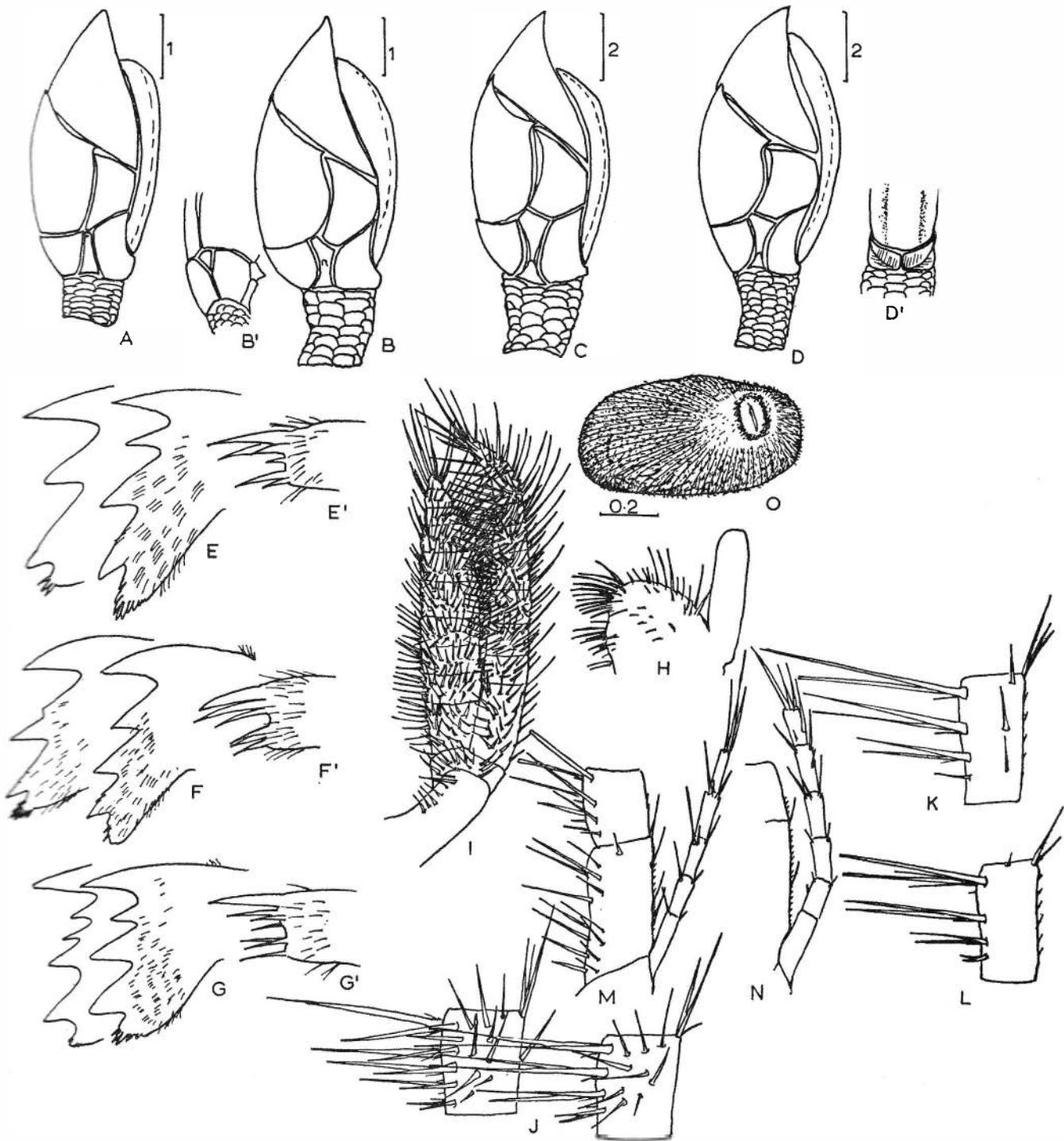


Fig. 40. *Arcoscalpellum raccidium* n.sp.: *A-D*, lateral views, females in order of increasing size and of capitulum lengths 4.3 mm (*A*), 5.3 mm (*B*), 8.7 mm (*C*), and 9.0 mm (*D*), with appropriate rostral and carinal views of lower part of capitulum; *E, E'*, both mandibles and a maxillule, 5.3-mm specimen; *F, F'*, same, 8.7-mm specimen; *G, G'*, same, 9.0-mm specimen; *H*, maxilla of 8.7-mm specimen; *I*, cirrus I of 9.0-mm specimen; *J*, inner view, intermediate segments of anterior (left) and posterior (right) rami of cirrus II, 8.7-mm specimen; *K*, outer view intermediate segment of posterior ramus, cirrus IV of 5.3-mm specimen; *L*, same, anterior ramus of cirrus VI, 8.7-mm specimen; *M*, caudal appendage and pedicel of cirrus VI, 5.3-mm specimen; *O*, dwarf male from specimen *D* (scales in mm).

but at 4–5 mm capitular length shell added apically, with a subsequent basal shift of umbo. Inframedian latus with upper part wide, a longer upper lateral margin than scutal margin, and whole plate in shape of hour-glass, waisted at umbo. Umbos of carinolatera do not project much beyond base of carina, and 2 plates occlude simply. Rostrum visible externally as a small, triangular plate between apices of rostrilatera. Peduncle has closely set and overlapping scales.

Males borne in scutal pouches, and have numerous, minute, external spines, but no traces of plates or their rudiments.

Mouthparts: Mandible with 3–5 teeth, upper 1 and lower 2 largest. If more than 3 teeth, smaller extra teeth placed below upper tooth. Maxillule with group of stout setae at upper angle, separated by a gap from a group of 3 setae at lower angle.

Cirri: Basal segments of rami of cirri indistinctly demarcated. Counting the basal section as one, segment numbers in rami of cirri are as follows, anterior ramus 1st:

cap. length	I	II	III	IV	V	VI
5.3 mm	7, 9	14, 14	14, 16	17, 18	18, 18	18, 19
8.7 mm	8, 10	13, 14	18, 18	18, 18	19, 19	21, 22
9.0 mm	8, 11	13, 16	19, 18	22, 21	20, 21	21, 22

Middle segments of anterior ramus of cirrus I approx. 1.5× as wide as those of posterior ramus. Setae on medial faces of segments decrease in abundance from cirrus II posteriorly as well as distally in each ramus. Intermediate segments of anterior ramus of cirrus II bear single seta on posterior interarticular edge. Intermediate segments of posterior cirri bear 4 pairs of setae on anterior edge, with a single, small seta between bases of each pair. Central setae of distal group of each segment of anterior ramus much longer than in posterior

ramus. Longest setae of posterior distal group less than ½ length of segment. Posterior edge of segments, particularly in basal half of rami, and of pedicels, bear minute, upwardly-directed spines. Caudal appendages of 5 or 6 segments, and exceed length of pedicel of cirrus VI. Penis absent.

HOLOTYPE: NZOI 204, the larger of the specimens from station F872 (Plate 8E, right).

REMARKS: This species is readily distinguished from *A. novaezelandiae*, with which it might be confused, by the squatter and more rounded capitulum, and the overlapping peduncular scales. Other differences include the evenly rounded scutal occludent margin, the lateral ridges to the roof of the carina, the more pronounced hourglass shape of the inframedian latus, and such internal differences as the greater dentition of the mandible but lesser pectination of the maxillule, the proportionately narrower anterior ramus of the first cirrus, and the serrations on the posterior edges of the basal segments of the posterior rami.

It externally resembles *A. carinatum* (Hoek), collected from off Tristan da Cunha, and *A. idioplax* (Pilsbry), taken from the Caribbean Sea, neither of which has had the appendages described. The present species differs from both these Atlantic species in details of capitular and peduncular plate shape and arrangement, which are not encompassed by the ontogenetic changes shown by the present limited material. It has therefore seemed prudent to give the specimens in hand a different name.

The most interesting feature of the species is the tendency to increase the dentition of the mandible, recalling the calanticoid condition, and being somewhat different from the stable 3-toothed mandible of the other arcoscelpellid species considered here.

Suborder VERRUCOMORPHA Pilsbry, 1916

Thoracican cirripedes which lack a peduncle. Shells asymmetrical, wall composed of carina, rostrum, tergum, and scutum, and in fossil forms, a carinolatus and a rostrolatus. Other tergum and scutum together form a movable lid to shell. Base may be membranous or calcareous.

Family VERRUCIDAE Darwin, 1854

Characters as for the suborder.

Genus *Verruca* Schumacher, 1817

Verrucidae with a shell wall of rostrum, carina, and fixed scutum and tergum.

REMARKS: Five subgenera have been recognised. Three have the lid in a plane nearly parallel to the base: *Verruca*, which has a very narrow radiolar area between the parietes of the fixed tergum and scutum, the apex of the rostrum marginal, and the fixed scutum without an adductor ridge;

Metaverruca, in which the fixed scutum has an adductor ridge forming a tongue-shaped myophore, and the apex of the rostrum is marginal;

Rostratoverruca, which is like *Verruca* except that the apex of the rostrum is removed from the edge of the plate.

The other two subgenera have the lid in a plane nearly vertical to the base:

Altiverruca, in which the fixed scutum is without an adductor ridge;

Cameraverruca, in which the fixed scutum has an

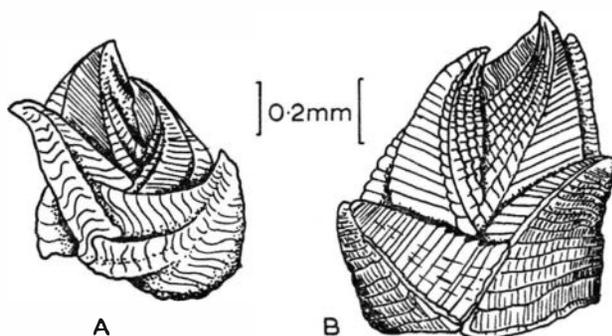


Fig. 41. Verrucids recorded from near New Zealand: A, *Verruca gibbosa* Hoek, after Hoek (1883); B, *Verruca navicula* Hoek, after Hoek (1913).

adductor ridge forming a myophore, and the fixed tergum and rostrum have internal apical recesses.

The only representatives of this genus examined in the present study are the comparatively numerous specimens of *Verruca (Metaverruca) halothea* described below. This species has not previously been reported from the South Pacific. Other species taken from near New Zealand are *V. (Altiverruca) navicula* Hoek, recorded by Nilsson-Cantell (1927), and *V. (Altiverruca) gibbosa* Hoek, recorded as *V. sulcata* by Hoek (1883); these are illustrated in Figure 41. They can be distinguished from *V. halothea* by their more ornate appearance. In *V. navicula*, the movable plates are large and supplied with a relatively large number of articular ridges; in *V. gibbosa*, the apex of the rostrum stands away from the terga to give a more splayed appearance to the shell. *V. navicula* was taken at 37°S, 163°30'E at 2745 m (Nilsson-Cantell 1927), and *V. gibbosa* was taken near the Kermadecs at either 960 m or 1160 m. Their absence from the NZOI collections might be taken to indicate that they are more characteristic of waters deeper than those on the New Zealand shelf in which dredging has been done.

***Verruca (Metaverruca) halothea* Pilsbry**
(Plate 8F; Fig. 42)

Verruca halothea Pilsbry, 1907b: 188; Pilsbry 1916: 46.
Verruca capsula Hoek, 1913: 130.

MATERIAL EXAMINED: NZOI: Stns D159 (1 specimen), D160 (2 shells), D169 (1 shell), E906 (1 specimen), F120 (1), F122 (1), F146 (3).

DISTRIBUTION: Hawaii, Malaysia, New Zealand, 252–1680 m. In New Zealand, throughout, 252–896 m (Fig. 43).

DESCRIPTION: *Externals and shell:* Shells very neat and compact, sides steep, and lid in a plane more

parallel to base than to vertical axis. Plates with external concentric growth ridges. Rostrum and carina abut by radiolar teeth forming a zigzag suture, upper margins of upper teeth form a straight line for articulation of movable tergum and scutum. Fixed scutum has a triangular radiolar area on rostral side, and internally a depending myophore. Fixed tergum has triangular radiolar areas on both scutal and carinal sides. Basal margins of all wall plates inflected.

Opercular plates: Orifice semicircular in outline. Movable scutum and tergum together form a straight rostrocarinal hinge, and each has 3 interarticular ridges forming a zigzag suture as a continuation of that between rostrum and carina. Movable scutum smaller than tergum, former triangular with an acute apex, latter quadrate with an obtuse apex. Inner surfaces of both movable plates inornate. Of 10 specimens, 6 had right tergum and scutum movable, oriented so carina anterior, and 4 were “left-handed”.

Mouthparts: Labrum shallowly concave with a row of small teeth. Mandibles have 3 teeth and a pectinate lower cutting edge and angle, spines here arranged in 2 groups, one at lower angle and other between it and 3rd tooth. Maxillule has very stout and long seta at upper angle, 2 smaller setae immediately below it, then a short plateau with some very small setae, and rest of cutting edge rounded and protuberant, with setae of various lengths.

Cirri: Cirrus I has subequal rami. Cirrus II has anterior ramus about $\frac{1}{2}$ as long as posterior ramus, latter only slightly shorter than rami of remainder of cirri. Each intermediate segment of anterior ramus of cirrus III has 4 pairs of setae on anterior edge and a few setae medially and distally. Posterior ramus of cirrus III has 3 pairs of anterior setae and fewer medial setae. Segments of cirri IV–VI tend to fuse proximally, but medial ones have 3 pairs of setae on anterior edge, a row of spines at distal lateral-to-posterior edge, and a few longer setae at posterior angle. Caudal appendages almost as long as basal segment of pedicel of cirrus VI, and of 7 or 8 segments, each with many setae. Penis short, about $\frac{1}{2}$ length of pedicel of cirrus VI.

REMARKS: This species is notable for its relatively large size for the genus, the “absence of salient umbos and the generally inornate appearance” (Pilsbry 1916), and the “scutal margin of the rostrum and the tergal margin of the carina forming together a straight line” (Hoek 1913). These New Zealand records are a little shallower than previous records, and confirm a wide Pacific distribution. Both Hoek (1913) and Pilsbry (1916) drew attention to the similarity of *V. halothea* to *V. magna* Gruvel from the North Atlantic. It also seems to be closely related to *V. recta* Aurivillius (= *V. linearis* Gruvel) and *V. coraliophila* Pilsbry, also from the Atlantic Ocean (see Southward & Southward 1958). Future comparative studies may prove that these are one cosmopolitan species, as Nilsson-Cantell (1928a) concluded for *Verruca gibbosa*.

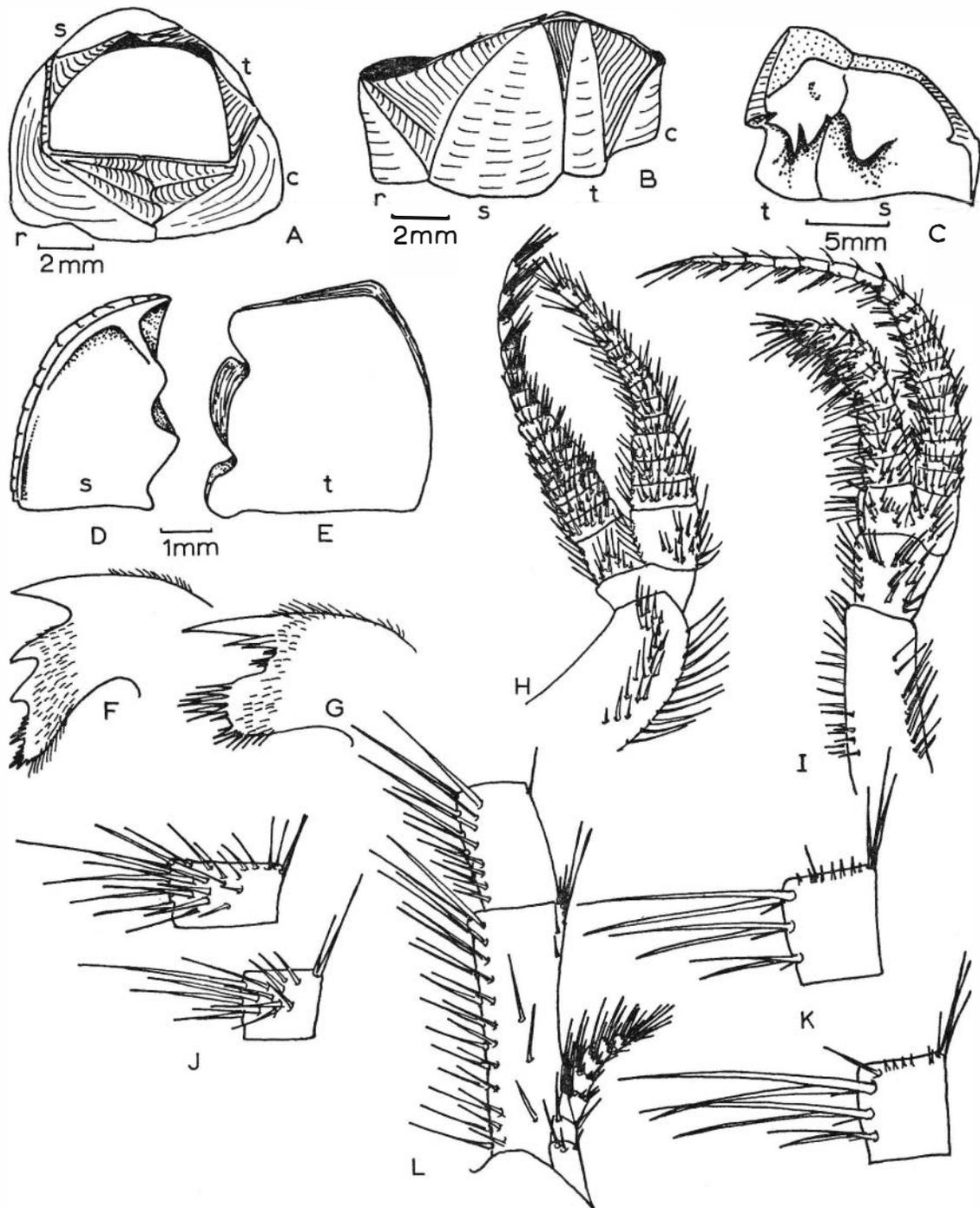
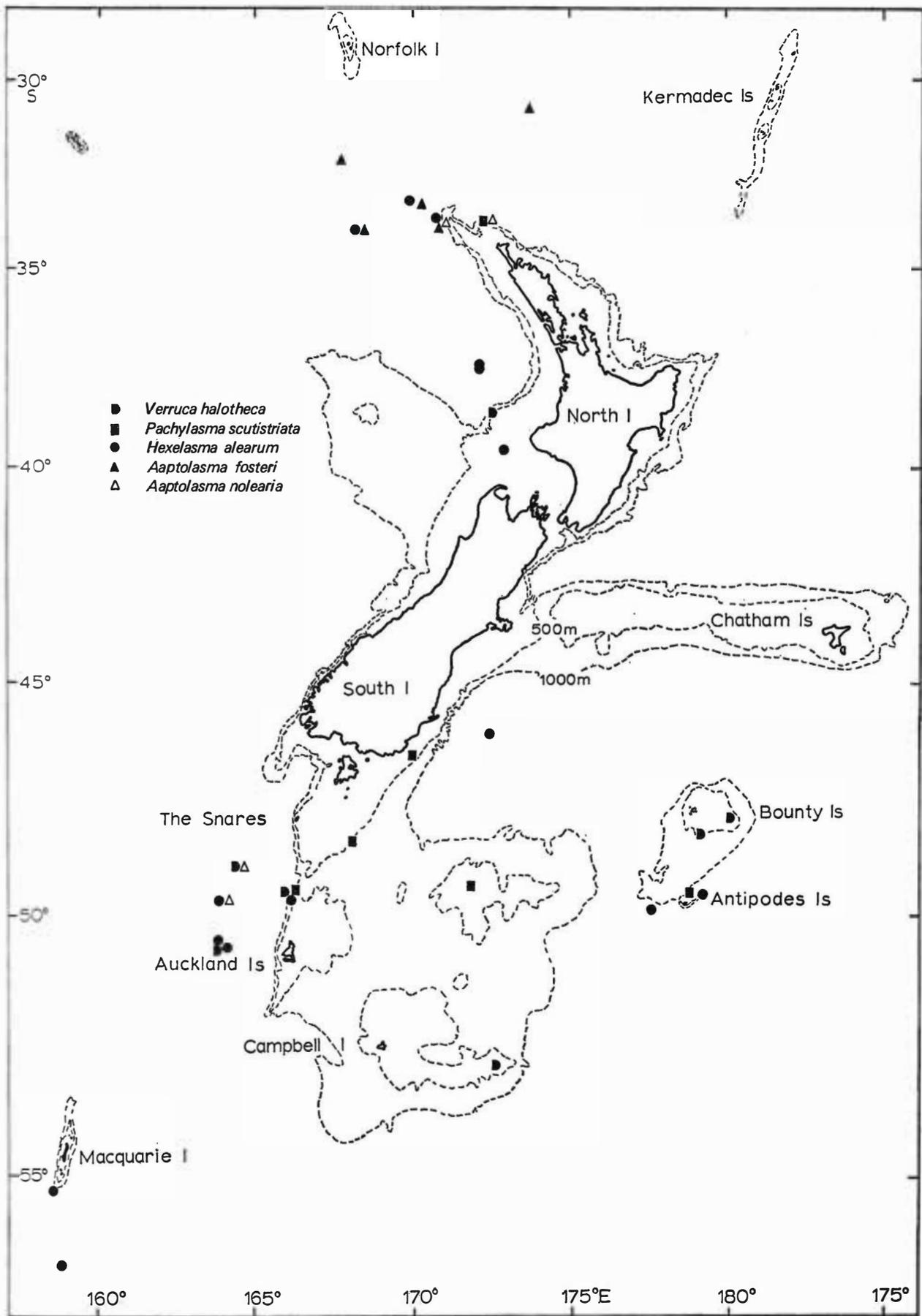


Fig. 42. *Verruca halotheca* Pilsbry: *A*, apical view, empty 'right-handed' shell; *B*, lateral view, 'left-handed' shell; *C*, inner view, fixed tergum and scutum; *D*, *E*, inner views, movable scutum and tergum; *F*, mandible; *G*, maxillule; *H*, cirrus I; *I*, cirrus II; *J*, inner view, intermediate segments of anterior (upper) and posterior (lower) rami of cirrus III; *K*, outer view, intermediate segments of anterior (upper) and posterior (lower) rami of cirrus VI; *L*, caudal appendage and pedicel of cirrus VI.

Fig. 43. Records of species of Verrucidae and Pachylasmidae in the New Zealand region.



Suborder BALANOMORPHA Pilsbry, 1916

Thoracican cirripedes which lack a peduncle, and with shells bilaterally symmetrical on either side of rostro-carinal axis. Primary shell wall made up of a number of parietal plates; including a carina, rostrum, and 1–3 pairs of lateral plates, all separate from one another, variously fused, or totally conrescent. Two genera have accessory plates outside primary shell wall. Shell closed on top by opercular plates, paired terga and scuta, of which members of each pair may be separate, articulated, conrescent, or degenerate. Base of shell may be membranous or calcareous.

Family CHTHAMALIDAE Darwin, 1854

Balanomorpha with a primary shell wall of 8, 6, or 4 plates, separate, variously fused, or totally conrescent. One genus, *Catophragmus*, has accessory lateral plates. Rostrum overlapped on either side by rostrolatera. Orifice enlargement primarily occurs by apical attrition of shell. Parietal plates may interlock by superficial, chevron-like flanges, but these obliterated with external shell erosion. All extant species intertidal. Anterior edge of labrum bullate, crest without median incision. Cirrus III resembles in length cirrus IV more than II, sometimes has antenniform rami. Caudal appendages present in some species. Penis without basidorsal point.

REMARKS: The evolution of each of the balanomorph families has involved reduction in the number of shell plates (Fig. 72). The genus with the most shell plates is *Catophragmus* of the Chthamalidae, in which the primary shell wall of 8 plates is encircled by accessory whorls of plates, very reminiscent of the pollicipid condition amongst the Lepadomorpha. *Octomeris* has only the primary wall of 8 plates, which remain distinct throughout ontogeny. From the octomerid condition the 6-plated condition of *Chthamalus* can be derived, like *Octomeris* except that the carinolatera do not develop. From the chthamalid condition, the genera *Chamaesipho* and *Tetrachthamalus* can be separately derived, the former showing during ontogeny fusion of the rostrolatera with the latera and then complete conrescence, whereas in *Tetrachthamalus* the rostrolatera fuse with the rostrum before complete conrescence.

The only chthamalid genus known with certainty from New Zealand waters is *Chamaesipho*. Recently, Utinomi (1968a) listed *Chthamalus antennatus* as collected by *Galathea* from a South I locality: "Stony Shore, Harrison Cove, Milford Sound, tidal zone. Two specimens (about 10 mm in carino-rostral diameter and

2 mm high) on mytilid mussels, together with *Elminius modestus*". This record is seriously doubted, because any species of *Chthamalus* is foreign to New Zealand shores, and the Fiordland area has been ecologically surveyed by Batham (1965). The specimens are unlikely to be non-conrescent *Chamaesipho columna*, because if they were the size quoted they would almost certainly reveal a solid parietal whorl. More likely, the sample may be a New South Wales one that has been inadvertently mislabelled.

It is more certain that the record of *Chthamalus stellatus* from the Bay of Islands by Borradaile (1916) is a misnomer; it must in fact refer to specimens of *Chamaesipho brunnea*, very common and conspicuous on northern shores, but not named until quite recently (Moore 1944).

The family Chthamalidae has to date contained the deep-sea genus *Chionelasmus*, which has an accessory whorl of plates, and the deep-sea genera *Pachylasma* and *Hexelasma*. Utinomi (1968b) subdivided the Chthamalidae into the deep-sea and intertidal Cato-phragminae for the species with accessory shell plates, the intertidal Chthamalinae, and the deep-sea Pachylasminae. Independently, Newman & Ross (1971) recognised some special features of deep-sea hexelasmids, and proposed a new family, Bathylasmatidae, for *Hexelasma* and some newly named genera, but excluding *Pachylasma*. On reconsideration of some new material and existing descriptions, I feel that the family of deep-sea balanomorphs should be extended to include the deep-sea genera *Chionelasmus* and *Pachylasma*, and accorded the prior family-group name of Utinomi (1968b). By this decision Utinomi's subfamily Cato-phragminae is heterogeneous.

Genus *Chamaesipho* Darwin, 1854

Shell wall initially of 6 plates including carina, rostrum, paired latera, and paired rostrolatera, but early during ontogeny rostrolatera fuse with latera and soon after, all parietal plates fuse. Stout grapple-like setae borne on distal segments of anterior ramus of cirrus II, basal segments of anterior ramus of cirrus III, and sometimes distal segments of posterior ramus of cirrus I. Caudal appendages absent.

REMARKS: Three species have been assigned to this genus, two of which occur in New Zealand waters. *C. columna* (Spengler) and *C. brunnea* Moore occur commonly on New Zealand shores, the latter only in the north (Fig. 46). Oliver (1923) and Cranwell & Moore

(1938) recognised the existence of two chthamalids on New Zealand shores on ecological grounds. The intertidally higher and north-centred species, *C. brunnea*, was described by Moore (1944). There is some doubt about the proper designation of names, but Pope (1965) presents convincing arguments that Spengler's name *columna* should apply to the Australian and New Zealand forms subsequently so designated, at least as long as the Australian and New Zealand forms are held as the same species. Certainly, Darwin's material, now in the British Museum, does not now include any *C. brunnea* (sensu Moore). The third species of *Chamaesipho*, *C. scutelliformis* Darwin, "attached to *Pollicipes mitella*, probably from the seas of China", has received little attention since Darwin's description, despite the intensive studies of Oriental cirripedes.

The types of setae on the anterior cirri are described by Pope (1965) for a number of chthamalid genera. Whereas most cirral setae of barnacles have fine lateral setules, and are then called plumose or pinnate setae, some species have more strongly pinnate types (see Plate 1). *C. columna* and *C. brunnea* have on certain segments of the anterior cirri, and in addition to pinnate setae, much stouter setae which look like stag's antlers ("strongly pectinate" of Moore, and "grapple-like" of Pope) (Plate 1). Very similar setae occur on *Chthamalus intertextus* of high tidal habitats of Pacific shores. In the opinion of Pope (1965), these strongly barbed setae are developed with the need for a more efficient feeding mechanism in the short and infrequent periods of submersion in intertidal habitats. In support of this hypothesis, strongly barbed setae on the anterior cirri also occur in the intertidal Tetraclitidae, but are apparently absent in the deep-water Pachylasmidae chthamalids dealt with later in this paper.

The shell growth of intertidal chthamalids produces a thick shell, to offset external erosion and also, no doubt, to reduce the permeability of the shell and hence water loss. To this end, too, the complete concrescence of the parietal plates in *Chamaesipho* is appropriate. Shell plate increments occur by calcite deposition on the inner surface of the shell, and particularly at the basal edge of the shell adjacent to the substratum. Successive periods of growth are marked by laminations in the shell matrix. The opercular valves likewise increase in thickness as well as in area by shell secretion on their inner surfaces and basal margins. The apical regions and the whole outer surface, progressively from the apex to the basal margin, is eroded away by the effects of sun, salt, and water. This is the prime and probably basic means of orifice enlargement with growth; if the erosive conditions of the intertidal habitat are sufficient, there is no need to employ extra growth gradients in the shell, such as alae or radii, to effect diametric shell growth at the apices of the parietal plates. In *Chamaesipho* the shell is strengthened by plate concrescence. In tetraclitids and balanids, adjacent parietal plates develop interlocking sutural surfaces to improve shell rigidity.

***Chamaesipho columna* (Spengler) (Plate 9A, B; Fig. 44)**

Chamaesipho columna. Darwin 1854: 407–72 (see for earlier citations); Weltner 1899: 445; Broch 1922: 308–9; Moore 1944: 316–20; Pope 1965: 67–70; Foster 1967: 84–5.

MATERIAL EXAMINED: BAF: shore collecting throughout New Zealand. NZOI: Stns E767, E768, E809, F930 (in all cases on shells of *Epopella plicata*). There are numerous specimens in the Auckland, National, Canterbury, and Otago Museums.

DISTRIBUTION: Australia and New Zealand, intertidally. In New Zealand, one record from Kermadec Is (Linzey 1942a), not in Chatham Is or the southern islands (Fig. 46).

DESCRIPTION: Tergum elongate with crests for carinal depressor muscles separated by deep pits. Scutum with sinuous tergal margin of which central projection rounded, distinct adductor ridge, and a shallow pit for lateral depressor muscle overhung by tergal margin. Body navy blue. Mandible has 4 teeth, and a short, pectinated lower edge with a 5th tooth in centre and a conspicuous spine at lower angle. Grapple-like setae have 1 or 2, occasionally 3, pairs of side hooks, and situated on distal segments of anterior ramus of cirrus II and basal segments of anterior ramus of cirrus III. Posterior rami of cirrus III sometimes antenniform. Segments of posterior rami have a few short setae between 4 or 5 pairs of major setae on anterior edge.

REMARKS: see after *Chamaesipho brunnea*.

***Chamaesipho brunnea* Moore (Plate 9C, D; Fig. 45)**

Chthamalus stellatus Borradaile 1916: 135.

Chamaesipho brunnea Moore, 1944: 320–5; Foster 1967: 85.

MATERIAL EXAMINED: BAF: shore collection from northern part of New Zealand. NZOI: Stns D881 (34 specimens), D892 (11), E115 (1), E844 (2), F927 (2). There are specimens in the Auckland, National, Canterbury, and Otago Museums.

DISTRIBUTION: New Zealand; North I, including the Three Kings Is, Chatham Is, and South I south to Banks Peninsula and Cape Foulwind (Fig. 46).

DESCRIPTION: Tergum elongate with crests for carinal depressor muscles separated by deep pits. Scutum has a sinuous tergal margin, central projection truncate, without a distinct adductor ridge but with a shallow pit for lateral depressor muscles not overhung by tergal margin. Body brown. Mandible has 3 teeth and a pectinated lower edge, lower few spines longer than others. Grapple-like setae have 3 or more pairs of side hooks (Plate 1E), situated on distal segments of posterior ramus of cirrus I, distal segments of anterior ramus of cirrus II, and basal segments of anterior ramus and upper pedicel segment of cirrus III. Antenniform rami absent. Segments of posterior cirri have tufts of short setae between 4 pairs of major setae on anterior edge.

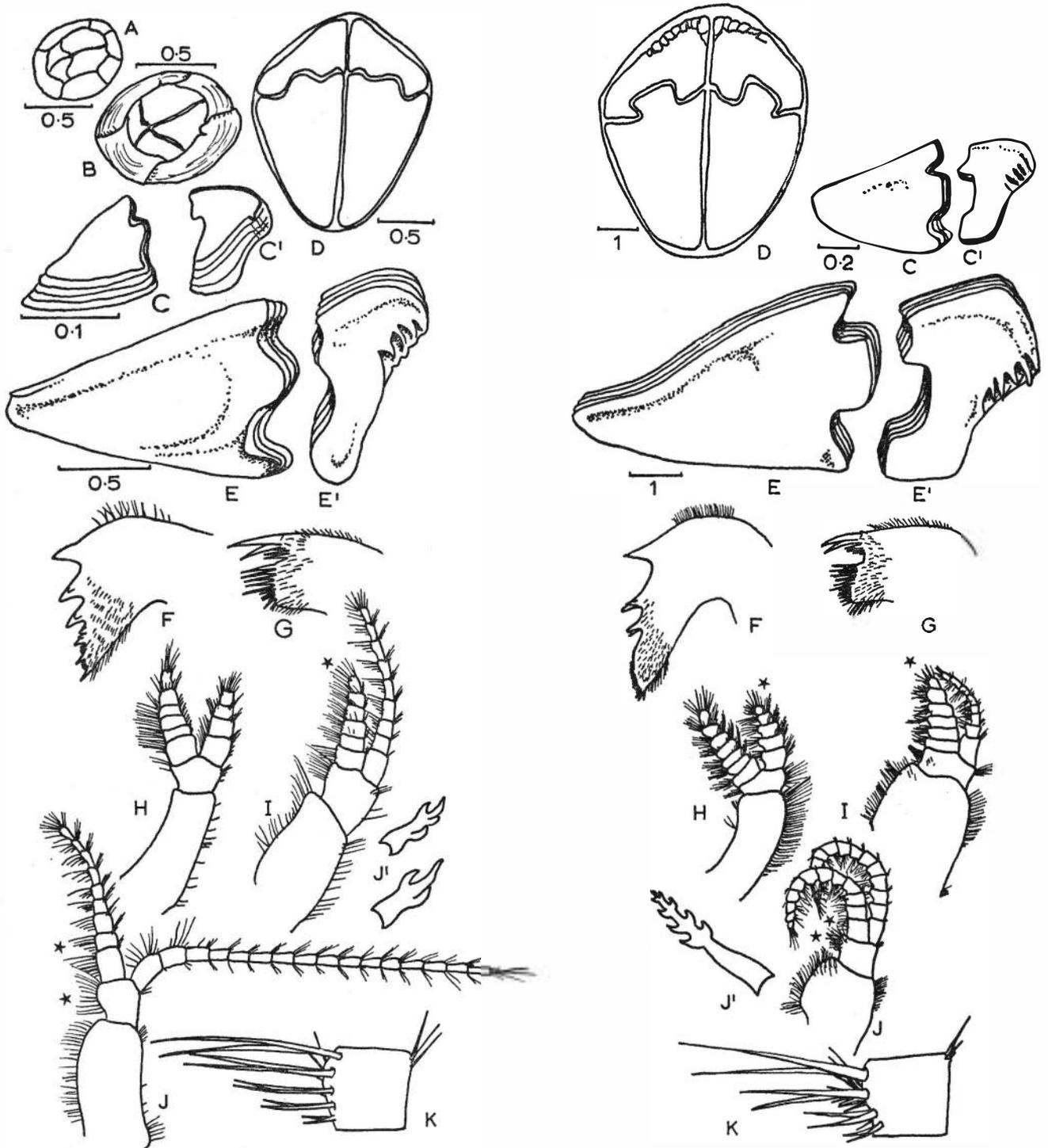


Fig. 44. (left). *Chamaesipho columna* (Spengler), and Fig. 45 (right). *Chamaesipho brunnea* Moore; A, B, juvenile *C. columna*; C, C', scutum and tergum, specimens of 0.9-mm *C. columna* and 2.4-mm *C. brunnea*; D, plan of opercular valves, specimens of 4-mm *C. columna* and 19-mm *C. brunnea*; E, E', inner views, scuta and terga of specimens in D; F, mandible; G, maxillule; H, cirrus I; I, cirrus II; J, cirrus III with the grapple-spines from segments marked * shown in J'; K, intermediate segments of cirrus VI (scales in mm; measurements are rostrocarinal diameters).

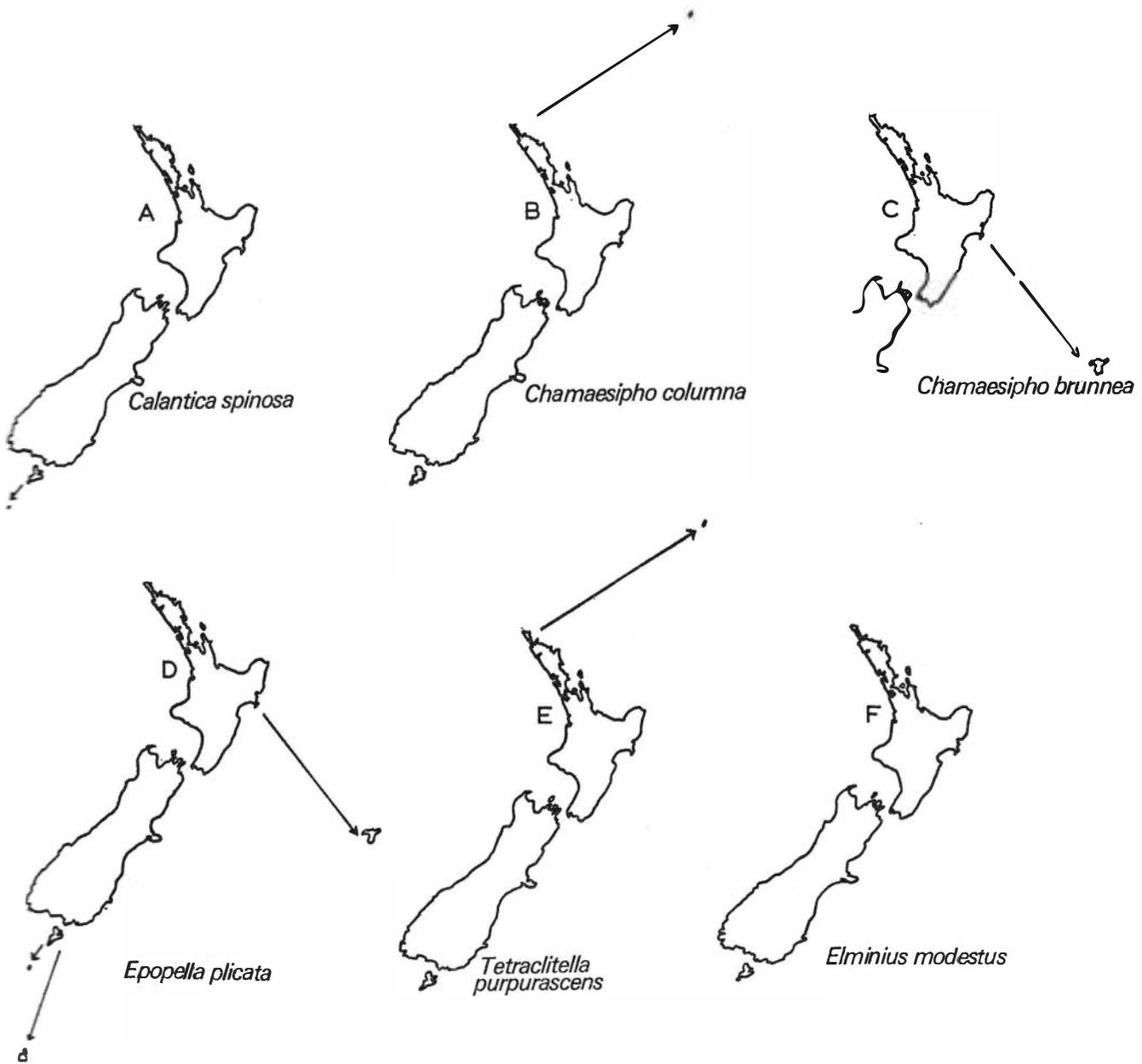


FIG. 46. Distribution of intertidal barnacle species in the New Zealand region. The maps indicate the shoreline where each species may be expected to be found, given appropriate local conditions. The Kermadec Is are indicated to the north-east, the Chatham Is to the west, and The Snares and Auckland Is to the south.

REMARKS: Most accounts of the ecology of New Zealand shores will contain some reference to one or both of the species of *Chamaesipho*. Any shore that experiences some measure of wave action and provides a stable substratum will have many *C. columna* on sun-exposed rock surfaces, and in crevices. Under some conditions, the populations will be so dense that large areas of the rock are covered by a honey-comb formation of this barnacle alone. In the north-east of New Zealand, at high tidal levels, *C. brunnea* can likewise form ex-

tensive "mats", which reach their greatest development on shores exposed to the full fetch of the ocean. The mats may reach up to 4 m above the level of the highest spring tides, but generally not further down the shore than about mean high tide level, where they abut on to or slightly intergrade with *C. columna*. With a decrease in the degree of wave exposure, the vertical extent of *C. brunnea* is markedly reduced. Near the southern limit of the distribution of *C. brunnea*, the vertical shore range is also restricted, and on shores with small tidal

ranges, e.g., Oteranga Bay and Chatham Is, *C. columna* is absent, and *C. brunnea* extends the short distance to the upper limit of the large kelps. Space utilisation on shores by these barnacles, and also the other common barnacle of New Zealand shores, *Epopella plicata*, is governed by interspecific competition and predation by thaid gastropods (Luckens 1970).

Intertidal barnacles can be difficult to identify in the field, because of the erosion of the shell plates. With the two species of *Chamaesipho*, erosion of external surfaces produces specimens of the same species that look very different. On the other hand, uneroded juvenile specimens of both species look alike. The best of the taxonomic characters for field use is: (i) the shape of tergal-scutal articulation. Other, less reliable, characters are: (ii) the orifice shape in *C. columna* has the greatest width towards the rostral side of the tergal-scutal articulation, whereas in *C. brunnea* the greatest width is at the tergal-scutal articulation; (iii) with erosion of the apex of the tergum, the crests for the lateral depressor muscles become evident from above, and as *C. brunnea* is longer-lived, the upstanding crests are more obvious in this species; (iv) uneroded plates of both species are covered with a brownish integument, but with erosion this may be evident only at the edges of the opercular valves and at the base of the shell, as a plain covering in *C. columna*, and as protruding laminations overlying zones of shell growth in *C. brunnea*; (v) crowded specimens of *C. brunnea* abut at the bases of their shells, and the orifice diameter remains less than the basal diameter, but in *C. columna* crowding leads to a honeycomb appearance, the specimens abut throughout the lengths of the shell plates, the orifice diameter equals the basal diameter, and the shell may be much longer than it is wide. *C. columna* may reach a height of 16 mm and a basal diameter of 9 mm; *C. brunnea* may attain a shell height of 8 mm and a diameter of 24 mm.

Family PACHYLASMIDAE Utinomi, n. stat.

Pachylasminae Utinomi, 1968b: 37.

Bathylasmatidae Newman & Ross, 1971: 138.

Shell wall of 8, 6, or 4 plates, separate or usually with just rostrilatera fused with rostrum. One genus, *Chionelasmus*, has free rostrilatera and accessory lateral plates. Diametric growth of shell effected by alar growth of carina, carinolatera, and latera, and of rostrum when distinct. Radii absent. Sutural edges not interlocked. Labrum more-or-less bullate, its crest without median incision. Cirrus III intermediate in length between II and IV, sometimes with antenniform rami. Caudal appendages present in some species. Penis without a basidorsal point. All extant species live in the deep sea.

REMARKS: The similarity of *Pachylasma* and *Hexelasma* was noted by Pilsbry (1916, p. 327): "with the progress of deep water exploration. . . the division into [these] two genera will become increasingly difficult". Because of the generally unmodified nature of the appendages and the presence of caudal appendages in some species of *Pachylasma*, Pilsbry (1916) placed the two genera into the Chthamalidae. Utinomi (1968b) recognised the identity of the deep-sea hexelasmids as a new subfamily of the Chthamalidae but, strangely, included *Bathybalanus* Hoek into the subfamily. Newman & Ross (1971) also recognised a natural group of deep-sea hexelasmids which "although presently included in the Chthamalidae, are in many respects more similar to certain solid walled balanids". They properly assigned *Bathybalanus* to the Balanidae, designated a new family, the Bathylasmatidae, to accommodate *Hexelasma* and some new forms from deep-sea stations, but maintained *Pachylasma* in the Chthamalidae. The relationship between *Pachylasma* and *Hexelasma* is obvious; they are both weakly constructed, deep-sea forms with wide parietal alae and no radial interlocking of the plates. Their shells differ in growth and construction from the intertidal chthamalid genera. Furthermore, the deep-sea genus *Chionelasmus* apparently also has primary parietes with wide alae which do not interlock (Pilsbry 1911, Nilsson-Cantell 1928b). *Chionelasmus*, too, should be grouped with *Pachylasma* and *Hexelasma*. The three genera illustrate a trend from an 8-plated barnacle with accessory plates, of which *Chionelasmus* is a derivative, to a 6-plated shell, with evidence of a compound rostral plate (*Pachylasma*), to the 6-plated *Hexelasma* (see Fig. 72). The 4-plated *Tetrachaelasma southwardi*, described by Newman & Ross (1971), is also obviously of this deep-sea group and completes the shellplate reduction tendency, as independently demonstrated in the intertidal Chthamalidae and in the Balanidae.

The family-group name of Utinomi (1968b) has priority over that of Newman & Ross (1971). In any case, there are reasons for suspecting that the genus *Bathylasma* is not distinct from *Hexelasma*, as discussed below under *Hexelasma*.

Genus *Pachylasma* Darwin, 1854

Shell wall of 6 solid plates including a carina, a rostral plate formed by fusion of rostrum and rostrilatera, and paired latera and carinolatera. External alar growth lines parallel inferior alar margin, no welting along superior alar margin. Terga and scuta with prominent articular ridges. Caudal appendages present. Segments of posterior cirri with graded series of 3 or more pairs of anterior setae.

Pachylasma scutistriata Broch (Plate 9E, F; Fig. 47)

Pachylasma scutistriata Broch, 1922: 301; Nilsson-Cantell 1927: 781; Utinomi 1968b: 26.

MATERIAL EXAMINED: NZOI: Stns D160 (2 specimens), D210 (2), E407 (1), F94 (3), F921 (1), A745 (shell plate).

DISTRIBUTION: Indian Ocean, Malaysia, Tasmania, China Sea, and New Zealand, 130–2060 m. In New Zealand, 309–722 m (Fig. 43).

DESCRIPTION: *Shell*: Plates very pale pink with faint external growth lines without hairs. Algae with regularly placed external growth lines paralleling inferior alar margin, continuing on to inner surfaces as growth ridges of sheath. Apicobasal ridge curved internally, on carinal side faint replications of external alar growth ridges of adjacent plate. Internal surface of parietal plates below sheath smooth in specimens up to 7.5-mm rostrocarinal diameter, but in specimens of 12+-mm diameter

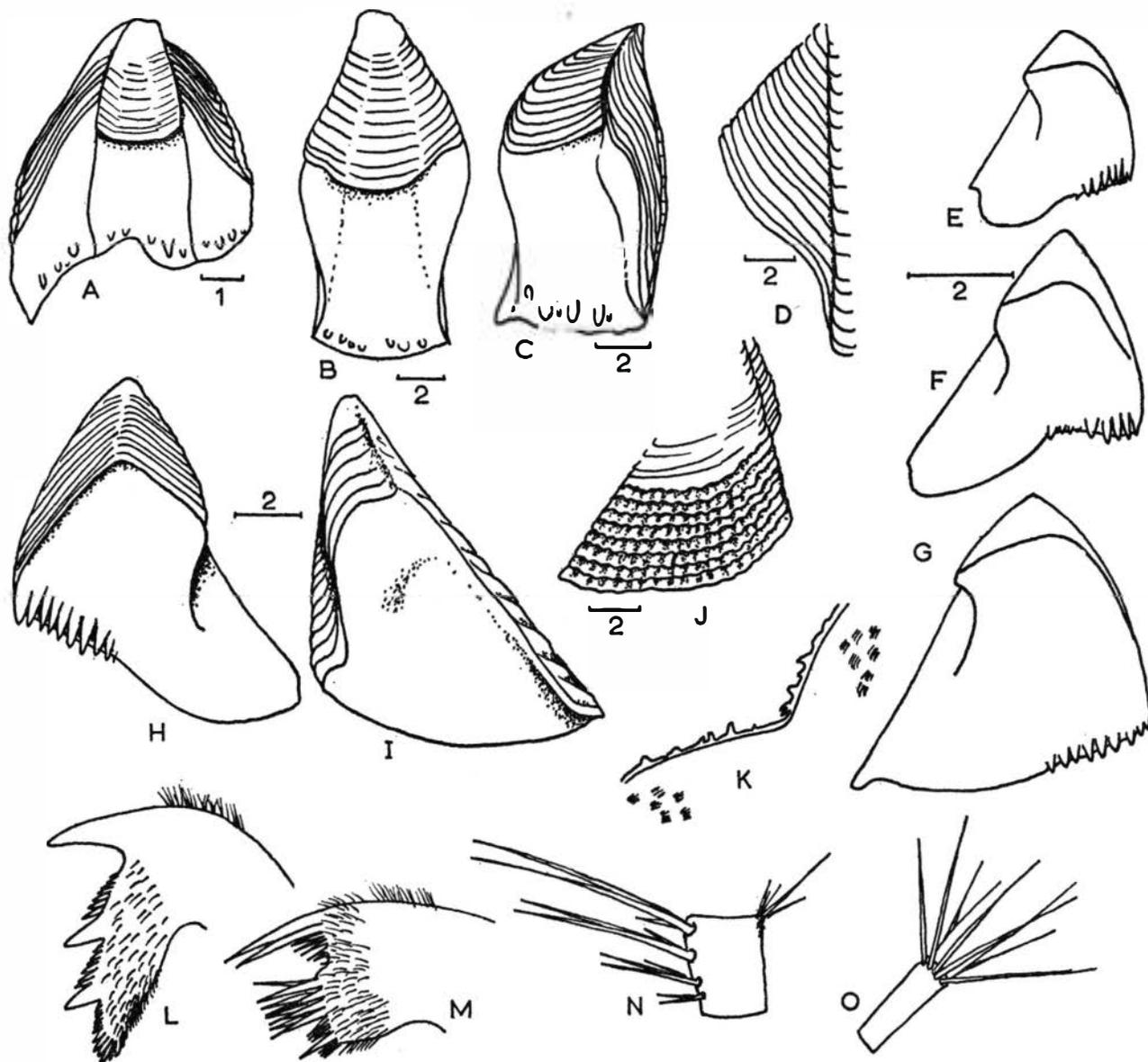


Fig. 47. *Pachylasma scutistriata* Broch: A, inner view, rostral plate; B, same of carina; C, same of carinolatus; D, external sculpturing on ala of carina; E, F, G, outlines of terga of three different specimens, to same scale; H, I, inner views, tergum and scutum of another specimen; J, external sculpturing of part of scutum; K, labral crest; L, mandible; M, maxillule; N, intermediate segment of cirrus VI; O, segment of caudal appendage (scales in mm).

with irregular, blunt projections in lower part. In only one specimen (of 14.5-mm diameter) evidence of a calcareous base, as a 3-mm peripheral shelf. Sutures between rostralatera and rostrum clearly visible internally and sometimes evident externally. Rostral plate broad and not much curved when viewed from above. Carina notably keeled in upper part because of diverging alae. Carinolatera from $\frac{1}{2}$ to as wide as latera.

Opercular plates: Tergum triangular with straight scutal margin, spur only slightly separated from basiscutal angle. Spur sometimes broad, sometimes barely indicated, and sometimes tapering. Carinal depressor muscle crests extend below basal margin. A prominent but short articular ridge projects beyond scutal articular margin. External growth lines faint, but with faint radial striations from apex to depressor muscle crests on basal margin. Scutum triangular, with a straight articular ridge extending for about $\frac{1}{2}$ of articular margin, internal surface smooth, with a very faintly indicated adductor muscle scar, without depressor muscle crests, external growth ridges very distinct and crinkled, curves of successive ridges so lined up as to give impression of radial striations.

Mouthparts: Labral crest shallowly concave, with irregularly placed sharp and blunt teeth on crest. Mandible bears 3 teeth, and lower angle has 8–17 spines extending around it. Maxillule bears 2 major setae at upper angle, and some shorter setae extending into a notch at same level as base of major setae. Cutting edge of maxillule raised and straight, with paired, stout setae in its upper part and a row of smaller setae to and at lower angle, usually including 1 rather prominent one.

Cirri: Number of segments in rami of cirri and caudal appendages increases with age, as follows, anterior ramus 1st:

Stn	shell diam.	actual length	I	II	III	IV	V	VI	c.a.
D210	3.7 mm	2.0 mm	6, 5	7, 9	5+6, 4+7	13, 14	15, 13	18, 17	9, 9
F94	7.1 mm	4.4 mm	7, 8	9, 12	6+7, 4+11	15, 18	21, 20	17, 19	14, 17
F94	7.5 mm	4.8 mm	10, 9	11, 16	6+12, 6+14	22, 23	24, 25	24, 24	16, 18
F921	?	7.4 mm	10, 9	13, 17	7+10, 7+13	21, 23	23, 24	25, 25	11, 13
D210	11.9 mm	9.4 mm	11, 10	14, 17	8+13, 7+13	24, 26	25, 25	26, 27	18, 18
F94	14.5 mm	9.5 mm	11, 7	14, 16	8+12, 7+16	22, 23	25, 24	28, 26	21, 19

Rami of cirrus III with basal segments like those of anterior cirri, but distal segments like those of posterior cirri. For this cirrus, above counts distinguish between basal (first) and distal (second) segment types. Basal segments of anterior rami of cirri I and II almost 2× as wide as corresponding segments of posterior rami. Basal segments of both rami protrude anteriorly, well provided with medial setae. Rami taper distally to elongate and not protuberant segments. Basal segments of anterior ramus of cirrus III wider than those of posterior ramus, distal segments bear 3 pairs of setae on anterior margin, a tuft of setae at posterior distal

angle, and generally resemble segments of more posterior cirri except for a few scattered setae at distal medial margin. Segments of cirri IV–VI have 3 pairs of setae on anterior edge, a single, small seta between bases of each pair, usually a proximal 4th pair of setae of same size as medial setae, and a group of 3 or 4 setae at distal posterior angle, together with a number of very short spines. Bases of rami represent fused segments, and bear minute, upwardly-directed spines on posterior edge. Caudal appendages a little longer than protopod of cirrus VI, and all its segments have distal setae. Penis annulate and, in preserved condition in largest specimen examined, a little over $\frac{1}{2}$ length of cirrus VI.

REMARKS: None of the specimens was attached to substratum, and only two were intact. The others had partially or completely disarticulated, a consequence of their fragile construction. However, the parts are readily recognisable, being distinguished from species of *Hexelasma* or *Aptolasma*, with which they occur, by the hairless and ridgeless parietal plates, the external growth lines of the alae not diverging from the inferior alar margin nor forming a “welting” along the superior alar margin, the irregular bumps internally at the base of the parietes of larger specimens, the crinkled external growth ridges of the scuta, and in the body the multidenticulate lower angle of the mandible and the presence of caudal appendages.

Pachylasma scutistriata was described initially by Broch (1922) from near Tasmania, and later by Nilsson-Cantell (1927) from the Indian Ocean and off New Guinea. The known range was extended to Japan by Utinomi (1968b). The species resembles *P. darwinianum*

Pilsbry from the Philippines, but in the latter species the caudal appendages are rudimentary (Pilsbry 1916, p. 327). The caudal appendages of *P. scutistriata* are as well developed as in *P. giganteum* of the Mediterranean Sea, in which species, however, the rostral sutures are obscured. Following the remarks by Darwin (1854, p. 478) and Nilsson-Cantell (1927), as well as the evident variation in the relative width of the carinolatera and latera, it would not be surprising if a revision of the genus revealed some synonymies.



Shell wall of 6 solid plates, including a carina, paired latera and carinolatera, and a single-piece rostral plate. Parietal plates with external growth ridges lined with conspicuous cuticular hairs. External alar growth lines parallel or diverging from inferior alar margin. Superior alar margin has a welting. Terga and scuta have prominent articular ridges. Caudal appendages absent. Segments of posterior cirri with graded series of 3 or more pairs of anterior setae.

REMARKS: The construction of the shell wall in *Hexelasma* is similar to that in *Pachylasma*. The angle of the alae abuts on to an internal, apicobasal ridge of the sheath of the adjacent plate. In *Hexelasma*, and in *Aptolasma*, the alar angle is truncated and strengthened, resulting with growth in a pronounced welting along the superior alar margin.

Growth ridges are pronounced on the external surfaces of the plates, especially on the free edges of the alae and on the whole of the outer surface of the parietes, where the ridges bear rows of chitinous hairs. This feature is not seen in *Pachylasma*, but has been seen in *Octomeris brunnea*, tetractitids, *Aptolasma*, and balanids. The ridges and hairs are apparent only when external erosion or encrustation has not occurred, perhaps one reason why the feature is more characteristic of deep-water species than of shallow-water and intertidal balanomorphs.

The rostral plate of *Hexelasma* shows no evidence of its assumed compound origin. One of the better-known species is the Antarctic *Hexelasma corolliforme*, described under the names *Balanus corolliforme* by Hoek (1883), *Hexelasma antarcticum* by Borradaile (1916), and *Bathylasma corolliforme* by Newman & Ross (1971). A small specimen of this species in a sample from a Ross Sea station (NZOI Stn E189) was examined in the course of the present deliberations on the hexelasmids. Diagrams are given in Fig. 48. Even in this juvenile specimen no sutures could be traced in the rostral plate, nor could the rostral plate be broken along any likely sutural lines. The specimen had undergone 4 moults since metamorphosis, and while it is clear that the carinolatera had not appeared until after the second moult, there was no trace of separate rostralatera. The appendages of the specimen were mounted, and are discussed further below.

Newman & Ross (1971) differentiated *Hexelasma* and *Bathylasma* on slight characters, including the number of paired setae on the anterior edge of the segments of cirrus VI and the shape of the spur of the tergum. It is my belief that the confounding of two taxa in the description of *Hexelasma velutinum*, which was designated type-species of the genus by Utinomi (1965), was not fully resolved by Newman & Ross (1971). The latter authors point out that Hoek's material

included two species, the larger, columnar form which, by priority, would be *Hexelasma velutinum*, and two lower, conical specimens which had internal laminations in the shell plates and which Newman & Ross (1971) designated into a new genus as *Aptolasma leptoderma*.

Aptolasma leptoderma and *A. britoni*, as described by Newman & Ross (1971), and *A. americanum* (Pilsbry) and *A. callistoderma* (Pilsbry) have a very characteristic setation on the posterior cirri. The segments are square in outline, with 2 pairs of very long, stiff setae on the anterior edge, with some very small spines at the bases of these, and sometimes a smaller third pair proximally. The figure of cirrus VI given for *H. velutinum* (Hoek 1913, pl. 26, fig. 14) is of this type, but there is no indication of the specimen from which this was drawn; it could have been one of the conical specimens now known under the name *Aptolasma leptoderma*. In other words, the nature of the setation of the segments of the posterior cirri of the type species of *Hexelasma* is in doubt.

Further, the single specimen that Hoek (1913) named *Hexelasma arafurae* had the segments of the posterior cirri "furnished with 2 pairs of very long stiff, needle-like spines along their inner face, at the base and between which 2 or 3 very short bristles are regularly inserted". The description of this species accords so well with the characters of *Aptolasma* that it is most likely that it, too, should be reassigned.

