THE LIGHT AND SMITH MANUAL

INTERTIDAL INVERTEBRATES *from* CENTRAL CALIFORNIA *to* OREGON

EDITED BY JAMES T. CARLTON

FOURTH EDITION, COMPLETELY REVISED AND EXPANDED

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Bivalvia

EUGENE V. COAN AND PAUL VALENTICH-SCOTT

(Plates 393–434)

The Bivalvia, which includes clams, cockles, scallops, oysters, mussels, piddocks, and shipworms, are fundamentally bilaterally symmetrical mollusks in which the mantle encloses the head, foot, and visceral mass and secretes a shell in the form of two lateral valves, hinged dorsally. With the retreat of the body from direct contact with the substratum, a unique mode of feeding using the ctenidia has developed.

Although the exact mode of feeding of ancestral bivalves is not known, it is likely that suspension feeding by palps and ctenidia was developed with the enclosure of the body by the mantle and shell. Modern representatives of the order Nuculoida retain several primitive morphological characters and are suspension feeders. However, such forms also possess specialized, elongate, palp appendages that can be extended from within the shell to sweep up detritus with cilia and convey it to the mouth. The radula and other structures of the head were lost as this indirect mode of feeding developed. The protobranch ctenidia of the primitive bivalve, presumably similar to those of *Ennucula* or of *Acila,* consist of a central axis bearing, on either side, a series of flattened, ciliated filaments.

The evolution of lamellibranch ctenidia, which characterize the vast majority of modern bivalves, was accomplished by the elongation of the filaments, their folding back on themselves so each ctenidium commonly resembles a tall, narrow W in cross-section, and the binding of adjacent filaments into extensive lamellae. Diagrams of the various types of fusions and shapes of the resulting demibranchs are available in invertebrate zoology textbooks. Complex feeding and rejection tracts of cilia on the ctenidia transport food and rejecta (pseudofeces) respectively, and the palps further sort the food before passing it into the mouth (plate 393A). Thus equipped, bivalves have become nearly complete introverts, using their ciliated ctenidia both for respiration and filtering food from the water. To keep in touch with their environments, they have developed sensory tentacles on mantle edges and at siphonal apertures and may even possess distinctive eyes along the edges of the mantle, as in *Crassadoma* and other scallops.

Ctenidial food collecting, successful as it is, has imposed certain limitations; no bivalve can lead a terrestrial existence, and enclosure of the body within the mantle precludes a really active life. The ability to collect food from the water has ensured a steady source of nutrition, and this has made possible the retreat of many bivalves into protected crevices or burrows.

Bivalves furnish splendid examples of evolutionary diversification and adaptive radiation. Easily recognizable adaptive modifications create features of taxonomic importance. On one hand, this is of great value to the student because closely related families, superfamilies, and orders generally show uniformity in way of life. On the other hand, similar ways of life have also produced parallelisms in structure and adaptation, like we see among distantly related genera that attach themselves to hard substrata (e.g., *Chama, Pododesmus,* and *Crassadoma*). Certain structures, such as the hinge, often permit the recognition of affinities despite outward dissimilarity. Thus, the ligament and cardinal teeth in *Tivela, Mactrotoma,* and *Tresus* readily demonstrate the taxonomic affinity of the latter two genera, whereas in outward form and way of life, *Mactrotoma* and *Tivela* are most similar.

Modern classification of bivalves is based on a wide spectrum of characters, the most important of which are: (1) the structure of the ctenidia, including their relationship to the palps and the types of cilia on them; (2) the mode of life, such as burrowing, boring, attaching with a byssus, cementing to a substratum, or free-living; (3) the morphology of the shell, particularly the hinge teeth and the ligament and the relative sizes and degree of gape of the two valves; (4) the surface sculpture of the valves; (5) the size and position of the adductor muscles that pull the shells closed, which create distinctive scars on the insides of the valves; (6) the degree of fusion of the mantle edges and the presence and nature of siphons, reflected by readily visible scars on the insides of the valves; (7) the microstructure and mineralogy of the shell; (8) the morphology of the stomach; (9) the form of the foot and the presence on it of attachment threads forming a byssus, and (10) information now available through biochemical and genetic methods.

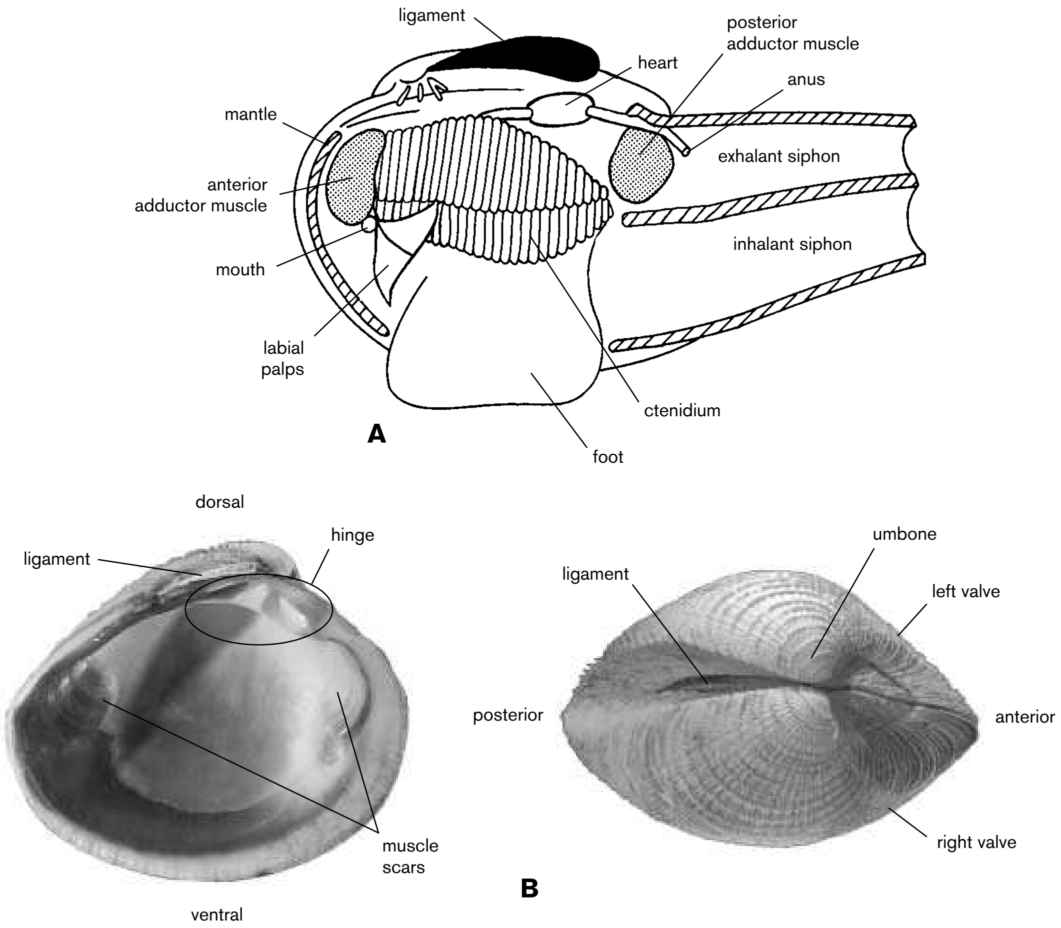

PLATE 393 A, diagrammatic anatomy of a heterodont bivalve; B, diagnostic characters that aid in the identification of bivalve mollusks.

A long and abundant bivalve fossil record has also enabled systematists to establish relationships and rankings that would be difficult to discern using only living forms. The number of characters now employed in bivalve classification, and the degree of parallel evolution in the expression of these features, has led workers to adopt names for orders not based on any one set of characters.

Bivalve Diversity and Classification

PROTOBRANCHIA

A compact, probably natural group composed of two orders.

SOLEMYOIDA

The genera *Solemya* and *Acharax* have primitive, protobranch ctenidia, which are the main organs of feeding, and, as in the Nuculoida, a flattened foot. Solemyoida are subtidal, with *Solemya valvulus* and *S. reidi* occurring offshore in waters of moderate depth in central California.

NUCULOIDA

These have protobranch ctenidia, a primitive taxodont hinge with a row of similar teeth, and they feed in large part by the palps. They are also subtidal. Valves of *Nuculana taphria* and *Yoldia cooperi* are occasionally washed ashore, and *Acila castrensis* and *Ennucula tenuis* may be dredged in water of moderate depth.

PTERIOMORPHA

Most systematists agree that this subclass is a natural group, a conclusion based both on fossil evidence and on the overall similarity of living representatives. Most members are epifaunal, attached to surfaces by a byssus or by cementation, and, as a result, the foot is reduced or entirely absent. The mantle margins are less fused than in the subclass Heterodonta.

ARCOIDA

This order has filter-feeding, filibranch ctenidia in which the elongate filaments are reflected, so each gill appears as a tall, narrow W in cross-section; adjacent filaments are united by patches of interlocking cilia to form lamellae. This is chiefly but not exclusively a tropical order, and most have a taxodont hinge. Of the Arcidae, only *Acar bailyi* has occasionally been found in the intertidal zone of central California, and of the Glycymerididae, shells of *Glycymeris septentrionalis* have been found washed ashore. The Philobryidae, represented locally by *Philobrya setosa,* which resembles a small mytilid, is also placed here.

MYTILOIDA

Members of this order have either filibranch or eulamellibranch ctenidia, the latter with actual bridges of tissue between adjacent filaments. The adductor muscles are unequal in size (heteromyarian). The order includes the Mytilidae, the well-known mussels, which lack conspicuous hinge teeth. Most are found epifaunally attached to rocks or pilings by a byssus, although some are infaunal in soft substrata and others bore into shale.

PTERIOIDA

This group includes many taxa that are mostly tropical, with only the Ostreidae (true oysters) found in central California.

LIMOIDA

This order contains the family Limidae, two species of which occur offshore in water of moderate depth in central California.

PECTINOIDA

Members of this order include two families in the central California intertidal zone, Pectinidae (scallops) and Anomiidae (rock jingles or rock oysters). Only the much-enlarged posterior adductor muscle is present, a condition termed "monomyarian." Some attach to the substratum, whereas others are free living.

HETERODONTA

This group includes most of the familiar clams. Ctenidia are eulamellibranchiate; the mantle margins are well fused, and elongate siphons are present in most. Distinctive patterns of hinge teeth and ligament characterize the different families.

VENEROIDA

Most heterodonts are members of this order, in which hinge teeth are generally well developed. Many veneroids are shallow to deep burrowers. Local families include Lucinidae, Thyasiridae, Ungulinidae, Carditidae, Chamidae, Galeommatidae, Lasaeidae, Corbiculidae, Pisidiidae, Cardiidae, Neoleptonidae, Veneridae, Petricolidae, Tellinidae, Donacidae, Psammobiidae, Semelidae, Solecurtidae, Solenidae, Pharidae, Mactridae, and Hiatellidae.

MYOIDA

In this group, burrowing and boring are characteristic ways of life; most have long siphons, and the hinge has few teeth. Local families include Myidae, Corbulidae, Pholadidae, and Teredinidae (shipworms).

PHOLADOMYOIDA

Members of this group have siphons, and many burrow into the substratum; the shells are generally thin, and many are nacreous within; hinge teeth are inconspicuous or absent. There is only one order, the Pholadamyoida. In the central California intertidal zone, there are a few members of this order, which also includes the offshore, carnivorous Septibranchia. The only local intertidal families are the Lyonsiidae, Thraciidae, and Laternulidae. Taxa occasionally dredged in water of moderate depth include *Pandora punctata*, *P. bilirata*, and *P. filosa* of the Pandoridae, *Thracia trapezoides* of the Thraciidae, *Periploma discus* of the Periplomatidae, *Cardiomya pectinata* of the Cuspidariidae, and *Trigonulina novemcostatus* of the Verticordiidae.

Ecology and Habitats

Most local bivalves are free-living infaunal burrowers or nestlers, or epifaunal and attach to the substratum by cementation or a byssus. A number of species often occupy empty pholad holes; the external shape in these and other nestlers may vary considerably, and such situs forms have sometimes been given separate names of no taxonomic significance. Only a few of our local species are commensal; for example, *Cryptomya californica* lives in association with *Urechis* and burrowing anomuran shrimps, tapping their burrows with its short siphons; *Mytilimeria nuttallii* lives embedded in compound ascidian tests; *Neaeromya rugifera* occurs byssally attached beneath the abdomen of *Upogebia*; and *Mysella pedroana* is found on the legs and gills of the large sand crab *Blepharipoda occidentalis*.

Other galeommatoideans, such as *Lasaea* and *Kellia,* are nestlers among the byssal threads of mussels, in crevices, even in marine-laboratory seawater systems. Best represented in our intertidal zone fauna are the mytilids (with about 16 species), the venerids (about 12 species), the tellinids (about 10 species), and the pholads (about 10 species).

It may be noted that some of the most abundant bivalves in our bays and lagoons were introduced from other provinces; these include *Mytilus galloprovincialis, Geukensia demissa, Gemma gemma, Petricolaria pholadiformis, Mya arenaria, Lyrodus pedicellatus,* and *Teredo navalis* from the Atlantic, and *Musculista senhousia, Venerupis philippinarum, Nuttallia obscurata, Theora lubrica, Corbula amurensis,* and *Laternula marilina* from Asia. Others, such as the quahog *Mercenaria mercenaria,* are not established locally, but specimens may be encountered. The Asian oysters *Crassostrea sikamea* and *Crassostrea gigas,* and the eastern oyster, *Crassostrea virginica,* although raised commercially in Tomales Bay, Drake's Estero, and other areas, do not usually reproduce here; rare free-living individuals are occasionally reported. However, *Crassostrea gigas,* the most important commercially raised oyster, reproduces in southern California. Further introductions may be expected.

Morphology and Identification

Plate 393B illustrates most of the basic terminology used in the keys to the bivalves. The first-formed part of the shell is the beak. The highest or most prominent point of each valve, at or near the beak, is called the umbo (pleural, umbones). The outer surface of the valves may be covered with a fibrous or horny layer, the periostracum. Beneath this is the calcareous shell, which may be variously sculptured with radial and/or commarginal ridges. The valves are joined dorsally at the hinge, where there is a horny, elastic ligament. The ligament may be partly or entirely internal; if within, it is called a resilium, housed in a resilifer, and if a projecting calcareous shelf is built up for it, this structure is called a chondrophore. In most bivalves, interlocking teeth strengthen the hinge. In bivalves with a few strong teeth, those radiating directly from the beaks are cardinals, whereas those lying posterior or anterior to the beaks are called laterals. In the boring pholads, there may be a calcareous projection in each valve below the hinge called a myophore for the attachment of muscles.

