Chapter 25

Brachyura: *The True Crabs*

John S. Garth and Donald P. Abbott

The Brachyura represent the highest development attained by articulated animals in the sea. Their hormonally controlled molting cycle, autotomy reflex, and ability to regenerate lost limbs excite the physiologist; their highly organized nervous systems, complex organs of sight and sound production, and incipient social organization beguile the animal behaviorist as well. Their commensal and mutualistic relationships with other invertebrates intrigue the marine ecologist, and their role as hosts to invading arthropods engages the parasitologist's attention.

Crabs first appear in the fossil record early in the Jurassic period of the Mesozoic, nearly 200 million years ago. As a group they show a continuation of the trend toward shortening the body and reducing the abdomen expressed in various anomuran groups (Chapter 24). The crab cephalothorax, formed by fusion of head and thorax and covered by the carapace, is short and broad, and forms virtually the whole body. The crab abdomen (corresponding to what gourmets call the "tail" of a lobster) is reduced to a thin, flat plate, tucked forward out of sight below the cephalothorax, hence the name "Brachyura," or "short-tailed" crabs.

The original metamerism, or serial segmentation, of the cephalothorax is largely obscured except as represented by the appendages. The five pairs of head appendages include the first and second antennae and the innermost three pairs of mouthparts (the mandibles and the first and second maxillae). The eight pairs of thoracic appendages include the outermost three pairs of mouth-

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parts (the first, second, and third maxillipeds) and the five pairs of walking legs, the first of which are modified as chelipeds, or pincers.

The abdomen in crabs usually retains some external indications of serial segmentation, and some, but not all, of the original abdominal limbs. Female crabs possess four pairs of pleopods, which are used to carry eggs during the reproductive season. The males bear two pairs of pleopods, used as copulatory organs. Uropods are lacking in the adult stages of all but the most primitive crabs, and in most crabs they are absent even in the hatched larvae.

Crabs show some very effective locomotory innovations. Below their short, wide bodies the bases of the right and left members of each pair of walking legs are well separated; moreover, the legs themselves are relatively long and are hinged and suspended for the sideways gait that is so characteristic of true crabs. Many crabs can take relatively large steps, some species are capable of very rapid running, and nearly all can cling firmly to hard substrata when at rest. The limbs consist of non-repetitive segments or articles, separated by joints. The movable segments, starting at the body and moving outward on a leg, are called the coxa, basiischium, merus, carpus, propodus, and dactylus. Analogy of the cheliped and the human forelimb equates the merus with the forearm, the carpus with the wrist, the propodus with the hand or manus, the movable dactylus with the forefinger, and an opposable projection of the propodus with the pollex or thumb. The pollex is sometimes referred to as the fixed or immovable finger. Carcinologists (those who study crabs) often use the crustacean and human anatomical terms interchangeably.

A crab whose leg becomes trapped or is gripped by a predator

can escape by quickly autotomizing (shedding) the limb and running away. Locomotory effectiveness is scarcely affected by the loss. Detachment of the limb is brought about by special muscles, and occurs at a preformed fracture plane in the basi-ischium.

The crab body is covered by a hard exoskeleton that offers protection but limits growth. Periodically, a crab seeks a sheltered hiding place, resorbs some materials from its exoskeleton, then splits the remaining shell and crawls out of it. In a short time the new exoskeleton, already partly formed inside the old shell but still thin and soft, thickens and hardens, but before it does the crab body absorbs considerable water and expands to a size larger than before the molt. Missing limbs, if any, are regenerated along with molting, provided the loss has occurred sufficiently early in the intermolt period to permit their internal preformation.

In crabs, as in other arthropods, increase in size must always be accomplished by molting, from the larval stages onward. The fertilized eggs, carried on special hairs on the pleopods of females, hatch as protozoea larvae and immediately molt to zoea larvae. These larvae are much more shrimplike in appearance than the adults. During the zoeal period the young exist as part of the plankton. They swim actively by means of appendages on the cephalothorax that become the antennae and mandibles of the adult and feed on metazoans, larval forms, and protozoa even smaller than themselves. Periodically they molt their larval exoskeletons, the body enlarging and undergoing some change in form at each molt. The stages between molts are called instars, and different species of crabs exhibit one to five zoeal instars. The last zoeal instar is followed by a molt and metamorphosis to the megalops stage. The megalops looks a bit like a small crab. The abdomen is somewhat flattened and can be folded forward below the cephalothorax, allowing the animal to sit on the substratum like an adult. The abdomen can also be extended posteriorly, allowing the megalops to swim swiftly by the beating of its strong pleopods. The megalops instar represents a transitional stage in the life of a crab, during which the animal swims about but settles from time to time, testing the bottom. The megalops molts to produce the first juvenile crab instar, which in nearly all crabs remains on the bottom and commences an adult type of existence. Molting occurs less frequently as crabs get larger and older. Some species cease molting on becoming sexually mature; others continue to molt throughout life.

Nearly 4,500 living species of crabs have been described. Some

occur in brackish or fresh water, or in damp habitats on land; some occur in the ocean deeps, and others are pelagic in the open sea; still others live on or in the bodies of other organisms. However, the great majority of species are free-living and benthic, and inhabit the sea floor on continental shelves and slopes in comparatively shallow water. In terms of ecological diversity, they occupy a great variety of specific habitats and consume a great variety of foods. Body form varies along with habitat and way of life.

The intertidal Brachyura fall into three large groups: the spider crabs, the cancroid crabs, and the grapsoid crabs (Rathbun, 1918, 1925, 1930). Additional groups occur in deeper water off our coast (Rathbun, 1937). The carapace tends to be longer than broad in spider crabs, its shape pyriform (pear-shaped), lyrate (broadly triangular), or alate (winged). In other crabs the carapace tends to be broader than long: in cancroid crabs like *Cancer* it is broadly oval; in grapsoid crabs like *Pachygrapsus* it is rectangular or squarish. In spider crabs the frontal portion of the carapace develops into a prominent rostrum (beak) consisting of a single or a double horn; in other crabs the front is either straight and flat or many-toothed. Hooked hairs are present in spider crabs for the attachment of foreign objects; body hairs (setae) in other crabs, when present, are never of the hooked kind.

For both the serious student of crabs and the amateur beachcomber who enjoys the pastime of crab watching, California is ideally situated. Between Crescent City (Del Norte Co.) and Monterey one may find cold-water species that occur north to Alaska; between Santa Barbara and San Diego one may discover warm-water species that occur south to Bahía Magdalena (Baja California). Some crabs collectible at low tide in northern California are obtainable only by dredging in southern California, whereas crabs that occupy middle intertidal levels in California may dominate high intertidal levels in Puget Sound (Washington). A roll call of crab families illustrates the diversity to be found in the California intertidal region.

The spider crabs, family Majidae, include the decorators, such as *Loxorhynchus* (25.10, 25.11) and *Scyra* (25.9), which disguise themselves with bits of hydroids, sponges, and algae, and the kelp crabs *Pugettia* (25.4–7) and *Taliepus* (25.3), which are usually free of adornment.

Among cancroid crabs are the Portunidae, a tropical family ranging as far north as Santa Barbara. These swimming crabs may be

recognized by the paddle-shaped last pair of legs. The family Cancridae is well represented, with nine species. A commercially important fishery is based on the Dungeness crab, *Cancer magister* (25.20), and several species of *Cancer* have been used in significant experimental studies. The pebble crabs, family Xanthidae, are abundant in the tropics; *Cycloxanthops* (25.23) and *Paraxanthias* (25.28) extend northward to Monterey, and some *Lophopanopeus* (e.g., 25.24) reach Alaska. An eastern xanthid, *Rhithropanopeus harrisii* (25.27), recently introduced into San Francisco Bay, has spread into even severely polluted areas.

Among grapsoid crabs, the family Grapsidae includes the shore crabs *Pachygrapsus* (25.43) and *Hemigrapsus* (25.44, 25.45), which dominate the higher intertidal region of rocky or muddy beaches. Semi-terrestrial and relatively hardy, they have been favorite experimental subjects for a variety of physiological studies (e.g., Bollenbacher, Borst & O'Conner, 1972; R. I. Smith & Rudy, 1972). The family Ocypodidae includes the fiddler crabs of the genus *Uca* (e.g., 25.46), whose ritualistic courtship patterns have been studied by animal behaviorists (Altevogt, 1957; Crane, 1957, 1975; Dembrowski, 1926), and whose color changes, sexual dimorphism, and acclimation are of interest to physiologists and ecologists (e.g., Fingerman, 1966; Valiela et al., 1974; Vernberg, 1969). The family Goneplacidae is represented by *Malacoplax* (25.30), usually found burrowing with *Uca* on intertidal mud flats, but ranging into the subtidal as well. Finally, the family Pinnotheridae embraces the pea crabs that usually live as commensals with other invertebrates (Cheng, 1967; Clark, 1956; Quayle, 1960). Free-living males of some genera bear little resemblance to females, which are animated egg sacs imprisoned within their unresisting hosts. Invertebrate species with which pinnotherids have been found as commensals are listed in Schmitt, McCain & Davidson (1973).

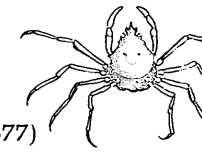
Crabs contribute to human welfare both directly as food for man (Frey, 1971) and indirectly as food for fishes and other animals (Quast, 1968). Crab claws excavated from kitchen middens testify to the importance of this food source to early California Indians (Hubbs, 1967). A single species of crab, *Cancer magister*, now accounts for 99 percent of the commercial catch in California waters, annually averaging 4,850 metric tons for the state, and over 16,000 metric tons for the west coast. The planktonic larvae of this species are consumed in vast quantities by such pelagic fishes as the herring, pilchard, and salmon; these in turn are fed upon by the tuna,

fur seal, and bear, respectively. Juvenile *Cancer productus* (25.22) are eaten in large numbers by the sculpin *Scorpaena guttata*, the kelp bass *Paralabrax clathratus*, and the sand bass *P. nebulifer*. The rock crab *Cancer antennarius* (25.16) is a delicacy esteemed by the sea otter of the Monterey coast, and adults of *Pachygrapsus crassipes* (25.43) are devoured by rats, raccoons, and sea gulls. Mink, ducks, and octopuses are crab predators in British Columbia. *Hemigrapsus oregonensis* (25.45) is stalked by the willet and other shorebirds, and is used by fishermen as bait for the pile perch in the Monterey area. *Loxorhynchus crispatus* (25.11) and *Paraxanthias taylori* (25.28) are important food sources for some fishes, notably the black croaker and the cabezon; *P. taylori* is eaten by the scorpion fish as well. *Lophopanopeus frontalis* (25.26), *Mimulus foliatus* (25.8), and *Pugettia* spp. have been found among stomach contents of the tidepool fish *Gibbonsia elegans* in the Los Angeles area.

Rathbun (1926), Menzies (1951), and more recently Zullo & Chivers (1969) and Nations (1970, 1975) have contributed to our knowledge of fossil crabs of the Pacific coast. Of these the Cancridae are best known because their heavy claws fossilize readily. Of living species *Cancer magister* (25.20) appeared in the Lower Pliocene, *C. antennarius* (25.16), *C. anthonyi* (25.17), *C. gracilis* (25.18), *C. oregonensis* (25.21), and C. *productus* (25.22) in the Middle Pliocene, *C. branneri* in the Upper Pliocene, and *C. jordani* (25.19) in the Lower Pleistocene. When these and other living species are found as fossils either north or south of their present range, we have the best possible evidence of climatic change, assuming that past and present ecological requirements are similar.

Warner (1977) provides an excellent modern introduction to the biology of crabs. For further general reading and reference the following are also recommended: for crustacean biology, Green (1961), Kaestner (1970), and Schmitt (1965); for crustacean physiology, Lockwood (1967) and Waterman (1960, 1961); for life history studies, Costlow & Bookhout (1960), Gurney (1960), Lebour (1928), and Wear (1970); for economic importance, Frey (1971) and Scheuerman (1958); for fossil crustaceans, Glaessner (1969); and for phylogeny and evolution, Whittington & Rolfe (1963), and Williamson (1974). Carlton & Kuris (1975) offers a key to species common in the intertidal zone in central California. Planktonic larvae found off the California coast may be identified to the family level using the key in Hart (1971a).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Majidae



25.1 **Pyromaia tuberculata tuberculata** (Lockington, 1877)
(=Inachoides tuberculatus)

Common under rocks in bays and on protected wharf pilings, low intertidal zone; subtidal to 411 m; Tomales Bay (Marin Co.) to Cabo Corrientes (Colombia); Japan; Pleistocene fossils from San Pedro (Los Angeles Co.) and San Diego Bay.

Carapace pyriform, tuberculate, to 17.7 mm wide in males and 15.1 mm in females; rostrum bearing a single spine; postorbital spine curving around eye; manus of cheliped inflated in male; walking legs long and slender; body and appendages often heavily overgrown with sponges and seaweeds, providing excellent camouflage; movements sluggish.

Although this crab may be collected intertidally in the southern part of the state, it is more properly considered a subtidal species; northern and central California collections have been made with a dredge or trawl, as in Tomales Bay (Marin Co.) and Monterey Bay.

See Garth (1958), Rathbun (1925, 1926), Ricketts & Calvin (1968), Sakai (1976), Schmitt (1921), and Willett (1937); the figure used in Schmitt and in Rathbun (1925) is of the Gulf of California subspecies, *P. tuberculata mexicana* (Rathbun).

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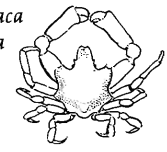

25.2 **Epialtoides hiltoni** (Rathbun, 1923)
(=Epialtus hiltoni) Small Kelp Crab

Among holdfasts of eelgrass (*Zostera*) and surfgrass (*Phyllospadix*), low intertidal zone; Santa Catalina Island (Channel Islands) and Laguna Beach (Orange Co.) to Bahía Magdalena, also Isla Guadalupe, Islas San Benito, and Isla Cedros (Baja California).

Carapace width to 15.7 mm in males, to 9.6 mm in females; species distinguished from the young of *Pugettia* (25.4–7) or *Taliepus* (25.3) by the oblong rostrum with bilobed tip, the

broad and advancing anterior marginal lobes, the prominent preorbital tooth, and the elongated manus of the cheliped in the male.

The discovery of this small kelp crab in an eelgrass holdfast in a cave at La Jolla (San Diego Co.) provided the clue that enabled others to obtain it in goodly numbers and to extend its known range to Mexico and offshore islands.

See Garth (1958) and Rathbun (1925).