In *Hexelasma hirsutum* of the North Atlantic, as well as in the Antarctic *H. corolliforme*, the leading edge of the segments of the posterior cirri bear from 3 pairs of setae in juveniles (Fig. 48) to 5 pairs in larger specimens, the setae grading from the longest distally to the shortest proximally, and with occasional short setae at the base of the major pairs.

On the point concerning the tergal spur, Newman & Ross (1971) claim that in *Bathylasma* it is "confluent with the basal margin and continuous with the articular margin", and in *Hexelasma* it is "distinct from the basal margin and effectively continuous with the articular margin". In the single species of *Hexelasma* in the New Zealand material described below, the tergal spur is sometimes confluent with both margins and sometimes distinct from one or both. In all pachylasmids the spur is situated at or very near to the articular margin, as in chthamalids, and slight variation in its position is scant basis for a generic distinction.

Newman & Ross (1971) described a small specimen of a hexelasmid barnacle taken by the *Tui* Expedition to the north of New Zealand. This specimen they placed in *Hexelasma* (sensu Newman & Ross), and named it *H. fosteri*. However, the presence of 2 pairs of long setae on the segments of the posterior cirri and the lack of a prominent tergal articular ridge indicate the affinities of this specimen with *Aptolasma*. The beaded external surface of the parietes is so like the condition found in disarticulated specimens of the present specimens, which in other respects are clearly aptolasmid, that I have effected the synonymy.

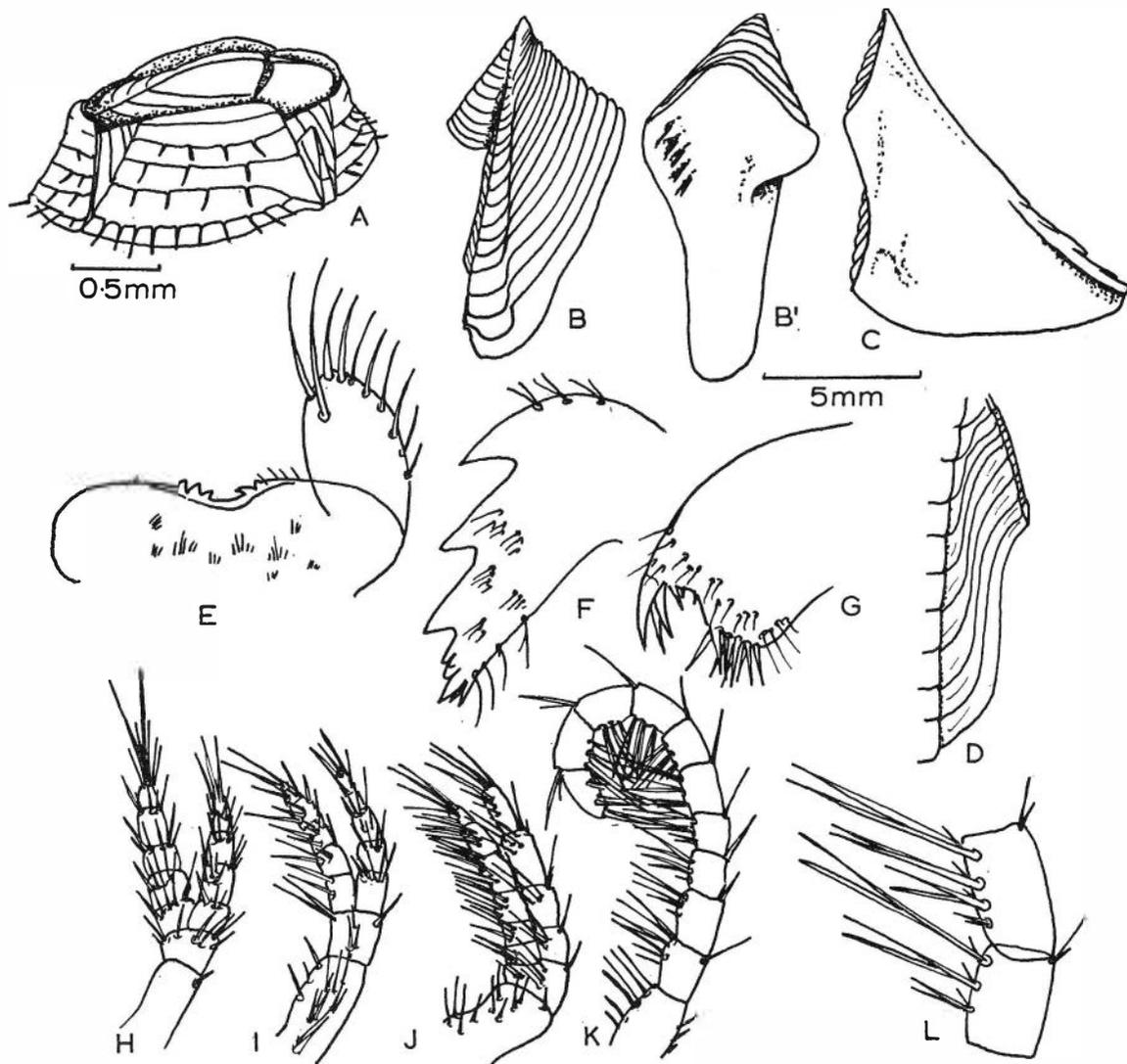


Fig. 48. *Hexelasma corolliforme* (Hoek), specimens from NZOI Stn E189 (Ross Sea): *A*, juvenile; *B*, *B'*, outer and inner views, tergum of 2-cm high specimen; *C*, same, inner view of scutum; *D*, same, external alar sculpturing; *E-L*, body of the juvenile *A—E*, labrum and mandibular palp; *F*, mandible; *G*, maxillule; *H*, cirrus I; *I*, cirrus II; *J*, cirrus III; *K*, pedicel and one ramus of cirrus VI; *L*, intermediate segments of cirrus VI.

The following species of *Hexelasma* are thus recognised:
Hexelasma velutinum Hoek, 1913 (type, S.D. Utinomi, 1965)
Hexelasma corolliforme (Hoek, 1883)
Hexelasma hirsutum (Hoek, 1883)
Hexelasma aucklandicum (Hector, 1888)
Hexelasma alearum n. sp.

***Hexelasma alearum* n. sp.** (Plate 10A, B; Fig. 49)

MATERIAL EXAMINED: NZOI: Stns F132 (2 specimens, 1 intact; and numerous shell plates); shell plates only from C171, D5, D6, D22, D160, D166, D169, E81 E852, E855, E870, E902, E903, F117, G704.

DISTRIBUTION: New Zealand shelf, 414–1600 m (Fig. 43).

DESCRIPTION: *Shell:* Parietal plates not flared out from orifice, with prominent rows of hairs on external growth ridges but not between growth ridges. Alae have conspicuous welting along upper alar margin, and external growth lines not parallel with inferior alar margin, leaving a smooth triangular extension of internal alar surface on outside towards alar angle beneath lowest growth line. Parietes internally smooth except for ridges on sheath and faint replication of alar growth lines on carinal side of apico-basal ridge. No evidence of a calcareous base.

Opercular plates: Tergum with prominent triangular articular ridge extending for about $\frac{1}{2}$ articular margin in

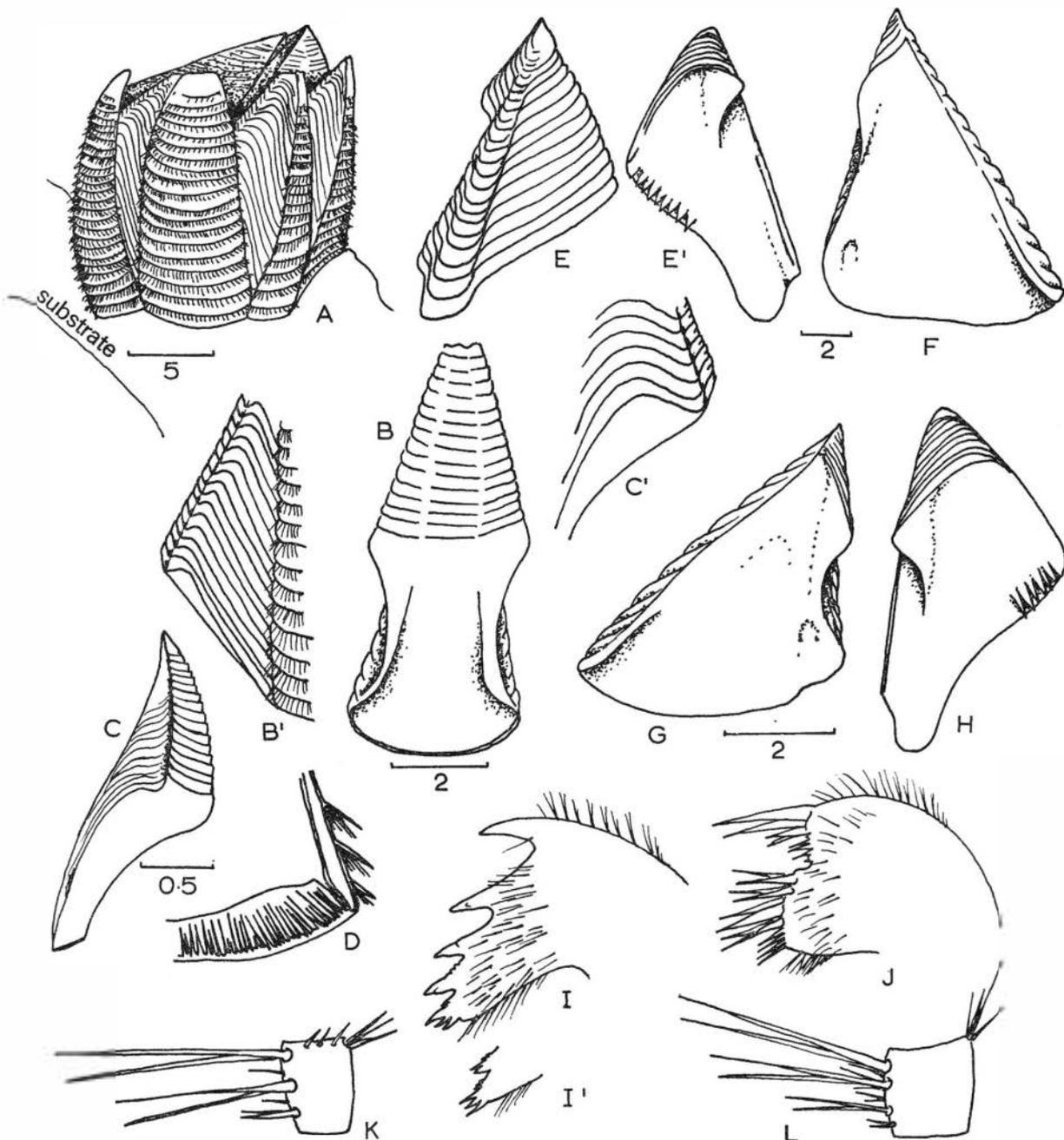


Fig. 49. *Hexelasma alearum* n.sp.: A, lateral view of 16-mm specimen; B, inner view of carina of a separate shell; B', external alar growth lines of B; C, inner view of carinolatus of a separate shell; C', external alar growth line and welting of C; D, infolded chitinous spines at base of shell plate; E, E', outer and inner views, tergum of A; F, inner view, scutum of A; G, H, scutum and tergum of a smaller intact specimen, 9 mm diameter; I-L, specimen A-I, mandible; I', detail of lower angle; J, maxillule; K, 16th segment, posterior ramus of cirrus II; L, intermediate segment of cirrus VI (scales in mm).

smaller specimens, but proportionately shorter in larger specimens; articular margin practically straight, and spur placed near basitergal angle; prominent carinal depressor muscle crests depend slightly below basal

margin. Scutum triangular, with a moderately prominent articular ridge, without an adductor ridge or scar or pit for adductor muscle, but with a very shallow pit for attachment of internal depressor muscle. The foregoing

description based on a number of shells; the following description of appendages based on 2 live specimens.

Mouthparts: Labrum of smaller specimen (9-mm basal diameter) without conspicuous teeth on crest, but that of larger specimen (16 mm) with a row of blunt teeth; inner surface well supplied with trifid setae. Mandible in both specimens bears 4 teeth, lower ones with side teeth and with minute teeth on upper side of both 4th tooth and lower angle; lower angle has 3 spines. Maxillule bears 2 stout setae at upper angle and a few shorter setae extending into notch; cutting edge straight, and bears an upper group of paired, stout setae and a lower group of shorter setae.

Cirri: Number of segments in cirri as follows; anterior ramus 1st:

Shell diam.	I	II	III	IV	V	VI
9 mm	8, 8	6+5, 7+11	8+11, 8+11	18, 22	21, 22	21, 26
16 mm	12, 11	18, 22	24, 24	33, 27	31, 34	35, 33

Anterior ramus of cirrus I longer than posterior ramus. Cirrus II with posterior ramus markedly longer than anterior ramus; basal segments of each ramus wider than long, protuberant anteriorly, and with numerous setae on inner face; more distal segments elongate, with 3 pairs of setae confined to distal edge. Cirrus III has subequal rami as long as posterior ramus of cirrus II; basal segments of anterior ramus like those of anterior cirri, and those of both rami with copious medial setae; distal segments of both rami like distal ones of cirrus II and all segments of posterior cirri. Cirri IV–VI have subequal rami, each segment with 3 or 4 pairs of setae on anterior edge, grading from longest pair distally to shortest pair proximally; 4th pair of setae, when present, no longer than few short unpaired setae between bases of large setae. Penis very short in smaller specimen, almost hairless, but in larger specimen fully length of cirrus VI, and annulate and setose.

HOLOTYPE: NZOI 205, the larger intact specimen from station F132 (Plate 10 A, B).

REMARKS: This species is closely related to *Hexelasma velutinum*, which name is now applied to the specimen from Stn 105 of *Siboga* and so named by Hoek (1913). According to Hoek (1913), *H. velutinum* is covered by a velvety epicuticle, but it is possible that this describes the externals of one of the other specimens. The description is taken to mean that cuticular hairs occur between those lining the growth ridges. In the present species, this area is quite smooth. The tergal spur of *H. velutinum* is broadly truncate, contrasting with the narrowly rounded condition in the present species. The scutum of *H. velutinum* has two external longitudinal folds not seen in the present species. As the description of the body of *H. velutinum* is unreliable for the reasons given above, comparison of the appendages is not profitable.

Hexelasma hirsutum of the North Atlantic Ocean has a more concave tergal articular margin and a distinct scutal adductor muscle pit, in contrast to the condition seen in the opercular plates of the present species. The

appendages of *H. hirsutum* and the present species are, however, quite comparable. *H. corolliforme* differs from all other known species of *Hexelasma* in that the external alar growth lines parallel the inferior alar margin. Differences from the fossil *H. aucklandicum* are discussed below.

Most of the samples of this species are composed of numerous shell plates in various stages of erosion. There are evidently areas of sea bed that have a hexelasmoid plate gravel, recorded as “barnacle plates” in the sediment records of NZOI. This phenomenon also occurs in the Ross Sea with the plates of *H. corolliforme* (Bullivant 1967). The plates may have been aggregated by current systems, or may represent accumulations of slowly decomposing and eroding solid parts of overlying changing populations of the barnacle. Evidently, similar processes have led to some of the Miocene deposits of the basal Waitemata series being rich in the plates of *H. aucklandicum*.

Hexelasma aucklandicum (Hector) (Plate 10C-E)

Scalpellum aucklandicum Hector, 1888: 440.

Hexelasma aucklandicum. Withers 1913: 841; Withers 1924: 18.

Bathylasma aucklandicum. Newman & Ross 1971: 151.

MATERIAL EXAMINED: Department of Geology, Auckland University: disarticulated fossil plates from Motutapu I, Motuihe I, and Mathesons Bay in the Hauraki Gulf. BAF: Isolated and broken fossil plates, from Motutapu I.

DESCRIPTION AND DISCUSSION: Parietal plates of this species have been well described by Withers (1913, 1924), and the present material does not amplify his accounts of the wall plates. Newman & Ross (1971) discovered in the single plate they had to examine a very wide welting along the upper alar margin, “half the width of the entire ala”. The numerous plates of the present material show no more than a very narrow welting.

The carina shown in Plate 10C has Catalogue no. A. 122 in the Geology Department, Auckland University. Of particular interest amongst the present material are two incomplete opercular plates (Plate 10D, E), which because of their size and evident hexelasmoid features are taken as a scutum and tergum of *H. aucklandicum*. These have not previously been described. The questioned tergum figured by Withers (1913, pl. 35, fig. 13) appears unrelated.

In both the tergum (Cat. no. A.123) and the scutum (Cat. no. A.124), the articular ridge is truncated along a line almost parallel to the articular margin. This feature is apparent when the plates are viewed externally. The ridge thus appears 4-sided, in contrast to the triangular articular ridges in the described extant forms of *Hexelasma*.

The straight articular margin of the tergum resembles that of *H. corolliforme* (Fig. 48) and *H. alearum* (Fig. 49). *H. aucklandicum* can be distinguished from *H. corolliforme* on the basis of the course of the external alar growth lines, but the chief difference between *H. alearum* and *H. aucklandicum* is at present one of size. The latter species can attain a shell height of 187 mm (Withers 1924), and the largest plate of the present material is 102 mm long and broken. Borradaile (1916) figures a carina of *H. corolliforme* 82 mm long, and the longest plate of *H. alearum* found is a carina 74 mm long. The largest tergum of *H. alearum* found is not much longer than the entire articular ridge of the fossil tergum of *H. aucklandicum*. It is possible that the change in outline of the articular ridge from triangular to quadrangular is an ontogenetic consequence of the attainment of larger size. It is tempting to link these Miocene and Recent New Zealand hexelasmids.

Withers (1924, p. 23) described from New Zealand 2 sets of fossil barnacle remains that lack radii. The first of these, "*Hexelasma* sp.", has the compartments with "the outer walls thrown into comparatively wide longitudinal folds", "a well-developed sheath", and "strong ribs on the inner surface". These plates are abundant in the Motutapu deposits, and are clearly not *Hexelasma*. Although radii are not developed, the external sutural edges of the parietes interlock. These plates will be described further in a future paper.

The second species of Withers, "*Hexelasma* sp. (cf. *aucklandicum*)", has external characters as for *Hexelasma*, a not very well developed sheath, but "on its inner surface near the base . . . traces of feebly developed ribs". From this information, the specimen (a rostral plate) might be better assigned to either *Pachylasma* or *Aptolasma*.

Genus *Aptolasma* Newman & Ross, 1971

Shell wall of 6 plates that develop internal chitinous laminae, including a carina, paired latera and carino-latera, and a single-piece rostral plate; with external growth ridges lined with cuticular hairs; external alar growth lines diverging from inferior alar margin; superior alar margin with a conspicuous welting. Terga and scuta without prominent articular ridges. Caudal appendages absent. Segments of posterior cirri with 2 pairs of long setae on anterior edge.

REMARKS: As discussed under *Hexelasma*, the confounding of two taxa in the description of *Hexelasma velutinum* by Hoek (1913) probably led to an insufficient diagnosis for *Aptolasma* as given by Newman & Ross (1971), particularly with regard to the nature of the cirral setation.

The presence of chitinous laminae in the wall plates, as discovered by Newman & Ross (1971), clearly warrants generic recognition. The chitin may occur as a continuous lamina, or be subdivided into a row of chitinous ribbons or columns. When situated close to the inner face of the plate, the ribbons may show through as longitudinal lines which alternate with internal, basal, longitudinal ribs. The presence of the chitinous laminae appears to be correlated with the formation of extra shell internally which, when formed as ribs, interlock basally with a calcareous base secreted by the basal tissues. This imparts extra rigidity to the shell construction and anchoring. The chitinous laminae and the calcareous base are not present in the early stages, and the shells of young specimens are often similar to *Hexelasma*.

However the chitin is formed, or for whatever purpose, the way in which it is layered in the parietal wall provides a useful specific character. Chitinous laminae are not unique to *Aptolasma*; they also occur in the shells of some of the Tetracitidae.

Chionelasmus, *Pachylasma*, *Hexelasma*, and *Tetrachaelasma* have very prominent tergal articular ridges, but in the described species of *Aptolasma*, the tergal articular ridge is more slender. Further, the internal surface of the tergum of *Aptolasma* is more-or-less roughened by irregular rows of calcareous beads radiating from the apex, in contrast to the quite smooth internal surfaces of the terga of *Hexelasma*. In many respects *Aptolasma* approaches *Epopella* of the Tetracitidae, but is distinguished from it by the absence of interlocking parietal plates.

The following species are included in *Aptolasma*:

- A. callistoderma* (Pilsbry) (type, subsequent designation Newman & Ross, 1971)
- A. arafuræ* (Hoek) (see p. 79)
- A. americanum* (Pilsbry)
- A. ecaudatum* (Hiro)
- A. leptoderma* Newman & Ross
- A. britoni* Newman & Ross
- A. triderma* Newman & Ross
- A. fosteri* (Newman & Ross)
- A. nolearia* n. sp.

Aptolasma fosteri (Newman & Ross)

(Plate 10F; Fig. 50)

Hexelasma fosteri Newman & Ross, 1971: 155.

MATERIAL EXAMINED: *Tui* Expedition: holotype (now deposited in USNM, Cat. no. 125310). NZOI: Stns E852 (1 disarticulated, incomplete and dry specimen); shell plates from E854, E860, E870.

DISTRIBUTION: New Zealand shelf, 538–1556 m (Fig. 43)

DESCRIPTION: *Shell*: Parietal plates externally with rows of small beads between and on growth lines, and with external alar growth lines diverging from inferior alar margin; internally orange and longitudinally striped but not ribbed. Base represented in larger

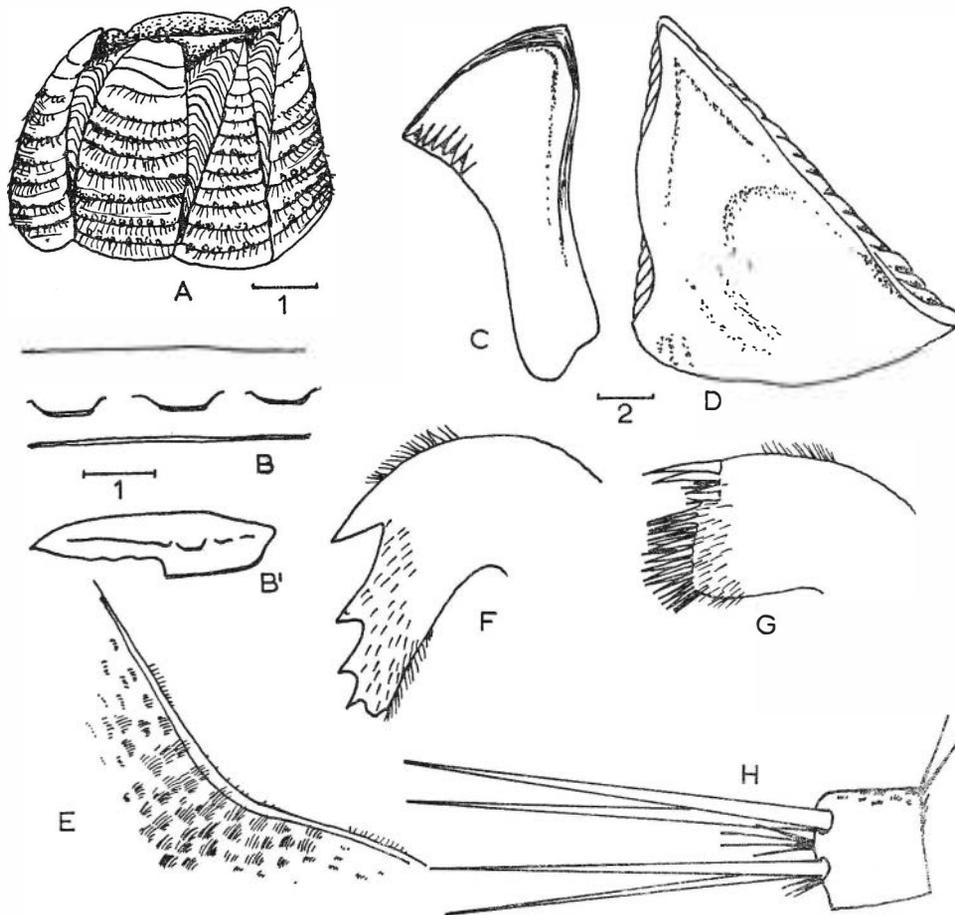


Fig. 50. *Aptolasma fosteri* (Newman and Ross): A, lateral view of holotype; B-H, disarticulated specimen from NZOI Stn E852— B, B', cross-sections across base of latus (B) and towards apex of carinolatus (B') to show arrangement of chitin between outer (below) and inner (above) shell faces; C, inner view of tergum; D, same of scutum; E, medial labral crest; F, mandible; G, maxillule; H, intermediate segment of cirrus VI (scales in mm).

specimens as a wide, peripheral ledge, with crescentic chitinous ribbons dividing parietal part of shell plates into inner and outer shell laminae of equal width.

Opercular plates: Opercular plates internally dull orange. Tergum with a long and slightly concave articular margin; faint crests for carinal depressor muscles reaching but not extending below basal margin; basal margin concave to rounded spur set slightly apart from basitergal angle. Scutum with tergal and basal margins meeting at 90°; scutal articular ridge moderately prominent; adductor ridge faintly developed, extending towards basal margin; adductor muscle pit demarcated apically; faint crests for lateral depressor muscles; and externally well sculptured, but without longitudinal furrows.

Mouthparts: Appendages of specimen from station E852 were mounted, and were sufficiently preserved to show chitinous structures. Labral crest broadly concave, without teeth but with minute spines on edge, and set in rows below crest. Mandible has 4 teeth, and a rounded lower angle. Maxillule bears 2 large setae at upper angle, below which several short setae extend into a shallow notch; main cutting edge distinctly elevated from upper angle, bearing paired setae in its upper part and a comb of shorter setae at lower angle.

Cirri: Cirrus I has equal rami of 15 segments, very wide and copiously setose but not protuberant. Cirrus II with subequal rami with 19 and 21 segments similar to those of cirrus I. Cirrus III with 21 and 25 segments in anterior and posterior rami respectively, lower 12 or so being like those of anterior cirri, more distal ones like those of posterior cirri except with more longer setae on distal border of lateral face. Cirri IV-VI similar to each other, with 31-36 segments in each ramus showing some basal fusion; each segment bearing 2 pairs of long setae on anterior edge, more distal pair being only slightly longer, with a tuft of short setae between, and at bases of, 2 major pairs, and a few just below bases of proximal pair; posterior borders of segments serrated by minute, upwardly directed spines, more extensive in basal part of rami, and especially pronounced distally in each segment; groups of small spines extend across medial distal border. Penis annulated, with distal circlet of setae, and slightly longer than pedicel of cirrus VI.

REMARKS: The shape of the opercular plates and the sculpturing of the external parietal surfaces indicates that the present material is the same as the immature *Tui* specimen. The relative lengths of the rami of the cirri also agree. The external growth lines of the alae shown in the figure of the holotype (Newman & Ross

1971, fig. 75B) are inaccurately drawn. According to my own figures of this specimen (Fig. 50A), drawn before sending it to the U.S.A., the external alar growth lines are normal.

The absence of the internal chitinous laminae in the shell of the holotype is possibly due to the immaturity of the specimen. At this size a calcareous base may not have formed, and internal thickenings and ribbing not commenced.

The shape of the chitinous laminae in the parietal plates of larger specimens resembles the condition in *Aaptolasma callistoderma*, in which species, however, the inner shell lamina is twice as thick as the outer lamina. The opercular plates also differ; the scuta are not apicobasally elongate, and the basitergal angle is more pronounced than in the corresponding structures of *A. callistoderma*.

The orange coloration of the opercular plates recalls the condition reported in *A. americanum* and *A. arafurcae*.

***Aaptolasma nolearia* n. sp.** (Plate 10G, H; Fig. 51)

MATERIAL EXAMINED: NZOI: Stns D159 (2 specimens), F921 (1), E850 (3); shell plates from D166.

DISTRIBUTION: New Zealand, 70–508 m (Fig. 43).

DESCRIPTION: *Shell:* Plates externally with distinct growth ridges; alar growth lines diverging from inferior alar margin; internally ribbed at base where ribs interlock with a calcareous base. Chitinous ribbons divide parietes into thicker outer and thinner inner shell laminae; ribbons in pairs, each pair extending from between internal shell ribs.

Opercular plates: Tergum has a convex articular margin; prominent crests for carinal depressor muscles which extend over about $\frac{1}{2}$ basal margin; a somewhat indistinct spur merging with basiscutal angle. Scutum apicobasally elongated; articular margin as long as, or longer than, basal margin, which together subtend an obtuse angle; a prominent adductor ridge extends from sunken apical part enclosed between folded articular and occludent ridges, curves beneath a faint adductor muscle pit to basal margin, and continues almost parallel to basal margin towards rostral angle, and with a few faint crests for lateral depressor muscles.

Mouthparts: Crest of labrum lined with bluntish teeth, without setae below crest. Mandible 4-toothed and bears a tridentate lower angle, upper spine usually largest. Maxillule bears 2 sets of setae on cutting edge.

Cirri: Cirral counts as follows; anterior ramus 1st.

Stn	scutal length	I	II	III	IV	V	VI
E850	4.8 mm	9, 7	9, 10	10+3, 10+8+17	23, 20	26, 25	26, 25
E850	8.0 mm	11, 8	10, 12	10+6, 10+6+14	26, 30	31, 33	34, 33
D159	9.5 mm	10, 8	10, 15	10+6, 10+10+27	30, 31	34, 33	32, 31
F921	10.1 mm	13, 11	12, 13	12+6, 12+10	36, —	38, 42	42, 41
E850	10.6 mm	11, 8	11, 13	12+6, 12+9+30	28, 31	33, 34	35, 35
<i>A. fosteri</i> : E852	12.8 mm	15, 15	19, 21	13+8, 12+13	31, 33	36, 36	32, 34)

All but one of specimens (that from station D159, figured in Plate 10) disarticulated, and length of scutum taken to rank specimens to size. Cirrus I with anterior ramus slightly longer than posterior ramus, segments wide basally, only slightly protuberant, and well provided with setae on anterior, posterior, and medial faces. Cirrus II has posterior ramus longer than anterior ramus, and segments of both rami similar to those of cirrus I, but more distal segments of posterior ramus have setae confined to distal regions of segment. Cirrus III with 2 types of segments; anterior ramus has basal segments similar to those of cirrus I, and more distal segments like those of posterior cirri in bearing 2 major pairs of setae on anterior edge, but differ in that some distal setae borne on medial face; posterior ramus, in all but one specimen, antenniform, where a 3rd type of segment occurs distally bearing short setae at distal anterior and posterior angles. These antenniform segments become more elongate towards tip of ramus. Cirri IV–VI similar to each other; segments of rami tend to fuse basally where posterior margins of rami bear minute, upwardly directed spines; intermediate segments bear 2 pairs of setae on anterior edge, longest pair distally, with 1 or 2 small, medial setae at base of minor pair or between bases of 2 pairs; medial, lateral, and distal edges of each segment with rows of small setae. Penis a little longer than pedicel of cirrus VI, annulated, and with a distal whorl of setae.

HOLOTYPE: NZOI 206, the specimen from Stn D159 (Plate 10G, H).

REMARKS: This species closely resembles *A. leptoderma* in that the chitin-filled tubes or ribbons are close to the internal surface of the shell plates, but the chitin does not occur as a continuous lamina as in *A. leptoderma*. The opercular valves also differ in the extensive and prominent scutal adductor ridge, the convex articular margin of the tergum, and the indistinct tergal spur. The internal ribbing is more evident in this species than in any other thus far described.

The significance of antenniform anterior cirri is not yet understood, but they seem to be sensory in function. They are found in a number of balanomorph genera, but not invariably in all species of a genus, nor in all specimens of a species. They may be transient developments, perhaps associated with the reproductive cycle.

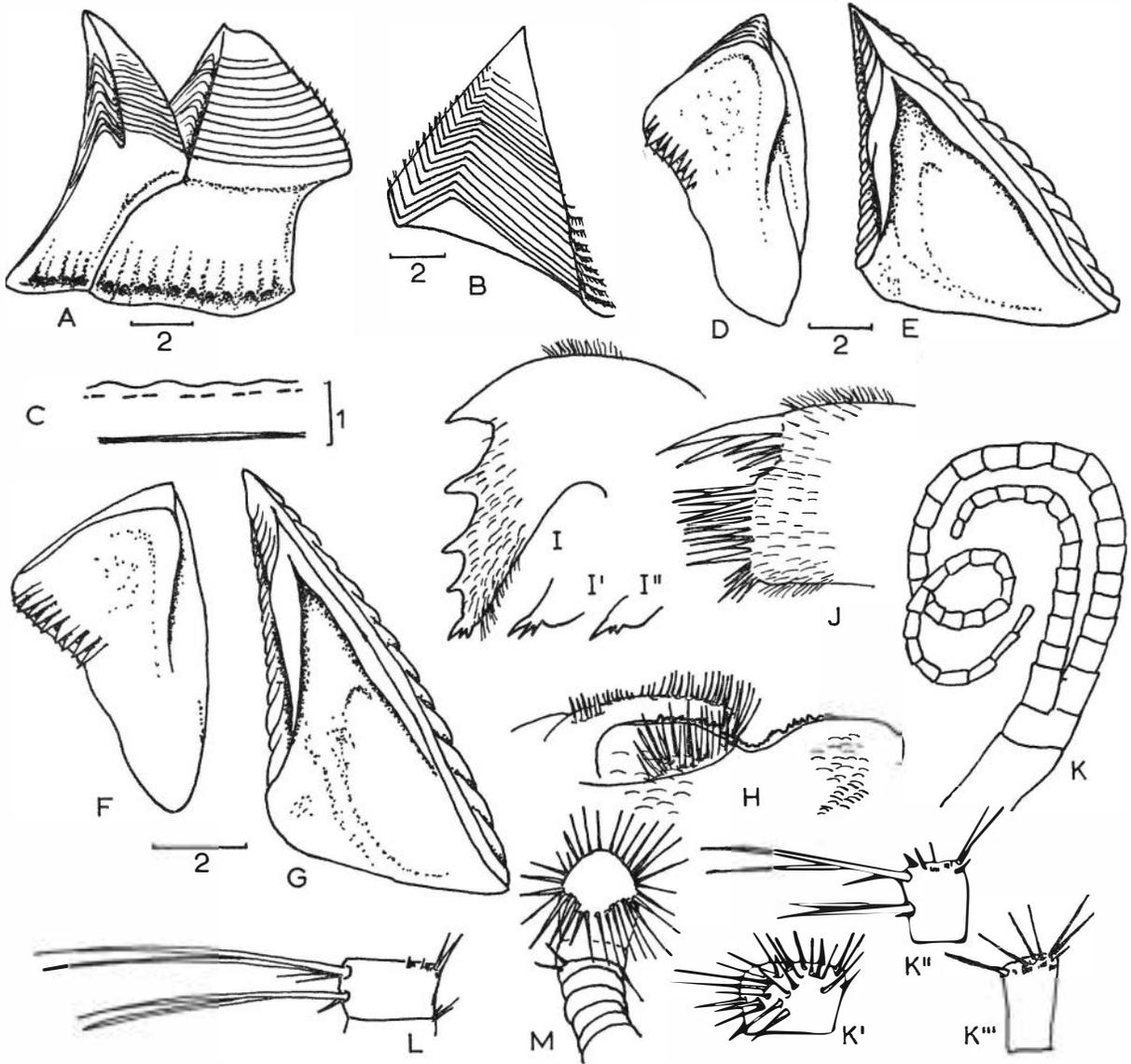


Fig. 51. *Aptolasma nolera* n.sp.: *A*, inner views of adjacent latus and carinolatus; *B*, external alar growth lines of latus; *C*, cross-sections of paries near base to show arrangement of chitin between outer (below) and inner (upper) shell faces; *D*, inner view of tergum; *E*, same scutum of same specimen; *F*, *G*, inner views, tergum and scutum of another specimen; *H*, labral crest and mandibular palp; *I*, mandible, with variants of the lower angle in *I'*, *I''*; *J*, maxillule; *K*, plan of cirrus III, with details of 4th (*K'*), 13th (*K''*), and 31st (*K'''*) segments of posterior ramus; *L*, intermediate segment of posterior ramus of cirrus VI; *M*, tip of penis (scales in mm).

Family TETRACLITIDAE Gruvel, 1903

Balanomorpha with 4 parietal plates, which may be concrescent in larger specimens. Plates either non-porous with internal ribs (*Epopella*), or porous with 1 (*Tesseropora*) or several (*Tetraclita* and *Tetraclitella*) rows of longitudinal tubes. Radii more-or-less developed, with denticulate sutural edges. Rostral plate overlaps adjacent latera. Labrum not bullate, crest without a deep medial incision. Cirrus III resembles II more than IV, its rami in some species sometimes antenniform.

Caudal appendages absent. Penis without a basidorsal point.

REMARKS: The tetraclitids were given independent family rank by Ross (1968), who later (1969) presented a familial diagnosis. On re-examining antipodean material which was originally described by Broch (1922) as *Tetraclita purpurascens breviscutum*, Ross (1970) proposed the genus *Epopella* to be included in the Tetraclitidae. A distinctive feature of *Epopella* is that the shell walls are essentially solid, and it holds the same relationship with the tubiferous tetraclitids as the solid-walled species of *Balanus* (sensu lato) do to the tubiferous balanids (see Fig. 72).

The shell wall plates of *Epopella* develop longitudinal internal ribs and these provide a greater area of attachment to the substratum. Compared with intertidal chthamalids (*Chthamalus* and *Chamaesipho*), which increase the shell thickness by solid internal and basal additions to the shell plates, the tetracitids effect greater tenacity with the substratum along with greater efficiency of calcite deposition, by forming ribs and tubes. The tubiferous construction of the plates in tetracitids other than *Epopella* could be a hazard when environmental factors result in erosion of the older, apical parts of the shell. To counteract this the tissues in the tubes secondarily fill the tubes apically with solid, supposedly chitinous material, which apparently withstands erosion better than the surrounding shell matrix. Tropical intertidal tetracitids characteristically have the external surface roughened by the upstanding, filled parietal tubes.

The chitinous laminae in the shell plates of *Epopella* seem to serve a similar purpose of slowing down shell erosion. In *E. plicata*, which has a continuous sheet of yellow chitin in each parietal plate, plus layers of the same material apically in the parietes and in the opercular valves, the yellow laminae lend a characteristic colour to eroding specimens. If not too eroded, the exposed yellow laminations are frequently wider than the interspersed white shell zones.

Newman & Ross (1971) suggest that the chitinous layers function (in *Aptolasma*) as protection against the borings of predators. It is difficult to see how chitin would deter a drilling gastropod, which in any case will have to penetrate chitin layers before reaching the mantle cavity of the barnacle. Rather, the early deposition of chitin in *Epopella*, and its late deposition in the apices of the tubes in the tubiferous tetracitids, is seen as an adaptation to mitigate the erosive conditions of intertidal life. The deeper-water species of *Aptolasma*, are in this respect, and by the development of other features such as increased basal attachment area and increased parietal plate interlocking, preadapted for intertidal life. *Aptolasma* ancestors may have led to the tetracitid condition.

Primitively in the sublittoral habitat, enlargement of the orifice with growth was brought about by diametric growth of the alae; external shell erosion, bringing about attrition of the thinner and older apical parts, was evidently in itself not sufficient. However, in the intertidal zone, increased erosive factors lead to orifice enlargement without the need for alar diametric growth, allowing for parietal interlocking. In this case the radii are narrow, solid, and have dentate edges. Possibly, with reoccupation of hypobiotic habitats on the shore by species of *Tetracitella*, diametric orifice enlargement is again necessary, and is brought about by alar growth and the development of the radii to completely overlap the alae, while still interlocking with the edge of the adjacent parietes.

The development of radii interlocking with adjacent parietes has apparently occurred separately in the

chthamalid, tetracitid, and balanid lineages. The radii of the intertidal chthamalids are solid, chevron-shaped flanges, but do not provide for diametric growth. In the tetracitids, the tubes of the radii of *Tetracitella* are redirected parietal tubes. In the balanids, the tubes of the radii, when porous, are quite separate from the parietes, and alternate with the teeth of the sutural edges of the radii.

Apart from the chitinous laminae, another similarity between the tetracitids and *Aptolasma* is the possession of rows of pronounced, external, chitinous hairs paralleling the parietal growth ridges. These, and the integument from which they arise, persist over much of the shell of adults in deep-water pachylasmids, but are soon lost in intertidal tetracitids subject to shell erosion. Species of *Tetracitella*, however, even as large adults, may have persistent rows of chitinous hairs.

The non-thickened labrum and the complicated nature of the shell plates render the tetracitids more advanced than the chthamalids. The lack of a basidorsal point on the penis, the presence of coarsely pectinate spines on the anterior cirri, and the lack of a deeply incised labrum denies their inclusion in the Balanidae. It is possible that the Tetracitidae and Balanidae have had independent origins from a sublittoral, pachylasmid ancestor.

Genus *Epopella* Ross, 1970

Parietal shells without pores but permeated by laminae of chitin, and with internal basal ribs. Radii solid and narrow.

Epopella plicata (Gray) (Plate 11A, B; Fig. 52)

Elminius plicatus Gray, 1843: 269; Darwin 1854: 351; Hutton 1879: 328; Hoek 1883: 32; Filhol 1885: 489; Weltner 1899: 443; Gruvel 1905: 296; Pilsbry 1916: 261; Jennings 1918: 62; Broch 1922: 341; Nilsson-Cantell 1930b: 211; Moore 1944: 326; Foster 1967: 84.

Elminius rugosus Hutton, 1879: 328; Hoek 1883: 32; Filhol 1885: 489; Gruvel 1907: 1.

Tetracitella purpurascens forma *breviscutum* Broch, 1922: 337; Hiro 1939: 275.

Epopella breviscutum. Ross 1970: 3.

MATERIAL EXAMINED: NZOI: Stns A970, D102, D140, D186, D190, D886, E767, E768, E809, E834, E909, F930, F934. BAF: shores, from Spirits Bay in the far north to Stewart I. Nat. Mus.: numerous specimens from mainland shores, and also from Chatham and Auckland Is.

DISTRIBUTION: New Zealand, intertidal, excluding the Kermadec Is but including the Chatham Is, the Snares, and the Auckland Is (Fig. 46).

DESCRIPTION: *Shell*: In juvenile and uneroded specimens, with external longitudinal folds and cuticular hairs lining growth ridges; a yellow chitinous lamina

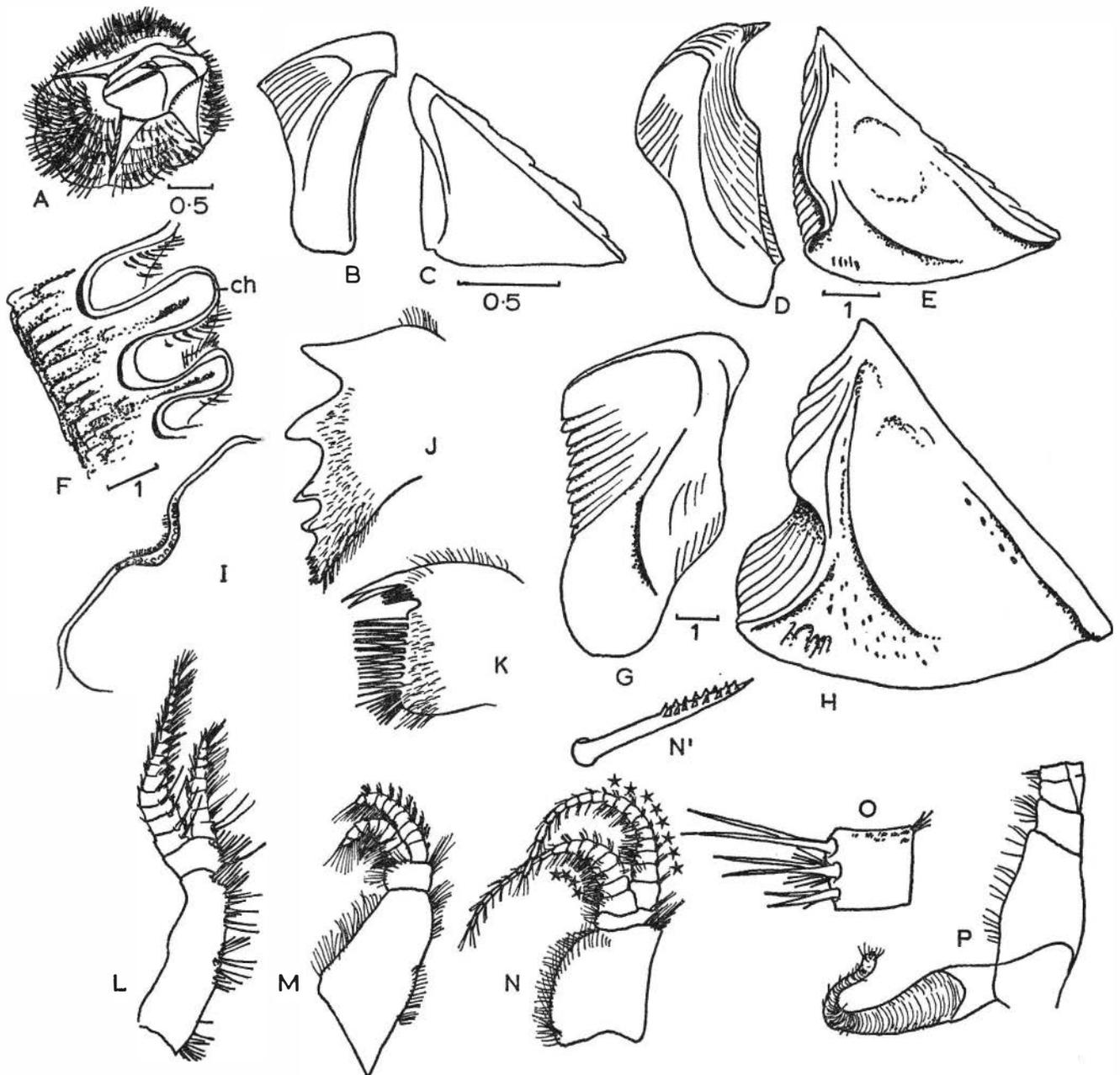


Fig. 52. *Epopella plicata* (Gray): *A*, juvenile specimen; *B*, *C*, tergum and scutum, specimen *A*; *D*, *E*, tergum and scutum, specimen of 11-mm diameter; *F*, sketch of shell base, 22-mm diameter specimen, to show chitinous lamina (*ch*) paralleling outer edge of shell, and ridged inner shell to the left; *G*, *H*, tergum and scutum, specimen of 30-mm diameter; *I*–*P*, appendages of 12-mm diameter specimen—*I*, labrum; *J*, mandible; *K*, maxillule; *L*, cirrus I; *M*, cirrus II; *N*, cirrus III, with *N'* a pectinate seta from the segments of cirrus III marked *; *O*, intermediate segment, ramus of cirrus VI; *P*, penis and pedicel of cirrus VI (scales in mm).

closely paralleling external shell surface; further laminae occur apically in association with sheath; with external erosion laminae show alternating smooth yellow and chalky white. In larger specimens, external folds develop into close-set ribs, and with erosion surface becomes minutely ridged longitudinally, and uniformly grey-brown; parietes provided internally with “a large number of irregular gill-like ridges more or less coalescing, or even produced into downwardly directed pegs” (Moore 1944), as shown in Plate 11B. Radii

narrow, transversely ribbed, with crenate margins, not contributing much to diametric growth for orifice enlargement.

Opercular plates: Scutum triangular, with occludent margin inflected at rostral end; articular ridge short, not very prominent; deep articular furrow; prominent adductor ridge, adductor muscle pit, crests for lateral depressor muscles, and sometimes indications of rostral depressor muscle crests; internal surface may have deep pits in a line in groove behind occludent edge, and in

radiating lines in area below junction of adductor ridge and lower part of articular margin; adductor muscle ridge and articular margin may unite at level of lower part of articular ridge, and contain a deep, narrowing pit between them, or they may unite further down, at base of adductor muscle scar with a row of pits continued up to level of articular ridge. Tergum waisted, narrowing towards basiscutal angle; spur rounded and indistinct, often confluent with basiscutal angle; articular ridge prominent, with a wide articular furrow to one side and a deep groove reaching to basiscutal angle on other; prominent, numerous crests for carinal depressor muscles; apex sometimes beaked, but usually worn and rounded. External surfaces of opercular valves normally eroded with growth lines only against sheath, along basal margin of scutum, and over basal $\frac{1}{2}$ of tergum.

Mouthparts: Labrum with concave centre, fringed with hairs and with teeth on oral aspect. Mandible has 4 teeth, lower 3 with 2 or more cusps; lower angle coarsely serrated, with overlapping spines.

Cirri: Cirrus I with anterior ramus longer than posterior. Cirrus II with subequal rami just longer than posterior ramus of cirrus I. Cirrus III has subequal rami, sometimes antenniform; basal segments about as long as rami of cirrus II, stout, with numerous plumose setae and some coarsely pectinate setae of very stout build (Plate 1F); distally, setae restricted to distal border of each segment, with plumose setae distal to pectinate ones, and ultimately restricted to posterior and anterior distal tufts. Cirri IV–VI much longer than even antenniform rami of cirrus III; all of subequal length; each segment bears anteriorly 3 main pairs of setae, rarely a minute basal 4th pair, although distal segments have only 2 pairs; between pairs of major setae a number of shorter setae, with 1 or 2 rows of minute, grouped spines along lateral distal edge, more prominent towards posterior edge. Penis as long as posterior cirri, with a smooth basal part, and otherwise annulate with sparse, fine setae.

REMARKS: This is a common New Zealand intertidal barnacle, occurring on the mainland and immediate offshore islands, and also on the Chatham Is, The Snares, and the Auckland Is (Foster 1967). The Australian records by Darwin (1854) are doubtful. This species has certainly not been mentioned in the numerous surveys of Australian shores (e.g., Bennett & Pope 1960). Rather, a near relative, *Epopella simplex* (Darwin), occurs on southern Australian shores.

There can be no doubt that the removal of *E. plicata* and *E. simplex* from the Balanidae is warranted. There is less similarity between *E. plicata* and the type-species of *Elminius*, namely *Elminius kingii* from South America, than between *E. kingii* and the genus *Balanus*. Apart from morphological grounds, *E. plicata* occupies mid-tidal stations on New Zealand shores, as do other tetraclitid species on temperate and tropical shores. Furthermore, the nauplii of *E. plicata* (Fig. 2E) also indicate a tetraclitid rather than a balanid affinity,

whereas the nauplii of *Elminius modestus* are more obviously balanid. The structure of the base of the penis in *E. plicata* is also somewhat anomalous among the Balanidae (Barnes & Klepal 1971).

Like most intertidal barnacles, *Epopella plicata* shows a diverse array of external appearances. The descriptions by Broch (1922) of *Tetraclita purpurascens* forma *breviscutum*, and by Ross (1970) of the same material and others from the Auckland Is, do not diverge from the descriptions for *E. plicata* given by Darwin (1854) and Moore (1944). As well as the two extremes of shell shape noted by Moore (1944), viz., “tall, tubulo-conical with the orifice little smaller than the base” and the low conical form with an outwardly concave carina and an outwardly convex rostral plate (*E. rugosus* of Hutton 1879), Darwin specifically mentions forms with “the whole surface deeply corroded in which case they are finely striated longitudinally, or pitted, and are of a gray or brown colour”. Such forms have been collected in the Otago Harbour, and one is shown in Plate 11A. The features of these large, eroded specimens particularly, agree with the description of Ross (1970) for the Auckland I material. Indeed, inspection of the material in the National Museum collected by Dr Yaldwyn from Auckland I and studied by Ross confirms the identity. This growth-form seems to result from conditions near the limits of the ecological range into wave-sheltered situations, where settlement is sparse but, once established, the barnacles live for a long time, reach quite large sizes, and become much eroded. Normal yellowish and ribbed specimens of *E. plicata* have also been examined in collections by Professor G. A. Knox from the Auckland Is.

***Epopella kermadeca* n. sp. (Fig. 53)**

Elminius simplex. Linzey 1942a: 280.
not *Elminius simplex* Darwin, 1854.

MATERIAL EXAMINED: Cant. Mus.: the 2 shells on a fragment of a mussel collected from Sunday I, Kermadec Is, by W. R. B. Oliver and listed by Linzey (1942a), Cat. no. AQ.3320; bodies missing.

DISTRIBUTION: Kermadec Is, intertidal.

DESCRIPTION: *Shell:* Parietes with more-or-less pronounced external longitudinal folds; when uneroded, covered by cuticle and rows of cuticular hairs. Internally and basally, parietes have irregular and faint ribs. Chitinous laminae included in shell matrix in association with sheath, but without laminae or columns towards base. Radii narrow, with smooth or faintly crenate edges.

Opercular plates: Scutum slightly elongated transversely, articular ridge occupying about $\frac{1}{2}$ articular margin, and with prominent adductor ridge, adductor muscle pit, and crests for lateral depressor muscle. Tergum slightly waisted, with a wide, truncated spur set near basiscutal angle, wide articular furrow, and a few crests for depressor muscles.

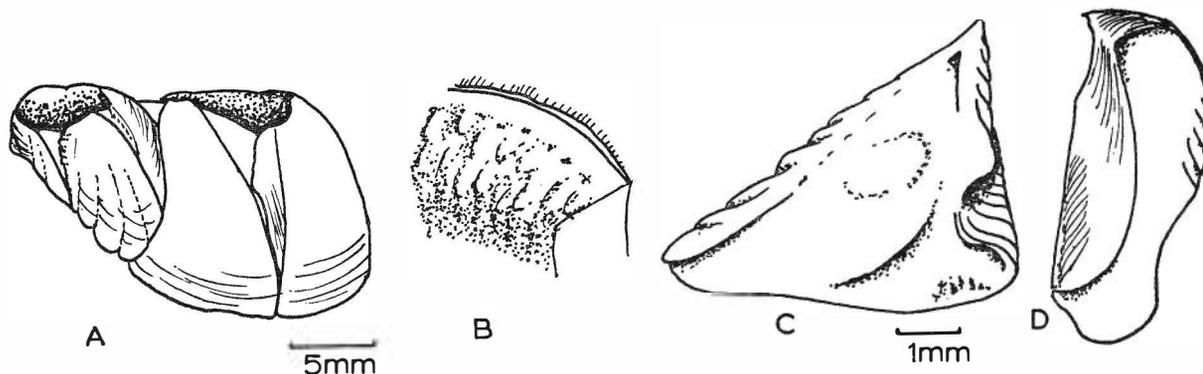


Fig. 53. *Epopella kermadeca* n.sp.: A, lateral view of the two type specimens; B, sketch of shell base, inner face to the left; C, D, inner views, scutum and tergum of the larger specimen in A.

HOLOTYPE: Canterbury Museum, cat. no. AQ. 3320.

REMARKS: Re-examination of the Kermadec material studied by Linzey (1942a) reveals that the specimens he identified as *Elminius simplex* differ from the descriptions of *E. simplex* given by Darwin (1854), Pope (1945), and Newman & Ross (1971), and specimens of *E. simplex* in the National Museum, in that the parietes are not permeated by yellow, chitinous ribbons such that "when broken transversely, a row of microscopically minute orange-coloured dots can generally be distinguished between the inner and outer laminae" (Darwin 1854). Furthermore, the terga of the present species are not as slender as that illustrated for *E. simplex* by Pope (1945). On the present evidence, I am compelled to distinguish the Kermadec specimens from both the Australian *E. simplex* and the mainland New Zealand *E. plicata*.

Genus *Tesseropora* (Pilsbry, 1916)

Parietal plates with 1 complete row of tubes; accessory but incomplete rows of tubes may be formed towards outer edge; radii solid and narrow.

***Tesseropora rosea* (Krauss)** (Plate 11C; Fig. 54)

Tetraclita rosea. Darwin 1854: 335 (see for earlier citations); Linzey 1942a: 280.

Tetraclita (Tesseropora) rosea. Pilsbry 1916: 260; Nilsson-Cantell 1927: 786; Pope 1945: 366.

MATERIAL EXAMINED: Nat. Mus.: 32 specimens from McCauley I, Kermadecs (J. C. Yaldwyn), and others from Sunday I, Kermadecs; and Lord Howe I (W. R. B. Oliver). Cant. Mus.: the specimens identified by Linzey from Sunday I, Kermadecs. BAF: 21 specimens, *Tui*, from Meyer I, Kermadecs.

DISTRIBUTION: Australia, from the Victoria/New South Wales border to Magnetic I on the Queensland coast (i.e., between 20°S and 38°S); Lord Howe I and the Kermadec Is. Intertidal. The South African record (Darwin 1854) requires confirmation.

DESCRIPTION: *Shell:* Conical, white tinged with pink; when eroded, pillared in upper part where secondarily filled parietal tubes exposed. Parietal tubes large and quadrangular; basally, outer shell laminae with longitudinal and approximate ridges, but without spines, extending into tubes.

Opercular plates: Scuta with occludent margin longest, long articular ridge, short but deep articular furrow, prominent adductor ridge that meets articular ridge towards apex to form a narrowing trench; and faint crests for lateral and sometimes rostral depressor muscles. Tergum with broad spur over $\frac{1}{2}$ width of basal margin and set slightly apart from basiscutal angle, prominent crests for carinal depressor muscles, and a very wide articular furrow.

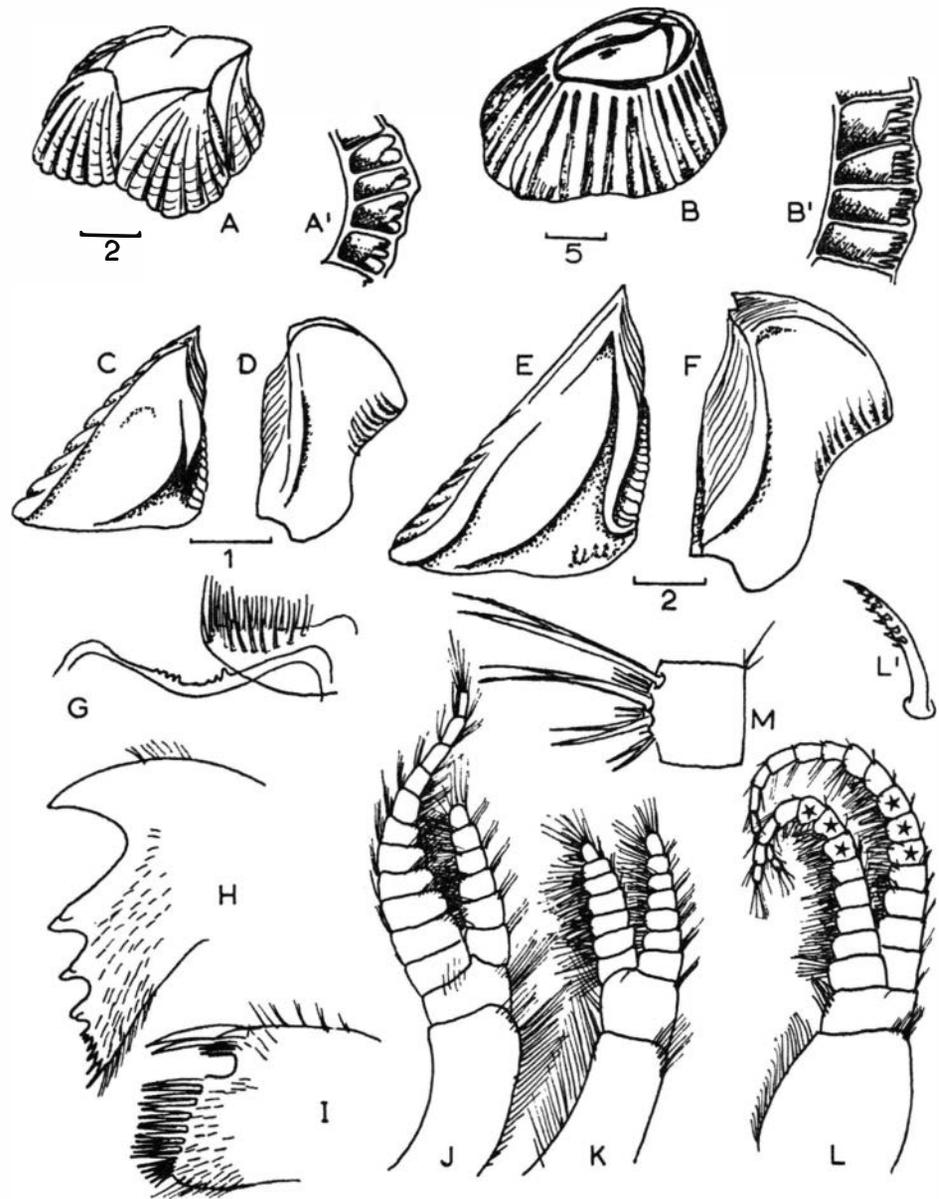
Mouthparts: Labrum with edge shallowly concave, with teeth on either side of centre. Mandible has 4 teeth, lower 3 with side teeth, and lower edge with a row of spines, of which lowest are longest. Maxillule bears 2 large and a few smaller setae at upper angle, and below subapical notch 2 groups of setae, upper group longer.