The inner surface of the valves bears the scars of muscle attachments, the most prominent being those of the adductors. The pallial line marks the attachment of the mantle. Posteriorly, this line may be indented to form a pallial sinus, marking the position of muscles for the siphons, if present.

There is no single technique for relaxing all species of bivalves. We have had varying results relaxing bivalves by adding menthol crystals, magnesium chloride (7% in seawater), or dilute ethyl alcohol (approximately 3%) to native seawater until the specimens are not responsive to touch. Members of the family Veneridae can be especially difficult to relax, and we have had to resort to a combination of the above methodologies to properly relax them.

When a specimen is nonresponsive to touch it can then be fixed in 5% buffered formalin (a handful of sodium borate [Borax] per gallon sample—not scientific but the reality of fieldwork). Formalin should be buffered to prevent decalcification, especially of small shells that can rapidly dissolve. Most bivalve specimens should not be allowed to remain in formalin for more than 48 hours, or severe damage can occur to the shell. As usual, use care with formalin; this carcinogen should only be used outdoors or in well-ventilated conditions.

After fixation, bivalves should be rinsed and soaked in distilled water to remove any formalin residue. Finally, they should be place in 80% ethyl alcohol for long-term preservation. If DNA studies are anticipated, formalin should not used. Instead, the specimens should be frozen or placed directly into 95% alcohol, although this makes the specimens poorer candidates for histological examination.

Perhaps the most difficult process in examining a bivalve is to safely open tightly closed (and frequently fragile) valves to observe details of the hinge, pallial line, and muscle scars. Depending on the final deposition of the specimens, one of the following two techniques should provide acceptable results. With either method one must be sure to examine the outside characters (e.g., ligament, lunule, escutcheon, etc.) of the specimen first, as these may be unobservable once the specimen is opened.

If there is no need to examine the soft parts of the bivalve, the specimen can be placed in a dilute solution (approximately 30%–50%) of household bleach in distilled water. Usually after 15 minutes for small shells, longer for larger specimens, all soft tissue will dissolve, allowing easy access to the inside of the shell. This method destroys all soft tissue and the periostracum.

To preserve the soft tissue and periostracum of the specimen, one can open a bivalve shell by using a single-edge razor blade. Carefully place the specimen, ventral side up, in a stiff adhesive (e.g., poster mount) or clay. Then, while carefully holding the specimen with forceps, gently slice the blade into the opening between the valves. With small bivalves, one must accomplish this task while viewing the specimen through a dissecting microscope. While this technique takes practice, it is possible to open specimens as small as 1 mm in length with little or no damage. This method is usually not effective with species that have a heavily crenulated ventral margin.

External observations should include shell sculpture, ligament (if external), beak size and orientation, lunule and escutcheon (if present), and periostracum. Internal shell observations should include type and number of teeth, type of resilifer (if present), pallial line and sinus (if present), and adductor muscle scars (plate 393B).

In smaller specimens, it is often difficult to observe the pallial line and muscle scars. Dyeing the shell in crystal violet allows easier examination of these features. Place the specimen in a solution of crystal violet (no definite concentration, just mix a small amount—maybe 3 g—in 30 cc–50 cc of water and dispense from a dropper bottle) for approximately 15 minutes, or until the pallial line becomes more visible. Crystal violet stain can be removed from the shell by soaking it in ethyl alcohol.

The following keys attempt to achieve a balance between demonstrating adaptive, phylogenetically related groups and providing somewhat artificial keys for easy identification. The keys will be most useful for fresh, mature, unworn specimens and are designed for intertidal species occurring between the Oregon coast and Point Conception. The keys contain both dichotomous and multichotomous choices.

In addition to the general references on Bivalvia, the general references on Mollusca include valuable sources of information on the ecology, biology, physiology, and systematics of bivalves. See especially Coan et al. (2000).

Key to Intertidal Zone Bivalve Families

1. Shell with file-like denticulations anteriorly (plate 394A), and internally with a myophore (except in *Netastoma*) (plate 394B); boring into heavy mud, clay, shale, wood, or shell 2
— Shell various, not as above 3
2. Boring into wood; pallets at siphon tips (plate 394C); anterior end of shell indented with an angular notch (plate 394D) (shipworms). . . . . Teredinidae
— Boring into a variety of substrata; no pallets on siphon tips; anterior end pointed or evenly curved, not notched (plate 394A, 394B). . . . . Pholadidae
3. Dorsal margin produced into triangular "ears" at least in young; sculpture of radial ribs (plate 394E) . . . . Pectinidae
— Dorsal margin without ears 4
4. Shell firmly cemented to substratum (plate 394F); valves irregular and/or distinctly different from one another 5
— Shell not cemented to substratum; valves more or less regular, similar 7
5. Adductor muscles coalesced (plate 394G), resulting in one large, sometimes complex, muscle scar near center of shell 6
— Adductor muscles at opposite ends of shell, not coalesced (plate 394F) . . . . Chamidae
6. Adductor muscle scar complex, with central area showing two to three superimposed secondary scars; one valve with a hole ventral to beaks in most (plate 394H); attached to hard substrata . . . . Anomiidae
— Adductor muscle scar simple (plate 395A); in bays, often attached to rocks and other shells by left valve . . . . . Ostreidae
7. Without a chondrophore or projecting, interlocking teeth on hinge (irregular denticles or a nonprojecting resilifer may be present) 8
— Hinge plate with a projecting chondrophore and/or true teeth. 11
8. Shell minute, triangular, with a single central adductor muscle scar (plate 395B). . . . . Philobryidae
— Shell with two adductor muscle scars 9
9. Adductor muscles and their scars not equal in size (plate 395C); anterior muscle smaller, located at or near beaks; shell

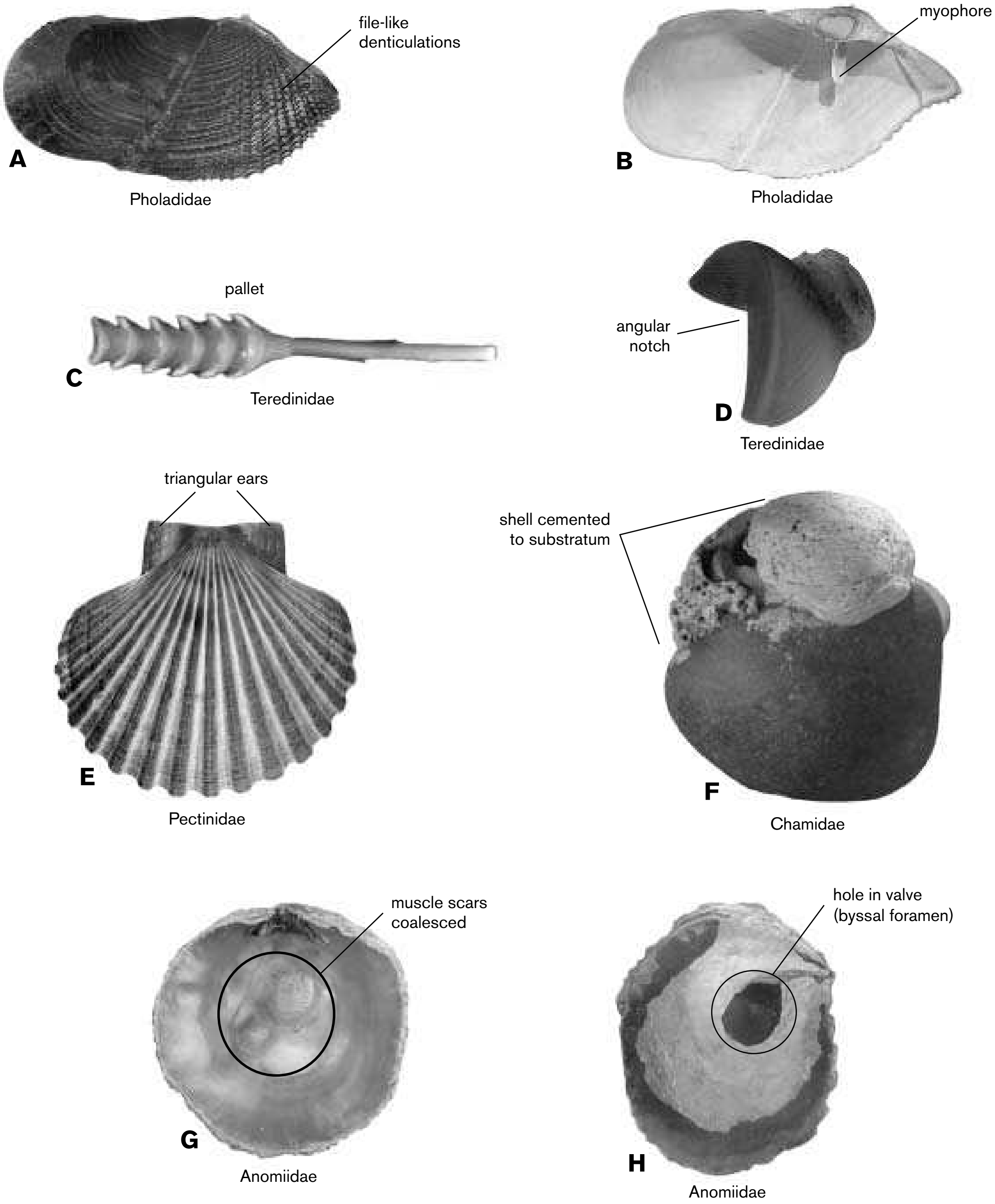

PLATE 394 A, file-like denticulations of Pholadidae; B, projecting myophore of Pholadidae; C, pallet attached to siphons of Teredinidae; D, notch in shell of Teredinidae; E, triangular ears of Pectinidae; F, Chamidae shell cemented to rock; G, coalesced muscle scars of Anomiidae; H, byssal foramen of some Anomiidae.

brown or black, cylindrical or tapering anteriorly . . . . Mytilidae

— Adductor muscles and their scars approximately equal in size (but not necessarily in shape) 10

10. Ligament external; shell porcelaneous within; pallial line broken into patches (plate 395D) in some (others not in patches) . . . . Hiatellidae (in part)

— Ligament both external and internal in a resilifer; shell porcelaneous; pallial line never in patches (plate 395E). . . . . Thraciidae

— Ligament only internal; shell nacreous within (plate 395F); pallial line not in patches . . . . Lyonsiidae

11. Hinge with a row of many similar appearing teeth (taxodont) (plate 395G) . . . . Arcidae

— With only a few (heterodont) teeth and/or a projecting chondrophore (plates 395H, 396D, 396H). 12

12. Hinge with an internal ligament in a distinct resilifer or chondrophore (an external ligament may also be present) (plates 395H, 396A). 13

— Hinge with ligament entirely external, on dorsal surface (or slightly sunken into dorsal margin of hinge plate) (plate 397F) 20

13. Hinge with a spoon- or peg-shaped chondrophore in left valve only (plate 395H). 14

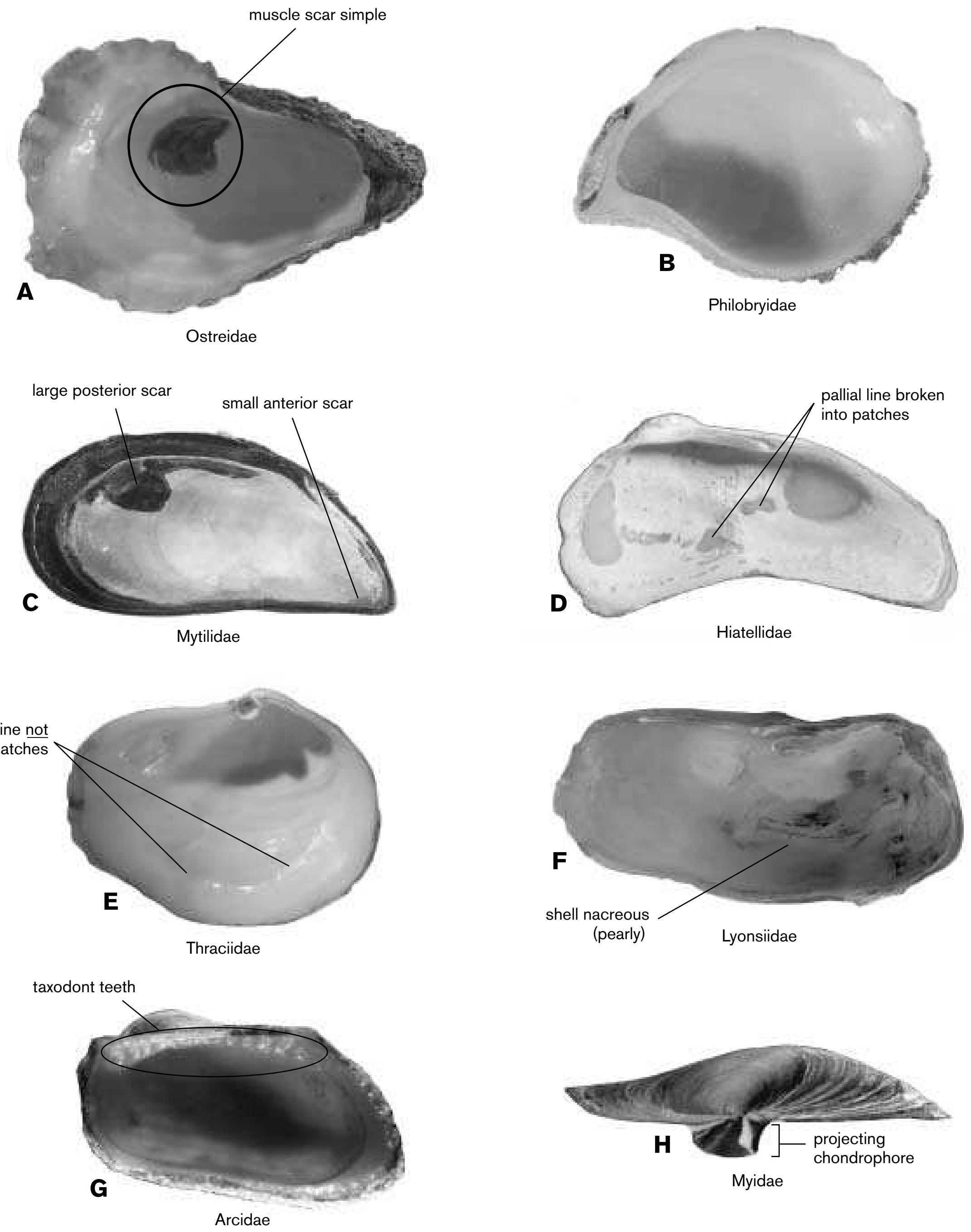

PLATE 395 A, simple muscle scar of Ostreidae; B, triangular shape of Philobryidae; C, unequal adductor scars of Mytilidae; D, patchy pallial line of some Hiatellidae; E, unbroken pallial line of Thraciidae; F, nacreous interior of Lyonsiidae; G, taxodont teeth of Arcidae; H, projecting chondrophore of Myidae.