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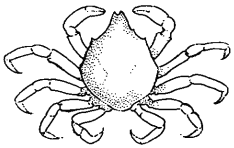

25.3 **Taliepus nuttallii** (Randall, 1839)
(=Epialtus nuttallii) Southern Kelp Crab, Globose Kelp Crab

Clinging to larger brown algae, low intertidal zone on rocky shores, and among kelp beds offshore; subtidal to 93 m; Santa Barbara to Bahía Magdalena (Baja California); less abundant than formerly, owing to absence of large kelps; Pleistocene fossils from Playa del Rey (Los Angeles Co.).

Carapace to 92 mm wide in males, to half that in females; species differing from *Pugettia producta* (25.4) in having a more convex carapace and a more prominent rostrum with a small triangular notch at the tip, and in lacking the small tooth in front of the eye; color dark red-brown.

Rather than a replacement of *Pugettia producta* (25.4) south of Point Conception (Santa Barbara Co.), as suggested in Ricketts & Calvin (1968), *T. nuttallii* is the northern hemispheric analogue of the south-temperate *T. marginatus* (Bell, 1835) from north Chile and Peru, and as such defines a north-temperate region.

This herbivorous crab shows a marked preference for large brown algae, especially *Macrocystis* and *Egregia*.

See Garth (1955, 1958), Hinton (1969), Johnson & Snook (1927), Leighton (1966), North (1964), Rathbun (1925), Ricketts & Calvin (1968), Schmitt (1921), and Willett (1937).

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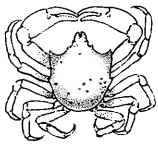

25.4 **Pugettia producta** (Randall, 1839)
(= Epialtus productus) Shield-Backed Kelp Crab, Kelp Crab

Young animals common among rocks or on the brown alga *Egregia*, low intertidal zone on rocky shores of protected outer coast in winter, migrating to floating kelp (*Macrocystis*) in summer as they grow older; subtidal to 73 m; Prince of Wales Island (Alaska) to Punta Asunción (Baja California); Pleistocene fossils from Santa Monica and San Pedro (both Los Angeles Co.).

Carapace width to 93 mm in males, 78 mm in females; color reddish or olive-brown, mottled with small round spots of darker shade, frequently lighter in young; species distinguished from *Taliepus nuttallii* (25.3) by its depressed and alate margins.

Both this species and *T. nuttallii*, the other large kelp crab of the California coast, were once placed in the genus *Epialtus*, now restricted to the smaller kelp crabs.

Pugettia producta is mainly an herbivore on larger brown algae, aggregating in densities up to 27 per m^2 of kelp holdfast in the Monterey region. In California waters the preferred foods are *Macrocystis*, *Egregia*, and *Pterygophora*. In Puget Sound (Washington) the main summer diet is brown algae (*Fucus*, *Sargassum*, and *Nereocystis*); in winter, on pilings where the normal plant foods were not available, individuals changed to a carnivorous diet including barnacles, hydroids, and bryozoans. Brackish conditions are not tolerated; the crabs do not osmoregulate, and the body wall is several times more permeable than that of the common shore crabs *Pachygrapsus crassipes* (25.43) and *Hemigrapsus nudus* (25.44).

Breeding in California occurs all year. Females mate while hard-shelled, and at least half the females are found carrying eggs at all months of the year. Pairs have been observed to mate in a male-under-female position, while eggs were still attached to the pleopods of the female. In Monterey Bay, eggs are carried for 28–31 days before hatching. Females held in the laboratory typically deposited a new brood of eggs within 2 days after the hatching of the previous brood, and appear

capable of producing a new crop of offspring approximately every 30 days. In Puget Sound populations, brood size for females 41–56 mm in carapace width averaged about 61,000 (range 34,000–84,000). In Monterey Bay, 66 percent of the ovigerous females examined had egg masses infested with the small (1–2 mm long) nemertean worm *Carcinonemertes epialti*. About 3 percent of all crabs were parasitized by the highly modified barnacle *Heterosaccus californicus* (20.34), which is visible beneath the abdomen (see Fig. 20.34) and interferes with normal reproductive activity.

Additional studies have been conducted on the structure of the reproductive and nervous systems, the composition of the exoskeleton, and the physiology of respiration.

See Andrews (1945), Boolootian et al. (1959), Fasten (1915), Garth (1958), Gross (1957a), Hart (1940, 1968), Heath (1941), Hewatt (1938), Hines (1978), Hinton (1969), Huang & Giese (1958), Johnson & Snook (1927), Knudsen (1964a,b), Leighton (1966), MacGinitie (1935), MacGinitie & MacGinitie (1968), McLean (1962), North (1964), Rathbun (1925, 1926), Ricketts & Calvin (1968), Schmitt (1921), Thompson & Chow (1955), Weymouth et al. (1944), and Willett (1937).

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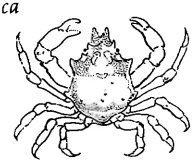

25.5 **Pugettia gracilis** Dana, 1851
Graceful Kelp Crab

In eelgrass and kelp, low intertidal zone on rocky shores; subtidal to at least 73 m depth; Attu Island (Aleutian Islands, Alaska) to Monterey Bay.

Carapace width to 39.2 mm in males, to 28.0 mm in females; species differing from *Pugettia richii* (25.6) in having the anterior marginal tooth broad and completely joined to the postorbital, in having the merus of the male cheliped with a superior (dorsal) crest, and in having the legs stout rather than slender.

Like the larger kelp crab *P. producta* (25.4), the graceful kelp crab keeps its carapace naked and smooth. It is active and has hooked and clawed legs, and does not disguise itself with bits of sponge, bryozoan, or algae, as do the more sluggish of the

spider crabs. In places it is quite numerous, and up to 92 per m^2 of kelp holdfast have been reported in Monterey Bay.

Mating occurs as in *Pachygrapsus* (25.43) and *Hemigrapsus* (25.44, 25.45), with the male supine on his back and the female above, facing him. Good reproductive data are lacking, but ovigerous females have been taken almost throughout the year in Puget Sound (Washington) and through much of the year in Oregon and California. Number of eggs per brood, for five females of carapace width 20–25 mm, ranged from 6,200 to 13,300, and averaged 10,500.

Small crabs found in the stomachs of the tidepool fishes *Gibbonsia metzi* and *Clinocottus analis* in the Los Angeles area were probably *P. richii* (25.6), rather than this species as reported.

See Andrews (1945), Fasten (1915), Garth (1958), Hart (1940), Johnson & Snook (1927), Kundsen (1964b), Mitchell (1953), Rathbun (1925), Ricketts & Calvin (1968), and Schmitt (1921).

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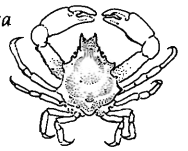

25.6 **Pugettia richii** Dana, 1851

Under stones, low intertidal zone on rocky shores; subtidal to 97 m; Prince of Wales Island (Alaska) to Isla San Gerónimo (Baja California); Pleistocene fossils from Playa del Rey (Los Angeles Co.) and San Diego.

Carapace to 36.0 mm wide in males, to 26.5 mm wide in females, constricted at base of anterior marginal tooth, this tooth narrow and incompletely joined to postorbital tooth; merus of cheliped with a few tubercles but lacking the superior crest present in *P. gracilis* (25.5); color variable, red to brown, the slender legs usually with light and dark bands.

This is another species in which the body is often effectively masked by an overgrowth of hydroids, bryozoans, and algae. In places the crabs are very abundant: up to 245 per m^2 of kelp holdfast were reported from Monterey Bay. Reproductive data are sketchy, but ovigerous females have been noted in Monterey Bay throughout the year, and in the Los Angeles area in September.

Small individuals found in the stomachs of the tidepool fishes *Gibbonsia metzi* and *Clinocottus analis* in the Los Angeles area were probably this species, rather than *P. gracilis* (25.5) as reported.

See Andrews (1945), Garth (1958), Hart (1940, 1953, 1962, 1968), Hewatt (1938), Hines (1978), Johnson & Snook (1927), McLean (1962), Mitchell (1953), Rathbun (1925, 1926), Schmitt (1921), Turner, Ebert & Given (1969), and Willett (1937).

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25.7 **Pugettia dalli** Rathbun, 1893

Among holdfasts of various marine plants and sessile animals, low intertidal zone on rocky shores, and on harbor floats; subtidal to 117 m; San Miguel Island (Channel Islands) to Cabo Thurloe (Baja California).

Carapace to 13.8 mm wide in males, to 10.3 mm wide in females, covered with minute vesicles; anterior marginal projection a transverse spine, the postorbital projection an ovate lobe inclined at a right angle to it; propodus of male cheliped crested, carpus doubly so; walking legs slender; color varying with algal surroundings.

Within its range this crab is distinguished from *P. richii* (25.6) by its slender walking legs and transverse anterior marginal spine. The body is frequently clothed with calcareous algae and the bryozoan *Holoporella*. The species is known from all of the Channel Islands and from numerous mainland localities from Los Angeles Co. southward. At Santa Catalina Island it is found in holdfasts of the kelp *Eisenia* and in clumps of the red algae *Lithothrix* and *Liagora*. At Redondo Beach it is common among hydroids on floating docks and on pilings, and at Corona del Mar it occurs on the surfgrass *Phyllospadix*.

Ovigerous females may be found in any month, but most abundantly in August. The young have proportionately longer rostral spines than do the adults.

See Garth (1958), Johnson & Snook (1927), Rathbun (1925), and Schmitt (1921).

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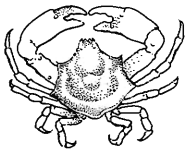
25.8 **Mimulus foliatus** Stimpson, 1860



Uncommon under rocks, low intertidal zone on protected outer coast; common on kelp (*Macrocystis*) holdfasts in subtidal waters offshore and ranging to depths of 128 m; Captain's Bay (Unalaska, Alaska) to Point Arguello (Santa Barbara Co.) and Santa Cruz Island (Channel Islands), and occasionally San Diego.

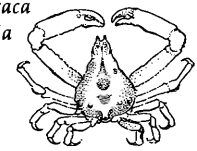
Carapace to 39 mm wide in males, 32.4 mm wide in females, the lateral expansions leaflike and overlapping at lateral fissures, the two rostral horns short, narrowly separated; predominant color red or red-brown, lighter on chelae than on carapace, with a white "V" and red-and-white striped legs (neither shown in photograph).

Adults may have a covering growth of bryozoans or sponges. In the kelp forests off Pacific Grove in Monterey Bay, populations of up to 73 crabs per m^2 of kelp holdfast have been reported. Individuals are more abundant among the kelp in summer and fall than in late winter, but ovigerous females occur in the population throughout the year. *Macrocystis* is a major element in the diet.

Specimens of *M. foliatus* taken from the stomach of the tidepool fish *Gibbonsia metzi* in the Los Angeles area and from the surface of a rock cod in 9 m of water near Point Loma (San Diego Co.; unpublished record) confirm the presence of this cold-water species in regions of upwelling well south of its normal range.

See Andrews (1945), Garth (1958), Hart (1940), Hewatt (1938), Hines (1978), Johnson & Snook (1927), McLean (1962), Mitchell (1953), Rathbun (1925), Ricketts & Calvin (1968), and Schmitt (1921).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Majidae



25.9 **Scyra acutifrons** Dana, 1851
Sharp-Nosed Crab

Among algae and associated sessile animals, on and under rocks, low intertidal zone on protected outer coast; also among fouling growth on pilings; subtidal to 91 m; Kachemak Bay (Cook Inlet, Alaska) to Punta San Carlos (Baja California); Pleistocene fossils from San Pedro (Los Angeles Co.).

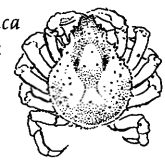
Carapace to 37.7 mm wide in males, 30 mm in females, pyriform, tuberculate but not spinose, the rostrum composed of two flattened horns; chelipeds of male enlarged, the propodus compressed and crested.

The carapace of larger specimens is usually covered with an encrustation of sponges, tunicates, barnacles, bryozoans, and hydroids. Although not so efficient a masker as *Loxorhynchus crispatus* (25.11), *S. acutifrons* is more truly an intertidal crab than the larger species. Like other spider crabs, it usually sits with the anterior end pointed down.

Ovigerous females may be found almost any month of the year. In females 19.5–30 mm across the carapace, the number of eggs carried ranged from 2,700 to 16,300, averaging 8,600. A second batch of eggs may be produced shortly after the first has hatched.

See Garth (1958), Hart (1940), Hines (1978), Johnson & Snook (1927), Knudsen (1964b), McLean (1962), Rathbun (1925, 1926), Ricketts & Calvin (1968), Schmitt (1921), and Turner, Ebert & Given (1969).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Majidae



25.10 **Loxorhynchus grandis** Stimpson, 1857
Sheep Crab

Occasional, low intertidal zone (as at Hedionda Lagoon, San Diego Co.); characteristically subtidal to depth of 124 m; Cordell Bank (Marin Co.) to Punta San Bartolomé (Baja Cali-

fornia); Upper Oligocene fossils from Washington; Pliocene fossils from central California; Pleistocene fossils from Santa Monica and Playa del Rey (both Los Angeles Co.).

Carapace to 159 mm wide in males, 115 mm wide in females, inflated, ovate, sparsely tuberculate but with two anterior marginal tubercles; rostrum strongly deflexed; chelipeds of males greatly enlarged, especially in old individuals.

Because of its large size, peculiar shape, and deliberate movements, the sheep crab presents a ludicrous appearance. The young mask themselves with living barnacles, bryozoans, hydroids, and algae and tend to remain in environments where they match the background. The adults have less need for concealment; they lose the instinct to decorate themselves, and divers report seeing them walking on open, sandy, subtidal bottoms. The animals are carnivores and scavengers; hungry crabs in aquaria have been observed to take apart and feed on starfishes, clams, and even octopuses.

Mating has been noted in the spring and early summer off southern California.

The polychaete *Iphitime loxorhynchi* is found in the branchial cavity.

See Garth (1958), Hartman (1952), Johnson & Snook (1927), MacGinitie (1937), MacGinitie & MacGinitie (1968), Nations (1975), Rathbun (1925, 1926), Schmitt (1921), Turner, Ebert & Given (1969), Wicksten (1979b), and Willett (1937).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Majidae

25.11 **Loxorhynchus crispatus** Stimpson, 1857
Masking Crab, Moss Crab

Scarce in low intertidal zone on rocky shores of protected outer coast, much more common on subtidal pilings, kelp holdfasts, and rocks to 183 m depth; Redding Rock (Humboldt Co.) to Isla Natividad (Baja California)—unpublished records; Pleistocene fossils from Santa Monica and San Pedro (both Los Angeles Co.).