Cirri: Number of segments in rami of cirri of 2 specimens as follows, anterior ramus 1st:

shell diam.	I	II	III	IV	V	VI
7.6 mm	11, 7	7, 7	11, 17	13, 16	17, 17	18, 17
21.0 mm	20, 11	11, 11	21, 19	18, 20	24, 24	24, 24

Anterior ramus of cirrus I and both rami of cirrus III taper and end in elongate segments. Basal segments of these rami, and all segments of cirrus II have many setae. Intermediate segments of both rami of cirrus III have stoutly pectinate setae. Segments of cirri IV–VI have 3 major pairs and a minor, proximal pair of setae on anterior edge, with clumps of smaller setae at and between bases of larger pairs.

Fig. 54. *Tesseropora rosea* (Krauss): A, uneroded specimen, 7.6-mm diameter, with A' base of paries; B, eroded specimen, 21.0-mm diameter, with B' base of paries; C, D, inner views, scutum and tergum of specimen A; E, F, same of specimen B; G-L, appendages of specimen A—G, labrum and mandibular palp; H, mandible; I, maxillule; J, cirrus I; K, cirrus II; L, cirrus III, with L' pectinate setae from segments of cirrus III marked *; M, intermediate segment, ramus of cirrus VI (scales in mm).



REMARKS: The Kermadec Is specimens in no way depart from the descriptions of Australian *T. rosea* given by Darwin (1854), Nilsson-Cantell (1927), and Pope (1945). The Kermadecs are within the latitude range of the species on the east Australian coast, but so is the northern part of the New Zealand mainland. As yet, *T. rosea* has not been found on the mainland of New Zealand. *Tesseropora* is represented in New Caledonia and the Fiji Is by *Tesseropora pacifica* (Pilsbry), which develops secondary tubes towards the outer perimeter of the shell (Foster 1974). There are specimens of *T. pacifica* in the National Museum collected by C. Kensler from Minerva Reef, almost midway between the Fiji and Kermadec Is.

Genus *Tetraclita* Schumacher, 1817

Parietes permeated by many rows of tubes; radii solid, very narrow, or obsolete, and have oblique summits.

Tetraclita aoranga n. sp. (Plate 11D-F; Fig. 55)

MATERIAL EXAMINED: BAF: several lots on *Balanus tintinnabulum* from low tide on the Poor Knights Is (A. M. Ayling, R. Grace, and C. I. Milligan); 3 specimens under boulders at Anawhata (R. Willan). Nat. Mus.: 14 specimens on a shell of *B. tintinnabulum* from White I (M. A. Crozier).

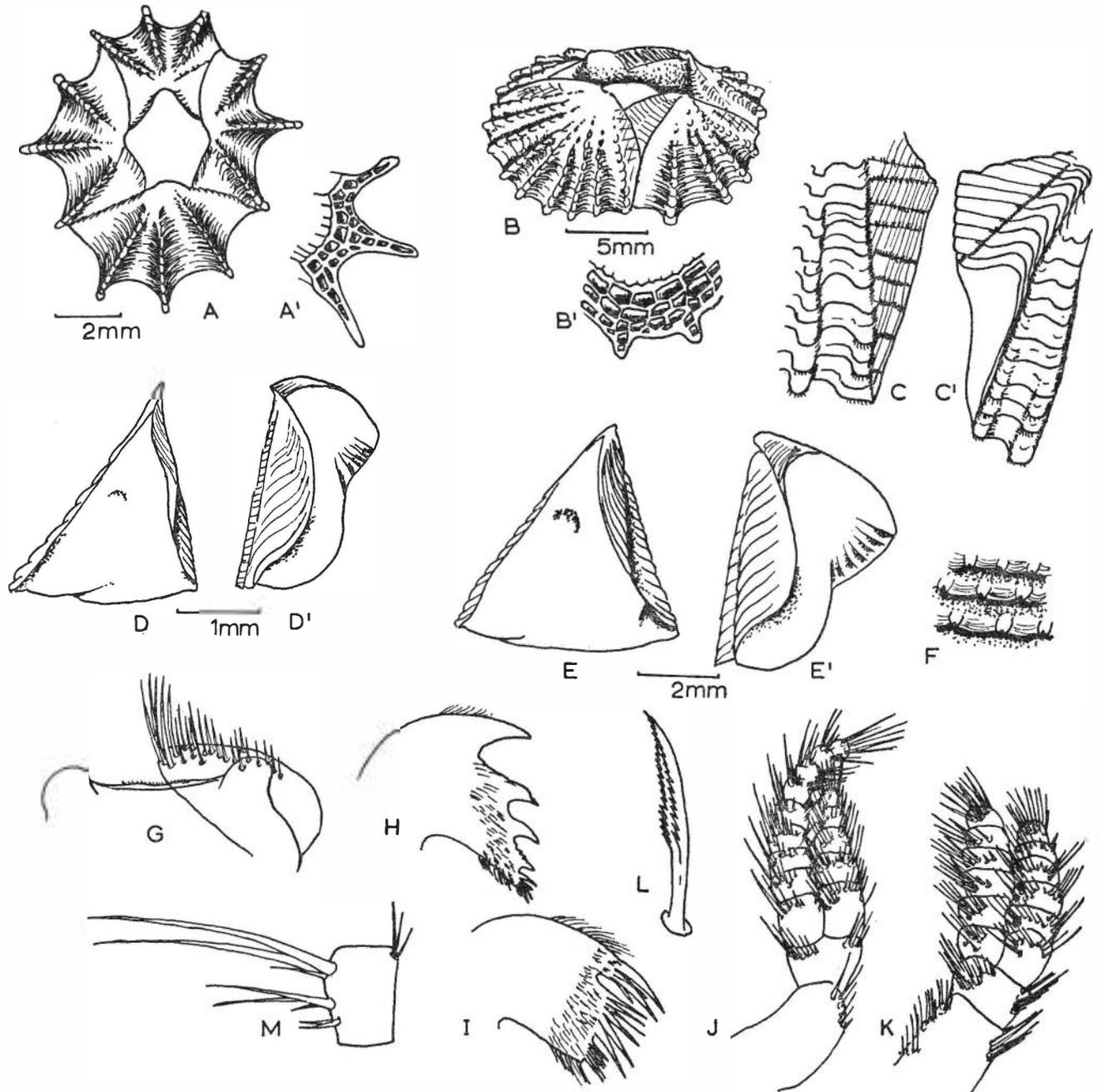


Fig. 55. *Tetracrita aoranga* n.sp.: A, apical view, shell of 10-mm diameter specimen, with A' base of paries; B, lateral view, shell of 20-mm diameter specimen, with B' base of paries; C, C', external views, radius of rostral plate (left) and ala of the adjacent latus; D, D', inner views, scutum and tergum of specimen A; E, E', same, specimen B; F, crenated external growth ridges, scutum in E; G—M, appendages of specimen B—G, labrum; H, mandible; I, maxillule; J, cirrus I; K, cirrus II; L, pectinate seta from cirrus III; M, 11th segment, anterior ramus of cirrus VI.

DISTRIBUTION: New Zealand, the Poor Knights Is (Fig. 66).

DESCRIPTION: *Shell*: Parietes with prominent, narrow, and widely spaced longitudinal ribs, 3 per plate in young specimens, in which basal circumference particularly stellate, but increasing in number in larger specimens; rows of rhomboidal tubes increase in number with growth; orifice enlarged by diametric growth of alae;

radii present, abutting on to adjacent parietes basally; summits of radii much more oblique than those of alae; base calcareous, without pores or radial striations.

Opercular plates: Tergum with wide articular furrow and rounded spur merging with basicutal angle. Scutum nearly equitriangular, with moderately prominent articular ridge, and faint adductor ridge near basal margin; depressor muscle crests absent; external growth ridges like overlapping curtains, gathered at intervals to give a beaded appearance.

Mouthparts: Labrum without a notch and without teeth. Mandible has 4 teeth, and a group of narrow spines at lower angle. Maxillule bears 2 large and a few smaller setae above a subapical notch on cutting edge, then 2 groups of setae below, of which uppermost is of longer setae.

Cirri: In a specimen of 10-mm basal diameter, cirri had following numbers of segments; anterior ramus 1st:

I	II	III	IV	V	VI
9,5	6,6	5,5	14,15	17,14	15,16

Cirri I–III similar in length, heavily setose on medial faces; strongly pectinate setae borne on distal segments of posterior ramus of cirrus I, both rami of cirrus II, anterior ramus of cirrus III, and most of segments of posterior ramus of cirrus III. No antenniform rami found. Segments of posterior cirri carry 3 pairs of setae on anterior edge, with a single, small seta at and between bases of larger 2 pairs. Penis as long as cirrus VI, annulate, and sparsely hairy for its entire length.

HOLOTYPE: Nat. Mus. NMNZ Z.Cr. 1967; Paratype (not syntype) NMNZ Z.Cr. 1968; from Poor Knights Is; also syntypes.

REMARKS: This species was first collected on *Balanus tintinnabulum* at the Poor Knights Is, where the latter species forms a low-tidal band of clumped specimens in surge channels shaded from direct insolation (C. Milligan, pers. comm.). It seems a more likely explanation of the identity of "*Tetraclita porosa* (Gmelin) Darwin (?)" of Cranwell & Moore (1938) from just this habitat, than the identity suggested by Foster (1967).

Apart from the hypobiotic habitat, *T. aoranga* superficially resembles *Tetraclitella* spp. in the buttress-like parietal ribs, the low form of the shell, and the lack of depressor muscle crests on the scutum. However, tubiferous radii are not developed, so this species must be classified in *Tetraclita*, as currently defined. In tetraclitids that live in more sun-exposed places, orifice enlargement is by apical erosion, even though there is limited diametric growth of the alae in juveniles. In *T. aoranga*, diametric orifice enlargement occurs throughout ontogeny, and is aided by secondary alar growth. This manner of shell growth may have preceded the development of radii to overlap the alae as in *Tetraclitella*. *T. aoranga* may lie close to a common ancestor to *Tetraclita* and *Tetraclitella*; the closeness of the tergal spur to the basiscutal angle seems a primitive feature.

Genus *Tetraclitella* Hiro, 1939

Parietes discrete, permeated by many rows of longitudinal tubes; radii broad, completely overlapping adjacent alae, and have uniform-sized tubes like those of parietes; radii with summits parallel to base.

Tetraclitella purpurascens (Wood) (Plates 11F, 12A, B; Fig. 56)

Conia depressa Gray, 1843: 269.

Tetraclita purpurascens. Darwin 1854: 337; Hutton 1879: 828; Weltner 1899: 443; Jennings 1918: 61; Linzey 1942a: 279; Pope 1945: 367; Foster 1967: 83.

not *Tetraclita purpurascens* forma *breviscutum* Broch, 1922: 337 (= *Epopella plicata*).

MATERIAL EXAMINED: NZOI: Stn E809. Nat. Mus.: specimens from McCauley I, Kermadecs (J. C. Yaldwyn), and from Hen I, Waiwera I, Piha, Cape Runaway, Worser Bay in Wellington Harbour, Queen Charlotte Sound, Sandfly Bay on the Otago Peninsula, Dusky Sound, and Stewart I. Cant. Mus.: those from the Kermadecs listed by Linzey (1942a), and others from mainland localities. BAF: numerous specimens from shore collecting from the far north to Otago Peninsula.

DISTRIBUTION: Intertidal in Australasia; in Australia, on southern shores north to latitude 25° S; in New Zealand, from Kermadec Is to Stewart I (Fig. 46).

DESCRIPTION: *Shell:* Low conical pale purple or dirty white in uneroded and eroded specimens respectively; surface with longitudinal, radiating ribs, which may have transverse growth ridges lined with chitinous hairs, but with erosion surface features become indistinct. Radii at first solid, but later develop horizontal tubes, externally striated at 90° to base. Base not calcified.

Opercular plates: Scuta transversely elongated to varying degrees, with a slight articular ridge, a shallow articular furrow, a long adductor ridge, faint crests for lateral depressor muscles, and externally with distinct growth ridges, and sometimes 1 or 2 slight apicobasal furrows. Terga smaller than scuta, with a short, broad, rounded spur, a faint articular ridge, a wide articular furrow, prominent crests for carinal depressor muscles which depend below basal margin, and externally with faint growth lines, no furrows, but faint striations backing muscle crests.

Mouthparts: Labrum has a median depression and bears a few teeth on crest on each side. Mandible with 4 teeth, of which lower 3 may have more than 1 cusp and lowest may be insignificant, lower angle with spines of various lengths, distal-most rather longer than others. Maxillule bears 2 or 3 large setae at upper angle, major setae on cutting edge below notch almost as long.

Cirri: Anterior ramus of cirrus I about $\frac{1}{2}$ as long again as posterior ramus. Rami of cirri II and III all subequal, about as long as anterior ramus of cirrus I. All rami of anterior cirri heavily setose. Except for anterior ramus of cirrus I, distal 1 or 2 segments of rami of cirri I–III bear a few pectinate setae. Basal segment of pedicel of cirrus III particularly wide and oval. Cirri IV–VI have subequal rami, segments with 3 pairs of setae on anterior edge and tufts of smaller setae at and between bases of the pairs, and sometimes,

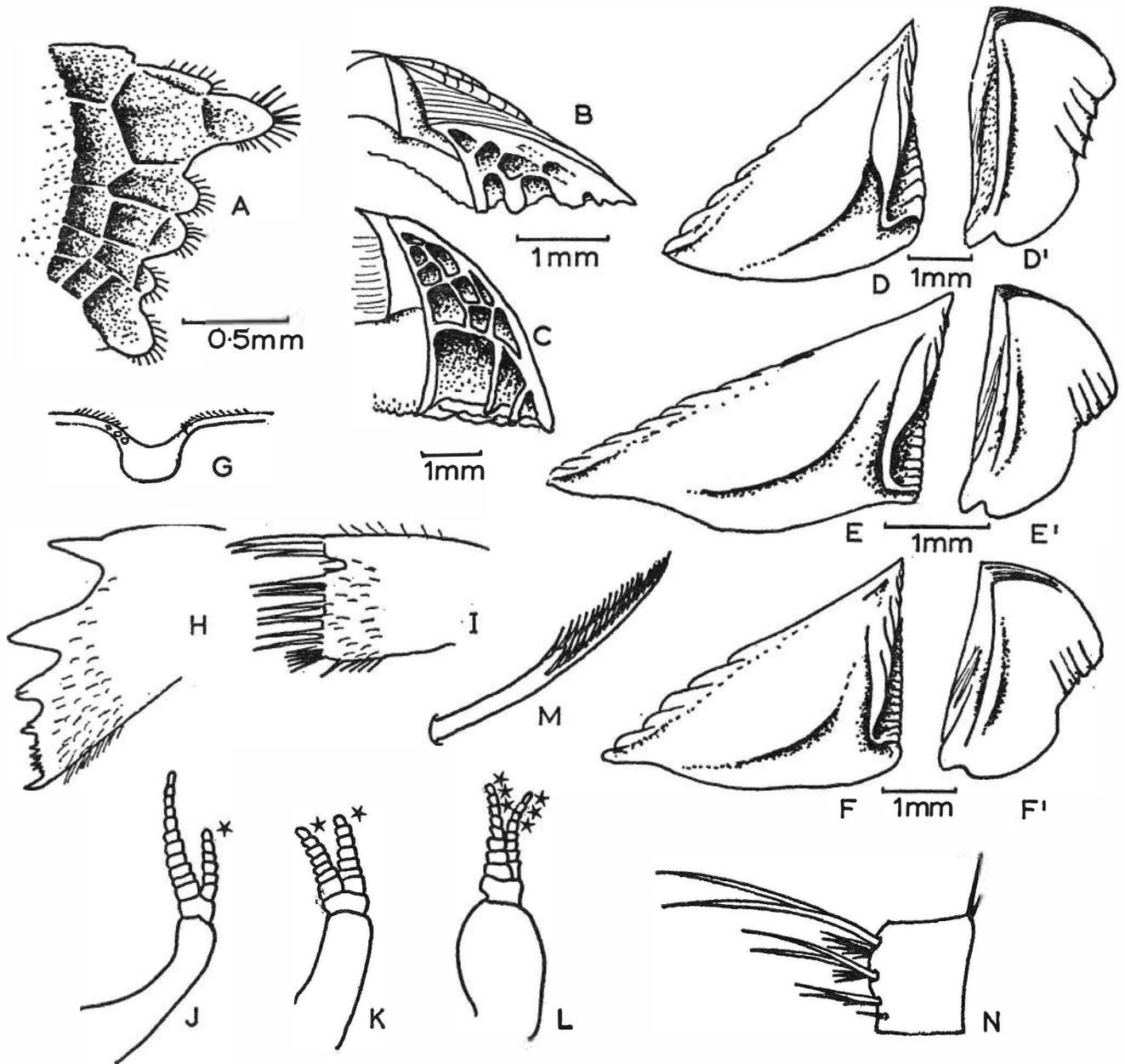


Fig. 56. *Tetracitella purpurascens* (Wood): A, basal view, latus of 5-mm diameter specimen; B, sutural edge, radius of rostral plate, 10-mm diameter specimen; C, same, 15-mm specimen; D-F, scuta and terga of three different specimens, to show variation in the degree of scuta elongation; G, labral crest; H, mandible; I, maxillule; J, cirrus I; K, cirrus II; L, cirrus III; M, pectinate seta from the segments of cirri I-III marked *; N, intermediate segment of cirrus VI.

particularly on cirrus VI, a single, extra, medial and basal seta. Penis long and annulated.

REMARKS: This is a common barnacle in New Zealand, occurring over the lower half of unsilted shores as a characteristic part of the "hypobion", i.e., the fauna under stones, in crevices, or in caves; in effect, in places which are not exposed to excessive desiccation risk. It is frequently found attached to the capitular plates of *Calantica spinosa*, and on the shells of mussels. The species was first recorded from New Zealand waters by

Gray (1843) as *Conia depressa* on *Haliotis* shells from the Bay of Islands.

The eroded nature of the specimen figured by Darwin (1854, pl. 11, fig. 1a) has not been re-encountered amongst New Zealand material. Dry Australian specimens in the National Museum labelled *Tetracitella purpurascens* by Pope are all of this appearance, but no differences could be detected in the features of the opercular valves. It may be that the Australian and New Zealand forms are different.

The distribution of *Tetraclitella purpurascens* in Australasia indicates that it is a cool temperate species. There are some early records of the species from more northern seas, but the oriental forms are now recognised as a separate species, *T. chinensis* (Utinomi, 1949). The locality for specimens of *T. purpurascens* on *Pollicipes mitella* from the South Atlantic Ocean by Nilsson-Cantell (1921) was later corrected to Java (Nilsson-Cantell 1930a), and it seems that these might be the same as the variety *multicostata* (see Nilsson-Cantell 1930a) from the East Indies, and since identified from the Fiji Is (Foster 1974). This latter Malaysian-to-west-Pacific form seems a valid species, and holds a similar geographic relationship to *T. purpurascens* as *Tesseropora pacifica* does to *Tesseropora rosea*.

Family BALANIDAE Leach, 1817

Shell wall of 6 or 4 plates, separate or totally concrescent, solid or permeated by longitudinal tubes, which contain living tissue or are secondarily filled with calcareous and chitinous material; radii more-or-less developed; rostral plate overlaps adjacent laterals. Labrum not bullate, its crest with a medial, deep, V-shaped incision; cirrus III resembles II more than IV, its rami usually not antenniform; caudal appendages absent; penis with a basidorsal point (except in *Elminius*).

REMARKS: Newman *et al.* (1969) recognise 4 subfamilies of the Balanidae. The tetraclitids have since been given family ranking, leaving the Chelonibinae, Balaninae, and Coronulinae. The Chelonibinae, or turtle barnacles, have not been recorded in New Zealand. They are of interest because the rostral plate is tripartite, indicating the primitive 8-plated shell condition for the Balanidae, like that of *Pachylasma* does for the Chthamalidae (see Fig. 72). In the Balaninae and Coronulinae the rostral plate is solid, and most likely represents the rostral plate fused with the rostrum.

Subfamily BALANINAE Leach, 1817

Rostral plate without fissures; scuta and terga fill orifice, those on each side articulate or joined together; shells solid or porous, or secondarily filled; sheath occupies a part of inner parietal wall and has its lower edge straight.

Genus *Elminius* Leach, 1825

Shell plates 4, loosely articulated, thin and solid; radii with smooth edges; penis without basidorsal point.

REMARKS: Darwin (1854) assigned 4 Southern Hemisphere species to *Elminius*. Hutton's (1879) *Elminius sinuatus* and *E. rugosus* are synonyms of two of Darwin's species. Pilsbry (1916, p. 261) mentions *Elminius cristallinus*, described by Gruvel from the Azores, but nothing more has been made of this unusual northern record, and it may be no more than a juvenile *Balanus*. It is true that *Elminius modestus* now occurs in the northern hemisphere, but it is clear that this has been the result of its introduction on shipping.

Following the proposal of Ross (1970), *Elminius plicatus* Gray is now placed in the genus *Epopella* in Tetraclitidae, and along with it must go *Elminius simplex* Darwin. This move strengthens the diagnosis of the Balanidae, and overcomes a lot of inexactness in the discussion of the genus *Elminius* given by Darwin (1854). The genus is now represented by only two certain species: the type (subsequent determination by Pilsbry 1916) *Elminius kingii* Gray, from temperate South America; and *Elminius modestus*, initially from temperate Australasia.

Elminius modestus Darwin (Plate 12C; Fig. 57)

Elminius modestus Darwin, 1854: 350; Hutton 1879: 328; Filhol 1885: 489; Jennings 1918: 62; Nilsson-Cantell 1921: 351; Nilsson-Cantell 1930b: 212; Moore 1944: 329; Powell 1947: 42; Southward & Crisp 1963: 24; Foster 1967: 84; Utinomi 1968a: 178.

Elminius sinuatus Hutton, 1879: 328; Broch 1922: 342.

MATERIAL EXAMINED: NZOI: Stns E795, E808, E815. BAF: specimens from shores in the far north to Stewart I, and from Britain. There are numerous specimens in the Auckland, National, Otago, and Canterbury Museums.

DISTRIBUTION: New Zealand: North I, South I, Stewart I. Chatham Is record by Young (1929) requires confirmation; Knox (1963, p. 391) states *E. modestus* to be absent from the Chathams (Fig. 46). Australia: South Australia, Victoria, Tasmania, and New South Wales. Recently introduced to Europe, and South Africa (Sandison 1950).

DESCRIPTION: *Shell:* Conical to tubular, white or grey; basal outline sinuous; plates thin, and usually with 2 wide, longitudinal and whiter folds, but there may be numerous ridges basally on each plate in crowded specimens; internally without ribs; radii with very oblique summits, and growth lines parallel to parietal edge of adjacent plate, so that only inferior margin of radius abuts smoothly against adjacent plates; alae wider than radii, but also have oblique summits; orifice diamond-shaped in outline, and toothed; base membranous.

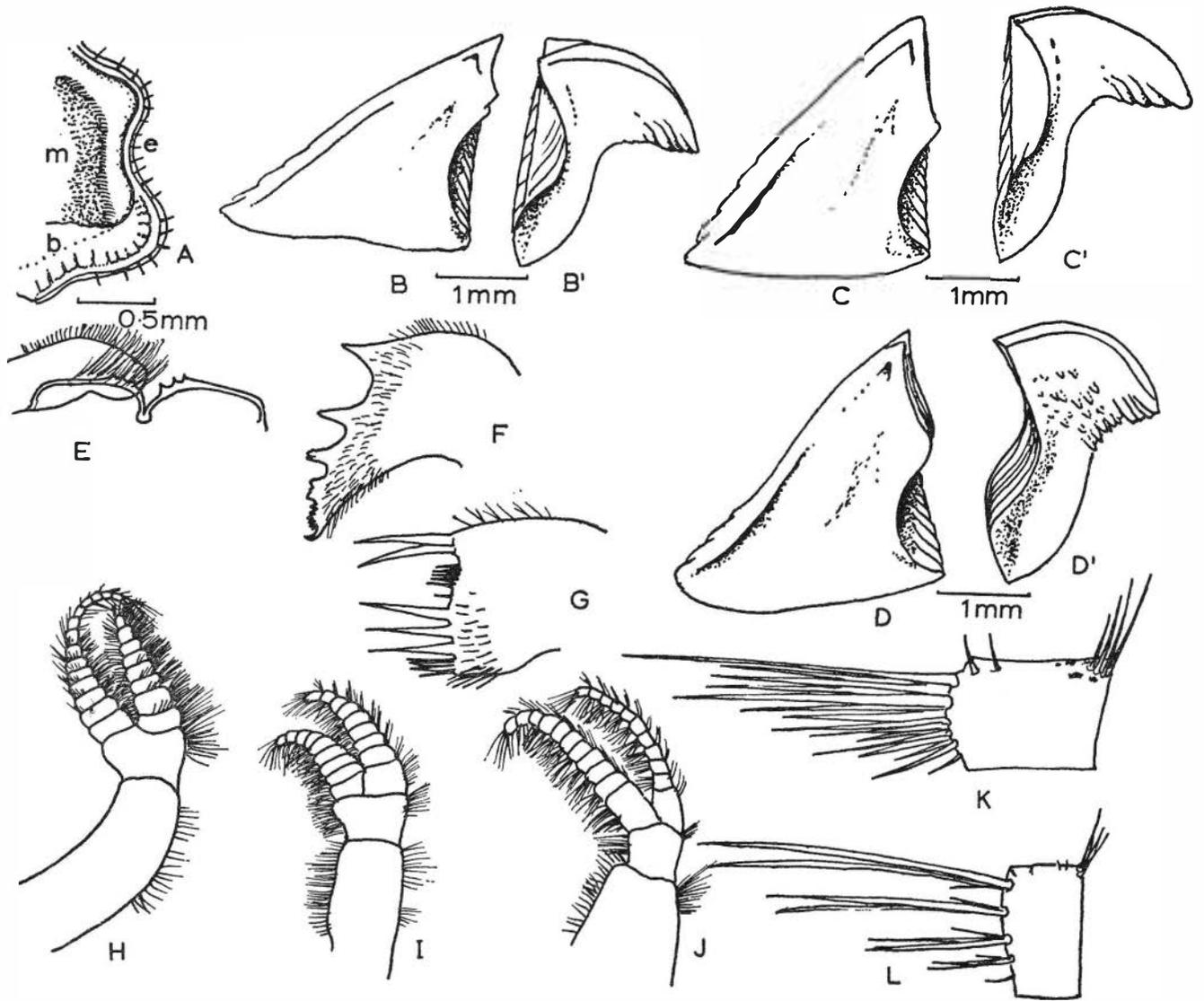


Fig. 57. *Elminius modestus* Darwin: *A*, basal edge, latus of uneroded specimen of 6.5-mm diameter, with fixation muscle fibres (*m*), basal membrane (*b*) attached in the lower part, and external integument with chitinous hairs (*e*); *B-D'*, inner views, scutum and tergum pairs from same-sized specimens of 5.5-mm diameter but showing different degrees of erosion, increasing from *B* through *C* to *D*; *E*, labrum and mandibular palp; *F*, mandible; *G*, maxillule; *H*, cirrus I; *I*, cirrus II; *J*, cirrus III; *K*, outer view, intermediate segment, anterior ramus of cirrus III; *L*, same, cirrus VI.

Opercular plates: Scutum triangular; externally with 2 longitudinal, dark bands; internally with a moderately prominent articular ridge, but without an adductor ridge or pits or scars for depressor muscles. Tergum with wide articular furrow; prominent articular ridge confluent with basitergal angle which is protruded from basal margin and folded on itself to form a channelled spur confluent with basitergal angle; concave basal margin with crests for depressor muscles, depending at carinal end; carinal margin convex and somewhat thicker than central part of valve, which bears minute, calcareous projections.

Mouthparts: Labrum has 2 or 3 teeth on its crest on each side of central notch. Mandible has 5 teeth, 5th

set close to a series of 4 or 5 spines, last at lower angle curved and more prominent. Maxillule has a notch with a row of short setae beneath an upper pair of stout setae; rest of cutting edge with 3 major setae on upper part and a group of shorter setae at lower angle.

Cirri: Cirrus I has anterior ramus longer than posterior ramus. Cirrus II has subequal rami, about as long as posterior ramus of cirrus I. Cirrus III has anterior ramus slightly longer than posterior ramus, which is as long as anterior ramus of cirrus I. Cirri IV-VI all subequal in length, segments have 4 pairs of setae on anterior face and, in intermediate segments, an extra, small, proximal pair of setae no longer than short spines at and between bases of major pairs. Penis without a basidorsal point.

REMARKS: *Elminius modestus* is a common barnacle on New Zealand shores. It is not present on the Kermadec Is, nor on the islands south of Stewart I. In Australia it is apparently not present much north of Port Jackson (Pope 1945). *E. modestus* is especially characteristic of shores where wave action is not too severe, and this correlates with the weak construction of the shell. In contrast to the other zoning species on New Zealand shores, viz., *Chamaesipho brunnea*, *C. columna*, and *Epopella plicata*, the present species also occurs subtidally, and may be the dominant barnacle in harbour-fouling communities. Because of the importation of this species to European ports as a part of ship fouling, *E. modestus* is a well-studied barnacle. Much is known about its rate of dispersal, rate of growth, breeding, and physiological ecology, but little has been made of its phylogenetic status. Despite the subdivision of Darwin's genus, and the removal of 2 of the species to the Tetralitidae, Darwin's 4 species still have some common primitive features: the solid shell, the pectinated lower angle of the mandible, the position of the tergal spur at the basiscutal angle, and the way the radii and adjacent parietal edges abut without interlocking. Although included in the Balanidae by virtue of the structure of the labrum, *Elminius*, as herein defined, still stands apart from the majority of the Balaninae by the lack of a basidorsal point to the penis, as well as by the weak shell construction. *Elminius* may thus be a derivative of an early 6-plated balanid, before the articulation of radii and adjacent parietes occurred (see Fig. 72), and may warrant separate subfamily ranking.

Genus *Balanus* da Costa, 1778

Shell of 6 interlocked wall plates, including paired latera and carinolatera, and a carina and rostral plate; plates solid, or with tubes in direction of shell growth; radii have denticulate sutural edges; penis generally with a basidorsal point.

REMARKS: It has long been held that the large number of species of *Balanus* represents a number of diverse lineages. Newman *et al.* (1969) list 12 subgenera, and they appear to have left out *Bathybalanus* Hoek. No doubt some synonymies will be established; Henry & McLaughlin (1967) suggest that *Hesperibalanus* and *Solidobalanus* are the same, and Newman & Ross (1971) suggest that *Bathybalanus* and *Solidobalanus* are the same. Tarasov & Zevina (1957, cited in Newman & Ross 1971) include *Metabalanus* with *Chirona*. Clarification of balanid phylogeny will probably come with rethinking on the place of these solid-walled or poreless balani. On the other hand, subgenera like *Megabalanus*, *Balanus*, and *Conopea* seem more integral, and probably warrant full generic recognition as much as does *Acasta*.

The New Zealand material contains 2 solid-walled species, *Balanus (Austrobalanus) vestitus* and *B. (Solidobalanus) auricoma*, 3 species of *Megabalanus*, and 3 of *Balanus* (sensu stricto). None of these are new, and give no new information for reinterpretation of 6-plated balanid phylogeny.

The tubes in the plates of *Balanus* are essentially in a single row, and are bordered by the outer primary shell lamina and the inner shell lamina, the latter formed by the lateral growth of the inner ends of the septae that demarcate the tubes. A porous structure can develop in the parietes, the radii, and the base, and the tubes always run in the direction of shell growth. There is a tendency for secondary filling of the tubes, and this prevents the opening of the tubes when apical attrition of the parietes and radii occurs. The combinations of porosity and solidity of the parietes and radii can in some cases be used to characterise the subgenera. For example, *Megabalanus* has both the parietes and radii with open tubes, but *Balanus* (sensu stricto) has tubiferous parietes and the tubes of the radii secondarily and completely filled up. *Balanus* thus seems an advancement over *Megabalanus*. Yet, such characters alone are not the crux of the subgenera. For example, some specimens of *Balanus*, like *B. (Megabalanus) campbelli*, have the radiolar tubes secondarily filled up, the condition of the subgenus *Balanus*, yet the cirri confirm the affinity with other species of *Megabalanus*. The subgenera quoted herein are those assigned by Pilsbry (1916).

Among the fossil barnacles known from New Zealand, Withers (1924) describes *Balanus (Chirona) zelandica* from the Miocene, *Balanus (Megabalanus) tubulatus* from the Pliocene, and *Balanus (Balanus) amphitrite acutus* from the Miocene and Pliocene. These are not considered further herein. Withers (1924) also describes fossils of *Balanus (Megabalanus) decorus* from the Miocene and Pliocene, and *Balanus (Balanus) amphitrite* from the Pliocene. These two species are part of the Recent fauna. The specimens of *Balanus (Megabalanus) tintinnabulum* and *Balanus (Balanus) trigonus* from "Otago", described by Withers (1924), are probably Recent specimens, and are probably not from Otago.

Balanus (Austrobalanus) vestitus Darwin

(Plate 12D, E; Fig. 58)

Balanus vestitus Darwin, 1854: 286; Hutton 1879: 328; Weltner 1899: 445; Gruvel 1905: 248; Pilsbry 1916: 219; Broch 1922: 322; Foster 1967: 83.

Balanus (Austrobalanus) vestitus Withers, 1924: 36; Withers 1953: 77; Newman & Ross 1971: 169.

MATERIAL EXAMINED: NZOI: Stns A702, A705, A713, A746, A747, A751, B181, B260, B271, C617, C653, C856, D52, D59, D62, D80, D83, D109, D121, D185, D907, E106, E817, G655, G660, G661, G662, G669, G673, G674, G680, G681, G685, G686, G695, G707.

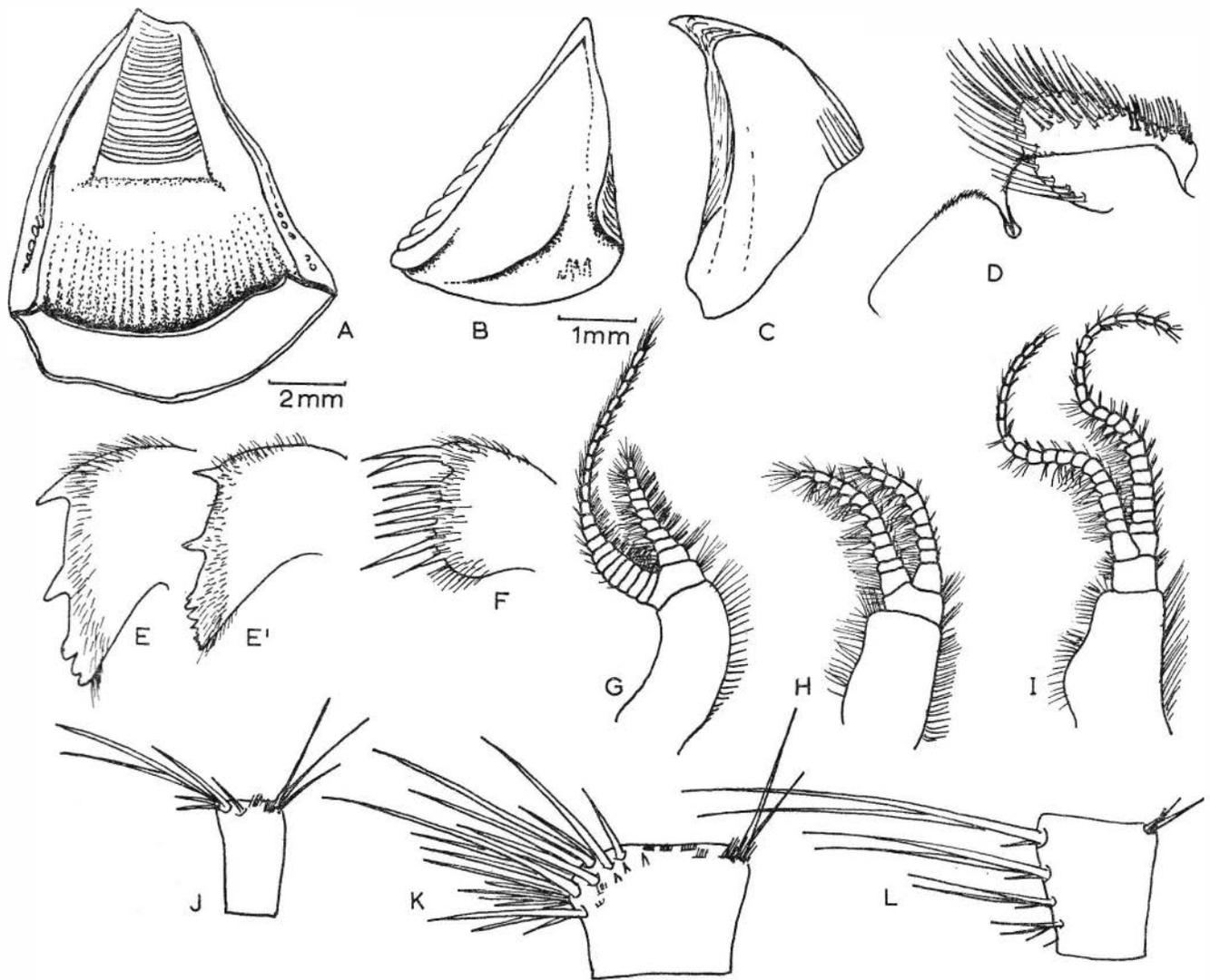


Fig. 58. *Balarus vestitus* Darwin: A, inner view, rostral plate with portion of calcareous base attached; B, C, scutum and tergum, 8-mm diameter specimen; D, labrum and mandibular palp; E, E', mandibles of two different specimens; F, maxillule; G, cirrus I; H, cirrus II; I, cirrus III; J, 17th segment, anterior ramus of cirrus III; K, 9th segment, anterior ramus of cirrus III; L, intermediate segment of a ramus of cirrus VI.

Shells only from Stns A704, A715, A748, A750, B176, B189, B192, B195, B197, B562, B566, B569, B601, B609, C118, C125, C591, C595, D1, D32, D53, D55, D57, D58, D78, D876, D897.

Nat. Mus.: Specimens from Mercury Bay, Chatham Is, and Auckland Is, and from various mainland localities. BAF: Specimens collected on shores from North Cape to Otago Peninsula, and on shelf off Otago Peninsula.

DISTRIBUTION: New Zealand: North Cape to Campbell I, including Chatham Is; shore to 400 m (Fig. 59).

DESCRIPTION: *Shell*: Conical, generally with a very small orifice; radii very poorly developed or absent, interparietal space a mere fissure; occludent edges of parietes dentate; alae well developed; plate white, with more-or-less pronounced pink tinting, especially apically and on alae and sheath, but whole shell covered by a

hairless, yellow, chitinous epidermis; plates solid, and externally smooth or ribbed; sheath occupies about $\frac{1}{2}$ inner parietal surface; regular internal ribs interlock basally with a solid calcareous base.

Opercular plates: Set well within orifice, often with only beaked apices of terga apparent.

Tergum has a long, concave articular margin, articular ridge very slight, rostral margin convex, 5 or 6 well developed crests for carinal depressor muscles; a short, truncated spur, fully $\frac{1}{3}$ or more basal width of valve, and standing close to basiscutal angle.

Scutum longer apicobasally than laterally; externally with closely set growth ridges; internally with a slight articular ridge occupying about $\frac{2}{3}$ of tergal margin; basitergal angle rounded; a few distinct crests for lateral depressor muscle, adductor ridge well developed, curving below a well marked adductor muscle scar almost to basal margin and towards rostral angle.

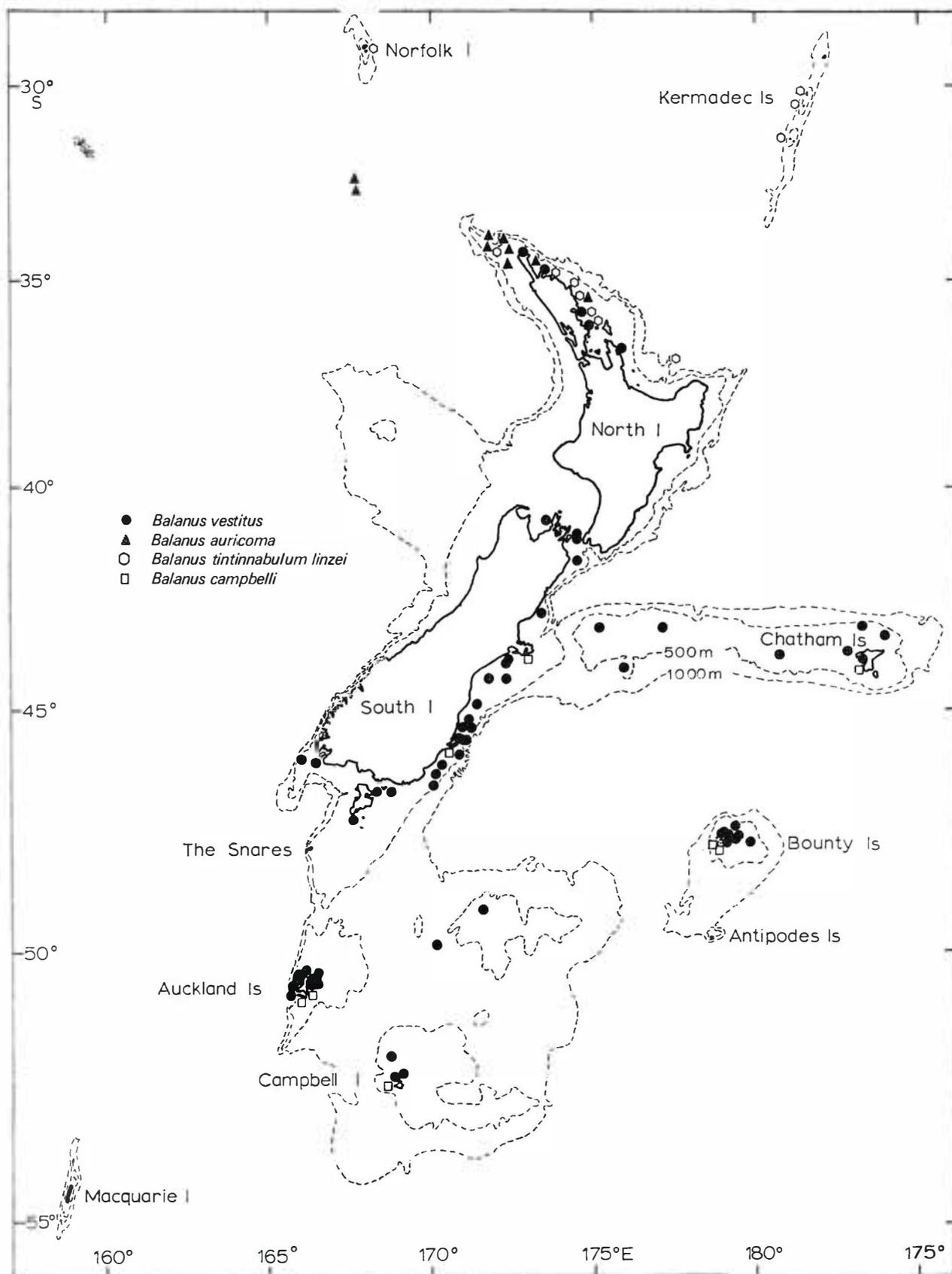


Fig. 59. Records of some *Balanus* species in the New Zealand region.

Mouthparts: Labrum deeply notched, with up to 4 small teeth on crest on either side of notch. Mandibular palps wide and leaf-like. Mandibles have 3 upper teeth nearly equally separated, but 3rd tooth set close to a thickened lower angle containing 3 more cusps. Maxillule has 2 large setae at upper angle, separated by a more-or-less pronounced notch from a single series of setae, of which penultimate one is as large as largest at upper angle. Maxillae elongate, concave on their anterior edge.

Cirrus I with anterior ramus at least $2\times$ as long as posterior ramus, no segments protuberant, and distal ones on anterior ramus elongate, with medial setae confined to distal edge of each segment. Cirrus II with rami a little longer than posterior ramus of cirrus I, with segments slightly protuberant anteriorly, protuberant parts with copious medially and anteriorly directed setae. Cirrus III with basal segments similar in shape and setation to those of cirrus II; distal segments, of which there may be so many for cirrus to equal in length the more posterior cirri, elongate, with distal, anterior, and posterior tufts of setae. Cirri IV–VI subequal; their segments with 3 or 4 pairs of setae, sometimes with an extra single, proximal seta on anterior edge; sometimes an articulated, short, and centrally placed seta on distal border; posterior margin at base of rami, and both anterior and posterior faces of pedicel segments, provided with small, upwardly directed spines which gives a distinct serration when viewed from side. Penis long, with a small basidorsal point.

REMARKS: This species is widely distributed in the shallow seas around New Zealand, commonly occurring on mollusc shells, worm tubes, crab carapaces, and stones. It is surprising that NZOI shelf-dredging in the northern part of New Zealand has not yielded this barnacle; it certainly occurs on the east Northland coast, having been taken at a number of low tidal sites and found washed up on shells. New South Wales was given as a locality by Darwin (1854), and this locality has been quoted by Pilsbry (1916), Gruvel (1905), and Broch (1922, p. 351). Miss E. Pope (pers. comm.) has not identified this species from Australian shores, nor from dredged material. This is apparently another case of confused early (pre-Darwin) locality records.

The absence of radii may represent the primitive condition, before lateral growth of radii occurred in the balanid lineage (see Fig. 72). The characteristic yellow, chitinous epidermis, formed at the junction of the base and the parietes and ending up lying outside the shell, recalls the chitin included in the shell of *Aptolasma* and *Epopella*. The antenniform nature of the rami of cirrus III is somewhat exceptional in *Balanus*, and again recalls the occurrence of antenniformity in *Aptolasma*, *Epopella*, and other chthamalid and tetracelitid genera. The basiscutal position of the tergal spur is taken to be its primitive position. In contrast to other species of *Austrobalanus*, *B. (A.) vestitus* has a thick, calcareous base.

The beautiful *Balanus imperator* of Australian shores

also exhibits antenniformity in cirrus III, and has a very thin base. This large, intertidal barnacle is remarkable not only for its shell colour, but also for the development of thick parietes, with the broad, basal part provided with depending plates and points. This is also a feature of the South American species *Balanus flosculus* Darwin, the only other species in the subgenus, and of *Epopella plicata*. *Epopella* is now considered to stem from close to the base of tetracelitid lineage. Darwin (1854, p. 352) noted the similarity of *Epopella plicata* not only to porous tetracelitids such as *Tetracelita porosa*, but also to *Balanus imperator* and *B. flosculus*, and when he discussed the affinities of *B. imperator* (Darwin 1854, p. 290) he remarked on the resemblance to *Tetracelita* and *Chelonibia*.

All the foregoing suggests that *Austrobalanus* retains many basic features. It can hardly be coincidence that the species considered primitive in both tetracelitid and balanid lines have restricted distributions in Australia, New Zealand, and South America.

***Balanus (Solidobalanus) auricoma* Hoek**

(Plate 12F; Fig. 60)

Balanus auricoma Hoek, 1913: 198; Broch 1922: 323; Nilsson-Cantell 1938: 49.

Balanus (Solidobalanus) auricoma. Broch 1931: 71.

MATERIAL EXAMINED: NZOI: Stns E292 (2 specimens), E312 (27), E861 (1), E864 (4); and fragments from E265, E319, E333, E349. BAF: attached to antipatharian, Poor Knights Is.

DISTRIBUTION: From Persian Gulf through Malaysian waters to Australasian seas, 85–376 m. In New Zealand, in north-eastern waters 62–376 m (Fig. 59).

DESCRIPTION: *Shell:* Parietes and radii without tubes, externally white with pink to red transverse lines in groups on low longitudinal ribs, giving parietes appearance of radiating rows of white blotches; radii well developed with growth lines parallel to base, and with oblique summits; radii have denticulate sutural edges, coloured white or pink; alae and sheath deep pink; parietes ribbed internally and basally; base calcareous, without tubes or pores.

Opercular plates: Scutum longer apicobasally than laterally; with a long but not very prominent articular ridge; without an adductor ridge or crests for depressor muscles. Tergum has a produced basiscutal angle, with spur placed quite close to angle and protruding beyond it; a slight articular ridge; a few short crests for carinal depressor muscles close to basicarinal angle; slightly roughened internally and apically. Along apical occludent edges of both scuta and terga persistent epidermal hairs present.

Mouthparts: Labrum bears 2 to 5 teeth on either side of notch. Mandible has 4 teeth, 2nd to 4th with accessory

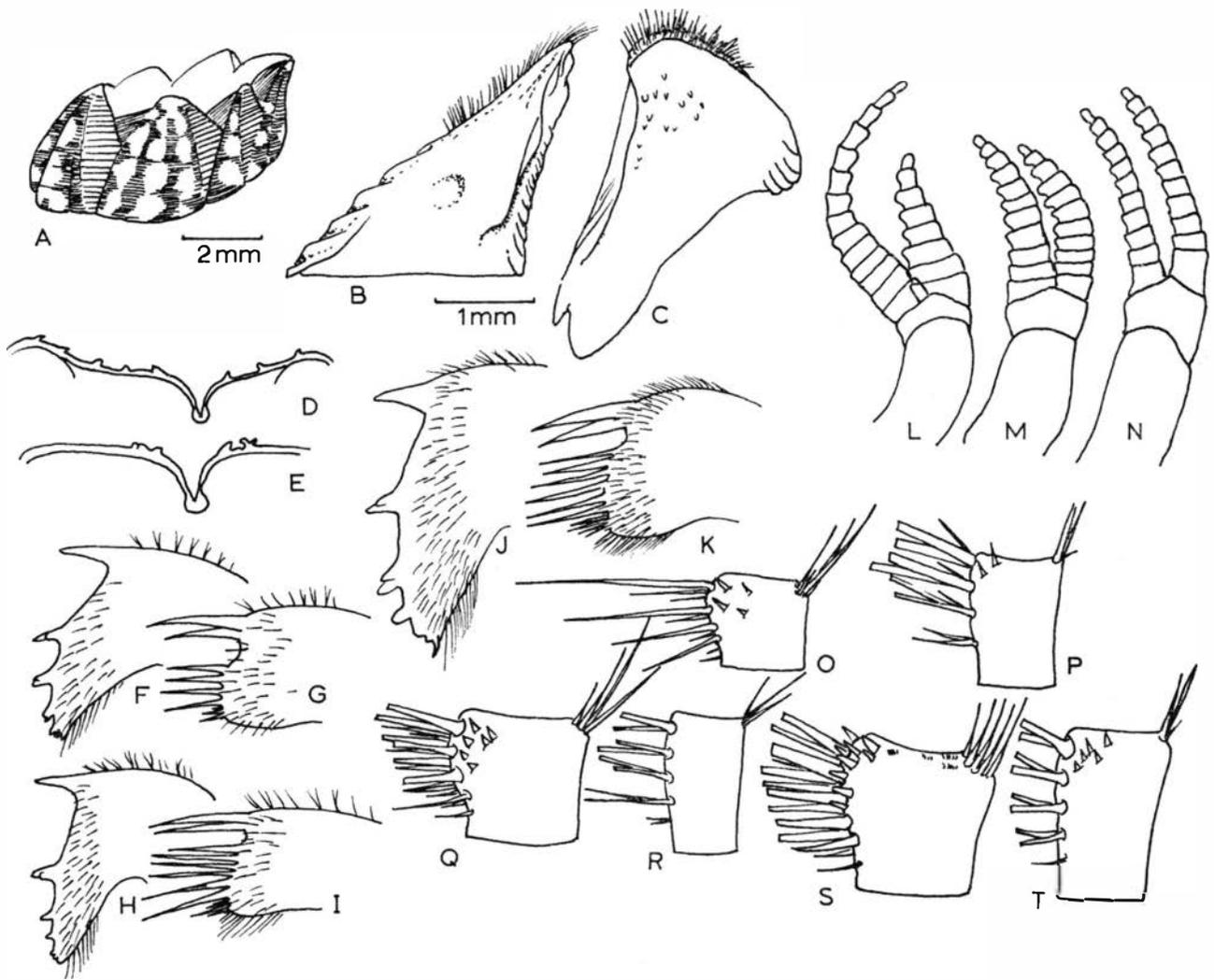


Fig. 60. *Balanus auricoma* Hoek: *A* lateral view, shell of 6-mm specimen; *B, C*, inner views, scutum and tergum of specimen *A*; *D, E*, labral crests of a 2.2-mm and 16.0-mm diameter specimens respectively; *F, G*, mandible and maxillule, 2.2-mm diameter specimen; *H, I*, same, 6.5-mm diameter specimen; *J, K*, same, 16.0-mm diameter specimen; *L, M, N*, cirrus I, M, cirrus II, and *N*, cirrus III of 6.5-mm diameter specimen; *O*, outer view, intermediate segment, posterior ramus of cirrus III, 2.2-mm specimen; *P*, same, cirrus IV of 2.2-mm diameter specimen; *Q*, same, cirrus III of 6.5-mm diameter specimen; *R*, same, cirrus IV of 6.5-mm diameter specimen; *S*, same, cirrus III of 16.0-mm diameter specimen; *T*, same, cirrus IV of 16.0-mm diameter specimen.

cusps, a molariform lower angle with 3 more-or-less blunt cusps in a series, and a row of stiff setae on lower edge. Maxillule with 2 large setae at upper angle, a more-or-less distinct notch with a series of long setae and a basal bunch of shorter setae on main cutting edge.

Cirri: Cirral counts of 4 specimens as follows, anterior ramus 1st:

shell diam.	I	II	III	IV	V	VI
2.2 mm	8, 6	7, 7	9, 9	12, 13	15, 16	16, 17
2.5 mm	10, 6	7, 7	9, 8	13, 15	—, —	17, 18
6.5 mm	15, 8	10, 10	10+, 10	21, 21	20, 21	22, 23
16.0 mm	15, 10	11, 11	15, 14	21, 22	22, 23	24, 23

Cirrus I with anterior ramus exceeding posterior ramus by about 6 segments; rami basally of wide segments,

but distally taper to more elongate segments with distal setae; segments of posterior ramus protuberant anteriorly. Cirrus II has rami of equal numbers of segments, but anterior ramus slightly exceeds length of posterior; all segments protuberant anteriorly, with copious setae on antero-medial faces; upper segment of pedicel bears on its lateral-posterior-distal aspect numerous groups of minute spines, and a series of upwardly directed spines along distal part of posterior edge of segment (this condition repeated in pedicels of cirri III–VI, especially in larger specimens, but becomes less pronounced towards posterior). Cirrus III with anterior ramus slightly longer than posterior ramus; each segment bears copious setae on anteromedial faces, and

near lateral anterodistal border some stout, peg- or tooth-like spines (these spines more pronounced and numerous on posterior ramus, and in larger specimens). Cirri IV–VI subequal in length and segment numbers; each segment with 5 pairs of anterior setae, or four in smaller specimens and basally in rami; a single, occasionally double, medial, short seta between bases of major pairs; near lateral anterodistal border of segments of cirrus IV only one to several short, tooth-like spines, in posterior ramus only in small specimens, but on both rami and more numerous in larger specimens. Penis with a rounded basidorsal point, longer than cirrus VI even in specimens as small as 2.2-mm diameter.

REMARKS: The record of Broch (1922) for this species at 38°12'S, 149°40'E is not "north of New Zealand" as he states it in his discussion on biogeography, and as quoted by Broch (1931) and Nilsson-Cantell (1938). However, it now appears that this error contained an element of prophecy.

The available descriptions permit some measure of the variation in this sublittoral and not very commonly encountered species. The colour varies from quite white to very dark red or brown. The notch beneath the upper pair of spines on the maxillule is more-or-less pronounced. The form of the lower angle of the mandible is also variable. Sometimes the lowest tooth may be longer and more pointed than shown in Fig. 60J, giving the impression that the cusps are the worn bases of more acute spines. A minor contention in the existing descriptions are the short lateral spines on the segments of cirri III and IV. Hoek's specimens were small, at the most 2.5 mm in diameter, and he makes no mention of teeth on the segments of these rami. Broch (1922) had a specimen of 13-mm diameter, and does not mention these spines nor specifically notes their absence. Broch (1931) stated that, in material from Malaysia, "all specimens lack small hooks or spines in the third cirrus and must accordingly be designated as *Balanus auricoma*". Nilsson-Cantell (1925) expressed doubt as to the validity of *Balanus ciliatus*, which Hoek (1913) described as having teeth on the 3rd and 4th cirri, but later (Nilsson-Cantell 1934a) stated: "I do not think that the absence of these teeth on the cirri is a character of great specific value. . . . Possibly the teeth may be better developed in older specimens". Later still, Nilsson-Cantell (1938) upheld the distinction between *B. ciliatus* and *B. auricoma* on the basis of the shape of the opercular valves. The present specimens are definitely not *B. ciliatus*, and only differ materially from previous descriptions of *B. auricoma* in the presence of these contentious teeth. It is clear that they increase in numbers during ontogeny, and they are more numerous on some rami than others. Broch (1931) gives no measurements of his Malaysian specimens; they may have been small.

The teeth in *Solidobalanus* are not the recurved hooks of subgenera like *Armatobalanus* and *Balanus*, but are better developed than the lateral spines seen in *Balanus (Austrobalanus) vestitus*.

***Balanus (Megabalanus) tintinnabulum linzei* n. ssp.**
(Plate 13A, B; Fig. 61)

Balanus (Megabalanus) tintinnabulum. Withers 1924: 24.
Balanus tintinnabulum concinnus. Cranwell & Moore 1938: 400.
Balanus tintinnabulum tintinnabulum. Linzey 1942a: 279.
Balanus tintinnabulum. Foster 1967: 81.

MATERIAL EXAMINED: NZOI: Stn E844 (1 specimen). Nat. Mus.: Esperance Rock, Kermadecs (J. C. Yaldwyn), Great King I (F. M. Climo), Spirits Bay, White I (M. A. Crozier). Also empty shell from "raised barnacle band" of Curtis I, Kermadecs (J. C. Yaldwyn). BAF: Norfolk I (W. J. Ballantine), Meyer I, Kermadecs (*Tui*), Cape Karikari, Poor Knights Is (R. Grace, A. Ayling, and C. Milligan), Whangarei Heads, Cape Rodney.

DISTRIBUTION: Norfolk I, Kermadec Is, and north-east waters of North I of New Zealand; low tidal on wave-exposed coasts (Figs 59, 66).

DESCRIPTION: *Shell:* Steeply conical to globulo-conical; blackish purple; parietes strongly ridged externally, regularly in juveniles, but only apically in older specimens; parietes with narrow, longitudinal tubes separated by thin septa, short lamellae on inner face of outer shell lamina, and internally with basal ribs corresponding to fluted inner parts of septa; radii well developed, with tubes (i.e., spaces between septa not filled up); externally with square ridges and grooves, former corresponding with tubes which run parallel to base of shell; radii with summits slightly oblique, and sutural edges of septa denticulate on both sides (Plate 13F); orifice rhomboidal in shape, but not markedly toothed; base calcareous, with tubes. Shells attain a large size; specimens up to 65-mm basal diameter have been collected.

