Chapter 20

Cirripedia: *The Barnacles*

William A. Newman and Donald P. Abbott

The Cirripedia are crustaceans that as adults are usually sessile, attached to hard substrata or to other organisms. The carapace (mantle) completely envelops the body, and in most forms it secretes a calcareous shell—a trait that led some earlier zoologists to place barnacles in the phylum Mollusca. In adapting to life in the protected environment of the mantle cavity, the barnacle body has undergone an evolutionary reduction or loss of such features as the compound eyes and the abdomen and its appendages, but most adult cirripeds are still easily recognizable as crustaceans upon dissection. This is not the case with the more highly modified parasitic species, whose true cirriped nature is clear only from a study of their larvae.

The barnacles are an ancient group. There are published accounts of Silurian fossil remains, and barnacles have been discovered very recently in the Burgess Shale deposits in British Columbia (D. H. Collins, pers. comm.), beds that date from the middle Cambrian period of the Paleozoic. Barnacles remain a very successful group today, both in number of species—about 1,445 living species are known—and abundance. Charles Darwin, whose superb monographs on Cirripedia (1851, 1854) are still valuable references, once remarked that the present epoch may go down in the fossil record as the "Age of Barnacles," so abundant and widespread are their remains. Barnacle shells make up 50 percent of the carbonate sediments on the Florida shelf (Milliman, 1974), and, in many parts of the world, rock surfaces in the middle intertidal zone bear extensive carpets of barnacles (Stephenson & Stephenson, 1972). Those seeking recreation at the shore may regard barnacles as an unnecessarily abrasive nuisance, but to the biologist interested in ecology and evolution they are among the most intriguing of all invertebrates.

The subclass Cirripedia encompasses four orders: the Ascothoracica, Acrothoracica, Thoracica, and Rhizocephala. Representatives of each order occur in waters off California. The Thoracica, or true barnacles, are ecologically more important by virtue of their abundance and conspicuousness. Therefore only a few comments on the other orders will be made here, a fuller understanding being obtainable from the sources given in the bibliography.

Species of Thoracica occur in virtually all marine environments, from the highest reaches of the tides to the depths of the oceans. Some occur in estuaries, but none completes its life cycle in fresh water. Diversity is greatest in the tropical Indo-Pacific, less in the northeast Pacific, and far less in the North Atlantic (Cornwall, 1951, 1955; Henry, 1940, 1942; Ross, 1962; Zullo, 1966). Size is generally moderate, a few centimeters in greatest dimension, but some barnacles exceed 10 cm and others are but a few millimeters. All are permanently attached as adults. Most retain their calcareous shells throughout life and strain food (small plankton and edible detritus particles) from the water with biramous thoracic limbs called cirri. In some, the cirri are modified for grasping and rasping. Many of the Thoracica form intricate symbiotic associations with larger organisms such as whales, sea snakes, lobsters, medusae, corals, and sponges. A few have become nutritionally dependent on sharks, worms, or corals, which in earlier stages of their evolution they exploited simply for support or protection (Krüger, 1940; Newman,

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Zullo & Withers, 1969). Although most barnacles living symbiotically with other organisms do not occur in the intertidal zone, several species from California's offshore and subtidal waters have been included in this chapter because of their very great biological interest. Some of these forms are periodically washed ashore, and others may be brought in by divers.

The order Thoracica is divided into three suborders: the Lepadomorpha (stalked barnacles), the Verrucomorpha (asymmetrical sessile barnacles), and the Balanomorpha (symmetrical sessile barnacles). In the stalked barnacles the body is divided into a capitulum containing feeding appendages (cirri and mouthparts) and most other organs, and a peduncle or stalk by which the animal is attached to the substratum. The capitulum and sometimes the peduncle are armored with characteristic calcareous plates. The sessile barnacles differ from stalked barnacles mainly in having lost the peduncle, bringing what was the capitulum into direct contact with the substratum. In the process, certain of the capitular plates became articulated to form a rigid wall; others (anteriorly the scuta, posteriorly the terga) formed the movable lid or operculum. This arrangement is generally considered better adapted to shore environments, but radiation of sessile barnacles into a wide array of habitats indicates other advantages. Most Verrucomorpha are found in deep water, and one yet undescribed species is known from the west coast of North America. The Balanomorpha, commonly called acorn barnacles, constitute the majority of species found along the shore.

In general, the true barnacles are classified by the number, arrangement, and specialization of the plates and the details of the appendages (Darwin, 1851, 1854; Krüger, 1940; Newman & Ross, 1976; Newman, Zullo & Withers, 1969; Pilsbry, 1907, 1916). Most common forms are cross-fertilizing hermaphrodites, each barnacle reaching out and depositing sperm in the mantle cavity of another barnacle nearby and in turn, but not simultaneously, receiving sperm. However, there are species in which the hermaphrodites are accompanied by dwarf, complemental males and still others in which the sexes are separate, the female being accompanied by one or more dwarf males (Darwin, 1851, 1854).

Individual barnacles brood their fertilized eggs in the mantle cavity within the shell. Nauplius larvae (nauplii), bearing three pairs of appendages, hatch out, swim, feed, grow, undergo a series of molts, and then metamorphose into cyprid larvae. The cyprid has a bivalved shell and a body organization somewhat like that of the adult. It cannot feed, but swims using its six pairs of thoracic legs. Periodically it settles to the bottom and crawls about on its first antennae, testing the substratum for suitable places to attach. Settlement in a spot favorable for the rest of the life history is important for sessile animals, and the cyprid's "choice" of settlement site is influenced by a variety of physical and chemical stimuli (reviewed by Lewis, 1978). The cyprid larvae of most species are especially attracted by the presence of attached adults of their own kind. When ready to settle, the cyprids attach their heads to the substratum by their first antennae (which contain cement glands), and then undergo a second metamorphosis to become juvenile barnacles, essentially miniatures of the adults. Adults of some species live only a matter of weeks or a few months; in other species they may persist for several years to a decade or more.

The remaining three orders may be treated more briefly. The Ascothoracica contains forms ranging from semi-predaceous carnivores to obligate parasites on various corals and echinoderms (Newman, 1974; Wagin, 1946). It is an obscure group, but important in understanding the characteristics that distinguish cirripeds from other crustaceans as well as the generalized form from which the extraordinary radiation and diversity of the subclass has evolved. Ascothoracicans differ from all other adult cirripeds in having a bivalved shell, in using their thoracic limbs for swimming rather than feeding, and in being unable to attach permanently by their first antennae. A few rather specialized, wholly parasitic species are known from deeper waters off California (Fisher, 1911). None is included in this chapter.

The Acrothoracica are generally very small. They most commonly burrow in calcareous substrata and show their greatest diversity in coral seas (Tomlinson, 1969). These burrowing barnacles differ from the true barnacles (Thoracica) in having limbs situated at the end of the thorax rather than evenly distributed along it. Otherwise their biologies are similar. All species have separate sexes, the female being accompanied by a dwarf non-feeding male. One highly specialized species, *Trypetesa lateralis* (20.1), is known from California.

The Rhizocephala are highly modified parasites, primarily on decapod crustaceans. The adults are unrecognizable as crustaceans, much less cirripeds, but life histories include the planktonic nauplius and/or cyprid larval stages characteristic of the subclass

(Boschma, 1953; Smith, 1906; Yanagimachi, 1961). In general, a female cyprid attaches and injects its cellular content into the host, where it develops into a complex of tubular rhizoids (the interna). After the interna has become established, a reproductive body develops and appears as the externa, usually on or under the abdomen of the host after a molt. A male cyprid then attaches and injects its undifferentiated content into the virgin externa. This eventually differentiates into the male gametes that fertilize the next generation of eggs. The cycle starts over with the liberation of larvae. The presence of the parasite generally castrates the host and in males feminizes the form of certain appendages and the abdomen. Several rhizocephalans are known from California; accounts of three species (20.34–36) are included in this chapter.

Barnacles have been the subjects of a broad range of scientific research. The true barnacles have long caused problems as fouling organisms on ships and docks, where they add weight and resistance and can cause deterioration of submerged surfaces. Much study has therefore been devoted to understanding their habits and seeking methods to control their settling and growth. On the other hand, barnacles have their direct uses to man, as well. In Japan certain species are cultivated for fertilizer, and in countries like Chile, Spain, and Portugal, some species are prized as food. The ability of barnacle larvae to attach to wet surfaces has recently led to investigations of "barnacle cement" in dental research (anon., 1968; Manly, 1970; Walker, 1972).

Many barnacle species are used in basic biological research. Their reproductive relationships are of interest in studies of sexual mechanisms and determination (Gomez, 1975; Henry & McLaughlin, 1967; Landau, 1976; McLaughlin & Henry, 1972; Tomlinson, 1966; Yanagimachi, 1961). Organic acids have been found to stimulate mating behavior (Collier, Ray & Wilson, 1956), and proteinaceous substances in the shells of attached individuals encourage cyprid larvae to settle (Crisp & Meadows, 1963). Insect juvenile hormone and juvenile hormone mimics induce abnormal metamorphosis (Gomez et al., 1973; Ramenofsky, Faulkner & Ireland, 1974). Many species have very simple photoreceptors (Gwilliam, 1965); others have the largest single muscle fibers known (Hoyle & Smyth, 1963), and these are useful in physiological research (Hagiwara & Takahashi, 1967; Krebs & Schaten, 1976). Barnacles often figure prominently in ecological, biogeographical, and evolutionary studies, and in his work on cirripeds, before professing the theory of natural selection, Darwin (1851, 1854) formulated such principles as neoteny and specialization through simplification.

In terms of taxonomy and geographical distribution the barnacles are among the best-known marine invertebrates of the west coast. They thus contribute readily to the delineation of biogeographical provinces along the shore, providing a model probably applicable to most other benthic invertebrate groups as well. The figure on the facing page summarizes the distribution of those shore

Latitudinal ranges of benthic cirripeds of the Oregonian and Californian Provinces (from Newman, 1979). The 23 species shown are divided into four groups; see text.

Group I

1. *Semibalanus cariosus* (20.23)
2. *Chthamalus dalli* (see under 20.12)
3. *Balanus glandula* (20.24)
4. *Pollicipes polymerus* (20.11)
5. *Chthamalus fissus* (20.12)
6. *Tetraclita rubescens* (20.18)