Carapace width to 88 mm in males, 68 mm in females; spe-

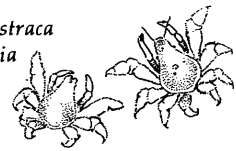
cies distinguished from *L. grandis* (25.10) by: (1) smaller size, (2) a carapace with fewer tubercles and only one anterior marginal tubercle, (3) a rostrum not strongly deflexed, and (4) a plushlike coat of short, thick hairs; chelipeds much longer in males than in females, to 335 mm long in old males; walking legs short for a spider crab.

These slow-moving crabs are generally found so thickly covered with foreign growth, such as hydroids, anemones, seaweeds, bryozoans, and sponges, that in their natural environment they are scarcely recognizable as crabs at all. Crabs experimentally denuded quickly redecorate themselves, using scraps of whatever is available. Masking materials are attached by wedging them among strong hooked setae provided with spines or barbs. Crabs with these setae removed are unable to decorate themselves until the setae are regenerated, at the next molt. Secretions from glands on the mouthparts play no role in attachment of masking materials.

Large individuals are often found clinging, head down, on vertical walls and pilings. They eat a wide variety of materials including algae, sponges, small crustaceans, erect bryozoan colonies, and several other invertebrates. Under aquarium conditions the purple sea urchin, *Strongylocentrotus purpuratus* (11.5), is torn apart and consumed. Sessile or sedentary prey are preferred. The crabs, in turn, form an important food for some fishes, including the black croaker and the cabezon.

See Garth (1958), Haderlie (1968, 1969), Haig & Wicksten (1975), Hines (1978), Holmes (1900), Johnson & Snook (1927), Limbaugh (1961), McLean (1962), O'Connell (1953), Rathbun (1925, 1926), Schmitt (1921), Turner, Ebert & Given (1969), and Wicksten (1975, 1977a,b, 1978, 1979b).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Suborder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Majidae



25.12 **Pelia tumida** (Lockington, 1877)
Dwarf Crab

Under stones, low intertidal zone on rocky shores; subtidal to 100 m; Monterey Bay to Bahía de Petatlán (Mexico), including Gulf of California.

Carapace small, to 14.5 mm wide in males, 13 mm in females, pear-shaped, covered with pubescence to which sponges and other foreign particles adhere; rostrum bifid; walking legs compressed, bearing stiff setae on margins.

When turned on its back, the dwarf crab usually remains motionless with legs upcurved, almost indistinguishable from its surroundings. When placed in an aquarium and deprived of its normal covering, it decorates itself with any material available. A common inhabitant of kelp holdfasts, up to 65 per m^2 of *Macrocystis* holdfasts were reported in Monterey Bay.

See Andrews (1945), Garth (1958), Johnson & Snook (1927), Rathbun (1925), and Schmitt (1921).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Majidae

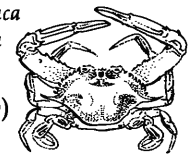
25.13 **Herbstia parvifrons** Randall, 1839
Spider Crab

Infrequent, under stones, low intertidal zone; occasionally dredged to 73 m; Monterey Bay to Bahía Magdalena (Baja California).

Carapace to 41.6 mm wide in males, 17.1 mm wide in females, flattened, ovate, usually overgrown with sponges; rostrum short; legs long, spiny; color (not shown well in the photograph) light tan to mottled brown, the chelipeds a more pronounced red with tips of fingers white, the walking legs banded with reddish brown.

This species, not likely to be confused with any other spider crab within its range, is distinguished from *H. camptacantha* of the Gulf of California by having two teeth between the inner and outer orbital teeth, instead of only one.

See Garth (1958), Rathbun (1925), Schmitt (1921), and Weymouth (1910).



25.14 **Portunus xantusii xantusii** (Stimpson, 1860)
Swimming Crab

On sand flats, low intertidal zone; in beds of eelgrass (*Zostera*) in Mission Bay (San Diego Co.); subtidal to 179 m; occasionally found swimming at water surface, attracted to ship's lights at night; Santa Barbara to Topolobampo (Mexico); not likely to be found intertidally north of Newport Bay (Orange Co.); Pleistocene fossils from Playa del Rey (Los Angeles Co.) and San Diego.

Carapace broad, flat, finely pubescent, each lateral angle armed with a long spine; body width (including spines) to 70.7 mm in males, 73.1 mm in females; last pair of legs paddlelike, each merus armed with spinules but no spine.

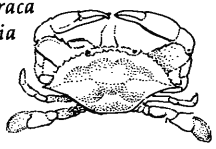
These crabs swim by sculling with the flattened last pair of legs. Swimming, like walking, is sideways, with one "elbow" leading and the cheliped and legs of the opposite side trailing. Predation of *Portunus* on the mole crab *Emerita analoga* (24.4) has been described by the MacGinities. A portunid moving across a bed of *Emerita* pauses frequently to push one of the large claws straight down into the sand. If an *Emerita* is found and grasped, *Portunus* starts running in a circle about the submerged claw while pulling it upward till the prey breaks the sand surface.

Ovigerous females of *Portunus* are found from May through September.

This crab has close relatives to the south. A subspecies, *P. xantusii minimus* Rathbun, occurs in the Gulf of California, and another subspecies, *P. xantusii affinis* (Faxon), extends south to Ecuador and Peru.

See Ally (1974), Garth & Stephenson (1966), Glassell (1935), Johnson & Snook (1927), MacGinitie & MacGinitie (1968), Rathbun (1926, 1930), Ricketts & Calvin (1968), Schmitt (1921), and Willett (1937).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Portunidae



25.15 **Callinectes arcuatus** Ordway, 1863
Swimming Crab

On sand and mud bottoms of lagoons and estuaries, often seined at mouths of shallow sloughs such as Anaheim Slough (Orange Co.), low intertidal zone to 27 m depth; Los Angeles harbor to Peru, including Gulf of California.

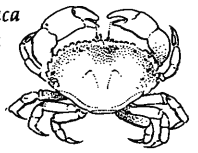
Carapace width, including lateral spines, to 120.5 mm in males, 98.5 mm in females; species differing from *Portunus xantusii* (25.14) in having the male abdomen in the shape of an inverted letter "T" and in lacking the inner spine on the wrist of the cheliped.

Along the California coast, *C. arcuatus* could be confused only with its congener **C. bellicosus** (Stimpson), which has been reported from San Diego and Point Loma (San Diego Co.) and as a Pleistocene fossil from Playa del Rey and Long Beach (both Los Angeles Co.). Both species are related to the edible blue crab of the east coast, *C. sapidus*, which is marketed in the soft-shelled condition, and they are said to be as savory.

Ovigerous females have been found from March to September.

See Garth & Stephenson (1966), Rathbun (1926, 1930), and Willett (1937).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Cancridae



25.16 **Cancer antennarius** Stimpson, 1856
Rock Crab

Common in some areas, low intertidal region on rocky shores; subtidal around bases of kelp and on gravel bottoms to 40 m depth; Coos Bay, Oregon (unpublished record) to Baja California, including Islas de Todos Santos; probably not British Columbia as reported; Pliocene fossils from central and southern California; Pleistocene fossils from Playa del Rey and San Pedro (both Los Angeles Co.).

Carapace to 118 mm wide in males, to 78 mm wide in females; juveniles pubescent, adults with only a fringe of hair on the lower surface, abdomen, and walking legs; species readily recognized by the red speckling on the lower surface, especially anteriorly.

Considered by some to be as tasty as the Dungeness crab, *C. antennarius* supports only a very limited sport fishery. The animals are caught by hand or with a baited hoop net. Crabs 4 inches (10 cm) or more across the carapace may be taken at any season; the bag limit for this and all other members of the genus *Cancer* except the Dungeness crab (*C. magister*, 25.20) is 35 crabs of all species combined (1979 State Department of Fish and Game regulations, subject to change).

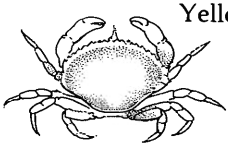
The rock crab is mainly an inhabitant of the outer coast. Although it may invade sloughs, it does not tolerate brackish conditions and cannot osmoregulate. It is both a scavenger and an active predator, eating a wide variety of other animals. It captures hermit crabs by walking over them and sitting on them, or several may be flicked under the body by the walking legs and held there in a cage formed by the body and appendages. A crab in its shell is then removed from the cage, held in both chelae, and inspected. The fingers of both large claws are then inserted into the aperture of the hermit crab's shell, and the shell cracked away a bit at a time until the hermit crab can withdraw no further and is removed and eaten. The rock crab itself is often eaten by the California sea otter in the Monterey area. The polychaete *Iphitime holobranchiata* lives in the branchial cavity.

Mating occurs after female crabs molt and while they are still soft-shelled. Ripe females ready to molt release a substance (pheromone) in the urine, which attracts the male and stimulates courtship behavior. Ovigerous females are most common from November to January, but a few may be found at other seasons in southern California. The first zoeal stage has been described.

See Case (1964), Cook (1965), Frey (1971), Ghiradella, Cronshaw & Case (1970), Giese (1966), Gross (1957a), Johnson & Snook (1927), Jones (1941), Kittredge, Terry & Takahashi (1971), MacGinitie (1935), McLean (1962), Mir (1961), Nations (1975), Phillips (1939), Pilger (1971), Rathbun (1930), Ricketts & Calvin (1968), Schmitt (1921), Thompson & Chow (1955), Turner, Ebert & Given (1969), and Willett (1937).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Cancridae

25.17 **Cancer anthonyi** Rathbun, 1897
Yellow Crab



In rocky areas of bays and estuaries, low intertidal zone; subtidal to 132 m; Humboldt Bay to Bahía Magdalena (Baja California); uncommon north of San Pedro (Los Angeles Co.); Pliocene and Pleistocene fossils from central California; Pleistocene fossils also from San Pedro and San Diego.

Carapace to 152 mm wide in males, to 98.7 mm wide in females; carpus of cheliped bearing only one spine, no spines on hand; black color of fingers extending less than half the length of outer margins; underparts uniformly light, not red-spotted as in *C. antennarius* (25.16).

This is an edible crab frequently taken in southern California by sport fishermen using baited hoop nets; size, season, and bag limits are the same as those listed under *C. antennarius*. The yellow crab is especially abundant on artificial reefs off southern California in April and May, and in Elkhorn Slough (Monterey Co.) in June and July.

Mating, which occurs immediately after the females molt, has been observed in June. Females ripe and ready to molt emit substances (pheromones) that attract males and stimulate courtship behavior. The first zoeal stage has been described.

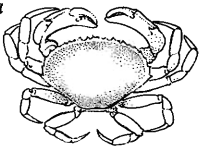
Divers off southern California noted a yellow crab actively removing ectoparasites from a sand bass 46 cm long. Juvenile crabs are eaten by a variety of reef fishes.

A smaller species, **C. amphioetus** Rathbun, has been taken intertidally at Newport Bay and Anaheim Landing (both Orange Co.). It occurs on sandy and muddy bottoms of shallow bays and in deeper water on bottoms of rock, pebbles, sand, and broken shells. Commonest subtidally, it ranges to depths of 148 m in American waters and to 309 m in Japanese waters. It is known from El Segundo, Los Angeles Co. (unpublished record) to Bahía Magdalena (Baja California) and the Gulf of California, and from Japan, Korea, and northern China; Pleistocene fossils are found at San Pedro (Los Angeles Co.) It is distinguished by having a carapace that is rela-

tively small (width to 29.5 mm in American specimens, to 41.4 mm in Japanese specimens), not hairy, strongly areolated (especially in the female), with marginal teeth broadly triangular and moderately produced. It differs from *Cancer anthonyi* in having the edges of the lateral teeth non-serrated and the median tooth of the front blunted.

For *C. anthonyi*, see Carlisle (1969), Frey (1971), Johnson & Snook (1927), Kittredge, Terry & Takahashi (1971), MacGinitie (1935), Mir (1961), Nations (1975), Phillips (1939), Rathbun (1926, 1930), Schmitt (1921), Turner, Ebert & Given (1969), and Willis (1968). For *C. amphioetus*, see Johnson & Snook (1927), Kim (1973), Nations (1975), Rathbun (1904, 1930), Sakai (1965, 1976), Schmitt (1921), and Shen (1932).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Cancridae



25.18 **Cancer gracilis** Dana, 1852
Slender Crab, Graceful Crab

Sometimes common on mud flats and in beds of eelgrass (*Zostera*), low intertidal zone in bays; subtidal to 174 m offshore; Prince William Sound (Alaska) to Bahía Playa María (Baja California); usually not taken intertidally south of central California; Pliocene fossils from Los Angeles; Pleistocene fossils from Santa Monica (Los Angeles Co.) to San Diego.

Carapace to 91 mm wide in males, to 64 mm wide in females; species distinguished from *C. magister* (25.20) by its smaller size, more convex carapace, and absence of tubercles upon its surface; walking legs slender and graceful, suggesting the specific name.

Although seasonally found in bays, the slender crab does not tolerate brackish conditions; its body wall is relatively permeable to water and salts, and it does not osmoregulate. It feeds mainly on animal remains, and on barnacles when available. Young crabs (carapace 8–35 mm wide) are a major food of the starry flounder, *Platichthys stellatus*, in Monterey Bay. Some adults are taken for human consumption. California sport fishing regulations (1979, and subject to change) are the same as for *C. antennarius* (25.16).

In Elkhorn Slough (Monterey Co.), mating is common in November, and ovigerous females were noted in July and August. Farther north, in Puget Sound (Washington), animals held in the laboratory bore eggs from December to April, and a few females produced a small second brood. The males remain with the females after mating, and appear to protect them. Larval stages are planktonic, as in other crabs, and the megalops larvae and juvenile crabs are frequently found crawling unharmed on and under the bells, and even in the stomachs, of the larger jellyfishes, especially *Pelagia colorata* (3.21).

See Gross (1957a), Hart (1968), Johnson & Snook (1927), Knudsen (1964b), MacGinitie (1935), Nations (1975), Orcutt (1950), Phillips (1939), Rathbun (1926, 1930), Schmitt (1921), Turner, Ebert & Given (1969), and Weymouth (1910).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Cancridae

25.19 **Cancer jordani** Rathbun, 1900
Hairy Cancer Crab

Under rocks, low intertidal zone; subtidal to 104 m; Coos Bay (Oregon; unpublished record) to Cabo Thurloe (Baja California); Pleistocene fossils from San Pedro (Los Angeles Co.).