— Ligament chiefly internal; projecting chondrophore, if present, in both valves 15

14. Chondrophore strongly projecting (plate 395H) . . . . Myidae

— Chondrophore weakly or not projecting (plate 396A). . . . . Corbulidae

15. Adult shells mostly small (<25 mm); pallial line without a sinus. 16

— Adult shells mostly large (>25 mm); pallial line with a distinct sinus (plate 396G) 18

16. Hinge with two to three cardinal teeth and at least one lateral tooth in each valve (plate 396B) . . . . Neoleptonidae

— Hinge simple, with only one to two hinge teeth 17

17. Animal larger than shell (plate 396C) . . . . Galeommatidae

— Shell able to cover entire animal . . . . Lasaeidae

18. Shell nacreous within (plate 396E) . . . . Laternulidae

— Shell porcelaneous within (plate 396G). 19

19. Anterior cardinal tooth in left valve inverted V-shaped (plate 396F) . . . . Mactridae

— Cardinal teeth not inverted V-shaped (plate 396G) . . . . Semelidae

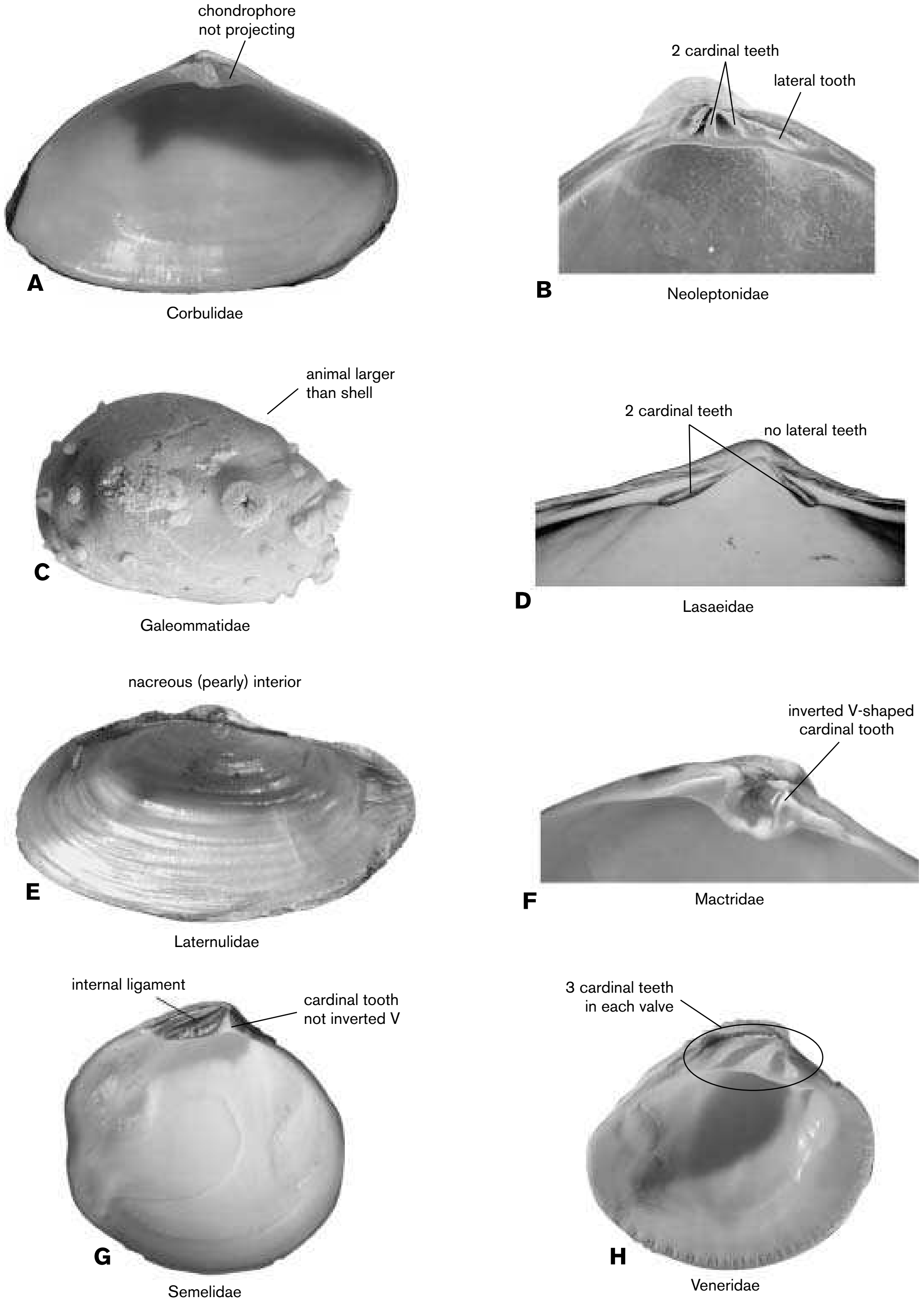

PLATE 396 A, nonprojecting chondrophore of Corbulidae; B, two cardinal teeth and one lateral tooth of Neoleptonidae; C, shell completely internal, Galeommatidae; D, two cardinal teeth of Lasaeidae; E, nacreous interior of Laternulidae; F, inverted V-shaped cardinal tooth of Mactridae; G, porcelaneous interior and simple cardinal tooth of Semelidae; H, three cardinal teeth of Veneridae.

20. Sculpture predominately of radial ribs corrugating all or part of surface (plate 397C) 21

— Sculpture various, including cancellate, not predominately radial 24

21. Hinge without lateral teeth. 22

— Hinge with lateral teeth (plate 397B) 23

22. Three cardinal teeth in each valve (plate 396H) . . . . Veneridae (in part)

— Three cardinal teeth in one valve, two in the other (plate 397A) . . . . Petricolidae (in part)

23. Shell ovate, inflated; beaks central (plate 397B) . . . . Cardiidae

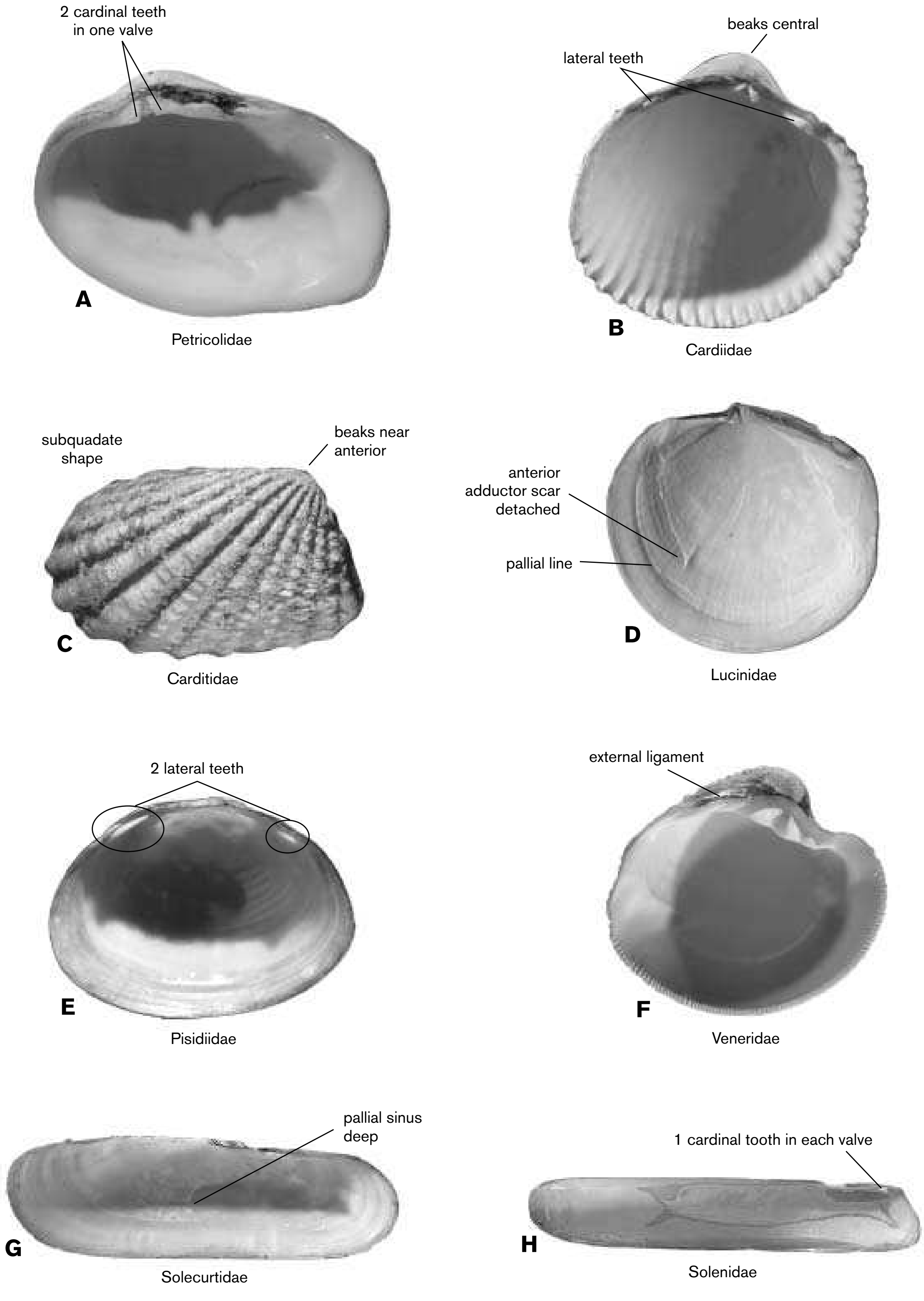

PLATE 397 A, two cardinal teeth of Petricolidae; B, lateral teeth of Cardiidae; C, anteriorly placed beaks of Carditidae; D, detached adductor muscle scar of Lucinidae; E, two lateral teeth of Pisidiidae; F, external ligament of Veneridae; G, deep pallial sinus of Solecurtidae; H, single cardinal tooth of Solenidae.

— Shell subquadrate, not particularly inflated; beaks near anterior end (plate 397C) . . . . Carditidae

24. Anterior adductor muscle scar narrower than posterior, its lower end detached from pallial line and bent inward (plate 397D) . . . . Lucinidae

— Adductor muscle scars approximately equal in shape. 25

25. Adult small to minute, <15 mm in length 26

— Adult >15 mm in length 27

26. Shell thin; ligament partly sunken below dorsal surface; hinge with one to two cardinal and two lateral teeth in each valve (plate 397E) . . . . Pisidiidae

— Shell relatively thick and heavy; ligament completely external; hinge with three cardinal teeth in each valve and,

at most, one lateral tooth in each valve (plate 397F) . . . . Veneridae (in part)
27 Shell evenly cylindrical, length about 2.5 times height (plate 397G, 397H) 28
— Shell otherwise 30
28. Beaks at or near anterior end; pallial sinus relatively shallow; some with a prominent internal radial rib 29
— Beaks nearly central; pallial sinus relatively deep; never with prominent radial strengthening rib (plate 397G) . . . . Solecurtidae
29. One cardinal tooth in each valve (plate 397H) . . . . Solenidae
— One valve with two cardinal teeth, the other with four (plate 398A) . . . . Pharidae
30. Fewer than three cardinal teeth in each valve 31
— Three cardinal teeth in one or both valves (plate 398C) 32
31. Hinge with very elongate, serrate lateral teeth (plate 398B) . . . . Corbiculidae
— Lateral teeth, if present, not very elongate or serrate 33
32. Three cardinal teeth in each valve (plate 398C) . . . . Veneridae (in part)
— Three cardinal teeth in one valve, two in the other (plate 398D) . . . . Petricolidae (in part)
33. Pallial sinus deep (plate 398E) . . . . Psammobiidae, Tellinidae
— Pallial sinus shallow or absent 34
34. Shell oval; pallial line narrow, simple (plate 398F) . . . . Ungulinidae
— Shell elongate; pallial line thick, patchy in some (plate 398G) . . . . Hiatellidae

Species Keys and Lists

SOLEMYIDAE

Solemya reidi Bernard, 1980 (plate 399A). Offshore on soft bottoms with high organic content and low oxygen level. Coan et al. 2000: 65, 67.

**Solemya valvulus* Carpenter, 1864 (plate 399B). Offshore in fine sediments as far north as Monterey Bay in warm-water years. Coan et al. 2000: 66–67.

NUCULIDAE

**Acila castrensis* (Hinds, 1843) (plate 399C). Offshore in fine sediments. Coan et al. 2000: 75–76.

**Ennucula tenuis* (Montagu, 1808) (plate 399D). Offshore in fine sediments. Coan et al. 2000: 76–77.

NUCULANIDAE

**Nuculana taphria* (Dall, 1896) (plate 399E). Offshore in fine sediments, occasionally washed up on beaches. Coan et al. 2000: 89–90.

YOLDIIDAE

**Yoldia cooperii* Gabb, 1865 (plate 399F). Offshore in fine sediments, occasionally washed up on beaches. Coan et al. 2000: 112–113.

ARCIDAE

The southern Californian *Acar bailyi* (Bartsch, 1931) (plate 400A), has been found in the intertidal zone as far north as Cayucos, San Luis Obispo County. Coan et al. 2000: 130–131; Rost 1955, Alan Hancock Pacific Exped. 20: 190–191.

GLYCYMERIDIDAE

**Glycymeris septentrionalis* (Middendorff, 1849) (plate 400B). Occasionally washed ashore on Californian beaches. Coan et al. 2000: 143–144.

PHILOBRYIDAE

**Philobrya setosa* (Carpenter, 1864) (plate 400C). Resembles a small mussel (height to about 5 mm), lives attached to rocks or algae by a byssus in the low intertidal zone. Coan et al. 2000: 151.