Group II

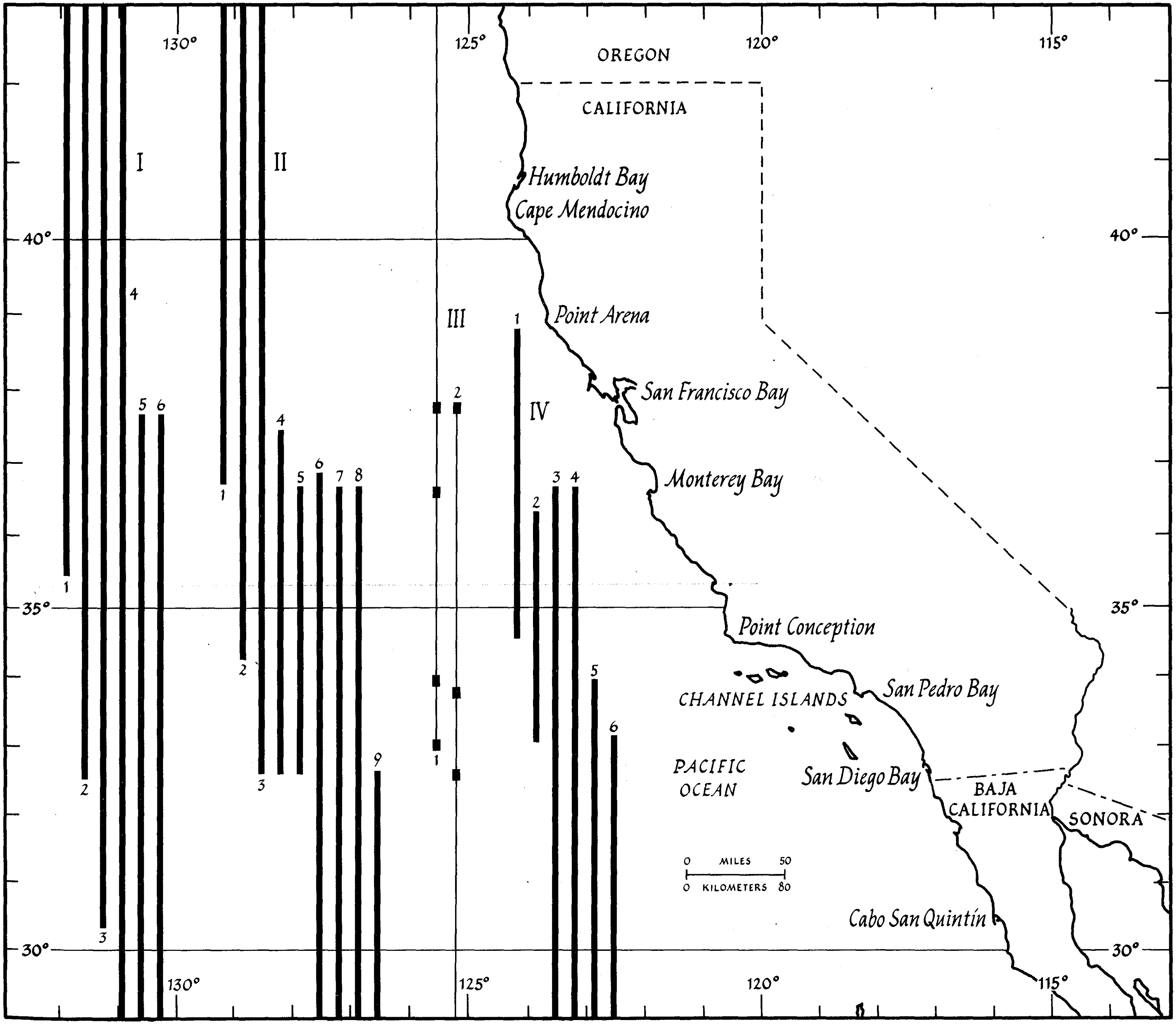
1. *Solidobalanus hesperius* (20.20)
2. *Balanus crenatus* (20.25)
3. *Balanus nubilus* (20.32)
4. *Balanus aquila* (20.31)
5. *Arcoscalpellum californicum* (20.10)
6. *Megabalanus californicus* (20.33)
7. *Balanus pacificus* (20.27)
8. *Balanus trigonus* (20.26)
9. *Balanus regalis* (20.30)

Group III

1. *Balanus improvisus* (20.29)
2. *Balanus amphitrite amphitrite* (20.28)

Group IV

1. *Trypetesa lateralis* (20.1)
2. *Armatobalanus nefrens* (20.19)
3. *Conopea galeata* (20.22)
4. *Octolasmis californiana* (20.3)
5. *Membranobalanus orcutti* (20.21)
6. *Oxynaspis rossi* (20.2)



OREGON
CALIFORNIA
Humboldt Bay
Cape Mendocino
Point Arena
San Francisco Bay
Monterey Bay
Point Conception
San Pedro Bay
CHANNEL ISLANDS
PACIFIC OCEAN
San Diego Bay
BAJA CALIFORNIA
SONORA
Cabo San Quintín
I
II
III
IV
130°
125°
120°
115°
40°
35°
30°
0 MILES 50
0 KILOMETERS 80

barnacles treated in this chapter that are attached to fixed substrata such as rocks and pilings, or to benthic organisms that move about little if at all (forms attached to such moving hosts as whales, turtles, or ships are omitted).

It is clear from the figure that most of the species encountered near Cape Mendocino in northern California are different from those found in the vicinity of San Diego, and they are usually designated as members of the Oregonian and Californian Provinces, respectively (see, for example, Newell, 1948; Valentine, 1966). The species of each province extend well to the north or south of the political boundaries of California. The region of overlap, the Californian Transition Zone, centering on Point Conception, contains a mixture of species that totals more than the number of species found immediately to the north or south. In addition, the Transition Zone contains a number of short-range endemic species.

There is a marked climatic difference between Oregonian and Californian Provinces, and the change in the Transition Zone is rather abrupt. Differences in ocean temperature are believed to play an important role in sustaining the position of biogeographical boundaries. This conclusion is borne out by the finding that high-latitude shallow-water species occur in deeper (therefore colder) water at the southern ends of their ranges, and by the discovery of cold-water species well to the south of their normal distributional ranges in isolated areas where upwelling of cold deep-ocean water occurs. The importance of temperature in sustaining the boundary is also shown by laboratory studies of thermal tolerances, the temperature optima for enzyme action, and the role of temperature regimes in regulating reproductive cycles. Moreover, studies of paleoecology (e.g., Addicott, 1966) demonstrate that the boundary shifted its latitudinal position with rapid climatic changes during the Pleistocene.

The benthic cirripeds shown in the figure have been divided into four ecological groups: (I) intertidal species (those species native to the coast that are largely restricted to the intertidal zone), (II) shallow-water species (species that, though sometimes found in the low intertidal zone, occur mainly at subtidal depths on the continental shelf), (III) introduced bay and estuarine species (species occurring in both intertidal and shallow subtidal waters), and (IV) obligate commensal species (forms living on or in other living organisms that are themselves sessile or relatively sedentary).

Group I contains the only highly eurytopic form, *Pollicipes polymerus*, which ranges through both provinces. All other species in Groups I–IV terminate one end of their latitudinal range in, or reside wholly in, the Transition Zone.

All Group I species are represented by aggregations of individuals that are community dominants. *Chthamalus* generally ranges higher into the intertidal zone than *Balanus* and *Tetraclita*. The northern forms, *Chthamalus dalli* and *Semibalanus cariosus*, are largely replaced in the south by *C. fissus* and *Tetraclita rubescens*, respectively. *Balanus glandula*, occurring for the most part between the northern and southern species in vertical distribution, ranges farther south than *S. cariosus* and is eventually replaced in part by *B. regalis*. As adults, in various species combinations, these species compete for space and food along both horizontal and vertical gradients.

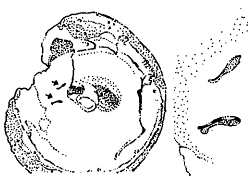
Group II, from continental-shelf waters, follows a similar pattern, the northern *Solidobalanus hesperius*, *B. crenatus*, and *B. nubilus* being replaced by *Megabalanus californicus*, *B. pacificus*, and *B. trigonus* in the south. All these species, with the possible exception of *B. nubilus* and *B. crenatus* in the northern parts of their ranges, are relatively opportunistic. That is, they neither dominate, nor become long-standing members of, the subtidal community.

Two of the four short-range endemic species of the Transition Zone, *B. aquila* and *Arcoscalpellum californicum*, are encountered in this group. The former occurs with *B. nubilus* in the northern part of its range, but both undergo submergence south of Point Conception, where they are replaced by a close relative of *B. aquila*, *B. regalis*. Being at the ends of their respective ranges, apparently neither *B. nubilus* nor *B. regalis* is capable of fully exploiting the available resources, and this has left space for *B. aquila*. The situation for *Arcoscalpellum* appears quite different. The genus occurs primarily in deep water, but *A. californicum* ranges up into shallower water (less than 30 m) in the Transition Zone.

Group III contains two bay and estuarine species. Both have been introduced to California, probably by ships or along with transplanted oysters. *Balanus improvisus*, from the North Atlantic, ranges into the Transition Zone from the north. *B. amphitrite amphitrite*, probably from the Indo-West Pacific, does likewise but from the south.

Members of Group IV, being obligate commensals, do not interact with other barnacle species, at least in the adult stage. They receive varying degrees of protection by their hosts, and are usually limited by host distribution. All are warm-temperate/subtropical derivatives that have cognates in other regions. All are the sole representatives of their groups in the eastern Pacific. Two of the species, *Armatobalanus nefrens* and *Trypetesa lateralis*, are short-range endemics. *A. nefrens* occurs on hydrocorals, sometimes *Errinopora pourtalesii* but more commonly *Allopora californica*, which is itself a short-range endemic. *Trypetesa*, an acrothoracican, burrows in the interior of gastropod shells inhabited by hermit crabs. Although hermit crabs range widely in temperate and tropical regions, and into deep water, *T. lateralis* is found only in the northern part of the Transition Zone.

Thus it can be seen that the Californian Transition Zone is rich in barnacle species, owing to the overlap of the Oregonian and Californian Provinces and to the presence of the short-range endemics. This is the case with the mollusks and undoubtedly many other invertebrates. The disharmony between overlapping provincial communities caused by the steep latitudinal temperature gradient in the vicinity of Point Conception apparently results in incomplete utilization of the resources upon which the short-range endemics depend (Newman, 1979). Identifying these resources and how they are shared by so many species offers a whole area of interesting research.



Phylum Arthropoda / Class Crustacea / Subclass Cirripedia
Order Acrothoracica / Suborder Apygophora / Family Trypetesidae

20.1 **Trypetesa lateralis** Tomlinson, 1953

Common in some localities, burrowed into shells of gastropods (particularly *Tegula* species) occupied by hermit crabs, middle and low intertidal zones; Point Arena (Mendocino Co.) to Point Conception (Santa Barbara Co.); the only member of the order known from north of Mexico on the Pacific coast.

Females to 5 mm long, distinguished from all other California cirripeds by habitat, and in having but three pairs of uniramous cirri arranged on posterior end of thorax; males microscopic.

The females of this remarkable species form slitlike burrows parallel to the shell surface in shells of gastropods *Tegula brunnea* (13.31) and *T. funebralis* (13.32), and occasionally *Calliostoma costatum* and *Acanthina spirata* (13.81). They are best seen by breaking the tops (apices) off shells occupied by hermit crabs (*Pagurus samuelis, P. hirsutiusculus, P. hemphilli*, and *P. granosimanus*, 24.10–24.13) and removing the crabs. If the shells are then illuminated by a bright spot of light from below (aperture side), and the columella and adjacent areas on the "floor" of the whorls are viewed from above (apical side), the burrows appear as translucent areas in the wall of the shell, often colored yellow, orange, or red.

The body of the female barnacle is partly encased in a muscular mantle provided externally with chitinous teeth that are renewed at each molt. Shell boring involves the rasping action of the teeth and probably chemical action as well; in a related species, *T. nassaroides*, the enzyme carbonic anhydrase reaches high levels in the body during periods of boring activity. The cirri of the female are greatly reduced in *T. lateralis*, but appear to be involved in feeding as in the more familiar acorn barnacles. They are not constantly active, but when in motion they beat regularly, about once every 2 seconds at 17°C, accompanied by regular pulsations of the mantle. These actions create a flow of water in and out of the mantle cavity and past the mouth, a circulation probably involved in both feeding and respiration. The food is uncertain, but probably consists of minute organic particles dropped by the hermit crab in its feeding, or brought in with currents created by movements of the crab within its shell. The gut of the female barnacle is remarkable in lacking both intestine and anus; the muscular esophagus opens into a stomach that is a large, lobulated, blind sac. Experiments show that elimination of undigested particles is probably by regurgitation.

On reaching adult size, females form an external mantle flap, a tongue of tissue provided with rasping teeth, that bores a hole through to the outside of the gastropod shell, leaving the burrow open to the sea on both inner and outer surfaces of the host shell. Once the new hole is completed, water is pumped in a jerky flow from outside to inside the shell, the flow reversing only if the outer hole becomes clogged. The flow provides males and embryos with fresh seawater.

The males are tiny, non-feeding dwarfs, averaging about 0.4 mm in greatest length. They are smaller in size than even the cyprid larvae from which they develop, and lack both gut and feeding appendages. Their most prominent organs are a single testis and seminal vesicle, a nauplius eye, and paired first antennae. In some species of *Trypetesa* the mature males develop a penis much longer than the body, but this is lacking in *T. lateralis*. The sperm are threadlike, and become motile after release into the seawater filling the mantle cavity. They need move only a millimeter or two to reach the eggs. One to several males may be present with a given female, either partly embedded in the mantle of the female or attached by their first antennae to the wall of the cavity near the female's external mantle flap.