A small species of *Cancer* with a hairy carapace to 33.4 mm wide in males and 19.5 mm wide in females (the only small hairy *Cancer* besides *C. branneri*, see below); anterolateral carapace margin with sharp teeth, alternately large and small, the tenth (most posterior) tooth inconspicuous; carpus of cheliped bearing two spines at distal end.

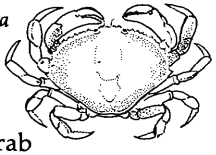
Up to 78 *C. jordani* were recorded per m^2 of kelp holdfast in Monterey Bay. The natural history of this crab is poorly known, but ovigerous females have been noted in Monterey Bay in October and November.

A similar species, **C. branneri** Rathbun, ranges from Alaska to Isla Cedros, Baja California (unpublished record), and is known from Pliocene fossils at Santa Barbara and Los Angeles and from Pleistocene fossils at Tomales Bay (Marin Co.) and San Pedro (Los Angeles Co.). *C. branneri* differs from *C.*

jordani in having the tenth (most posterior) of the teeth on the anterolateral carapace margin spiniform, in having the middle orbital tooth resembling the two outer teeth but less advanced, and in having a markedly areolated carapace.

See Andrews (1945), Garth (1961), Hewatt (1938), Johnson & Snook (1927), MacGinitie (1935), McLean (1962), Nations (1975), Rathbun (1930), Reish & Winter (1954), and Schmitt (1921).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Cancridae



25.20 **Cancer magister** Dana, 1852
Dungeness Crab, Market Crab, Common Edible Crab

Sometimes in sandy pools between low intertidal rock outcroppings, but more commonly from deeper sandy bottoms; subtidal to 230 m, but not abundant below 90 m; Tanaga Island (Aleutian Islands, Alaska) to Pismo Beach, San Luis Obispo Co. (unpublished record) and rarely to Santa Barbara (unpublished record), but probably not Bahía Magdalena (Baja California) as reported; Pliocene fossils from Coos Bay (Oregon) to Ventura and Pleistocene fossils from Cape Blanco (Oregon) to San Pedro (Los Angeles Co.).

Carapace to 230 mm wide in males, to about 165 mm wide in females, granular, its anterolateral margins each bearing ten small teeth or denticles, the posterior one the largest.

This crab, the largest edible true crab on the west coast, supports a large fishery from California to British Columbia. Annual catch for the whole coast averages over 16 million kg (35 million lbs), with an annual price to the fishermen of about $5.5 million. This species alone accounts for more than 99 percent of all crab species taken commercially in California. In California waters there appear to be five subpopulations, which show little or no mixing, centering in the following areas: (1) Avila/Morro Bay (San Luis Obispo Co.), (2) Monterey Bay, (3) San Francisco, (4) the region from Fort Bragg (Mendocino Co.) to Cape Mendocino (Humboldt Co.), and (5) the Eureka/Crescent City region, north of Cape Mendocino (Humboldt and Del Norte Cos.). The three southern areas now yield few crabs, and the bulk of California's catch

comes from Fort Bragg northward to the Oregon border. Crabs are taken in traps, mainly at 10–45 m depth; the California catch alone has averaged over 4.8 million kg (about 10.7 million lbs) annually over the past 25 years, but the catch fluctuates greatly from year to year. Both commercial and sport fishing for the species is strictly controlled. According to the 1979 sport fishing regulations of the California Department of Fish and Game (subject to change), the bag limit is 10 crabs, and only male animals measuring 6.25 inches (16 cm) or more across the carapace may be taken; south of Mendocino Co. the fishing season is from the second Tuesday in November through June 30, and in Mendocino Co. and northward it is from December 1 through July 30. No crabs may be taken in San Francisco and San Pablo Bays.

The crabs are carnivores, and 40 different identifiable food items have been found in their stomachs. Smaller crustaceans of all sorts are favored foods; small clams and oysters are also eaten, the shells being crushed or opened by chipping away the margins with the strong claws. Some worms are taken, and even some fishes caught with the chelipeds. Dead animal flesh is eaten only if fresh and unspoiled. On a soft bottom the crabs often bury themselves with only their eyes and antennae exposed. Water is circulated through the gill chamber even while the crabs are buried; normally water enters from below and passes out anteriorly, but currents can be reversed to flush the gill chamber. Gill surface area is large, about 877 cm^2 in a crab 11.8 cm across the carapace.

Mating occurs from April to September in British Columbia, and may begin earlier in California. Female crabs may store viable sperm for several months before use. California females spawn from September to December, and most adult females are found with eggs from November through February. The smallest females with eggs are about 10 cm across the carapace. The number of eggs carried in a brood varies with the size of the female, ranging from 700,000 to about 2.5 million. Hatching starts in December and reaches a peak in March. Molting of the adults follows reproduction, from May to September, with a peak in the summer.

The eggs hatch as protozoea larvae, a stage lasting only a few minutes, then pass through five successive zoeal stages to a megalops stage. The larval period, from hatching through

the megalops phase, lasts 3–5 months, depending on temperature, salinity, and other factors. These larval stages are pelagic, and tend to stay in the upper 20 m of the sea; enormous numbers are eaten, especially by such fishes as the herring, pilchard, and salmon.

Metamorphosis of the megalops larvae into juvenile crabs occurs mainly from April through June off California. The young crabs take up residence on the bottom, where many more are consumed by bottom predators. At this stage males and females can be told apart by differences in primary sex organs. Thereafter it takes about 1.5 years and about 11 molts to reach sexual maturity (at a carapace width of about 10 cm). Males reach legal size at an age of 3.5–4 years in California waters, and after sexual maturity both males and females molt only once a year. The largest animals, about 23 cm across, are probably about 6 years old in California, and perhaps 1–2 years older in more northerly waters. Hermaphroditism has been reported only once.

The megalops larvae of *Cancer magister* often attach to the bells of pelagic jellyfishes and to the tentacles of the chondrophoran *Velella velella* (3.18). Off Bodega Bay (Sonoma Co.) and outside San Francisco Bay, up to 88 percent of the *Velella* carried from one to three megalopa, and the guts of the crab larvae were full of undischarged *Velella* nematocysts.

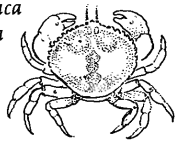
Recent studies on *C. magister*, largely carried out or sponsored by the California Department of Fish and Game, include investigations of the yearly migrations of tagged crabs, the life history of the crab under laboratory and field conditions, the distribution and behavior of the pelagic larval stages, and the possible causes of recent declines in commercial catches. It has been discovered that in general, from Fort Bragg northward, male crabs in most areas move farther offshore from November to March and closer inshore from March through June. North of Cape Mendocino there are population shifts northward or southward with season, but the movements differ in different areas. Causes of fluctuations in the crab populations in nature are difficult to pinpoint, but among those suggested and investigated are (1) the effects of pesticides, sewage, and industrial pollutants on the mortality of larval and adult crabs and on crab reproduction, (2) predation by a nemertean worm, *Carcinonemertes errantia*,

on the fertilized eggs and embryos carried on the pleopods by brooding female crabs, and (3) predation on the pelagic larval stages of the crab by such fishes as the coho salmon, recently successfully introduced into rivers not far from the fishery area. *Velella* may serve to transport crab larvae to the nearshore habitats of juvenile Dungeness crabs, and the presence of the hydrozoan in coastal waters may also contribute to the fluctuations in abundance.

Fossil remains of species of *Cancer* first appear in the Eocene epoch, about 60 million years ago. The species known today are confined mainly to temperate seas where annual mean temperatures range between 4° and 24°C (40–75°F).

See Butler (1967) for a bibliography of 131 papers dealing with various aspects of this crab; sources for the present account, some not listed in Butler's bibliography, include Buchanan & Millemann (1969), Fasten (1915), Frey (1971), Giese (1966), Gotshall (1977, 1978a,b,c), Johnson & Snook (1927), Jones (1941), MacGinitie (1935), MacKay (1934, 1937, 1942, 1943a,b), Mir (1961), Nations (1975), Phillips (1935, 1939), Poole (1966a, 1967), Rathbun (1926, 1930), Reed (1969), Ricketts & Calvin (1968), Scheer & Meenakshi (1961), Scheffer (1959), Schmitt (1921), M. Smith (1963), Snow & Nielsen (1966), Snow & Wagner (1965), Thompson & Chow (1955), Waldron (1958), Welsh (1974), Weymouth (1915, 1916), Weymouth & MacKay (1934), Wickham (1977, 1979), Wickham, Schleser & Schuur (1976), and Willis (1971).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Cancridae



25.21 **Cancer oregonensis** (Dana, 1852)
Oregon Cancer Crab

Occasionally found under rocks or wedged in crevices and holes, low intertidal zone on rocky shores, also on pilings heavily encrusted with barnacles and mussels; more abundant subtidally, to 435 m depth; St. George Island (Pribilof Islands, Alaska) to Palos Verdes (Los Angeles Co.): probably not Bahía Magdalena (Baja California) as reported; Pliocene fossils from Trinidad (Humboldt Co.) to San Diego; Pleistocene fossils from Oregon to San Pedro (Los Angeles Co.).

Carapace to 31.9 mm wide in males, 47.1 mm wide in females, widest opposite the seventh or eighth tooth, differing

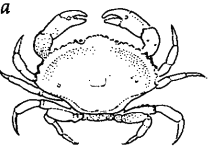
from the carapace in all other *Cancer* species in not having the anterolateral and posterolateral margins meeting at an angle, thus body appears more rounded when viewed from above; walking legs hairy; body dark red above, lighter below; chelipeds with dark-colored claws.

Biological studies have been carried out mainly on populations from Puget Sound (Washington). The crabs are primarily carnivores. Barnacles, the staple food when available, are crushed with the chelipeds. Polychaete worms and smaller crustaceans are also taken, along with a few scraps (possibly incidental) of smaller green algae.

Courtship, molting, and mating occur in late spring and summer, mainly from April to June. The male grasps and carries a female for several days before she molts, and mating occurs after the molting. Courting pairs conceal themselves well, and the male remains with his mate until her shell has hardened enough for normal activity. Sperm are stored by the female until the eggs are laid, and ovigerous females are seen mainly from November to February. One brood a year seems normal, but occasional ovigerous females found from April to June are probably carrying a second brood. The number of eggs borne by ovigerous females of carapace width 17–26 mm ranged from 10,000 to 33,000, averaging 20,540.

See especially Knudsen (1964a); see also Hart (1940), Johnson & Snook (1927), Nations (1975), Rathbun (1930), Ricketts & Calvin (1968), Schmitt (1921), and Wicksten (1979a).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Cancridae



25.22 **Cancer productus** Randall, 1839
Red Crab

Often half buried in sandy substratum under rocks, low intertidal zone, primarily in bays and estuaries, but also on protected rocky coasts; subtidal to 79 m; Kodiak Island (Alaska) to San Diego; probably not Bahía Magdalena (Baja California) as reported; Pliocene fossils from Trinidad (Humboldt Co.) to San Ysidro (Baja California); Pleistocene fossils from Cape Blanco (Oregon) to Punta Descanso (Baja California).

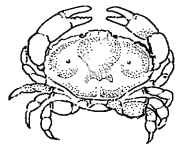
Carapace to 158 mm wide in both sexes, smooth, the margins serrate, the anterolateral teeth closely spaced; front produced beyond orbital angles as five equally spaced teeth; adults usually with upper surface dark red, lower surface yellowish white; young pure white or exhibiting a striking variety of color patterns including bands of brown and white, stripes of red and white, and brown stripes (as shown in Figs. 25.22c–h).

According to Rathbun (1930), many specimens formerly referred to the young of the common species *C. magister* (25.20), *C. productus*, and *C. antennarius* (25.16) were later found to belong to the more recently defined species *C. anthonyi* (25.17), *C. jordani* (25.19), and *C. branneri*. For this reason, reported occurrences prior to 1900 are questionable unless specimens are available for verification.

Like other *Cancer* species, *C. productus* is a carnivore, and any animal matter available is eaten. In Puget Sound (Washington), barnacles are crushed with the large claw and passed to the mouth. Small living crabs and dead fishes are also eaten.

Mating occurs when females are soft-shelled, especially in the summer months. Ovigerous females occur from October to June (especially December to March) in Puget Sound, and from January to August (especially April to June) in southern California. The larvae have been reared in the laboratory and are similar to those of *C. magister*. Juvenile crabs, common in southern California in the fall and winter, are eaten in large numbers by the sculpin *Scorpaena guttata*, the sand bass *Paralabrax nebulifer*, and the kelp bass *P. clathratus*. Adults are taken in small numbers by fishermen for food. Under 1979 sport fishing regulations there is no closed season; size and bag limits are the same as those listed under *C. antennarius* (25.16).

See Case (1964), Fasten (1915), Frey (1971), Ghiradella, Cronshaw & Case (1970), Hart (1940), Johnson & Snook (1927), Knudsen (1964b), MacGinitie (1935), McLean (1962), Nations (1975), Phillips (1939), Poole (1966b), Rathbun (1926, 1930), Schmitt (1921), Thompson & Chow (1955), Trask (1970), and Turner, Ebert & Given (1969).



25.23 **Cycloxanthops novemdentatus** (Lockington, 1877)
Large Pebble Crab

Common in pools and under rocks, low intertidal zone; young in crevices or in spaces between snail tubes; subtidal to 73 m; Monterey Bay to Punta Abreojos (Baja California), including offshore islands; not common in northern part of range, but conspicuous in the intertidal zone at La Jolla (San Diego Co.); Pleistocene fossils from Santa Monica and Playa del Rey (both Los Angeles Co.).

Carapace to 94 mm wide in males and 52.4 mm wide in females, flattened, granular and rugose anteriorly, smoother posteriorly, its anterolateral border bearing nine small teeth; color brown, tinged with purple and occasionally red, the chelae black.

This is the largest California pebble crab and the subject of extensive studies by Knudsen. The animals feed mainly on coralline algae and other red algae, but some green algae and surfgrass (*Phyllospadix*) are taken, and some animals, such as crustaceans and worms. Crabs in the field have been observed to break open and eat purple sea urchins (*Strongylocentrotus purpuratus*, 11.5) and to attempt to dislodge black abalones (*Haliotis cracherodii*, 13.4). In turn, they are preyed upon by larger crabs, fishes, and probably octopuses.

The crabs have cryptic habits, seek shelter if exposed, and tend to run toward dark places; they can bury themselves rapidly in sand if no other cover is available. When running, the last pair of legs is often held above the ground, serving as rear "feelers." Crabs backed against a wall use the back legs to walk along, or to grip, the wall, and crabs in low tunnels use the rear legs to gauge the height of the ceiling. Suddenly disturbed crabs may freeze motionless, some even exhibiting a cataleptic rigidity if roughly handled.