Opercular plates: Scutum with prominent external growth ridges in small specimens, but these may be worn in older specimens; internally with a prominent, reflexed articular ridge, a deep articular furrow, an adductor ridge almost parallel to articular ridge bordering a deep cavity for attachment of lateral depressor muscles. Tergum less ridged externally than scutum, and has a deep furrow extending from apex to spur in younger specimens, but this is closed up in older specimens; spur long and narrow, placed at its own width from basitergal angle and not centrally on basal margin; basal margin on either side of spur forms a straight line; a prominent articular ridge in young specimens extends for about $\frac{3}{4}$ articular margin (shorter in older specimens), slightly curved ending at scutal side of base of spur; carinal margin distinctly convex; and with a few faint crests for carinal depressor muscle. In living specimens, colour of opercular tissues between opercular valves characteristic: a deep wine-red with an almost iridescent blue spot on either side (*see* frontispiece).

Mouthparts: Labrum with up to 3 teeth on either side of notch, but these may be worn down or absent. Mandible has 5 teeth, 5th close to lower angle, which

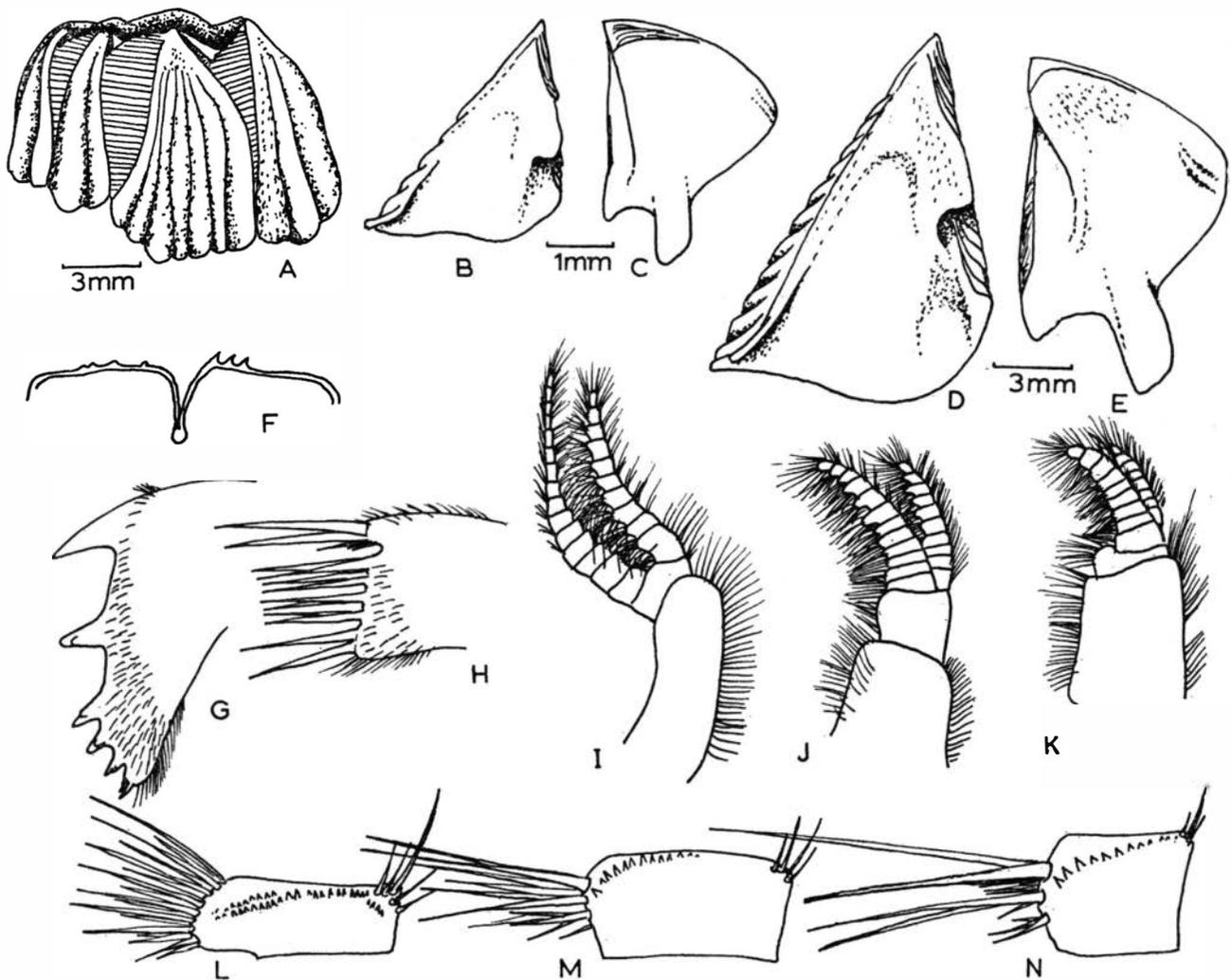


Fig. 61. *Balanus tintinnabulum linzei* n.ssp.: A, lateral view, shell of uneroded 12.5-mm diameter specimen; B, C, inner views, scutum and tergum of 5-mm diameter specimen; D, E, same, 45-mm diameter specimen; F, labral crest; G, mandible; H, maxillule; I, cirrus I; J, cirrus II; K, cirrus III; L, outer view, intermediate segment, posterior ramus of cirrus II; M, same, anterior ramus of cirrus III; N, same of cirrus IV.

may bear a group of spines (Darwin: "more or less spinose"). Maxillule has a small notch which separates upper pair of large setae from a double series of setae and lower single series of setae, lowest 2 of which as long as 2 at upper angle; lower angle fringed with short, fine setae.

Cirri: Cirrus I with rami nearly subequal in length, posterior ramus with anteriorly protuberant segments. Cirri II and III both short, rami of cirrus III shorter than those of cirrus II. Cirrus II has anterior ramus slightly longer than posterior, all segments with protuberant anterior edges with copious anteromedial setae, and outer face with distal rows of short spines. Cirrus III has anterior ramus slightly longer than posterior, segments not protuberant, with copious anteromedial setae, and outer faces with a distal row of short spines. Cirri IV-VI similar and subequal; seg-

ments each have 3 pairs of setae on anterior face, with tufts of short setae between major pairs, sometimes, especially medially, a single, downward-directed, short proximal seta, and an oblique row of short spines extending onto lateral and medial faces.

HOLOTYPE: Nat. Mus. NMNZ Z.Cr. 1964; Paratypes (not syntypes) NMNZ Z.Cr. 1965 and NMNZ Z.Cr. 1966; from Cape Karikari

REMARKS: Because of the tendency of *Balanus tintinnabulum* to foul ships, Pilsbry (1916) could not define the "natural habitat" of *Balanus tintinnabulum tintinnabulum*. His material evidently came from ships that had sailed from Oriental seas. Linzey (1942a) assigned Kermadec Is specimens to the subspecies *tintinnabulum*, although noting certain features that differed from Pilsbry's description, chiefly the rounded carinal border of the

tergum, the spur not centrally placed on the basal margin, and the deep pit for the scutal depressor muscle attachment. In these respects the tergum approaches that of *B. tintinnabulum concinnus* of the Pacific coast of South America. This may have swayed the decision on the identity of Poor Knights Is specimens by Cranwell & Moore (1938). Their specimens are no longer available, but all Poor Knights Is specimens examined since are as described above, and do not have the coloration or the external opercular valve sculpturing as described by Pilsbry (1916) for *B. t. concinnus*, nor do the segments of cirrus VI bear 6 pairs of setae as described by Darwin (1854). The parietal tubes of the New Zealand material are narrow, numerous, and have thin septa, more like the condition described for *B. t. californicus* than for *B. t. tintinnabulum*. *B. t. californicus* of the Pacific coast of North America also has a deep pit for the scutal depressor muscle, and although the tergal spur is wide it is not situated centrally on the basal margin. The south-west Pacific form deserves equal rank to the North and South American forms.

A form of *Balanus tintinnabulum* was taken from the hull of the *Terra Nova* in Lyttelton Harbour in 1910 and 1912, and recorded by Jennings (1918) as *B. tintinnabulum* var. *concinnus*. Re-examination of these specimens in the Canterbury Museum reveals that they are quite comparable with the above-described *B. tintinnabulum linzei*. They are for the most part not much bigger than 20-mm basal diameter, and many of them are coated by small (up to 5-mm diameter) *Balanus decorus*. This last fact indicates that the fouling probably occurred in New Zealand waters.

Included in T. M. Skerman's collection of fouling barnacles (from NZOI Stn Z1060) are 2 specimens of a *B. tintinnabulum* with the external surface of the parietes with downwardly directed spines and the summits of the radii parallel to the base of the shell. The opercular valves and bodies are missing, so identification is uncertain, but the shells agree with the descriptions of *B. tintinnabulum peninsularis* Pilsbry. However, as the material was collected off a ship's hull, like the *Terra Nova* barnacles, it is not admitted to the New Zealand fauna.

***Balanus (Megabalanus) decorus* Darwin**

(Plate 13C, D; Fig. 62)

Balanus decorus Darwin, 1854: 212; Hutton 1879: 328; Filhol 1885: 486; Weltner 1899: 443; Chilton 1909: 670; Chilton 1911b: 311; Pilsbry 1916: 77; Jennings 1918: 60; Linzey 1942a: 1; Linzey 1942b: 279; Powell 1947: 41; Foster 1967: 81. *Balanus amphitrite communis*. Borradaile 1916: 132 (see Withers 1924).

Balanus (Megabalanus) decorus. Withers 1924: 25; Newman & Ross 1971: 176.

MATERIAL EXAMINED: NZOI: intact specimens from Stns B169, B233, B248, B250, B264A, B270, B565, C210, C617, C844, C856, C863, D62, D72, D121, E106,

E159, E328, E720, E780, F94, F145, F146, F936, G161, G655, G659, G660, G662, G670, G671, G672, G673, G681, G685, G695; shells only from Stns A433, A489, A704, A706, A748, A749, A751, A850, A852, A853, A862, A877, A891, A892, A893, A898, B176, B184, B215, B216, B219, B220, B221, B222, B224, B225, B226, B227, B228, B229, B230, B235, B237, B238, B245, B251, B252, B253, B254, B256, B258, B264, B265, B268, B271, B272, B554, B562, B563, B564, B567, B568, B569, B595, B619, B632, B650, B690, B873, C80, C104, C106, C111, C118, C125, C132, C188, C272, C275, C287, C309, C325, C334, C342, C344, C369, C380, C381, C423, C429, C430, C438, C442, C444, C445, C447, C448, C449, C450, C451, C452, C453, C454, C456, C458, C460, C461, C462, C466, C468, C469, C471, C472, C473, C474, C476, C479, C480, C482, C483, C486, C520, C591, C596, C649, C650, C734, C765, C771, C773, C778, C789, C801, C812, C814, C852, C853, C861, C907, C908, C909, C910, C911, C912, C913, C914, C915, C919, C921, C924, C936, C937, C957, D10, D31, D32, D42, D47, D55, D80, D127, D164, D175, D193, D194, D269, D272, D876, D893, D898, E96, E113, E114, E127, E136, E139, E142, E162, E248, E252, E278, E280, E281, E292, E294, E302, E313, E319, E325, E326, E327, E332, E340, E342, E344, E348, E350, E353, E360, E363, E365, E366, E372, E380, E381, E382, E384, E385, E386, E387, E388, E391, E393, E394, E720, E738, E746, E779, E795, E832, E840, E841, E845, E847, F82, F146, F867, F933, G163, G854, G866, G694, G707, H69. Nat. Mus.: numerous specimens, including empty shells from the "raised barnacle band" of Curtis I, Kermadecs (J. C. Yaldwyn). BAF: Numerous specimens from shells and rocks at low tide on shores from the far north of the North I to Otago; dredged specimens on shells on shelf off Otago Peninsula; fouling specimens in Manukau Harbour; specimens on sublittoral shells cast up on beaches throughout N.Z. main islands; specimens from *Tui* benthic station off North Cape.

DISTRIBUTION: New Zealand, from Kermadecs to subantarctic islands including Macquarie I, from desiccation-protected shore habitats to 729 m (Fig. 63).

DESCRIPTION: *Shell:* Pale rose colour, radii often darker; parietes without prominent external ribbing or ridging, and in younger specimens quite smooth, with longitudinal stripes of darker pink; parietes with tubes square in cross-section with thin septa, and internal parietal ribs corresponding with septa between tubes; radii externally quite smooth, with tubes, and with septa between tubes with sutural edge denticulate only on lower side (Plate 13F); orifice broad, rhomboidal, and toothed; base calcareous. Shells up to 76-mm basal diameter have been dredged.

Opercular plates: Scutum externally concave; internally with a faint articular ridge extending for about $\frac{1}{2}$ articular margin, sometimes ending basally in a small hook, with an obvious adductor ridge running more-or-less parallel to tergal margin, and bordering a deep groove

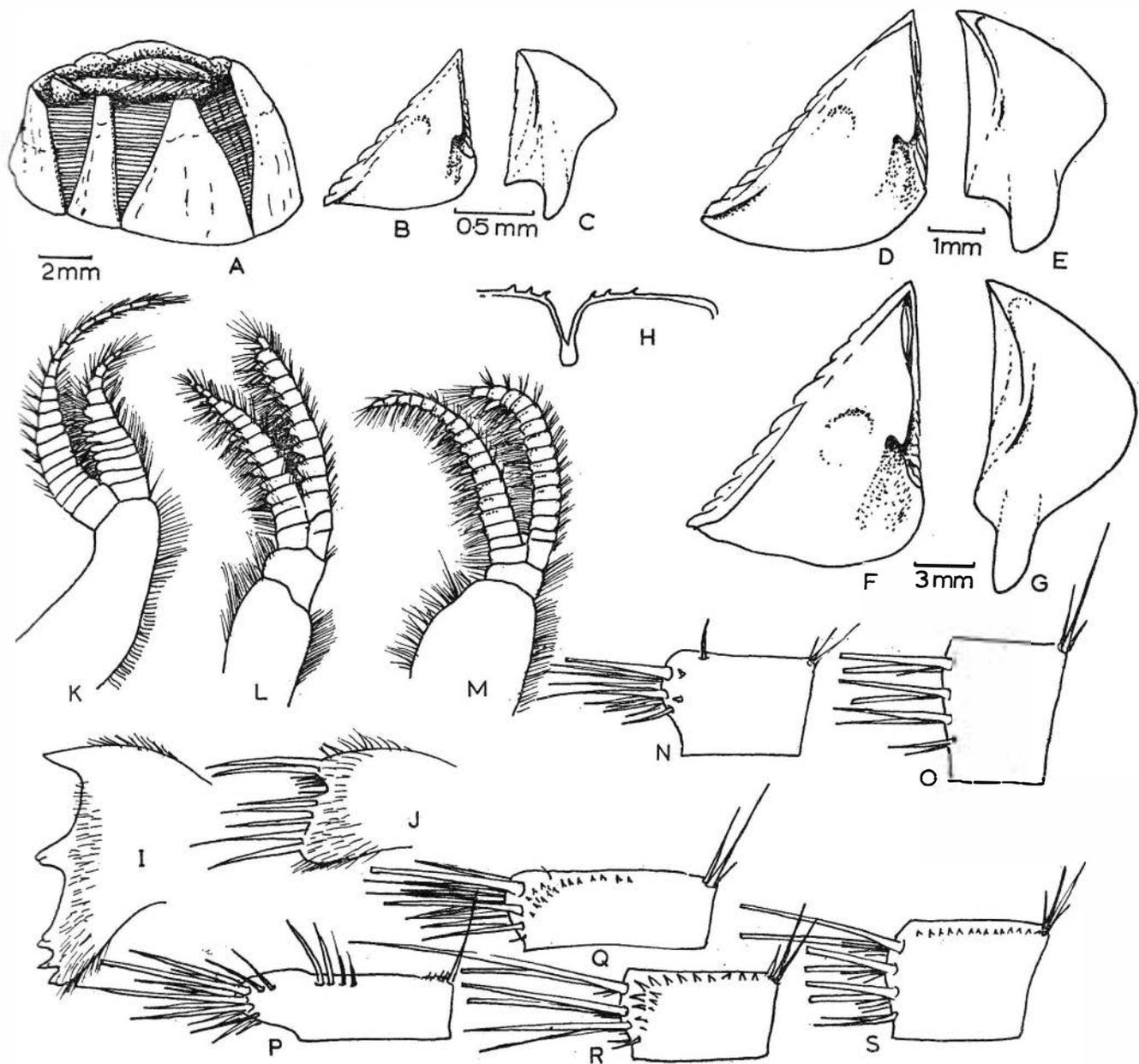


Fig. 62. *Balanus decorus* Darwin: A, lateral view, shell of 11-mm diameter specimen; B, C, inner views, scutum and tergum of 2.8-mm diameter specimen; D, E, same, 11-mm diameter specimen; F, G, same, 25-mm diameter specimen; H, labrum; I, mandible; J, maxillule; K, cirrus I; L, cirrus II; M, cirrus III; N, outer view, intermediate segment of cirrus II, 2.8-mm diameter specimen; O, same, cirrus IV of 2.8-mm diameter specimen; P, Q, R, and S, same of cirri II, III, IV, and VI of 25-mm diameter specimen.

for depressor muscle, but pit for adductor muscle attachment barely indicated.

Tergum has a shallow furrow externally; spur with bevelled, truncated end, situated at its own width from basiscutal angle; basal margin slopes towards spur on both sides, scutal part being concave; carinal margin slightly convex; and without crests for carinal depressor muscles.

The tissues between gape of opercular valves pink in live specimens (see frontispiece).

The appendages have been well described by Linzey (1942b), who pointed out the differences between the three New Zealand megabalanids.

Mouthparts: Mandible with its 3rd tooth set close to molariform lower angle; maxillule rounded towards lower angle, bearing setae on prominence as large as those at upper angle.

Cirri: Number of segments in cirri of 3 specimens as follows, anterior ramus 1st:

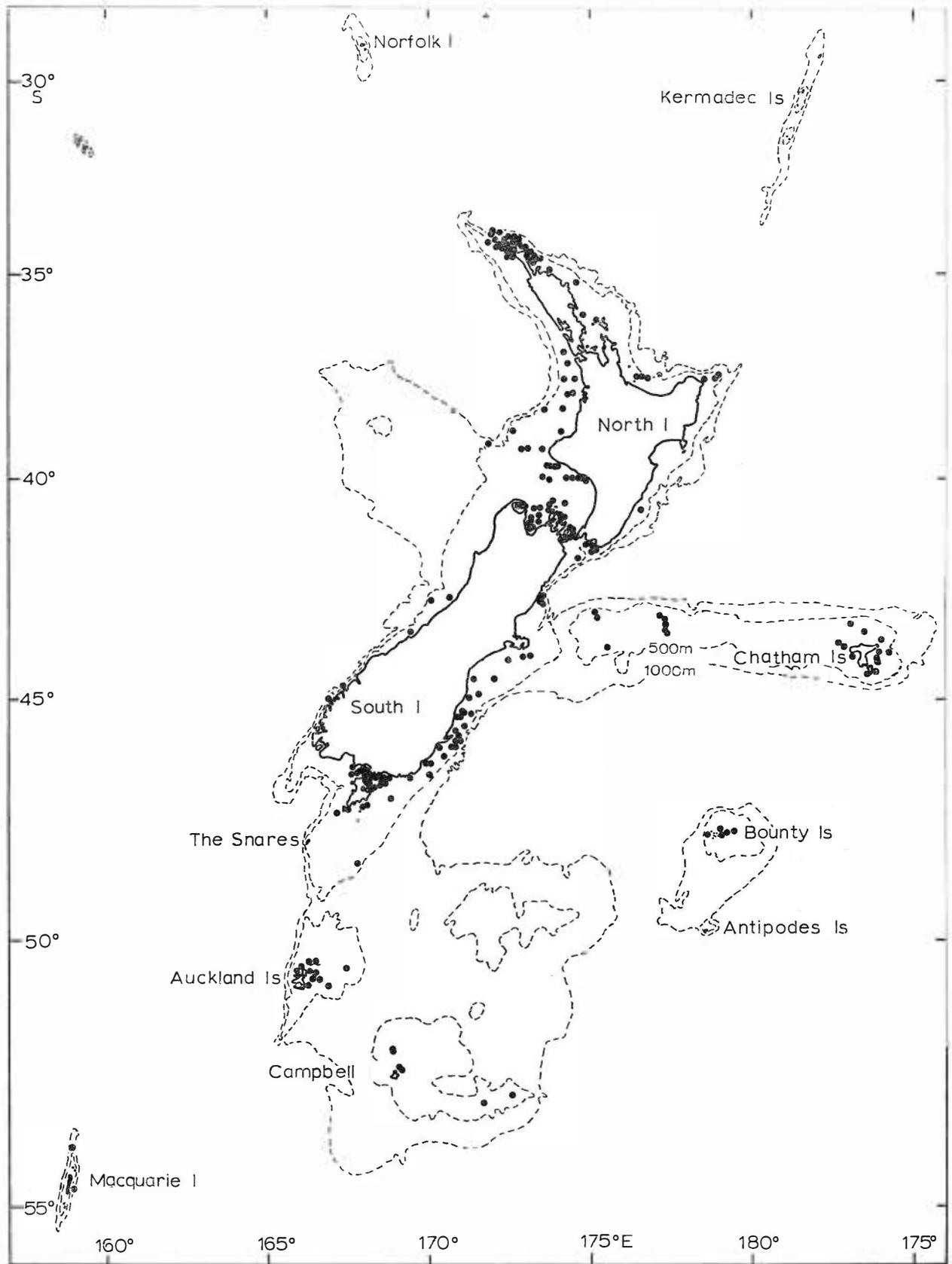


Fig. 63. Stations of collection of *Balanus decorus* represented in the NZOI collections.

shell diam.	I	II	III	IV	V	VI
2.8 mm	10, 6	8, 7	9, 8	12, 14	17, 17	17, 17
11.0 mm	18, 12	12, 12	15, 13	20, 21	28, 26	27, 27
25.0 mm	24, 17	18, 15	17, 13	28, 30	31, 35	36, 37

Cirrus I with anterior ramus a few segments longer than posterior. Cirrus III with rami longer than those of cirrus II. Cirri III–VI with the lateral faces of the segments bearing 1 or 2 distal rows of short spines, decreasing in abundance posteriorly from cirrus III, and more numerous and prominent in larger specimens; segments of rami with 4 pairs of setae on anterior edges, with short, medial setae between bases of major pairs, but sometimes, especially medially in ramus, with a single, short, downwardly-directed proximal seta.

REMARKS: *Balanus decorus* is the most characteristic and well known barnacle of the New Zealand shelf, from the Kermadec Is in the north to the subantarctic islands in the south. Despite the reference to Recent specimens in South Australia (Withers 1924) *B. decorus* is probably now endemic to the New Zealand region. Once it was more widespread, occurring in the Upper Oligocene, Miocene, and Pliocene in New Zealand, and in the Upper Miocene and Pliocene deposits of Victoria, Australia (Withers 1953).

***Balanus (Megabalanus) campbelli* Filhol**
(Plate 13E; Fig. 64)

Balanus campbelli Filhol, 1885: 487; Gruvel 1905: 214; Chilton 1909: 670; Broch 1922: 310; Foster 1967: 82; Maxwell 1970: 18.

?*Balanus porcatus*. Filhol 1885: 487; Hutton 1879: 328; Chilton 1909: 670.

?*Balanus psittacus*. Gruvel 1907: 1.

Balanus (Megabalanus) campbelli. Withers 1924: 27.

MATERIAL EXAMINED: NZOI: Stns A705 (2 specimens), A756 (2), D104 (fragments), D109 (1 plus fragments), D891 (2). BAF: specimens from shore collecting on Otago Peninsula; also Campbell I (G. S. Maxwell), Auckland Is (G. A. Knox).

DISTRIBUTION: New Zealand; southern part of the shelf from low tidal, desiccation-protected habitats to 64 m (Fig. 59).

DESCRIPTION: *Shell:* Conical, off-white; parietes externally with large radiating ridges not corresponding to more numerous tubes within, but with internal ribs corresponding to longitudinal septa; radii smooth externally, with summits parallel to base, sutural edges with denticulations on lower side only (Plate 13F), and with a tendency for tubes to secondarily fill with calcareous material; orifice broad and rhomboidal; base calcareous and porous, and in larger specimens, a thick, underlying, 'cellular' layer.

Opercular plates: Scutum has internally a slight articular ridge extending for about $\frac{3}{4}$ tergal margin and ending in a small point; an obvious but short ridge extending from base of articular furrow to form, with

lower part of articular margin, a deep cavity below articular ridge; a well demarcated adductor muscle scar and a rounded basal margin.

Tergum has a wide but shallow external furrow, a truncated spur set at about, or less than, its own width from basitergal angle; basal margin sloping on each side towards spur, short scutal part concave; carinal margin slightly convex; crests for carinal depressor muscles very faint or absent; articular ridge long and sweeping, terminating at basitergal angle.

In living specimens, tissues between opercular valves brightly coloured; golden-yellow at edge with red internally and blue patches towards rostral angle (see frontispiece).

Mouthparts: Labrum has up to 3 teeth on either side of a central notch. Mandible has 3rd set close to a molariform lower angle, upper cusp usually more prominent. Maxillule has a wide notch with shorter setae in a double series below pair at upper angle, an oblique section with similar setae, and a lower part of cutting edge rounded, with 3 or 4 large single setae.

Cirri: Cirrus I has an evenly tapering anterior ramus only slightly longer than posterior ramus, latter with very protuberant segments. Cirrus II has subequal rami, both with very protuberant segments. Cirrus III also has subequal rami, slightly longer than those of cirrus II, but segments not so protuberant; outer faces of segments bear distal, oblique rows of tooth-like spines, more numerous and prominent in larger specimens. Cirri IV–VI with subequal rami; segments with 5 pairs of setae on anterior face, with groups of short setae between and at bases of major pairs, and 1 or 2 rows of small teeth on lateral distal border, more prominent towards anterior of each segment, in anterior rami, and in larger specimens.

REMARKS: *Balanus campbelli* can be distinguished from *Balanus decorus*, with which it occurs, by the ridged, white parietes, as opposed to the smooth, pink ones of *B. decorus*. In living specimens, the colours of the tissues lining the opercular valves readily separate the species (Foster 1967).

The existence of *B. campbelli* in the southern part of the New Zealand region has no doubt led to some confusion of identity in the past. Although for long recorded only from Campbell I, it is now apparent that the species ranges to the Bounty, Auckland, and Chatham Is, and also to the South I at least as far north as Banks Peninsula. In a small collection of intertidal barnacles in the Canterbury Museum, collected in 1927 from Banks Peninsula by E. W. Bennett, there is a single specimen of *B. campbelli* among mostly *B. decorus* and *E. plicatus*. On the Otago Peninsula, *B. campbelli* occurs quite commonly in low tidal, wave-exposed situations with *B. decorus*, *E. plicatus*, *B. vestitus*, and *T. purpurascens*. It seems unlikely that it could have been missed by early collectors.

B. campbelli is superficially like *Balanus balanus* (= *porcatus*), and the likeness is enhanced by the tendency in some specimens of the former species to have the

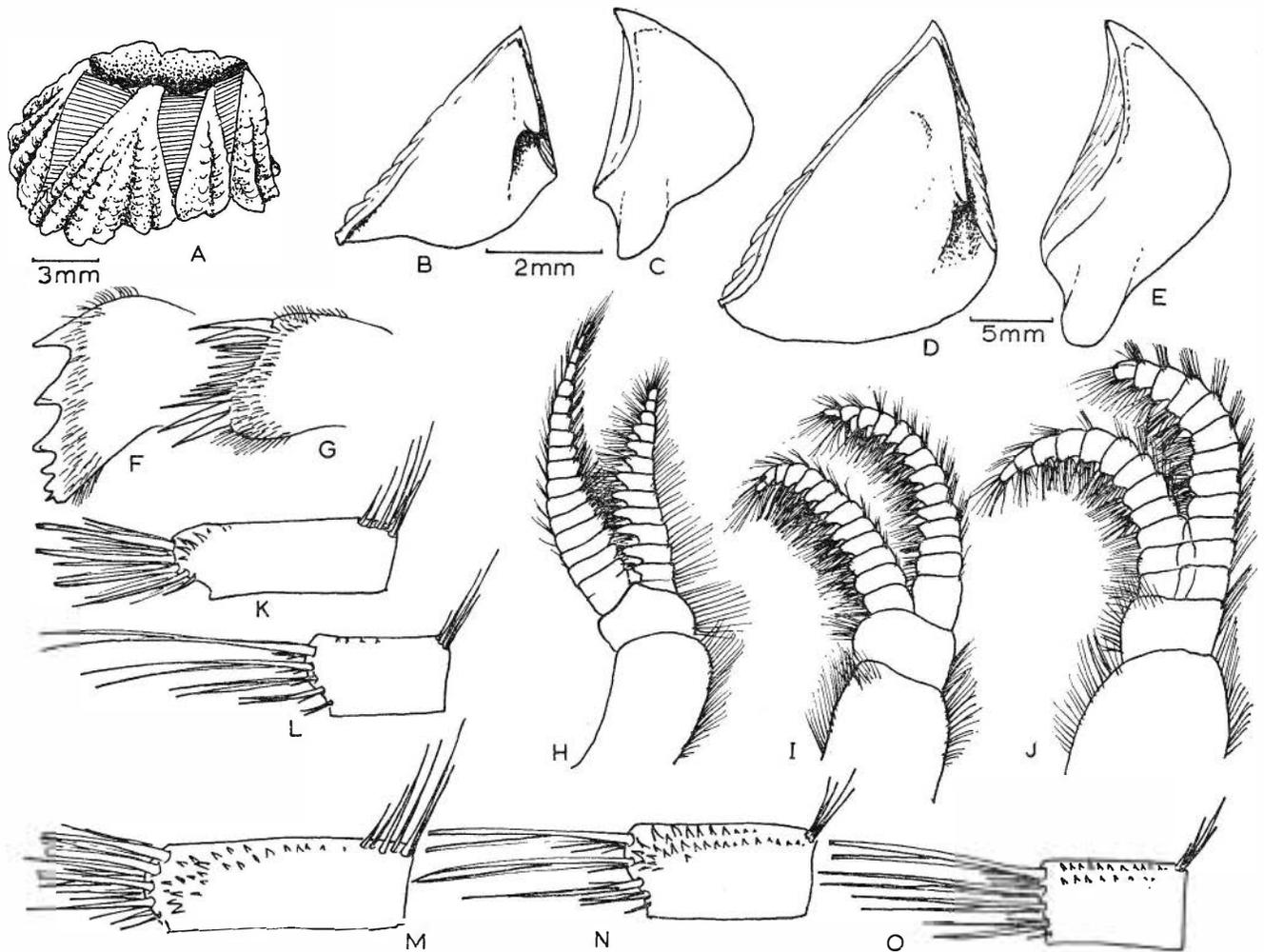


Fig. 64. *Balanus campbelli* Filhol: A, lateral view, shell of 12-mm diameter specimen from the intertidal zone; B, C, inner views, scutum and tergum of 6-mm diameter specimen; D, E, same, 40-mm diameter specimen; F, mandible; G, maxillule; H, cirrus I; I, cirrus II; J, cirrus III; K, outer view, intermediate segment, anterior ramus of cirrus III, 15-mm diameter specimen; L, same, cirrus VI of 15-mm diameter specimen; M, N, and O, same, cirri III, IV, and VI of 40-mm diameter specimen.

tubes of the radii almost totally occluded with calcareous material. *Balanus balanus*, under its old name of *B. porcatus*, is recorded from Campbell I, and Stewart I, by Hutton (1879), Filhol (1885), and Chilton (1909). None of Hutton's or Chilton's so-named material has been located. In connection with the record of *B. porcatus* by Jennings (1918), Withers (1924) "had an idea that the specimens so determined might possibly be examples of *B. campbelli* or *Balanus tubulatus*". Some of this material was re-examined by Dr Pilsbry and identified as *Balanus trigonus* (Chilton 1920), but Withers (1924, p. 34) re-examined a further lot, and found among them specimens of *Balanus vestitus*. Specimens in the Canterbury Museum (cat. no. AQ.3161) labelled "*Balanus porcatus*" are certainly *B. vestitus*.

Under *B. vestitus*, Withers reports on his re-examination of specimens collected by the *Discovery* from Auckland Is and identified by Gruvel (1907) as *Balanus psittacus*. On these specimens Withers found 12 small specimens of *B. vestitus*, the first record of this species from the subantarctic islands. The larger shells,

which were without opercular valves, Withers felt could as well be the Australian *Balanus nigrescens* as the South American *B. psittacus*, favouring *B. nigrescens* because of the association with *B. vestitus*. *B. nigrescens* may resemble *B. campbelli*, but *B. vestitus* does not occur in Australia, and *B. nigrescens* does not occur in New Zealand. A more likely interpretation of Gruvel's specimens would be that they are *B. campbelli*, because both this species and *B. vestitus* have been taken together subsequently from the Auckland Is. If so, then the *Discovery* specimens also represent an early record of *B. campbelli* from outside Campbell I.

All this makes good sense in the light of present-day knowledge on distribution; it removes *B. balanus* and *B. psittacus* from the New Zealand fauna. Neither have been subsequently found in the region. Jennings' (1918) record of *B. porcatus* for *B. trigonus* is for specimens from either of "Auckland" or "New Zealand"; the former is more accurate in view of the now apparent distribution of that species, as discussed below.

Balanus (Balanus) amphitrite amphitrite Darwin
(Plate 14A; Fig. 65)

Balanus amphitrite var. (1) *communis* Darwin, 1854: 240; Broch 1922: 314; Pope 1945: 362.

Balanus amphitrite hawaiiensis Broch, 1922: 314; Utinomi 1960: 43.

Balanus amphitrite amphitrite. Harding 1962: 274; Stubbings 1967: 271; Utinomi 1967b: 200.

Balanus amphitrite. Southward & Crisp 1963: 27; Foster 1967: 83 (in part).

MATERIAL EXAMINED: BAF: specimens from boat fouling, Auckland Harbour; numerous specimens from Orakei Basin, an artificially controlled sea-water lagoon in Waitemata Harbour, Auckland.

DISTRIBUTION: Cosmopolitan in tropical and warm temperate seas; in New Zealand, so far only found in Waitemata Harbour (Fig. 66).

DESCRIPTION: *Shell:* Parietes smooth externally; off-white with longitudinal pink, brownish, or purplish stripes; stripes may be in 2 distinct groups on any or all of rostral, lateral, and carinal plates; without transverse coloured markings; parietes contain evenly spaced, rounded tubes placed alternately to internal fluted ribs; radii well developed, with summits oblique to interlocking margin and with transverse flecks of same colour as in parietes; radii with denticulated sutural edges, but interspaces between denticulations filled up; orifice toothed; base calcareous and porous, tubes radiating from point of attachment of larval barnacle, and with ridges interlocking with internal parietal ribs.

Opercular plates: Scutum with prominent articular ridge occupying about $\frac{1}{2}$ articular margin, latter at 90° to basal margin; adductor ridge straight, and parallel

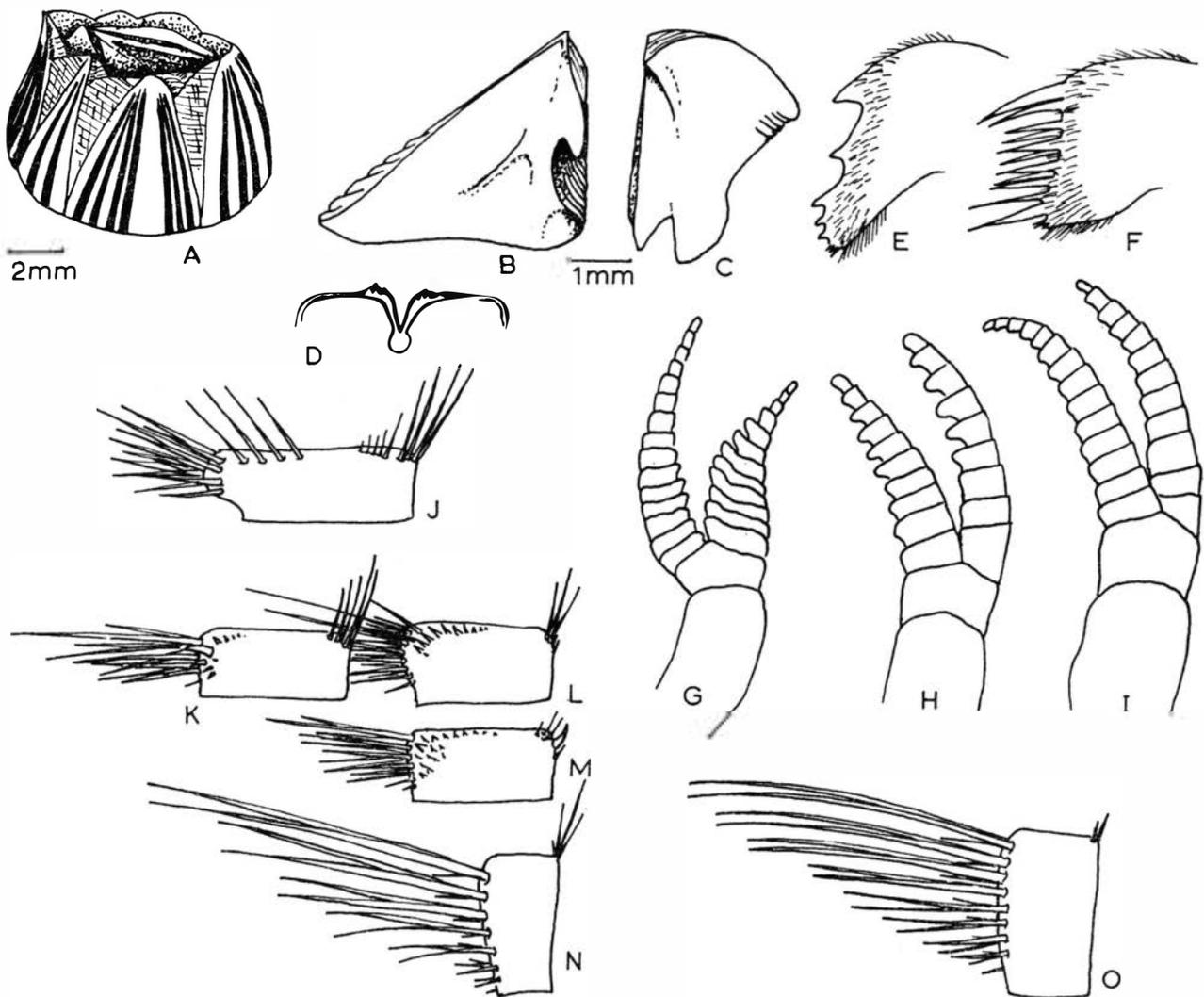


Fig. 65. *Balanus amphitrite amphitrite* Darwin: A, lateral view, shell of 10-mm diameter specimen; B, C, inner views, scutum and tergum of specimen A; D, labral crest; E, mandible; F, maxillule; G, cirrus I; H, cirrus II; I, cirrus III; J, outer aspect, intermediate segment, anterior ramus of cirrus II; K, same, cirrus III; L, same, posterior ramus of cirrus III; M, basal segment, posterior ramus of cirrus III; N, outer view, intermediate segment, anterior ramus of cirrus IV; O, same, anterior ramus of cirrus VI.

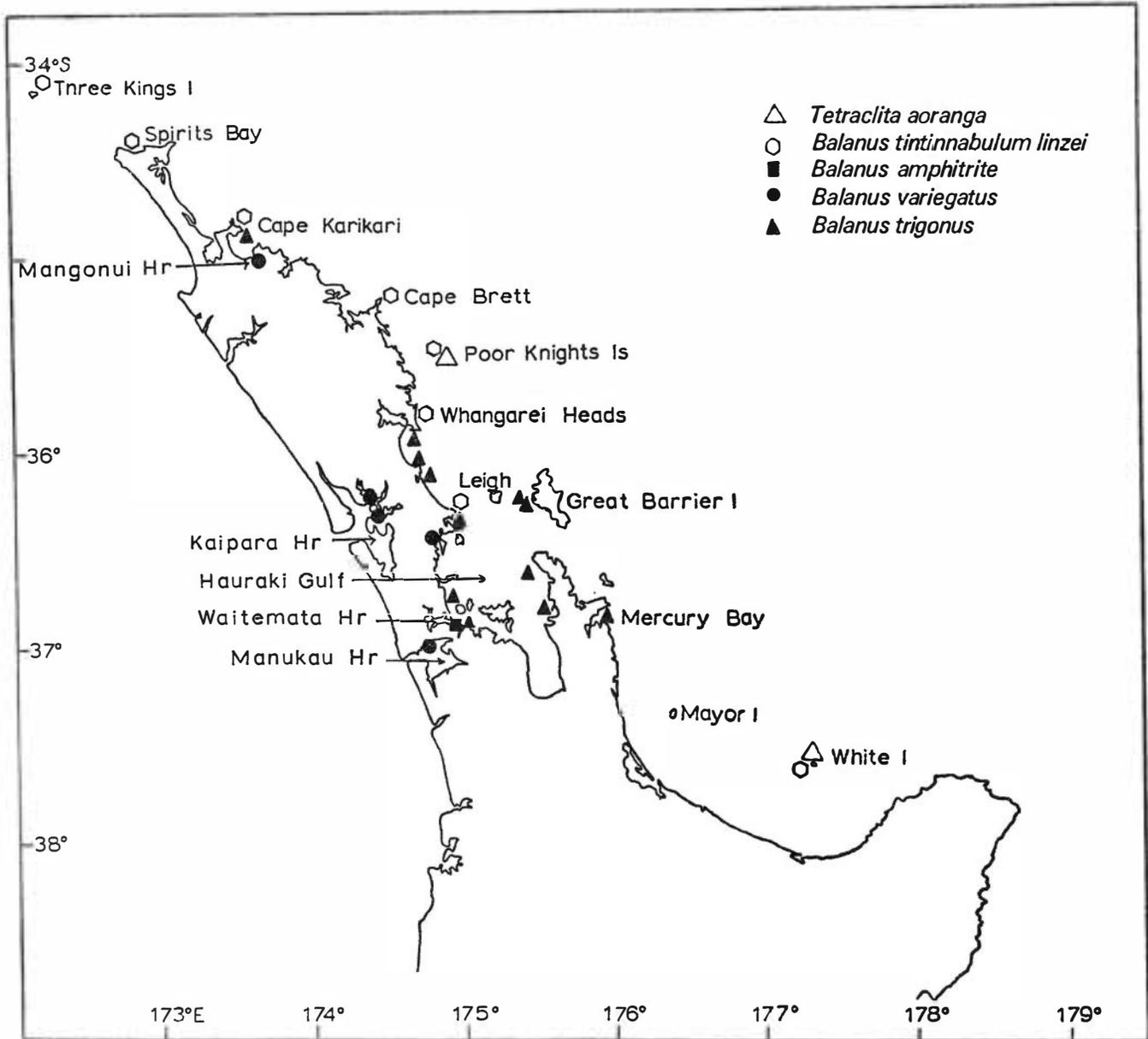


Fig. 66. Records of some shallow water balanomorphs that are restricted to the northern part of the North Island of New Zealand.

to occludent margin; a shallow pit for attachment of lateral depressor muscles.

Tergum broad, basal margin forming nearly a straight line on either side of spur, placed at about its own width from basiscutal angle, spur truncated or bluntly pointed; several crests for attachment of carinal depressor muscles; carinal margin convex, prominent articular ridge in upper part; a wide articular furrow; and a straight to slightly concave articular margin.

Opercular valves may be uniformly white or contain more-or-less pronounced longitudinal stripes of same colour as parietes. Tissue lining gape of opercular valves whitish, with 2 or 3 dark purple spots on either side (*see frontispiece*).

Mouthparts: Labrum has numerous teeth on each side of notch, teeth extend down into notch, where they become smaller. Mandible has 5 teeth, lower 3 set close to a molariform lower angle. Maxillule with a prominence towards lower angle which bears 2 or 3 setae that reach as far as large pair at upper angle.

Cirri: Cirrus I with anterior ramus longer than posterior ramus, basal segments of each ramus protuberant towards posterior in anterior ramus and anteriorly in posterior ramus. Cirri II and III have subequal rami, those of cirrus II shorter than those of cirrus III, and segments of cirrus II protuberant anteriorly.

Segments of Cirrus III with outer faces bearing tooth-like spines anterodistally, 1 or 2 more pronounced in the

anterior ramus; both rami with basal segments bearing distally on posterior edge an upwardly directed spine, instead of long seta of more distal segments. Cirri IV–VI subequal in length, with intermediate segments bearing 7 or 8 pairs of setae on anterior edge, with a short seta at and between bases of each of pairs, and without tooth-like spines on outer faces.

REMARKS: Darwin (1854) described 9 varieties of *B. amphitrite*. Harding (1962) reworked Darwin's specimens and changed a few names. More progress will depend on investigations of new material from various localities (e.g., Stubbings 1967, Utinomi 1967b). The validity of subspecies with continuous longitudinal stripes on a smooth white background is still not clear. The present specimens seem to be the first variety that Darwin designated, and the subsequently determined valid name is here retained, even though the status of the subspecies may prove invalid.

Balanus amphitrite is a fouling species, and whether or not it has been distributed to New Zealand by ships, breeding populations are established in Auckland. Skerman (1960) reports it (as *B. amphitrite communis*), along with *B. variegatus* (as *B. amphitrite cirratus*) and *B. trigonus*, as a ship-fouling species only at Auckland in New Zealand. No specimens from other New Zealand localities are in the various museum collections, nor have any been found in likely habitats in Wellington and Dunedin Harbours. The record of *Balanus amphitrite* by Filhol (1885) is evidently a restatement of the listing of Hutton (1879) for specimens of *Balanus variegatus* found in "Dunedin, on seaweed and shells". These specimens are not in the Otago Museum, nor do they appear to have been available to Jennings (1918), who omitted any form of *Balanus amphitrite* (sensu Darwin) from his list.

***Balanus (Balanus) variegatus variegatus* Darwin**
(Plate 14B; Fig. 67)

Balanus amphitrite variegatus Darwin, 1854: 241; ?Hutton 1879: 328; Nilsson-Cantell 1934a: 60; Nilsson-Cantell 1934b: 57; Nilsson-Cantell 1938: 39.

Balanus amphitrite cirratus. Pope 1945: 362.

Balanus variegatus variegatus. Harding 1962: 291; Utinomi 1968a: 171.

Balanus variegatus cirratus. Pope 1966: 179.

Balanus amphitrite. Foster 1967: 83 (in part).

MATERIAL EXAMINED: BAF: specimens from Mangonui, Kaipara, Mahurangi, Waitemata, and Manukau Harbours, in the north of New Zealand.

DISTRIBUTION: Indomalaysia to Australasia. In New Zealand, possibly only in the north (Fig. 66).

DESCRIPTION: *Shell*: Parietes externally smooth; off-white colour with a cross-hatching effect produced by radiating longitudinal stripes and parallel transverse purple stripes which are more-or-less pronounced; parietes contain evenly spaced tubes with thin septa, and internally have fluted ribs corresponding to expanded inner ends of septa; radii well developed and solid, whitish, or uniformly of colour of parietes, with oblique summits and denticulate sutural edges; orifice toothed, base with pores radiating from centre, and ridges on its upper surface interlocking with those of parietes.

Opercular plates: Scutum with a prominent articular ridge occupying about $\frac{1}{4}$ tergal margin, a short but pronounced adductor ridge; a well-defined pit for attachment of lateral depressor muscle, and externally 2 radiating purple bands. Tergum broad, with basal margin either nearly straight or deeply hollowed out on either side of a long, narrow, and nearly centrally placed spur, either pointed or truncated distally; a few crests for attachment of carinal depressor muscles; carinal margin convex; articular ridge prominent in upper part, and slopes to base of spur; externally a furrow from apex to spur. Colour of opercular valves varies from white to general colour of parietes. Tissues lining gape of opercular valves white, with 3 dark purple spots on either side (see frontispiece).

Mouthparts: Labrum with a deep, central notch with 3 teeth on crest to either side of notch. Mandible with 3 equally spaced teeth, lowest closely placed to a molariform lower angle bearing 2 noticeable teeth and a small spinule at lower angle. Maxillule with 2 large setae at upper angle, no notch, and lower angle separated from main cutting edge by a prominence bearing 2 setae that reach as far as those at upper angle.

Cirri: Cirrus I with tapering anterior ramus slightly longer than posterior ramus; basal segments of the posterior ramus with protuberant anterior edges. Cirrus II with protuberant segments, cirrus III with rami slightly longer than those of cirrus II, and segments not as protuberant; outer faces of segments with numerous small spines on anterior half, more numerous in basal segments. Cirri IV–VI have subequal rami; segments with 3 major pairs of setae on anterior edge, with 1 or 2 small medial setae between major pairs, and proximally sometimes a small 4th pair; outer face of segments of anterior ramus of cirrus IV with spines like those in cirrus III; outer faces of segments of both rami of cirri V and VI with a row of spines at anteriodistal margin; posterior edges of pedicels, and basal parts of rami provided with minute, upwardly-directed scales. Penis with prominent basidorsal point.

REMARKS: Following Harding's (1962) re-examination of Darwin's *Balanus amphitrite* material, the forms *variegatus* and *cirratus* are held distinct from the rest, because of colour patterns on the shell and the shape of the opercular valves. Harding was unable to distinguish empty shells labelled *cirratus* by Darwin from

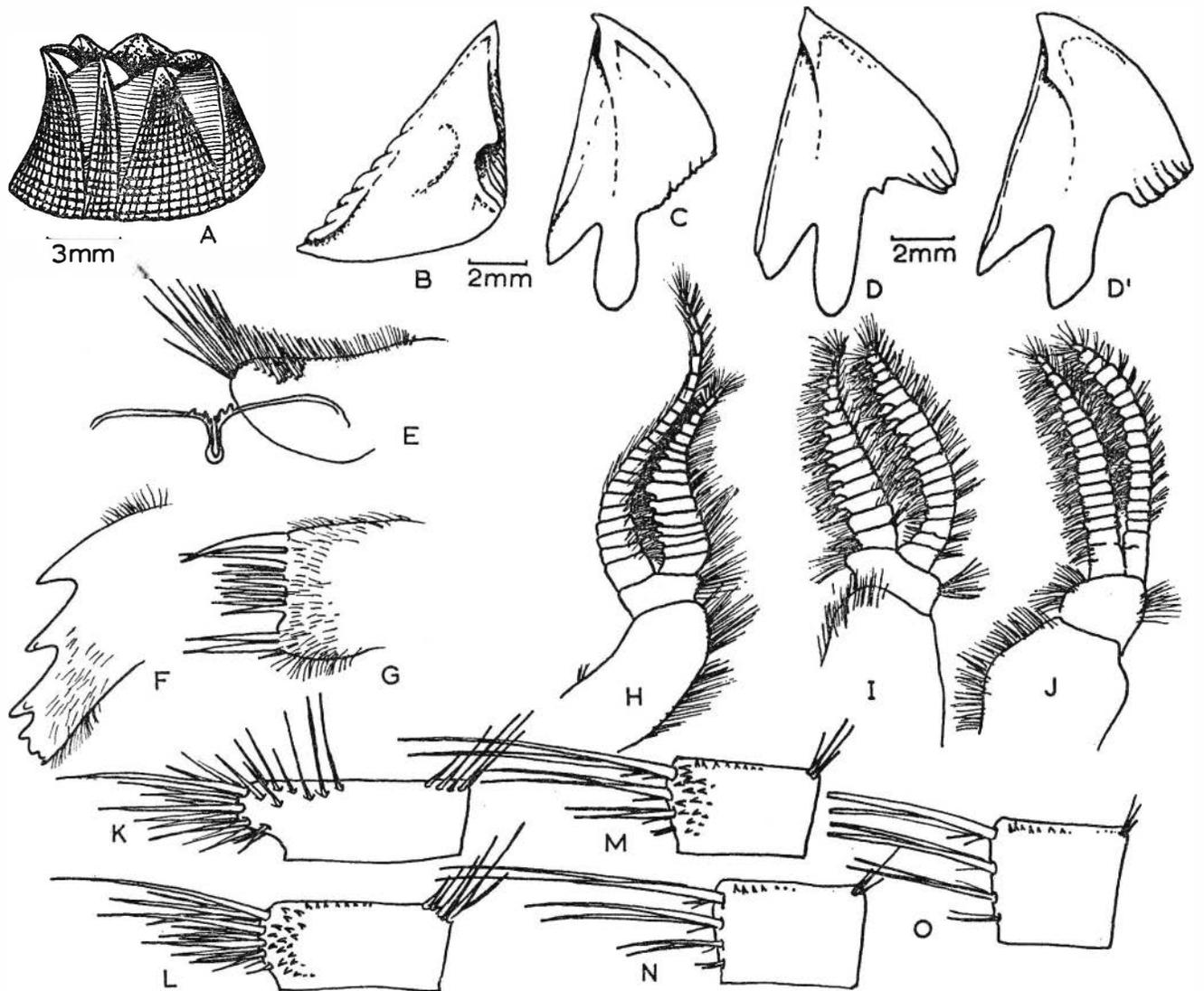


Fig. 67. *Balanus variegatus variegatus* Darwin: A, lateral view, shell of 17-mm diameter specimen; B, C, inner views, scutum and tergum of specimen A; D, D', other terga; E, labral crest and mandibular palp; F, mandible; G, maxillule; H, cirrus I; I, cirrus II; J, cirrus III; K, outer aspect, intermediate segment, anterior ramus of cirrus II; L, same, cirrus III; M, same, cirrus IV; N, same, posterior ramus of cirrus IV; O, same, cirrus VI.

variegatus, but regarded the former as a variety of *B. variegatus*. The latter species is recorded from the Indian Ocean through the Malay Archipelago to China, Australia, and New Zealand, and *cirratu*s has the same distribution except for New Zealand (*vide* Nilsson-Cantell 1938). Skerman (1959, 1960) identified specimens from overseas ships docked at Auckland as *cirratu*s. Pope (1945) recorded *cirratu*s as a common fouling barnacle at Sydney, which identification Utinomi (1967b) put into the synonymy of *variegatus* distinct from the subspecies *cirratu*s. However, the distinction between *variegatus* and *cirratu*s is still not clear. The specimens examined here show some variation with respect to the colour and its intensity, in the prominence of the tergal spur, and the degree of hollowing out of the basal

margin to either side of the spur, and these variations encompass the characters of *cirratu*s.

The forms of *B. amphitrite* named var. *malayensis* by Hoek (1913) are characterised by the lack of an adductor ridge in the scutum, and it is doubtful whether they should be synonymised with *B. variegatus* as done by Utinomi (1967b).

The record of *B. variegatus* from Dunedin by Hutton (1879), repeated by Filhol (1885), may have represented an introduction of the species into Port Chalmers, but these specimens have not been traced in the Otago Museum, nor has the species been found since in southern harbours (*see also* Skerman 1960). The species is restricted to wave-sheltered waters.

Balanus (Balanus) trigonus Darwin (Plate 14C; Fig. 68)

Balanus trigonus Darwin, 1854: 223; Pilsbry 1916: 111; Jennings 1918: 61; Broch 1922: 320; Pope 1945: 361; Foster 1967: 82; Stubbings 1967: 267; Utinomi 1968a: 173.

Balanus porcatus. Jennings 1918: 61 (in part); probably not *B. porcatus* of Hutton (1879), Filhol (1885), and Chilton (1909). *Balanus (Balanus) trigonus*. Withers 1924: 33.

MATERIAL EXAMINED: NZOI: Stns C779, C786, C790. Nat. Mus.: specimens from north-eastern shore localities as far south as Mercury Bay, and from between Little and Great Barrier Is at 55 m. BAF: numerous specimens from shore and sublittoral substrata and boats, from Waitemata Harbour to Whangarei.

DISTRIBUTION: Cosmopolitan in tropical and warm temperate seas to 450 m (Utinomi 1968a). In New Zealand, apparently restricted to north-east waters from shore to 55 m (Fig. 66).

DESCRIPTION: *Shell:* Parietes with prominent and more-or-less regularly spaced white ribs against a pink to purplish-red ground colour; parietes with tubes, each external rib overlying a tube; septa produced as fluted ribs on inner surfaces, and these interlock basally with ribs of porous base; radii solid, and of same ground colour as parietes, with summits set slightly oblique to interlocking edge; orifice markedly triangular with acute angle towards carina. Specimens of up to 16-mm diameter have been collected in New Zealand waters.

Opercular plates: Scutum with external longitudinal furrows crossed by growth ridges to give up to 6 longitudinal rows of pits; internally, a slight articular ridge extending over $\frac{1}{2}$ length of tergal margin, a short adductor ridge, and without crests for attachment of depressor muscles.

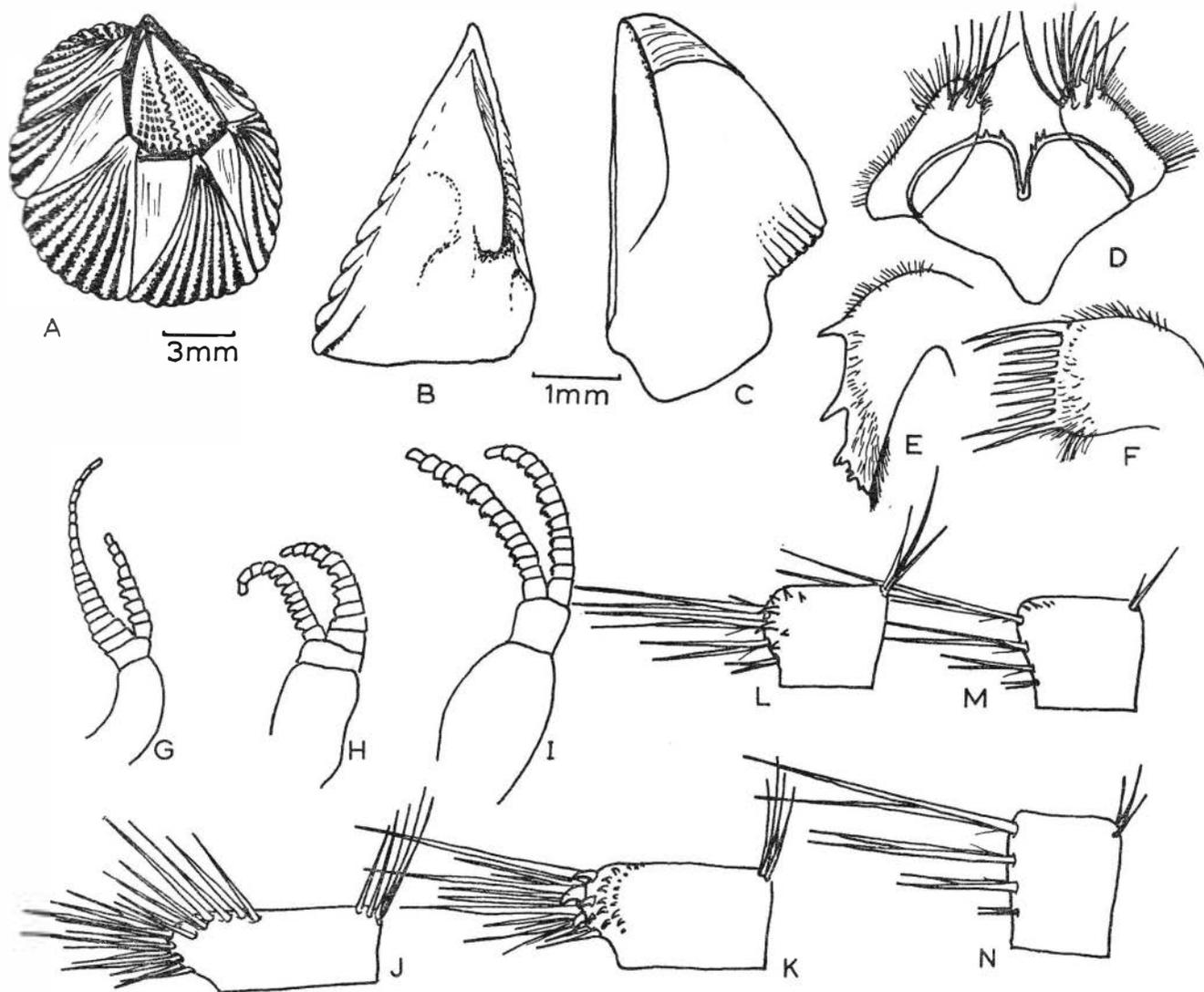


Fig. 68. *Balanus trigonus* Darwin: *A*, apical view, 15-mm basal diameter specimen; *B*, *C*, inner views, scutum and tergum, specimen *A*; *D*, labrum and mandibular palps; *E*, mandible; *F*, maxillule; *G*, cirrus I; *H*, cirrus II; *I*, cirrus III; *J*, outer aspect, intermediate segment, anterior ramus of cirrus II; *K*, same, cirrus III; *L*, same, cirrus IV; *M*, same, posterior ramus of cirrus IV; *N*, same, cirrus VI.