The females discharge their eggs into the mantle cavity, where they are brooded. The eggs are oval, averaging about 0.25 mm in greatest length; at least 180 have been observed in a single brood. They develop past the nauplius stage within the egg membranes, hatching as non-feeding, weak-swimming cyprid larvae about 0.5 mm long. The lack of free nauplius stages, together with a tendency of hermit crabs to remain within a localized area, may account for the rather patchy distribution of *T. lateralis* along the shore in areas where it is known to occur. The greatest settlement of the larvae is in the winter (November through January), with a smaller peak in June. The life span, which is not known, may depend on the durability of the shell; the animals have been kept in seawater in a cold box for more than a year without noticeable growth.

The genus *Trypetesa* is a small one, including two known species from the North Atlantic, one from California, one from Japan, and one from Madagascar. The species are generally endemic to a limited geographical area that marks the transition between major biogeographical provinces. It is curious that apparently suitable gastropod shells, inhabited by hermit crabs and ranging from north to south and into deep water, are not inhabited by these barnacles.

For *T. lateralis*, see Tomlinson (1953, 1955, 1960, 1969a,b). For related species, see Darwin (1854), Tomlinson (1969a,b), Turquier (1971), Utinomi (1964), and White (1970).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Lepadomorpha / Family Oxynaspididae

20.2 **Oxynaspis rossi** Newman, 1972

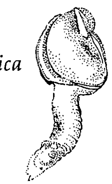
On black coral in deep water; recorded from 183 m depth off Santa Catalina Island (Channel Islands) and south and from 55 m depth off Baja California (22°55′N).

Small, to 2 cm in length; distantly related to *Lepas* (e.g., 20.4–6) and *Octolasmis* (e.g., 20.3), but differing from both in having the growth center (umbo) of the carina subcentral rather than basal.

With the exception of one species that lives on a sponge, all members of this genus live on black or horny corals (Cnidaria: Anthozoa: Antipatharia). The group to which *Oxynaspis* belongs is an ancient one, considered by some workers to be transitional between lepadid and scalpellid barnacles. Because of their deep-water habitat, nothing is known of their biology.

See Newman (1972).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Lepadomorpha / Family Poecilasmatidae



20.3 **Octolasmis californiana** Newman, 1960

In gill chambers of large decapod crustaceans such as *Panulirus, Loxorhynchus grandis* (25.10), *Pugettia producta* (25.4), and *Cancer* spp. (e.g., *C. antennarius*, 25.16, and *C. productus*, 25.22), low intertidal zone and continental shelf; Monterey Co. to Panama.

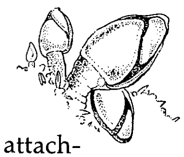
Small, to 1.5 cm in length; similar to lepadids in having five capitular plates, these reduced in extent, the scutum with two slender arms; differing from lepadids in having uniarticulate caudal appendages.

No other representatives of the diverse tropical family to which this species belongs are known from the northeastern Pacific. *Octolasmis* feeds on plankton carried in the respiratory current of the host. The barnacles are shed along with the exoskeleton of the host when the host molts. Nothing else is known about the biology of the animal.

A closely related east coast species occurs on the gills of blue crabs. The particular portion of the gills that becomes infected is related to the distribution and effectiveness of the host's gill-cleaning mechanisms. The reason *Octolasmis* does not settle on caridean and anomuran crustaceans is probably that these animals have more efficient methods of gill cleaning.

See Newman (1960). For related species, see Bowers (1968) and Walker (1974, on east coast species).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Lepadomorpha / Family Lepadidae



20.4 **Lepas (Lepas) anatifera** Linnaeus, 1758
Goose Barnacle

Common, oceanic, gregarious; numerous individuals attaching in clusters to such floating objects as logs, bottles, glass fishing floats, and shells of the pelagic snail *Janthina*; not usually seen washed ashore south of Point Conception (Santa Barbara Co.); cosmopolitan.

Length to about 15 cm; species distinguished from the smaller *L.* (*L.*) *pacifica* (20.5) in having a thicker, opaque scutum and two filament-like appendages at the base of each first cirrus; species determination generally requires dissection.

All lepadids, or goose barnacles, differ from scalpellids in having no more than five capitular plates and a naked peduncle. *Lepas* (*Lepas*) is distinguished from the subgenus *Dosima* by its heavier valves and in not producing a float of its own.

The many fine setae on the cirri of species in the subgenus *Lepas* permit the capture of tiny organisms and particles. Relatively large planktonic organisms can also be captured and eaten, and material too bulky to be completely devoured by one individual may be relinquished to another. The diet includes young fishes, and large pelagic hydrozoan cnidarians such as *Physalia*, *Porpita*, and *Velella* (3.18). *Lepas* attached to the pelagic gastropod *Janthina* and dependent on it for flotation reach further and hold prey more tightly than *Lepas* attached to other substrata. Such *Lepas* benefit their hosts by passing on to them surplus or partially consumed prey; thus the association with *Janthina* appears to be mutualistic.

Lepas (*Lepas*) *anatifera* individuals have been observed to settle gregariously on the less brightly illuminated portions of floating survey beacons, and they prefer the rougher surfaces. When the barnacles are closely crowded, growth of the capitulum appears to be retarded, whereas that of the peduncle is accelerated. Ovigerous lamellae commonly appear in individuals about 23 mm in capitular length, several weeks after settling. Nauplius larvae appear a week or so thereafter, from individuals with 27 mm capitula.

Adults survive and breed in the laboratory if fed an appropriate diet and maintained in running seawater. After copulation, the individual acting as the female sheds ova into the mantle cavity by contraction of the peduncle. Ovigerous lamellae are attached to ovigerous frenae (membranous extensions of the interior of the mantle) whereas in *Pollicipes* (e.g., 20.11) they are free within the mantle cavity. Embryos develop normally at 19–25°C, and gravid females refrain from molting until during or shortly after the release of nauplii. Molting rate increases with temperature between 10 and 25°C, but falls with further rise in temperature.

See Barnes & Klepal (1971), Bieri (1966), Bigelow (1902), Boëtius (1952), Burnett (1975), Crisp & Southward (1961), Gwilliam (1963), Howard & Scott (1959), E. Jones (1968), Lacombe & Liguori (1969), Mahmoud (1959), Patel (1959), Pilsbry (1907), and Skerman (1958a,b).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Lepadomorpha / Family Lepadidae

20.5 **Lepas (Lepas) pacifica** Henry, 1940

Oceanic, in clusters on floating objects such as *Lepas* (*Dosima*) *fascicularis* (20.6), *Velella velella* (3.18), seaweeds, wood, feathers, cardboard; Alaska to San Diego and south.

Length to about 2.5 cm; similar to *L.* (*L.*) *anatifera* (20.4) but distinguished from other species of the subgenus *Lepas* in California by small size, thin shell with underlying bluish tissues visible through scutum, and only a single short filamentary appendage at base of each first cirrus.

This species, along with *L.* (*D.*) *fascicularis*, is commonly stranded by seasonal onshore winds in southern California. This has provided an opportunity to observe large numbers of the two species and to analyze their settling preferences. In general *L. pacifica* is more often found attached to tar and less often to floating feathers, eelgrass blades, and bits of intertidal brown algae. Occasionally it is found growing on the back of the northern elephant seal, *Mirounga angustirostris*. Curiously, the two barnacle species are found attached in about equal numbers to debris of terrestrial origin.

The circulatory system of *L.* (*L.*) *pacifica*, like that of the other lepadids (*L.* (*D.*) *fascicularis*, *L.* (*L.*) *anatifera* (20.4), and *Conchoderma virgatum*, 20.7), is relatively simple and primitive compared to that of more advanced barnacles, such as *Pollicipes* (e.g., 20.11) and *Megabalanus* (e.g., 20.33). The rostral vessel has been interpreted as a vestige of the heart, and the rostral sinus equivalent to the pericardial sinus of ordinary crustaceans. Curiously, the smaller lepadid species, *L.* (*L.*) *pacifica* and *L.* (*D.*) *fascicularis*, have larger blood vessels in proportion to body size than do the larger species *L.* (*L.*) *anatifera* and *Conchoderma virgatum*. The ladderlike nervous system of *Lepas* is also relatively generalized. In higher forms ganglia coalesce into a large neural mass.

Experiments have shown that *Lepas* can live, grow, and reproduce in certain situations along the shore, but only if protected from predation. Apparently this ancient stock has found its last refuge in the open sea.

Little is known of the natural history of this species.

See Baldridge (1977), Burnett (1975), Cheng & Lewin (1976), Cornwall (1953), and Henry (1940).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Lepadomorpha / Family Lepadidae

20.6 **Lepas (Dosima) fascicularis** Ellis & Solander, 1786

Common, oceanic; cypris larvae settling on small objects, commonly feathers; developing juveniles and adults forming gas-filled floats of their own; cosmopolitan.

To 5–6 cm in length; distinguished from species of *Lepas* (*Lepas*) in having thin, papery calcareous plates, in not being as markedly laterally flattened, and in secreting a float from the base of the peduncle rather than depending on floating objects as adults.

Although adults of the subgenera *Lepas* and *Dosima* use different methods for staying afloat, their sizes are generally comparable, and one might expect them to share many of the same resources. However, even though members of both subgenera can handle larger prey, in *Lepas* (*Lepas*) species the cirri are equipped for straining out tiny particles, whereas those in *L.* (*Dosima*) species are shorter and stouter and are equipped with spinelike setae unsuited for fine filtering. The stomachs of *L.* (*Dosima*) species are commonly packed with copepods, whose pigment is the source of the carotenoprotein providing the barnacle's blue color.

The abundance of *Lepas* (*Lepas*) is in good part limited by the availability of floating objects (feathers, wood, seaweed, pumice, coconuts, tar, etc.). *Lepas* (*Dosima*) has partially circumvented this limitation. Initially it attaches to a small floating object and then, as the barnacle grows further, it forms a gas-filled float of its own. If the cyprid formed a float during metamorphosis, the species could become completely independent of floating objects. Although this evolutionary step has not been made, it would appear to be an easy one, because the cement by which the cyprid attaches itself to an object, and the substance forming the float, are believed to come from the same glands.

See Ankel (1962), Bainbridge & Roskell (1966), Ball (1944), Barnes & Klepal (1971), Boëtius (1952), Cheng & Lewin (1976), Darwin (1851), Fox & Crozier (1967), Fox, Smith & Wolfson (1967), Knudsen (1963), and Thorner & Ankel (1966).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Lepadomorpha / Family Lepadidae

20.7 **Conchoderma virgatum** (Spengler, 1790)

Oceanic, on a wide variety of objects including ships, buoys, telegraph cables, seaweeds, decapod crustaceans, fishes, marine reptiles, and whales; cosmopolitan.

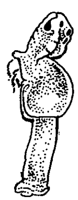
To about 5 cm in length, with five capitular plates much reduced in extent; capitulum and peduncle leathery, usually with several purplish-brown, longitudinal stripes; species differing from *C. auritum* (20.8) in having five rather than two plates, and in lacking fleshy perforate lobes at top of capitulum.

This is an opportunistic species that settles on any hard substratum away from the shore. It attaches to the parasitic copepod *Pennella* that infects flying fish, and to the hard surfaces of swimming crabs and turtles. The occurrence of *C. virgatum* on fishes is unusual, but it has been reported on species of *Mola*, *Gymnothorax*, *Tylosurus*, *Diodon*, and *Remora*, the *Remora* having been removed from the blue shark *Prionace glauca*. A close relative of *Conchoderma virgatum*, *C. auritum*, occurs on whales, and a distant relative, *Anelasma*, occurs on certain sharks, but these barnacles are obligate commensals; the occurence of *C. virgatum* on fishes appears to be largely fortuitous.

Conchoderma virgatum grows rapidly. Specimens became mature in less than 17 days after settling on a buoy at approximately 30°S off Australia; the largest animals had capitular lengths approaching 20 mm and contained ovigerous lamellae. During Darwin's visit to the Galápagos Islands, *C. virgatum* seriously fouled the *Beagle* in 33 days. In another case, recorded here with some skepticism, *Conchoderma* individuals were reported to reach a total length of 13–19 mm on instruments immersed for 2.5 days at 50–150 m depth in cold waters off Greenland. On the same occasion, *Balanus amphitrite* was reported to have reached a diameter of 13 mm.