MYTILIDAE

KEY TO MYTILIDAE

1. Adult shell minute (5 mm or less), stubby, inflated, with a forwardly directed, anteroventral protuberance; ventral margin sinuous posteriorly (plate 401A) . . “*Musculus*” *pygmaeus*
— Adult shell not minute 2
2. Beaks terminal, at anterior end of shell (plates 401B, 402A) 3
— Beaks near anterior end, but not terminal (plate 402C) 6
3. Anterior end bridged by a shelly septum internally; shell with prominent radial ribs; black externally, purplish internally (plates 401B, 402A) . . . . *Septifer bifurcatus*
— Anterior end without internal septum . . . . *Mytilus* 4
4. Shell generally with irregular radial ribs especially on posterior end (plate 401C) . . . . *Mytilus californianus*
— Shell generally smooth, without strong radial ribs 5
5. Members of this group can not be reliably diagnosed by shell characters (see text) (plate 401D–401F) . . . . *Mytilus trossulus, Mytilus galloprovincialis, Mytilus edulis*
6. Shell cylindrical, with dorsal and ventral margins more or less parallel (plates 402B, 403A–403D) 7
— Shell not cylindrical 10
7. Posterodorsal slope with rough, chalky encrustations; boring in rock (plates 402B, 403A) . . . . . . *Lithophaga plumula*
— Posterodorsal slope with a thick mat or wrinkles, often with mud and debris, not chalky encrustations . . . . *Adula* 8
8. Periostracum with irregular striae; boring in soft shale (plate 403B) . . . . *Adula gruneri*
— Smooth or with a few radiating striations anteriorly 9
9. Shell elongate, generally tapering posteriorly, posterior end not wider than anterior end; generally boring in soft shale (plate 403C) . . . . *Adula californiensis*
— Shell stout, generally distinctly wider posteriorly; free-living (plate 403D) . . . . *Adula diegensis*
10. Shell with prominent radial ribbing; dark brown to blackish (plate 403E) . . . . *Geukensia demissa*
— Shell without ribs 11
11. Shell smooth, thin, without hairs; often with wavy brown bands on greenish background (plate 403F) . . . .

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* = Not in key.

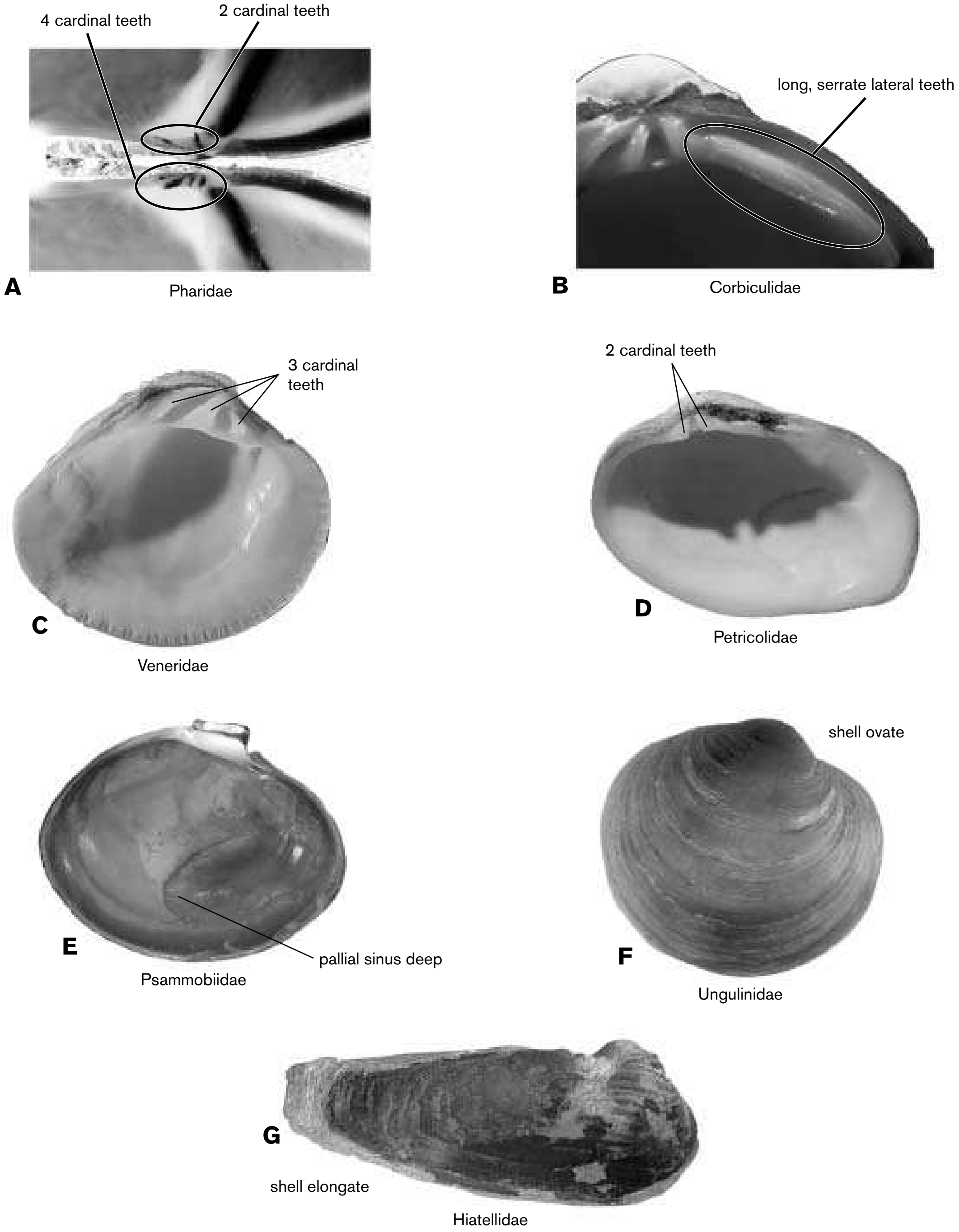

PLATE 398 A, four cardinal teeth of Pharidae; B, long, serrate lateral teeth of Corbiculidae; C, three cardinal teeth of Veneridae; D, two cardinal teeth of Petricolidae; E, deep pallial sinus of Psammobiidae; F, oval shell of Ungulinidae; G, elongate shell of Hiatellidae.

. . . . *Musculista senhousia*

— Shell with periostracal hairs (plate 402D–402E) . . . . *Modiolus* 12

12. Periostracum with serrate hairs (plates 402D, 404A) . . . . *Modiolus capax*

— Periostracal hairs smooth (plate 402E) 13

13. Shell elongate; umbones set well back from anterior margin; adult to 120 mm or more (plate 404B) . . . . . *Modiolus rectus*

— Shell rhomboidal; beaks not projecting beyond anterior end; adult to 140 mm (plates 402C, 404C) . . . . *Modiolus modiolus*

— Shell short, stout, inflated, umbones protruding beyond anterior margin; adult to about 40 mm (plate 404D) . . . . *Modiolus carpenteri*

— Shell short, stout; anteroventral margin projecting beyond beaks; adult to 70 mm (plates 402E, 402F, 404E) . . . . *Modiolus sacculifer*

LIST OF SPECIES

Soot-Ryen 1955, Allan Hancock Pac. Expeds. 20: 175 pp.

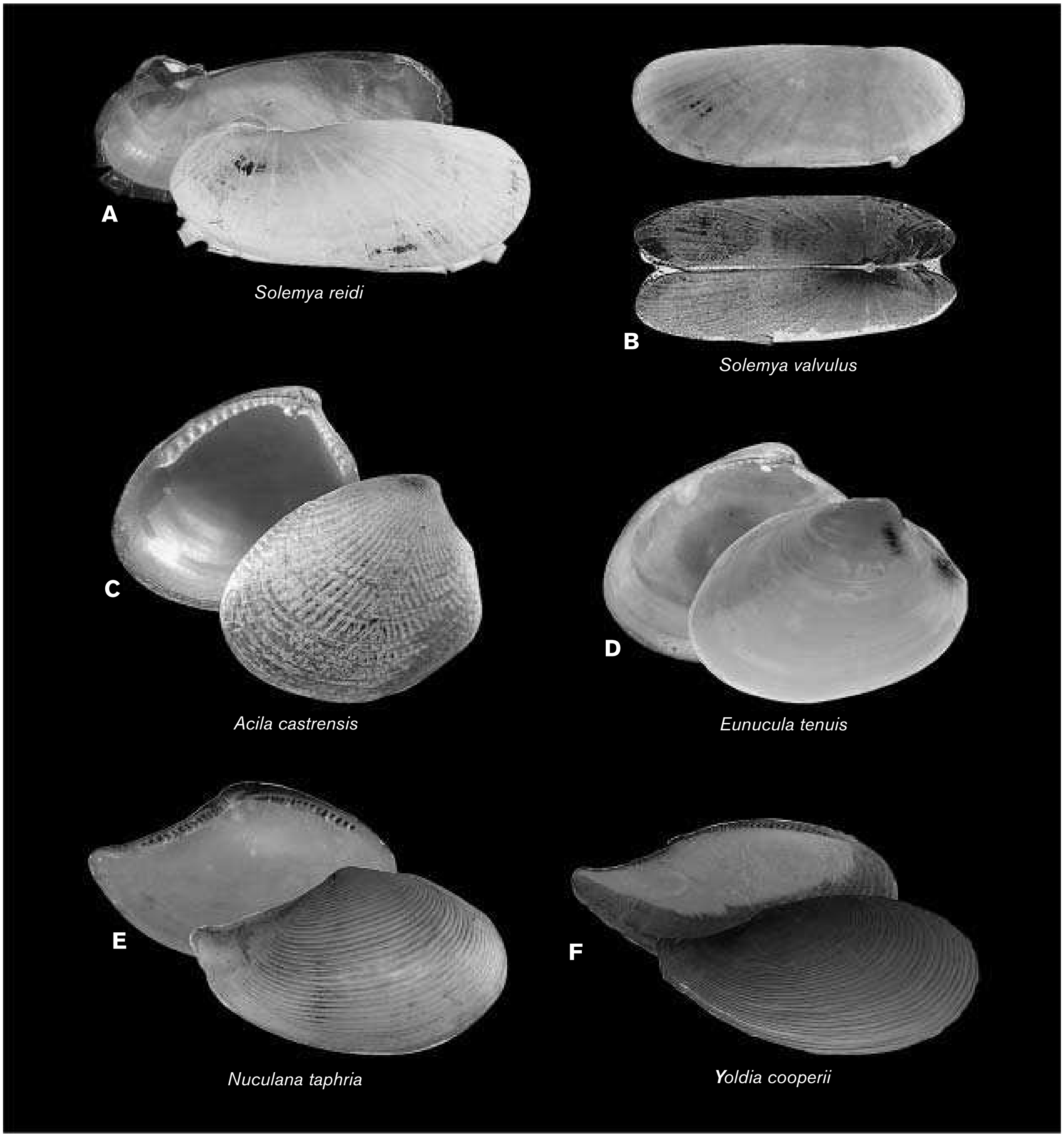

PLATE 399 A, *Solemya reidi,* length 35 mm; B, *Solemya valvulus,* length 11 mm; C, *Acila castrensis,* length 8 mm; D, *Ennucula tenuis,* length 4 mm; E, *Nuculana taphria,* length 5 mm; F, *Yoldia cooperii,* length 39 mm.

Adula californiensis (Philippi, 1847) (plate 403C). Boring mechanically in soft shale, mudstone, but occasionally free-living; intertidal to sublittoral zones. Coan et al. 2000: 176–178; Lough and Gonor 1971, Mar. Biol. 8: 118–125 (embryology, developmental rate); Lough and Gonor 1973, Mar. Biol. 22: 241–250 (larvae); Soot-Ryen 1955: 90–91; Yonge 1955, Quart. J. Micr. Sci. 96: 383–410 (boring).

Adula diegensis (Dall, 1911). Free-living on mud flats, pilings, with *Mytilus*; distinguished from *A. californiensis* by its more flaring dorsal margin and sparse periostracal mat on the posterior slope. Coan et al. 2000: 178; Soot-Ryen 1955: 91.

Adula gruneri (Philippi, 1851) (=*A. falcata* [Gould, 1851]). Boring mechanically in soft shale or clay. Coan et al. 2000: 159, 178–179; Fankboner 1971, Biol. Bull. 140: 28–45 (feeding, ciliary currents); Soot-Ryen 1955: 89–90; Yonge 1955, Quart. J. Micr. Sci. 96: 383–410 (boring).

Geukensia demissa (Dillwyn, 1817) (formerly placed in *Volsella, Modiolus, Arcuatula,* and *Ischadium*). An introduced western Atlantic mussel now abundant in mud in sloughs, bays, in cracks on pilings. There is a substantial literature on the biology of this species, chiefly in the western Atlantic; for a bibliography: Coan et al. 2000: 187–188.

**Crenella decussata* (Montagu, 1808) (plate 405A). A small, rounded species in soft sediments just offshore. Coan et al. 2000: 163, 166.

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* = Not in key.

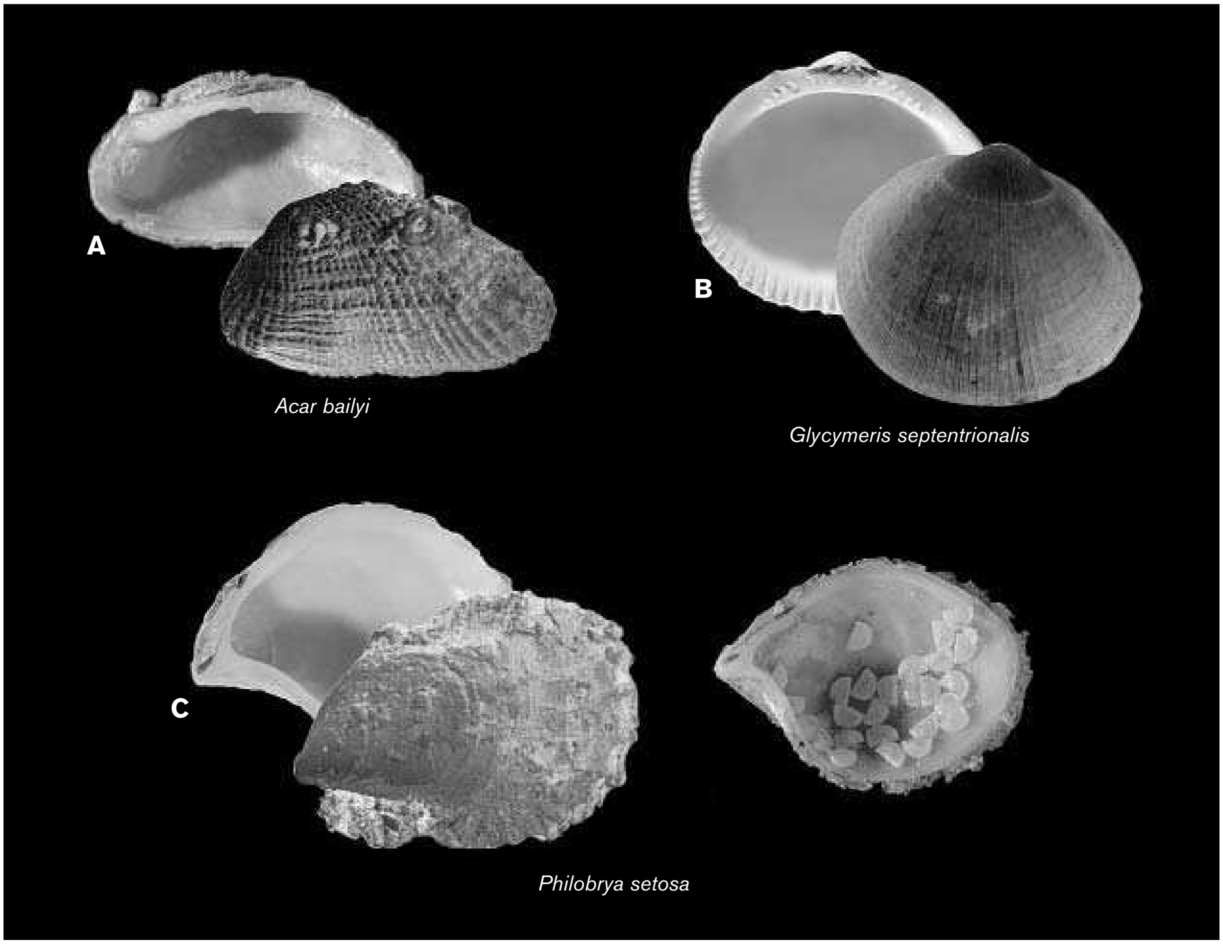

PLATE 400 A, *Acar bailyi,* length 7 mm; B, *Glycymeris septentrionalis,* length 17.5 mm; C, *Philobrya setosa,* length 6 mm (left pair), length 5 mm (right specimen with brood).