Tergum externally smooth; a truncated spur $\frac{1}{2}$ width of basal margin situated slightly apart from basiscutal angle; a not very prominent articular ridge, a wide articular furrow, and prominent crests for attachment of carinal depressor muscles.

In living specimens, tissues lining gap between opercular valves pink edged with white (*see* frontispiece).

Mouthparts: Labral crest generally with 3 teeth on either side of notch. Mandible with 3 teeth, and a molariform lower part into which 3rd tooth may be incorporated. Maxillule with a very slight notch beneath upper pair of setae, and lowest 2 spines of those on cutting edge longer than rest.

Cirri: Cirrus I with anterior ramus longer than posterior, and of tapering segments; anterior edges of posterior ramus protuberant. Cirri II–IV, with posterior edge of basal parts of anterior rami having strong, upwardly-directed teeth instead of long setae of more distal segments; anterior ramus of cirrus II and III slightly longer than posterior, those of III longer than II; segments of cirrus III with prominent, downwardly directed teeth on anterior face, plus smaller ones on outer face in anterior part; cirrus IV much longer than cirrus III; both rami with proximal segments with 4 pairs of setae on anterior face, decreasing to 2 pairs in distal segments, and with tooth-like spines on outer face of anterior ramus, and a few insignificant distal spines on segments of posterior ramus. Cirri V and VI with segments with 1 to 4 pairs of setae on anterior face. Penis with acute basidorsal point.

REMARKS: This species is a notable constituent of the sublittoral fouling fauna of the Waitemata Harbour and east Auckland coast. The sizable teeth in the third cirrus may possibly be used for dealing with large particles that tend to occlude the orifice; *Balanus trigonus* is frequently found nearly covered by encrusting ascidians and sponges, with just the trigonal orifice visible. In species of the genus *Acasta* (which is not represented in New Zealand) which occur sunk into sponges, very prominent teeth are developed on the segments of the cirrus IV.

Despite Wither's (1924) doubtful record of *Balanus trigonus* from "Otago", the species seems confined to the north-east of the New Zealand region (Skerman 1960). It has already been discussed in the remarks on *Balanus campbelli* how the *Balanus porcatus* of Jennings (1918) was a misidentification of *B. trigonus* for some of the specimens from either or both of two lots from "Auckland" and "New Zealand". Other specimens of these lots, and also the *B. porcatus* of Filhol (1885), Chilton (1909), and Hutton (1879), possibly refer to *Balanus campbelli* for the reasons already discussed. The wide New Zealand distribution of *B. trigonus* given by Moore (1944), and based on these identifications, is thus incorrect.

Chilton (1920) reports on the proper identification of at least some of Jennings' material, and in the same paper rightly rules on the inadmissibility of *Balanus* (*Balanus*)

crenatus, from off the *Terra Nova*, to the New Zealand fauna.

Three small balanids were found attached to the flippers of a hawksbill turtle in association with *Platylepas hexastylus*; the turtle was stranded on Piha Beach, Auckland. The barnacles had been poorly preserved, and the shell and opercular plates were very brittle and soft. Their identity is uncertain, but the lateral teeth on the cirri indicate the subgenus *Balanus*, and with the available details the specimens seem closest to *Balanus flos*, recorded by Pilsbry (1916) from seaweed and buoys off the Californian coast.

Genus *Creusia* Leach, 1817

Shell wall of 4 interlocked plates, including a rostral plate, a carina, and 2 laterals; parietes with internal ribs, which may be secondarily filled, may form irregular rows of tubes; base solidly calcareous, cup-shaped to cylindrical. The species lives embedded in corals.

Creusia spinulosa Leach

Creusia spinulosa. Darwin 1854: 376 (*see* for earlier citations); Linzey 1942a: 280.

REMARKS: There is only one species in *Creusia*. Although there is a wide range of variation in the shape of the opercular valves, the variations seemingly intergrade. Darwin recognised 11 varieties, but left it to "persons resident in the coral-bearing zones" to study "the forms fresh in their native site". Subsequent papers by Broch (1931), Hiro (1938), and Nilsson-Cantell (1938) have given names to some of Darwin's varieties and described 6 more, but have made no progress on whether there is one or more species.

Variety "8" of Darwin is not considered further by these authors dealing with Indian, Malaysian, and Japanese material, but specimens referable to this variety were collected in the Kermadec Is and commented on by Linzey (1942a). These specimens are embedded in coral, and are now in the Canterbury Museum. There is nothing more to add to Linzey's description.

Shell wall of 6 plates, including a rostral plate without fissures, 2 laterals, 2 carinolaterals, and a carina; parietes solid or with pores formed towards outside of shell; sheath occupies inner shell wall, but inner parietal lamina is present; opercular valves, when present, not articulating and not filling the orifice; base membranous.

REMARKS: The subfamily Coronulinae encompasses some 8 named genera and not many more species. They are all epizoid on marine vertebrates. They can be divided into two groups. The first includes *Coronula*, *Cryptolepas*, *Tubicinella*, and *Xenobalanus*, which are only found on whales, and in which the parietes are not inflected but may be provided with external ribs to strengthen the shell. The shell in *Xenobalanus* is vestigial, and contains only the basal parts of the animal. In all, the opercular membranes are extended at the carinal end to form a hood-like structure. In the other group, which includes *Cylindrolepas*, *Platylepas*, *Stephanolepas*, and *Stomatolepas*, the parietes have a median internal midrib or traces of a median infolding. They are more catholic in choice of hosts, living on turtles, sirenians, sea snakes, and fish.

The Coronulinae are as widespread as their hosts. In New Zealand, one species of whale barnacle, *Coronula diadema*, has long been known. There is also an old record of another whale barnacle, *Tubicinella major*, and more recently a further whale barnacle and two turtle barnacles have been found.

Body contained in a shell wall of 6 equal-sized plates, each with 4 radiating lamellar folds, which may be secondarily branched, terminating in cross flanges which unite to form an outer wall and enclose pores which are open below and occupied by the skin of the host whale; radii present; oral borders of opercular membranes project hood-like at carinal end. On whales.

***Coronula diadema* (Linné)** (Plates 3E, 14D; Fig. 69)

Lepas balaenaris. Gray 1843: 269.

Coronula diadema. Darwin 1854: 417 (see for earlier citations); Hutton 1879: 329; Filhol 1885: 489; Stead 1903: 944; Pilsbry 1916: 273; Jennings 1918: 62; Nilsson-Cantell 1921: 371; Powell 1947: 41; Beu 1971: 902.

MATERIAL EXAMINED: NZOI: Stns A706 (1 plate), D885 (1 plate). Auck. Mus.: specimens off whales from Whangamumu (Great Barrier I). There are also specimens in Canterbury Museum, National Museum (including material from Norfolk I), and Portobello Marine Biology Station.

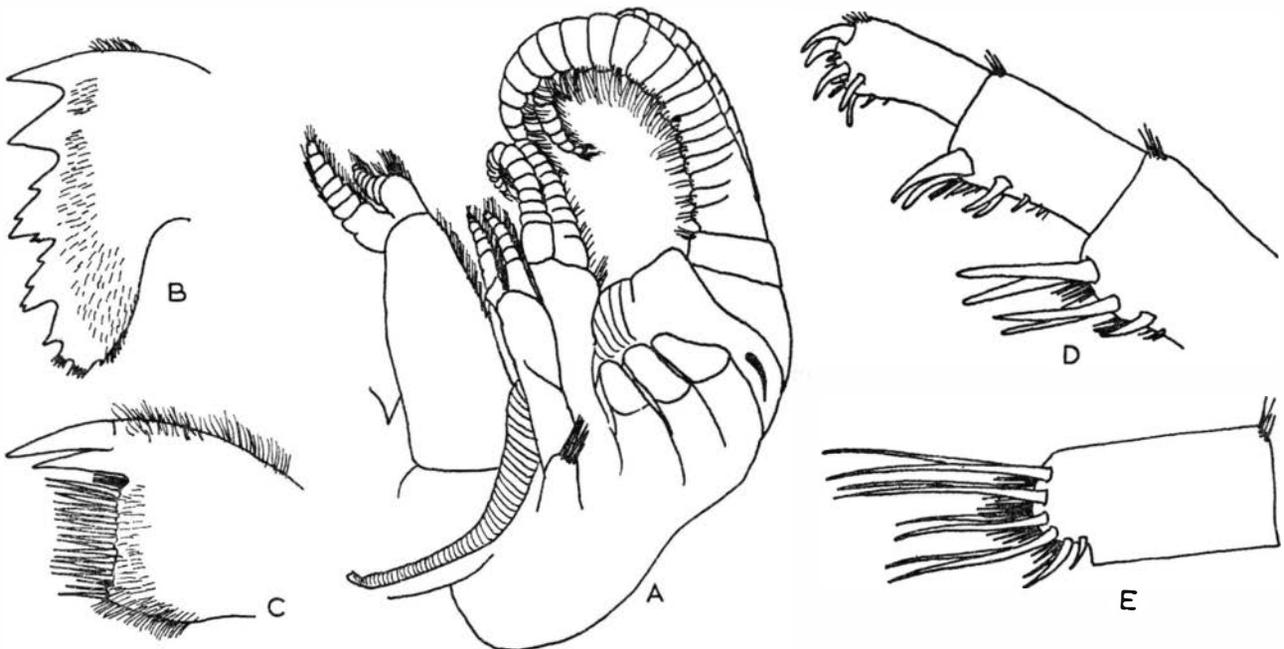


Fig. 69. *Coronula diadema* (L.): A, lateral view, whole prosoma showing cirri I to III and the bases of cirri IV to VI of the right side, and the penis and cirrus VI of the left side; B, mandible; C, maxillule; D, ultimate segments of cirrus VI; E, outer view, intermediate segments of cirrus VI.

DISTRIBUTION: Probably cosmopolitan (Nilsson-Cantell 1939).

DESCRIPTION: *Externals and shell plates:* Shell crown-shaped with convex ribs, crenated edges, crossed by narrow, beaded growth ridges; basal edges of ribs crenated; radii as wide in upper part as parietes in lower part, and about $\frac{1}{2}$ thickness of whole plate; orifice larger than basal opening; terga vestigial or absent; scuta small and embedded in thick opercular cuticle; sheath descends almost to basal inner edge of wall; outer edge of wall much deeper in host's skin than inner edge. Ribs of *C. diadema* branch much less frequently than in other species.

Mouthparts: Labral crest concave with a central notch, and with numerous teeth on crest. Mandible with 5 main teeth; 2nd, 3rd, and 4th double; a small tooth between 2nd and 3rd, and 3rd and 4th. Lower angle with groups of spines. Maxillule has 2 long, stout setae at upper angle, separated by a small notch from main cutting edge, which bears a double series of shorter setae.

Cirri: Cirrus I with a very broad and long pedicel; rami provided with short, spinose segments. Cirri II and III with protuberant segments which bear copious medial setae. Lateral tuft of setae at base of cirrus II. Cirri IV–VI with wide and flattened segments; each protuberant on its anterior face; basal ones with 5 pairs of stout setae on anterior edge, tufts of shorter setae between; distal ones with fewer paired setae, and on terminal segment setae short and claw-like. Penis long, with a rounded basidorsal point.

REMARKS: *C. diadema* differs from other species of *Coronula* in that only a small part of the total height is embedded in the skin of the whale. It frequently provides a site for the attachment of the lepadid *Conchoderma auritum* which, although part of the whale epifauna, is not directly attached to the skin of the whale (Plate 3E).

Coronula reginae Darwin (Plate 14E)

Coronula reginae Darwin, 1854: 419; Pilsbry 1916: 275; Beu 1971: 901, figs 3, 6.

MATERIAL EXAMINED: Nat. Mus.: numerous specimens from whales landed at a Tory Channel whaling station.

DISTRIBUTION: Probably cosmopolitan (Nilsson-Cantell 1939).

DESCRIPTION: *Externals and shell plates:* Shell low, conical with flattened ribs which have crenate lateral edges and crossed by delicate, beaded growth-ridges; basal edges of ribs crenulated; radii considerably narrower in upper part than lower part of parietes, and not more than $\frac{1}{3}$ thickness of the whole plate; orifice larger than basal opening, basal edge of sheath free.

Terga absent; scuta small and embedded in opercular cuticle; $\frac{1}{4}$ to $\frac{1}{3}$ whole diameter embedded in skin of whale.

Prosoma: Body appendages resemble those of *Coronula diadema*.

REMARKS: This species differs from *C. diadema* in its flatter shape, the flattened ribs, the narrower radii, and in being more deeply embedded in the skin of the whale. It resembles in appearance the third extant species, *Coronula balaenaris* (Ranzani) (= *C. complanata* Morch), which has 4 opercular valves, ribs which are symmetrically branched but not crenulated basally, and radii almost as thick as the whole plate. *C. balaenaris* has not been collected in New Zealand.

Genus **Tubicinella** Lamarck

Shell tubular, "wider at the top in adults, composed of 6 equal compartments, belted by several or many rounded ridges, the parietes longitudinally striated, the outer layer porose; radii narrow; sheath nearly as long as the tube, marked with circular grooves; lower layer of the opercular membrane limiting the shell nearly to the base; opercular valves four, rather larger" (Pilsbry 1916: 281).

Tubicinella major Lamarck

Tubicinella trachealis. Gray 1843: 269; Darwin 1854: 431 (see for earlier citations).

Tubicinella major. Pilsbry 1916: 281; Nilsson-Cantell 1921: 373.

Characters as for the genus.

REMARKS: This species was reported by Gray (1843) to inhabit the skin of whales around New Zealand. Pilsbry (1916) says it lives in the skin of the head of the southern right whale. There are no recent New Zealand records, nor have any specimens been located in any likely New Zealand institution.

Genus **Platylepas** Gray, 1825

Shell of 6 plates each with internal midrib, and supports an outwardly convex, membranous base larger in area than orifice; sheath $\frac{1}{2}$ length of plates; basal and inner edges of plates ribbed; opercular valves occupy whole length of orifice.

Platylepas hexastylus (Fabricius) (Fig. 70)

Platylepas bissexlobata. Darwin 1854: 428 (see for earlier citations).
Platylepas hexastylus. Pilsbry 1916: 285; Hiro 1937: 472.

MATERIAL EXAMINED: BAF: numerous specimens embedded in the skin of a hawksbill turtle (*Eretmochelys imbricata*) stranded on Piha Beach, Auckland, 19 Oct. 1970, in association with *Conchoderma virgatum*, *Lepas anatifera*, and *Balanus* (*Balanus*) sp.

DISTRIBUTION: Throughout tropical and subtropical seas.

DESCRIPTION: *Externals and shell plates*: The turtle had been preserved in formalin, and by the time of examination the barnacle shells were brittle and eroded. The latter condition may also have been due to rubbing with sand on the beach. Each plate bilobed, with an indistinct medial furrow externally, an internal triangular midrib, minute pores in the outer lamina, and a hollow beneath lower edge of sheath on each side of midrib.

MOUHPARTS: Labrum notched, with 4 or 5 teeth on crest to either side. Mandible with 5 teeth, 2nd, 3rd, and 4th double, with a small, simple tooth between 2nd and 3rd, and 3rd and 4th; lower angle spinose, lowest spine longer than rest. Maxillule with a very slight notch, main cutting edge straight, with a double series of setae and a group of shorter setae at lower angle. Maxillae bear a group of long setae distally.

Cirri: Cirri I–III with anterior rami slightly longer than posterior, segments with numerous medial setae, and lengths of rami increasing posteriorly. Cirri IV–VI with square segments, each with 4 or 5 pairs of setae on anterior face, and a small, single seta at and between bases of pairs of major setae.

REMARKS: These specimens are assigned to *P. hexastylus* because of the pores in the parietes, the hollow below the edge of the sheath, and the long, distal spines on the maxillae. *P. hexastylus* is cosmopolitan in tropical and subtropical seas, and has been recorded on various sea turtles, sirenians, and a fish (Pilsbry 1916). Darwin (1854) pointed out the similarity of *Platylepas* and

Coronula, and added that in some of the respects in which *Platylepas* differs from *Coronula* it approaches ordinary sessile cirripedes. The more catholic choice of host also possibly indicates an early coronulid status for *Platylepas*.

Genus Stomatolepas Pilsbry, 1910

Shell bowl-shaped; orifice much larger than base; each shell plate sulcate down middle; outer lamina composed of imbricating calcareous scales arranged in a chevron pattern; internal midrib absent; inner lamina projects, fingernail-like, above outer lamina; basal edge thin and smooth; sheath long and transversely grooved; opercular valves long, narrow, and thin.

The genus occurs on sea turtles. It is now held that *Stomatolepas* is monospecific.

Stomatolepas elegans (Costa) (Plate 14F)

Stomatolepas elegans. Pilsbry 1916: 289 (see for earlier citations);
Hiro 1937: 473; McCann 1969: 154.
Stomatolepas praegustator Pilsbry, 1916: 289.

MATERIAL EXAMINED: Nat. Mus.: 4 specimens from loggerhead turtle, *Lepidochelys olivacea*, Flat Point; 3 specimens from leatherback turtle, *Dermochelys coriacea*, Whareama River mouth (C. McCann).

DISTRIBUTION: Throughout tropical to temperate seas.

DESCRIPTION: Characters as for the genus.

REMARKS: The more recently collected set of specimens were described and illustrated by McCann (1969). The illustrations by McCann are poorly orientated, possibly leading to the statement that this barnacle "affixes itself so that its appendages are turned towards the substratum". The specimens in Plate 14F are of the earlier lot from Flat Point. I can see no reason for supposing this barnacle operates upside down.

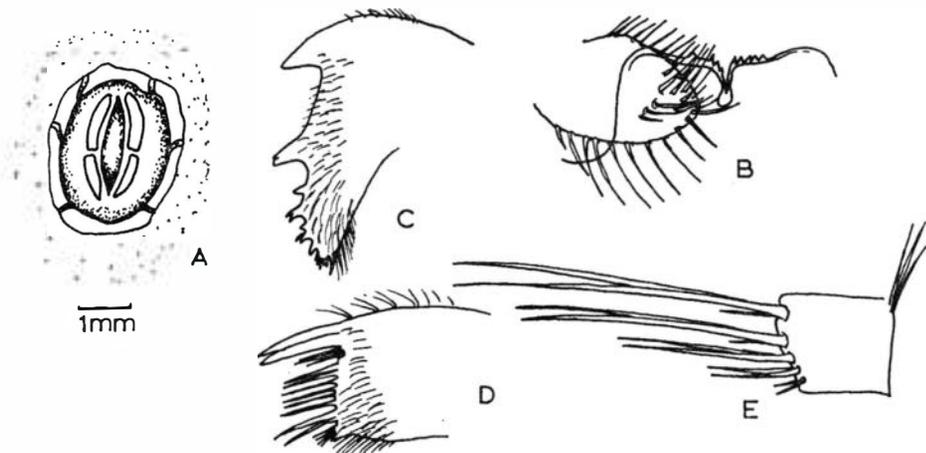


Fig. 70. *Platylepas hexastylus* (Fabricius): A, appearance of barnacle embedded in skin of host; B, labral crest and mandibular palp; C, mandible; D, maxillule; E, intermediate segment of cirrus VI.

DISTRIBUTION OF BARNACLES WITHIN THE NEW ZEALAND REGION

In this report, all barnacle records between latitudes 29°S and 57°S and longitudes 158°E and 170°W are considered. These have been mostly in depths less than 2000 m. The localities of many records, particularly of the deeper water species, are mapped in Figs 4 (heteralepads through poecilasmatids), 15 (*Lepas*), 25 (calanticids), 32 (*Arcoscalpellum*), 43 (*Verruca* and pachylasmatids), and 59, 63, and 66 (*Balanus* spp.). Overall ranges are better known for the shore species, and are mapped in Fig. 46. The species are categorised according to bathymetric and latitudinal distribution in Table 2.

Bathymetrically, four species groups are recognised: (1) species that occur only on shores; (2) species that characteristically occur on the lower shore, but also in the sublittoral; (3) species that occur only in the sublittoral, to or between various depths; and (4) species that occur on floating and nektonic objects. The intertidal barnacles occur in definite zonal arrays, such as *Chamaesiphon brunnea* always occurring high on the shore and above *C. columna*, but the bathymetric limits of sublittoral species cannot be so clearly recognised. The best-documented species, *Balanus decorus*, extends from the lower shore to a recorded maximum of 729 m,

Table 2. The barnacle species of the New Zealand region grouped according to available evidence of their latitudinal and depth distribution (order of listing in each block corresponds very approximately to known bathymetric ranges; endemic species marked by an asterisk).

	Kermadec Is only	northern species, not found in South I waters	species found in North and South I waters	southern species not found in North I waters
shore only	<i>Tesseropora rosea</i> * <i>Epopella kermadeca</i>	* <i>Tetraclita aoranga</i> <i>Balanus tintinnabulum</i>	* <i>Chamaesiphon brunnea</i> * <i>Epopella plicata</i> <i>Chamaesiphon columna</i> <i>Tetraclitella purpurascens</i> * <i>Calantica spinosa</i>	
lower shore and sublittoral	<i>Creusia spinulosa</i>	<i>Balanus trigonus</i> <i>Balanus amphitrite</i> <i>Balanus variegatus</i>	<i>Elminius modestus</i> * <i>Balanus vestitus</i> * <i>Balanus decorus</i> * <i>Calantica villosa</i> * <i>Ibla idiotica</i>	* <i>Balanus campbelli</i>
always sublittoral		<i>Balanus auricomus</i> <i>Calantica studeri</i> <i>Paralepas quadrata</i> <i>Heteralepas japonica</i> <i>Oxynaspis indica</i> * <i>Oxynaspis terranova</i> <i>Trilasmis kaempferi</i> <i>Paralepas minuta</i> <i>Megalasma striatum</i> <i>Smilium zancleanum</i> <i>Megalasma carinatum</i> <i>Arcoscalpellum intermedium</i> * <i>Arcoscalpellum raccidium</i> <i>Arcoscalpellum vitreum</i>	* <i>Calantica spinilatera</i> <i>Verruca halothea</i> <i>Pachylasma scutistriata</i> * <i>Aptolasma nolera</i> * <i>Hexelasma alearum</i> * <i>Aptolasma fosteri</i> <i>Smilium acutum</i> * <i>Arcoscalpellum pedunculatum</i> * <i>Arcoscalpellum affricatum</i> <i>Arcoscalpellum costellatum</i> * <i>Arcoscalpellum trochelatum</i> <i>Arcoscalpellum novaezelandiae</i>	<i>Calantica gemma</i> * <i>Arcoscalpellum pertosum</i>
pelagic	<i>Lepas denticulata</i>	<i>Alepas pacifica</i> <i>Platylepas hexastylus</i> <i>Stomatolepas elegans</i>	<i>Lepas anatifera</i> <i>Lepas pectinata</i> <i>Lepas testudinata</i> <i>Lepas fascicularis</i> <i>Conchoderma virgatum</i> <i>Conchoderma auritum</i> <i>Coronula diadema</i> <i>Coronula reginae</i> <i>Tubicinella major</i>	<i>Lepas australis</i>

which is beyond the lower recorded depths of some purely sublittoral species. Within the quite shallow limits of the present sampling, distribution may be more a factor of availability of adequate substrata than of physical factors associated with increasing depth.

Within the New Zealand region, there is a decrease in the numbers of barnacle species from the north to the south. The Kermadec Is to the north have a few intertidal species not found further south; the southern islands are notable for their relative paucity of species rather than for any peculiar species of their own. Apart from the Kermadec Is species, the northern species are generally restricted to the north-eastern sector of the North I and extend towards the Chatham Is to the east. These are the regions receiving the warm, subtropical waters of the East Auckland Current. The deeper-water species of this group, such as the heteralepads, the oxynaspid, the pocilasmatids, and such species as *Calantica studeri*, *Smilium zancleanum*, *Arcoscalpellum intermedium*, and *Balanus auricomus* probably represent the fringes of widespread distributions in tropical Pacific waters. Their restriction to the north may be due to the counterflow of the southern currents preventing their dispersal to more southerly latitudes.

In shallow water, climatic factors contribute towards hydrological ones in influencing distribution. The species of *Lepas* illustrate this (see Fig. 15). Three species, *L. anatifera*, *L. testudinata*, and *L. pectinata*, are not commonly encountered south of Cook Strait, and are found in the Chatham Islands; *L. australis*, however, has not been recorded north of a latitude of about 39°S. The central part of the New Zealand region is an area of overlap of these species, and their occurrence north or south is probably determined by surface currents and the extent that wind can influence the direction of drift of floating objects. The limits of distribution may reflect temperature limitation to some part of the life cycle, or possibly, and more likely, separate derivations of the surface waters from the north and south, introducing cosmopolitan tropic-centred species from the north and circumantarctic *L. australis* from the south.

The distributions of intertidal and subtidal balanomorphs in the islands of the New Zealand region are shown in Table 3. Some benthic and immediate subtidal species are quite definitely north-centred. *Balanus tintinnabulum linzei* is a good example, ranging from Norfolk I and the Kermadec Is to a southern limit on the north-eastern coast of the North I, occurring there on wave-exposed parts of the coast influenced by the East Auckland Current (see Figs 59, 66). The south-west Pacific seems to have its own discrete subspecies of *Balanus tintinnabulum*, a wide-ranging species in tropical seas, as are *B. trigonus*, *B. amphitrite*, and *B. variegatus*, which also have restricted northern distributions in New Zealand. Specimens of these last

Table 3. The distribution of intertidal and shallow-water barnacles in the islands of the New Zealand region (x, recorded; —, not collected and identified).

	<i>Chamaesipho brunnea</i>	<i>Chamaesipho columna</i>	<i>Epopella plicata</i>	<i>Elminius modestus</i>	<i>Tetraclitella purpurascens</i>	<i>Balanus tintinnabulum linzei</i>	<i>Balanus decorus</i>	<i>Balanus campbelli</i>
Kermadec Is	—	x	—	—	x	x	x	—
North I	x	x	x	x	x	x	x	—
South I	x	x	x	x	x	—	x	x
Chatham Is	x	—	x	x	x	—	x	x
Stewart I	—	x	x	x	x	—	x	x
The Snares	—	—	x	—	—	—	x	—
Auckland Is	—	—	x	—	—	—	x	x
Campbell I	—	—	—	—	—	—	x	x
Bounty I	—	—	—	—	—	—	x	—
Antipodes Is	—	—	—	—	—	—	x	—
Macquarie I	—	—	—	—	—	—	x	—

three species from New Zealand do not seem distinct from descriptions of material from elsewhere.

The highest-occurring intertidal barnacle, *Chamaesipho brunnea*, extends southward to latitude 43–44°S in the South I, and also occurs in the Chatham Is (see Fig. 46). The southern limit is probably set as much by climatic as by hydrological environmental factors. At lower shore levels *Chamaesipho columna* extends from the Kermadec Is to Stewart I, but it does not occur in the Chatham Is nor the more southern outlying islands. The existence of *C. brunnea* and the absence of *C. columna* in the Chatham Is is suggestive of the former species being phylogenetically older, isolated in the Chathams since the submergence of the Chatham Rise, and prior to the arrival of *C. columna* on the mainland.

The southern and south-eastern islands have sparse barnacle faunas in the intertidal zones, both in numbers of individuals and numbers of species (Table 3). The only definite southern benthic species is *Balanus campbelli* (see Fig. 59). The paucity of shallow-water barnacles in the far south may be due to the submergence of the Campbell Plateau before the start of balanomorph radiation, to limiting low temperatures, or to counterflow of currents against the necessary direction of larval dispersal from the north and north-west.

GEOGRAPHIC AFFINITIES OF THE NEW ZEALAND BARNACLE FAUNA

An assessment of the geographical range of a species is as good as the number of collection records and the existing taxonomic status of the species. Intertidal barnacles are fairly well known, but for many of the deeper-water shelf species, geographic and taxonomic information is still sparse. For example, the arcoscaltellids and pachylasmids are still not adequately worked on a world-wide basis, and it is probable that, as more deep sea material becomes available, a number of synonymies will become apparent.

The barnacle species of the New Zealand region are listed in Table 4 according to whether (1) they are endemic to New Zealand, (2) they occur in New Zealand and Australia only, (3) they have also been collected from Indomalayan and west Pacific localities, or (4) they are more cosmopolitan in distribution. Only the benthic species are listed; the pelagic species are generally cosmopolitan.

The impression gained from consideration of the deeper-water species is of the cosmopolitan nature of some of the scalpellids and the Indomalayan affinity of other scalpellids and the pachylasmids, bearing in mind the uncertainty over edemicity caused by lack of data. An Indomalayan element is particularly apparent in the north-eastern species already discussed. Such affinities are not restricted to the Cirripedia; other marine ben-

thic forms are held to have extended their range south-eastwards to the New Zealand region via formerly elevated submarine ridges. Independent migrations from the Indomalayan area to New Zealand as well as Australia may account for the present isolation of the common intertidal barnacles *Chamaesipho columna*, *Tetraclitella purpurascens*, and *Elminius modestus* on both sides of the Tasman Sea. It is possible that subsequent far-reaching dispersal of larvae has occurred for these species, but the absence of these species from the Chatham Is weakens such an argument.

It is among the intertidal and high sublittoral barnacles that endemism can be certain and revealing. *Chamaesipho brunnea* is certainly unique to New Zealand, and for a number of reasons appears phylogenetically older than *C. columna*. If the only other species of this genus, *C. scutelliformis*, really exists in the China Sea (as stated by Darwin 1854), then *Chamaesipho* could be an orientally derived genus with two Australasian species. *Epopella* is definitely Australasian, with different species in Australia (*E. simplex*), the Kermadec Is (*E. kermadeca*), and New Zealand (*E. plicata*). *Elminius* is now represented by two species, *E. modestus* in Australia and New Zealand, and *E. kingii* in South America, and like the species of *Epopella* these too

Table 4. The non-pelagic barnacle species of the New Zealand region grouped according to available evidence of their geographic affinities outside New Zealand.

	endemic species	common with Australia only	Indomalayan-Pacific affinities	cosmopolitan
shore only	<i>Epopella kermadeca</i> <i>Tetraclitella aoranga</i> <i>Chamaesipho brunnea</i> <i>Epopella plicata</i> <i>Calantica spinosa</i>	<i>Tesseropora rosea</i> <i>Chamaesipho columna</i> <i>Tetraclitella purpurascens</i>		<i>Balanus tintinnabulum</i>
lower shore and sublittoral	<i>Balanus vestitus</i> <i>Balanus decorus</i> <i>Balanus campbelli</i> <i>Calantica villosa</i> <i>Ibla idiotica</i>	<i>Elminius modestus</i>	<i>Balanus variegatus</i>	<i>Creusia spinulosa</i> <i>Balanus trigonus</i> <i>Balanus amphitrite</i>
always sublittoral	<i>Oxynaspis terranova</i> <i>Calantica spinilatera</i> <i>Aptolasma noleria</i> <i>Aptolasma fosteri</i> <i>Hexelasma alearum</i> <i>Arcoscalpellum raccidium</i> <i>Arcoscalpellum pedunculatum</i> <i>Arcoscalpellum affricatum</i> <i>Arcoscalpellum trochelatum</i> <i>Arcoscalpellum pertosum</i>	<i>Calantica studeri</i>	<i>Balanus auricoma</i> <i>Oxynaspis indica</i> <i>Paralepas quadrata</i> <i>Heteralepas japonica</i> <i>Pachylasma scutistriata</i> <i>Verruca halothea</i> <i>Megalasma striatum</i> <i>Smilium zancleanum</i> <i>Arcoscalpellum intermedium</i> <i>Arcoscalpellum vitreum</i>	<i>Calantica gemma</i> <i>Trilasmis kaempferi</i> <i>Paralepas minuta</i> <i>Megalasma carinatum</i> <i>Smilium acutum</i> <i>Arcoscalpellum costellatum</i> <i>Arcoscalpellum novaezelandiae</i>

would seem to be relict species of a once more widely distributed ancestor. The same may also apply to the subgenus *Austrobalanus* of *Balanus*, with *B. vestitus* in New Zealand, *B. imperator* in Australia, and *B. flosculus* in South America. Two further interesting endemic species are the intertidal *Calantica spinosa* and the lower-shore-to-shelf *C. villosa*. Both retain primitive scalpellid characteristics, and were probably derived from a pollicipoid ancestor, as also was the archetypal balanomorph. The relict balanomorph genera *Epopella*,

Elminius, and *Austrobalanus* occupy fairly basic positions in their respective families.

Although the concentration of species in the north, and the apparent north-westerly affinities of many of the species indicate likely sources and routes of barnacle influxes, particularly recent ones, to the New Zealand region, the isolation of certain key scalpellids and balanomorphs as shore forms in New Zealand may help to clarify the time of isolation of the New Zealand region.

EVOLUTION OF THE LEPADOMORPHA

The major discussions on thoracican phylogeny have been those of Broch (1922), Withers (1928, 1935, 1953), and Newman *et al.* (1969). To some extent, the last of these reconciles some conflicting views of the first two authors and presents a balanced theory based on available palaeontological and neontological evidence. It is generally agreed that lepadomorph barnacles are more basic than the balanomorphs, and it is apparent that much of the balanomorph radiation has occurred at the same time as the scalpellid radiation. A diagrammatic interpretation of lepadomorph phylogeny is given in Fig. 71. This recapitulates much of the morphological evidence and reasoning in the systematic part of this paper, and differs in some ways from the theories proposed by the above authors. Ecological considerations have played a part in the formulation of the phylogeny, and these are further propounded below.

The stalk or peduncle is a fundamental lepadomorph feature, and seems primarily to permit orientation of the capitulum to water currents and to alleviate crowding of closely settled and growing individuals where living space is limited. The stalk also serves to elevate the barnacle from silts or from confined habitats such as the body surface of other arthropods.

The earliest certain fossil barnacle is *Cyprilepas*, an unshelled cyprid-like but stalked form that occurred epizoically on eurypterid arthropods in Upper Silurian seas (Wills 1963). Significant features of *Cyprilepas* are its epizoic way of life and the lack of calcareous plates on the capitulum.

Of the extant genera, *Paralepas* is close in appearance and habit to *Cyprilepas*; it is uncalcified, and occurs

epizoically on arthropods. The non-shelled capitulum of the Heteralepadidae may be quite primitive. The carapace of *Cyprilepas* was probably shed at each moult (Newman *et al.* 1969), but that of the heteralepads is not. In *Paralepas* the carapace can be built up into a thick, protective, chitinous capitulum, so that the animal can become independent of the protection of the exoskeleton of other arthropods. Today *Heteralepas* occupies a wide range of habitats, sometimes epizoically but not necessarily so. Both *Paralepas* and *Heteralepas* have a specialised cirral setation termed 'acanthopod', in which the setae are restricted to the distal margin of the segments as they are in the segments of multi-articulated caudal appendages of those barnacles that have them. This type of setation seems to be primitive. Acanthopod setation is not to be confused with the short, claw-like setae of some species of *Paralepas*, also seen in genera such as *Lepas*, *Alepas*, and *Coronula*, and seemingly associated with the type of feeding in such pelagic and epizoic barnacles.

Darwin (1851, p. 160) noted an affinity of *Ibla* with *Heteralepas* (his *Alepas*) in the curved oesophagus, the multiarticulated caudal appendages, the general and basic character of the cirri and trophi (except for the setation in the heteralepadids), and the lack of calcification on the capitulum. Broch (1922) regarded the heteralepadids as reduced poecilasmatisids, and Newman *et al.* (1969) placed them as advanced and shell-less scalpellids. Broch (1922) also derived the Iblidae from scalpellid ancestors, but Newman *et al.* (1969) suspected their fairly basic position in barnacle phylogeny. There seems much to commend a primitive position for both

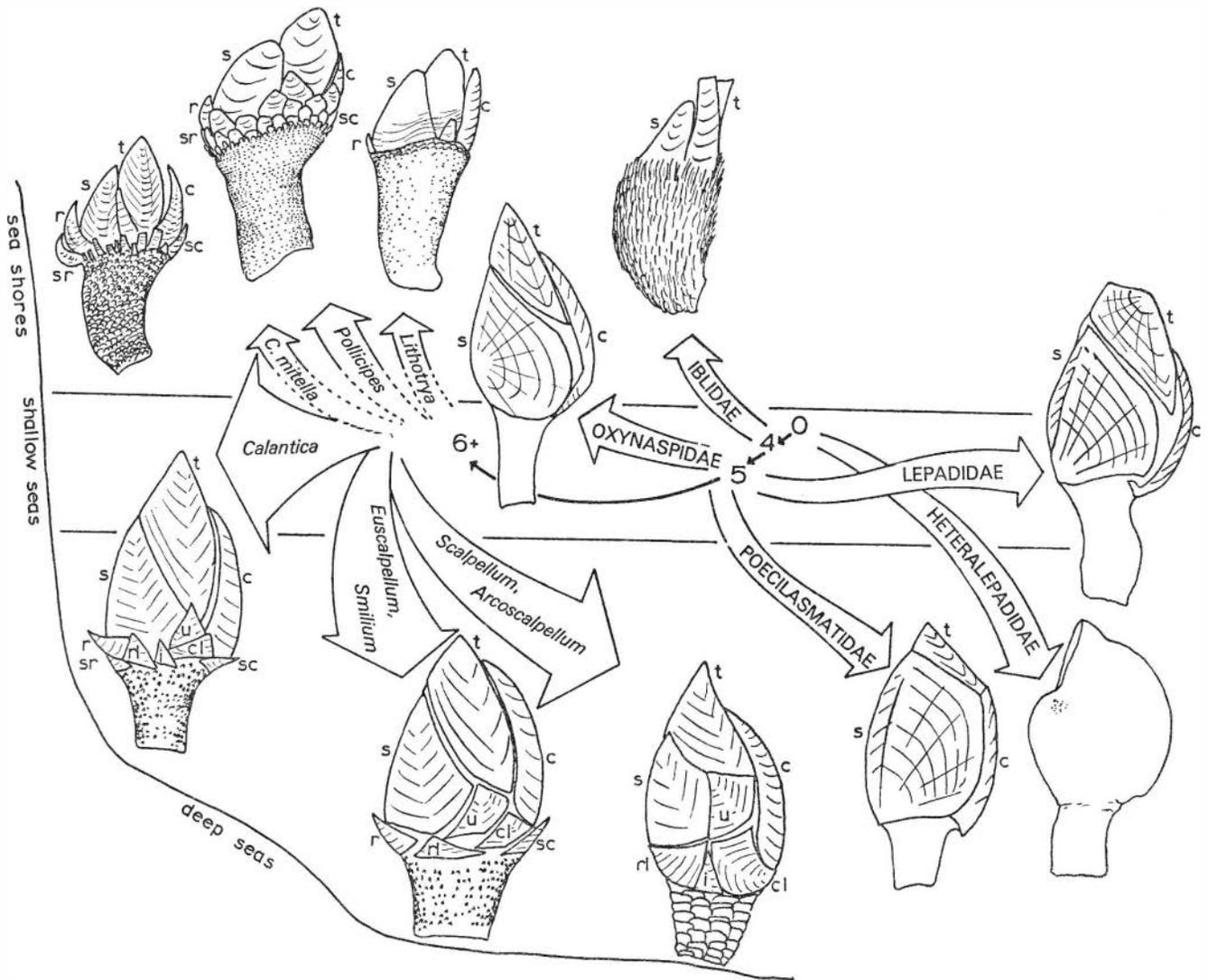


Fig. 71. Radiation of the Lepadomorpha. The numbers refer to the total number of shell plates on the capitulum. Shell plates: c, carina; cl, carinolatus; i, inframedian latus; r, rostrum; rl, rostrolatus; s, scutum; sc, subcarina; sr, subrostrum; t, tergum; u, upper latus.

the Iblidae and the Heteralepadidae, as shown in Fig. 71.

The surviving species of the Iblidae are known mostly from intertidal habitats, where they usually occur epizoically on other invertebrates; certain species also occur to some depth in the sublittoral. The sexual differentiation of some *Ibla* spp. may be a development to meet the scarcity of substrata in deeper waters (as discussed below for the Scalpellidae). Their present-day occurrence on sea shores may indicate their relative antiquity and their seeking of refuge habitats; this may also be the case for *Lithotrypa*, *Pollicipes*, the Chthamaliidae, and the Tetraclitidae.

The development of shell plates on the capitulum is probably foreshadowed by the chitinous terga and scuta of *Ibla*, but the first definite calcification was probably on a five-plated form such as *Praelepas* of the Carboniferous. The possession of five capitular plates is basic to the Lepadidae, Oxynaspidae, and

Poecilasmataidae, and also to the Scalpellidae judging by the appearance of only five primordial plates before and just after the cypris-to-adult metamorphosis. *Praelepas* is not unlike *Oxynaspis*, a genus epizoic mainly on antipatharians and more distantly related to the poecilasmataids, which are also epizoic but on arthropod and echinoid hosts.

Possibly also from an early five-plated condition, a step towards non-living substrata occurred when the Lepadidae associated with floating and drifting objects in the sea, maintaining a position in the rich photic zones and capitalising on the dispersal benefits of such objects. The pelagic habitat is not subject to the mechanical forces of shallow-water habitats, or indeed the habitats on or near the moving parts of arthropod and echinoid hosts. There has been a trend towards reducing the significance of the shell plates: the shells of some species of *Lepas* are thin, and do not necessarily cover

the capitulum; in the epizoic and pelagic lepads *Conchoderma* and *Alepas*, the shells are practically absent.

In the Oxynaspidae, Poecilasmatidae, and Lepadidae the umbos of the scuta and carina are not apical. The umbos of the scuta of *Ibla*, and of both scuta and carina of *Praelepas* and what appear to be primitive scalpellids, are apical. Consequently, the subapical umbos in the shell plates of the former three families, or at least in their living representatives, would seem best regarded as a secondary development towards redirection of shell growth to cover an enlarging capitulum from a few centres of calcification.

The Scalpellidae occur on a wide variety of substrata, and not always on specific animal hosts. It is now generally agreed that, although initially derived from non-shelled forms, the primitive scalpellids as such were multi-plated, and later underwent shell-plate reduction to result in the range of scalpellids known today. It is a contention of this paper that *Pollicipes* is a relatively unmodified descendant of early multiplated forms, and that the survival today of a few relict species on the coasts of America and Europe is due to their adaptation to shallow-sea habitats and their refuge in the intertidal zone. The armouring of the capitulum protects against the buffeting of surf or near-surf conditions, permitting utilisation of the food-rich inshore currents and full realisation of the sessile, free-living habit.

The tropical rock-boring genus *Lithotrya* may also be an intertidal refugee of early scalpellid evolution, finding protection by boring into coral boulders. The few capitular plates, viz., a rostrum and in some species a latus in addition to the basic five, may be a pollicipoid condition in scalpellid evolution.

It may have been that the ancestral pollicipids occurred in the subtidal, but perhaps predation pressure or competition for suitable substrate became too severe, and they came to occur characteristically in the intertidal zone — a sort of refuge habitat. The pollicipids occur where there is no danger of desiccation, such as in caves or crevices, or among the clusters of other organisms on the flatter rock surfaces, always on surf-soaked shores. In these habitats the stalk is a valuable asset in elevating the capitulum towards the water.

With the development of closely interlocking plates and appropriate behavioural control of the opercular opening, the susceptibility of the animal to water loss could have been reduced enough for the occupation of more exposed rock surfaces, when the stalk would have been an unnecessary encumbrance. The balanomorph condition thus perhaps arose as a further adaptation to the free-living, sessile habit in the high-energy environment of wave-exposed rocky shores. Withers (1928) supposed that domination of shore habitats by barnacles was only possible when lepadomorphs lost the stalk and became more compactly armoured against wave buffeting.

Apart from *Lithotrya*, *Pollicipes*, and the Balanomorphs, the multi-plated ancestral scalpellids possibly

also gave rise to most of the present-day scalpellids which are more characteristic of the sub-littoral than of shores, and which show progressive loss of the capitular plates. The calanticoid stock is probably an early derivative. The New Zealand species *Calantica spinosa* and *C. villosa* both retain the subrostrum, which is not a very common plate in the Scalpellidae apart from *Pollicipes*. *C. spinosa* is more closely related to *Pollicipes*, than is *C. villosa*, and is characteristically intertidal in habitat; *C. villosa* occurs in moist shore habitats, as well as sublittorally. This is suggestive that the pollicipid-scalpellid transition has thus been preserved in New Zealand in the form of these two species.

A significant feature of scalpellid evolution is the suppression of the free-living larval stages, such that ambulatory cyprid larvae are released from the adult to find suitable substrata for attachment. Consequently, once a substratum is colonised, a population can build up and cross-fertilisation is enhanced. Suitable hard surfaces probably become sparser with increasing depth, and because below the photic zone a planktonic larval existence is inept, the suppression of the nauplius larvae permits colonisation of greater depths.

A further refinement of the reproductive cycle is the retention of some of the cyprids in close association with the hermaphrodite, where their sexual development into males is encouraged and their normal growth and ovarian development is suppressed. Thus, the chances of cross-fertilisation are improved. It is in fact a reversion towards the unisexual condition. In some species of *Arcoscalpellum* the sexual differentiation has been taken to the extreme; the freely growing form is entirely female, and cyprids which lodge beneath the integument on the inside of the tergum become degenerate males.

The calanticoids show the first step in the reduction of the shell-plate armature associated with radiation to sublittoral habitats. They were in the ways described above pre-adapted to the special conditions of the deep sea, where the various scalpellid lineages with even further reduced shells, *Smilium*, *Euscalpellum*, *Scalpellum*, and *Arcoscalpellum*, are now found. The number of deep-sea species of *Arcoscalpellum* today rivals that of *Balanus* in the shallow seas of the world.

The tendency to develop complementary males in the Scalpellidae, the Iblidae, and even in some species of *Balanus*, can be interpreted as a trend away from the hermaphrodite condition, and towards the unisexual dioecious condition predominant in free-living animals. It is suspected that the origins of the Thoracica are even more basic than the epizoic habit of *Cyprilepas* suggests; the parasitic habit of the Ascothoracica, and their more marked body segmentation and retained abdomen, indicate that the ancestral cirripede may have been a parasite. The hermaphrodite condition is more common in internal parasites, and its existence in barnacles makes it difficult to accept the free-living, bivalved crustacean of Annandale (1910) or Withers (1928) as an ancestral thoracican.

EVOLUTION OF THE BALANOMORPHA

It has long been realised that the evolution of the Balanomorpha has involved reduction in the number of parietal shell plates surrounding the body and supporting the terga and scuta. This reduction has occurred independently in separate lines of evolution, and these lines, or families, have also evolved ways to enlarge the shell orifice with growth, and to effect rigidity of shell construction, including parietal plate interlocking and basal attachment. Fig. 72 is a schematic representation of the course of balanomorph phylogeny, and although it specifically shows parietal plate structure and arrangement, it is also based on anatomical features.

The shell construction of *Catophragmus* (see Pope 1965) is so like the capitulum of *Pollicipes* that the derivation of *Catophragmus* from a pollicipoid ancestor is quite probable. It seems more than coincidental that *Pollicipes* and *Catophragmus* are, in their respective suborders, the most heavily armoured genera, and that both are intertidal surf barnacles. The assumption is that the more radially symmetrical shell of balanomorphs is an adaption to conditions on the upper surfaces of rocks on wave-exposed shores.

There can be little doubt about the relative antiquity of the chthamalid genera *Catophragmus* and *Octomeris*,

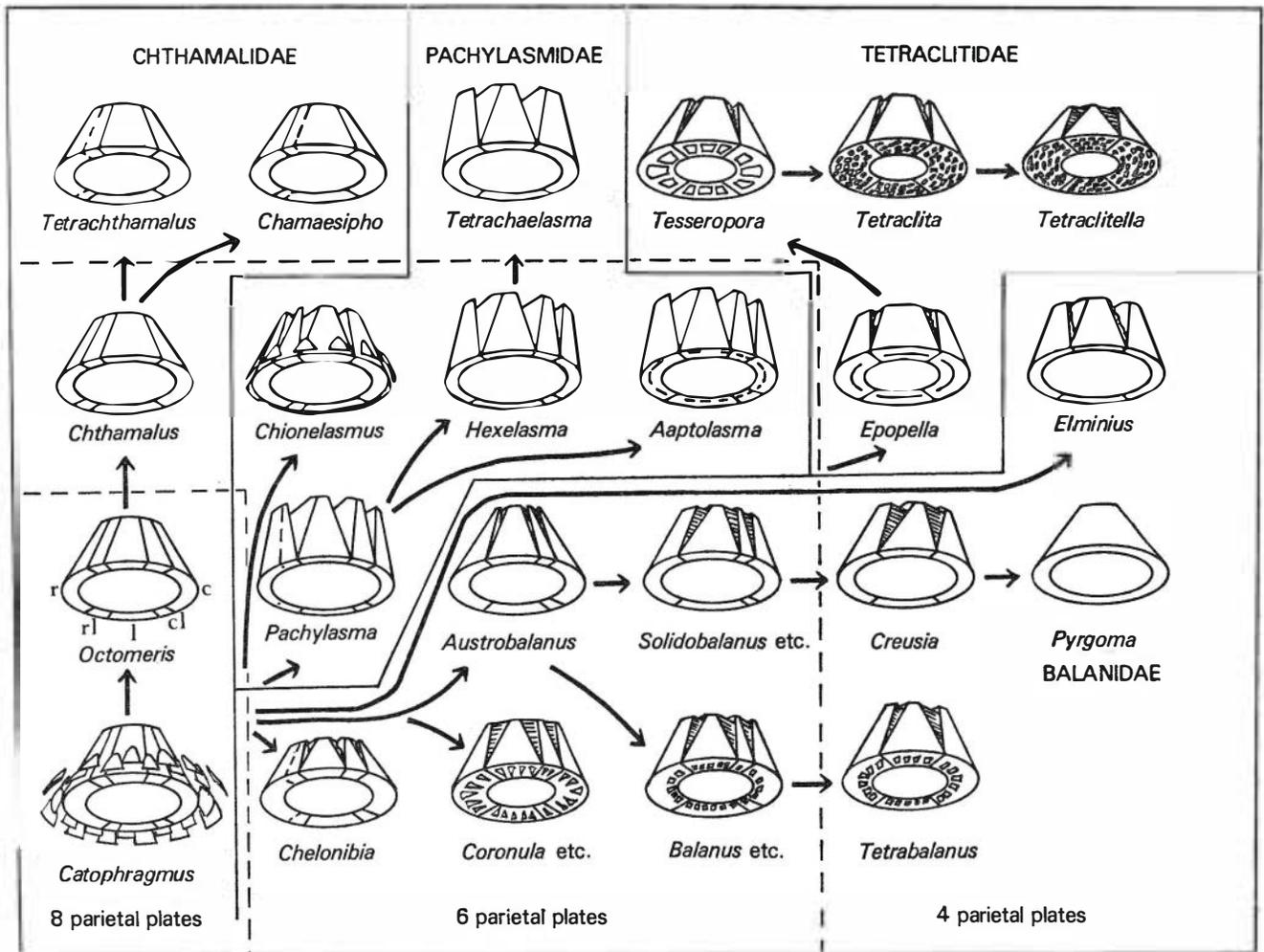


Fig. 72. Balanomorph genera arranged to show the structure, arrangement, and interlocking of the parietes, and showing possible phylogenetic trends within the families. The shells are all similarly orientated, according to the nomenclature in *Octomeris*: c, carina; cl, carinolatus; l, latus; r, rostrum; rl, rostrolatus.

which survive today as isolated species on shores in various parts of the world. Details of their anatomy not only reveal a relationship with pollicipids, but also suggest close relation with the intertidal genera *Chthamalus*, *Tetrachthamalus*, and *Chamaesipho*. On shores, the effects of alternating immersion and emersion lead to complete erosion of the apical parts of the shell, and the enlargement of the shell orifice. In some species of *Chthamalus* and *Octomeris*, particularly when young, the adjoining surfaces of the parietes are interlocked by chevron-shaped flanges, but these are quite superficial and are eroded with the surface shell layers. These 'radii' doubtfully provide for any diametric enlargement of the orifice; chthamalids rely very much on shell erosion, to enlarge the orifice, in order to allow for and keep pace with growth of the animal within the shell. The eroded adult chthamalid shell is commonly made more rigid by the parietal plates becoming fused into a cylinder by extensive internal secretion of calcite, a feature assumed more readily by *Chamaesipho* than any of the other chthamalid genera.

Chionelasmus was formerly classified with the Chthamalidae. However, even though it is like *Catophragmus* in having extra parietal plates outside the primary whorl, and distinct rostrilatera, it is not a shore species, and orifice enlargement is by alar growth of all the parietes except the rostrilatera. Diametric orifice enlargement is necessary when there is insufficient apical erosion. Alar enlargement is characteristic of the deep-sea Pachylasmidae, taken in this paper to include *Chionelasmus* and *Pachylasma*. The relationship of these two genera has been stressed by Pilsbry (1911), and in common with primitive chthamalids they show the primitive features of the rostro-latera and multiarticulated caudal appendages. The relatively fragile pachylasmid shell reflects the calm conditions of the deep-sea environment; specimens are generally disarticulated when collected by dredges. The shells of pachylasmids are also relatively simple; as in chthamalids, the shell is mostly solidly calcareous, though the base is uncalcified. The genus *Aptolasma*, however, has the parietal plates permeated in the direction of shell elongation by strips of chitin-like substance, and in some species there are regular internal and basal ribs on the parietes which interlock with a calcareous base.

The chitin-like laminae and the basal ribbing of the parietes of *Aptolasma* resemble the condition in the primitive tetraclitid genus *Epopella*. The Tetraclitidae are like the Chthamalidae in being intertidal in habitat. However, the affinities with *Aptolasma* may indicate a sublittoral origin of the Tetraclitidae, in contrast to a probable littoral origin of the Chthamalidae. The tetraclitids have alae on the carina and latera, but the alae are not as well developed as in the pachylasmids; due to the intertidal habitat, orifice enlargement is mostly effected by shell erosion. With the secretion of calcite on to the insides of the shell plates, the sutures between the plates can become quite obliterated in older, and particularly larger, tetraclitid specimens.

In contrast to the pachylasmids, the plates of tetraclitids can be interlocked by outgrowths (radii) of the rostral and lateral plates overlying the alae of adjacent plates. These denticulate-edged radii generally only engage with the adjacent parietes towards the base, but this basal strengthening of the shell is of obvious advantage in wave-exposed shore environments. Species of *Epopella*, *Tesseropora*, and *Tetraclita* can assume markedly limpet-like shapes, from extensive thickening of the parietes basally and erosion of the shell apically. The internally depending plates and pegs of *Epopella*, and the parietal tubes of the other genera, provide for structural reinforcement and perhaps efficiency of calcite secretion, and the tubes themselves provide extravisceral water reservoirs. All these features are of advantage in exposed shore habitats, so long as the intra-shell spaces are protected from the possible effects of apical shell erosion. To this end, the tubes of tetraclitids are secondarily filled with a chitin-like substance which tends to stand up above the eroded shell surface, thus probably helping to retard the pace of erosion. The chitinous laminae in *Epopella* may be analogous, and probably serve the same purpose.

The tetraclitid adaptations towards intertidal life would seem to be quite successful, despite the severe climates of shores. For example *Tetraclita squamosa viridis*, a large and very tubiferous barnacle, is conspicuous on fully sun-exposed rocks of tropical Pacific shores. The genus *Tetraclitella*, however, characteristically occurs on shaded surfaces, and without the regular heating/cooling and drying/wetting needed to effect shell erosion, diametric orifice enlargement is achieved by wide alar growth, with completely overlapping radial extensions of the parietes for structural reinforcement.

The Balanidae is a large and not yet properly subdivided family, at present comprising all those balanomorphs with a deep V-notch in the labrum. These are mostly lower-shore to shallow-sea species, but many occur epizoically on a variety of 'host' animals. The plates are generally interlocked by denticulate-edged radii, perhaps indicative of a shallow-sea origin, where wave action was a significant factor. The epizoic barnacle *Chelonibia* ranks as a primitive balanid, as it still shows evidence of eight parietal plates, has radially interlocking parietes only basally and, unlike other epizoic balanids, is rather versatile in its choice of host. The extensive infolding of the bases of the parietes of *Chelonibia* resembles the condition seen in adult *Epopella plicata* of the Tetraclitidae, and also in *Balanus (Austrobalanus) imperator*. *Chelonibia* seems to be a specialised early offshoot of the balanid line.

Elminius differs from other balanids except *Chelonibia* in lacking a basidorsal point on the penis, and in the weakly constructed but solidly calcareous shell. The radii are quite narrow, and abut on to the adjacent parietes only basally. With these features it is not surprising that *Elminius modestus* occupies habitats not prone to severe wave action. Nevertheless, *E. modestus* is a very modern barnacle, an 'opportunist' in that it can

quickly grow to maturity and is not too fussy about its choice of substratum. It can rapidly colonise available surfaces and build up breeding populations. In New Zealand it is one of the commonest 'fouling' barnacles. *E. modestus* shows that a relatively primitive morphology can lend itself to ecological diversification. This is in part due to its greater repertoire of cirral activity (Crisp & Southward 1961), whereby it can successfully utilise a wider range of habitats than can, say, the chthamalids, with their more stereotyped cirral extension responses. Chthamalids are wave-exposed shore forms; *E. modestus* is a wave-sheltered shore and sublittoral species.

Like *Chelonibia*, *Elminius* probably evolved from the balanid line before the bulk of the present day balanids, with their basidorsal point to the penis, and interlocking radii and parietes. Of these, the subgenus *Austrobalanus*, with its solidly calcareous shell, slightly diametrically enlarging shell orifice, and antenniform third cirrus (which is somewhat anomalous amongst the Balanidae), would seem as primitive as any. The restriction of the three extant species of *Austrobalanus* to temperate Australasian and South American habitats might also be taken to indicate a phylogenetic position near *Epopella* and *Elminius*. The Australian *Balanus* (*Austrobalanus*) *imperator* is an intertidal species, and the shell growth is such that there is a wide base to the adult parietes, with depending ridges and plates like those in older specimens of *Epopella* and *Chelonibia*.

Despite the wealth of material, or perhaps because of it, the taxonomic status of the genus *Balanus* and the so-called higher balanids (*Acasta*, *Creusia*, *Pyrgoma*, *Tetralbanus*, *Coronula*, and other whale barnacles) leaves much room for improvement. The large number of species, some of which are hard to distinguish, may reflect a still-evolving balanid plan. In other words, the wealth of species may represent the realisation of the potential in a shell with diametric orifice enlargement and structural reinforcement by interlocking of parietes and radii for most of their lengths. The balanids today occupy a wide variety of marine substrata, from surf-beaten rocky shores to enclosed harbour shores, from mid-tidal levels to the depths of the sea, and from rock to various animals such as sponges (*Acasta*), gorgonids (*Conopea*), corals (*Creusia* and *Pyrgoma*), and vertebrates (*Coronula* through to *Xenobalanus*, and *Cylindrolepas* through to *Stomatolepas*). Some species readily 'foul' man-made structures, rapidly colonising any available surface by means of high reproductive efficiency. Many of the fouling balanids are now cosmopolitan, e.g., *Balanus amphitrite* and *B. trigonus*. Many balanids parallel the tetracitids in having a tubiferous structure in the parietes and/or radii, and these include the largest balanids, which are species of the subgenera *Megabalanus* (e.g., *B. tintinnabulum* and *B. psittacus*) or *Balanus* (e.g., *B. nubilus* and *B. cariosus*). As in the Tetracitidae, tubiferous parietes and large shell size are related developments.