See Clarke (1966), Darwin (1851), E. Jones, Rothschild & Shomura (1968), MacIntyre (1966), and Roskell (1969).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Lepadomorpha / Family Lepadidae



20.8 **Conchoderma auritum** (Linnaeus, 1758)
Rabbit-Eared Barnacle

Attached to the sessile barnacle *Coronula* (e.g., 20.15) on baleen whales, or to teeth of the sperm whale or other toothed cetaceans; cosmopolitan.

Length to 12 cm; species differing from *C. virgatum* (20.7) in having two fleshy tubular structures projecting from top of capitulum, connecting mantle cavity with exterior, and in having two rather than five calcareous plates.

This species is wholly adapted to living on cetaceans, although it occasionally settles on other organisms and sometimes even on the hulls of submarines. Apparently unable to attach directly to whale skin, it requires a hard surface such as a barnacle or the whale's teeth, where these are continuously exposed due to lip or jaw damage. Both *Conchoderma auritum* and the sessile whale barnacle *Coronula diadema*, to which it most commonly attaches, orient themselves so the cirral net faces in the direction the whale swims, taking full advantage of the water flow. Water bearing food enters the anterior slit and strained water exits by way of the paired tubes, or "ears." As much as 98 percent of the humpback whale population carries some *Conchoderma*. The incidence is higher in female whales, presumably owing to their longer sojourns from high latitudes into warm waters.

Nothing is known of the biology of *C. auritum*, although individuals are apparently reproductively inactive when the hosts migrate into higher latitudes.

See Barnes & Klepal (1971), Clarke (1966), Cornwall (1924), Darwin (1851), MacIntyre (1966), and Petriconi (1969).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Lepadomorpha / Family Lepadidae

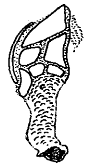
20.9 **Alepas pacifica** Pilsbry, 1907

Oceanic, attached to the bells of large jellyfishes; occasionally washed inshore; Indian, Pacific, and South Atlantic Oceans.

To about 6 cm in length; species distinguished from other lepadids in having the number of plates reduced, from a normal complement of five, to a pair of Y-shaped scuta; capitulum globular; entire animal translucent.

Aside from its habit of attaching to jelly fishes, and its occurrence in the few widely distributed localities where it has been reported, nothing is known about this species. As in *Lepas* (*Dosima*), the cirri are short and spiny rather than long and setose, but how this characteristic relates to its food habits is not understood.

See Pilsbry (1907) and Utinomi (1958).



Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Lepadomorpha / Family Scalpellidae

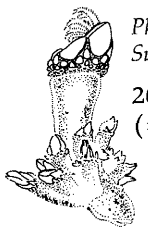
20.10 **Arcoscalpellum californicum** (Pilsbry, 1907)
(=Scalpellum)

On rocks and other organisms at subtidal depths of 18–400 m; in shallow water ranging from Monterey (but usually south of Point Conception, Santa Barbara Co.) to San Diego; in deep water ranging from approximately Point Arena (Mendocino Co.) to Bahía Magdalena (Baja California).

Length to 4 cm; like *Pollicipes polymerus* (20.11) in having capitulum covered with more than five plates, but with a single whorl of basal plates and a peduncle armored by conspicuous scales.

This species appears to be synonymous with *A. osseum* (Pilsbry), which differs mainly in being more heavily calcified. Nothing is known of *A. californicum* other than its geographical distribution. It appears to be hermaphroditic. In related deep-water forms the hermaphrodite may be accompanied by complemental males; or the sexes may be separate, with large females accompanied by dwarf males.

See Cornwall (1951) and Pilsbry (1907).



Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Lepadomorpha / Family Scalpellidae

20.11 **Pollicipes polymerus** Sowerby, 1833
(=Mitella polymerus) Leaf Barnacle

Common, usually in clusters but also mixed with *Mytilus californianus* (15.9), middle intertidal zone on wave-swept rocky shores; British Columbia south at least to Punta Abreojos (Baja California); replaced along western Mexico by *P. elegans*.

To 8 cm in length; capitulum covered with more than five plates and surrounded basally by several whorls of imbricate scales; peduncle tough, roughened by inconspicuous calcareous spicules.

This species feeds by directing its cirral net into currents, usually the backwash of waves. It captures mainly large particles of detritus, but crustaceans up to 1 cm long are also commonly ingested.

The barnacle's body temperature is frequently lower in air than would be expected from the heat load, and evaporation from the peduncle is responsible, a loss of 35–40 percent of the body water being tolerated during periods of exposure of less than 9 hours. The species is an osmoconformer: the salinity of the body fluids increases in sunshine and decreases in rain, and the urine is isosmotic with the blood. Blood pressure averages 250 cm of water, remarkably high for a crustacean. *Pollicipes* has a four-part circulatory system and a blood pump formed by three pairs of skeletal muscles, which are apparently unstriated.

Reproduction, at least in northern California and Washington, occurs in the summer. At Monterey, the seminal vesicles begin to enlarge with spring warming (above 12°C) and decrease in size in the fall, bracketing the occurrence of embryos. The fertilized eggs, expelled on either side of the thorax, adhere to one another and form a pair of flattened disks (ovigerous lamellae). The lamellae are brooded in the mantle cavity within the shell, one on each side. The time from fertilization to the release of swimming nauplius larvae is about 30 days. An individual may produce three to seven broods a year, with 100,000–240,000 larvae per brood, depending on age and size. Only early development is especially sensitive to temperature changes. Growth is slow in attached juvenile barnacles over 10 mm in length. It has been inferred that maturity is reached in 5 years and that fully grown individuals may be 20 years old.

This is a hermaphroditic species, but cross fertilization is thought to be the rule, since isolated individuals have not been found to contain embryos.

Although it is not known to foul ships, the leaf barnacle has been reported on a humpback whale, associated with *Conchoderma* (e.g., 20.8) attached to *Coronula* (e.g., 20.15), and it occasionally becomes established in large numbers in the laboratory seawater system at Scripps Institution of Oceanography at La Jolla (San Diego Co.). The closely related European species, *Pollicipes pollicipes*, is cooked and served as a delicacy in

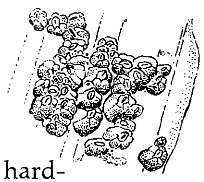
Portugal and Spain, but it has long been in short supply. In recent years *P. polymerus* has been exported from British Columbia to these countries. Gibbons (1964) pronounces it moderately good eating, and provides recipes.

See Barnes (1959, 1960), Barnes & Barnes (1959a), Barnes & Gonor (1958a,b), Barnes & Klepal (1971), Barnes & Reese (1959, 1960), Burnett (1972), Cornwall (1936, 1951, 1953), Darwin (1851), Dayton (1971), Dudley (1973), H. Fyhn, Petersen & Johansen (1972, 1973), Gwilliam (1963), Hilgard (1960), Holter (1969), Howard & Scott (1959), Lewis (1975a,b, 1977), Lewis, Chia & Schroeder (1973), Paine (1974, 1979), Petersen, Fyhn & Johansen (1974), Rice (1930), and Seapy & Littler (1978).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Balanomorpha / Superfamily Chthamaloidea / Family Chthamalidae

Chthamalus dalli Pilsbry, 1916

20.12 **Chthamalus fissus** Darwin, 1854
(=C. microtretus Cornwall)



Chthamalus dalli: common on rocks, pier pilings, and hard-shelled organisms, high and upper middle intertidal zones, Alaska to San Diego; northern Japan. *C. fissus*: common in similar habitats; San Francisco to Baja California.

Both species small, to 8 mm in diameter, externally similar; wall of shell with both end plates overlapped by adjacent plates (thus differing from balanids, in which one end plate, the rostrum, overlaps adjacent plates).

Reliable identification of these species usually requires removal of the scutal plates and examination of their inner surfaces under a good hand lens. The two scuta are triangular, with their apices meeting at the peak of the operculum. The lateral scutal depressor muscles attach near the basal angles of the scuta laterally. In *C. dalli* the muscle attachment scar bears strong ridges or crests, whereas in *C. fissus* it is a smooth-walled depression. Another character separating the species is the nature of the setae on the ends of the second cirri; under microscopic examination the setae of *C. dalli* appear finely bipectinate, but those of *C. fissus* are coarsely bipectinate and have a pair of basal pectinations enlarged as guards. Specimens of *C. fissus* with a narrow, slitlike orifice were formerly called *C. microtretus.*

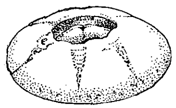
Chthamalus individuals can occupy higher intertidal situations than any other acorn barnacles, spending considerably more than half their lives out of water. Some species occur where they are only wetted by splash. On California shores, *Balanus glandula* (20.24) nearly equals *Chthamalus* in resistance to desiccation. Where both *Chthamalus* and *B. glandula* occur, the latter dominates, since a growing shell of *Balanus* pushes adjacent *Chthamalus* from the rocks. However, *Balanus* is preferred over *Chthamalus* by such predators as the gastropod *Nucella emarginata* (13.83) and the starfish *Pisaster ochraceus* (8.13), and this selective predation on *Balanus* apparently makes more space available for *Chthamalus.* Under optimum conditions, densities of 70,000 per m^2 are found.

Chthamalus is frequently parasitized by the epicaridean isopod *Cryptothir* (=*Hemioniscus*) *balani*; infected barnacles are infertile.

From field sampling, it has been inferred that both *C. dalli* and *C. fissus* that are separated by more than 5 cm from their nearest neighbor fertilize themselves, but cross-fertilization normally occurs. *C. fissus* in central California produces about 16 small broods from spring through fall, with reduced brooding activity in the winter. Brood production is limited by food availability, and depending on the size of the parent, 200–3,000 nauplius larvae are released per brood. Settlement occurs erratically year-round at all tide levels. Mortality in newly settled *C. fissus* on rock surfaces is apparently little affected by the grazing of limpets, owing to the small size of the cyprids and their ability to settle in tiny cracks and minute depressions. *C. fissus* individuals in central California reach reproductive maturity when 2–3 mm in diameter and about 2 months old. They may live to about 3 years, with better survival rate in the high than the low intertidal zone.

Adult *Chthamalus* feed by extending their cirri while splash or wave wash flows over them and retracting the cirri and closing the operculum when the water has flowed away. Although the activity of cirri has not been studied in local species, studies on other forms show it to be temperature-dependent, and its rate apparently differs among local races.

See Augenfeld (1967), Barnes & Barnes (1958), Barnes & Gonor (1958a), Barnes & Klepal (1971), Connell (1970), Cornwall (1953, 1955a), Dayton (1971), Henry (1960), Hines (1976, 1978, 1979), Klepal & Barnes (1975a,b), Newman & Ross (1976), Paine (1974), Pilsbry (1916), Rice (1930), Ross (1962), Seapy & Littler (1978), and Stallcup (1953). For related species, see Monterosso (1933) and Southward (1962, 1975).



Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Balanomorpha / Superfamily Coronuloidea / Family Coronulidae

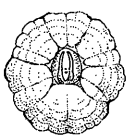
20.13 **Chelonibia testudinaria** (Linnaeus, 1758)
Turtle Barnacle

On shells of sea turtles; uncommon in southern California, common in all warm seas including eastern Pacific.

To 80 mm in diameter; wall smooth, low, dome-shaped, broadly attaching to turtle shell, supported internally by numerous septal buttresses.

There is a great diversity of barnacles on turtles. *Chelonibia* is the largest and least specialized genus. Superficially, the wall appears to be made up of six plates, but close inspection reveals that one, the rostrum, is formed of three fused together. The "tripartite" rostrum of *Chelonibia* is a vestige of the eight-plated ancestry of all balanomorphs.

See Darwin (1854), Newman & Ross (1976), Ross & Newman (1967), and Zullo (1966).



Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Balanomorpha / Superfamily Coronuloidea / Family Coronulidae

20.14 **Platylepas hexastylos** (Fabricius, 1798)

Uncommon on turtles in southern California; commoner elsewhere attached to skin of turtles, of mammals such as the American manatee and the dugong, and of gar fish (*Lepidosteus*); cosmopolitan in warm seas.

To 18 mm in diameter; species superficially resembling *Chelonibia testudinaria* (20.13) but differing markedly in structure of wall, in which six internal buttresses extend down to the membranous basis.

Even though this species is common on turtles, nothing is known about its biology.

See Darwin (1854), Newman & Ross (1976), Pilsbry (1916), and Utinomi (1970).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Balanomorpha / Superfamily Coronuloidea / Family Coronulidae

20.15 **Coronula diadema** (Linnaeus, 1767)

Found locally on the humpback whale (*Megaptera novaeangliae*), especially on the fins, the lips, the long grooves of the throat region, and the lips of the genital aperture; also reported from the fin, blue, and sperm whales; cosmopolitan.

To about 85 mm in diameter, white, dome-shaped, firmly anchored in skin of whale but not (like *Cryptolepas*, e.g., 20.16) completely embedded in it; bearing a single pair of opercular valves suspended in opercular membrane.

This species has undergone striking modification in connection with its life on whales. The outer wall of the barnacle shell bears large radiating ridges or buttresses, each of which develops, on its distal margin, flanges that meet and fuse with similar flanges on the buttresses on either side of it. The result is a roofing over of the buttresses, except on the side of the barnacle adjacent to the whale. The skin of the whale is pulled up between the concealed buttresses as the barnacle grows, firmly anchoring the shell to the whale.

The barnacles on the whale are generally oriented such that the rostrum, and the short extended cirri, face into the current as the whale swims along. This is surely an advantage in feeding. *C. diadema* are thought to live for only 1 year. Their shells frequently form an attachment surface for *Conchoderma auritum* (20.8) and, less often, *Conchoderma virgatum* (20.7). These pedunculate barnacles are borne on the posterior (carinal) edge of the *Coronula* shell, where they do not interfere with *Coronula*'s feeding.

See Cornwall (1955a,b), Crisp & Stubbings (1957), Darwin (1854), and Newman & Ross (1976).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Balanomorpha / Superfamily Coronuloidea / Family Coronulidae

20.16 **Cryptolepas rachianecti** Dall, 1872

On the fins and head of the California gray whale (*Eschrichtius robustus*); Bering Sea to Baja California; Korea; not Hawaii, as once reported.

Shell to 60 mm in diameter, white, depressed, deeply embedded in skin of whale, often with only the bright-yellow opercular membrane and a few ridges of shell visible.

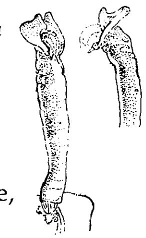
As in *Coronula diadema* (20.15), the wall of the shell in this species develops great radiating ridges or buttresses, but they do not form flanges, so the spaces between buttresses remain open (not roofed over). The shell grows down into the whale skin, as in *Coronula*, but the outer shell surface erodes away until it is virtually flush with the surface of the whale. This is a valuable adaptation, since gray whales have been noted to rub against objects on the sea floor and near shore.

More than a century ago the naturalist and geologist W. H. Dall observed the barnacles while still alive and wrote, "This species is found sessile on the California Gray whale. . . . I have observed them on specimens of that species hauled up on the beach at Monterey for cutting off the blubber . . . and the animal removed from its native element—protruding its bright yellow hood in every direction, to a surprising distance, as if gasping for breath—presented a truly singular appearance."

The surface of the shell of *C. rachianecti* is friable and easily eroded, which may help explain why the pedunculate barnacle *Conchoderma* is not found attached to it. On the other hand, the caprellid amphipod *Cyamus scammoni* (often called the "whale louse") is commonly found clinging to *Cryptolepas* (see the photograph).

See Cornwall (1955a), Dall (1872), Kasuya & Rice (1970), Newman & Ross (1976), and Pilsbry (1916).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Balanomorpha / Superfamily Coronuloidea / Family Coronulidae



20.17 **Xenobalanus globicipitis** Steenstrup, 1851

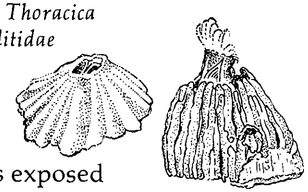
On various whalebone whales including the sei whale and common finback, also on the blackfish or Pacific pilot whale, usually attached to the fin tips; cosmopolitan.

Length to about 75 mm; species superficially resembling a stalked barnacle, but the six plates of the balanoid wall visible, forming a star-shaped anchor, embedded in skin of host.

This remarkable species has, through convergent evolution, come to resemble a pedunculate barnacle. The elongate tube is not actually a peduncle, but represents the greatly drawn-out opercular membrane. Opercular plates are lacking, but distally the membrane forms a hood with reflexed lips from which the short cirri protrude. This elongate form apparently represents an adaptation to feeding in the turbulent waters behind the trailing edge of whale fins. Little else is known of the biology of this unique species.

See Cornwall (1955a), Darwin (1854), and Newman & Ross (1976).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Balanomorpha / Superfamily Coronuloidea / Family Tetraclitidae



20.18 **Tetraclita rubescens** Darwin, 1854
(=T. squamosa rubescens)

Common, middle and low intertidal zones on rocks exposed to strong surf; occasionally subtidal on hard-shelled organisms such as abalones; San Francisco Bay to Cabo San Lucas (Baja California).

Diameter usually to 30 mm, rarely to 50 mm; wall consisting of only four plates (only balanomorph on this coast in which this is the case); shell of adult reddish, appearing "thatched" externally; shell of young (uneroded) individuals white, superficially resembling shell of *Semibalanus cariosus* (20.23) but with four wall plates instead of six.

Tetraclita is remarkable in that it relies mostly on erosion at the top of the wall rather than diametric growth to enlarge the orifice of the shell. Most balanomorphs grow laterally between wall plates, as well as upward from the base. Most *Tetraclita* do not, and if there is little erosion, the orifice remains remarkably small.

In central California this species produces about three broods in the summer, releasing 1,000–50,000 nauplius larvae per brood, depending on the size of the parent. Individuals do not begin to reproduce until they are about 18 mm in diameter and 2 years old. Like *Semibalanus cariosus*, its northern ecological equivalent, *T. rubescens* is an effective competitor for space in the lower intertidal zone, and individuals grow to a size large enough to exempt them from predation by many gastropods and sea stars. Some may live as long as 10–15 years.

Tetraclita rubescens var. **elegans** Darwin, 1854 (Fig. 20.18b), has the same general distribution as the common form, although it is more prevalent in the lower intertidal and subtidal waters and in the southern half of the geographical range. Up to 20 mm in diameter, it is distinguished from the type variety by its white uneroded wall and peltate form. It is often found on shelled mollusks and crabs that spend much of their time subtidally, and also on wharf piles in Monterey harbor. It is an ecotype, rather than a genetically distinct population.

See Barnes (1959), Barnes & Klepal (1971), Cornwall (1951), Darwin (1854), Emerson (1956), Henry (1960), Hewatt (1946), Hines (1976, 1978, 1979), Newman & Ross (1976), Pilsbry (1916), Rasmussen (1935), Ross (1962), Seapy & Littler (1978), and Willett (1937).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Balanomorpha / Superfamily Balanoidea / Family Archaeobalanidae

20.19 **Armatobalanus nefrens** (Zullo, 1963)
(=Balanus nefrens)

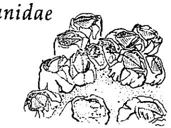
On and embedded in the hydrocorals *Allopora californica* and *Errinopora pourtalesii*, subtidal to 64 m; Monterey to Channel Islands.

Shell to 10 mm in diameter, white; only barnacle species in California known to infect hydrocorals.

Balanids have adapted in a variety of ways to living embedded in corals, and some forms found in the tropics are highly modified. However, apart from its specificity for hydrocorals, *A. nefrens* is hardly specialized at all, and one could envisage its living equally well on a rock. The methods it uses to get through the coral's defenses and establish itself, as well as other aspects of its biology, are unknown.

See Ross & Newman (1973) and Zullo (1963).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Balanomorpha / Superfamily Balanoidea / Family Archaeobalanidae



20.20 **Solidobalanus hesperius** (Pilsbry, 1916)
(=Balanus hesperius)

On hard-shelled organisms usually from soft bottoms, subtidal from 18 to 64 m depth; Bering Sea to Monterey Bay.

To 20 mm in diameter; walls dirty white, usually ribbed; species similar in appearance to *Balanus crenatus* (20.25), *B. glandula* (20.24), and when smooth (southern end of range), to *B. improvisus* (20.29), but distinguishable from all three in having strongly elevated callus above articular ridge on internal surface of scutum; distinguished from all except mature *B. glandula* in having the wall solid rather than permeated by longitudinal canals.

This species is rarely seen alive unless one resorts to dredging or diving. However, it occurs on mollusks and crabs and is commonly found on the Dungeness crab, *Cancer magister* (25.20), in markets or when washed ashore.

See Barnes & Barnes (1959c), Cornwall (1955a), Newman (1975), and Newman & Ross (1976).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Balanomorpha / Superfamily Balanoidea / Family Archaeobalanidae

20.21 **Membranobalanus orcutti** (Pilsbry, 1907)
(=Balanus orcutti) Sponge Barnacle

In sponges, very low intertidal zone and subtidal waters to 40 m; Point Conception (Santa Barbara Co.) to Cabo San Lucas (Baja California).

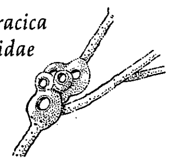
To 15 mm in length, white, thin-walled, with membranous basis; rostral plate much elongated and recurved basally.

Balanids frequently become overgrown and smothered by sponges, but they are usually attached to the substratum before the sponge becomes established. *M. orcutti*, on the other hand, settles on established sponges. After metamorphosis the barnacle becomes embedded in sponge tissue with only the opercular aperture exposed. The anterior cirri are armed with special hooks that apparently aid in removing sponge tissue that would otherwise tend to clog the aperture.

Sponge barnacles of the genus *Membranobalanus* are found in all tropical seas of the world but virtually nothing has been published on their biology. However, an intensive study of the sponge-barnacle relationship has recently been made, and the following are some of the results (L. L. Jones, pers. comm.). The apical portions of the shell plates in *M. orcutti* have rows of upturned spines that apparently prevent the young barnacles from pushing themselves out of the sponge as growth at the basal margins of the shell extends those margins deeper into the sponge. The barnacle is found in only two sponge species in California: the loggerhead sponge *Spheciospongia confoederata* (2.21), in shallow water (low intertidal zone to 18 m), and the boring sponge *Cliona celata* var. *californiana* (2.20), in deeper waters (18–40 m). Cyprid larvae show preference for, and actively select, the host species of their parents. Laboratory experiments indicate that the attractiveness of the alternate host species can be increased by exposure of the developing barnacle eggs to the alternate host.

See L. L. Jones (1978), Newman & Ross (1976), and Pilsbry (1907).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Balanomorpha / Superfamily Balanoidea / Family Archaeobalanidae



20.22 **Conopea galeata** (Linnaeus, 1771)
(=Balanus galeatus)

Embedded in sea fans (gorgonians), subtidal to 90 m; Monterey to Central America; Caribbean Sea.

To 15 mm in length; individuals aligning themselves with long axis of gorgonian branch, forming a boat-shaped basis attached to axial skeleton, and becoming overgrown by gorgonian tissue.

This species is remarkable not only in being an obligate commensal of gorgonians but in being one of the few balanomorphs in which the normal hermaphrodite is accompanied by small complemental males. Usually several of these males can be found attached within the hermaphrodite's orifice, mainly on the scuta. Males do not feed and apparently serve to ensure cross-fertilization, since the hermaphrodites are commonly widely separated on the gorgonian host. A larval cyprid sex ratio of one male to three hermaphrodites is evidently genetically determined. This suggests that the probability of male propagules finding a place to settle is much greater than that of hermaphroditic propagules. Hermaphrodite cyprids settle directly on the gorgonian axial skeleton, where it has been denuded of tissue by grazing gastropods or other predators. Male cyprids settle and metamorphose only on the hard parts of established hermaphrodites. However, mature cyprids can be induced to metamorphose in vitro without attaching to anything when treated with insect juvenile hormone and certain compounds that mimic them. Barnacle and insect hormones show many similarities.