**Gregariella coarctata* (Carpenter, 1857) (plate 405B). A trapezoidal species that nestles in offshore rocks. Coan et al. 2000: 163, 166–167.

Lithophaga plumula (Hanley, 1843) (=*L. subula* [Reeve, 1857] and *L. plumula kelseyi* [Hertlein and Strong, 1946]). Boring in calcareous shale, shells; inner mantle fold secretes acid mucus. Coan et al. 2000: 180; Hodgkin 1962, Veliger 4: 123–129 (boring); Kleemann 1990, Senckenbergiana Maritima 21: 101–154 (boring); Soot-Ryen 1955: 96–97; Yonge 1955 (boring, above, under *Adula*).

Modiolus capax (Conrad, 1837). Intertidal, on rocks, pilings; southern; central California records require confirmation. Coan et al. 2000: 183–185; Orduña, Rojas, and Farfán 1991, Veliger 34: 302–308 (development); Soot-Ryen 1955: 60–62.

Modiolus carpenteri Soot-Ryen, 1963. Occasional in low intertidal zone, largely sublittoral, and commonly washed ashore; among rocks, shells, gravel. Coan et al. 2000: 184–185; Soot-Ryen 1955: 62.

**Modiolus neglectus* Soot-Ryen, 1955 (plate 404F). Offshore in soft substrata. Coan et al. 2000: 184, 186; Soot-Ryen 1955: 64–65.

Modiolus modiolus (Linnaeus, 1758). This northern species has been found in the intertidal zone as far south as Monterey. In boreal waters of both the Atlantic and Pacific; there is a substantial literature on the biology of this species, cited in Coan et al. 2000: 185–186.

Modiolus rectus (Conrad, 1837) (=*M. flabellatus* [Gould, 1850]). Largely sublittoral, rare in low intertidal zone; in mud, anterior end embedded in soft substrata. Coan et al. 2000: 165, 184, 186–187; Soot-Ryen 1955: 63–64.

Modiolus sacculifer (Berry, 1953). Generally offshore in holdfasts, shell not elongate, umbones set back from produced anterior end, not overhanging anterior margin as in *M. carpenteri*. Coan et al. 2000: 184, 186; Soot-Ryen 1955: 65–66.

"*Musculus*" *pygmaeus* Glynn, 1964. High intertidal, attached to blades or holdfast of alga *Endocladia muricata* from Marin County to San Luis Obispo County. Coan et al. 2000: 169–170; Glynn 1964, Veliger 7: 121–128.

Musculista senhousia (Benson, 1842) (formerly placed in *Modiolus* and *Musculus*; *M. senhousei* is an invalid emendation). Abundant in mud, forming extensive mats; in fouling on pilings, among algae; introduced from Japan. Coan et al. 2000: 163, 167 (including references to many other papers); Morton 1974, Pac. Sci. 28: 19–33 (functional morphology, etc.); Soot-Ryen 1955: 74–75.

Mytilus californianus Conrad, 1837. California mussel; abundant in exposed intertidal rocks; also in bays, on pilings. Coan et al. 2000: 156–158 (with references to more than 60 papers); Coe and Fox 1942, J. Exp. Zool. 90: 1–30; Fox and Coe 1943, J. Exp. Zool. 93: 205–249; Coe and Fox 1944, Biol. Bull. 87:

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* = Not in key.

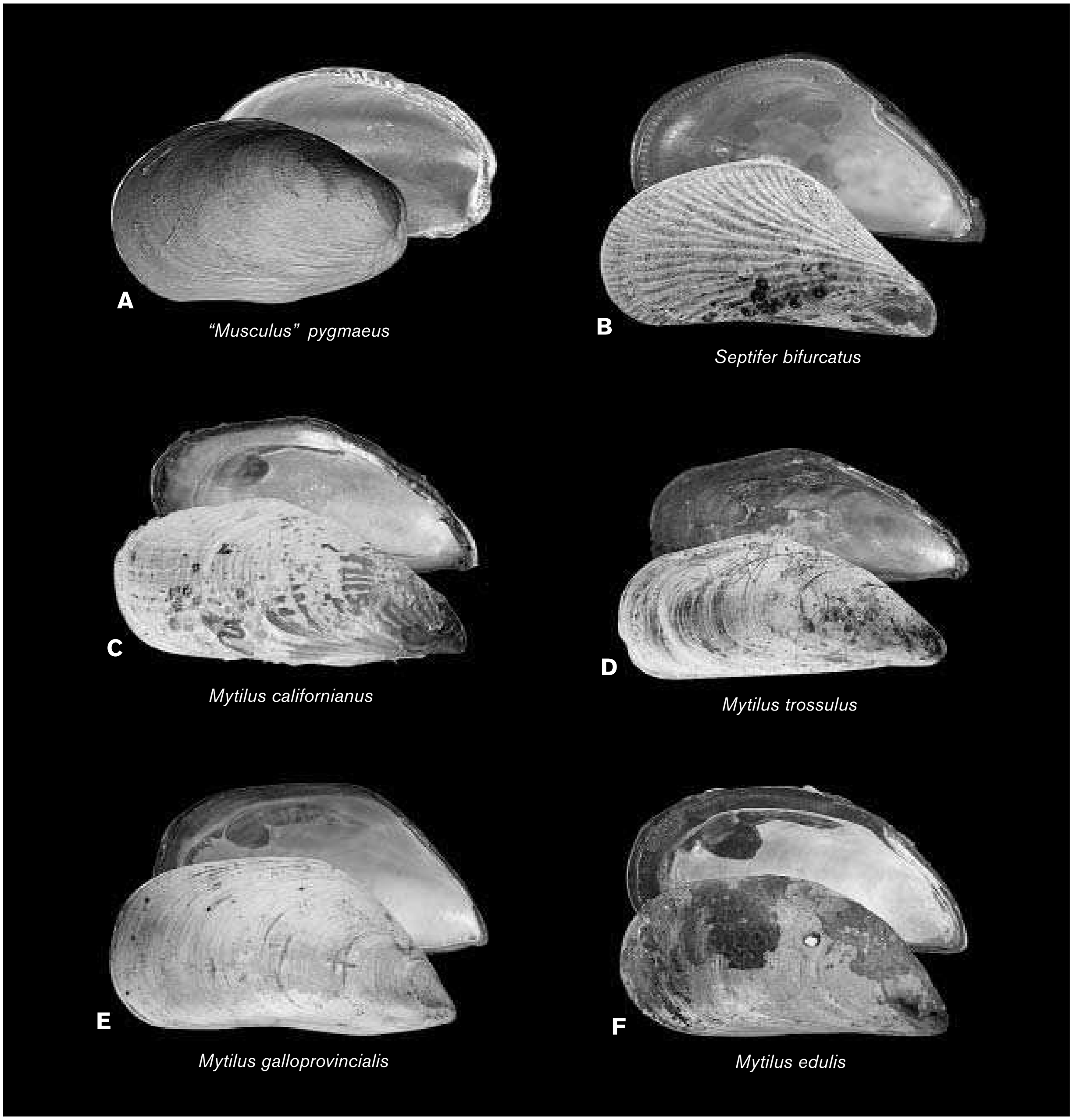

PLATE 401 A, *"Musculus" pygmaeus,* length 3.2 mm; B, *Septifer bifurcatus,* length 27 mm; C, *Mytilus californianus,* length 97 mm; D, *Mytilus trossulus,* length 46 mm; E, *Mytilus galloprovincialis,* length 87 mm; F, *Mytilus edulis,* length 64 mm.

59–72; Coe 1948, J. Mar. Res. 7: 586–601; aspects of biology; papers by Harger, and Harger and Landenberger, in Veliger 11–14 (1968–1971) on ecology, biology of *M. "edulis"* and *M. californianus*.

Mytilus trossulus Gould, 1851; *M. galloprovincialis* Lamarck, 1891; *M. edulis* Linnaeus, 1758. Genetic studies have shown that the native smooth mussel in the North Pacific is *M. trossulus,* which occurs from the Arctic south to central California, where it now forms a hybrid zone with the introduced European *M. galloprovincialis*; the latter occurs from central California to Baja California; wild specimens of *M. galloprovincialis* have also been found in southern British Columbia, but establishment there is uncertain. The native North Atlantic *M. edulis* is subject to experimental mariculture in British Columbia and may spread and hybridize as well. Members of this complex are widespread; abundant on wharf pilings, floats, docks, rocks; occasional on outer coast. There is a vast literature on all aspects of the biology of this group, with many papers cited in Coan et al. 2000: 157–160. Other important reviews of this group are in Gosling 1992, The genus Mytilus: ecology, physiology, genetics and culture, Amsterdam (Elsevier), 589 pp.; Bayne 1976, Marine mussels: their ecology and physiology, Cambridge, U.K. (Cambridge Univ.), 506 pp. See also Kafanov 1999, Bull. Inst. Malac., Tokyo 3: 103–108; Buianovskii 2000, Ruthenica 10: 43–48; Martel et al. 1999, Invert. Biol. 118: 149–164 (distinguishing early juveniles).

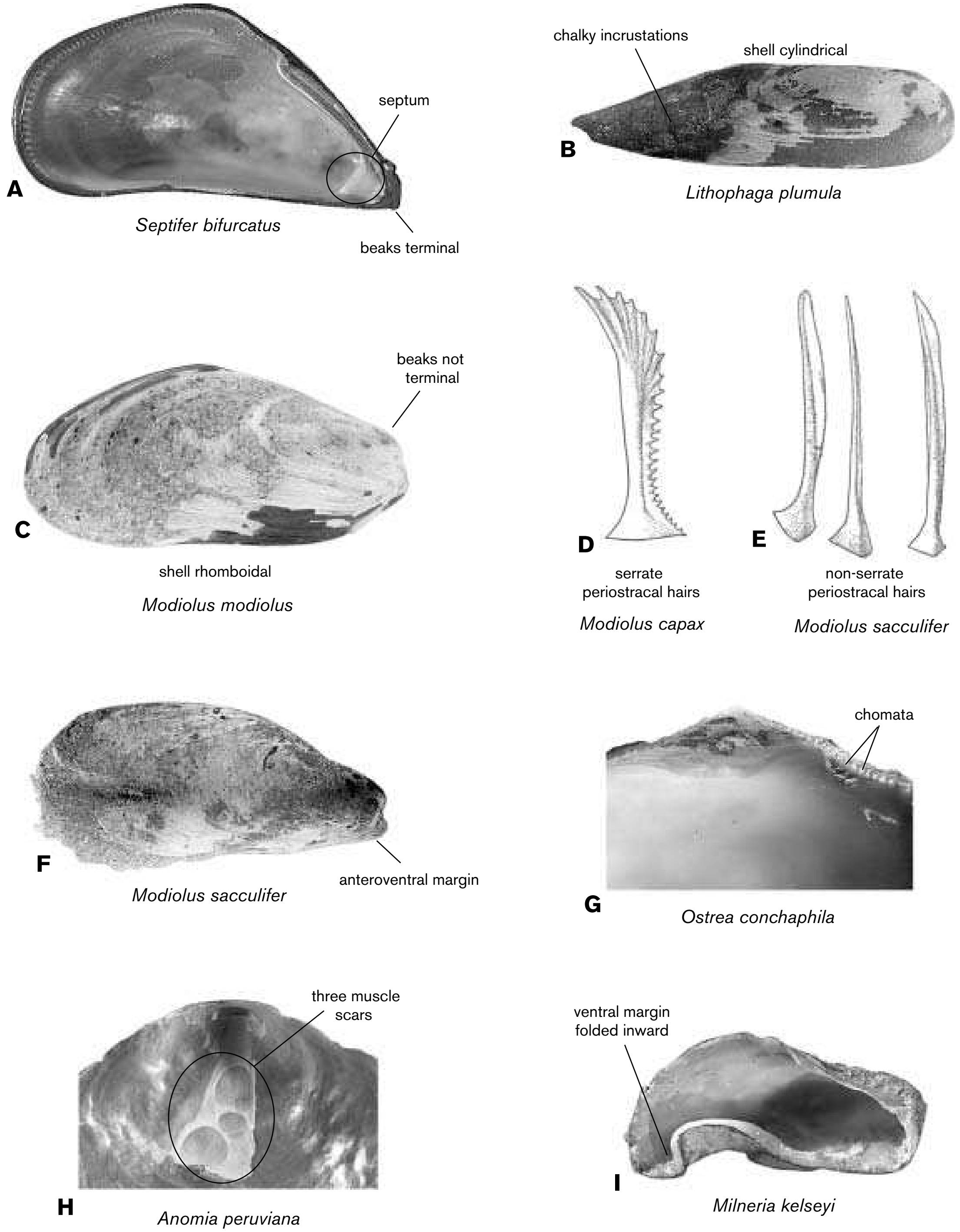

PLATE 402 A, *Septifer bifurcatus,* length 27 mm; B, *Lithophaga plumula,* length 51 mm; C, *Modiolus modiolus,* length 66 mm; D, detail of periostracal hair of *Modiolus capax*; E, detail of periostracal hair of *Modiolus sacculifer*; F, *Modiolus sacculifer,* length 74 mm; G, detail of chomata on dorsal margin of *Ostrea conchaphila*; H, three muscle scars of *Anomia peruviana*; I, infolded ventral margin of *Milneria kelseyi,* length 5 mm (D, E, from Soot-Ryen 1955).

Septifer bifurcatus (Conrad, 1837). Low intertidal, under rocks. Coan et al. 2000: 188, 190; Soot-Ryen 1955: 41–42; Yonge and Campbell 1968, Trans. Roy. Soc. Edinburgh 68: 34 (functional morphology).