ZONATION OF BARNACLES

The intertidal distribution of barnacles is well documented; the upper limits of some species provide useful 'bench-marks' for descriptions of the ecology of nearly all temperate shores around the world. As with many other dominant sessile organisms on shores, the upper and lower limits of distribution prescribe zones, and it is real to speak of barnacle zonation. Some barnacle species have zones that reach higher than others on the same shore; on other shores, the same species change their zonal levels in the absence of some of the other barnacles or other organisms, or in the presence of new ones, or with respect to changed climatic conditions. The subject of barnacle zonation and its causes is well investigated, and need not be reviewed in this paper. However, some of the facts of barnacle zonation may help to elucidate barnacle phylogenies, and the causes

of zonation may be more clearly understood in terms of the phyletic history of the barnacles.

In Fig. 73 the vertical occurrences of barnacles on northern and southern surf shores of New Zealand are indicated. The points to be made from these (regarding *Epopella plicata* as a tetraclitid) are that the Chthamalidae are represented higher on the shore than other barnacles, that the Tetraclitidae are represented higher on the shore than the Balanidae, and that balanids are often more conspicuous on the lower shore than lepadomorphs. The chthamalid-tetraclitid-balanid trend is fairly universal on warm temperate shores. It appears also to be the case on tropical shores (Foster 1974), and only becomes less clear on cold temperate, polar, or isolated shores, where one or more of the families is not represented.

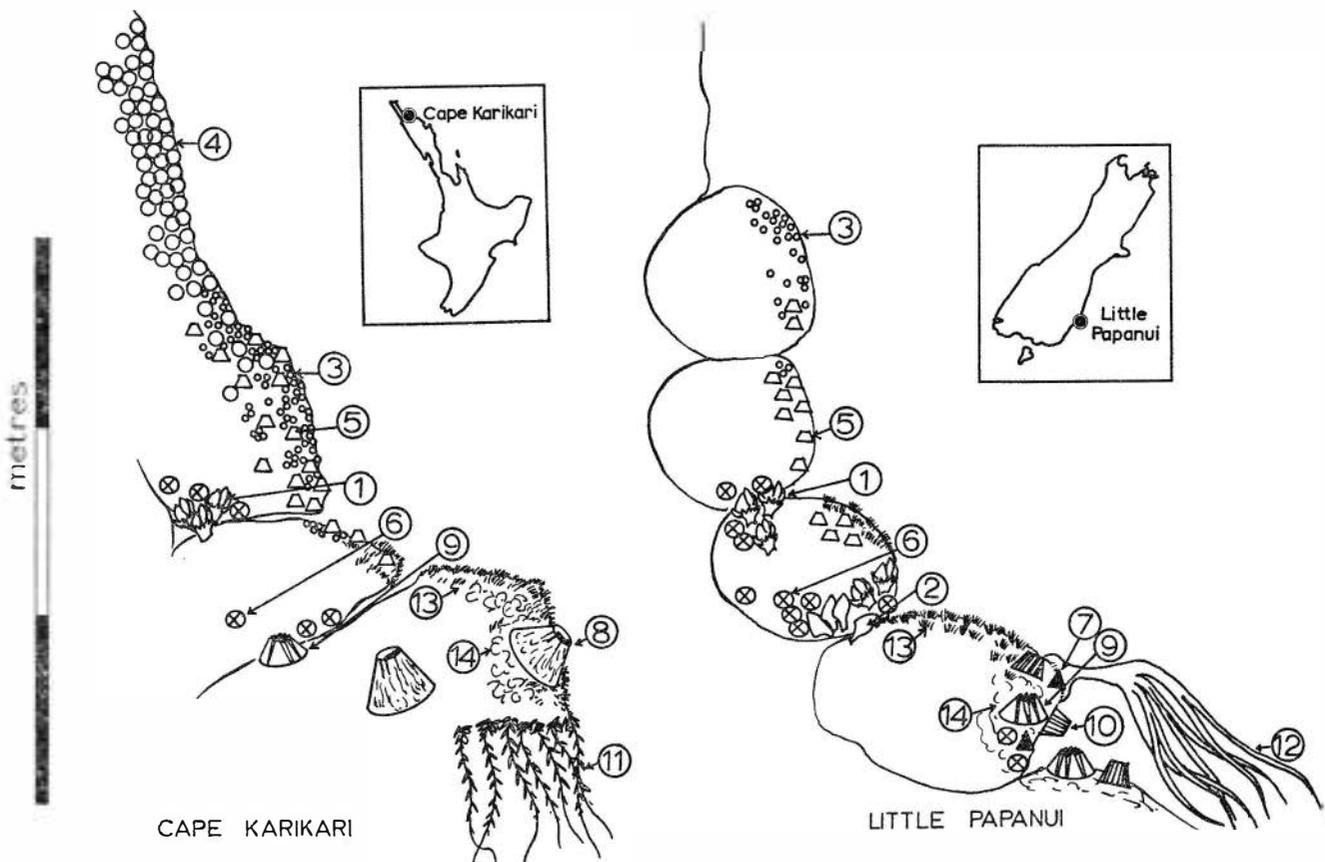


Fig. 73. Profiles of the shores at Cape Karikari and Little Papanui indicating the distribution of barnacles and visibly dominant algae.
 BARNACLES: 1, *Calantica spinosa*; 2, *Calantica villosa*; 3, *Chamaesipho columna*; 4, *Chamaesipho brunnea*; 5, *Epopella plicata*; 6, *Tetraclitella purpurascens*; 7, *Balanus vestitus*; 8, *Balanus tintinnabulum linzei*; 9, *Balanus decorus*; 10, *Balanus campbelli*
 ALGAE: 11, *Carpophyllum angustifolium*; 12, *Durvillea antarctica*; 13, tufted algae; 14, encrusting algae.

EVOLUTION OF BARNACLE ZONATION

In terms of barnacle phylogeny, the impression is that the balanids nowadays dominate the tropically rich, shallow-sea, sublittoral habitat; that first, the chthamalids and then the tetraclitids evolved in or towards the intertidal environment, and have progressively occupied higher intertidal levels; and that the pachylasmids have evolved towards, and are now restricted to, the deep sea (Fig. 74).

Life on the shore requires adaptations appropriate to the periods of emersion, particularly to avoid drying out. Barnacles with rigidly interlocked or concreted shells can not only survive wave action during immersion, but can also endure emersion periods, as long as they restrict their activity when emersed. The colonisation of low shore levels is possible to any marine form, as long as it selects desiccation-protected habitats and can compete for space, at least for long enough to become established. The vegetative growth of algae, sponges, coelenterates, and bryozoans would tend to smother barnacles, and must be an important factor in explaining the relative paucity of barnacle numbers (not species) in the shallow-sea habitat, compared with the dense and crowded barnacle populations that can occur higher on the shore. On New Zealand shores, intertidal specimens of *Calantica villosa*, *Ibla idiotica*, *Balanus vestitus*,

B. decorus, *B. campbelli*, *B. variegatus*, and even *Elminius modestus* can all be regarded as extensions of essentially sublittoral ranges into desiccation-protected habitats. *E. modestus* is apparently better equipped to do this than the other species, because it is an important constituent of the zonation patterns on wave-sheltered shores, where it can reach as high as high water of neap tides. The desiccation-protected shore habitats may be permanently protected, as for example under boulders, or in caves or crevices, and are then shared by the characteristically intertidal and hypobiotic barnacles *Calantica spinosa* and *Tetraclitella purpurascens*. In more southern latitudes the 'under-stone' species may not be as inaccessible among the rocks as they are in the north, a reflection of the lowered desiccation risk of the higher latitudes. The desiccation-protected habitats may also be seasonally governed; settling, metamorphosing, and growing barnacles will suffer more from the severer climatic effects of high temperatures and increased frequency of anticyclonic weather in the summer.

To varying extents all marine intertidal species suffer from periods of harsh climate, and the most vulnerable stage is the settling and metamorphosing larva. It has been shown that with increasing size of the barnacle

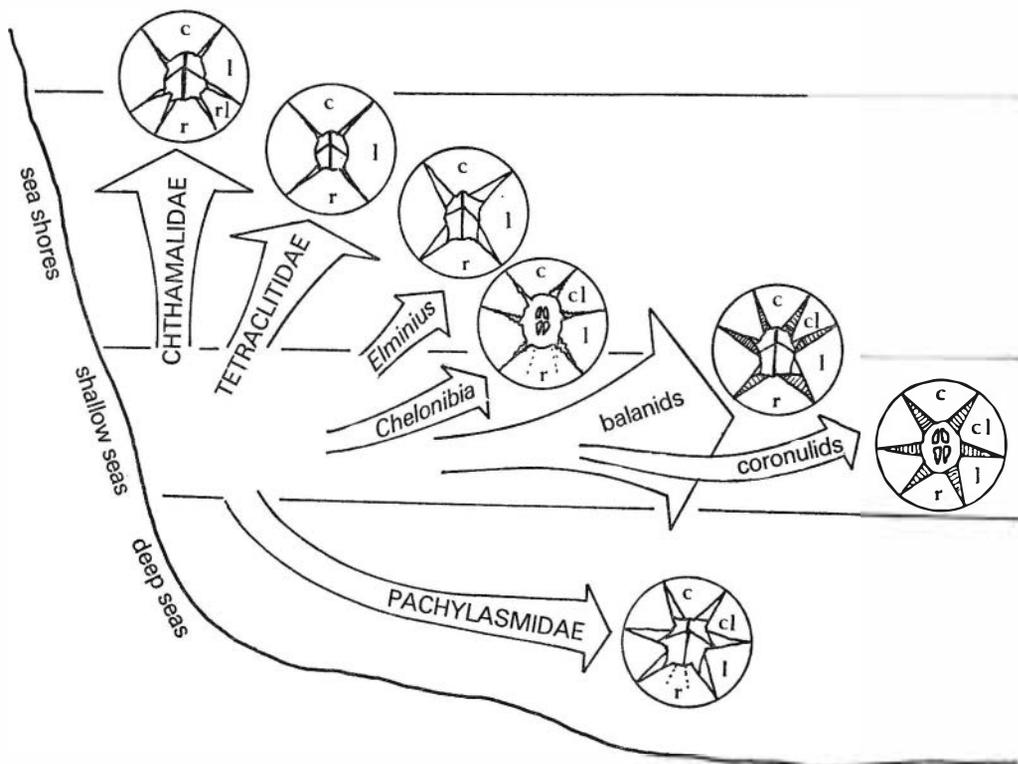


Fig. 74. Radiation of the Balanomorpha, with apical views of the plate arrangements: c, carina; cl, carinolatus; l, latus; r, rostrum or rostral plate; rl, rostrolatus; s, scutum; t, tergum.

the overall permeability decreases (Foster 1971a), and it follows that an established barnacle may become increasingly more immune to unpredictable periods when low spring tides, anticyclonic weather, and onshore breezes occur.

The larger specimens of *Balanus tintinnabulum linzei* in the north of New Zealand, although not abundant on sun-exposed shores, are conspicuous because of their size. This species is intolerant of emersion, but a few specimens evidently survive the low tidal surf conditions of rocky headlands and islands in the north-east of the country. Space in these habitats is restricted by the abundance of tufted and encrusting algae, but the adult *B. tintinnabulum* can counteract algal smothering with powerful cleaning movements of the apices of the terga around the shell orifice.

Soft-bodied, desiccation-prone, and spreading space competitors are barred from high shore levels, where species of barnacles with control over the opening of the opercular plates when the tide is out can survive. The up-shore limits of the various barnacle species reflect the nature and extent of their adaptation to emersion conditions. They must of course be increasingly eurythermal to meet the longer periods of exposure to wide-ranging atmospheric temperatures when the tide is out (Foster 1969). As long as the shell covering is complete, water loss (drying) or water gain (rain or land runoff) can be endured (Foster 1970, 1971a,b).

Intertidal barnacles use the mantle cavity as a lung during emersion, expelling surplus water and maintaining contact with the overlying air via a small pneumostome between the opercular plates, so that gaseous diffusion can occur with minimal water loss (Barnes *et al* 1963). The pneumostome is opened and closed for alternate periods; with prolonged emersion, the frequency and duration of the closed phase of the cycle increases, possibly in response to increasing water loss. Barnacles have receptors that penetrate the thick, chitinous integument at the occludent edges of the opercular plates, so that even when the plates are closed there is sensory contact with the external environment (Foster & Nott 1969). In all barnacles there is a reflexive closing response to light and mechanical stimuli, such as the approach of a predator, but the voluntary opening response probably involves these opercular receptors. Higher-shore barnacles are apparently more adept at interpreting and appropriately responding to stimuli associated with factors of the emersion environment, and do not open until appropriate clues associated with sea water are detected.

Any tendency to occupy higher and higher shore levels must be in response to considerable environmental pressure, for the upper shore can hardly be regarded as more hospitable to life. Perhaps nowhere else in the world is the substratum so subject to wide fluctuations of temperature, salinity, and drying and wetting by fresh or salt water, with diurnal and tidal regularity and climatic irregularity. For a marine animal the time spent feeding and reproducing must be small at high

tidal levels; and in supralittoral regions (above tidal predictions) is dependent on the effectiveness of waves. The harshness of the upper-shore environment is reflected in the abundance of bare rock surface and the paucity of permanent life; barnacles and lichens form the only permanent rock cover. *Chamaesipho brunnea* can occur 4 m above predicted tidal levels, and has at times to endure weeks without wetting by sea water. When transplanted to low shore levels, *C. brunnea* will function normally for as long as it is immersed, and will survive and grow as long as it is protected from predation and space competition. The barnacle is preyed on by carnivorous gastropod molluscs and cirri-snatching gobiomorph fishes, and competes for space with algae, encrusting invertebrates, other barnacles, oysters, and mussels. On Scottish shores, *Balanus balanoides* is faster-growing than *Chthamalus stellatus*, and can effectively crowd it out (Connell 1961). On New Zealand shores, the smaller but more densely settling and faster-growing *Chamaesipho columna* can, within a year, smother the slower-growing *C. brunnea* where the potential ranges of the two overlap; *C. brunnea* can survive at higher shore levels than *C. columna*, however (Luckens 1970).

The higher-shore habitats can thus be regarded as ecological refuges from biotic pressure. As the higher-shore species are better adapted to harsher shore conditions, they may have had longer to become so adapted, i.e., the higher-zoned species may be phylogenetically older. Certainly the contention 'chthamalids higher and older than tetracitids higher and older than balanids' is in accord with the order of antiquity of these families based on morphological grounds involving their relative divergence from a pollicipoid ancestor.

Of course, not all species of any one family may be equally as old; there are opportunist species in the Chthamalidae, as for example *Chthamalus malayensis*, which occurs practically ubiquitously on rocks, mangroves, mollusc shells, coral, and other barnacles on tropical south-west Pacific shores (Pope 1965, Foster 1974), and *Chamaesipho columna* on Australasian shores. This latter species is particularly "keen" in the north of its New Zealand range, where dense settlement can form a "honeycomb" covering on rocks and shells within months. In the Tetracitidae, opportunists are probably best exemplified by some of the hypobiotic *Tetracitella* species, such as *T. divisa* on many tropical shores, and *T. purpurascens* on temperate Australasian shores. In the Balanidae, *Elminius modestus*, *Balanus amphitrite*, *B. trigonus*, *B. improvisus*, and *B. balanoides* are examples of opportunist, shallow-sea to midtidal, fouling barnacles. The hallmarks of opportunist barnacles are a high metabolic rate, as typified by fast beating rates of the cirri and a wide repertoire of cirral activity, to meet a variety of conditions of water movement; and fast growth-rate to sexual maturity, in order to maintain a high "recolonising potential" of larvae in the plankton to take advantage of any available settlement space. Not surprisingly, it is the opportunist species of the Balanidae

that have particularly wide geographical and ecological distributions, many of them through the agency of shipping.

Throughout this paper little has been made taxonomically of the presence or absence of a calcareous base to the balanomorph shell. Even in one genus, some of the species may never form calcite in the basal tissues, or it may develop only in larger specimens. Apparently, the primitive condition is a non-calcareous base, corresponding to the condition of the pedal disc of lepadomorphs. Certainly, most chthamalids and the supposedly more primitive tetraclitids (*Epopella*) and balanids (*Chelonibia* and *Elminius*) do not deposit calcite basally.

The secretion of a calcareous base seems to separate the tissues from the substratum (of importance to forms that live on soft or porous substrata, such as coral, so that water retention may be enhanced), or it may provide a convenient substrate-adhering plate which can interlock peripherally with the basal edges of the parietes. High tidal barnacles can abut directly on to non-porous and solid rock, and most of the chthamalids and the temperate-shore tetraclitids and balanids have membranous bases. However, the predominant coral-rock substrate of tropical shores has perhaps dictated a water-conserving calcareous base for *Chthamalus intertextus* and the adults of many species of *Tetraclita*, *Tesseropora*, and *Tetraclitella*.

BARNACLE PALEOECOLOGY

The importance of the shore habitat, and particularly the surf-shore habitat, to balanomorph evolution may account for the indefiniteness of the palaeontological record of the suborder. The intertidal region is very restricted in area, and, although barnacles may be very dense on surf shores, the total numbers of any one intertidal species are probably not as great as for more widespread sublittoral species. Further, the rocky shore environment does not favour the deposition of its elements intact into sediments. Rather, it is a dynamic, eroding environment, grinding loose particles into sand.

The earliest known horizons of barnacle genera are listed in Table 5. These fossil ages are consistent with some of the foregoing ideas, and can in fact provide some tentative dates for the origins of the families of the

Balanomorpha. The existence of *Catophragmus* in the Upper Cretaceous is a fortuitous discovery, and indicates the relative antiquity of the Chthamalidae. The absence of other chthamalids and of tetracitids of equivalent age may be due to the unlikelihood of their fossilisation and geological discovery. The predominance of genera of the Balanidae as fossils possibly reflects their living in more fossil-prone habitats, such as the stiller regions of shallow seas and continental shelves. It is of interest that the earliest fossil balanid, *Hesperibalanus* of the Lower Eocene, is one of the solid balanid 'genera', as are *Kathpalmeria*, known only from the Eocene, and *Austrobalanus*, recorded from the Oligocene. The various epizoic balanids evolved during the Tertiary, the sponge-inhabiting *Acasta* by the Oligocene, the

Table 5. Earliest known fossil horizons of barnacle genera (extinct genera in parentheses; data mostly from Newman *et al.* 1969).

	Lepadomorpha	Chthamalidae	Pachylasmaeidae	Tetracitidae	Balanidae
Pleistocene				<i>Tetraclita</i>	<i>Membranobalanus</i> <i>Cryptolepas</i> <i>Platylepas</i>
Pliocene	U M L	<i>Chthamalus</i>		(<i>Tesseroplax</i>)	<i>Hexacreusia</i> <i>Semibalanus</i> <i>Pyrgoma</i>
Miocene	U L		<i>Hexelasma</i> <i>Pachylasma</i> (<i>Tesserelasma</i>)	? <i>Tetraclita</i>	<i>Coronula</i> <i>Armatobalanus</i> <i>Chirona</i> <i>Conopea</i> <i>Creusia</i> <i>Chelonibia</i>
Oligocene	L			<i>Tesseropora</i>	<i>Acasta</i> <i>Balanus</i> <i>Megabalanus</i> <i>Austrobalanus</i>
Eocene	U M L	<i>Trilasmis</i> <i>Lepas</i> <i>Pollicipes</i> <i>Scalpellum</i> <i>Oxynaspis</i>			(<i>Emersonius</i>) (<i>Kathpalmeria</i>) <i>Hesperibalanus</i>
Paleocene		<i>Calantica</i>			
Cretaceous	U L	<i>Arcoscalpellum</i> (<i>Cretiscalpellum</i>) (<i>Virgiscalpellum</i>)	<i>Catophragmus</i>		
Jurassic	U	(<i>Archeolepas</i>) (<i>Zeugmatolepas</i>)			
Triassic	U	(<i>Eolepas</i>)			
Carboniferous	M	(<i>Praeolepas</i>)			
Silurian	U	(<i>Cyprilepas</i>)			

coral-inhabiting *Creusia* by the early Miocene, and the whale barnacles also by the Miocene. It seems that much of the balanomorph radiation had taken place by the Oligocene, and that important clues to balanomorph radiation should be sought in Paleocene and Eocene deposits.

The New Zealand fossil barnacles have received some attention, particularly from Withers (1913, 1924) who assigned more accurate horizons to the known fossil species in the last of his monographs of fossil Cirripedia (Withers 1953). This information, plus a little more, is given in Table 6. Cenozoic marine sediments dating back to the lower Oligocene reveal a calanticoid, pachylasmid, and balanid barnacle fauna like that of the present-day New Zealand shelf. The extensive, *Hexelasma*-rich Miocene strata of Motutapu Island near Auckland seem to represent an environment similar to parts of the New Zealand shelf today, where dredging has produced accumulations of disarticulated hexelasmoid plates. A similar phenomenon has been reported in Antarctic seas for the circumantarctic extant species *Hexelasma corilliforme* (Bullivant 1967).

There is now scope for a fuller understanding of the New Zealand fossil Cirripedia, not only from as yet

undescribed specimens in various collections, but also from the more refined balanomorph taxonomy than existed even a few years back. It is possible that the unidentified species of *Hexelasma* of Withers may not even be of that genus. Some of the deposits on Motutapu Island contain fragments of barnacles with narrow radii, internal basal ribbing, and some with and some without calcareous bases. Detailed evaluation of these may assign them to any of the Pachylasmiidae, Tetraclitidae, or Balanidae, as these families are presently understood. Conglomerate deposits may contain the fragments of shore debris, and prove rewarding of examination.

Certainly, if much of the foregoing on balanomorph radiation is to be substantiated or otherwise, we must examine shore-derived fossil material. The presence today in New Zealand of such key genera to the Tetraclitidae and Balanidae as *Epopella*, *Elminius*, and *Austrobalanus* seems to indicate that New Zealand (along with temperate Australia and South America) is a refuge of certain trends of balanomorph evolution which became zoogeographically isolated during the Paleocene-Eocene period, at the dawn of tetraclitid and balanid radiation.

Table 6. The known fossil Cirripedia of New Zealand (from Withers 1953, *Fleming 1958, and †Grant-Mackie 1965)

	Lepadomorpha	Chthamalidae	Pachylasmiidae	Tetraclitidae	Balanidae
Pleistocene					* <i>Coronula diadema</i>
	U				<i>Balanus decorus</i>
Pliocene	M				* <i>Coronula aotea</i> <i>Balanus decorus</i> <i>B. tubulatus</i> <i>B. acutus</i>
	L				<i>B. decorus</i> <i>B. tubulatus</i> <i>B. acutus</i>
Miocene	U				<i>B. decorus</i>
	L	<i>Lepas harringtoni</i> <i>Calantica subplana</i> † <i>Arcoscalpellum distinctum</i>		<i>Hexelasma aucklandicum</i> <i>Hexelasma</i> sp.	
	U	<i>Arcoscalpellum unguatum</i>			<i>B. decorus</i> <i>B. acutus</i>
Oligocene	M	<i>A. unguatum</i> <i>A. striatulum</i>			<i>B. acutus</i>
	L	<i>A. unguatum</i> <i>A. complanatum</i> <i>Calantica arguta</i> <i>A. striatulum</i> <i>A. euglyphum</i>		<i>Hexelasma</i> sp.	<i>B. vestitus</i> <i>B. acutus</i>

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APPENDIX

New Zealand Oceanographic Institute stations which have yielded
barnacles or (species in parentheses) barnacle shells.

Stn no.	Lat. (°S)	Long. (°E)*	Depth (m)	Species represented	Stn no.	Lat. (°S)	Long. (°E)*	Depth (m)	Species represented
A426	4139	17433	150	<i>Arcoscalpellum affricatum</i>	B254	4637	16832	14	(<i>Balanus decorus</i>)
A433	4000	17340	110	(<i>Balanus decorus</i>)	B256	4637	16845	21	(<i>Balanus decorus</i>)
A444	4123	17431	276	<i>Calantica villosa</i>	B258	4640	16838	19	(<i>Balanus decorus</i>)
A489	4127	17451	101	(<i>Balanus decorus</i>)	B260	4645	16839	25	<i>Balanus vestitus</i>
A702	4741	17931	168	<i>Balanus vestitus</i>	B264	4640	16807	17	(<i>Balanus decorus</i>)
A704	4742	17927	154	(<i>Balanus vestitus</i>)	B264A	4643	16820	27-28	<i>Balanus decorus</i>
				(<i>Balanus decorus</i>)	B265	4656	16820	23	(<i>Balanus decorus</i>)
A705	4742	17906	48	<i>Balanus vestitus</i>	B268	4645	16853	60	(<i>Balanus decorus</i>)
				<i>Balanus campbelli</i>	B270	4642	16900	33	<i>Balanus decorus</i>
A706	4743	17848	311	(<i>Balanus decorus</i>)	B271	4642	16853	21	<i>Balanus vestitus</i>
				(<i>Coronula diadema</i>)					(<i>Balanus decorus</i>)
A713	4745	17953	201	<i>Balanus vestitus</i>	B272	4644	16831	21	(<i>Balanus decorus</i>)
A715	4741	17903	121	(<i>Balanus vestitus</i>)	B554	4400	17258	81	(<i>Balanus decorus</i>)
A745	4937	17851	399	(<i>Pachylasma scutistriata</i>)	B562	4518	17128	128	(<i>Balanus vestitus</i>)
A746	4730	17930	159	<i>Balanus vestitus</i>					(<i>Balanus decorus</i>)
A747	4741	17903	113	<i>Balanus vestitus</i>	B563	4518	17115	71	(<i>Balanus decorus</i>)
A748	4741	17904	62	(<i>Balanus vestitus</i>)	B564	4520	17054	22	(<i>Balanus decorus</i>)
				(<i>Balanus decorus</i>)	B565	4600	17018	22	<i>Balanus decorus</i>
A749	4742	17904	62	(<i>Balanus decorus</i>)	B566	4600	17059	346	(<i>Balanus vestitus</i>)
A750	4742	17908	135	(<i>Balanus vestitus</i>)	B567	4600	17055	124	(<i>Balanus decorus</i>)
A751	4745	17907	155	<i>Balanus vestitus</i>	B568	4600	17043	75	(<i>Balanus decorus</i>)
				(<i>Balanus decorus</i>)	B569	4640	17008	165	(<i>Balanus decorus</i>)
A756	Bounty Is, shore			<i>Balanus campbelli</i>					(<i>Balanus decorus</i>)
A850	4720	16726	135	(<i>Balanus decorus</i>)	B595	4640	16923	73	(<i>Balanus decorus</i>)
A852	4717	16749	135	(<i>Balanus decorus</i>)	B601	4715	16736	15	(<i>Balanus vestitus</i>)
A853	4715	16755	101	(<i>Balanus decorus</i>)	B609	4600	16622	220	(<i>Balanus vestitus</i>)
A862	4717	16721	146	(<i>Balanus decorus</i>)	B619	4442	16733	95	(<i>Balanus decorus</i>)
A877	4704	16848	112	(<i>Balanus decorus</i>)	B632	4241	17044	146-289	(<i>Balanus decorus</i>)
A891	4322	17711	263	(<i>Balanus decorus</i>)	B650	4000	17443	42	(<i>Balanus decorus</i>)
A892	4317	17711	253	(<i>Balanus decorus</i>)	B690	4100	17305	26	(<i>Balanus decorus</i>)
A893	4312	17711	263	(<i>Balanus decorus</i>)	B837	4059	17403	40	(<i>Balanus decorus</i>)
A898	4322	17717	231	(<i>Balanus decorus</i>)					
A901	4317	17704	251	<i>Calantica spinilatera</i>					
A970	Curio Bay, Southland, shore			<i>Epopella plicata</i>	C80	4115	17432	348	(<i>Balanus decorus</i>)
					C104	4119	17434	163	(<i>Balanus decorus</i>)
B176	5029	16631	84	(<i>Balanus vestitus</i>)	C106	4118	17433	183	(<i>Balanus decorus</i>)
				(<i>Balanus decorus</i>)	C111	4119	17433	172	(<i>Balanus decorus</i>)
B181	5054	16606	7	<i>Balanus vestitus</i>	C118	4119	17428	172	(<i>Balanus vestitus</i>)
B184	5237	16907	188	(<i>Balanus decorus</i>)					
B189	5233	16908	29	(<i>Balanus vestitus</i>)	C125	4117	17429	263	(<i>Balanus decorus</i>)
B192	5227	16921	165-192	(<i>Balanus vestitus</i>)					
B195	4915	17145	82-174	(<i>Balanus vestitus</i>)	C132	4118	17433	174	(<i>Balanus decorus</i>)
B196	4620	17028	135	<i>Balanus decorus</i>	C166	3937	17158	271	<i>Arcoscalpellum pedunculatum</i>
B197	4614	17032	110	(<i>Balanus vestitus</i>)	C171	3940	17253	163	(<i>Hexelasma allearum</i>)
B215	4650	16832	32	(<i>Balanus decorus</i>)	C175	3940	17344	84	<i>Calantica spinilatera</i>
B216	4650	16823	22	(<i>Balanus decorus</i>)	C188	4050	17317	44	(<i>Balanus decorus</i>)
B219	4645	16810	36	(<i>Balanus decorus</i>)	C210	4116	17434	95	<i>Balanus decorus</i>
B220	4640	16810	37	(<i>Balanus decorus</i>)	C272	3820	17412	91	(<i>Balanus decorus</i>)
B221	4640	16817	31	(<i>Balanus decorus</i>)	C275	3820	17344	137	(<i>Balanus decorus</i>)
B222	4640	16824	27	(<i>Balanus decorus</i>)	C287	3802	17433	68	(<i>Balanus decorus</i>)
B224	4645	16817	32	(<i>Balanus decorus</i>)	C309	3700	17426	22	(<i>Balanus decorus</i>)
B225	4650	16818	31	(<i>Balanus decorus</i>)	C325	3719	17422	55	(<i>Balanus decorus</i>)
B226	4655	16817	49	(<i>Balanus decorus</i>)	C334	3742	17437	49	(<i>Balanus decorus</i>)
B227	4659	16807	24	(<i>Balanus decorus</i>)	C342	3742	17414	155	(<i>Balanus decorus</i>)
B228	4645	16803	38	(<i>Balanus decorus</i>)	C344	3759	17434	55	(<i>Balanus decorus</i>)
B229	4640	16755	28	(<i>Balanus decorus</i>)	C363	3840	17240	146	(<i>Calantica spinilatera</i>)
B230	4640	16803	26	(<i>Balanus decorus</i>)	C369	3854	17258	143	(<i>Balanus decorus</i>)
B233	4640	16748	37	<i>Balanus decorus</i>	C380	3854	17422	37	(<i>Balanus decorus</i>)
B235	4635	16755	49	(<i>Balanus decorus</i>)	C381	4118	17437	24	(<i>Balanus decorus</i>)
B237	4635	16811	25	(<i>Balanus decorus</i>)	C423	3920	17332	108	(<i>Balanus decorus</i>)
B238	4635	16814	33	(<i>Balanus decorus</i>)	C429	3920	17308	124	(<i>Balanus decorus</i>)
B245	4630	16748	49	(<i>Balanus decorus</i>)	C430	3920	17255	130	(<i>Balanus decorus</i>)
B248	4625	16803	17	<i>Balanus decorus</i>	C438	4000	17337	84	(<i>Balanus decorus</i>)
B250	4623	16806	11	<i>Balanus decorus</i>	C442	4000	17428	55	(<i>Balanus decorus</i>)
B251	4625	16810	15	(<i>Balanus decorus</i>)	C444	4000	17441	38	(<i>Balanus decorus</i>)
B252	4631	16817	18	(<i>Balanus decorus</i>)	C447	4000	17449	29	(<i>Balanus decorus</i>)
B253	4640	16831	17	(<i>Balanus decorus</i>)	C445	4000	17444	31	(<i>Balanus decorus</i>)

*Or °W where indicated here and on succeeding pages



Stn no.	Lat. (°S)	Long. (°E)*	Depth (m)	Species represented	Stn no.	Lat. (°S)	Long. (°E)*	Depth (m)	Species represented
C448	4000	17451	31	(<i>Balanus decorus</i>)	D1	4418	17610	141	(<i>Balanus vestitus</i>)
C449	4000	17454	29	(<i>Balanus decorus</i>)	D5	5640	15845	1280	(<i>Hexelasma alearum</i>)
C450	4000	17457	27	(<i>Balanus decorus</i>)	D6	5529	15832	415	(<i>Hexelasma alearum</i>)
C451	4000	17458	26	(<i>Balanus decorus</i>)	D10	5440	15901	71	(<i>Balanus decorus</i>)
C452	4000	17500	22	(<i>Balanus decorus</i>)	D22	5038	16357	755	(<i>Hexelasma alearum</i>)
C453	4000	17501	22	(<i>Balanus decorus</i>)	D31	5235	16917	62	(<i>Balanus decorus</i>)
C454	3940	17416	24	(<i>Balanus decorus</i>)	D32	5208	16850	188	(<i>Balanus vestitus</i>)
C456	3940	17411	26	(<i>Balanus decorus</i>)					(<i>Balanus decorus</i>)
C458	3940	17452	24	(<i>Balanus decorus</i>)	D42	5047	16631	31-49	(<i>Balanus decorus</i>)
C460	3940	17400	33	(<i>Balanus decorus</i>)	D47	5055	16613	68	(<i>Balanus decorus</i>)
C461	3940	17357	44	(<i>Balanus decorus</i>)	D52	5042	16615	73	<i>Balanus vestitus</i>
C462	3940	17355	48	(<i>Balanus decorus</i>)	D53	5042	16624	81	(<i>Balanus vestitus</i>)
C466	4045	17246	11	(<i>Balanus decorus</i>)	D55	5039	16604	49	(<i>Balanus vestitus</i>)
C468	4039	17246	15	(<i>Balanus decorus</i>)					(<i>Balanus decorus</i>)
C469	4040	17252	29	(<i>Balanus decorus</i>)	D57	5037	16615	44	(<i>Balanus vestitus</i>)
C471	4038	17259	33	(<i>Balanus decorus</i>)	D58	5036	16616	49	(<i>Balanus vestitus</i>)
C472	4038	17252	26	(<i>Balanus decorus</i>)	D59	5035	16614	27	<i>Balanus vestitus</i>
C473	4038	17245	22	(<i>Balanus decorus</i>)	D62	5031	16617	27	<i>Balanus decorus</i>
C474	4037	17245	17	(<i>Balanus decorus</i>)					<i>Balanus decorus</i>
C476	4100	17305	20	(<i>Balanus decorus</i>)	D72	5020	16624	163	<i>Balanus decorus</i>
C479	4114	17314	9	(<i>Balanus decorus</i>)	D78	5040	16602	132-141	(<i>Balanus vestitus</i>)
C480	4110	17318	29	(<i>Balanus decorus</i>)	D80	5032	16559	104	<i>Balanus vestitus</i>
C482	4100	17331	46	(<i>Balanus decorus</i>)					(<i>Balanus decorus</i>)
C483	4050	17331	53	(<i>Balanus decorus</i>)	D83	4953	16709	150	<i>Balanus vestitus</i>
C486	4127	17506	27	(<i>Balanus decorus</i>)	D85	4950	17013	611	<i>Arcoscalpellum costellatum</i>
C520	4139	17510	112	(<i>Balanus decorus</i>)	D90	4350	17900W	399	<i>Ibla idiotica</i>
C591	4146	17446	108	(<i>Balanus vestitus</i>)	D102		Erebus Cove, Auck. Is, shore		<i>Epopella plicata</i>
				(<i>Balanus decorus</i>)	D104	5049	16616	95	(<i>Balanus campbelli</i>)
					D109	5049	16602	64	<i>Balanus vestitus</i>
C595	4323	17517	99	(<i>Balanus vestitus</i>)					<i>Balanus campbelli</i>
C596	4320	17512	124	(<i>Balanus decorus</i>)	D119	4345	17840	492	<i>Smilium acutum</i>
C607	4348	17900	421-431	<i>Arcoscalpellum trochelatum</i>	D121	4317	17711	210	<i>Calantica spinilatera</i>
C617	4358	17523	288-302	<i>Balanus vestitus</i>					<i>Balanus vestitus</i>
				<i>Balanus decorus</i>					<i>Balanus decorus</i>
C627	3913	17154	397	<i>Arcoscalpellum affbricatum</i>	D127	4642	16817	29	(<i>Balanus decorus</i>)
C636	3914	17153	681	<i>Smilium acutum</i>	D140	4801	16635	shore	<i>Calantica spinosa</i>
C640	3917	17153	364	(<i>Balanus decorus</i>)					<i>Epopella plicata</i>
C642	3916	17153	354	<i>Arcoscalpellum pedunculatum</i>	D159	4901	16430	741	<i>Verruca halothea</i>
C650	4250	17324	27	(<i>Balanus decorus</i>)					<i>Aaptolasma nolearia</i>
C653	4250	17331	95	<i>Balanus vestitus</i>	D160	4932	16616	722	<i>Calantica gemma</i>
C675	4244	17335	surface	<i>Lepas australis</i>					(<i>Verruca halothea</i>)
C729	5947	16931	surface	<i>Lepas australis</i>					<i>Pachylasma scutistriata</i>
C734	5355	15855	360	<i>Arcoscalpellum affbricatum</i>					(<i>Hexelasma alearum</i>)
				(<i>Balanus decorus</i>)	D164		Rose I, shore		(<i>Balanus decorus</i>)
C735	5339	15900	surface	<i>Lepas australis</i>	D166	4949	16351	668	(<i>Hexelasma alearum</i>)
C765	3427	17249	22	(<i>Balanus decorus</i>)					(<i>Aaptolasma nolearia</i>)
C771	3440	17327	192	(<i>Balanus decorus</i>)					(<i>Verruca halothea</i>)
C773	3502	17346	26	(<i>Balanus decorus</i>)	D169	5048	16358	896	(<i>Hexelasma alearum</i>)
C778	3520	17448	187	(<i>Balanus decorus</i>)					(<i>Calantica gemma</i>)
C779	3600	17433	20	<i>Balanus trigonus</i>	D171	5057	16547	501	(<i>Balanus decorus</i>)
C768	3640	17521	20	<i>Balanus trigonus</i>	D175	5037	16741	426	(<i>Balanus decorus</i>)
C789	3614	17518	59	(<i>Balanus decorus</i>)	D185		Carnley Harbour	64	<i>Balanus vestitus</i>
C790	3611	17521	20	<i>Balanus trigonus</i>	D186		Camp Cove Harbour, shore		(<i>Epopella plicata</i>)
C801	3740	17636	77	(<i>Balanus decorus</i>)	D190		Masked I Harbour, shore		<i>Epopella plicata</i>
C812	3740	17838	75	(<i>Balanus decorus</i>)	D193	5040	16622	72	(<i>Balanus decorus</i>)
C814	3740	17856	194	<i>Calantica studeri</i>	D194	5044	16621	75-95	(<i>Balanus decorus</i>)
				(<i>Balanus decorus</i>)	D210	4922	17153	353	<i>Pachylasma scutistriata</i>
C844	4138	17511	88	<i>Balanus decorus</i>					<i>Arcoscalpellum costellatum</i>
C852	4041	17420	132	(<i>Balanus decorus</i>)					<i>Arcoscalpellum affbricatum</i>
C853	4038	17405	91	(<i>Balanus decorus</i>)	D220	3932	17148	344	<i>Arcoscalpellum pedunculatum</i>
C586	4055	17351	22	<i>Balanus vestitus</i>	D227	3950	16943	752	<i>Arcoscalpellum affbricatum</i>
				<i>Balanus decorus</i>	D245	3954	17200	466	<i>Arcoscalpellum pedunculatum</i>
					D269	4045	17336	57	(<i>Balanus decorus</i>)
C361	4100	17316	38	(<i>Balanus decorus</i>)	D272	4040	17349	59	(<i>Balanus decorus</i>)
C863	4057	17402	71	<i>Balanus decorus</i>	D595		Waitangi, shore		<i>Lepas anatifera</i>
C907	4054	17420	90	(<i>Balanus decorus</i>)	D720	2905	17710W	surface	<i>Lepas anatifera</i>
C908	4055	17410	48	(<i>Balanus decorus</i>)	D876	4320	17650W	148	<i>Calantica studeri</i>
C909	4114	17352	17	(<i>Balanus decorus</i>)					(<i>Balanus vestitus</i>)
C910	4113	17353	24	(<i>Balanus decorus</i>)					(<i>Balanus decorus</i>)
C911	4113	17352	33	(<i>Balanus decorus</i>)	D878	4325	17640W	115	<i>Calantica studeri</i>
C912	4113	17352	22	(<i>Balanus decorus</i>)	D881		Wharekauri, shore		<i>Chamaespho brunnea</i>
C913	4113	17351	18	(<i>Balanus decorus</i>)	D885	4355	17640W	59	(<i>Coronula diadema</i>)
C914	4111	17352	31	(<i>Balanus decorus</i>)	D886		Waitangi, shore		<i>Epopella plicata</i>
C915	4109	17352	11	(<i>Balanus decorus</i>)	D891		Waihere Bay, shore		<i>Lepas anatifera</i>
C919	4107	17314	52	(<i>Balanus decorus</i>)					<i>Balanus campbelli</i>
C921	4105	17357	75	(<i>Balanus decorus</i>)					<i>Chamaespho brunnea</i>
C924	4103	17356	63	(<i>Balanus decorus</i>)	D892		Flower Pot Harbour, Piit I, shore		(<i>Balanus decorus</i>)
C936	4056	17405	100	(<i>Balanus decorus</i>)	D893	4410	17600W	56	(<i>Balanus decorus</i>)
C937	4055	17408	25	(<i>Balanus decorus</i>)	D897	4429	17558W	177	(<i>Balanus vestitus</i>)
C957	4309	17515	123	(<i>Balanus decorus</i>)	D898	4426	17614W	96	(<i>Balanus decorus</i>)

Stn no.	Lat. (°S)	Long. (°E)*	Depth (m)	Species represented	Stn no.	Lat. (°S)	Long. (°E)*	Depth (m)	Species represented
D904	4359	17840W	459	<i>Smilium acutum</i> <i>Arcoscalpellum costellatum</i> <i>Arcoscalpellum pertosum</i>	E720	3733	17835	249	<i>Ibla idiotica</i> <i>Calantica studeri</i> <i>Balanus decorus</i>
D905	4408	17846W	607	<i>Smilium acutum</i> <i>Arcoscalpellum costellatum</i>	E738	3735	17903	246	(<i>Balanus decorus</i>)
D906	4354	17914W	222	<i>Calantica studeri</i>	E746	4041	17642	261	(<i>Balanus decorus</i>)
D907	4354	17914W	202	<i>Balanus vestitus</i> <i>Calantica studeri</i>	E767	Port Underwood, shore			<i>Calantica villosa</i> <i>Chamaesiphon columnna</i> <i>Epopella plicata</i> <i>Calantica spinosa</i> <i>Calantica villosa</i>
E81	4303	17930W	534	(<i>Hexelasma alearum</i>)	E768	The Knobbys & Port Underwood, shore			<i>Chamaesiphon columnna</i> <i>Epopella plicata</i> (<i>Balanus decorus</i>)
E96	4256	17324	42	(<i>Balanus decorus</i>)	E779	4241	17007	215–225	(<i>Balanus decorus</i>)
E106	4353	17710W	176	<i>Balanus vestitus</i> <i>Balanus decorus</i>	E780	4324	16927	202–248	<i>Balanus decorus</i>
E113	4330	17630W	114	(<i>Balanus decorus</i>)	E784	4323	16805	1220	<i>Smilium acutum</i>
E114	4335	17615W	132	(<i>Balanus decorus</i>)	E795	Caswell I Head, shore			<i>Elminius modestus</i> (<i>Balanus decorus</i>)
E115	The Sisters, shore			<i>Chamaesiphon brunnea</i>	E803	4557	16609	515–535	<i>Arcoscalpellum costellatum</i>
E127	4355	17550W	125	(<i>Balanus decorus</i>)	E808	Preservation Inlet, shore			<i>Elminius modestus</i>
E136	4405	17615W	63	(<i>Balanus decorus</i>)	E809	Preservation Inlet, shore			<i>Calantica spinosa</i> <i>Chamaesiphon columnna</i> <i>Epopella plicata</i>
E139	4400	17600W	92	(<i>Balanus decorus</i>)	E815	Revalier Bay, shore			<i>Tetracitella purpurascens</i> <i>Elminius modestus</i>
E140	4430	17600W	191	<i>Calantica studeri</i>	E817	4614	16629	215–232	<i>Balanus vestitus</i>
E142	South-east I shore			(<i>Balanus decorus</i>)	E822	4651	16536	686	<i>Arcoscalpellum costellatum</i>
E159	4401	17659W	162	<i>Balanus decorus</i>	E830	4721	16700	685	<i>Arcoscalpellum costellatum</i>
E161	Waitangi, shore			<i>Le pas anatifera</i>	E832	4721	16706	249–222	(<i>Balanus decorus</i>)
E162	4345	17720W	169	(<i>Balanus decorus</i>)	E834	Halfmoon Bay, shore			<i>Epopella plicata</i> <i>Smilium acutum</i> (<i>Balanus decorus</i>)
E234	5455	15848	212	<i>Arcoscalpellum affricatum</i>	E840	3352	17216	722	(<i>Balanus decorus</i>)
E248	3435	17243	331	(<i>Balanus decorus</i>)	E841	3353	17217	421–472	(<i>Balanus decorus</i>)
E252	3435	17233	55	(<i>Balanus decorus</i>)	E844	Three Kings, Great I, shore			<i>Chamaesiphon brunnea</i> <i>Balanus tintinnabulum linzei</i>
E265	3432	17233	62	(<i>Balanus auricoma</i>)	E845	3408	17211	172–270	(<i>Balanus decorus</i>)
E278	3425	17215	138	(<i>Balanus decorus</i>)	E847	3407	17152	688	(<i>Balanus decorus</i>)
E280	3425	17225	92	(<i>Balanus decorus</i>)	E850	3349	17119	502–508	<i>Aaptolasma nolearia</i>
E281	3426	17230	68	(<i>Balanus decorus</i>)	E852	3338	17055	1020	(<i>Hexelasma alearum</i>) <i>Aaptolasma fosteri</i>
E292	3415	17200	169	<i>Balanus auricoma</i> (<i>Balanus decorus</i>)	E854	3318	17010	1160	(<i>Aaptolasma fosteri</i>)
E294	3417	17205	239	(<i>Balanus decorus</i>)	E855	3310	16956	710–736	(<i>Hexelasma alearum</i>)
E302	3407	17210	129	(<i>Balanus decorus</i>)	E860	3221	16741	1244	(<i>Aaptolasma fosteri</i>)
E312	3400	17148	116	<i>Balanus auricoma</i>	E861	3225	16735	311–376	<i>Balanus auricoma</i>
E313	3405	17155	730	(<i>Balanus decorus</i>)	E862	3228	16731	127	(<i>Smilium zancleanum</i>)
E319	3356	17217	101	(<i>Balanus decorus</i>) (<i>Balanus auricoma</i>)	E864	3236	16736	120	<i>Balanus auricoma</i>
E323	3400	17215	162	<i>Calantica studeri</i>	E869	3358	16745	1685	<i>Arcoscalpellum vitreum</i>
E325	3400	17220	158	(<i>Balanus decorus</i>)	E870	3405	16810	1556	(<i>Hexelasma alearum</i>) (<i>Aaptolasma fosteri</i>)
E326	3410	17223	184	(<i>Balanus decorus</i>)	E871	3409	16920	1936	<i>Arcoscalpellum novaezelandiae</i>
E327	3418	17225	116	(<i>Balanus decorus</i>)	E875	3439	17207	485	<i>Paralepas minuta</i> <i>Megalasma striatum</i>
E328	3424	17240	40	<i>Balanus decorus</i>	E880	3520	17220	1025–1070	<i>Smilium acutum</i>
E332	3418	17230	100	(<i>Balanus decorus</i>)	E893	3719	17351	975	<i>Smilium acutum</i>
E333	3410	17230	107	(<i>Balanus auricoma</i>)	E902	3734	17205	978	(<i>Hexelasma alearum</i>)
E340	3405	17240	100	(<i>Balanus decorus</i>)	E903	3733	17205	958	(<i>Hexelasma alearum</i>)
E342	3412	17235	103	(<i>Balanus decorus</i>)	E906	3839	17238	745–685	<i>Verruca halothea</i>
E344	3415	17240	100	(<i>Balanus decorus</i>)	E909	Greville Harbour, shore			<i>Epopella plicata</i>
E348	3437	17320	147	(<i>Balanus decorus</i>)	F81	4932	16701	401	<i>Calantica gemma</i>
E349	3437	17315	118	(<i>Balanus auricoma</i>)	F82	5051	16654	137	(<i>Balanus decorus</i>)
E350	3437	17310	100	(<i>Balanus decorus</i>)	F90	4931	16740	585	<i>Arcoscalpellum costellatum</i>
E353	3437	17303	24	(<i>Balanus decorus</i>)	F91	4900	16730	687	<i>Smilium acutum</i>
E360	3434	17325	316	(<i>Balanus decorus</i>)	F94	4831	16801	576	<i>Arcoscalpellum costellatum</i> <i>Arcoscalpellum costellatum</i>
E363	3430	17308	107	(<i>Balanus decorus</i>)	F122	4806	17957W	252	<i>Pachylasma scutistriata</i> <i>Balanus decorus</i>
E365	3430	17303	31	(<i>Balanus decorus</i>)	F132	4959	17732	1335	<i>Hexelasma alearum</i>
E366	3430	17301	9	(<i>Balanus decorus</i>)	F143	5306	17013	380	<i>Arcoscalpellum pertosum</i>
E372	3420	17305	132	(<i>Balanus decorus</i>)	F144	5329	17056	596	<i>Arcoscalpellum costellatum</i>
E380	3410	17255	368	(<i>Balanus decorus</i>)	F145	5314	17148	435	<i>Balanus decorus</i>
E381	3415	17259	147	(<i>Balanus decorus</i>)	F104	4840	17049	788–814	<i>Arcoscalpellum costellatum</i>
E382	3425	17259	26	(<i>Balanus decorus</i>)	F107	4845	17200	658	<i>Arcoscalpellum costellatum</i>
E384	3425	17250	26	(<i>Balanus decorus</i>)	F117	4940	17900	1202–1293	(<i>Hexelasma alearum</i>)
E385	3423	17250	50	(<i>Balanus decorus</i>)	F120	4818	17916	494–512	<i>Verruca halothea</i>
E386	3420	17250	63	(<i>Balanus decorus</i>)	F122	4806	17957W	252	<i>Verruca halothea</i>
E387	3416	17248	85	(<i>Balanus decorus</i>)	F132	4959	17732	1335	<i>Hexelasma alearum</i>
E388	3414	17250	97	(<i>Balanus decorus</i>)	F143	5306	17013	380	<i>Arcoscalpellum pertosum</i>
E391	3413	17245	92	(<i>Balanus decorus</i>)	F144	5329	17056	596	<i>Arcoscalpellum costellatum</i>
E393	3420	17245	66	(<i>Balanus decorus</i>)	F145	5314	17148	435	<i>Balanus decorus</i>
E394	3423	17245	36	(<i>Balanus decorus</i>)					
E399	4600	17133	1221–1300	<i>Smilium acutum</i> <i>Arcoscalpellum novaezelandiae</i>					
E400	4600	17102	625–723	<i>Smilium acutum</i> <i>Arcoscalpellum costellatum</i>					
E406	4720	17017	1220	<i>Arcoscalpellum novaezelandiae</i>					
E407	4640	17008	309	<i>Pachylasma scutistriata</i>					
E413	4512	17144	570	<i>Arcoscalpellum trochelatum</i>					
E421	4400	17500	493	<i>Arcoscalpellum pertosum</i>					
E433	4343	17430	570	<i>Smilium acutum</i> <i>Arcoscalpellum pertosum</i>					

Stn no.	Lat. (°S)	Long. (°E)*	Depth (m)	Species represented	Stn no.	Lat. (°S)	Long. (°E)*	Depth (m)	Species represented
F146	5300	17245	435	<i>Yerruca halothea</i>	G688	4610	17100	731	<i>Arcoscalpellum costellatum</i>
F867	3730	17900	307–340	<i>Balanus decorus</i>	G694	4620	16952	14	<i>Arcoscalpellum pertosum</i>
F868	3729	17904	808–924	(<i>Balanus decorus</i>) <i>Trilasmis kaempferi</i>	G695	4620	17012	73	<i>Balanus vestitus</i>
F870	3726	17811	254–263	<i>Smilium acutum</i>	G700	4620	17115	1116	<i>Balanus decorus</i>
F872	3721	17811	832–878	<i>Arcoscalpellum costellatum</i>	G702	4620	17145	1400	<i>Smilium acutum</i>
F873	3720	17811	1050–1053	<i>Arcoscalpellum raccidium</i>	G703	4620	17204	1480	<i>Arcoscalpellum pertosum</i>
F875	3734	17735	282–311	<i>Arcoscalpellum intermedium</i>	G704	4617	17237	1600	<i>Arcoscalpellum novaezelandiae</i>
F876	3733	17734	492–529	<i>Arcoscalpellum costellatum</i>	G707	4548	17057	59	<i>Arcoscalpellum novaezelandiae</i>
F878	3729	17732	942–997	<i>Arcoscalpellum affricatum</i>					(<i>Hexelasma alearum</i>)
F883	3722	17701	713–735	<i>Smilium acutum</i>					<i>Balanus decorus</i>
F884	3730	17651	652–684	<i>Arcoscalpellum novaezelandiae</i>	H55	4800	17000	600	<i>Arcoscalpellum costellatum</i>
F900	3613	17623	721–754	<i>Arcoscalpellum raccidium</i>	H69	4538	16753	50	<i>Arcoscalpellum intermedium</i>
F909	3506	17511	1002–1030	<i>Arcoscalpellum intermedium</i>	J35	3830	16926	546	<i>Arcoscalpellum raccidium</i>
F921	3402	17231	304–344	<i>Arcoscalpellum costellatum</i>	J45	3640	17000	2146	<i>Arcoscalpellum pertosum</i>
F924	3408	17247	315–439	<i>Trilasmis kaempferi</i>	Z360	3935	17753	on buoys	<i>Arcoscalpellum novaezelandiae</i>
F927	Three Kings, Great I, shore			<i>Chamaesipho brunnea</i>	Z365	3922	17742	on buoys	<i>Lepas testudinata</i>
F930	Maukin's Hook, shore			<i>Chamaesipho columna</i>	Z398	3933	17743	on buoys	<i>Lepas testudinata</i>
F932	3427	17308	64–117	<i>Epopella plicata</i>	Z540	3925	17717	on buoys	<i>Lepas testudinata</i>
F933	3424	17310	212–249	<i>Heteralepas japonica</i>	Z541	3938	17723	on buoys	<i>Lepas australis</i>
F934	Tom Bowling Bay, shore			<i>Lepas anatifera</i>	Z542	3923	17713	on buoys	<i>Lepas australis</i>
F936	3609	17445	53–55	(<i>Balanus decorus</i>)	Z543	3920	17710	on buoys	<i>Lepas testudinata</i>
G161	4248	17328	55	<i>Balanus decorus</i>	Z544	3930	17755	on buoys	<i>Lepas testudinata</i>
G163	4245	17338	128	(<i>Balanus decorus</i>)	Z545	3944	17726	on buoys	<i>Lepas australis</i>
G305	4313	17920W	455	<i>Smilium acutum</i>	Z546	3931	17722	on buoys	<i>Lepas testudinata</i>
G342	4352	17852W	417	<i>Arcoscalpellum novaezelandiae</i>	Z547	3926	17753	on buoys	<i>Lepas australis</i>
G403	4354	17944W	391	<i>Smilium acutum</i>	Z548	3910	17730	on buoys	<i>Lepas testudinata</i>
G651	4400	17431	572	<i>Smilium acutum</i>	Z549	3917	17731	on buoys	<i>Lepas testudinata</i>
G652	4400	17410	557	<i>Arcoscalpellum novaezelandiae</i>	Z550	3932	17731	on buoys	<i>Lepas testudinata</i>
G654	4400	17300	68	<i>Smilium acutum</i>	Z552	3921	17750	on buoys	<i>Lepas testudinata</i>
G655	4401	17230	47	<i>Arcoscalpellum novaezelandiae</i>	Z553	3929	17738	on buoys	<i>Lepas anatifera</i>
G659	4425	17118	18	(<i>Balanus decorus</i>)	Z554	3926	17747	on buoys	<i>Lepas testudinata</i>
G660	4425	17200	63	<i>Balanus vestitus</i>	Z555	3933	17743	on buoys	<i>Lepas anatifera</i>
G661	4425	17230	93	<i>Balanus decorus</i>	Z556	4311	17328	on buoys	<i>Lepas testudinata</i>
G662	4425	17200	153	<i>Balanus decorus</i>	Z557	4316	17308	on buoys	<i>Lepas australis</i>
G666	4452	17220	1000	<i>Balanus vestitus</i>	Z558	4323	17312	on buoys	<i>Lepas australis</i>
G667	4457	17205	872	<i>Balanus decorus</i>	Z559	4333	17520	on buoys	<i>Lepas australis</i>
G669	4457	17128	63	<i>Arcoscalpellum novaezelandiae</i>	Z1024	Raumati Beach, drift			<i>Lepas pectinata</i>
G670	4500	17110	13	<i>Smilium acutum</i>	Z1025	Raumati Beach, drift			<i>Lepas anatifera</i>
G671	4510	17104	23	<i>Arcoscalpellum costellatum</i>	Z1026	Pukerua Bay, drift			<i>Lepas testudinata</i>
G672	4520	17057	29	<i>Balanus vestitus</i>	Z1027	Makara Beach, drift			<i>Lepas australis</i>
G673	4527	17101	45	<i>Balanus decorus</i>	Z1028	3936	17731	surface	<i>Lepas testudinata</i>
G674	4527	17112	98	<i>Balanus decorus</i>	Z1060	Skerman's collection of fouling barnacles; incl.			<i>Conchoderma virgatum</i>
G675	4527	17124	792	<i>Balanus vestitus</i>	Z1236	3347	15600		<i>Conchoderma auritum</i>
G680	4543	17102	103	<i>Arcoscalpellum trochelatum</i>	Z1238	3518	16458	1126	<i>Lepas testudinata</i>
G681	4543	17050	33	<i>Balanus vestitus</i>	Z1913	3906	17359	shore	<i>Conchoderma virgatum</i>
G685	4553	17048	68	<i>Balanus decorus</i>	Z2114	Island Bay, drift			<i>Lepas pectinata</i>
G686	4553	17054	108	<i>Balanus vestitus</i>	Z2366	3719	17626	368	<i>Lepas australis</i>
				<i>Balanus decorus</i>	Z2368	3721	17624	184–202	<i>Calantica spinilatera</i>
				<i>Balanus decorus</i>	Z2374	4209	17036	366	<i>Arcoscalpellum affricatum</i>
									<i>Arcoscalpellum pedatumum</i>

INDEX

Major references are indicated by page numbers in bold type.

Author and collector index on page 143.