See Bebbington & Morgan (1976), Cornwall (1951), Darwin (1854), Gomez (1973, 1975), Gomez et al. (1973), McLaughlin & Henry (1962), Molenock & Gomez (1972), Newman & Ross (1976), Pilsbry (1916), and Ross (1962).

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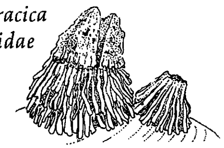
Suborder Balanomorpha / Superfamily Balanoidea / Family Archaeobalanidae



20.23 **Semibalanus cariosus** (Pallas, 1788)
(=Balanus cariosus)

Common in low intertidal zone on rocks along exposed shores; Bering Sea to Morro Bay (San Luis Obispo Co.); Japan.

To 60 mm in diameter; superficially resembling *Tetraclita rubescens* (20.18), especially when young, because of "thatched" texture of wall, but with six plates rather than four making up the wall; species distinguished from various California *Balanus* species by the white or gray, thatched wall permeated by numerous rows of longitudinal tubes, and by the membranous basis.

The thatched appearance of the walls derives from a series of basally directed, riblike buttresses that detach periodically as they are carried upward with growth. In central California individuals grow more or less separately, but in the Pacific northwest they form crowded colonies in which the thatched appearance is not as well developed.

The species is known to brood in winter, and larvae settle in the spring. Individuals grow large enough to be exempt from attack by many predators, and may live up to 10–15 years.

See Barnes (1959), Barnes & Klepal (1971), Batzli (1969), Connell (1970), Cornwall (1955a), Darwin (1854), Dayton (1971), Fahrenbach (1965), Gwilliam (1963, 1965), Gwilliam & Bradbury (1971), Millecchia & Gwilliam (1972), Newman & Ross (1976), Paine (1974), Pilsbry (1916), Rice (1930), Seapy & Littler (1978), Southward & Crisp (1965), Stickle (1973), Worley (1939), and Zullo (1969a).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Balanomorpha / Superfamily Balanoidea / Family Balanidae

20.24 **Balanus glandula** Darwin, 1854

Abundant on rocks, pier pilings, and hard-shelled animals, high and middle intertidal zones in bays and along outer coast; Aleutian Islands (Alaska) to Bahía de San Quintín (Baja California); recently reported to be introduced at Puerto de Mar del Plata (Argentina).

Shell to 22 mm in diameter, white to gray, variable in shape and texture but comparable in size and general form to *B. crenatus* (20.25) and to some extent to *Solidobalanus hesperius* (20.20); usually distinguishable from both by the dark area seen externally on each scutum, where underlying pigmented tissues show through thin central portion of shell plate, and by the more heavily ribbed wall.

This is probably the most common intertidal balanid along our shores. It is the ecological counterpart of *Semibalanus balanoides*, which occurs in both the North Pacific and Atlantic. Although *Balanus glandula* is found in bays and the polyhaline portions of estuaries, the main population occurs on the open coast where, throughout its latitudinal range, it forms a band a third of a meter or more in width, in association with the red alga *Endocladia muricata*. At Monterey this band centers at about 1.4 m above mean lower low water, and individuals are submerged 27 percent of the time. Their longest periods of continuous exposure to air and of submergence are about 20.25 and 6.5 hours, respectively. The maximum period of exposure above water at the upper limit of the band is in the order of 24 hours, if the sea is calm and without swell. *B. glandula* is moderately resistant to desiccation compared to other species of *Balanus* so far studied, losing less than 50 percent of its total water in 24 hours. On the other hand, it apparently osmoregulates more strongly than *B. amphitrite amphitrite* (20.28) and *B. improvisus* (20.29), although the last is more tolerant of dilute salinities. Nearly a hundred species of multicellular organisms live in the *Balanus-Endocladia* association. The average number of individuals of the 31 commonest species in the band has been estimated at 210,000 per m^2, with a dry weight biomass of 2,640 gms (157 gms of protein), of which *Balanus glandula* and *Endocladia muricata* form the greatest proportion. It is not known whether it can deposit salts of heavy metals, such as zinc, as granules in tissues surrounding the midgut; such deposition occurs in *S. balanoides*, where the amount deposited is proportional to environmental levels.

Balanus glandula produces two to six broods during the winter and spring in British Columbia and in central and southern California. It stores yolk in the summer and remains ripe in the fall until cold temperatures induce brooding. Depending on the size of the parent, 1,000–30,000 nauplius larvae are produced per brood. Settlement occurs in all but the highest part of the intertidal zone in the spring and summer. Peak settlement usually occurs in the spring and may result in dense "sets" of *B. glandula* smothering and crowding other organisms, especially *Chthamalus* species (e.g., 20.12). However, the presence of the crustose red alga *Petrocelis middendorffii* apparently inhibits barnacle settlement. Growth rates are variable but tend to be more rapid in the lower intertidal zone, if crowding is not too severe. Basal diameters reach 7–12 mm in 1 year, 10–16 mm in 2 years, and 14–17 mm in 3, with a maximum diameter of about 22 mm. *B. glandula* that settled in the spring are reproductive their first winter and may live up to 8–10 years.

Balanus glandula survives best in the narrow band on the high shore. The upper intertidal limit of the band is set by the species' ability to withstand desiccation; the lower limit appears to be set by both competition and predation. *B. glandula* tends to be crowded out at the bottom of the band by the mussel *Mytilus californianus* (15.9), in more northerly areas by the barnacle *Semibalanus cariosus* (20.23), and in more southerly areas by *Tetraclita rubescens* (20.18). Also, in this zone at the bottom of the band, barnacles can be preyed on effectively by the gastropod *Nucella emarginata* (13.83), and the sea stars *Pisaster ochraceus* (8.13) and *Leptasterias hexactis* (8.11). All three predators prefer *Balanus* to *Chthamalus* as prey; thus their depredation helps to counterbalance the physical dominance of *Balanus* over *Chthamalus*. The effect of limpets feeding on, or bulldozing off, cyprids and juvenile barnacles is more pronounced on *Balanus* than on *Chthamalus*.

See Augenfeld (1967), Barnes & Barnes (1956), Barnes & Gonor (1958a), Barnes & Healy (1969), Barnes & Klepal (1971), Batzli (1969), Bergen (1968), Connell (1970), Cornwall (1955a), Darwin (1854), Dayton (1971), Glynn (1965), Hines (1976, 1978, 1979), Johnson & Miller (1935), Newman (1967), Newman & Ross (1976), Paine (1974), Paine, Slocum & Duggins (1979), Pilsbry (1916), Rice (1930), Seapy & Littler (1978), Spight (1973), Stephenson & Stephenson (1972), Stickle (1973), Walker et al. (1975), Worley (1939), and Zullo (1969a).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Balanomorpha / Superfamily Balanoidea / Family Balanidae

20.25 **Balanus crenatus** Bruguière, 1789

Uncommon on rocks and, from Monterey Bay north, on deeply shaded pier pilings, low intertidal zone; common at subtidal depths to 182 m on various objects including seaweeds; northern Japan and Alaska south to Santa Barbara; North Atlantic.

Shell to 20 mm in diameter, white; species separable from *B. glandula* (20.24) and *Solidobalanus hesperius* (20.20), which it resembles, by (1) the smoother wall plates in California specimens of *B. crenatus*, and (2) the presence of large, regular, longitudinal tubes permeating the wall plates of *B. crenatus* (best seen from below, or in broken plates).

Balanus crenatus is in some respects the subtidal equivalent of *B. glandula* in the North Pacific and of *Semibalanus balanoides* of the North Pacific and Atlantic. Size for size *B. crenatus* is more susceptible to water loss through desiccation than some intertidal rock barnacles, especially *Chthamalus* (e.g., 20.12). This and its greater fragility correlates with its intertidal occurrence in relatively quiet waters. The species is found in polyhaline reaches of estuaries on both coasts of North America and on the west coast of Europe. In New Brunswick (Canada), for example, adults are abundant in Miramichi Bay but rare in the adjoining gulf. Plankton sampling revealed that early nauplius larval stages remain high in the water column and therefore move seaward, but later larvae descend deeper and undergo a net movement landward; the cyprids, being the deepest, are carried far into the bay with the saline wedge. Larvae likely spend 2–3 weeks in the plankton, and before they settle they are transported to areas where conditions approach the barnacle's lower salinity tolerance limits.

In years of exceptionally great larval "set," or settlement, extreme crowding occurs, with the result that barnacles with tall columnar walls develop. The individuals and clumps formed have small areas of attachment proportional to their size and are easily broken loose; consequently, relatively few members of heavy sets survive a season. Experiments involving containers suspended from a barge have shown that light has no significant effect on growth rate, fertilization, or development of embryos.

Balanus crenatus is sparsely distributed in the subtidal polyhaline reaches of San Francisco Bay, but it becomes an important subtidal species, in terms of numerical abundance, in the northwest. In Monterey Bay, *B. crenatus* settles erratically during most months of the year. After settlement, the animals can grow to a basal diameter of 20 mm in 1 year.

See Addicott (1966), Austin, Crisp & Patil (1958), Barnes (1953a,b,c, 1959), Barnes & Healy (1969), Barnes & Klepal (1971), Barnes, Klepal & Munn (1971), Barnes & Powell (1950), Barnes, Read & Topinka (1970), Bousefield (1955), Cornwall (1955a), Crisp (1955), Crisp & Barnes (1954), Crisp & Southward (1961), Crisp &

Stubbings (1957), Darwin (1854), Foster (1969, 1971), Haderlie (1974), Herz (1933), Kauri (1962, 1966), Newman (1967), Newman & Ross (1976), Southward & Crisp (1965), and Zullo (1969a).

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20.26 **Balanus trigonus** Darwin, 1854

On hard substrata, including hard-shelled invertebrates, or embedded in sponges or corals, low intertidal zone to 90 m depth; Monterey to Peru; cosmopolitan in warm seas.

Rarely more than 15 mm in diameter, usually less than 10 mm; wall ribbed, white usually mottled with some shade of red; orifice triangular in outline; exterior of scuta with one to several rows of pits, distinguishing it from all other species of *Balanus* occurring locally.

This species may form facultative associations with other organisms, and sometimes lives buried in corals or sponges. It has been found on the whale barnacle *Coronula* (e.g., 20.15), and it is therefore likely that whales have been in part responsible for its wide distribution. Its fossil record goes back to the Miocene. It arrived in the Hawaiian archipelago no later than the Pleistocene, at least a million years before the Polynesians. It is one of the few cosmopolitan shore barnacles not suspected of having become so via transport by ships.

This species has generally escaped the attention of west coast naturalists other than in Panama, where it contributes significantly to the sediments formed by coral reefs on offshore islands. Laboratory studies in Florida indicate that it and *Tetraclita stalactifera* are relatively intolerant of high and low temperature extremes (mid-40's and 0°C), compared with *Balanus amphitrite amphitrite* (20.28) and *Chthamalus stellatus*. Settling experiments and field observations indicate that this is primarily a subtidal species; there is no evidence that the larvae settle intertidally only to die later.

See Barnes & Klepal (1971), Darwin (1854), Henry (1960), Newman & Ross (1976), Pilsbry (1916), Ross, Cerame-Vivas & McCloskey (1964), and Werner (1967).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Balanomorpha / Superfamily Balanoidea / Family Balanidae

20.27 **Balanus pacificus** Pilsbry, 1916

Occasionally on rocks, usually on other organisms, low intertidal zone to 73 m depth; Monterey Bay to Baja California; replaced in Gulf of California by *B. pacificus mexicanus*, a form ranging south to Panama and perhaps Peru.

To 35 mm in diameter; wall smooth, white with reddish stripes; species distinguished from *B. amphitrite amphitrite* (20.28) by longitudinal striations across growth lines of scuta.