Females are sexually mature at a carapace width of 33 mm or more. There is no courtship prior to mating, and females mate while hard-shelled. Eggs are carried from mid-June to September in southern California, and ovigerous females move 1–2 m below the low tide level before extruding their

egg masses. An average female carries about 45,000 eggs, which hatch in 25–30 days. Larval stages include a prezoea, four zoeal instars, and a megalops stage, lasting altogether about 5 weeks under laboratory conditions. The larvae are active swimmers; the zoeae can cover a meter in 45–60 seconds, and the megalops nearly twice that.

See especially Knudsen (1960a,b,c); see also Johnson & Snook (1927), Rathbun (1926, 1930), Ricketts & Calvin (1968), Schmitt (1921), and Willett (1937).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Xanthidae

25.24 **Lophopanopeus bellus bellus** (Stimpson, 1860)
Black-Clawed Crab

Commonly burrowed in sand under rocks, low intertidal zone, especially in quiet waters of bays and estuaries where a single layer of rocks covers fine sand or mud; also in tidepools and kelp holdfasts on rocky shores; subtidal to 73 m; Resurrection Bay (Alaska) to Cayucos (San Luis Obispo Co.); Pleistocene fossils from Playa del Rey (Los Angeles Co.).

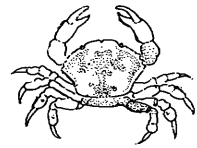
Carapace to 34.2 mm wide in males, 24.1 mm wide in females, pubescent; cheliped with the carpus smooth or rugose and bearing a deep dorsal groove, the propodus with a small lobe on upper margin, the dactylus with a large tooth at base; walking legs pubescent, the carpus slightly bilobed.

This crab has been studied in the Puget Sound area (Washington). The stomachs of the animals examined there contained brown algae, green plant matter, coralline algae, and some remains of mussels, barnacles, and other crustaceans. Females mate while hard-shelled, and most (60–70 percent) produce two broods of young a year. Brood 1 eggs are laid from December to April, and by early March over 90 percent of the females are ovigerous. Hatching occurs from April to August. Brood 2 eggs are deposited from May to mid-August, and hatching begins in August. Egg number per brood ranged from 6,000 to 36,000, averaging 15,640. For the population, egg production per female per year is about 25,000. The diploid chromosome number is 124.

A subspecies, **L. bellus diegensis** Rathbun, occurs from Monterey Bay to San Diego. It differs from *L. bellus bellus* in having the carpus of the cheliped tuberculated and the carpus of the walking legs markedly bilobed. The carapace of the males may be 21.8 mm wide, that of the females 19.3 mm wide. Studied extensively in southern California, this crab is similar in many ways to *L. bellus bellus*, but shows some differences. Ovigerous females occur from February through October. They carry fewer eggs (an average of 3,500), and there is evidence that some females may produce more than two broods per year. The crabs are mainly herbivores, but some animal matter is taken as well. Parasites found on the crabs include two species of rhizocephalan barnacles.

See especially Knudsen (1959a,b, 1960a,c, 1964b); see also Andrews (1945), Fasten (1921, 1926), Hart (1935, 1968), Johnson & Snook (1927), Menzies (1948), Rathbun (1930), Ricketts & Calvin (1968), Schmitt (1921), and Willett (1937).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Xanthidae



25.25 **Lophopanopeus leucomanus leucomanus** (Lockington, 1877)

Rather plentiful under rocks, buried in sand under rocks, among snail tubes, and in piles of drifted algae, low intertidal zone on protected outer rocky coast; subtidal to 200 m; Carmel (Monterey Co.) to beach at Rosarito (Baja California); Pleistocene fossils from San Pedro and Long Beach (both Los Angeles Co.).

Carapace to 20.8 mm wide in males and 17.3 mm wide in females, not pubescent; cheliped with the carpus bearing reticulations but no deep dorsal groove, the propodus with a large lobe on upper margin, the dactylus with a large tooth at base; walking legs not pubescent, the carpus not bilobed.

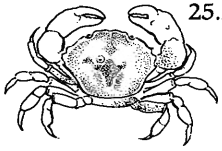
Lophopanopeus leucomanus leucomanus, investigated off southern California, feeds mainly on algae, especially encrusting species of coralline algae, but some animal material is also taken. Ovigerous females are found from February to October, and carry an average of 3,500 eggs (ranging from 1,000 to 6,400); they probably produce more than two broods of

young a year. Although the species extends into depths of 200 m, animals taken in deeper water are always small, suggesting that conditions there are less favorable.

Another subspecies, **L. leucomanus heathii** Rathbun (Fig. 25.25b–f), ranges from Moss Beach (San Mateo Co.) to La Jolla (San Diego Co.). It differs in that the carpus of the cheliped lacks reticulating ridges and the carpus of the walking legs is slightly bilobed. The carapace is up to 24.8 mm wide in males and 17.3 mm in females. Johnson & Snook (1927) first recognized that *Lophopanopeus heathii* was a northern replacement for *L. leucomanus*, a relationship formalized by Menzies (1948), who made the former a subspecies of the latter.

See especially Knudsen (1958, 1960a,c); see also Andrews (1945), Garth (1961), Hewatt (1938), Johnson & Snook (1927), Jones (1941), McLean (1962), Menzies (1948), Rathbun (1926, 1930), and Schmitt (1921).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Xanthidae



25.26 **Lophopanopeus frontalis** (Rathbun, 1893)

Under rocks in bays and in clusters of mussels on pilings, low intertidal zone; subtidal to 37 m; Santa Monica Bay (Los Angeles Co.) to Bahía Magdalena (Baja California), and Gulf of California; now rare in northern part of its range; Pleistocene fossils from Playa del Rey and San Pedro (both Los Angeles Co.).

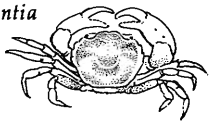
Carapace to 23.7 mm wide in males, 13 mm wide in females, lacking pubescence dorsally; cheliped with the carpus smooth or reticulate, with a deep dorsal groove, the propodus (hand) with a large lobe on upper margin, the dactylus (of major cheliped) lacking a large tooth; dark band on pollex (thumb) of chela extending far backward and upward on propodus.

The involved synonymy of this species includes *Xanthodes leucomanus* Lockington, 1877 (p. 100, not p. 32), which became *Lophopanopeus lockingtoni* Rathbun, 1900, which in turn became a synonym of *L. frontalis* (Rathbun, 1893). The distribution given above includes that recorded under these synonyms.

This species is recorded among the stomach contents of the tidepool fish *Gibbonsia elegans* in the Los Angeles area, but little is known of its natural history.

See Johnson & Snook (1927), Menzies (1948), Mitchell (1953), Rathbun (1926, 1930), Ricketts & Calvin (1968), Schmitt (1921), and Willett (1937).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Xanthidae



25.27 **Rhithropanopeus harrisii** (Gould, 1841)
Brackish-Water Crab

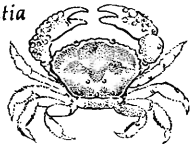
Locally common on muddy bottoms of sloughs and estuaries, and even into fresh water; subtidal to 10.5 m in San Francisco Bay (on the east coast to 36.5 m); sloughs south of Coos Bay (Oregon); San Francisco Bay and Delta areas as far upriver as Stockton (San Joaquin Co.); Atlantic coast from New Brunswick (Canada) to Tampico (Mexico); Europe.

Carapace to 19.1 mm wide in males, 10.6 mm wide in females, the first two anterolateral teeth on margin fused, the last three dentiform; front (rostrum) truncate, dorsal ridges prominent; walking legs slender.

This little crab has been introduced to both Europe and the Pacific coast from the Atlantic shores of North America. It was first reported from the west coast (San Francisco Bay), where it is now abundant, by Jones (1940). The crab tolerates brackish and even fresh water for prolonged periods; it osmoregulates efficiently at low salinities, and in dilute media may excrete a fourth of its body weight in urine each day. The permeability of the body wall appears to *decrease* at low salinities, a response found in a few other brackish-water crustaceans and in the annelid *Nereis*. In San Francisco Bay not only is it common near domestic sewage outfalls, but it is almost the only larger invertebrate that seems undisturbed by effluent from industrial outfalls that is toxic to most other macroscopic animal life. Development in Atlantic populations of this species has been studied from the standpoints of morphology, physiology, biochemistry, and behavior.

See Buitendijk & Holthuis (1949), Chamberlain (1962), Connolly (1925), Costlow (1966), Costlow & Bookhout (1971), Costlow, Bookhout & Monroe (1966), Filice (1958, 1959), Forward & Costlow (1974), Frank, Sulkin & Morgan (1975), Hood (1962), Jones (1940, 1941), Kalber (1970), Kalber & Costlow (1966), Kinne & Rotthauwe (1952), Morgan, Kramarsky & Sulkin (1978), Ott & Forward (1976), Pautsch, Lawinski & Turoboyski (1969), Payen, Costlow & Charniaux-Cotton (1971), Rathbun (1930), Ricketts & Calvin (1968), R. I. Smith (1967), Skorkowski (1972), Sulkin (1973, 1975), Via & Forward (1975), and Whitney (1969).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Xanthidae



25.28 **Paraxanthias taylori** (Stimpson, 1860)
(=Xanthias taylori) Lumpy Crab

Common, particularly in holes and crevices in region of algal turf, middle and low intertidal zones on rocky shores; subtidal to 100 m; Monterey Bay to Bahía Magdalena (Baja California).

Carapace width to 25.2 mm in males, 42 mm in females; carapace and chelipeds bearing blunt tubercles in adults and sharp curved teeth in juveniles; walking legs covered with stiff bristles; color dull red above, lower surface much lighter; chelae characteristically with dark-brown fingers.

A prominent feature of the intertidal region at La Jolla (San Diego Co.), these crabs are less common in the northern part of their range, though up to six per m^2 have been reported in kelp holdfasts in Monterey Bay. The diet is chiefly red and green algae, especially coralline algae. Some living and dead animal matter is eaten, and in aquaria nudibranch eggs may be taken if available. In turn, the crabs are a favorite food of the black croaker, and are also eaten by the cabezon and scorpionfish.

Out in the open on submerged rocks, individuals of *P. taylori* generally move only in the period between waves. They stop and cling firmly as a wave crest passes over them. Some stimulus, perhaps the "lift" exerted by the wave on the body or on the tactile hairs on the carapace or legs, signals the crabs to cling.

The abdomen of the female begins to acquire its feminine

characteristics when the carapace is only 6.5 mm wide, and at a width of 11.5–13.5 mm the first egg mass is produced. Mating occurs with the hard-shelled female on her back, the male astraddle above; mating may last up to 3 hours and is sometimes repeated several days in a row. Ovigerous females are abundant in southern California from April to September. The number of eggs per brood varies with the size of the female, from about 3,800 in a mother with a carapace 15 mm wide to about 40,000 in one 40 mm across the back; the average female carries about 21,000 eggs. More than two broods per year are probably produced. The larval stages have been described.

Individual crabs sometimes bear the rhizocephalan barnacle parasite *Thompsonia*, and occasional animals are overgrown with sponge or algae.

See especially Knudsen (1959b, 1960a,c); see also Andrews (1945), Johnson & Snook (1927), Limbaugh (1955), Rathbun (1930), Ricketts & Calvin (1968), and Schmitt (1921).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Xanthidae

25.29 **Pilumnus spinohirsutus** (Lockington, 1877)
Retiring Southerner, Hairy Crab

Under and among rocks, often hidden in sand, low intertidal zone; subtidal to 25 m; San Pedro (Los Angeles Co.) to Bahía Magdalena (Baja California); erroneously reported from tropical western Atlantic.

Carapace to 30.8 mm wide in males and 34.6 mm wide in females, easily recognizable by its hairs and spines.

This species is distinguished from *P. townsendi* Rathbun, which occurs in Bahía Magdalena and the Gulf of California, by having five anterolateral spines instead of four.

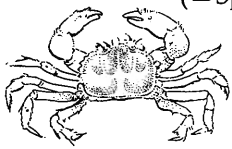
The retiring habits of *P. spinohirsutus* have earned it one common name. It hides in the sand under and among rocks, where its light-brown color makes it difficult to spot. The crabs *Cycloxanthops novemdentatus* (25.23) and *Paraxanthias taylori* (25.28) occur in the same habitat, sometimes even under the same rock. Formerly obtainable at San Pedro (Los Angeles

Co.) and at the entrance to Newport Bay (Orange Co.), this warm-temperate species is disappearing as harbors are dredged and deepened. It persists at outfalls of hydroelectric and nuclear power plants, where discharge water has been heated.

See Fabbiani (1972), Johnson & Snook (1927), Rathbun (1930), Ricketts & Calvin (1968), and Schmitt (1921).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Goneplacidae

25.30 **Malacoplax californiensis** (Lockington, 1877)
(=Speocarcinus californiensis) Burrowing Crab



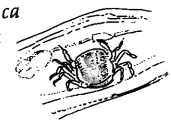
Sometimes common, burrowing in mud flats of bays and estuaries, middle and low intertidal zones; subtidal to 33 m; Mugu Lagoon (Ventura Co.) to Bahía Magdalena (Baja California); common in suitable situations.

Carapace width to 22.6 mm in males, the dorsal surface convex longitudinally, almost straight transversely, the margin bearing three anterolateral teeth; front and sides of carapace, tapering eyestalks, and legs all fringed with light-colored hairs; body brownish to white; chelae with tips of fingers black.

Like the fiddler crab, the burrowing crab is limited to the southern part of the state, where it may form deep burrows. It, too, threatens the intruder from the mouth of its burrow but retreats to safety when danger approaches. Unlike the fiddler, however, it ranges throughout the intertidal region and may be dredged from the bottom of the bay, as at Newport (Orange Co.) or San Diego.

See Guinot (1969) for name change; see also Johnson & Snook (1927), Rathbun (1918), Ricketts & Calvin (1968), and Schmitt (1921).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Pinnotheridae



25.31 **Fabia subquadrata** Dana, 1851
Mussel Crab, Pea Crab

Commensal in the mantle cavities of bivalve mollusks, especially *Mya arenaria* (15.67) and the mussels *Mytilus edulis* (15.10) and *M. californianus* (15.9); adults occasionally reported in the clams *Cyclocardia borealis, C. ventricosa, Tivela stultorum* (15.32), *Protothaca staminea* (15.41), *Saxidomus giganteus* (15.33), *Tresus capax* (15.47), *T. nuttallii* (15.48), and *Tapes* sp., the sea urchin *Strongylocentrotus purpuratus* (11.5), and the tunicate *Styela gibbsii*; low intertidal zone to 88 m depth; Akutan Pass (Aleutian Islands, Alaska) to La Jolla (San Diego Co.); uncommon south of San Pedro (Los Angeles Co.), where the related species *F. concharum* (25.32) predominates.