- Aaptolasma* 8, 78, 79, **83**, 87, 100, 124, 125
americanum 79, 83, 85
arafurae 83, 85
britoni 79, 83
callistoderma 79, 83, 85
ecaudatum 83
fosteri 14, 71, **83–85**, 118, 120, 155 (Plate 10)
leptoderma 79, 83, 85
nolearia 14, 71, 83, **85–86**, 118, 120, 137, 138, 139, 155 (Plate 10)
triderma 83
Acasta 97, 114, 126, 131
acutum; *Scalpellum*, *Smilium*
acutus; *Balanus*, *Balanus amphitrite*
 adductor muscle pit of scutum 9 (definition)
affricatum; *Arcoscalpellum*
affinis; *Lepas*
ala (pl. alae) 9, 10 (definition)
albatrossianum; *Arcoscalpellum*
 Aldermen Is 15, 27, 35, 53, 56
alearium; *Hexelasma*
Alepas 36, 38, 121, 123
japonica 15 (= *Heteralepas japonica*)
minuta 19 (= *Paralepas minuta*)
navigator 38
pacifica 14, **37–8**, 118
pellucida 38
quadrata 17 (= *Paralepas quadrata*)
spectrum 38
univalvis (= *parasita*) 38
Alert MV 19, 44, 51, 56, 60, 65
algae 127, 129
Alliverruca 68
americanum; *Aaptolasma*
amphitrite; *Balanus*
Anatifa elongata 7, 14, 31 (= *Lepas testudinata*), 32
spinosa 7, 8, 38, 39 (= *Calantica spinosa*), 41
tubulosa 7, 14, 17 (= *Heteralepas quadrata*), 19
anatifa; *Lepas*
 Anawhata 91
anserifera; *Lepas*
antarcticum; *Hexelasma*
 antenna 10, 11 (definition)
antennatus; *Chthamalus*
 antenniform rami 85, 100
 antennules 10, 11 (definition)
antillarum; *Arcoscalpellum*
 antipatharians as hosts 6, 22, 23, 24, 41, 100, 122, 146
 Antipodes I 119
aoranga; *Tetraclita*
aotea; *Coronula*
arafurae; *Aaptolasma*, *Hexelasma*
Archeolepas 131
Arcoscalpellum 7, 9, 42, 51, 53, 55, 118, 122, 123, 131
affricatum 14, 55, 60–2, 65, 118, 120, 136, 137, 138, 139, 151 (Plate 7)
albatrossianum 65
antillarum 62
aurivilli 65
buccinum 8, 56 (= *A. costellatum*)
carinatum 68
complanatum 132
costellatum 7, 8, 14, 55, 56–7, 58, 118, 120, 137, 138, 139, 151 (Plate 7)
darwinii 56
distinctum 132
euglyphum 132
flavum 65
gigas 56
gracilus 65
idioplax 68
intermedium 14, 53, 55, 62–3, 118, 119, 120, 139, 152 (Plate 8)
michelottianum 56
novaezelandiae 14, 55, 65–6, 68, 118, 120, 138, 139, 152 (Plate 8)
pedunculatum 14, 53–6, 118, 120, 136, 137, 139, 151 (Plate 7)
pertosum 14, 55, 63–5, 118, 120, 138, 139, 152 (Plate 8)
portoricanum 56
raccidium 14, 55, 65, 67–8, 118, 120, 139, 152 (Plate 8)
striatulum 132
trochelatum 14, 55, 59–60, 118, 120, 137, 138, 139, 152 (Plate 8)
ungulatum 132
utinomii 59
vitreum 14, 55, 58–9, 118, 120, 138, 151 (Plate 7)
arguta; *Calantica*
Armatobalanus 102, 131
 arthropods as hosts 121, 122
 articular furrow, margin, ridge of tergum and scutum 9 (definitions)
Ascothoracica 6, 13, 123
Astrolabe 7
 Atlantic Ocean 23, 38, 47, 48, 51, 56, 59, 65, 68, 69, 79, 82
atlantica; *Ibla*
 Auckland 30, 37, 44, 108, 109, 111, 112, 114, 132
 Museum 6, 8, 15, 17, 27, 35, 36, 39, 41, 49, 53, 56, 60, 73, 95, 115, 150
 University 6, 82
 Auckland Is 33, 47, 75, 87, 89, 98, 107, 108, 119, 137, 159
aucklandicum; *Bathylasma*, *Hexelasma*, *Scalpellum*
auricomma; *Balanus*
auritum; *Conchoderma*
aurivilli; *Arcoscalpellum*
 Australia, or Australasian 15, 20, 22, 23, 45, 47, 56, 62, 73, 89, 90, 91, 93, 94, 95, 97, 100, 107, 108, 111, 112, 120, 121, 126, 129
australis; *Lepas*
Austrobalanus 15, 97, 100, 121, 124, 126, 131, 132
balaenaris; *Coronula*, *Lepas*
 Balanidae 15, 87, 89, 95, 124, 125, 126, 127, 129, 131, 132
 Balaninae 95, 97
balanoides; *Balanus*
 Balanomorph 6, 8, 10, 12, 14, 72, 123, 131
 evolution of 124–6
Balanus 7, 13, 16, 86, 89, 97, 100, 102, 118, 121, 123, 124, 126, 131
acutus 132
amphitrite 7, 15, 97, **109–111**, 118, 119, 120, 126, 129, 160 (Plate 14), frontispiece
acutus 97
cirratus 111, 112
communis 104, 109, 111
hawaiensis 109
malayensis 112
variegatus 111
auricomma 15, 97, 99, 100–2, 118, 119, 120, 138, 157 (Plate 12)
balanoides 129
balanus 107, 108
campbelli 7, 15, 97, 99, 107–8, 114, 118, 119, 120, 127, 128, 136, 137, 159 (Plate 13), frontispiece
cariosus 126
ciliatus 102
corolliforme 79 (= *Hexelasma corolliforme*)
crenatus 7, 114
decorus 7, 8, 15, 97, 104–7, 118, 119, 120, 127, 128, 132, 136, 137, 138, 139, 159 (Plate 13), frontispiece
flos 114
flosculus 100, 121
imperator 100, 121, 125, 126
improvisus 129
negrescens 108
nubilus 126
porcatus (= *balanus*) 7, 107, 108, 113, 114
psittacus 107, 108, 126
tintinnabulum 7, 8, 15, 91, 93, 97, 102, 103, 104, 118, 119, 120, 126
californicus 104
concinus 102, 104
linzei 15, 99, 102–4, 110, 119, 127, 129, 138, 159 (Plate 13), frontispiece
peninsularis 104
trigonus 7, 15, 97, 108, 110, 111, 113–14, 118, 119, 120, 126, 129, 137, 160 (Plate 14), frontispiece
tubulatus 97, 108, 132
variegatus 15, 110, 111–12, 118, 119, 120, 128, 160 (Plate 14), frontispiece
vestitus 7, 15, 97–100, 102, 107, 108, 118, 120, 121, 127, 132, 136, 137, 138, 139, 157 (Plate 12)
zelandica 97
 Banks Peninsula 73, 107
 barnacle plate sediments 82, 132
 barnacles as hosts 26, 36, 73, 91, 94, 147, 159
Bathylasma 76, 97
Bathylasma 79
aucklandicum 82 (= *Hexelasma aucklandicum*)
corolliforme 79 (= *Hexelasma corolliforme*)
 Bathylasmatae 72, 76
 Bay of Islands 32, 36, 72, 94
 Bethells Beach 29
bissexlobata; *Platylepas*
 boats and ships as substrates 35, 36, 104, 112, 113 (see also fouling)
 Bounty I 107, 119
brevicinctum; *Epoppella*, *Tetraclita purpurascens*
 Britain 95, 129
 British Museum 7, 23, 73
britoni; *Aaptolasma*
brunnea; *Chamaesipho*, *Octomeris*
buccinum; *Arcoscalpellum*
Calantica 9, 38, 39, 41, 43, 45, 47, 49, 51, 122, 131
arguta 48, 132
eos 47
gemma 14, 43, 47–9, 118, 120, 137, 138, 150 (Plate 6)
grimaldi 47
kamperi 38, 41, 42, 49
krugeri 47
mortenseni 7, 14, 45 (= *C. studeri*)
pollicipedoides 41, 42, 49
quinquilatera 38, 42
scorpio (= *sexcornutum*) 42
spinifera 7, 8, 11, 14, 38, 39, 41–4, 49, 118, 120, 136, 137, 139, 149 (Plate 5)
spinosa 7, 8, 14, 39–41, 42, 43, 45, 75, 94, 118, 120, 121, 123, 127, 128, 137, 138, 144 (Plate 1), 149 (Plate 5)
studeri 7, 14, 21, 42, 43, 45–7, 118, 119, 120, 137, 138, 150 (Plate 6)
subplana 132
sulei 49
superba 47
trispinosa 47
villosa 7, 8, 14, 21, 43, 44–5, 49, 118, 120, 121, 123, 127, 128, 136, 138, 149 (Plate 5)
zancleana 49 (= *Smilium zancleanum*)
californicus; *Balanus tintinnabulum*
callistoderma; *Aaptolasma*
Cameraverruca 68
 Camp Cove Harbour 137
 Campbell I 33, 98, 107, 108, 119
 Campbell Plateau 8, 51, 56, 119
campbelli; *Balanus*
 Canterbury Museum 6, 34, 36, 41, 73, 89, 90, 93, 95, 104, 107, 108, 114, 115
 University 33
 Cape Brett 36
 Foulwind 73
 Egmont 44
 Karikari 102, 103, 127
 Rodney 102
 Runaway 93
Capitulum 41
mitella 122
 capitulum 8, 9 (definition)
capsula; *Verruca*
 carina 9 (definition)
carinatum; *Arcoscalpellum*, *Megalasma*, *Poecilasma*
carinulatus 9 (definition)
cariosus; *Balanus*
 Carnley Harbour 137
 Castlepoint 39
 Caswell I 138
Catophragma 38, 72, 124, 125, 131
 caudal appendages 11, 12 (definition)
celata; *Oxyaspis*
Chaetolepas segmentata 7, 14, 20, 21 (= *Ibla idiota*), 22
 Challenger 7, 51, 53, 56, 62, 65
 Challenger Plateau 26
Chamaesipho 45, 72–3, 75, 87, 120, 124, 125
brunnea 7, 8, 14, 72, 73–6, 97, 118, 119, 120, 127, 129, 137, 138, 139, 145 (Plate 1), 153 (Plate 9)
columna 7, 8, 14, 72, 73–6, 97, 118, 119, 120, 127, 129, 138, 139, 149 (Plate 5), 153 (Plate 9)
scutelliformis 73, 120
 Chatham Is 7, 31, 32, 33, 39, 43, 45, 73, 75, 76, 87, 89, 95, 98, 107, 119, 137, 138
 Chatham Rise 119
Chelonibia 100, 124, 125, 126, 128, 130, 131
 Chelonibiae 95
 China Sea; see Oriental Seas
chinensis; *Tetraclitella*
Chionelasma 72, 76, 83, 124, 125
Chirona 97, 131
Chthamaliae 14, 72, 76, 95, 122, 124, 125, 127, 128, 129, 131, 132
Chthamalus 72, 87, 124, 125, 131
antennatus 72
intertextus 73, 130
malayensis 129
stellatus 7, 8, 72, 73, 129
ciliatus; *Balanus*
cirratus; *Balanus amphitrite*
 cirrus (pl. cirri) 11, 12 (definition)
 climatic factors and intertidal distribution 119, 123, 125, 128–9
 Cloudy Bay 44
columna; *Chamaesipho*
communis; *Balanus amphitrite*
 competitors of barnacles 76, 128, 129
complanatum; *Arcoscalpellum*
 complemental males 13, 38, 41, 44, 47, 150 (Plate 6E)
Conchoderma 35, 123
auritum 7, 14, 36, 116, 118, 139, 147 (Plate 3)
virgatum 7, 14, 35, 117, 118, 139, 147 (Plate 3)
concinus; *Balanus tintinnabulum*
Conia depressa 7, 93 (= *Tetraclitella purpurascens*), 94
Conopea 97, 126, 131
 Cook Strait 60, 119
coraliophila; *Verruca*
 corals as hosts 6, 114, 123, 126
cornuta; *Heteralepas*



- corolliforme*; *Balanus*, *Bathylasma*, *Hexelasma*
Coronula 115, 117, 121, 124, 126, 131
aotea 132
balaenaris 116
diadema 7, 15, 36, 115–16, 118, 132, 136, 137, 147 (Plate 3), 160 (Plate 14)
reginae 15, 116, 118, 160 (Plate 14)
Coronulinae 95, 115
costellatum; *Arcoscalpellum*
crenatus; *Balanus*
Cretiscalpellum 131
Creusia 114, 124, 126, 131, 132
spinulosa 8, 15, 114, 118, 120
crystallinus; *Elminius*
crustaceans as hosts 6, 17 (*Jasus*), 25 (*Nephrops*), 26, 35 (*Penella*), 100 (crabs), 136, 147, 157
Cryptolepas 115, 131
cumingi; *Ibla*
Curio Bay 137
cygnus; *Heteralepas*
Cylindrolepas 115, 126
cyprid 11, 13
Cyprilepas 121, 123, 131
darwinianum; *Pachylasma*
darwini (i); *Arcoscalpellum*, *Pollicipes*
decorus; *Balanus*
denticulata; *Lepas*
depressa; *Conia*
diadema; *Coronula*
Disaster Bay 16
Discovery 108
dispersal of barnacles by boats 95, 97, 111, 129–130
distincta; *Paralepas*
distinctum; *Arcoscalpellum*
distribution of barnacles; outside N.Z. 120; with *depth* 118, 122; within N.Z. 118–19
divisa; *Tetraclitella*
Doubtful Sound 41
Doubtless Bay 17, 49, 157
dubia; *Heteralepas*
Dusky Sound 93
dwarf males 11, 20; *see also* complementary males
East Africa 20
East Auckland Current 119
East Cape 36, 62
ecaudatum; *Aptolasma*
echinoids as hosts 6, 19, 26, 122, 146, 147
elegans; *Megalasma*, *Pollicipes*, *Stomatolepas*
elephant seal as host 33
Elminius 89, 95, 97, 120, 121, 124, 125, 126, 128, 130, 132
crystallinus 95
kingii 89, 95, 120
modestus 7, 8, 15, 72, 75, 89, 95–7, 118, 119, 120, 125, 126, 128, 129, 138, 157 (Plate 12)
plicatus 7, 8, 14, 87 (= *Epopella plicata*), 95
rugosus 7, 87 (= *Epopella plicata*), 89, 95
simplex 8, 89, 90, 95
sinuatus 7, 95 (= *E. modestus*)
elongata (um); *Anatifa*, *Lepas*, *Scalpellum*
Eltanin 8, 51, 56
Emersonius 131
Endeavour 20, 22
endemic species 118, 120
Eolepas 131
eos; *Calantica*
Epopella 83, 86, 87, 95, 100, 120, 121, 124, 125, 126, 130, 132
brevicutum 87 (= *E. plicata*)
kermadeca 14, 89–90, 118, 120
plicata 7, 8, 11, 14, 75, 76, 87–9, 97, 100, 107, 118, 119, 120, 125, 127, 136, 137, 138, 139, 145 (Plate 1), 156 (Plate 11)
simplex 89, 90, 120
euglyphum; *Arcoscalpellum*
Euscalpellum 38, 42, 122, 123
fascicularis; *Lepas*
Fiji 20, 91, 95
filamentary processes 12, 32 (definition)
fish as hosts 35, 36, 115
flavum; *Arcoscalpellum*
floating objects as substrates 31, 32, 33, 35, 36, 118, 122, 139, 148
flos; *Balanus*
flosculus; *Balanus*
Formosa 17
formosum; *Scalpellum*
fossil barnacles 6, 8, 10, 48, 49, 51, 56, 82, 83, 97, 107, 121, 131–2, 155
fosteri; *Aptolasma*, *Hexelasma*
fouling by barnacles 97, 103, 109, 111, 126, 129
Foveaux Strait 41
French Pass 7
Galathea 8, 34, 72
Gazelle 7, 17, 20
gemma; *Calantica*, *Scalpellum*
gibbosa; *Verruca*
giganteum; *Pachylasma*
gigas; *Arcoscalpellum*, *Heteralepas*, *Megalasma*
Glyptelasma 26
gorgonids as hosts 126
gracilis; *Arcoscalpellum*
Great Barrier Island 15, 36, 113, 115
Greville Harbour 138
grimaldi; *Calantica*
Gulf of Mexico 62
halotheca; *Verruca*
harringtoni; *Lepas*
Hauraki Gulf 82
hawaiensis; *Balanus amphitrite*
Hawaii 69
Hawera 34
Hawke's Bay 30
Hen and Chickens Is 17, 39, 93
Hesperibalanus 97, 131
Heteralepadidae 6, 14, 15, 17, 121, 122
Heteralepas 15, 18, 19, 120, 121
cornuta 16
cygnus 16
dubia 7, 14, 15 (= *H. japonica*), 16
gigas 16
indica 15
japonica 7, 14, 15–6, 17, 118, 120, 139, 146 (Plate 2)
lankestri 16
nicobarica 16
quadrata 7, 17 (= *Paralepas quadrata*)
utinomi 16
Hexacreusia 131
hexastylus; *Platylepas*
Hexelasma 72, 76, 78, 79, 80, 82, 83, 124, 131, 132
aleurum 14, 71, 80–2, 83, 118, 120, 136, 137, 138, 139, 155 (Plate 10)
antarcticum (= *corolliforme*) 79
arafurae (= *Aptolasma arafurae*) 79
aucklandicum 8, 80, 82–3, 132, 155 (Plate 10)
corolliforme 79, 80, 82, 83, 132
fosteri 8, 79, 83 (= *Aptolasma fosteri*)
hirsutum 79, 80, 82
sp. Withers 83, 132
velutinum 79, 80, 82, 83
hilli; *Lepas*
hirsutum; *Hexelasma*
hosts; see antipatharians, arthropods, barnacles, corals, crustaceans, echinoids, elephant seal, fish, gorgonids, jellyfish, penguins, pennatulids, sea leopard, sponges, turtles, vertebrates, whales
Ibla 7, 8, 13, 20, 121, 122, 123
atlantica 20, 22
cumingi 20, 22
idiotica 8, 14, 17, 20, 21–2, 118, 120, 128, 137, 138, 146 (Plate 2)
pygmaea 20, 22
quadrivalvis 20, 22
segmentata 17, 21, 22
sibogae 20
Iblidae 14, 17, 20, 121, 122, 123
idioplax; *Arcoscalpellum*, *Scalpellum*
idiotica; *Ibla*
Ikateru 22, 25, 37, 41
imbricaria; *Scalpellum*
imperator; *Balanus*
inaequilaterale; *Poecilasma*
Indian Ocean 20, 22, 23, 27, 56, 65, 77, 78, 100, 112
indica; *Heteralepas*, *Oxynaspis*, *Oxynaspis celata*
Indomalaysia 15, 111, 120
inframedian latus 9 (definition)
intermedium; *Arcoscalpellum*, *Scalpellum*
intertextus; *Chthamalus*
intertidal zone as barnacle refuge 122, 123, 129; *see also* climatic factors
Iris 49
Japan 17, 19, 22, 23, 26, 27, 47, 58, 62, 78
japonica; *Alepas*, *Heteralepas*
Java Sea 17, 49, 51, 95
jellyfish as hosts 37, 38, 147
kaempferi; *Poecilasma*, *Trilasmis*
Kaipara Harbour 111
kampeni; *Calantica*
Kathpalmeria 131
Kermadec Islands 7, 8, 29, 31, 34, 51, 69, 73, 75, 87, 89, 90, 91, 93, 97, 102, 103, 104, 107, 114, 118, 119
kermadeca; *Epopella*
kingii; *Elminius*
krugeri; *Calantica*
labrum 10, 11 (definition)
lankestri; *Heteralepas*
latus (pl. latera) 9 (definition)
Leigh 29, 31, 33, 34, 35
Lepadidae 6, 14, 29, 122, 123
Lepadomorpha 8, 12, 14, 15
evolution of 121–3
Lepas 16, 29, 30, 32, 118, 119, 121, 122, 131
affinis 7, 31 (= *L. testudinata*)
anatifa, 7, 14, 29–31, 32, 117, 118, 119, 137, 138, 139, 148 (Plate 4)
anserifera 32
australis 7, 14, 30, 32–3, 118, 119, 137, 139, 148 (Plate 4)
balaenaris (= *Coronula diadema*) 115
elongata 31 (= *L. testudinata*), 32
denticulata 7, 14, 30, 34, 118, 148 (Plate 4)
fascicularis 7, 14, 30, 34, 118, 148 (Plate 4)
harringtoni 132
hilli 31, 32
pectinata 7, 14, 30, 33–4, 118, 119, 139, 148 (Plate 4)
testudinata 7, 14, 30, 31–2, 118, 119, 139, 148 (Plate 4)
leptoderma; *Aptolasma*
lichens 129
linzei; *Balanus tintinnabulum*
Lithotrya 38, 122, 123
lithotryae; *Paralepas*
Litoscalpellum nipponense 62 (= *Arcoscalpellum intermedium*)
Little Barrier I 22, 39, 41, 113
Little Papanui 21, 45, 127
Lord Howe I 90
Lyall Bay 29, 33, 44
Lyttelton Harbour 104
Macquarie I 104, 119
magna; *Verruca*
Mahia 41
Mahurangi Harbour 111
major; *Tubicinella*
malayensis; *Balanus amphitrite*, *Chthamalus*
Malaysia 20, 41, 44, 58, 62, 69, 77, 95, 100, 102, 112
males; see complementary males, dwarf males
Manawatu River mouth 34
mandible 10, 11 (definition)
Mangawhai 31, 33, 34
Manonui Harbour 111
Manukau Harbour 104, 111
Heads 34
Masked I Harbour 137
Matheson Bay 82
Maukin's Hook 139
maxilla 11, 12 (definition)
maxillule 11, 12 (definition)
Mayor I (Bay of Plenty) 29, 31, 33
Mediterranean Sea 19, 78
Megalobalanus 15, 97, 102, 104, 107, 126, 131
Megalasma 26, 29
carinatum 14, 17, 26–7, 118, 120, 147 (Plate 3)
elegans 29
gigas 26
striatum 14, 17, 27–9, 118, 120, 138, 147 (Plate 3)
Melanesia 20
Membranobalanus 131
Mercury Bay 98, 113
I 56
Mesoscalpellum 53
Metabalanus 97
Metaverruca 14, 68
michelottianum; *Arcoscalpellum*
Milford Sound 72
Minerva Reef 91
minuta; *Alepas*, *Paralepas*
Mitella (= *Pollicipes*) 38
sertus 8, 39 (= *Calantica spinosa*)
mitella; *Capitulum*, *Pollicipes*
modestus; *Elminius*
Mokohinau Islands 8, 41
mortensenii; *Calantica*
Motuie I 82
Motutapu I 82, 83, 132
mollusc shells as substrates 21 (*Fusitriton*), 94 (*Haliotis*), 100, 154
multicostata; *Tetraclitella*
Muriwai 29
Napier 41
National Museum 6, 22, 25, 26, 29, 31, 34, 35, 36, 39, 41, 44, 49, 51, 53, 56, 60, 63, 65, 73, 87, 89, 90, 91, 93, 95, 98, 102, 104, 113, 115, 116, 117, 161
nauplius (pl. nauplii) 11, 13, 89
navicula; *Verruca*
navigator; *Alepas*
Nelson 34
Neoscalpellum 53
New Brighton 7, 29
New Caledonia 91
New Guinea 78
New Zealand Marine Dept 25, 56
New Zealand Oceanographic Institute 6, 15, 19, 21, 25, 27, 29, 31, 33, 35, 36, 39, 41, 44, 45, 47, 49, 51, 53, 56, 58, 59, 60, 62, 63, 65, 69, 73, 77, 79, 80, 82, 83, 85, 87, 93, 95, 97, 98, 100, 102, 104, 107, 113, 115, 136–9, 146, 147, 149, 150, 151, 152, 153, 155, 157
nicobarica; *Heteralepas*
nigrescens; *Balanus*
nipponense; *Litoscalpellum*, *Scalpellum*
nodulosa; *Paralepas*
noleria; *Aptolasma*
Nora Niven 41
Norfolk I 29, 31, 33, 102, 115, 119
North Cape 16, 23, 24, 98, 104
novaezelandiae; *Arcoscalpellum*, *Scalpellum*
novaezelandiae; *Oxynaspis celata*
nubilus; *Balanus*
nudipes; *Scalpellum*
Nuggets, The 34
Octomeris 48, 72, 124, 125
brunnea 79
Omao Bay 29, 44
Opunake 29, 33
Orakei Basin 109
organic component of shell 83, 85, 87, 100, 125
Oriental Seas 44, 73, 77, 95, 103, 112, 120
Otago 44, 97, 104, 114
Harbour 89, 111, 112
Museum 6, 7, 32, 34, 36, 73, 95, 112
Peninsula 33, 39, 93, 98, 104, 107, 157, 159
Otaki 31

- Oteranga Bay 76
ovalis; *Paralepas*
 Oxynaspididae 14, 17, 22, 122, 123
Oxynaspis 6, 22, 23, 131
celata 22, 23
indica 22 (= *O. indica*)
novaezelandiae 14
indica 14, 17, 22-4, 118, 120, 146 (Plate 2)
terranovalis 7, 14, 17, 23, 24, 118, 120
- Pachylasma* 72, 76, 79, 83, 95, 124, 125, 131
darwinianum 78
giganteum 78
scutistriata 14, 71, 77-8, 118, 120, 136, 137, 138, 139, 153 (Plate 9)
Pachylasmatidae 14, 71, 73, 76, 124, 125, 128, 131, 132
 Pacific Ocean or shores 23, 27, 29, 56, 58, 69, 73, 104, 119, 120, 125, 129
pacifica; *Alepas*, *Tesseropora*
 Paekakariki 29
 Pakiri 31
palinuri; *Paralepas*
paradoxa; *Protomitella*
Paralepas 6, 17, 18, 19, 20, 121, 122
distincta 18
lithorayae 19
minuta 14, 17, 19-20, 118, 120, 138, 146 (Plate 2)
nodulosa 20
ovalis 20
palinuri 18
quadrata 14, 17-9, 118, 120, 146 (Plate 2)
scyllarusi 18, 19
 Paraparaumu 29
 paries (pl. parietes) 9 (definition)
pectinata; *Lepas*
 peduncle 8, 9 (definition)
pedunculatum; *Arcoscalpellum*, *Scalpellum*
 Pegasus Bay 30
pellucida; *Alepas*
 penguins as hosts 33
peninsularis; *Balanus tintinnabulum*
 pennatulids as hosts 15, 146
pertosum; *Arcoscalpellum*
 Philippine Is 34, 38, 47, 78
 Piha 31, 33, 35, 93, 114
Platylepas 115, 116, 117, 131
bissexlobata 117 (= *P. hexastylus*)
hexastylus 15, 114, 117, 118
plicatus; *Elminius*, *Epopella*
Poecilasma 14, 24, 26
carinatum 26 (= *Megalasma carinatum*)
inaequilaterale 25
kaempferi 24 (= *Trilasmis kaempferi*)
Poecilasmatidae 6, 14, 17, 24, 122, 123
pollicipedoides; *Calantica*
Pollicipes 10, 38, 39, 41, 42, 45, 122, 123, 124, 131
darwini 7, 39 (= *Calantica spinosa*)
elegans 38, 41
mitella 41, 49, 73, 95
pollicipes (= *cornucopia*) 38, 41
polymerus 10, 38, 39, 41, 149 (Plate 5)
sertus 7, 39 (= *Calantica spinosa*)
spinosus 7, 14, 38, 39 (= *Calantica spinosa*)
polymerus; *Pollicipes*
 Poor Knights Is 20, 22, 25, 26, 91, 92, 93, 100, 102, 104, 146, 156
porcatus; *Balanus*
 Port Underwood 138
porosa; *Tetraclita*
 Portobello Marine Biological Station 6, 33, 34, 41, 51, 56, 63, 115
portoricanum; *Arcoscalpellum*
praegustator; *Stomatolepas*
 predators of barnacles 76, 87, 129
 Preservation Inlet 138
Protomitella paradoxa 7, 39 (= *Calantica spinosa*)
psittacus; *Balanus*
purpurascens; *Tetraclita*, *Tetraclitella*
pygmaea; *Ibla*
Pyrgoma 124, 126, 131
- quadrata*; *Alepas*, *Heteralepas*, *Paralepas*
quadrivalvis; *Ibla*
 Queen Charlotte Sound 39, 44, 93
quinquilatera; *Calantica*
- raccidium*; *Arcoscalpellum*
 radius (pl. radii) 9, 10 (definition)
 Raglan 31
 Recorder 26, 49, 60
recta; *Verruca*
reginae; *Coronula*
 Revalier Bay 138
 Rose I 137
- rosea*; *Tesseropora*, *Tetraclita*
 Ross Sea 79, 80, 82
Rostratoverruca 68
 rostrulatus 9 (definition)
 rostrum 9 (definition)
rugosus; *Elminius*
- Saunders Canyon 21, 146
Scalpellidae 6, 10, 13, 14, 38, 122, 123
Scalpellum 42, 122, 123, 131
acutum 7, 51 (= *Smilium acutum*)
aff. imbricatum 60 (= *Arcoscalpellum affricatum*)
aucklandicum 82 (= *Hexelasma aucklandicum*)
elongatum 7, 56 (= *Arcoscalpellum costellatum*)
formosum 58 (= *Arcoscalpellum vitreum*)
gemma 47 (= *Calantica gemma*)
idioplax 65
imbricatum 62
intermedium 7, 62 (= *Arcoscalpellum intermedium*)
nipponense 62 (= *Arcoscalpellum intermedium*)
novaezelandiae 7, 65 (= *Arcoscalpellum novaezelandiae*)
nudipes 49 (= *Smilium zancleanum*)
pedunculatum 7, 53 (= *Arcoscalpellum pedunculatum*)
scorpio (= *Calantica scorpio*) 49
spinosum 7, 14, 41 (= *Calantica spinilatera*)
studerii 45 (= *Calantica studeri*)
subplanum (= *Smilium subplanum*) 49
talismani 59
villosum 44 (= *Calantica villosa*)
vitreum 58 (= *Arcoscalpellum vitreum*)
zancleanum (= *Smilium zancleanum*) 49
Scillaelepas 47, 48, 49
scorpio; *Calantica*, *Scalpellum*
scutelliformis; *Chamaesiphon*
scutistriata; *Pachylasma*
 scutum (pl. scuta) 9 (definition)
scyllarusi; *Paralepas*
 sea leopard as host 33
segmentata; *Chaetolepas*, *Ibla*
Semibalanus 131
sertus; *Mitella*, *Pollicipes*
 setation of cirri 12, 45, 73, 121, 145 (Plate 1)
 sex and sexual differentiation 13, 20, 22, 47, 122, 123
 shell growth 73, 76, 87, 89, 125
 shore zonation 75-76, 89, 97, 118-9, 120, 127-130.
Siboga 82
sibogae; *Ibla*
simplex; *Elminius*, *Epopella*
sinuatus; *Elminius*
Smilium 7, 38, 41, 43, 49, 51, 122, 123
acutum 14, 43, 51-2, 118, 120, 137, 138, 139, 150 (Plate 6)
spinosum 41 (= *Calantica spinosa*)
zancleanum 8, 14, 43, 49-51, 118, 119, 120, 138, 150 (Plate 6)
 Snares, The 39, 75, 87, 89, 119
Solidobalanus 15, 97, 100, 102, 124
 South Africa 90, 95
 South America 89, 95, 100, 104, 108, 120-1, 126
 southwardi; *Tetraclaelasma*
 spectrum; *Alepas*
spinilatera; *Calantica*
spinosa (us) (um); *Anatifa*, *Calantica*, *Pollicipes*.
Scalpellum, *Smilium*
spinulosa; *Cresida*
 Spirits Bay 39, 87, 102
 sponges as hosts 126, 131
squamosa; *Tetraclita*
 St. Clair Beach 33
stellatus; *Chthamalus*
Stephanolepas 115
 Stephen I 39, 44
 Stewart I 8, 39, 43, 44, 87, 93, 95, 97, 108, 119, 138
Stomatolepas 115, 117, 126
elegans 15, 117, 118, 160 (Plate 14)
praegustator 117 (= *S. elegans*)
striatum; *Arcoscalpellum*
striatum; *Megalasma*
studerii; *Calantica*, *Scalpellum*
 subcarina 9 (definition)
subplana (um); *Scalpellum*, *Calantica*
sulcata; *Verruca*
sulci; *Calantica*
superba; *Calantica*
- talismani*; *Scalpellum*
 Tasman Sea 120
 Tasmania 16, 20, 26, 38, 77, 78
Temnaspis 24
 tergum (pl. terga) 9 (definition)
Terra Nova 7, 17, 22, 32, 104, 114
terranovalis; *Oxynaspis*
Tesserelasma 131
Tesseroplax 131
- Tesseropora* 86, 90, 124, 125, 130, 131
pacifica 91, 95
rosea 14, 90-1, 95, 118, 120, 156 (Plate 11)
testudinata; *Lepas*
Tetrabalanus 124, 126
Tetraclaelasma 83, 124
 southwardi 76
Tetrachthamalus 72, 124, 125
Tetraclita 86, 91, 93, 100, 124, 125, 130, 131
aoranga 14, 91-3, 110, 118, 120, 156 (Plate 11)
porosa 93, 100
purpurascens 14, 93 (= *Tetraclitella purpurascens*), 94
breviscutum 86, 87 (= *Epopella plicata*), 89, 93
rosea 8, 90 (= *Tesseropora rosea*)
squamosa viridis 125
Tetraclitella 86, 87, 93, 124, 125, 129, 130
chinensis 129
divisa 129
multicostata 95
purpurascens 7, 14, 93-5, 107, 118, 119, 120, 127, 128, 129, 138, 156 (Plate 11), 157 (Plate 12)
Tetraclitidae 14, 73, 83, 86-7, 122, 124, 125, 126, 127, 128, 129
 Three Kings Is 7, 39, 43, 47, 73, 102, 138, 139
tintinnabulum; *Balanus*
 Tolaga Bay 19
 Tom Bowling Bay 139
 Tory Channel 35, 116
trachealis; *Tubicinella*
triderma; *Aptolasma*
trigonus; *Balanus*
Trilasmis 24, 131
kaempferi 14, 17, 24-6, 118, 120, 139, 147 (Plate 3)
trispinosa; *Calantica*
trochelum; *Arcoscalpellum*
Tubicinella 115, 116
major 7, 15, 115, 116, 118
trachealis 116 (= *T. major*)
tubulatus; *Balanus*
tubulosa; *Anatifa*
 Tu 25, 26, 27, 31, 33, 79, 83, 84, 90, 102, 104
 turtles as hosts 29, 35, 95, 114, 115, 117
- ungulatum*; *Arcoscalpellum*
 United States National Museum 83
univalvis; *Alepas*
 upper latus 9 (definition)
utinomi (1); *Arcoscalpellum*, *Heteralepas*
- Valkyrie* 15, 53
variegatus; *Balanus*, *Balanus amphitrite*
velutinum; *Hexelasma*
Venus 7
Verruca 68, 118
capsula 69 (= *V. halotheica*)
corallophila 69
gibbosa 69
halotheica 14, 69-72, 118, 120, 137, 138, 139, 152 (Plate 8)
magna 69
navicula 69
recta 69
sulcata (= *V. gibbosa*) 69
Verrucidae 14, 68, 71
Verrucomorpha 6, 8, 10, 14, 68
 vertebrates as hosts 115, 117, 126
vestitus; *Balanus*
villosa (um); *Calantica*, *Scalpellum*
virgatum; *Conchoderma*
Virgiscalpellum 131
vitreum; *Arcoscalpellum*, *Scalpellum*
- Waiheke I 31
 Waikanae 33
 Waipapakauri 31
 Waitemata Harbour 109, 111, 113, 114
 Waiterere Beach 34
 Waiuku 34
 Waiwera 93
 Wellington 26, 30, 44, 49, 93, 111
 West Africa 19
 whales as hosts 7, 36, 115, 116, 147
 Whangamata 31
 Whangarei Heads 102, 113
 Whareama River mouth 117
 White Beach 29
 White I 22, 39, 91, 102
 worm tubes as substrate 21, 100, 146
- Xenobalanus* 115, 126
- zancleana* (um); *Calantica*, *Scalpellum*, *Smilium*
zelandiae; *Balanus*
Zeugmatolepas 131

AUTHOR AND COLLECTOR INDEX

Collectors are indicated by page numbers in *italic type*.

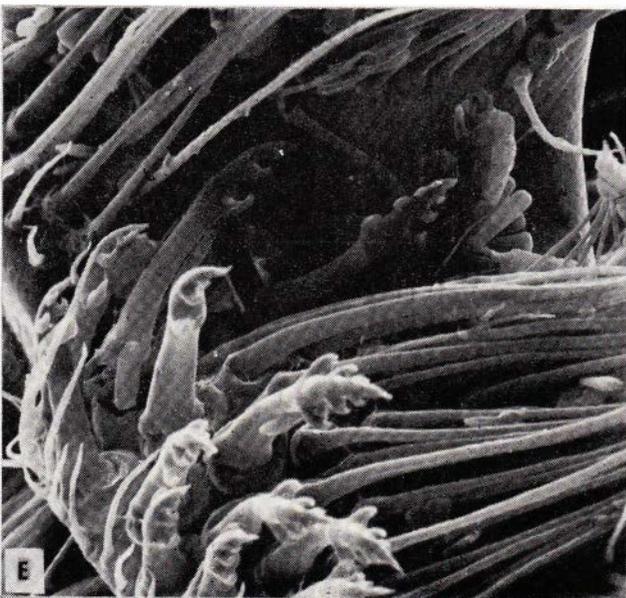
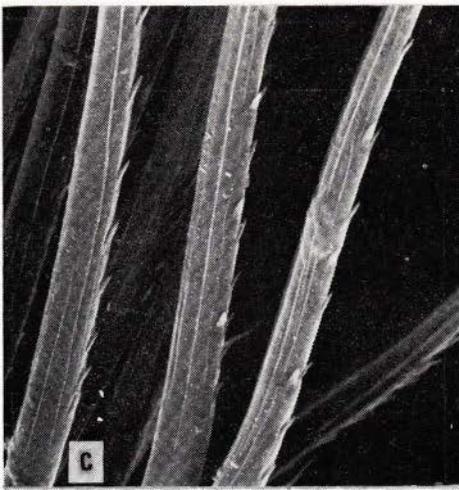
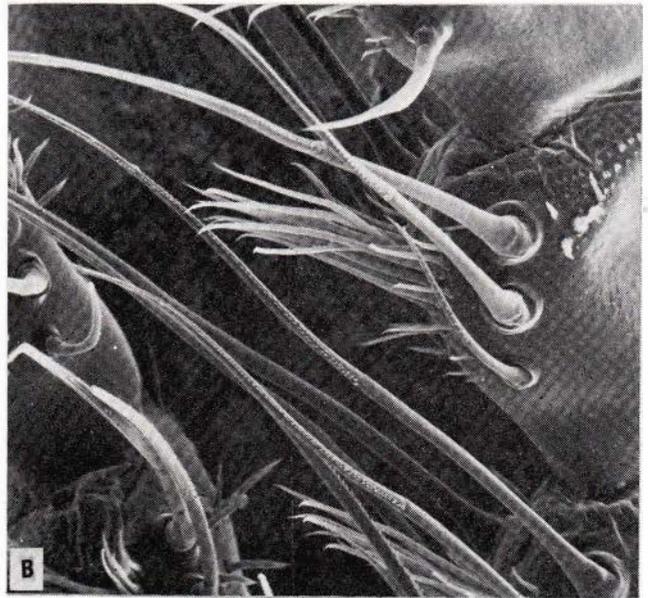
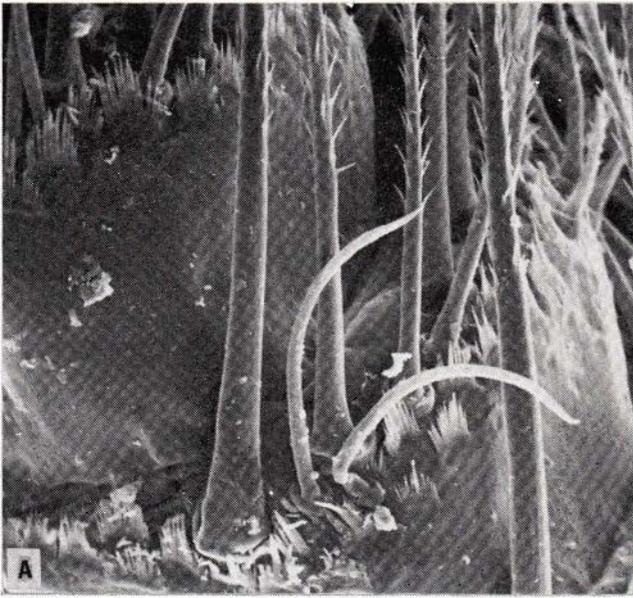
- Abernethy, F. 44
 Annandale, N. 7, 20, 22, 24, 26, 41, 49, 51, 65, 123
 133
 Aurivillius, C. W. 7, 15, 17, 31, 47, 48, 133
 Ayling, A. M. 91, 102
- Ballantine, W. J. 102
 Barnard, C. H. 24, 26, 133
 Barnes, H. 89, 129, 133
 Batham, E. J. 6, 8, 20, 21, 22, 39, 45, 72, 133, 146
 Bennett, E. W. 107
 Bennett, I. 89, 133
 Beil, R. S. 31
 Beu, A. G. 8, 115, 116, 133
 Borradaile, L. A. 7, 31, 33, 36, 41, 72, 73, 79, 83,
 104, 133
 Broch, H. 7, 15, 16, 19, 20, 21, 22, 23, 24, 26, 27, 33,
 39, 41, 42, 44, 45, 47, 51, 59, 60, 62, 73, 77, 78, 86,
 87, 89, 93, 95, 97, 100, 102, 107, 109, 113, 114, 121,
 133
 Bullivant, J. S. 82, 132, 133
- Calman, W. T. 26, 49, 51, 133
 Castle, P. J. 29, 31, 33
 Chilton, C. 7, 8, 29, 31, 33, 34, 41, 104, 107, 108,
 113, 114, 133
 Clark, A. G. 41
 Climo, F. 39, 102
 Cobham, W. S. 44
 Connell, J. H. 129, 133
 Crozier, M. A. 33, 39, 44, 91, 102
 Cranwell, L. M. 8, 72, 93, 102, 104, 133
 Crisp, D. J. 95, 109, 126, 133, 135
- Darwin, C. 7, 19, 20, 24, 29, 31, 32, 33, 34, 35, 36,
 38, 39, 44, 49, 73, 78, 87, 89, 90, 91, 93, 94, 95, 97,
 100, 104, 109, 111, 113, 114, 115, 116, 117, 120,
 121, 133
 Davidson, E. B. 29
 Dawson, E. W. 6
 Dell, R. K. 29, 31, 33, 39, 44
 Deveraii, T. 33
 Dieffenbach, E. 7
 Douglas, N. 34
- Eastern, T. 34
- Filhol, H. 7, 31, 32, 39, 87, 95, 104, 107, 108, 111,
 112, 113, 114, 115, 133
 Fleming, C. 8, 132, 133
 Foster, B. A. 8, 20, 73, 87, 89, 91, 93, 95, 97, 102,
 104, 107, 109, 111, 113, 129, 133
- Foster, W. 26, 49
 Gaimard, *see* Quoy
 Grace, R. 91, 102
 Grant-Mackie, J. A. 8, 132, 133
 Gray, J. E. 7, 87, 93, 94, 115, 116, 133
 Gruvel, A. 20, 31, 34, 59, 65, 87, 97, 100, 107, 108,
 133
- Harding, J. P. 109, 111, 134
 Hatton, C. 31
 Hector, J. 80, 82, 134
 Henry, D. P. 97, 134
 Hine, P. M. 25
 Hiro, F. 15, 17, 19, 35, 36, 37, 38, 47, 62, 114, 117,
 134
 Hoek, P. P. C. 7, 8, 19, 20, 26, 27, 33, 34, 41, 51, 53,
 56, 58, 62, 65, 69, 79, 80, 82, 83, 87, 100, 102, 112,
 134
 Hudson, D. 15
 Hutton, F. W. 7, 31, 32, 34, 39, 44, 87, 89, 93, 95,
 97, 104, 107, 108, 111, 112, 113, 114, 115, 134
- Jennings, L. S. 7, 29, 31, 32, 33, 34, 35, 36, 39, 41,
 44, 87, 93, 95, 104, 108, 111, 113, 114, 115, 134
 Johns, P. M. 33
- Kirton, N. S. 29
 Klepal, W. 89, 133
 Knox, G. A. 89, 95, 107, 134
- Laws, C. R. 8, 134
 Lindsay, C. J. 29
 Linzey, J. T. 8, 73, 89, 90, 93, 102, 103, 104,
 114, 134, 148
 Luckens, P. A. 6, 76, 129, 134
- McCann, C. 117, 134
 McLaughlin, P. A. 97, 134
 Marwick, H. 31, 33
 Maxwell, G. S. 107, 134
 Milligan, C. I. 91, 93, 102
 Moore, L. B. 7, 8, 72, 73, 87, 88, 89, 93, 95, 102,
 104, 114, 133, 134
- Newman, W. A. 8, 14, 16, 18, 19, 20, 32, 34, 35, 48,
 49, 51, 53, 56, 58, 59, 62, 72, 76, 79, 82, 83, 84, 87,
 90, 95, 97, 104, 121, 134, 135
 Nilsson-Cantell, C. 7, 8, 15, 16, 17, 23, 24, 26, 27,
 31, 32, 36, 37, 56, 58, 62, 69, 76, 77, 78, 87, 90, 91,
 95, 100, 102, 111, 112, 114, 115, 116, 134
 Nott, J. A. 129, 133
- Oliver, W. R. B. 8, 29, 31, 34, 39, 72, 89, 90, 134
- Phillips, W. J. 29
 Pilsbry, H. A. 15, 16, 24, 37, 38, 49, 56, 58, 59, 62,
 65, 69, 76, 78, 87, 90, 95, 97, 100, 103, 104, 113,
 114, 115, 116, 117, 134
 Pope, E. C. 45, 73, 89, 90, 91, 93, 97, 100, 109, 111,
 112, 113, 124, 129, 134
 Powell, A. W. B. 8, 35, 36, 39, 44, 49, 95, 104, 115,
 134
- Quoy, J. R. E. & Gaimard J. P. 7, 17, 19, 31, 32, 39,
 134
- Ross, A. 8, 14, 32, 34, 35, 51, 53, 56, 58, 59, 62, 72,
 76, 79, 82, 83, 84, 86, 87, 89, 90, 95, 97, 104, 134
 Russell, B. 35
 Rutland, G. A. 29
- Sandison, E. E. 95, 134
 Skerman, T. M. 35, 104, 111, 112, 114, 135
 Sketchley, R. 17
 Sorenson, J. H. 33
 Southward, A. J. 69, 95, 109, 126, 135
 Southward, E. C. 69, 135
 Stead, E. F. 115, 135
 Stubbings, H. G. 20, 23, 24, 56, 109, 111, 113, 135
 Studer, Th. 7, 20, 21, 22, 135
- Totton, A. K. 7, 22, 23, 24, 135
 Tubb, J. A. 37, 38, 135
- Utinomi, H. 7, 8, 14, 17, 18, 24, 27, 29, 32, 33, 34,
 45, 47, 58, 59, 72, 76, 77, 78, 79, 95, 109, 111, 112,
 113, 135
- Weltner, W. 7, 32, 33, 34, 39, 44, 45, 47, 73, 87, 93,
 97, 104, 135
 Wills, I. J. 121, 135
 Willan, R. C. 91
 Wilson, F. E. 34
 Withers, T. H. 7, 8, 22, 38, 41, 48, 49, 51, 82, 83, 97,
 102, 107, 108, 113, 114, 121, 123, 132, 134, 135
- Yaldwyn, J. 6, 29, 33, 90, 93, 102, 104
 Young, M. W. 31, 34, 39, 95, 135
- Zullo, V. A. 29, 134, 135



PLATES

Plate 1. Scanning electron micrographs of cirral setae of various barnacles.

- A the outer edge of cirrus I ramus, *Calantica spinosa*.
- B antero-lateral and distal view, cirrus III rami, *Calantica spinosa*.
- C long anterior setae, posterior cirri, *Calantica spinosa*.
- D anterior setae, cirrus III intermediate segments, *Calantica spinosa*.
- E anterior setae, cirrus III basal segments, *Chamaesipho brunnea*.
- F anterior setae, cirrus III basal segments, *Epopella plicata*.



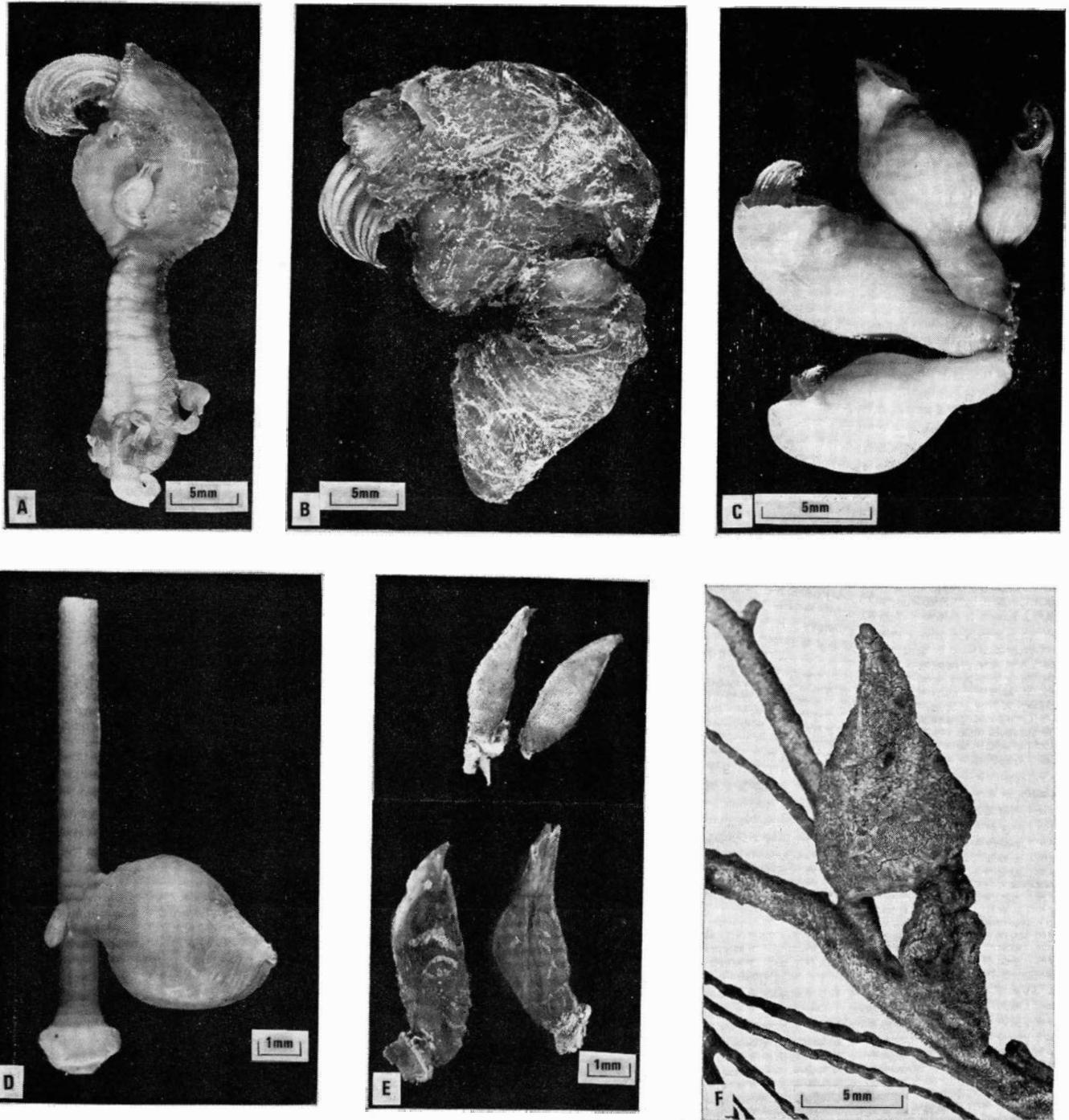


Plate 2. Heteralepadidae, Iblidae, and Oxynaspidae.

- A *Heteralepas japonica*, from pennatulids.
 B *H. japonica*, from submerged rope.
 C *Paralepas quadrata*, from spiny lobster.
 D *Paralepas minuta*, on echinoid spine (NZOI Stn E875).
 E *Ibla idiotica*, (above) Saunders Canyon, Otago (courtesy E. J. Batham), (below) from worm tube (NZOI Stn D90).
 F *Oxynaspis indica*, on antipatharian, Poor Knights Is.

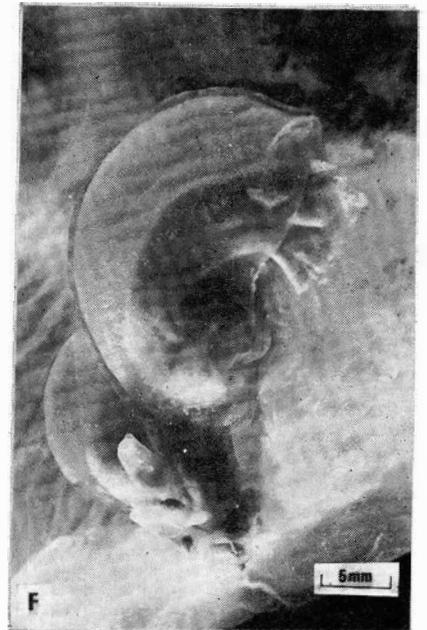
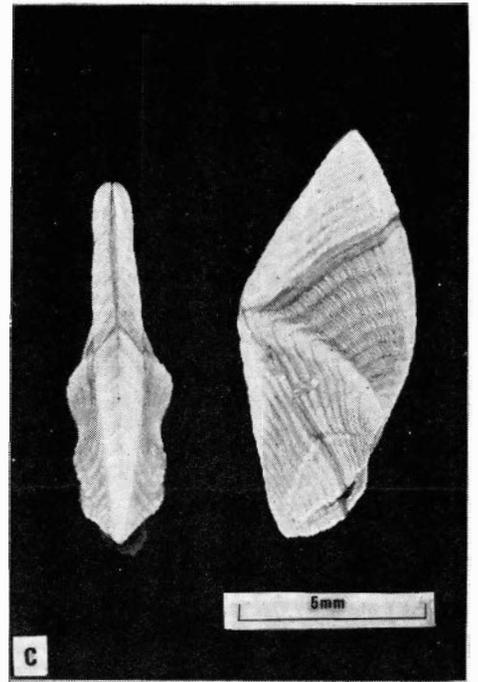
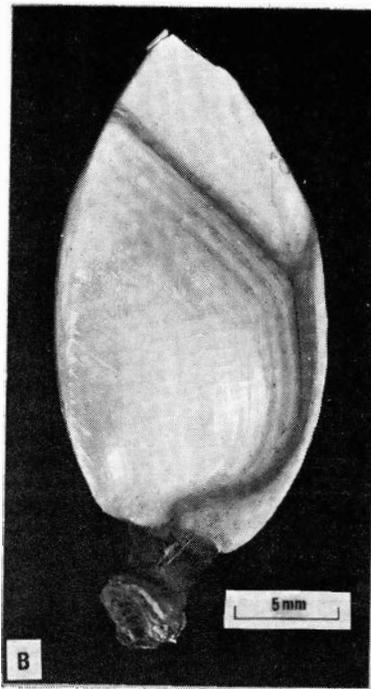
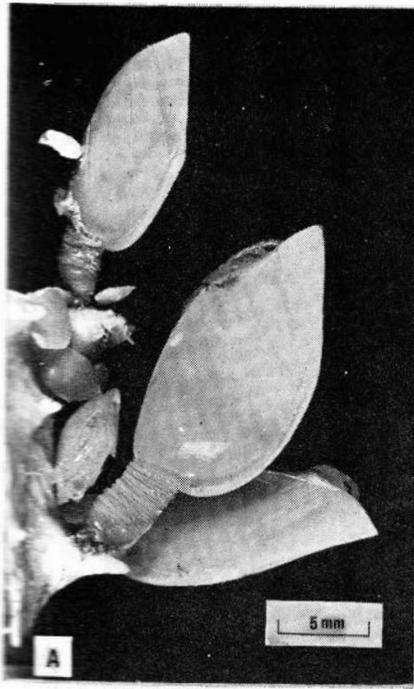


Plate 3. Poecilasmatidae and Lepadidae.

- A *Trilasmis kaempferi*, on crab carapace (NZOI Stn F924).
- B *Megalasma carinatum*, from cable.
- C *Megalasma striatum*, from echinoid spines (*Tui* specimens).
- D *Conchoderma virgatum*, on parasitic copepod *Penella*.
- E *Conchoderma auritum*, on *Coronula diadema* from a whale.
- F *Alepas pacifica*, on a scyphomedusan.

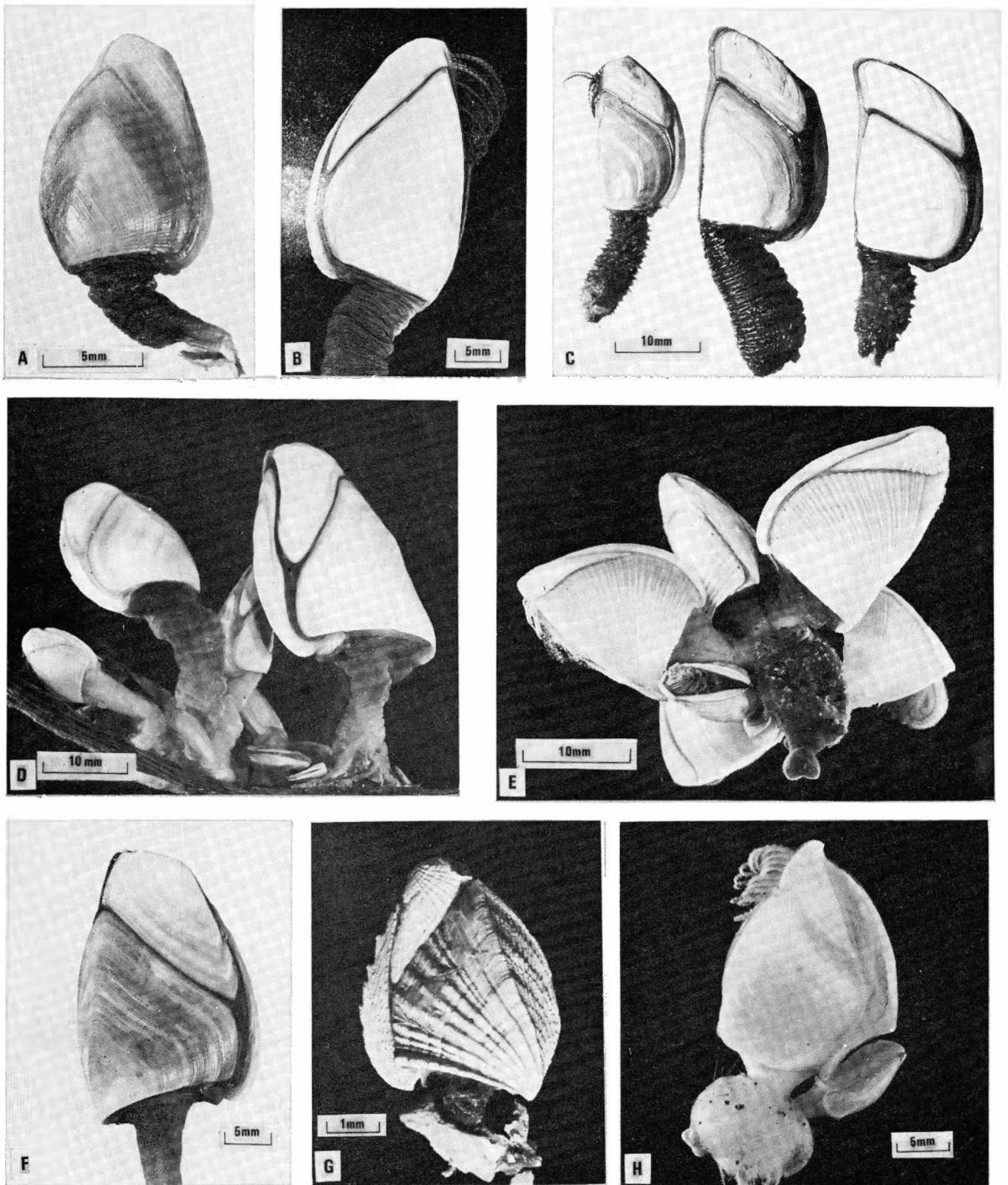


Plate 4. Lepadidae, *Lepas*.