Balanus pacificus produces many broods throughout the year in southern California. The larvae settle year-round on ephemeral substrata in subtidal sandy areas, rather than on rock bottom bearing well-established communities. In many sand dollar populations, up to 15–25 percent of the adults are fouled by *B. pacificus*, and the barnacles themselves become substrata for bryozoans, algae, and especially the hydroid *Clytia bakeri* (3.9). Many living sand dollars washed ashore during storms are fouled, and field observations indicate that the proportion of fouled sand dollars in established populations increases shorewards after storms. Thus, it appears that barnacle fouling increases the tendency of shoreward transport, adding to both sand dollar and barnacle mortality.

By settling on other organisms, *B. pacificus* tends to avoid many predators such as asteroids, gastropods, crustaceans, and fishes. Settling on organisms living in sand may be especially helpful in this regard. An unusual and apparently major cause of mortality is predation by two polyclad flatworms, *Stylochus tripartitus* (4.2) and *Notoplana inquieta*, against which the barnacle has no defenses. The flatworms can reach the barnacles as planktonic larvae. They enter the shell through the opercular aperture and eat the barnacle at a rate (in the laboratory) of 0.05 gms barnacle tissue per gm flatworm tissue per day. *Balanus pacificus* is opportunistic, taking advantage of surfaces freshly placed in the water or freshly cleaned by disturbances, but it does not form a permanent part of the bottom community.

See Cornwall (1962), Darwin (1854), Giltay (1934), Henry (1960), Houk & Duffy (1972), Hurley (1975, 1976), Merrill & Hobson (1970), Newman & Ross (1976), Pilsbry (1916), Ross (1962), and Zullo (1969b).

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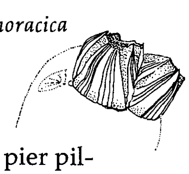


20.28 **Balanus amphitrite amphitrite** Darwin, 1854

Common on hard substrata such as rocks, shells, and pier pilings, low intertidal zone to 18 m depth in bays and estuaries; San Francisco to Panama; introduced into Salton Sea (Imperial and Riverside Cos.); cosmopolitan in warm seas.

To 20 mm in diameter, white with reddish-brown or purplish stripes; resembling young *B. pacificus* (20.27), but lacking longitudinal striations on scuta; similar to *B. improvisus* (20.29), but the latter never has dark-purple stripes on wall.

Although *B. amphitrite* is easy to identify in California, care must be taken to distinguish it from *B. inexpectatus* farther south, and from *B. reticulatus* in all tropical regions of the world, for the species have been much confused in the past.

Balanus amphitrite is a bay form, but does not survive long in very dilute seawater. A fouling barnacle, it is widely distributed in harbors of the world by ships. It becomes established only in bays in which the summer water temperatures reach 20°C, permitting breeding to take place.

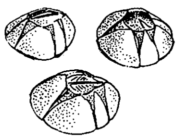
Certain Atlantic invertebrates were introduced to the west coast through the commercial importation of the east coast oyster *Crassostrea virginica*. *Balanus improvisus* (20.29) was apparently introduced in this way before 1853. *B. amphitrite* also grows on *C. virginica*, but the first records of this barnacle on our coast are those at San Diego (1921) and San Francisco (1939). It did not arrive with the oysters, apparently because the oysters were imported from north of Cape Hatteras (North Carolina), the barnacle's northern limit of distribution on the east coast. It seems likely that *B. amphitrite* came later, transported by ships. It was first collected in Hawaii and the Philippines between 1914 and 1916, at the Suez Canal in 1924, and in northern Europe in 1929. However, only in the past decade has this species been clearly defined. Therefore, only on the west coast and in northern Europe, where there are no closely related species, do the earlier records tell us clearly the approximate times of introduction.

The Salton Sea population (Imperial and Riverside Cos.) apparently became established early in World War II, when buoys from San Diego Bay used to mark seaplane lanes were hastily transported there. It differs somewhat in form from the coastal populations and has been formally considered a distinct subspecies. The differences could be genetic, owing to rapid selection in an artificial sea with an exceptionally short faunal list. Alternatively, the differences could be environmentally induced, for although the salinity of the Salton Sea approaches that of the ocean, the ionic composition is different, sulfates being markedly higher and chlorides proportionately lower than in normal seawater. The case for the Salton Sea barnacle being an ecotype rather than a genetically distinct form presently seems stronger, since a similar population has been identified statistically in Wilmington harbor (Los Angeles Co.) on the outer coast.

In general, larvae select suitable settling sites in relation to depth, illumination, surface contour, previous settlements of individuals of the same or related species, and the velocity of the currents. Cyprids of *Balanus amphitrite* settle with their tails to the current, in the absence of other stimuli, which orients the cirral net in the right direction (facing upstream) following metamorphosis. Although the cyprids are not responsive to the direction of light when searching for a suitable spot, they head into light while attaching, regardless of the normal current direction. Above all, the larva seeks a small pit in which to settle. Although some reorientation of the body to the current can be accommodated by differential growth after metamorphosis, it is limited after initial attachment has been made.

Shallow-water barnacles generally withdraw and close up when suddenly placed in shadow. Since the compound eyes of the cyprid are shed with the exoskeleton during metamorphosis, it has been presumed that the photoreceptors, or ocelli, are persisting elements of the nauplius larval eye. These ocelli can be seen, one on each side under the basal margins of the scuta, in freshly metamorphosed juveniles of *Balanus*, but their position becomes obscured with calcification, and dissection is necessary to locate them in adults. Each ocellus is composed of three large photoreceptor cells without ommatidial organization. The cell bodies have projections bearing microvilli and a large axon (15–20 μm in diameter). It has been shown electrophysiologically in a close relative, *B. eburneus*, that the primary event at the photoreceptor is an "on" response similar in form to that described for the retinular cells in a number of arthropods.

See Barnes, Klepal & Munn (1971), Barnes, Read & Topinka (1970), Costlow & Bookhout (1956, 1958a,b), Crisp & Costlow (1963), Crisp & Southward (1961), Davis, Fyhn & Fyhn (1973), Fahrenbach (1965), U. Fyhn & Costlow (1975, 1977), Graham & Gay (1945), Henry & McLaughlin (1975), Hillman et al. (1973), Lacombe (1970), Newman (1967), Newman & Ross (1976), Pilsbry (1916), and Zullo, Beach & Carlton (1972).



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Suborder Balanomorpha / Superfamily Balanoidea / Family Balanidae

20.29 **Balanus improvisus** Darwin, 1854

On rocks, pilings, and hard-shelled organisms, low intertidal zone to subtidal depths in estuaries; particularly tolerant of brackish waters; Columbia River (Oregon) to Salinas River (Monterey Co.), occasionally in harbors south of Point Conception (Santa Barbara Co.); Ecuador; Japan, Australia; North and South Atlantic; introduced into North Pacific.

Small, to 10 mm in diameter; closely related to *B. amphitrite amphitrite* (20.28), but shell wholly white, lacking purple stripes.

Another white, brackish-water form, *B. eburneus*, has been introduced from the east coast to Central America, Hawaii, and Japan, but it is not yet known from the west coast of North America. It is distinguished from both *B. improvisus* and *B. amphitrite* by the longitudinal striations of the exterior of the scuta.

Balanus improvisus is a truly estuarine barnacle, apparently introduced from the east coast before 1853, along with the eastern oyster, *Crassostrea virginica*. In the northern reaches of San Francisco Bay the barnacle spends as much as 10 months of the year in fresh water. Here, contrary to previous reports, it has recently been shown to osmoregulate if given sufficient time to acclimate. Specimens have been found attached to other freshwater organisms such as crayfish and water beetles in various parts of the world. In the North Sea this species is suffering from competition with a recently introduced Australian form, *Elminius modestus*. Comparisons of Baltic Sea *B. improvisus* living at salinities 75–90 percent that of ocean water with those living at salinities 15–18 percent of seawater show no significant differences between the two populations in a number of respects, including shell characters, ripe embryos, first nauplius larvae, ratio of shell volume to basal diameter, and ratio of shell weight to dry body weight. *Balanus improvisus* is evidently a well-adjusted estuarine species, in contrast to *Semibalanus balanoides*, which is not known to osmoregulate and which terminates its range into estuaries at salinities ranging from 30 to 75 percent that of normal seawater, accompanied by a marked reduction in size.

Studies of relative growth show that in *B. improvisus* the shell grows faster than the body, which provides the adult with a mantle cavity with plenty of room to accommodate developing embryos. In the Miramichi Bay (New Brunswick), larval planktonic life is estimated to last 18 days, the cyprid stage being reached by the fourteenth day. The stages show some vertical stratification with depth according to tidal stage. In general, cyprids are found nearer the surface at the head of the bay during flood tides, which ensures their transport into the intertidal reaches of the estuary where the adults are most commonly found.

In laboratory tests, *B. improvisus* grew more rapidly when fed the alga *Chlamydomonas* alone than a mixture of *Chlamydomonas* and *Nitzschia*, but growth was less than under field conditions. On the average, molting occurred every 2–3 days. Metamorphosed individuals passed through a stage possessing four wall plates in 2 days; this was followed by a stage showing the typical six-plated wall. Carbonic anhydrase inhibitors prevented the transition from four to six plates. At later stages the application of these inhibitors reduced the rate of growth, but individuals removed from the presence of inhibitors resumed normal growth. Treatment of the earliest juvenile, however, precluded further development, suggesting that mechanisms regulating growth must be initiated shortly after metamorphosis, and once blocked are not triggered again.

Three closely related barnacles, including *B. improvisus*, have been used in tissue and organ culture studies. Bovine embryo extract and yeastolate added to *Balanus* saline were favorable for cell outgrowth and organ maintenance; other additions had neutral or negative effects. Organs cultured include mantle parenchyma, ovarioles, and cement glands. Germinative tissue retained high mitotic activity for at least 7 days. Epithelial and fibroblast-like cells underwent extensive growth and migration. Success in this study may in part reflect the wise choice of materials; all three of the species selected are eurytopic, and *B. improvisus* is especially tolerant of estuarine conditions.

See Barnes & Barnes (1961), Barnes & Healy (1969), Barnes & Klepal (1971), Barnes, Klepal & Munn (1971), Barnes, Read & Topinka (1970), Bartha & Henriksson (1971), Bousfield (1955), Carlton & Zullo (1969), Costlow (1956, 1959), Costlow & Bookhout (1953, 1957), Crisp (1953), Crisp & Southward (1961), Darwin (1854), H. Fyhn (1976), U. Fyhn & Costlow (1975), Graham & Gay (1945), L. W. Jones & Crisp (1954), Kauri (1962, 1966), Meith-Avčin (1974), Newman (1967), Newman & Ross (1976), Törnävä (1948), Visscher (1928), and Zullo, Beach & Carlton (1972).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Balanomorpha / Superfamily Balanoidea / Family Balanidae

20.30 **Balanus regalis** Pilsbry, 1916

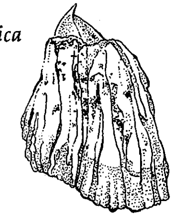
Low intertidal and subtidal zones on surf-washed rocks; Point Conception (Santa Barbara Co.) to western Mexico.

To 60 mm in diameter, closely related and similar in form to the larger northern species *B. aquila* (20.31), but distinguished by having fine, uniform, whitish ribs separated by brown to reddish-brown grooves on the walls, rather than a pure-white wall.

This little-known species, one of the more ornamental balanids, was only recently reported inhabiting wave-swept rocky outcrops in southern California.

See Henry (1960), Newman & Ross (1976), Pilsbry (1916), and Ross (1962).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Balanomorpha / Superfamily Balanoidea / Family Balanidae



20.31 **Balanus aquila** Pilsbry, 1907

On rocks, pier pilings, and abalone shells, low intertidal zone to 18 m depth; San Francisco to San Diego.

To 130 mm in diameter; species often confused with another large white species, *B. nubilus* (20.32), but distinguished from it by (1) the small rather than flaring orifice, (2) the beaked terga, and (3) the longitudinal striations on the scuta; distinguished from *B. regalis* (20.30) by the coarsely ribbed white wall.