Carapace width in males to 7.3 mm, in females to 16.2 mm; distinguished from *F. concharum* by the transverse groove across the front, the distally widened palm of the chela, and an outer maxilliped with the terminal segment reaching the end of the subterminal segment.

The strange life history of *F. subquadrata* has been studied in the Puget Sound area (Washington) by Pearce (1966a), and although some of the details are unknown, the whole is a remarkable story. The larger adult females have only a membranous outer shell, and their soft bodies are quite unsuited to life outside the protecting body of the host. The clams in which they live subsist by filtering the water for plankton, trapping this in mucus on the gills, and passing strings of mucus laden with food particles along food grooves to the mouth. The crab, huddled within the mantle cavity, plucks the food and mucus strings from *one* of the clam's two gills, often damaging that gill severely over a period of time; the other gill, relatively unharmed, provides food for the clam. Two such crabs in a single host might well destroy it, but two are almost never found together; females are hostile toward each other when confronted outside a clam, and if a second is inserted into an already occupied clam, one or both crabs shortly leave. In California the main host is *Mytilus californianus* (*Modiolus modiolus* is preferred in Puget Sound), and about 3 percent of the mussels contain pea crabs.

Some ovigerous females are found in mussels nearly all year; females carrying eggs are rare in August in the Puget Sound area, but increase in number to a peak from November to January and then decline steadily until the next August. One female examined bore about 1,200 eggs. Major hatching begins in February, and the liberated young pass through four zoeal stages and a megalops stage in the plankton before reaching the first crab instar. Development time from hatching to the first crab stage was about 52 days for animals reared in the laboratory at 11.6–13.6°C. The first crab stage, 0.76–0.9 mm across the carapace, has hairy legs and is adapted for swimming. It appears to be the stage that seeks a clam host, for the smallest crab found in a clam had a carapace width of 0.86 mm. Both males and females seek clam hosts, often such smaller species as *Astarte compacta, Cyclocardia ventricosa, Crenella columbiana,* and *Kellia* sp., in addition to *Modiolus.* Within the host's mantle cavity the crabs grow in April and May, probably molting at least seven times. The exoskeleton during this period is thin and soft.

Then, in late May, the crabs molt again, and this time both sexes produce a hard and calcified outer shell. Hard-shelled males average 4.1 mm in carapace width (range 1.3–6.8 mm), and females average 3.5 mm (range 1.5–6.2 mm). These tiny, hard-shelled crabs then leave their molluscan hosts and swarm into the plankton, where males and females meet and mate for the first and last time. This is the only period of their lives when the two sexes are found together. Females then return to a clam host, but never to the smaller species of clams they occupied as juveniles. Safe in the mantle cavities of mussels, the fertilized females molt and become soft-shelled again, then grow and start to produce eggs. Ovigerous females range in size from 5 to 13.4 mm across the carapace. The females do not molt the lining of their seminal receptacles (spermathecae); thus they appear to retain for a lifetime the store of sperm from their one mating in the plankton. Most females live only a year, but some may persist and produce broods a second year, still using the initial store of sperm.

The fate of males is less certain; a few appear to return to hosts, for a few males are found throughout the year (always alone) in mussels, where they remain small and hard-shelled.

The vast majority are never seen again, and it seems likely that, having done their essential job, they perish. There is no evidence that they ever visit clams containing the females, which shortly become so much larger than the males that further mating appears anatomically impossible.

Mussels more than 85 mm in length rarely contain pea crabs. Juvenile crabs and newly mated females usually seek mussels less than 15 mm long, and the larger *Modiolus* either were never infected or had outlived their symbionts.

See especially Pearce (1966a) and Schmitt, McCain, & Davidson (1973); see also Davidson (1968) and Irvine & Coffin (1960). Because of the confusion between *F. subquadrata* and *F. concharum*, references to older works are omitted.

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Pinnotheridae

25.32 **Fabia concharum** (Rathbun, 1893)
(=F. lowei, Pinnotheres concharum)

Commensal in the mantle cavities of bivalve mollusks, including *Barnea subtruncata* (15.71), *Donax gouldii* (15.54), *Mya arenaria* (15.67), *Cryptomya californica* (15.66), *Modiolus capax* (15.5), *M. modiolus*, *Tivela stultorum* (15.32), *Parapholas californica* (15.75), *Protothaca staminea* (15.41), and *Tapes* sp.; San Pedro (Los Angeles Co.) to Bahía de Tortuga (Baja California).

Distinguished from *F. subquadrata* (25.31) in having the front smooth and lacking a transverse groove, the palm of the chela not distally widened, and the terminal segment of the outer maxilliped not reaching the end of the subterminal segment.

This small commensal crab occupies some of the same bivalve hosts as the related species *F. subquadrata*. *F. concharum* predominates in southern California, where the two species overlap in distribution.

Although *F. concharum* is not known to inhabit ascidians, and *F. subquadrata* only occasionally does so, a somewhat similar pea crab, **Pinnotheres pugettensis** Holmes, typically occurs as a commensal in large tunicates. At Departure Bay (British Columbia) and Puget Sound (Washington) it is found

in *Halocynthia* (=*Tethyum*) *aurantium*, *H. hilgendorfi igaboja* (12.40), and *Ascidia paratropa* (12.26); in Monterey harbor it occurs in *Styela montereyensis* (12.33). The carapace is subpentagonal, and widest anteriorly (width 10.5 mm in females, unknown in males); the chela in females is widest behind the fingers, and the outer surface of the manus is brownish with light reticulations; the walking legs increase in length from first to last, and the dactylus of the fourth leg is the longest.

The type specimen, from Puget Sound, was found in the branchial cavity of *Cynthia* (=*Halocynthia*). Wells (1928) illustrates the enlargement of the atrial cavity of *H. aurantium* caused by the presence of this crab. The discovery of two specimens of *P. pugettensis* in *Styela montereyensis* at Monterey in 1978 (C. C. Lambert, pers. comm.) not only extends the range to central California, but adds a new host.

For *F. concharum*, see Davidson (1968) and the account and references for *F. subquadrata* (25.31). For *P. pugettensis*, see Holmes (1900), Pearce (1966a), Rathbun (1918), Schmitt, McCain & Davidson (1973), and Wells (1928).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Pinnotheridae

25.33 **Parapinnixa affinis** Holmes, 1900
Pea Crab

Commensal in tubes of the polychaete worms *Terebella californica* and *Loimia medusa* (=*L. montagui*) among clumps of shells and marine plants, low intertidal zone in protected situations; San Pedro (Los Angeles Co.), Anaheim Landing and Newport Bay (Orange Co.), and San Diego; Sakhalin and Kurile Islands (U.S.S.R.).

Carapace to 4.1 mm wide in males, 6 mm wide in females, less than twice as wide as long, smooth and shining; pollex (thumb) of cheliped with two teeth at tip and a large tooth at center; first pair of walking legs larger than others, the dactyli short and stout; carapace light amber mottled with ochre, legs pale ochre with greenish tinge (not shown in the photograph), dactyli yellow with white tips.

The worm that serves as host for this minute commensal

crab builds a mucus tube with embedded mud and sand. Generally one finds only one crab to a worm tube, but occasionally a male and female are found together. In one locality, females outnumbered males by three to one; in another spot males formed a two-to-one majority. Of 100 specimens examined, five were albino crabs.

See Berkeley & Berkeley (1941), Glassell (1933), Holmes (1900), and Kobjakova (1967).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Pinnotheridae

25.34 **Pinnixa barnharti** Rathbun, 1918
Pea Crab

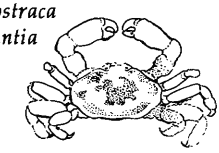
Commensal in the cloaca of the sea cucumber *Caudina arenicola*, low intertidal and subtidal sand flats of bays and estuaries; Venice (Los Angeles Co.) to Bahía Ballenas (Baja California); reported from Puget Sound (Washington), presumably in *Caudina intermedia*, and from Zihuatanejo (Mexico), in *Holothuria (Paraholothuria) riojai*.

Carapace to 15 mm wide in males, 16.2 mm wide in females, convex, laterally truncate; chelipeds massive, the fingers widely gaping, the dactylus with a strong tooth at the middle, the pollex (thumb) strap-shaped; walking legs with the dactyli straight.

The crab inhabiting the sweet potato sea cucumber was formerly thought to be invariably this species. However, 25 percent of the *Caudina* (=*Molpadia*) examined in the San Diego area were found to contain *Opisthopus transversus* (25.42) instead. Ricketts noted that the crabs often crawled out of the holothurian while the host was being relaxed with epsom salts prior to preservation.

See Caso (1963), Hopkins & Scanland (1964), Lie (1968), MacGinitie & MacGinitie (1968), Rathbun (1918), Ricketts & Calvin (1968), and Schmitt (1921).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Pinnotheridae



25.35 **Pinnixa faba** (Dana, 1851)
Large Pea Crab

Adults encountered intertidally as commensals in the mantle cavities of the burrowing bivalves *Tresus capax* (15.47; Puget Sound, Washington; Humboldt Bay) and *T. nuttallii* (15.48; Bodega Bay, Sonoma Co., and southward), in the mantle folds of the sea hare *Aplysia vaccaria* (14.9), in the atrial cavity of the tunicate *Styela gibbsii*, and in the cloaca of the holothurians *Caudina arenata* and *C. arenicola*; juveniles commensal in an assortment of clams (see below); Prince of Wales Island (Alaska) to Newport Bay (Orange Co.); Pleistocene fossils from Cape Blanco (Oregon).

Carapace width to 15 mm in males, 22.8 in females (see also Fig. 18.26); species distinguished from *P. littoralis* (25.36) by (1) carapace oblong, with orbits oval rather than pointed, (2) chelae with pollex (thumb) horizontal rather than deflexed in males, and fingers closed rather than gaping in females, and (3) merus of third leg in males more than twice as long as wide rather than only twice as long as wide.

Biologically, *P. faba* and its close relative *P. littoralis* show many similarities. Both species are best known from studies made in the Puget Sound area, where the adults occur only in *Tresus capax*. The two crabs occur in the same clam beds, but only one species of adult crab occupies a given clam host. Adult crabs occur in sexual pairs, often along with a few juveniles whose further development seems inhibited by the presence of adults of the same sex. Mature females hide under the visceral fold of *T. capax*, feeding on plankton and other particulate matter brought in with the clam's feeding current and trapped in its mucus. Food is scraped from the clam's visceral fold, where feeding activities cause some lesions but no damage to the clam's most important feeding organs, its gills and palps. The much smaller males and juvenile crabs range freely through the host's mantle cavity.

In Washington waters some females with eggs occur nearly all year. Breeding peaks for *P. faba* occur from January to April or May, and again in June and July, representing two

broods. Breeding peaks of *P. littoralis* are similar, but come about a month earlier. Average females of both species carry 7,000–8,000 eggs, though a large California specimen of *P. faba* carried more than 54,000 eggs. A hiatus in breeding occurs when the females molt, from late August through October. Hatched larvae of both crab species are planktonic, and take about 47 days (under laboratory conditions) to reach the last larval or megalops stage, which seeks a bivalve host.

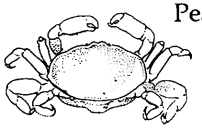
Males of both crabs subsequently pass through about 14 post-larval molts to reach terminal anecdysis (a final adult stage at which molting ceases), with an average carapace width of 13.1 mm. Females first become ovigerous at a carapace width of 12.8–14 mm (15 or 16 instars), but continue to grow to an average carapace width of 19.7 mm (23 or 24 instars). If an adult dies, it is replaced by the growth of one of the juvenile crabs, if any of that sex are present in the host clam.

California records are sparse, but both species of crabs, and both species of the host clam *Tresus*, occur in Humboldt Bay; today the crabs apparently inhabit only *T. capax*, but an earlier report put *P. faba* in *T. nuttallii*. *P. faba* has also been reported from *T. nuttallii* in Tomales Bay (Marin Co.), where it was collected by R. H. Morris, in Elkhorn Slough (Monterey Co.), Morro Bay (San Luis Obispo Co.), and Newport Bay (Orange Co.). *T. nuttallii* lacks the visceral fold present in *T. capax*, from which the *Pinnixa* females typically feed. Moreover, in California waters, *P. faba* has been reported from the clams *Macoma nasuta* (15.50), *Mya arenaria* (15.67), *Saxidomus giganteus* (15.33), *Siliqua gibbsi*, and *Protothaca staminea* (15.41), only one to a host under most circumstances. Further investigation of the biology of both *P. faba* and *P. littoralis* seems desirable, since older records need further verification.

See especially Pearce (1966b); see also Hart (1930), Johnson & Snook (1927), MacGinitie (1935), MacGinitie & MacGinitie (1968), Pearce (1962, 1965), Rathbun (1918), Ricketts & Calvin (1968), Schmitt (1921), Schmitt, McCain & Davidson (1973), Taylor (1912), Wells (1928, 1940), and Zullo & Chivers (1969).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Pinnotheridae

25.36 **Pinnixa littoralis** Holmes, 1894
Pea Crab



Found as a commensal in the mantle cavities of burrowing clams; in California, adults are reported in the gaper clams *Tresus capax* (15.47) and *T. nuttallii* (15.48) and the Washington clam *Saxidomus nuttallii* (15.34) (in Puget Sound they occur only in *T. capax*); juvenile crabs in a wide variety of bivalve hosts (see below); Prince William Sound (Alaska) to San Diego.

Carapace width to 16 mm in males, 26 mm in females; species differing from *P. faba* (25.35) in having (1) side walls of carapace less steep, the outline as seen from above not longitudinally truncate but inclined obliquely backward and outward, (2) orbits continuing laterally in an acute angle, not oval, (3) chelae with pollex (thumb) deflexed rather than horizontal in males, and fingers gaping rather than closed in females, and (4) merus of third leg in males no more than twice as long as wide; color gray or greenish white, with brown bands on walking legs; yellow liver and orange ovary ordinarily visible through transparent carapace (though not seen in the photograph).