- A, B *L. anatifera*, from floating wood. F *L. australis*, from floating algae.
 C *L. testudinata*, from floating wood and algae. G *L. denticulata*, from Kermadec Is (Linzey 1942a).
 D *L. anatifera* (left) and *L. australis* (right), on floating wood. H *L. fascicularis*, on its own float secreted round a feather.
 E *L. pectinata*, on floating algae.

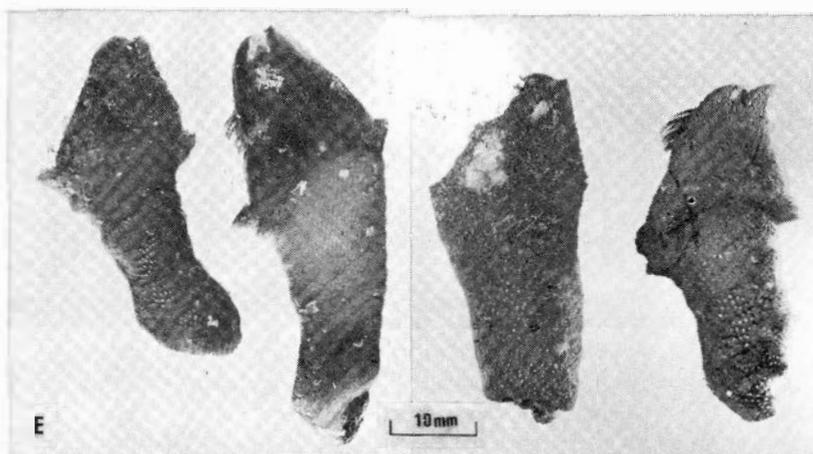
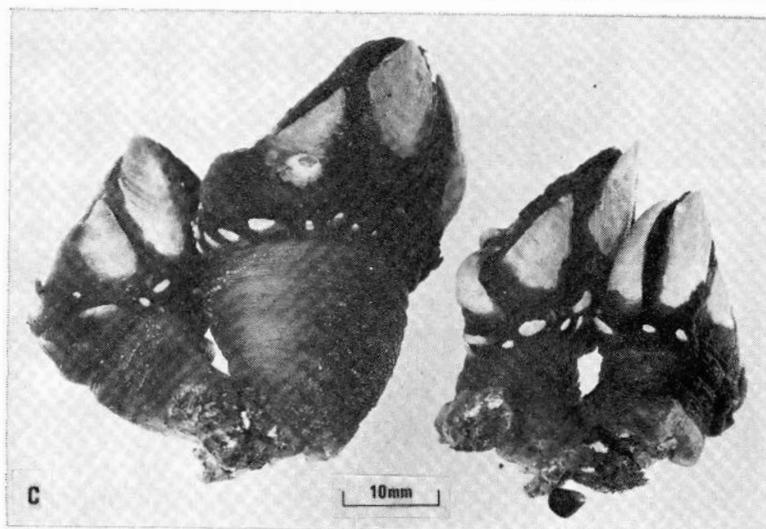
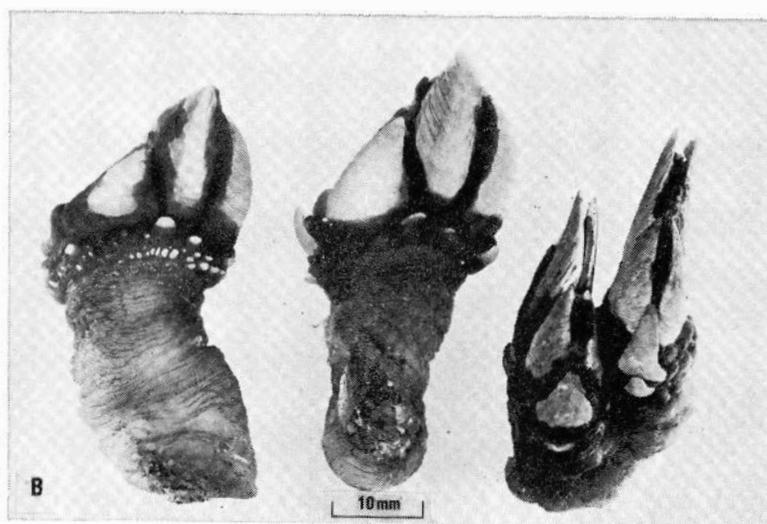
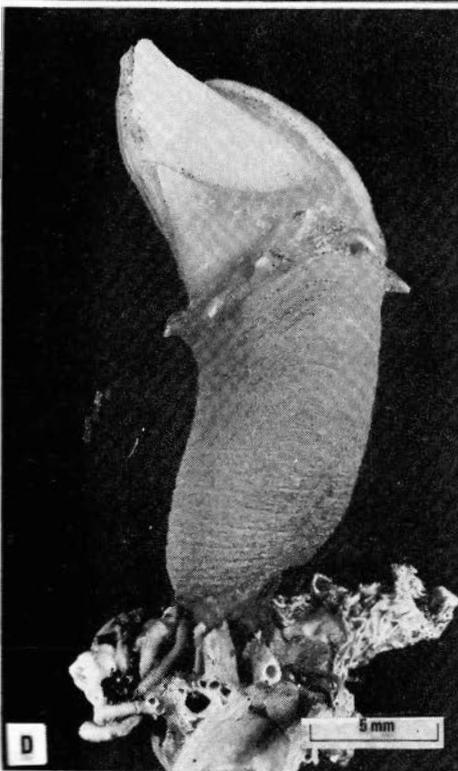
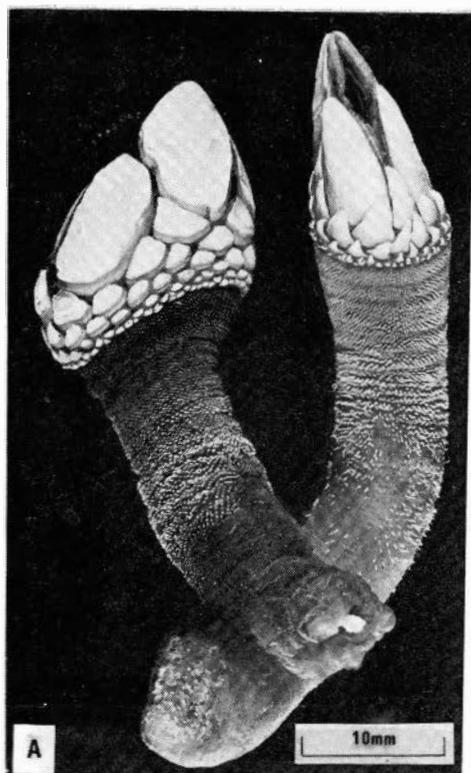


Plate 5. Scalpellidae.

A *Pollicipes polymerus*, from California.
 C *Calantica spinosa*, from northern New Zealand shores, one specimen in C with *Chamaesipho columna* on the right scutum.

D *Calantica spinilatera* (NZOI Stn D121).
 E *Calantica villosa*, from shore habitats.

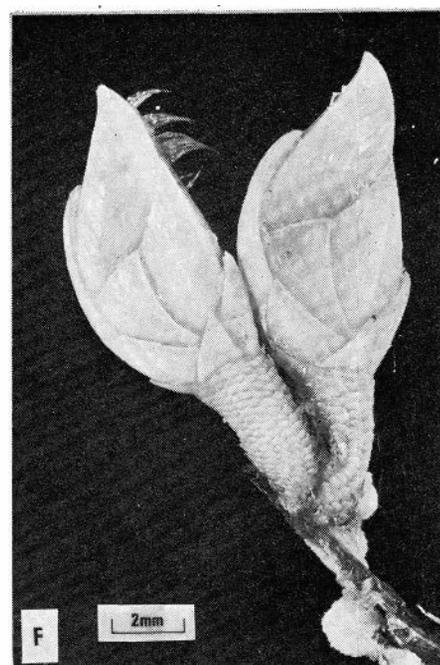
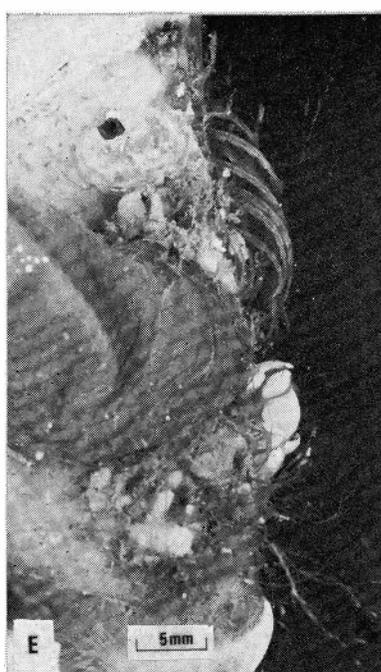
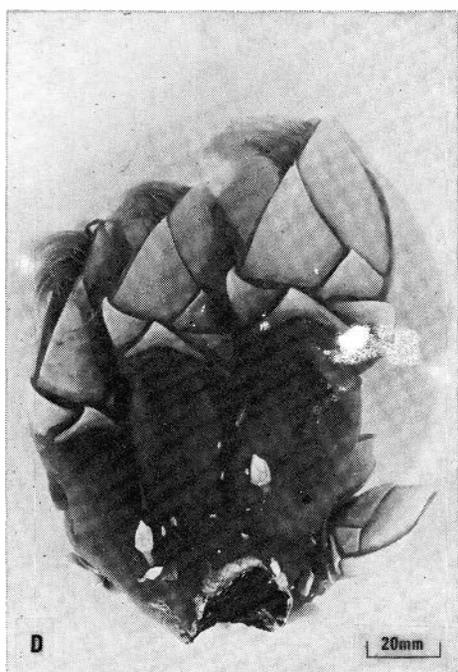
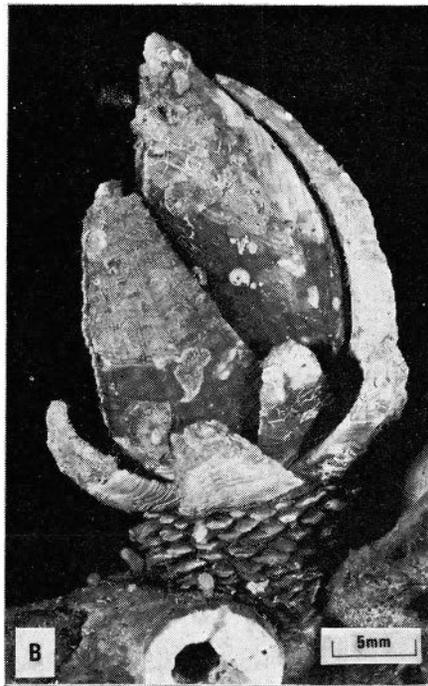
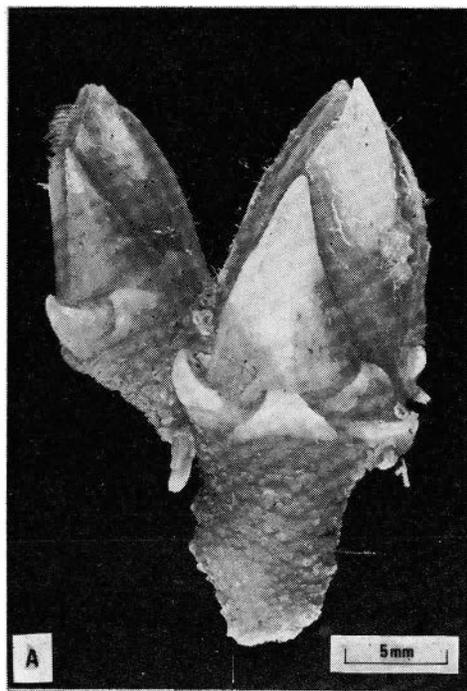


Plate 6. Scalpellidae.

- A** *Calantica studeri*, from shells (NZOI Stn E720).
B, C *Calantica gemma*, on rock, same specimen in **B** and (NZOI Stn F81).
D *Smilium zancleanum*, from cable (Auck. Mus.).
E males of *S. zancleanum* projecting beyond lower parts of scuta of a hermaphrodite.
F *Smilium acutum*, on a hydroid stalk (NZOI Stn D904).

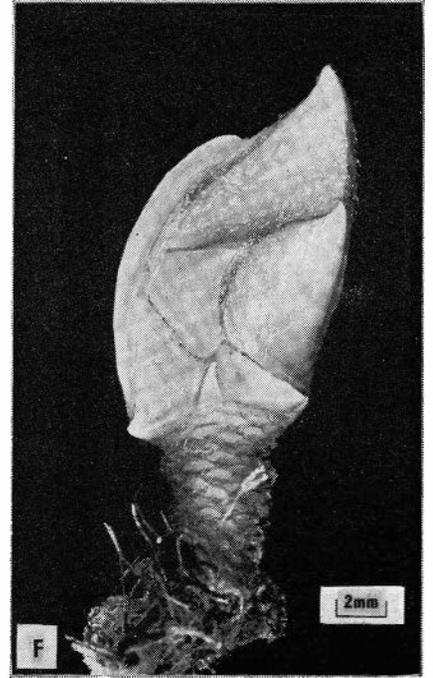
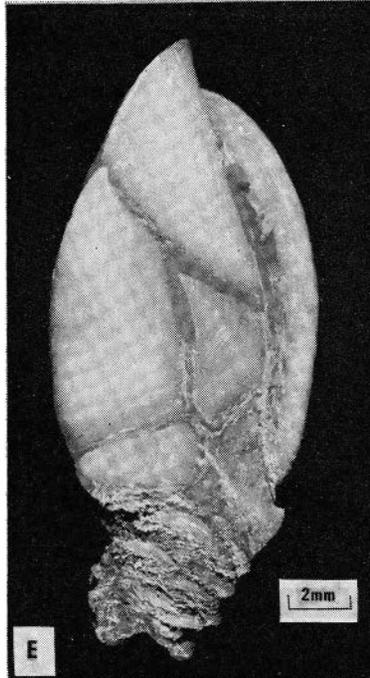
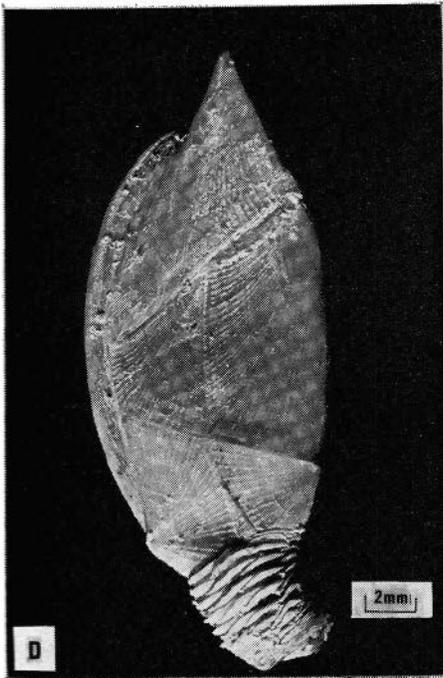
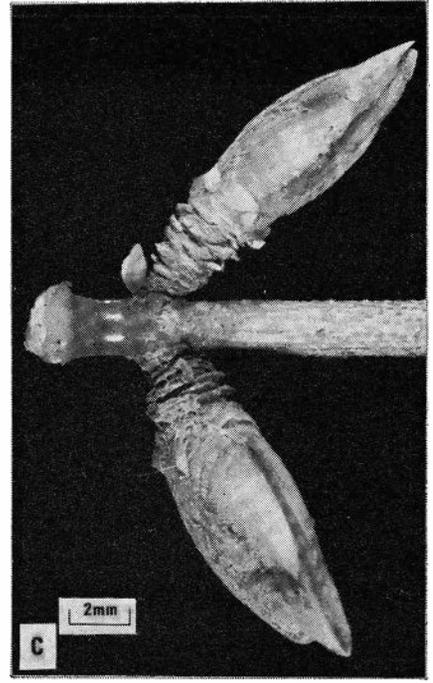
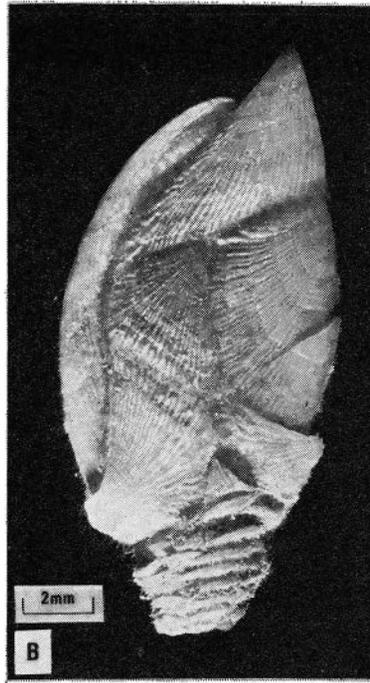
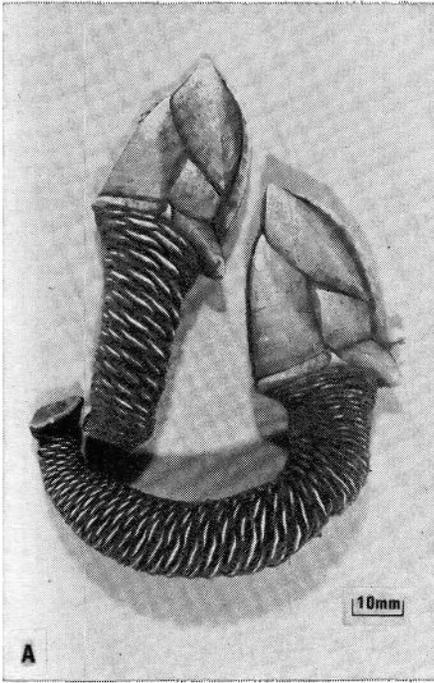


Plate 7. Scalpellidae, *Arcoscalpellum*.

- A *A. pedunculatum* (Auck. Mus.)
- B *A. costellatum* (NZOI Stn E830).
- C *A. costellatum* (NZOI Stn F870).
- D *A. vitreum* (NZOI Stn E869).
- E *A. affricatum* n.sp. (NZOI Stn C734).
- F *A. affricatum* n.sp. (NZOI Stn A426).

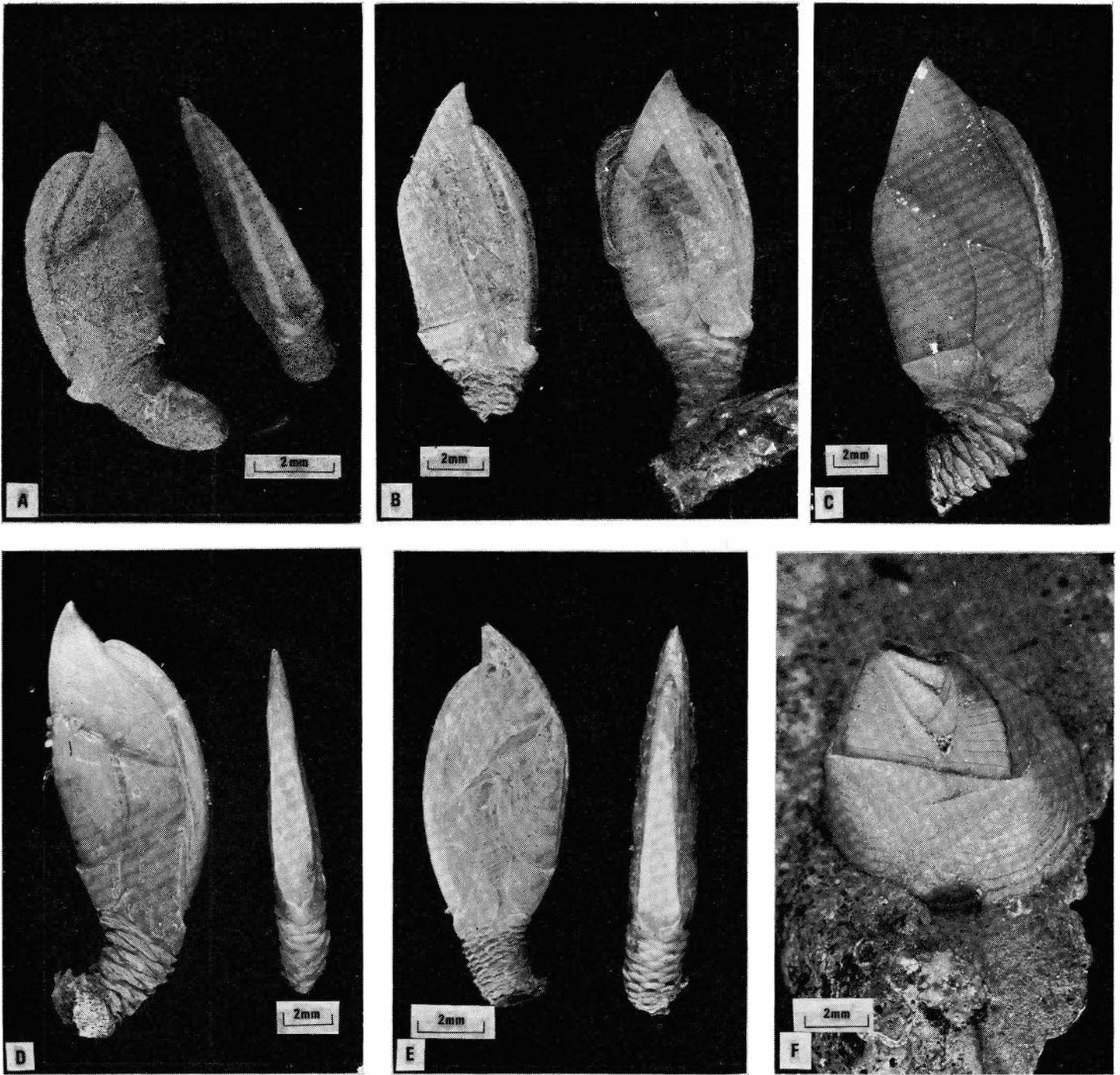


Plate 8. Scalpellidae and Verrucidae.

- | | | | |
|---|---|---|---|
| A | <i>Arcoscalpellum trochelatum</i> n.sp. (NZOI Stn E413). | D | <i>A. novaezealandiae</i> (NZOI Stn G700). |
| B | <i>A. intermedium</i> (NZOI Stn F883 on left, Stn F872 on right). | E | <i>A. raccidium</i> n.sp. (NZOI Stn F883 on left, Stn F872 on right). |
| C | <i>A. pertosum</i> n.sp. (NZOI Stn G700). | F | <i>Verruca halothea</i> (NZOI Stn D159). |

Plate 9 (facing). Chthamalidae and Pachylasmidae.

- | | | | |
|---|--|------|---|
| A | <i>Chamaesipho columna</i> , apical views of a range of specimens. | D | <i>C. brunnea</i> , 4 in apical view, 1 in lateral view. |
| B | <i>C. columna</i> , crowded together. | E, F | lateral and apical views of <i>Pachylasma scutistriata</i> (NZOI Stn D210). |
| C | <i>Chamaesipho brunnea</i> , crowded together. | | |

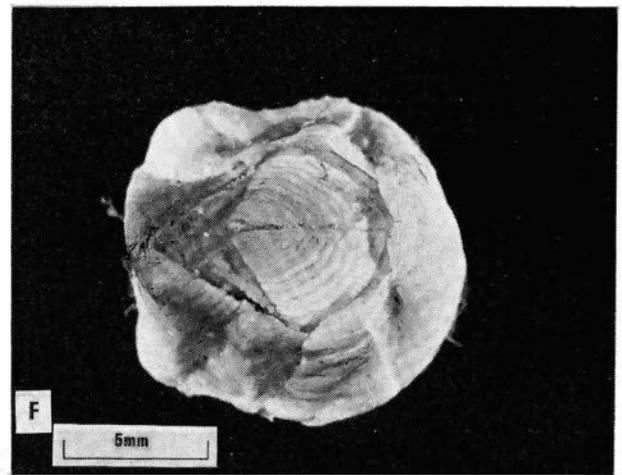
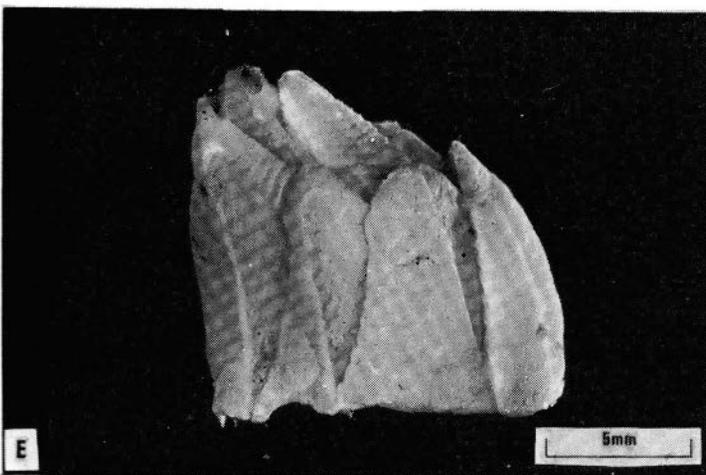
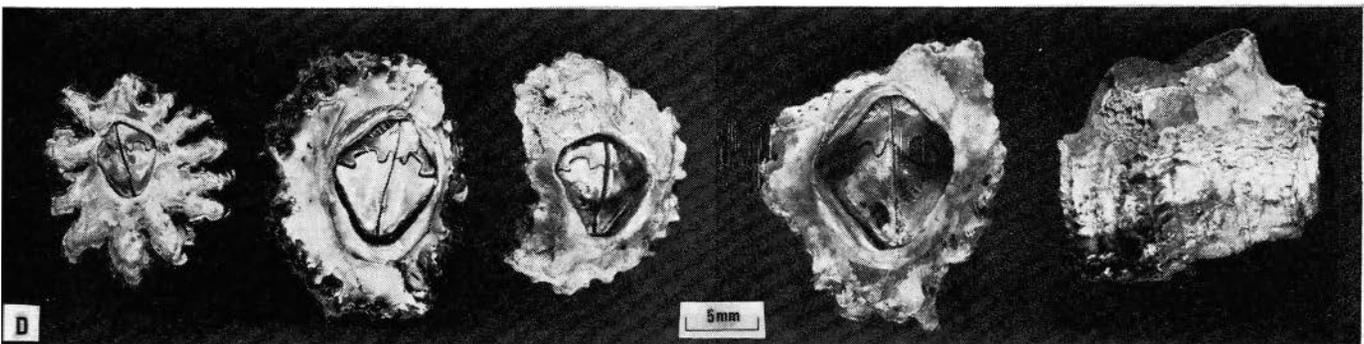
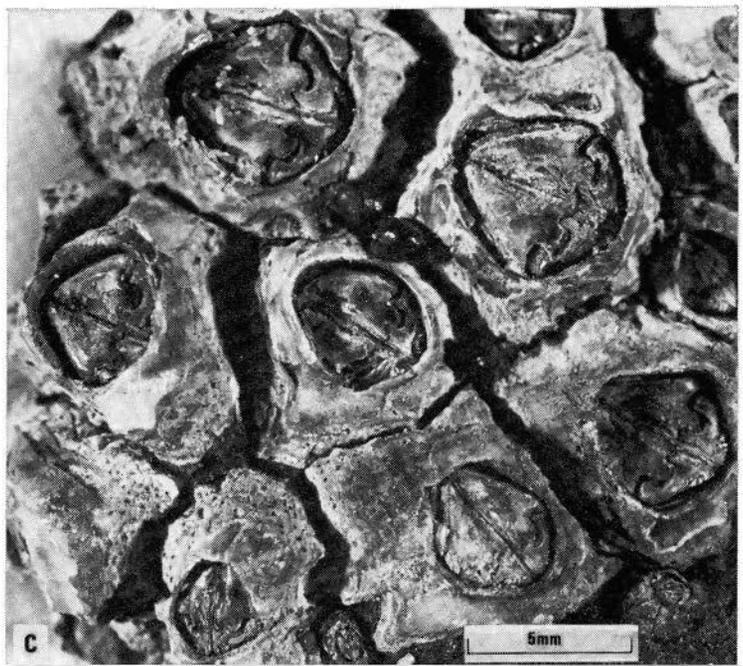
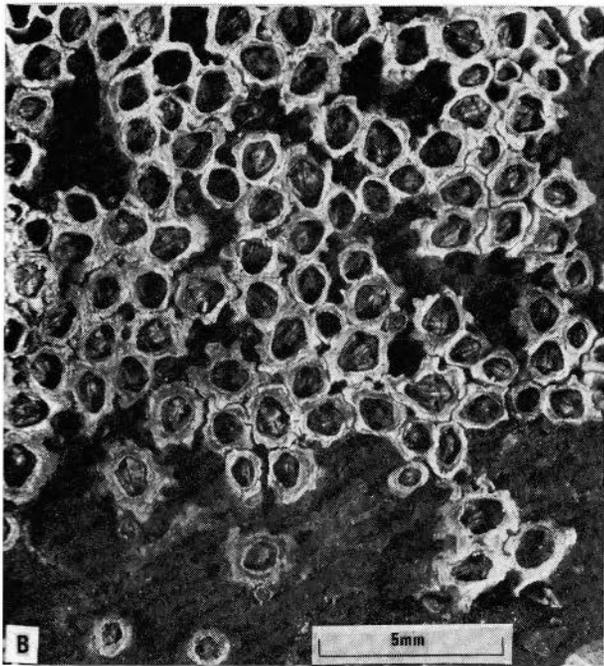
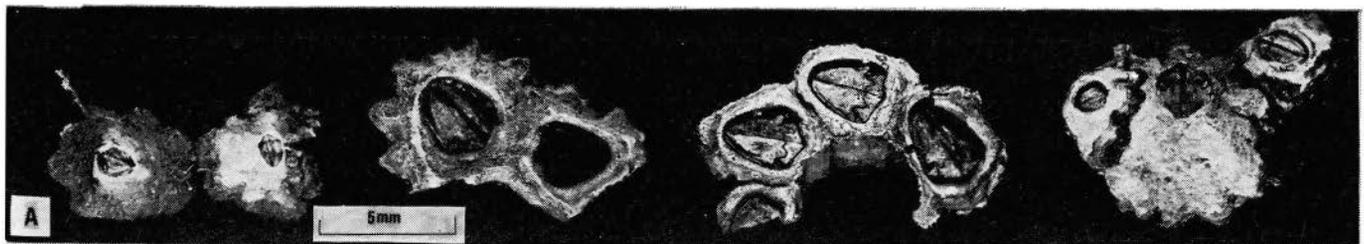


Plate 10 (*facing*). Pachylasmidae.

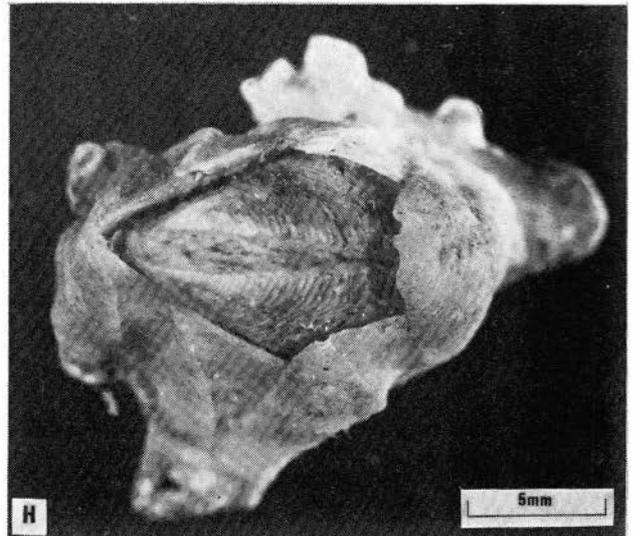
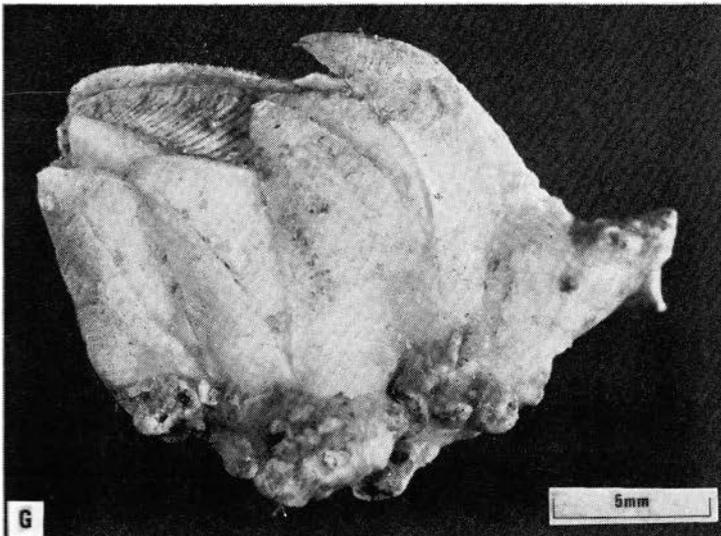
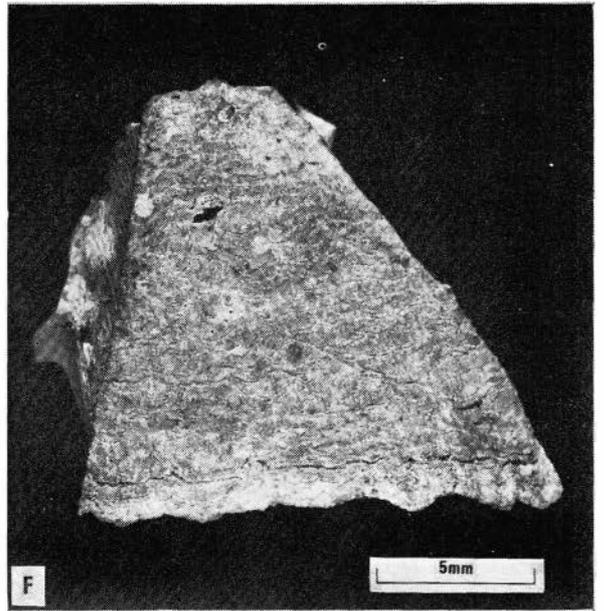
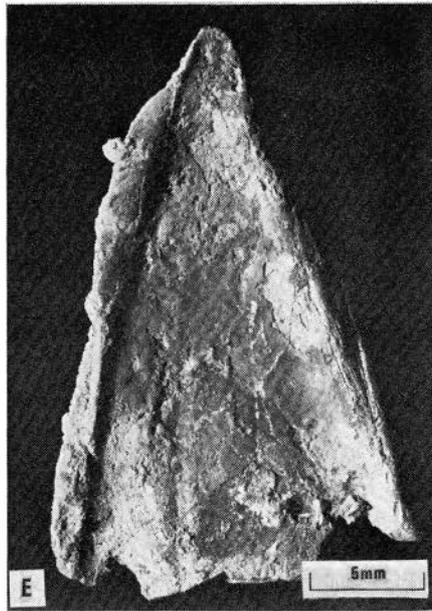
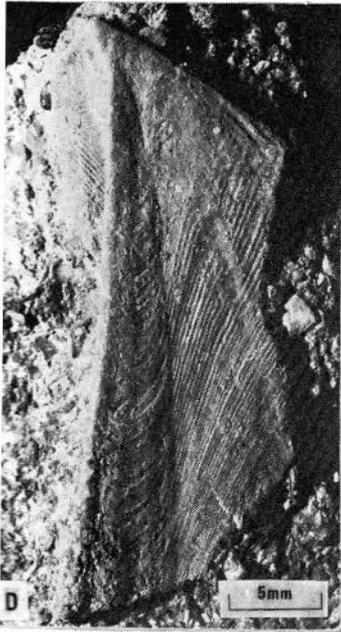
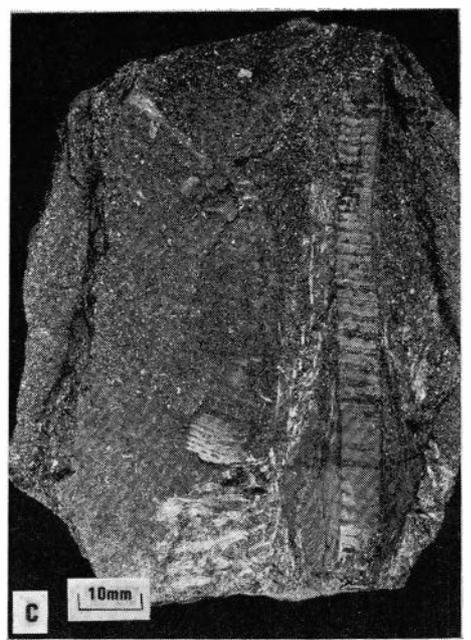
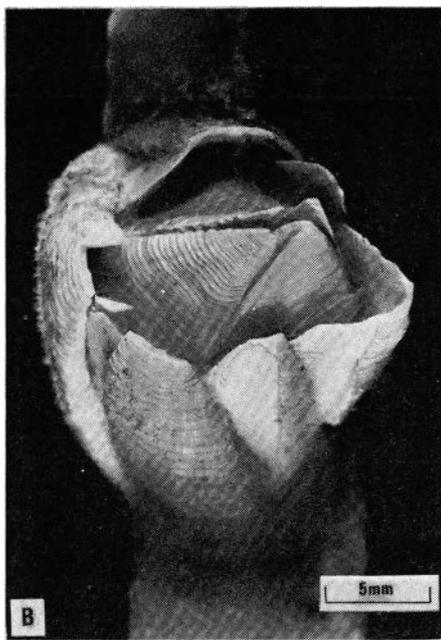
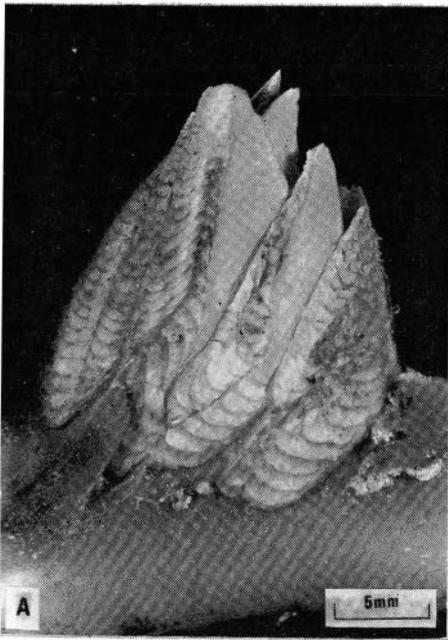
- A, B** lateral and apical views of *Hexelasma alearum* n.sp. (NZOI Stn F132.)
- C** *Hexelasma aucklandicum*, fossil carina.
- D** *H. aucklandicum*, fossil tergum.
- E** *H. aucklandicum*, fossil scutum.
- F** *Aptolasma fosteri*, latus only (NZOI Stn E852).
- G, H** *Aptolasma nolearia* n.sp., lateral and apical views (NZOI Stn D159).

Plate 11 (*page 156*). Tetracelitidae.

- A** *Epopella plicata*, range of specimens in apical view.
- B** View of basal edge of paries of *Epopella plicata*
- C** *Tesseropora rosea* from Kermadec Is, 2 in apical view, 1 in basal view.
- D, E** *Tetracelita aoranga* n.sp., on *Balanus tintinnabulum*, two lots from Poor Knights Is.
- F, G** views of basal edge of paries of *Tetracelita aoranga* and *Tetracelitella purpurascens* respectively.

Plate 12 (*page 157*). Tetracelitidae and Balanidae.

- A, B** *Tetracelitella purpurascens*, uneroded (A) and apically eroded (B) specimens on mussel shells.
- C** *Elminius modestus*, range of specimens in apical views.
- D, E** *Balanus vestitus*, on mollusc shell (Doubtless Bay) and crab carapace (off Otago Peninsula) respectively.
- F** *Balanus auricomus*, on hydroid (NZOI Stn F861).



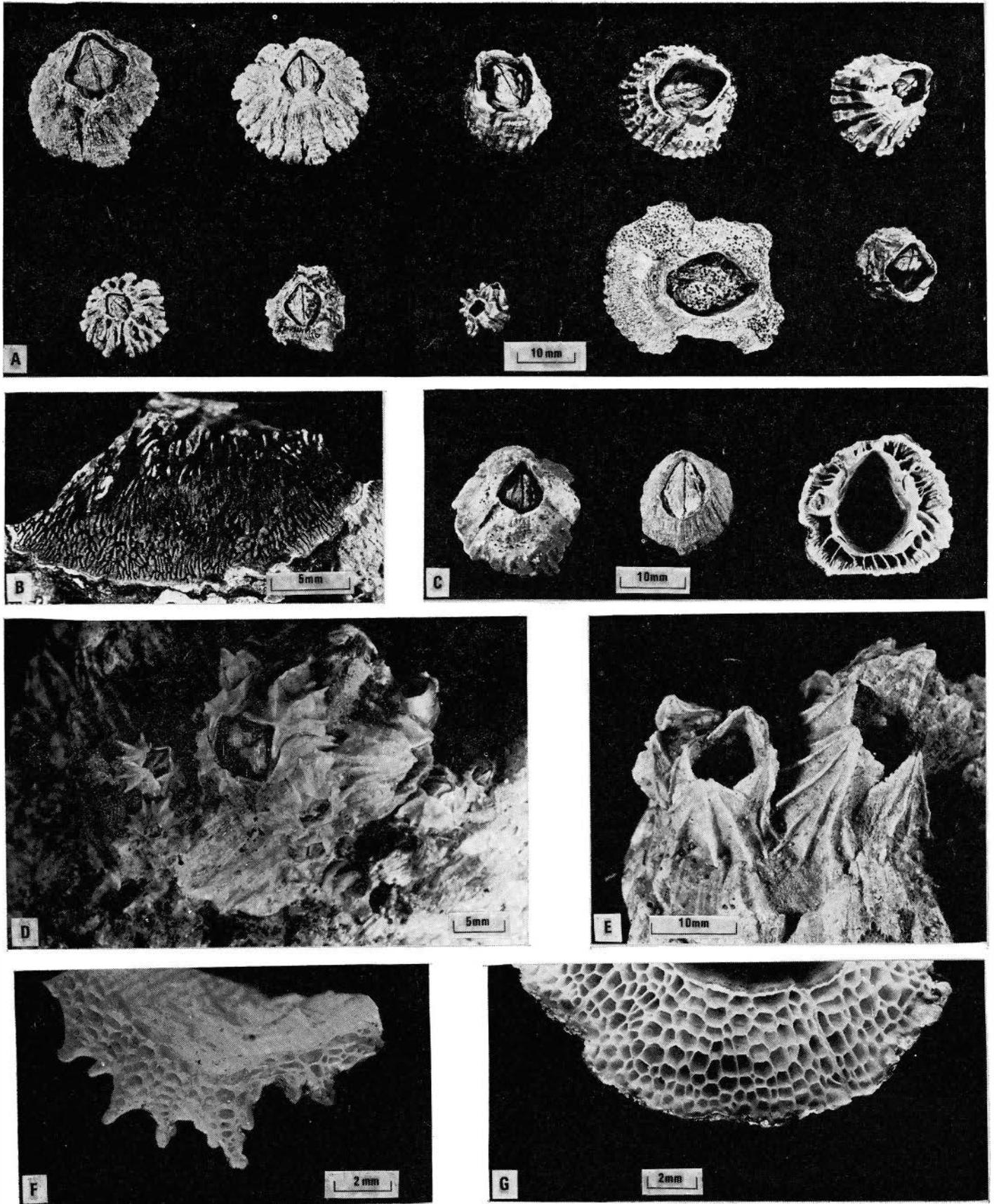


PLATE 11 — caption on page 154

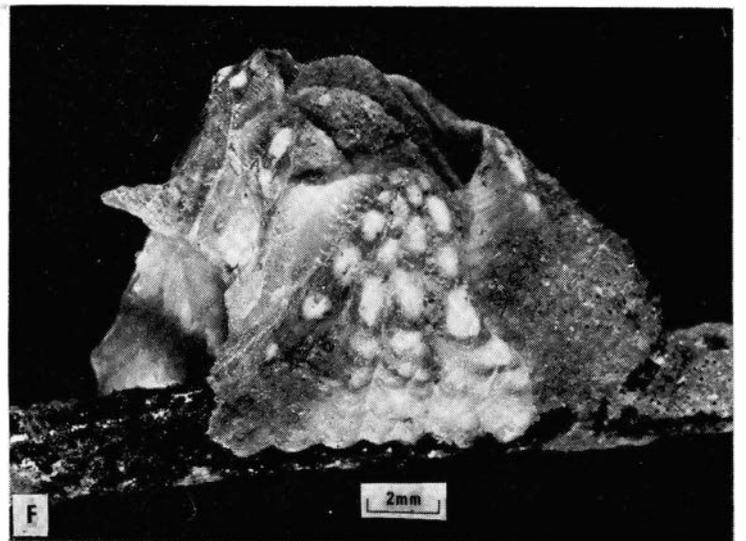
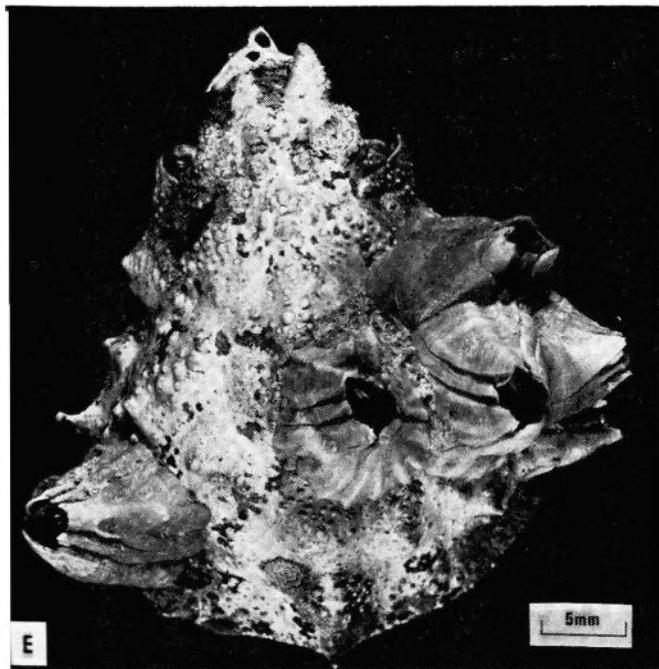
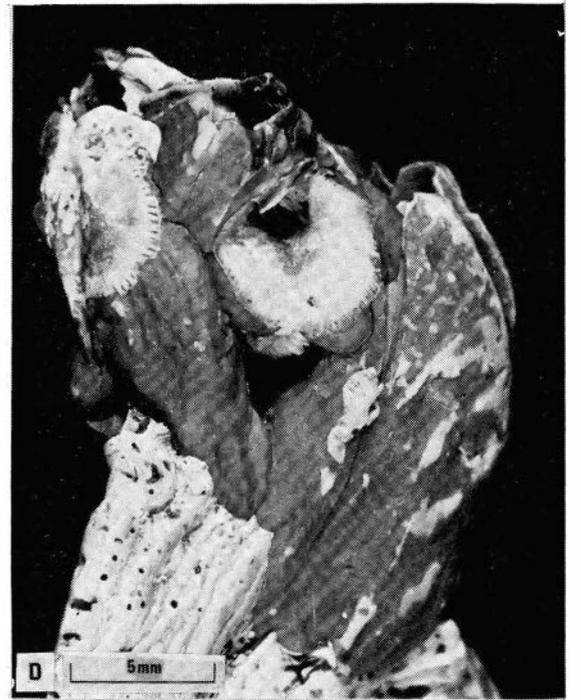
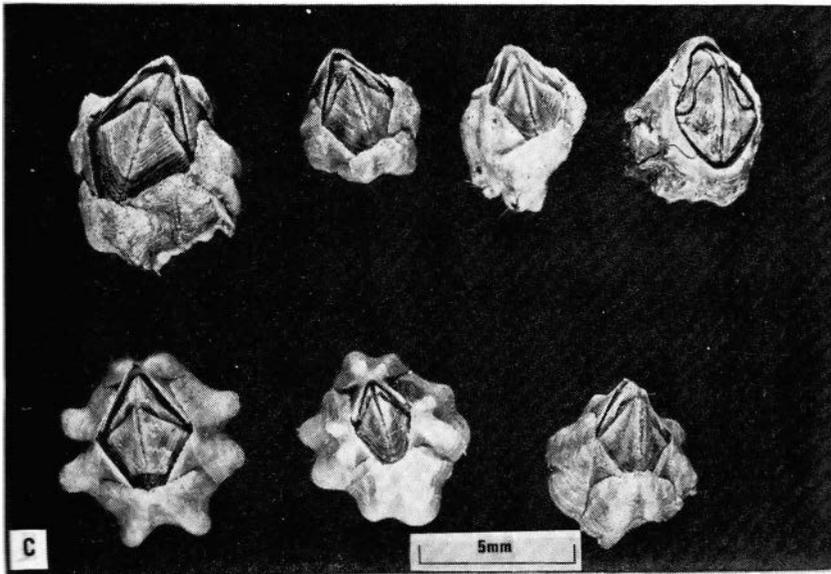
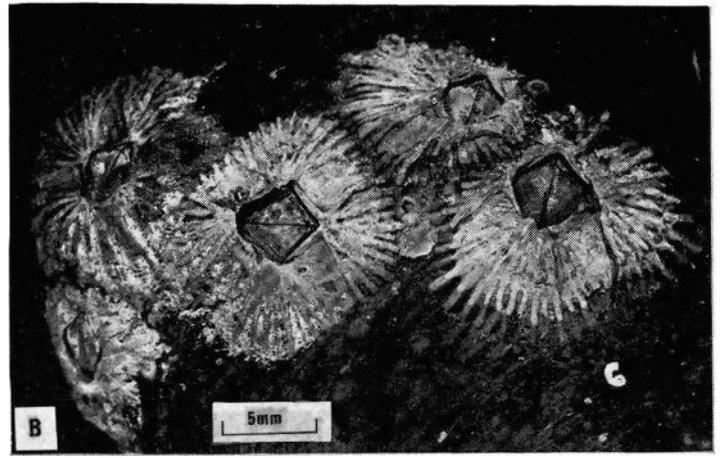
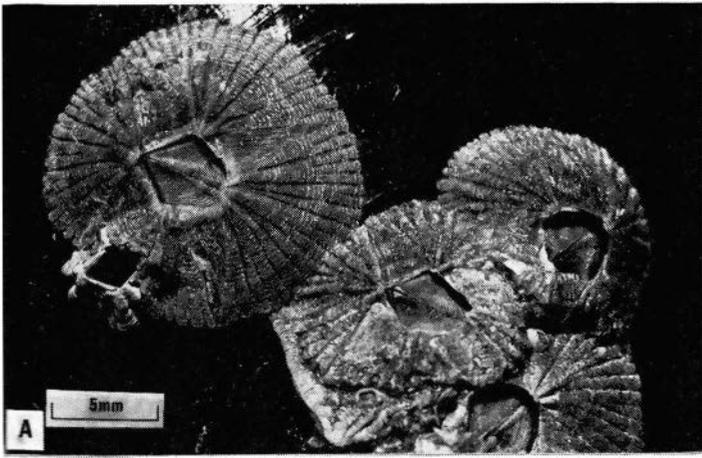


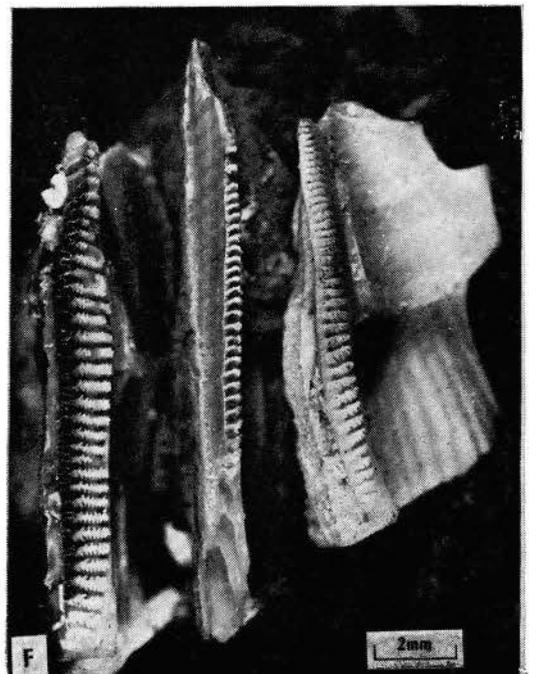
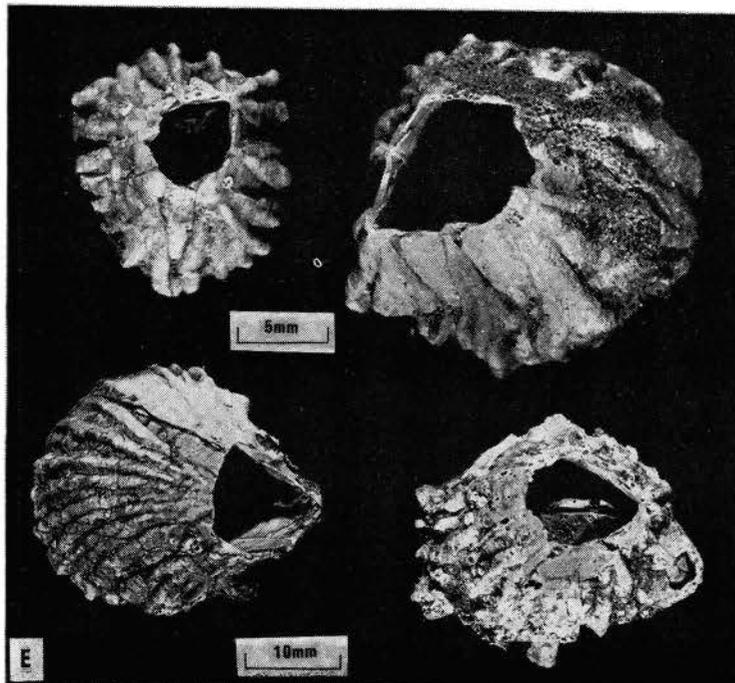
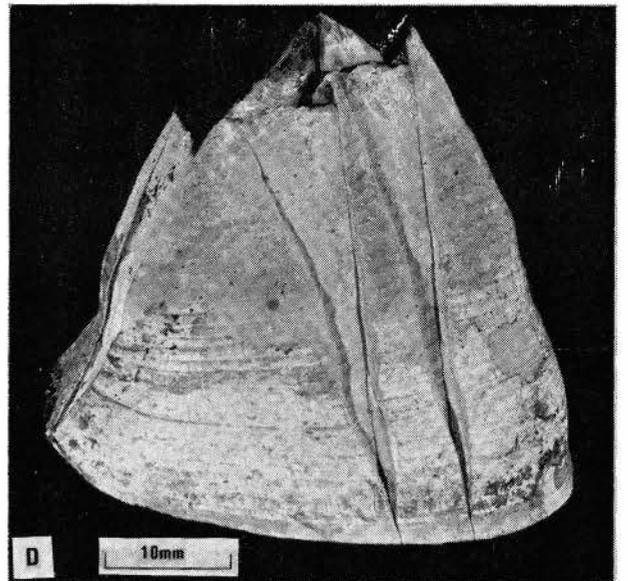
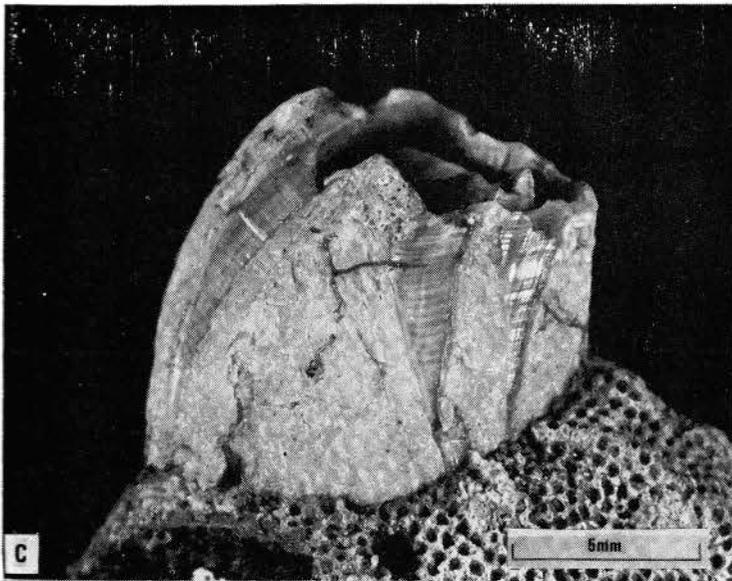
PLATE 12 — caption on page 154

Plate 13 (*facing*). Balanidae, *Balanus* (*Megabalanus*).

- A, B *Balanus tintinnabulum linzei* n.ssp., juvenile in A, medium sized specimen in B, the latter encrusted with *Epopella plicata* and *Tetraclitella purpurascens*.
- C, D *Balanus decorus*, small and large specimens respectively.
- E *Balanus campbelli*, range of specimens, 3 from Otago Peninsula, that on the bottom left from Auckland Is.
- F edges of the radii of the latera of (left to right), *B. tintinnabulum linzei*, *B. decorus*, and *B. campbelli*.

Plate 14 (*page 160*). Balanidae.

- A *Balanus amphitrite*, side (above) and apical views of two specimens.
- B *Balanus variegatus*, clustered.
- C *Balanus trigonus*, three different specimens.
- D *Coronula diadema* (Nat. Mus.).
- E *Coronula reginae* (Nat. Mus.).
- F *Stomatolepas elegans* (Nat. Mus.).



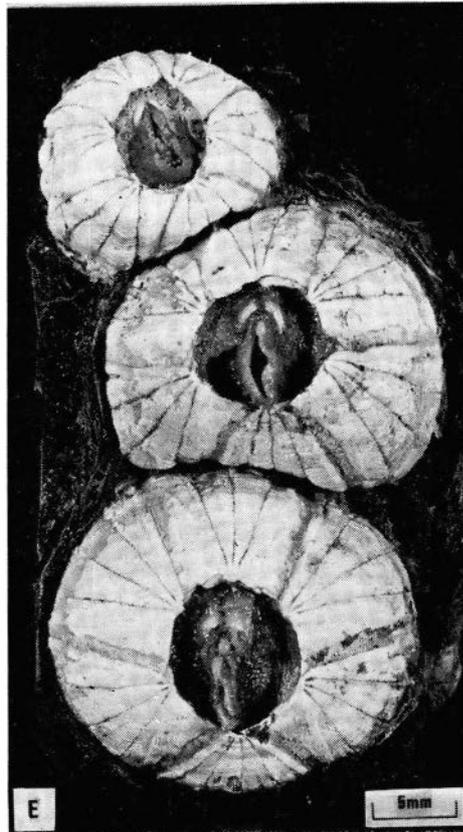
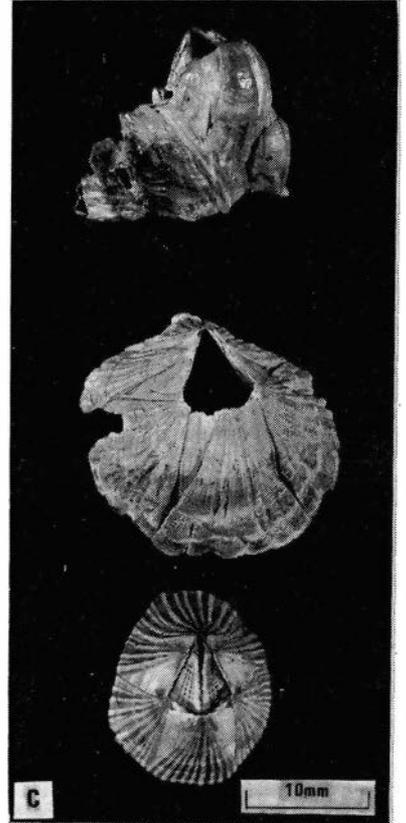


PLATE 14 — caption on page 158