This species, endemic to a limited region of California, is one of the last surviving members of the *concavus* group, known as fossils from the Oligocene-Pleistocene period in Europe and in North and South America and from the Pliocene period in northern Japan.

Because suppliers of biological materials have often misidentified *B. aquila* and sent it to investigators ordering *B. nubilus*, much of the membrane work reported for *B. nubilus* was actually done on *B. aquila*. Both species occur on pier pilings at Monterey. If there is an "endangered" barnacle species in California, it is *B. aquila*.

See Baskin et al. (1969), Cornwall (1960), Newman (1979), Newman & Ross (1976), Pilsbry (1916), and Zullo (1966).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Balanomorpha / Superfamily Balanoidea / Family Balanidae

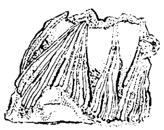
20.32 **Balanus nubilus** Darwin, 1854

Common on rocks, pier pilings, and hard-shelled animals, low intertidal zone to 90 m depth; southern Alaska to La Jolla (San Diego Co.).

To 110 mm in diameter; not easily confused with any other species except *B. aquila* (20.31), from which it is distinguished by a large, flaring (rather than small) aperture, and by the lack of longitudinal striations on the scuta.

Barnacles of this species are reputed to be eaten by the natives of the northwest, who cook them whole on open fires and then remove the operculum and eat them out of the shell. The animal contains the largest individual muscle fibers known to science and ostensibly has enjoyed considerable popularity in physiological research. However, much of this work was actually performed on *B. aquila*, through misidentification.

See Addicott (1966), Arvy & Lacombe (1968), Arvy, Lacombe & Shimony (1968), Arvy & Liguori (1968), Ashley, Ellory & Hainaut (1974), Barnes (1959), Barnes & Barnes (1959b), Barnes & Gonor (1958a), Carderelli (1968), Cornwall (1936, 1951), Darwin (1854), Devillez (1975), Emerson & Hertlein (1960), Hagiwara & Takahashi (1967), Hagiwara et al. (1968), Harnden (1968), Houk & Duffy (1972), Hoyle, McNeill & Selverston (1973), Hoyle & Smythe (1963), Lacombe (1970), Newman & Ross (1976), Pilsbry (1916), Ross (1962), Shelford et al. (1935), Tait & Emmons (1925), Whitney (1970), and Zullo (1969a,b).



Phylum Arthropoda / Class Crustacea / Subclass Cirripedia / Order Thoracica
Suborder Balanomorpha / Superfamily Balanoidea / Family Balanidae

20.33 **Megabalanus californicus** (Pilsbry, 1916)
(=Balanus tintinnabulum californicus)

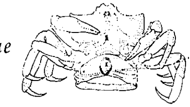
Uncommon in low intertidal zone; commonly subtidal to 9 m depth on rocks, pilings, buoys, kelp, mussels, and other hard-shelled organisms; Humboldt Bay to Guaymas (Mexico); very uncommon north of Monterey.

To 60 mm in diameter, with longitudinal red and white stripes; the only *Megabalanus* species known from California; genus distinguished from all other balanid genera in having radii permeated by transverse tubes rather than being solid.

This is one of the most colorful balanids and tends to be very gregarious. Crowding causes the basis to elongate into a deep cup so that the plates remain undistorted and individuals form spectacular clusters. A related species is considered a delicacy in Chile and is sold fresh or canned.

See Aleem (1957), Barnes & Klepal (1971), Coe (1932), Coe & Allen (1937), Graham & Gay (1945), Henry (1960), Hewatt (1946), Kanakoff & Emerson (1959), Newman & Ross (1976), Pilsbry (1916), Rasmussen (1935), Willett (1937), and Zullo (1968).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia
Order Rhizocephala / Suborder Kentrogonida / Family Sacculinidae



20.34 **Heterosaccus californicus** Boschma, 1933

Parasitic on the spider crabs *Loxorhynchus grandis* (25.10) and *L. crispatus* (25.11), *Pugettia producta* (25.4), and *Taliepus nuttallii* (25.3); known only from Monterey Bay to San Diego.

Externally visible portion of parasite (the "externa") attached to ventral surface of crab's abdomen, in same position that fertilized eggs are carried by ripe female crab; externa to 40 mm wide, globular, saclike, with a central orifice; similar to externa of another rhizocephalan barnacle reported from California, **Loxothylacus panopaei** (Gissler), which differs in parasitizing only crabs of the family Xanthidae.

Little has been published on the biology of *Heterosaccus*. However, its general life history probably resembles that of *Sacculina carcini*, a similar form carefully studied by the French zoologist Yves Delage and others nearly a century ago. In *Sacculina* the larvae hatch as nauplii that differ from those of free-living barnacles mainly in lacking a mouth and gut. The cyprid larval stage also lacks a gut and has only rudimentary mouthparts. Female cyprid larvae locate host crabs (*Carcinus*, *Portunus*, etc.) and attach themselves by one antennule at a place where the host's exoskeleton is very thin and soft. The cyprid then sheds much of its larval body, including thoracic limbs, muscles, and bivalved carapace. The small mass of tissue that survives this metamorphosis becomes surrounded with a new cuticle, one feature of which is a hollow needle or dart. This larval stage, the "kentrogon," extends its dart through the host cuticle and by muscular action injects the larval tissues into the crab's body. The kentrogon tissue then develops the "interna," a central lobe on the host's gut just back of the stomach, and, extending out from this lobe, a branching network of threadlike nutritive rootlets that range throughout the blood spaces of the crab's body. Some 9 months after initial penetration, the interna extends a lobe that emerges on the ventral abdomen of the crab, forming the sacklike externa. The externa contains the large ovary and a sack containing sperm probably derived from a male cyprid (see the account of *Peltogasterella gracilis*, 20.35, and Ichikawa & Yanagimachi, 1960). Eggs and sperm are both shed into an enclosed space, the mantle cavity, where fertilization occurs, and the embryos are brooded until they hatch as nauplius larvae and escape by the orifice. The presence of the parasite inhibits molting and normal sexual development of the host, but seems to cause little damage in other respects. After the parasite reproduces, the externa is sometimes shed or lost, but may persist on the host for at least a year and possibly a lifetime.

All of the rhizocephalans included in this chapter are "kentrogonids," that is, they pass through a kentrogon stage and undergo a period of internal development between initial infection of the crab and the emergence of the externa. This is in contrast to the "akentrogonid" type of rhizocephalan, recently described by Bocquet-Védrine (1972), in which the parasite always remains in communication with the exterior.

See Bocquet-Védrine (1972), Boschma (1953), Day (1935), Delage (1884), Foxon (1940), Fratello (1968), Ichikawa & Yanagimachi (1960), and O'Brien (1977).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia
Order Rhizocephala / Suborder Kentrogonida/Family Peltogasteridae

20.35 **Peltogasterella gracilis** (Boschma, 1927)

On abdomens of hermit crabs (*Pagurus* spp.); Bering Sea to Chile; Japan; only member of family Peltogasteridae known from California.

External portion of parasite ("externa") to 10 mm long, with mantle aperture terminal (rather than medial as in other California rhizocephalans); one host usually bearing several externae.

Classical studies of rhizocephalan barnacles suggested that they were self-fertilizing hermaphrodites. Some were known to be accompanied by males, presumed to be non-functional. Recent studies of this species in Japan show that the stage parasitizing crabs is not hermaphroditic, but female. The so-called "testes" are actually pockets in the female (analogous to seminal receptacles) in which male tissue has come to reside following the attachment of a male cyprid.

In *Peltogasterella gracilis* two types of females have been reported. Their externae are similar, but one type produces only small eggs (140–150 μm diameter). When fertilized, they give rise to small nauplius larvae, and later small cyprids. The cyprid locates a crab host, attaches by an antennule, sheds its thoracic limbs and carapace, and metamorphoses into a kentrogon larva (see the account of *Heterosaccus californicus*, 20.34). The kentrogon penetrates the host with a hollow dart, and injects tissues that proliferate to form the interna, or internal portion, of the parasite. The central cell mass of the interna grows in the abdomen and sends nutritive rootlets ramifying into the rest of the host body. Eventually the rudiment of the externa arises as a bud on the central cell mass, grows, and pushes out through the abdominal wall of the host, while remaining firmly attached to the root system. The female parasite develops ovaries in the externa, and also a pair of small sacs of "male-cell receptacles" that lack gametes.

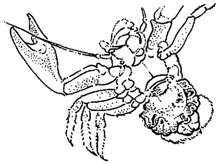
A second type of female parasite, from another crab host, produces only large eggs (160–170 μm diameter). When these are fertilized, they yield large nauplius larvae and later large cyprids, which become males. The large male cyprids swim and settle, not on crab hosts like the small cyprids, but on the apertures of the mantle cavities of *Peltogasterella gracilis* externae, which are all females. A large cyprid does not metamorphose into a kentrogon stage, but through one of its antennules it injects a cell mass into the mantle cavity of the female parasite. Both types of females receive such male-cell masses, which migrate through the mantle cavity and take up residence in the male-cell receptacles. Here the male cells differentiate to form sperm.

Female parasites may produce several successive batches of eggs, after which the externa dies and is shed, leaving the interna intact. New externae may develop from the same interna. When several externae are present on a host, they are probably (but not certainly) all budded from the same interna. Occasional exceptional female parasites were found that produce both large and small eggs, yielding, respectively, large and small larvae; it is possible that the female actually alternates between large and small cyprid production, as is the case in *Lernaeodiscus porcellanae* (20.36).

See Bocquet-Védrine (1972), Reinhard (1942), and Yanagimachi (1961a,b).

Phylum Arthropoda / Class Crustacea / Subclass Cirripedia
Order Rhizocephala / Suborder Kentrogonida / Family Lernaeodiscidae

20.36 **Lernaeodiscus porcellanae** F. Müller, 1862



On the porcelain crab *Petrolisthes cabrilloi* (24.17), middle and low intertidal zones on rocky shores; La Jolla (San Diego Co.), only member of family Lernaeodiscidae known from west coast of North America; if identification is correct, previously known only from southern Brazil.

To 10 mm wide, distinguished from other solitary California rhizocephalans by fluted edges of external sac.

Although the species was only recently discovered in California, an intensive study of the host-parasite relationship has been made by the late L. Ritchie. The following are some of his results (pers. comm.).

Sexes are separate in *Lernaeodiscus;* the smaller female-producing cyprid enters the gill chamber of the crab, where it attaches to a gill lamella by both first antennae. In the next few days the kentrogon stage forms (see the account of *Heterosaccus californicus*, 20.34). Unless the crab has successfully removed the parasite in the process of cleaning its gills, the latter invades the host through a trough formed by the cyprid labrum (upper lip), rather than by a tube inserted through one of its first antennae. Gill cleaning is accomplished by the posterior pair of thoracic legs, especially modified in connection with this cleaning function. The mere presence of female cyprids initiates vigorous gill cleaning in *P. cabrilloi*, but not in other porcelain crabs of the region. Between 5 and 60 percent of the host population can be infected, the incidence of infection being significantly increased in the laboratory by damaging or removing the last thoracic legs. Infection castrates both sexes and feminizes male crabs. Such non-reproductive individuals have normal life expectancies and continue to draw on the resources of the crab population. Upon completion of maturation the tissues of the parasite inside the crab's body develop an incipient externa, between the proximal abdominal sterna. This forms the externa on the next molt of the host. One to several male cyprids of *L. porcellanae* locate the virgin externa, attach, and extrude their cellular contents into it. These male cells come to reside in receptacles and differentiate into spermatozoa in time to fertilize the first and successive broods of eggs produced in the externa. The maturing externa takes on the general form, and occupies the same position on the crab's abdomen, as the eggs being brooded by a normal female crab; and it is cared for and cleaned by the last pair of thoracic legs as if it were indeed the crab's egg mass. Mature externae wither and die if experimentally deprived of this care, in good part for lack of assistance in molting. Lost externae are regenerated, but normally they are long-lived, producing successive broods of nauplius larvae that develop into female, mixed female and male, or male cyprids, in a succession that is apparently seasonal.

See Boschma (1969).

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