Juvenile crabs appear to be far less specific than adults in their choice of hosts. In California, juveniles have been found in the clams *Mya arenaria* (15.67), *Clinocardium nuttallii* (15.29), and *Macoma secta* (15.51), as well as in the definitive hosts; in Puget Sound they inhabit these species and in addition the clams *Entodesma saxicola* (15.81), *Saxidomus giganteus* (15.33), *Macoma nasuta* (15.50), *M. inquinata, M. indentata, M. secta* (15.51), *Serripes groenlandicus, Siliqua patula* (15.65), *Protothaca staminea* (15.41), and *Tapes,* and are sometimes found in the pallial cavities of the larger limpets *Notoacmea* and *Collisella* spp. Further details of biology are included under *P. faba.* Because of the similarity of these two crabs, the close resemblance of the two species of *Tresus* that serve as their definitive hosts, and the fact that reports seldom distinguished the crabs as sexually mature or immature, there is considerable doubt about the validity of early California records. This is

particularly true south of Monterey, where some reports of *P. faba* may actually refer to *P. littoralis*.

See especially Pearce (1966b); see also Hart (1930, 1940, 1968), Johnson & Snook (1927), Rathbun (1918), Ricketts & Calvin (1968), Schmitt (1921), Schmitt, McCain and Davidson (1973), and Wells (1928, 1940).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
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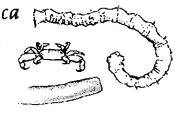

25.37 **Pinnixa longipes** (Lockington, 1877)
Pea Crab

Commensal in tubes of the annelid worm *Axiothella* (= *Clymenella*) *rubrocincta*, abundant on sand bars exposed at low tide; also in tubes of the polychaete worms *Pectinaria californiensis* (18.32) and *Pista elongata* (18.33), and occasionally in burrows of the echiuroid worm *Urechis caupo* (19.7); subtidal to 128 m; Bodega Bay harbor (Sonoma Co.) to Ensenada (Baja California); reported erroneously from the east coast of North America.

Carapace to 6 mm wide in males, to 6.3 mm wide in females, nearly three times as wide as long; third leg greatly enlarged, the merus bearing a flange on posterior margin; fourth leg small, not reaching beyond merus of third.

The transverse elongation of the body expressly adapts this little crab for life in long, slender worm tubes. The crab insinuates itself through the narrow opening by inserting one of the enormously elongated third legs first, then carefully edging itself in sideways.

Ovigerous females were found in July and August in Elkhorn Slough (Monterey Co.).

See Carlisle (1969), Glassell (1935), Johnson & Snook (1927), MacGinitie (1935), MacGinitie & MacGinitie (1968), Rathbun (1918), Ricketts & Calvin (1968), Schmitt (1921), and Schmitt, McCain & Davidson (1973).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
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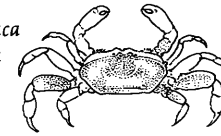


25.38 **Pinnixa franciscana** Rathbun, 1918
Pea Crab

Usually commensal in burrows of the echiuroid worm *Urechis caupo* (19.7), sometimes in tunnels with the burrowing crustaceans *Callianassa californiensis* (24.2) and *Upogebia pugettensis* (24.1); juveniles in tubes of the terebellid polychaete *Neoamphitrite robusta* and the scale worm *Grubeopolynoe* (formerly *Hololepidella*) *tuta;* middle and low intertidal zones and adjacent subtidal waters, sand flats and mud flats of bays; San Francisco Bay to Bahía de Tortuga, Baja California (unpublished record).

Carapace to 22.7 mm wide in males, to 11 mm wide in females, the sides pointed; cheliped with the dactylus (thumb) horizontal, the propodus bearing a sharp, raised line of granules near lower edge; merus of the third leg broadened (about 1.7 times as long as wide).

Pinnixa schmitti Rathbun, which occupies tunnels of *Callianassa californiensis* and *Upogebia pugettensis* from Alaska to San Francisco Bay, differs from this species by having a more oblong carapace, the cheliped with a less prominent line of granules on the propodus extending onto the distally inclined pollex (thumb), and the merus of the third leg narrower (twice as long as wide).

The crab *Scleroplax granulata* (25.41), which also occurs in *Urechis* burrows, is smaller than *P. franciscana.* Both crabs filter particles from the water using the second pair of maxillipeds, and may also eat bits of detritus. The males migrate from burrow to burrow.

Ovigerous females of *P. franciscana* have been found in March at Elkhorn Slough (Monterey Co.) and Morro Bay (San Luis Obispo Co.), and in July at Morro Bay.

See MacGinitie (1935), MacGinitie & MacGinitie (1968), Rathbun (1918), Reish (1961b), Ricketts & Calvin (1968), Schmitt (1921), and Schmitt, McCain & Davidson (1973).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Pinnotheridae

25.39 **Pinnixa tubicola** Holmes, 1894
Pea Crab

Commensal in tubes of polychaete worms, particularly *Neoamphitrite robusta* but also *Eupolymnia heterobranchia, Thelepus crispus* (18.35), and *Chaetopterus variopedatus* (18.20), and associated with the scale worms *Halosydna brevisetosa* (18.4) and *H. californica*, under rocks, middle and low intertidal zones on protected rocky shores; Prince Rupert (British Columbia) to San Diego; reported from Alaska without specific locality.

Carapace to 9 mm wide in males, 13 mm wide in females, smooth.

Pinnixa tubicola, P. schmitti (see under 25.38), and *P. weymouthi* (25.40) all have smooth carapaces, swollen propodi on the chelae, and nearly straight dactyli on the legs. The male abdomen of *P. tubicola* is more triangular, that of *P. schmitti* more convexly margined, and that of *P. weymouthi* more slender than the other two. **Pinnixa tomentosa** Lockington (San Clemente Island, Channel Islands; Mission Bay, San Diego Co.; San Felipe and Bahía de Los Angeles, Baja California) is morphologically similar to *P. tubicola* but differs in having the propodus of the third walking leg terminally spinulous, the palm of the chelae in males smooth. *P. tomentosa* shares the tubes of the polychaete *Chaetopterus variopedatus* with *P. tubicola* where their ranges overlap at San Diego.

Terebellid worms, the most frequent hosts of *P. tubicola*, extend their feeding tentacles into the sediments surrounding their tubes and use cilia and mucus to transport back to the tube a supply of detritus particles. The filter feeder *Chaetopterus* traps plankton and suspended detritus from the water. In both cases the food intended for the worm consists of organic particles in mucus. Possibly the commensal crabs take a share for themselves. The crabs usually occur in the host tube in pairs. Females have not been reported outside of worm tubes, and males have been noted free only once, in Elkhorn Slough (Monterey Co.).

Ovigerous females were reported in Monterey Bay in June and August.

See Hart (1930), Johnson & Snook (1927), MacGinitie (1935), MacKay (1931), Pearce (1966b), Pearse (1913), Rathbun (1918), Ricketts & Calvin (1968), Scanland & Hopkins (1978), Schmitt (1921), and Schmitt, McCain and Davidson (1973).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Pinnotheridae

25.40 **Pinnixa weymouthi** Rathbun, 1918
Pea Crab

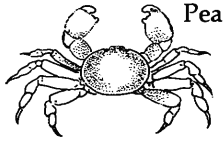
Reported in unoccupied tubes of annelids on undersides of rocks, low intertidal zone; Monterey Bay and Peninsula.

Carapace about 5.3 mm wide in males, 6.2 mm wide in females; species distinguished from *P. tubicola* (25.39) by its narrower body, truncated sides, and more prominent anterolateral angle.

Almost nothing is known of the natural history of this small crab.

See Rathbun (1918), Schmitt (1921), and Schmitt, McCain & Davidson (1973).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Pinnotheridae



25.41 **Scleroplax granulata** Rathbun, 1893
Pea Crab

A common commensal in burrows of the echiuroid worm *Urechis caupo* (19.7) and tunnels of the burrowing shrimps *Callianassa californiensis* (24.2) and *Upogebia pugettensis* (24.1), middle and low intertidal zones on sandy mud and mud flats in protected bays; Roller Bay (Hope Island, off northern tip of Vancouver Island, British Columbia) to Ensenada (Baja California).

Carapace to 11.5 mm wide in males, 12.9 mm wide in females, hard, highly convex, the anterolateral margins not forming an angle with posterolateral margins (as they do in *Pinnixa*, e.g., 25.34–40) but curving gradually into them; chela

in male much larger than in female, the short pollex (thumb) bearing a large tooth filling gape caused by curved dactylus (finger); walking legs similar, fourth leg not noticeably smaller than others.

Up to six crabs have been found in a single *Urechis* burrow in Elkhorn Slough (Monterey Co.), but the animals often occur singly. They feed on particles of flesh and detritus and can also strain plankton from the water with their outer mouthparts. The bryozoan *Triticella elongata* is often found growing on the carapace and appendages and in the gill chamber of this crab (see Fig. 6.19).

Ovigerous females (some only 4.9 mm across the carapace) are most abundant in Elkhorn Slough in February, March and April, but a few were noted from June to August. Females with eggs were seen in Humboldt Bay in January and in Morro Bay (San Luis Obispo Co.) in February. Males may migrate from burrow to burrow. Some crabs "play possum" for a few seconds or up to 2 minutes when disturbed; crabs in *Urechis* burrows may move to the host worm and cling to its body.

See Hart (1930, 1935, 1937, 1940, 1971b), Johnson & Snook (1927), MacGinitie (1935), MacGinitie & MacGinitie (1968), Rathbun (1918), Ricketts & Calvin (1968), Schmitt (1921), Schmitt, McCain & Davidson (1973), and Wells (1928).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Pinnotheridae

25.42 **Opisthopus transversus** Rathbun, 1893
Mottled Pea Crab

A commensal crab found in the cloaca of the sea cucumbers *Parastichopus californicus* (9.7), *P. parvimensis* (9.8), and *Caudina* (formerly *Molpadia*) *arenicola*, in the tubes of the polychaete *Chaetopterus variopedatus* (18.20), on the gills of the amphineuran *Cryptochiton stelleri* (16.25), and in the mantle cavities or pallial grooves of a variety of clams and gastropods (see below); low intertidal zone and adjacent subtidal waters on rocky shores and in mud flats of protected bays; Monterey to Laguna San Ignacio, Baja California (unpublished record); San Felipe (Baja California).

Carapace to 11.8 mm wide in males, 21 mm wide in females, squarish, a little wider than long, firm, harder in male than in female; chelipeds pubescent; walking legs pubescent, similar in form, the second pair slightly longer than others; carapace richly spotted with vermilion to deep red, polished to almost pearly smoothness.

Unlike most commensal crabs, this little species is found living with a wide variety of hosts, always in a protected place. In addition to the above hosts, *Opisthopus* has been found in the mantle cavities or mantle folds of the giant keyhole limpet *Megathura crenulata* (13.8), the bubble snail *Bulla gouldiana* (14.6), the sea hare *Aplysia vaccaria* (14.9), the slug *Navanax inermis* (14.4), the cone snail *Conus californicus* (13.103), and the large snails *Polinices lewisii* (13.62) and *Astraea undosa* (13.39). Clams likewise may serve as hosts, though less commonly, and the crab has been found in the mantle cavities or siphon tubes of the gaper *Tresus nuttallii* (15.48), the clay borer *Zirfaea pilsbryi* (15.72), the rock borer *Parapholas californica* (15.75), the mussels *Modiolus modiolus, Mytilus edulis* (15.10), and *Megapitaria squalida,* the scallop *Hinnites multirugosus,* and the bivalves *Sanguinolaria nuttallii, Platyodon cancellatus* (15.68), and *Dinocardium* (= *Trachycardium*) *robustum.*

In the San Diego area alone Hopkins and Scanland (1964) found *O. transversus* in association with 13 different species of hosts distributed among three phyla. They found the largest and most mature crabs (ovigerous females) in the mantle cavity of *Hinnites,* the intestine of *Caudina,* and the siphon of *Zirfaea.* Crabs inhabiting the gastropods *Astraea* and *Megathura* and the sea cucumber *Parastichopus* were somewhat smaller, and those inhabiting the gastropod *Bulla* and the tubes of *Chaetopterus* were smaller still, suggesting that the size of the cavity available may limit the size of the resident crab. Regarding color, they found that the bright-red mottling of the young crabs persists in individuals having a food supply independent of that of the host, such as the crabs inhabiting hosts like *Astraea, Bulla,* and *Megathura;* however, the color is lost in crabs that use food already gathered by filter-feeding hosts such as *Hinnites, Dinocardium,* and *Zirfaea.* This suggests that, indirectly, the host may influence the color of crabs by limiting the amount of carotenoid pigments available to them. In sea cucumber hosts, which ingest large quantities of

mud rich in carotenoids, crabs maintain a color pattern of reddish brown and white (in *Caudina*) or a pale red mottling (in *Parastichopus*). The similarity of pattern in the crabs inhabiting *Caudina* to that in *Pinnixa barnharti* (25.34), at one time thought to be the only pinnotherid commensal with this holothurian, suggests convergence, since this pattern was not found among *O. transversus* specimens occurring in any other host. Of 53 *Caudina* from the San Diego area, 52 contained a commensal crab, and of this number, 13 (or 25 percent) were *O. transversus*.

See especially Hopkins & Scanland (1964); see also Beondé (1968), Glassell (1935), Johnson & Snook (1927), MacGinitie (1935), MacGinitie & MacGinitie (1968), Rathbun (1904, 1918), Ricketts & Calvin (1968), Schmitt (1921), Schmitt, McCain and Davidson (1973), Webster (1968), and Wolfson (1974).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Grapsidae

25.43 **Pachygrapsus crassipes** Randall, 1839
Striped Shore Crab, Lined Shore Crab

Abundant in crevices, tidepools, and mussel beds, high and middle intertidal zones on rocky shores; occasionally on pilings in harbors; sometimes on hard muddy shores of bays and estuaries, at the mouths of burrows; Charleston (Oregon) to Isla de Santa Margarita (Baja California), and Gulf of California; Japan and Korea.

Carapace to 47.8 mm wide in males, 40.8 mm wide in females, squarish, broader than long, the sides converging posteriorly, the upper surface transversely striated anteriorly; distinguished from *Hemigrapsus* species (25.44, 25.45) by its darker coloration, marked with shades of red, purple, or green, and by having only one lateral tooth, and from *P. transversus* (Gibbes) of the Panamic region by the smooth merus of the last walking leg.

This abundant crab, a familiar resident of higher pools and crevices, has been the object of many investigations. Native to the west coast of North America, it was not reported from Asia until 1890; it may have been introduced to the Orient by ships carrying zoea larvae in water ballast.