**Solamen columbianum* (Dall, 1897) (plate 405C). A rounded, inflated species characteristic of offshore soft sediments; larger than *Crenella decussata*, with finer sculpture. Coan et al. 2000: 171–172.

LIMIDAE

**Limaria hemphilli* (Hertlein and Strong, 1946) (plate 405D). In shallow water offshore in warm-water years. Coan et al. 2000: 205–206.

**Limatula saturna* Bernard, 1978 (plate 405E). In shallow offshore waters. Coan et al. 2000: 206–208.

* = Not in key.

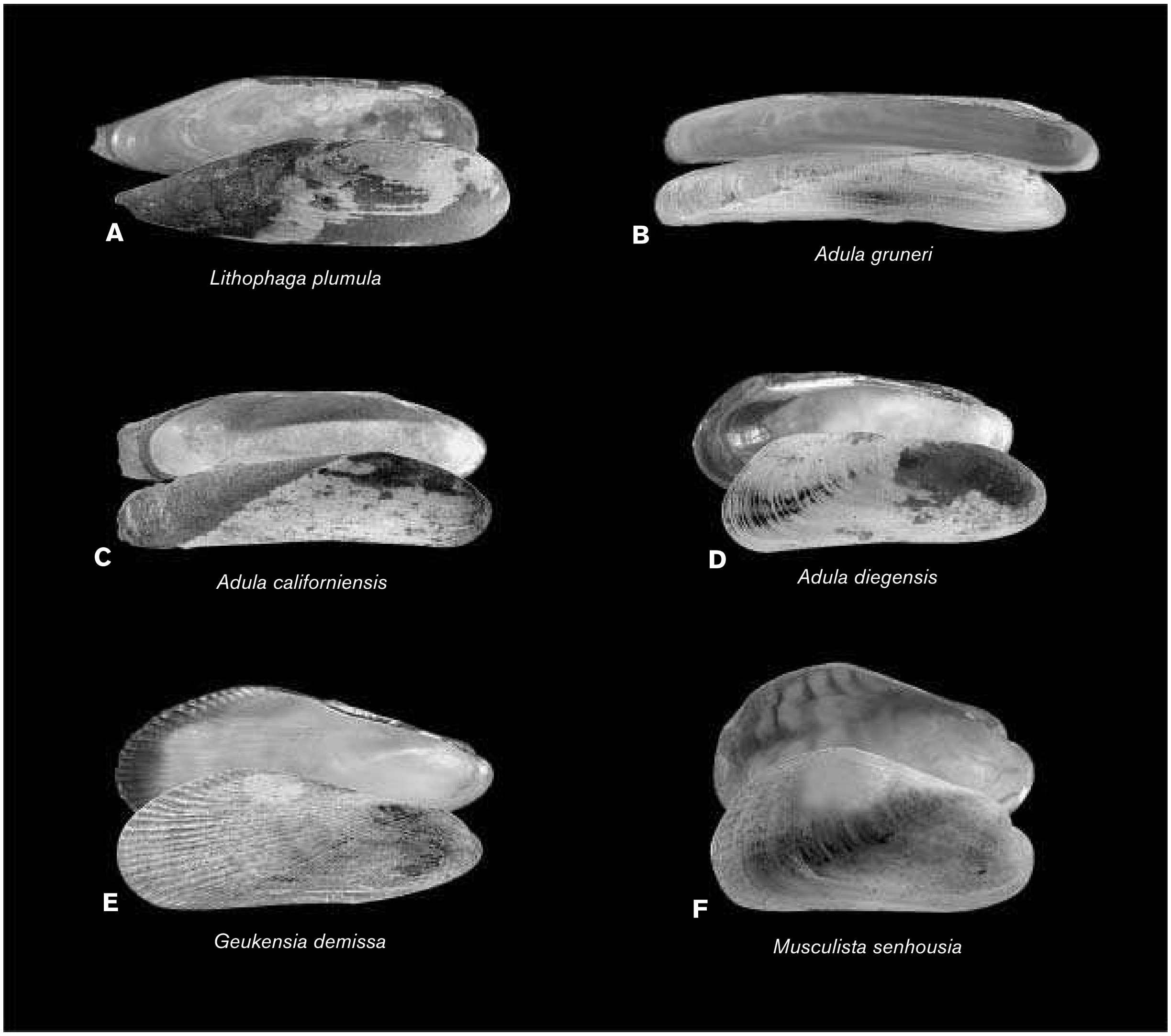

PLATE 403 A, *Lithophaga plumula,* length 51 mm; B, *Adula gruneri,* length 64 mm; C, *Adula californiensis,* length 38 mm; D, *Adula diegensis,* length 24 mm; E, *Geukensia demissa,* length 61 mm; F, *Musculista senhousia,* length 20 mm.

OSTREIDAE

KEY TO OSTREIDAE

(With assistance from Patrick Baker, Andrew Cohen, and James Carlton)

1. Hinge region with chomata in most specimens (plate 402G) 2
— Hinge region without chomata 3
2. Outline of shell usually circular or broadly oval; sculpture of right (upper) valve usually with conspicuous, thin, frilly, concentric lamellae; ventral margin of shell (opposite hinge) may be undulate, but not plicate; maximum shell height 170 mm (plate 406C). . . . . *Ostrea edulis*
— Shell outline variable; sculpture of right valve variable, with obscure concentric lamellae, frequently abraded; ventral margin of shell may be smooth or distinctly plicate (shell edges interlock in wavy pattern); maximum shell height 80 mm (plate 406A) . . . . *Ostrea conchaphila*
3. Maximum shell height 60 mm; left (attached) valve deeply cupped, with three or more distinct radial ridges; right valve relatively smooth; ventral shell margin usually plicate (plate 406E) . . . . *Crassostrea sikamea*
— Maximum shell height exceeding 60 mm; left valve may be deeply cupped when compared to right valve; right (upper) valve often with spine-like features or fluting, well-raised above the shell; ventral shell margin often plicate (plate 406B) . . . . *Crassostrea gigas*
— Maximum shell height exceeding 60 mm; left valve usually not deeply cupped when compared to right valve. . 4
4. Adductor muscle scar usually solid deep violet or dark brown (plate 406F). . . . . *Crassostrea virginica*
— Adductor muscle scar frequently white, or with blotchy dark color, usually not a solid color (plate 406D) . . . . *Crassostrea ariakensis*

LIST OF SPECIES

Yonge 1960, Oysters, London: Collins, 209 pp.; Stenzel 1971, Treatise on Invertebrate Paleontology, N (Mollusca) (6)3: 953–1224. Introduced species do not generally reproduce on the central California coast.

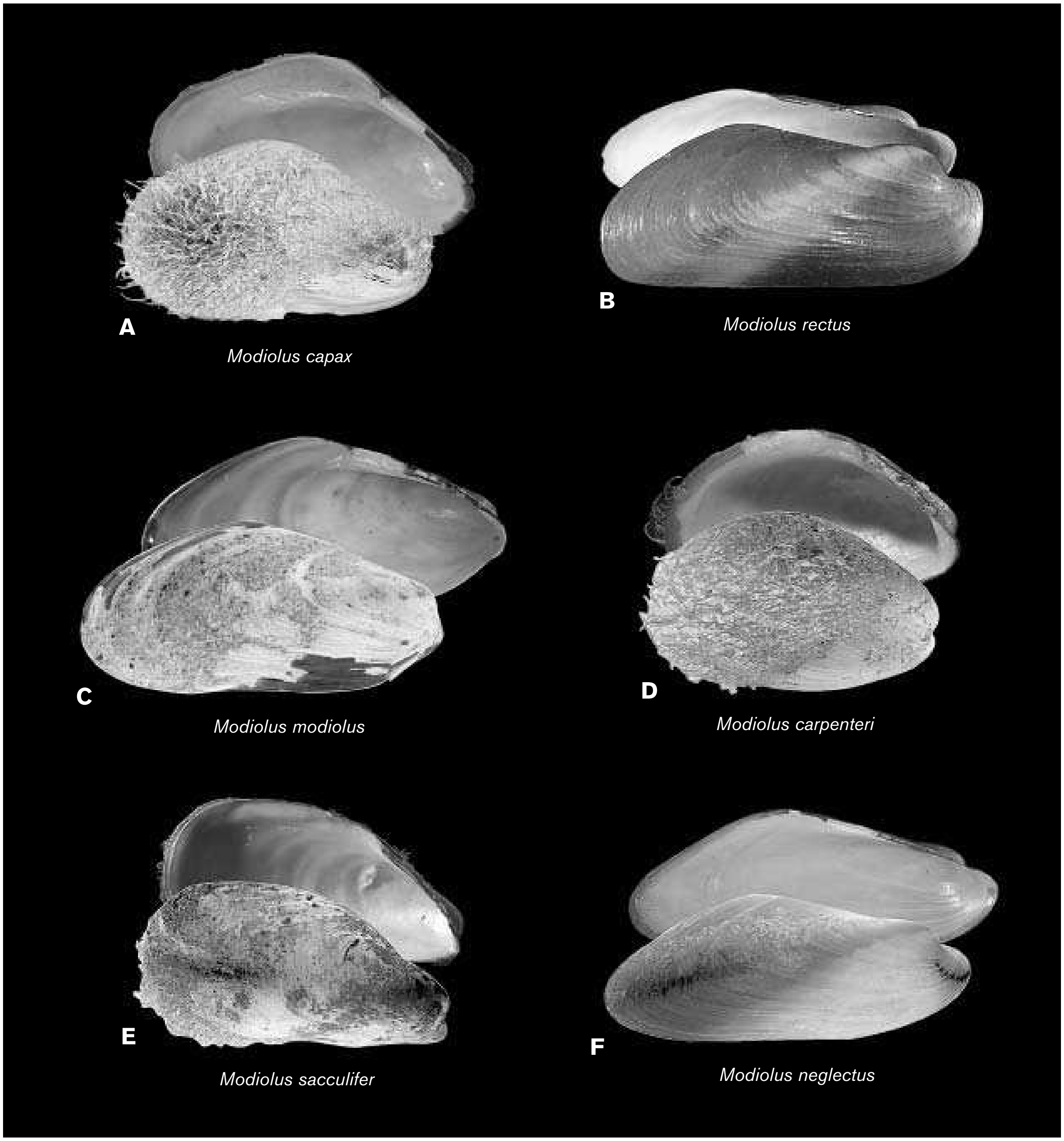

PLATE 404 A, *Modiolus capax,* length 65 mm; B, *Modiolus rectus,* length 67 mm; C, *Modiolus modiolus,* length 66 mm; D, *Modiolus carpenteri,* length 18 mm; E, *Modiolus sacculifer,* length 74 mm; F, *Modiolus neglectus,* length 55 mm.

Ostrea conchaphila Carpenter, 1857 (=*Ostrea lurida* Carpenter, 1864; in the subgenus *Ostreola*, treated by some as a genus). Olympia or native oyster; common in mud, on rocks, pilings, in bays, often in clumps. Locally abundant in Humboldt Bay and Tomales Bay; still common in parts of San Francisco Bay but rare on open coastline. Adults normally 2 cm–6 cm in shell height. Coan et al. 2000: 214–215; Hopkins 1936, Ecology 17: 551–566; 1937, Bull. Bur. Fish. 48: 439–503 (reproduction, larval development); Barrett, below; Baker 1996, J. Shellfish Res. 14: 501–518 (ecology, fishery); Couch and Hassler 1989, U.S. Fish Wildl. Serv. Biol. Rep. 82 (11.124, 8 pp., review of biology).

Ostrea edulis Linnaeus, 1758. European flat oyster, native to western Europe; plantings have been made in Tomales Bay and Drake's Estero. Adults 6 cm–10 cm in shell height, rarely to 17 cm. Seldom reproduces or occurs in the wild in this range. Coan et al. 2000: 215–216; Leonard 1969, Veliger 11: 382–390.

Crassostrea ariakensis (Fujita, 1913). Suminoe oyster; native to eastern Asia and occasionally cultured in bays and estuaries north of San Francisco Bay. Adults 10 cm–15 cm in shell height, rarely to 20 cm. Reproductive status in this range unknown. Also mistakenly known as *C. rivularis*. Langdon and Robinson 1996, Aquaculture 144: 321–338; Torigoe 1981, J.

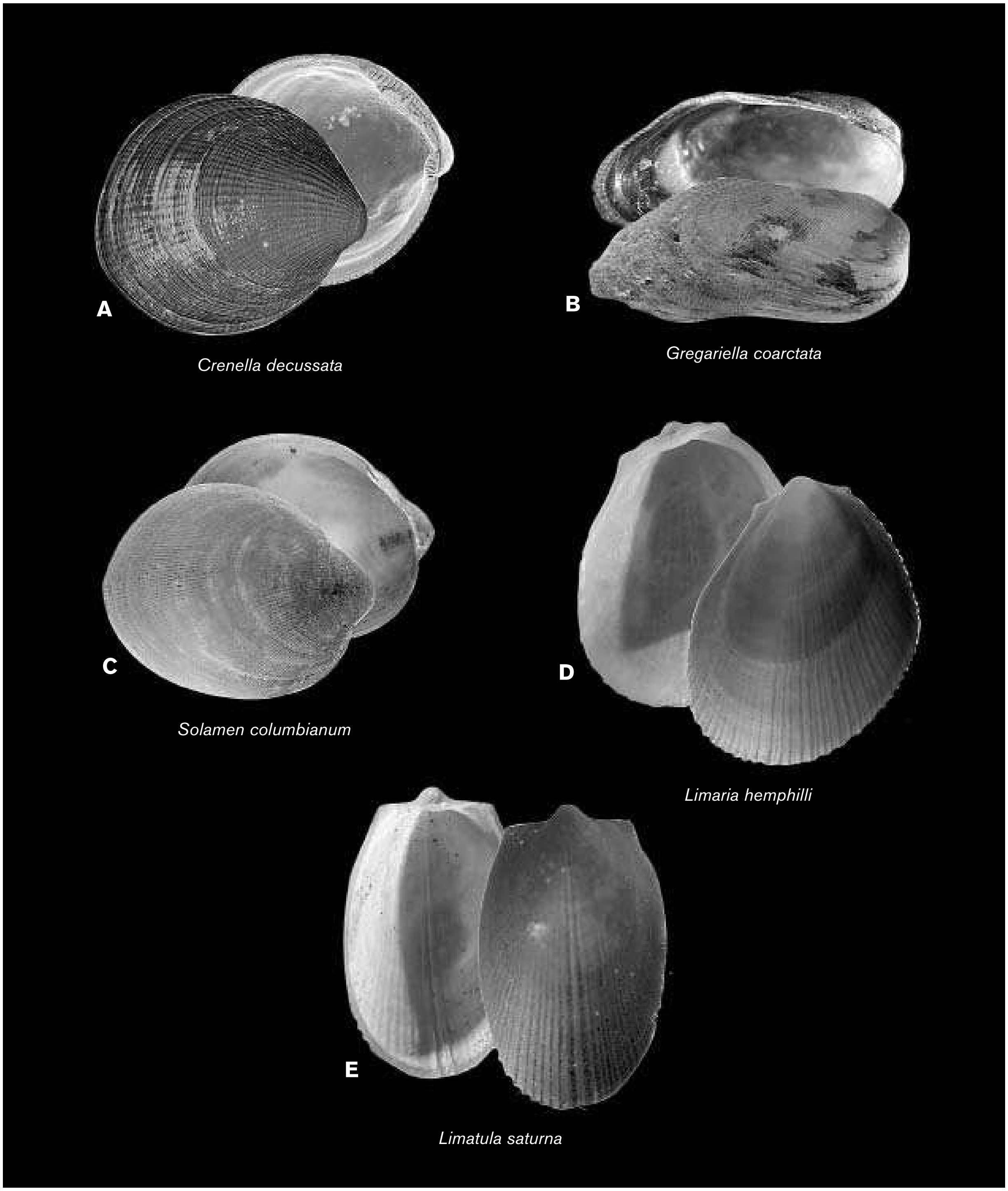

PLATE 405 A, *Crenella decussata,* length 3.8 mm; B, *Gregariella coarctata,* length 12 mm; C, *Solamen columbianum,* holotype, length 12 mm; D, *Limaria hemphilli,* height 28 mm; E, *Limatula saturna,* height 8 mm.