More than any other north-temperate, west coast crab, *P. crassipes* is adapted to a semi-terrestrial life. In the field the animals spend at least half their time out of water, but visit pools at intervals to feed and to moisten the gills. Water (about 3 percent of the body volume) is retained in the gill chamber when the crabs are above the surface, and in experiments some animals have remained alive high and dry in shaded enclosures for up to 70 hours. Respiratory rate decreases as the crabs get drier. Partly desiccated crabs take to water quickly when immersed, and they can even absorb water from saline media against a diffusion gradient. The crabs regulate osmotically in both brackish and hypersaline media; given a choice of waters of different salinities, individuals choose normal seawater, even if found living under other conditions. *P. crassipes* tolerates a wide range of environmental temperatures. The composition of the pool of free amino acids found in the tissues is intermediate between that of typical marine crustaceans, like the lobsters and shrimps, and that of such semi-terrestrial forms as the isopod *Ligia* and the beachhopper *Orchestoidea*.

The main food of *Pachygrapsus* on rocky shores is the film of algae and diatoms growing on rocks in higher pools and crevices, which the animal scrapes off by means of the small spoon-shaped cups at the tips of the chelae. Some larger algae are also eaten, especially the green algae *Ulva* and *Enteromorpha*, the brown seaweed *Fucus*, and the red algae *Endocladia*, *Rhodoglossum*, and *Grateloupia*. Dead animal matter and detritus are also eaten when available. Living prey, such as limpets, the snails *Littorina* and *Tegula*, hermit crabs, and isopods, are occasionally taken. The limpets *Notoacmea scutum* (13.23) and *Collisella limatula* (13.14) are attacked; the crab presses the fingertips of its open chela straight down on top of the shell and pinches, popping the top off the limpet shell with the exertion of relatively little force. The crabs have also been observed catching flies that settle nearby; a quick lunge and sudden snap of the chela often results in a successful catch. In turn, *P. crassipes* adults are eaten by such air-breathing predators as sea gulls, rats, raccoons, and even man. Juvenile crabs and larvae are consumed by sea anemones and fishes. There is even some cannibalism, especially on crabs that have just molted and have soft shells. Out of water, food is located

mainly by vision and by tactile stimuli, and the crab's excellent eyesight plays an important role in much of its behavior. Regular shifts in position of retinal pigments adapt the eyes for both day and night vision. Crabs held in constant darkness (but not in constant light) show a similar shift in retinal pigments, and the daily changes appear to be regulated by a "biological clock."

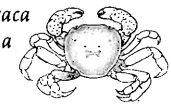
The crabs are rather aggressive toward one another. They do not defend feeding territories, but they may defend a food item, and often defend a crevice refuge against intruders when under water. Two crabs in confrontation often engage in a "boxing match," their chelae held outspread and gaping. The larger animal almost always dominates the smaller, and males tend to dominate females, but the major weapon here is bluff; crabs rarely injure each other in such bouts in the field.

Fertile females that are ready to molt emit a chemical signal, or pheromone, called crustecdysone, which attracts and stimulates males. Mating occurs after the female molts, while she is still soft-shelled. A courtship dance precedes the act, after which the male rolls over on his back and the female walks above him. Ovigerous females are found from March or April to August or September in central California, and from late February to October in southern California; peak reproduction occurs in June and July in both regions. A medium-sized female carries about 50,000 eggs and produces one or two broods a year. Larval stages occur in the plankton, and juvenile crabs are found in tufts of the alga *Endocladia*, well up in the intertidal zone, from January to July in the Monterey area. It takes at least 3 years after hatching for adults to reach full size; this involves 21 molts for females and 18 molts for males. Males reach sexual maturity 7 months after hatching; females require 11–12 months. The smallest ovigerous females reported were only 19 mm in carapace width. Old crabs are sometimes seen encrusted with bryozoans and barnacles, suggesting that they may have ceased to molt.

See especially Hiatt (1948); see also Baker (1912), Bliss (1968), Bollenbacher, Borst & O'Conner (1972), Boolootian (1965), Boolootian et al. (1959), Bovbjerg (1960a,b), Chapin (1968), Glynn (1965), Gross (1955, 1957a,b, 1958, 1959, 1961), Gross & Marshall (1960),

Hewatt (1935, 1937, 1938), Johnson & Snook (1927), Jones (1941), Kittredge, Terry & Takahashi (1971), Kittredge et al. (1962), MacGinitie (1935), MacGinitie & MacGinitie (1968), Prosser, Green & Chow (1955), Rathbun (1918), Ricketts & Calvin (1968), Roberts (1957), Sakai (1965, 1976), Schmitt (1921), and R. I. Smith (1948).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Grapsidae



25.44 **Hemigrapsus nudus** (Dana, 1851)
Purple Shore Crab

Common in some areas under stones and among seaweeds, middle and low intertidal zones on rocky shores; less commonly along clay banks in sloughs and estuaries, but never in burrows; Yakobi Island (Alaska) to Bahía de Tortuga (Baja California); uncommon in southern California and southward; Pleistocene fossils from San Pedro (Los Angeles Co.) to San Diego Bay.

Carapace to 56.2 mm wide in males, 34 mm wide in females, smooth and convex anteriorly, flat and punctate posteriorly, the anterolateral margins rounded and bearing two teeth; chelae of males with a patch of hair inside; color usually purple, sometimes greenish yellow or reddish brown; easily distinguished from *H. oregonensis* (25.45) and from the slimmer *Pachygrapsus crassipes* (25.43) by the red or purplish spots on the chelae.

In the southern part of its range, which it shares with *Pachygrapsus crassipes*, *H. nudus* remains at middle intertidal levels and below, generally lower down than *Pachygrapsus*. In the Puget Sound region (Washington), however, it inhabits also the higher intertidal levels on rocky shores and invades the gravel-shore habitat of *H. oregonensis*. The purple shore crab tolerates both brackish and hypersaline conditions, regulating osmotically in both media. The body wall is slightly more permeable to water than in *Pachygrapsus*, but less so than in *H. oregonensis*. Osmotic activity increases with degree of osmotic stress.

The diet in Puget Sound, where studies have been made, consists mainly of diatoms, desmids, and small green algae scraped from rocks with the cup-shaped tips of the chelae, as in *Pachygrapsus*. A small amount of animal material is also

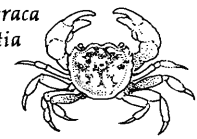
found in the gut. Vision appears to be an important sense, and the retinal pigments shift in position regularly to adapt the eye for day and night seeing. These shifts continue under experimental conditions of constant darkness, but not under constant illumination, and appear to be controlled by a "biological clock."

In the Monterey Bay area, breeding occurs in winter; ovigerous females are found only from November to April. In Puget Sound, where the season is a bit later, ovigerous females are present from early January to mid-July, with a seasonal peak in April. Copulation is much as in *Pachygrapsus*, but without preliminary courtship. Size of the brood varies with the size of the female, from a mere 441 eggs in a female 11.9 mm in carapace width to over 36,400 in a female 34 mm across the back; the average for 51 ovigerous females was about 13,000 eggs. One brood per year is the rule, and second broods appear to be rare. Hatched larvae enter the plankton and pass through five zoeal stages and a megalops stage before the first juvenile crab instar. Larvae have been raised in the laboratory and the instars described.

The parasitic isopod *Portunion conformis* occurs in the perivisceral cavity in some individuals of *H. nudis*.

See Boolootian et al. (1959), Dehnel (1958, 1960, 1962, 1966), Dehnel & Carefoot (1965), Dehnel & McCaughran (1964), Dehnel & Stone (1964), Fasten (1915), Gross (1957a), Hart (1935, 1940, 1968), Hu (1958), Johnson & Snook (1927), Jones (1941), Knudsen (1964b), MacGinitie (1935), MacGinitie & MacGinitie (1968), McWhinnie & Scheer (1958), Meenakshi & Scheer (1959), Piltz (1969), Rathbun (1918, 1926), Ricketts & Calvin (1968), Scheer & Meenakshi (1961), Schmitt (1921), R. I. Smith (1948), R. I. Smith & Rudy (1972), Thompson & Chow (1955), and Todd & Dehnel (1960).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Grapsidae



25.45 **Hemigrapsus oregonensis** (Dana, 1851)
Yellow Shore Crab, Mud-Flat Crab

On open mud flats, in mats of the green alga *Enteromorpha*, and in beds of the eelgrass *Zostera*, high to low intertidal zones in bays and estuaries: Resurrection Bay (Alaska) to

Bahía de Todos Santos (Baja California); not Gulf of California (specimens reported from there are now recognized as *Goetice americanus* Rathbun); Pleistocene fossils from San Pedro (Los Angeles Co.).

Carapace width to 34.7 mm in males and 29.1 mm in females; color yellow or gray, the carapace and legs mottled with brownish purple or black, the claw tips light yellow or white; species distinguished from *H. nudus* (25.44) by its dull color, hairy legs, and four-lobed anterior margin of carapace, and by absence of red spots on chelipeds.

This species tends to replace *Pachygrapsus crassipes* (25.43) and *Hemigrapsus nudus* in bays, on mud flats, and on gravel shores. Though its body is more permeable to water than those of the other two species, it osmoregulates effectively in both brackish and hypersaline media. The crabs are common in parts of San Francisco Bay where the salinity averages 73 percent that of seawater, and a population in Los Peñasquitos Lagoon (San Diego Co.) was found living at a salinity of 175 percent that of seawater, far beyond the tolerance limits of most members of the species. The crabs endure moderately polluted conditions in Los Angeles harbor.

The mud-flat crab feeds mainly at night, primarily on diatoms and green algae. Although largely an herbivore, it takes meat when available and can locate it at a distance under water by means of chemoreceptors on the first antennae. The eyes are not essential in finding food, but they show adaptive changes for day and night vision; as in other grapsoid crabs, these changes continue to occur when the crabs are held in constant darkness, but not when they are constantly illuminated. The crabs are good diggers and can bury themselves rapidly, providing some protection against such important predators as the western willet, a marsh bird.

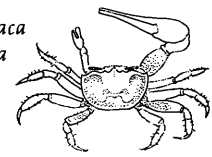
Reproduction in the mud-flat crab is best known in populations in Washington and adjacent British Columbia. Mating occurs much as in *Pachygrapsus crassipes* and *H. nudus*. Under laboratory conditions a female may mate with several males, and observations suggest that males may be stimulated to mate by substances secreted by the female. In northern waters ovigerous females are seen from February to September, and by May some 90 percent are carrying eggs. Hatching occurs from May to July, and in August some fe-

males produce a second brood. The number of eggs carried by individual females ranges from 800 to 11,000 (averaging 4,500). The larval stages have been described and illustrated by Hart (1935). Detailed studies of reproduction in California waters are lacking, but females with eggs have been noted in Monterey Bay from November through February and in May. Young crabs are abundant from May to August and are sometimes used by fishermen as bait for the pile perch, *Rhacochilus vacca*.

The parasitic isopod *Portunion conformis* occurs in the perivisceral cavity of *H. oregonensis*. Infected hosts appear normal, and the presence of the parasites (one to four per infected host) can be determined only by dissection. Infection was present in 21.2 percent of the 372 crabs sampled from San Francisco Bay, and 12.3 percent of the 122 crabs from Bodega Bay.

See Bowman (1949), Dehnel (1958, 1960, 1962), Dehnel & Carefoot (1965), Dehnel & McCaughran (1964), Dehnel & Stone (1964), Easton (1972), Filice (1958), Gross (1957a, 1961), Hart (1935, 1940, 1968), Holmes (1900), Johnson & Snook (1927), Jones (1941), Knudsen (1964b), MacGinitie (1935), MacGinitie & MacGinitie (1968), MacKay (1943a), Muscatine (1956), Piltz (1969), Rathbun (1918, 1926), Reeder (1951), Reish (1961a), Reish & Winter (1954), Ricketts & Calvin (1968), Schmitt (1921), R. I. Smith (1948), Symons (1964), Todd & Dehnel (1960), Turner & Sexsmith (1964), and Vassallo (1969).

Phylum Arthropoda / Class Crustacea / Subclass Malacostraca
Superorder Eucarida / Order Decapoda / Suborder Reptantia
Section Brachyura / Family Ocypodidae



25.46 **Uca crenulata crenulata** (Lockington, 1877)
Fiddler Crab

On sand and mud flats, high and middle intertidal zones in protected bays and estuaries, forming permanent burrows marked by presence of sand and mud pellets around openings; Playa del Rey, Los Angeles Co. (existence of small colony recently verified) to Isla de los Mangles (Baja California); former large colonies at Newport Bay (Orange Co.) and Mission Bay (San Diego Co.) now facing extinction.

Carapace up to 19.7 mm wide in males, 17 mm wide in fe-

males, rectangular, wider than long, convex, smooth; females with chelae small and of equal size; males with one chela small, the other greatly enlarged, the large one with an oblique ridge inside propodus, bending at an obtuse angle and continuing to upper margin.

Another subspecies, *U. crenulata coloradensis* (Rathbun), occurs in the Gulf of California (Bahía San Felipe to Bahía de Tenacatita).

Fiddler crabs dig burrows at the levels of the highest tides and feed on minute plants and animals contained in sandy mud. Females feed with both chelae, but males use only the small claw in taking food. Feeding is selective, and the rejected mud remains as pellets about the burrows. Males use the large claw in ritualistic encounters with other males (which seldom result in injury), and in beckoning to the females, which are lured into the male's burrow for mating. Motions of the large and small claw in males were probably responsible for the name "fiddler crab," although some species stridulate, producing a rasping sound; one of the more common of these is *Uca musica* Rathbun, which occurs from Baja California and the Gulf of California to Puerto Pizarro, Peru, and perhaps formerly near San Diego as well.

Uca crenulata tolerates brackish conditions well and also occurs in lagoons where salinities are high (up to 150 percent seawater). The animals osmoregulate in both dilute and hypersaline media. In other respects *U. crenulata* has not been the object of much study, but a great deal is known of the behavior and physiology of other species of fiddler crabs.

Although subgenera are not used in this account, it should be noted that the correct subgeneric name for both *Uca crenulata* and *U. musica* is *Leptuca* Bott, 1973, rather than *Celuca* Crane, 1975 (see von Hagen, 1976).

See especially Crane (1975); see also Altevogt (1957), Bliss & Mantel (1968), Bott (1973), Crane (1941, 1957), Dembrowski (1926), Fingerman (1966), Gross (1961), Johnson & Snook (1927), Jones (1941), Peters (1955), Rathbun (1918), Ricketts & Calvin (1968), Schmitt (1921), Valiela et al. (1974), Vernberg (1969), von Hagen (1976), and Waterman (1960, 1961, indexes).

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