Sci. Hiroshima Univ. Ser. B, Div. 1, 29: 291–419; Zhou and Allen 2003, J. Shellfish Res. 22: 1–20 (literature review).

Crassostrea gigas (Thunberg, 1795). Japanese or Pacific oyster, native to Asia; introduced; large oyster farms in Drake's Estero and Tomales Bay in central California; shells are common. Adults 8 cm–20 cm in shell height, rarely to 40 cm. Frequently reproduces; scattered individuals common in estuaries with oyster culture, and rare on open coastline. Coan et al. 2000: 215, 217–218; Barrett 1963, Calif. Fish Game Fish Bull. 123: 103 pp.; Quayle 1988, Pacific oyster culture in British Columbia. Can. Bull. Fish. Aquatic Sci. 218, 241 pp.; Berg 1969, Veliger 12: 27–36; 1971, Calif. Fish Game 57: 69–75 (causes of mortality); see also Torigoe, above.

Crassostrea sikamea (Amemiya, 1928). Kumamoto oyster; native to Japan. Cultured in bays and estuaries north of San Francisco Bay. Adults 4 cm–8 cm in shell height. Reproduction in California unknown. Morphology frequently overlaps strongly with small *C. gigas,* of which it was formerly considered a subspecies

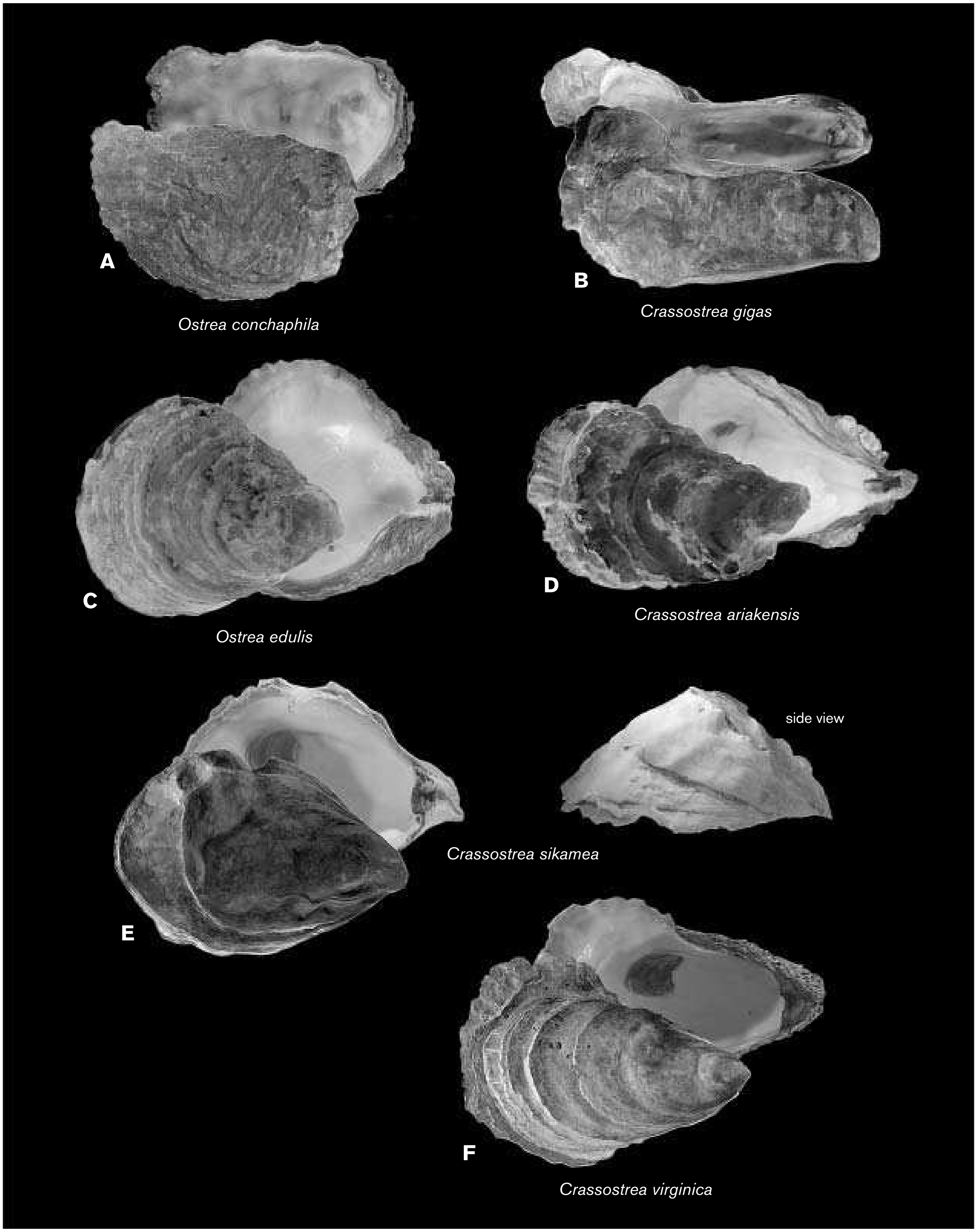

PLATE 406 A, *Ostrea conchaphila,* height 50 mm; B, *Crassostrea gigas,* height 105 mm; C, *Ostrea edulis,* height 67 mm; D, *Crassostrea ariakensis,* height 170 mm; E, *Crassostrea sikamea,* height 58 mm, width of sideview 39 mm; F, *Crassostrea virginica,* height 96 mm.

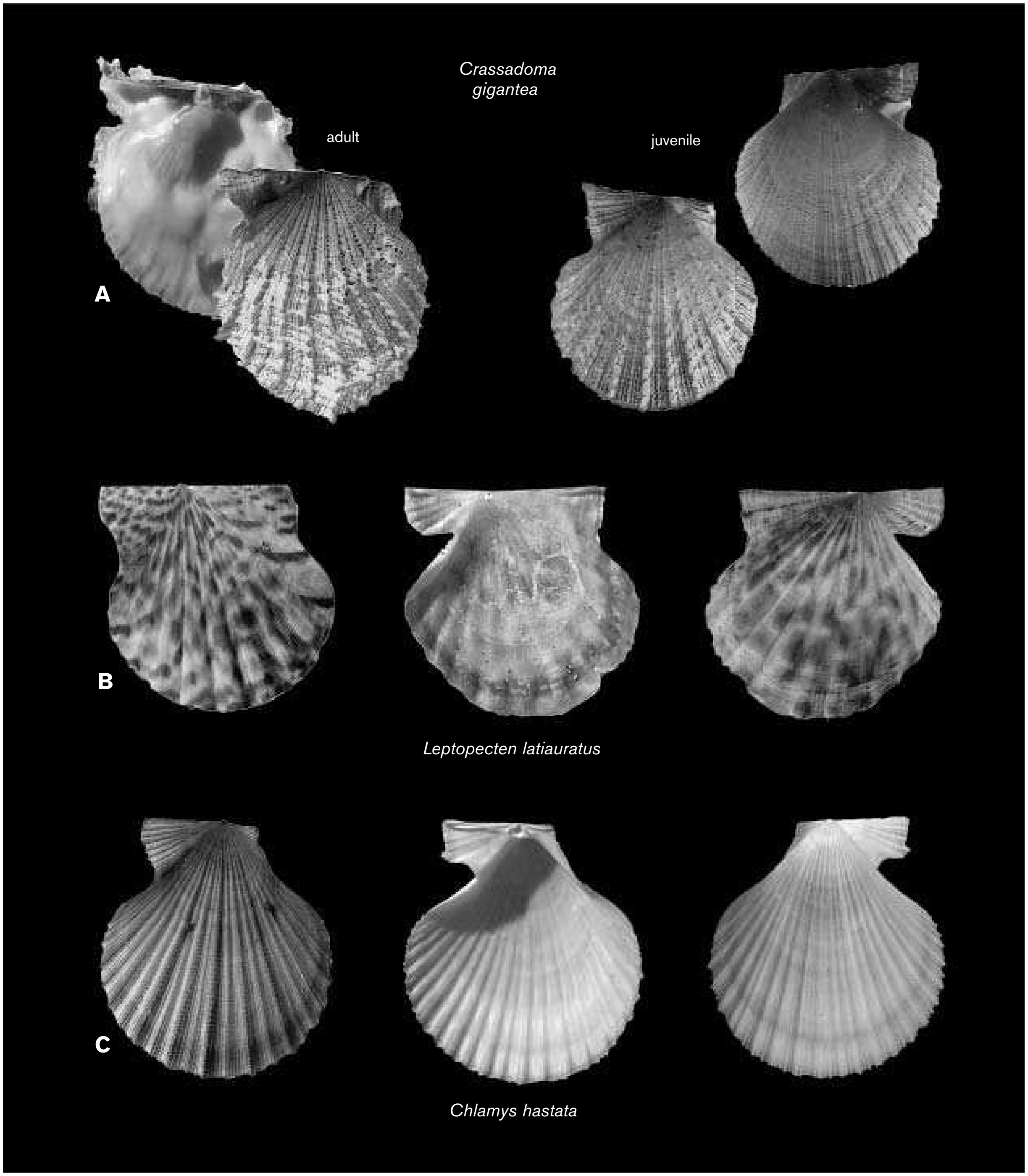

PLATE 407 A, *Crassadoma gigantea,* height (adult) 53 mm, height (juvenile) 35 mm; B, *Leptopecten latiauratus,* height 17 mm; C, *Chlamys hastata,* height 56 mm.

or variety. Coan et al. 2000: 218–219; Banks et al. 1994, Mar. Biol. 121: 127–135; Hedgecock et al. 1993, J. Shellfish Res. 12: 215–221.

Crassostrea virginica (Gmelin, 1791). The eastern oyster, native to Atlantic and Gulf of Mexico coasts, occasionally cultured in bays and estuaries from San Francisco Bay north. Adults 7 cm–15 cm in shell height, rarely to 20 cm. Reproduction in this range rare. A comprehensive treatment with references to hundreds of papers is in Kennedy et al. 1996, The eastern oyster, Crassostrea virginica, College Park, Maryland, Maryland Sea Grant Book, 734 pp.; Coan et al. 2000: 218–219.

PECTINIDAE

KEY TO PECTINIDAE

— Radial ribs imbricated (with shingle-like spines); height greater than length in small specimens; hinge purple; adult attached to rocks or pilings (plate 407A). . . . . . *Crassadoma gigantea*

— Radial ribs not imbricated; length greater than height; hinge not purple; adults free-living (plate 407B). . . . . *Leptopecten latiauratus*

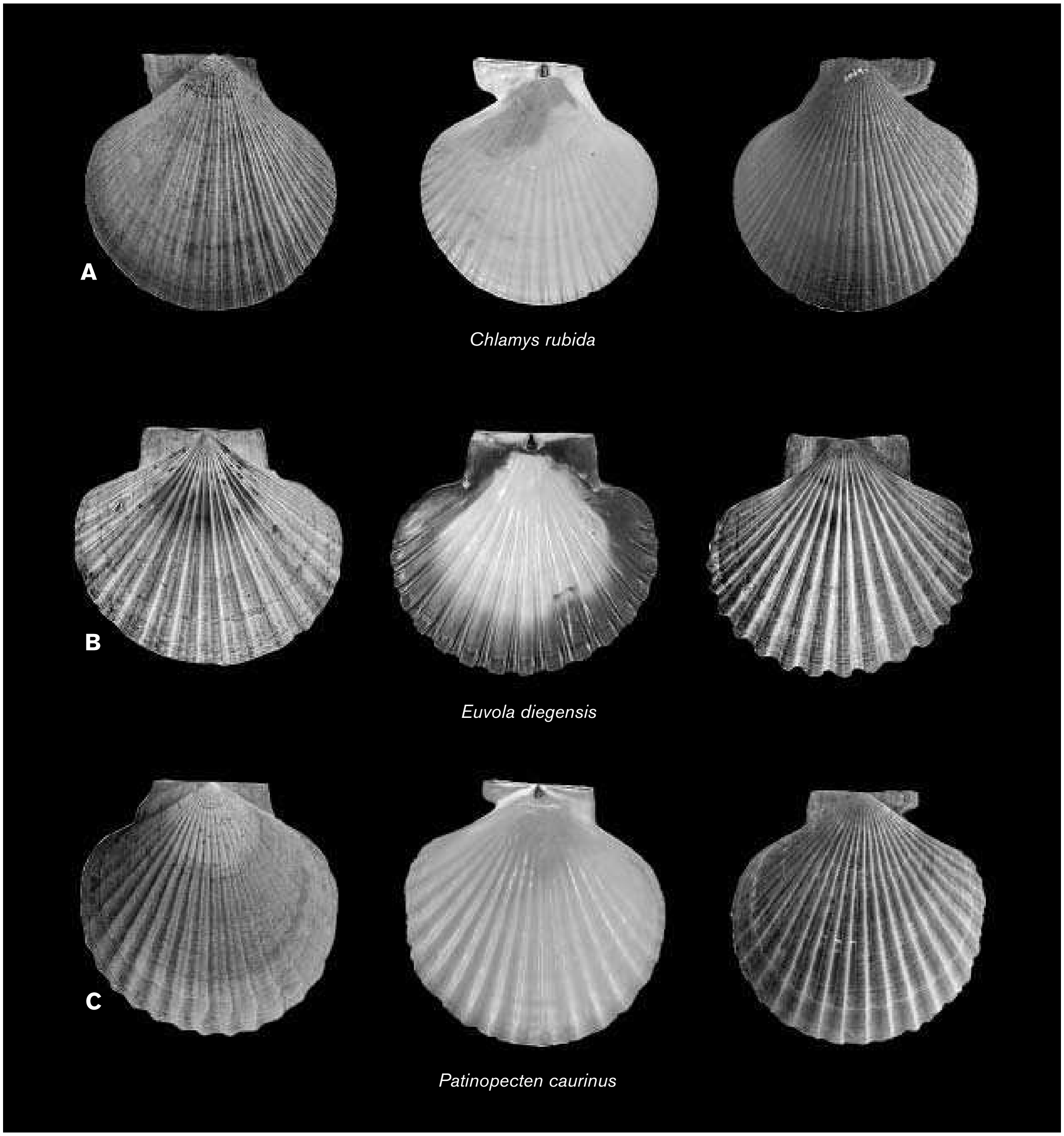

PLATE 408 A, *Chlamys rubida,* height 60 mm; B, *Euvola diegensis,* height 90 mm; C, *Patinopecten caurinus,* height 117 mm.

LIST OF SPECIES

Grau 1959, Pectinidae of the eastern Pacific, Allan Hancock Pacific Expeditions 23, 308 pp.

**Chlamys hastata* (G. B. Sowerby II, 1842) (plate 407C). The spiny scallop is most common offshore pectinid in central California. Coan et al. 2000: 232–234; Grau 1959: 85–91.

**Chlamys rubida* (Hinds, 1845) (plate 408A). Less common, the red scallop is occasionally dredged offshore. Coan et al. 2000: 232, 234; Grau 1959: 76–81.

Crassadoma gigantea (Gray, 1838) (=*Hinnites giganteus*). The giant rock-scallop is free-living when young, attaching as an adult to rocks and pilings, where growth becomes irregular. Coan et al. 2000: 236, 238; Grau 1959: 134–137; Yonge 1951, Univ. Calif. Publ. Zool. 55: 409–420.

**Euvola diegensis* (Dall, 1898) (plate 408B). The San Diego scallop is occasionally found in shallow water as far north as Bodega Bay. Coan et al. 2000: 225–226; Grau 1959: 143–145.

Leptopecten latiauratus (Conrad, 1837). Coan et al. 2000: 236–237; Grau 1959: 107–113; McPeak and Glantz 1982, Festivus 14: 63–69 (ecology); Morton 1994,Veliger 37: 5–22 (functional morphology).

**Patinopecten caurinus* (Gould, 1850) (plate 408C). The weathervane scallop occurs offshore. In Alaska it has supported a modest fishery. Coan et al. 2000: 240–241; Grau 1959: 221–222.

* = Not in key.

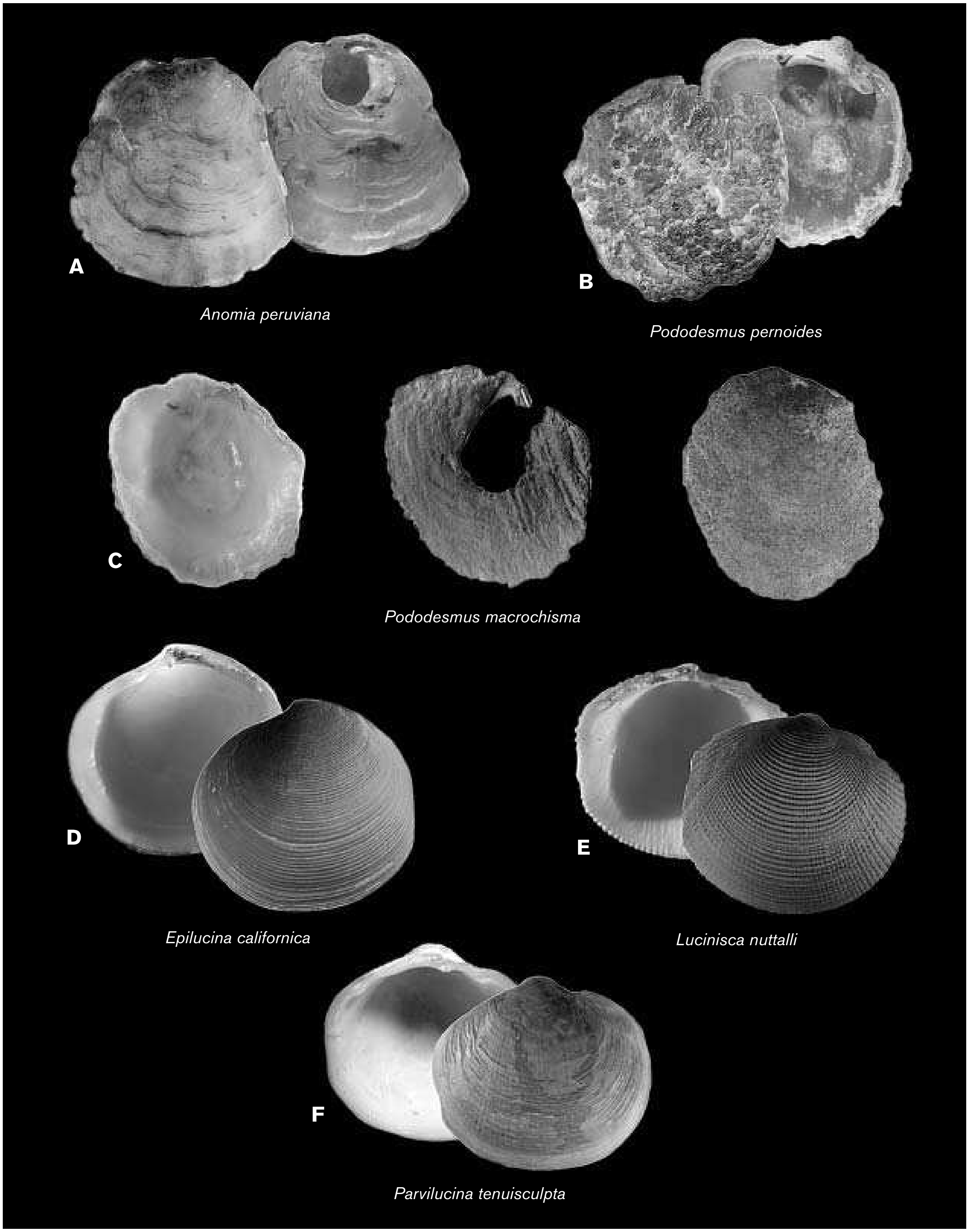

PLATE 409 A, *Anomia peruviana,* height 20 mm; B, *Pododesmus pernoides,* height 36 mm; C, *Pododesmus macrochisma,* height 91 mm; D, *Epilucina californica,* length 35 mm; E, *Lucinisca nuttalli,* length 25 mm; F, *Parvilucina tenuisculpta,* length 9 mm.

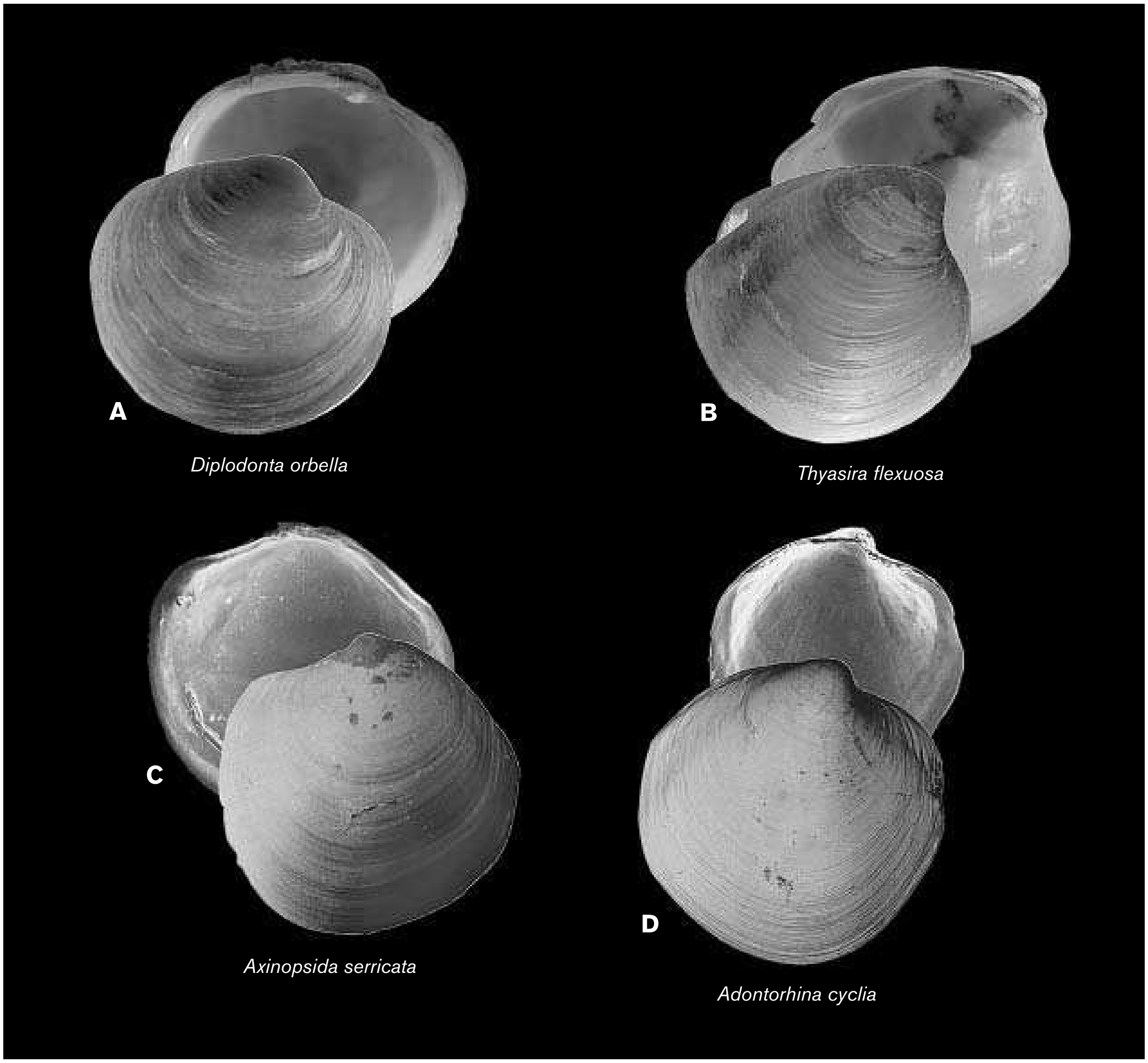

PLATE 410 A, *Diplodonta orbella,* length 27 mm; B, *Thyasira flexuosa,* length 17 mm; C, *Axinopsida serricata,* length 4 mm; D, *Adontorhina cyclia,* length 2 mm.

ANOMIIDAE

KEY TO ANOMIIDAE

1. Two smaller muscle scars inside central area of valves (plate 394G) . . . . *Pododesmus* 2
— Three scars inside central area (plates 402H, 409A). . . . . *Anomia peruviana*
2. Hole in right valve for attachment of calcified byssus medium-size to large; shell greenish (plate 409C). . . . . *Pododesmus macrochisma*
— Hole in right valve small; shell chocolate in color (plate 409B) . . . . *Pododesmus pernoides*

LIST OF SPECIES

Pododesmus macrochisma (Deshayes, 1839) (=*P. cepio* [Gray, 1850]; *P. macroschisma*, invalid emendation). Conclusive proof has yet to be offered that Alaskan material, described as *P. macrochisma,* represents a different species than *P. cepio,* described from California. This species is green because of algae within the shell and is common on rocks, abalone shells, and in dead shells. Coan et al. 2000: 256–257; Yonge 1977, Philos. Trans. Roy. Soc. London (B) 276: 459–476 (functional morphology); Leonard 1969,Veliger 11: 382–390 (reproduction); Anderson 2000, Festivus 32: 139–142 (algae in shell).

Pododesmus pernoides (Gray, 1853). Much less common, it is generally attached to the shells of other mollusks. Coan et al. 2000: 255–257.

Anomia peruviana Orbigny, 1846. Reported as far north as Monterey in association with El Niño years. Coan et al. 2000: 255, 257.

LUCINIDAE

Taylor and Glover 2000, pp. 207–225, in: Harper et al., eds., The evolutionary biology of the Bivalvia. Geol. Soc. London, Spec.

Publ. 177; Taylor and Glover 2006, Zool. J. Linn. Soc. 148: 421–438 (functional anatomy, evolution).

Epilucina californica (Conrad, 1837) (plate 409D). In the intertidal zone nestling in gravel and crevices on rocky coast. Coan et al. 2000: 263–264.

Lucinisca nuttalli (Conrad, 1837) (plate 409E). A southern Californian species recorded as far north as Monterey in El Niño years. Coan et al. 2000: 263–265.

Parvilucina tenuisculpta (Carpenter, 1864) (plate 409F). Very common in soft bottoms immediately offshore. Coan et al. 2000: 264–266; Hickman 1994, Veliger 37: 53–55.

UNGULINIDAE

Represented in local rocky intertidal zone by *Diplodonta orbella* (Gould, 1851) (plate 410A), which lives in holes in rocks and forming a nest of agglutinated detritus and sand under rocks. Coan et al. 2000: 270–271; Haas 1943, Zool. Ser. Field Mus. Natl. Hist. 29: 9–12; Hertz et al. 1982, Festivus 14: 76–87.

THYASIRIDAE

Although not present in the intertidal zone of central California, the following members of this family are relatively common on soft bottoms immediately offshore.

**Thyasira flexuosa* (Montagu, 1803) (plate 410B). There is a considerable literature about the biology of this species, listed in Coan et al. 2000: 275–276.

**Axinopsida serricata* (Carpenter, 1864) (plate 410C). Coan et al. 2000: 278–280.

**Adontorhina cyclia* Berry, 1947 (plate 410D). Coan et al. 2000: 279–280.

CARDITIDAE

KEY TO CARDITIDAE

1. Ventral margin of shell folded inward (in female); radial ribs absent anteroventrally (plate 402I) 2
— Ventral margin evenly arched, not bent inward; strong radial ribs throughout (plate 411C) . . . . *Glans carpenteri*
2. With a strong keel, 10 strong ribs, and a narrow, short lunule (plates 402I, 411A). . . . . *Milneria kelseyi*
— Without a keel, four strong ribs, and a long, broad lunule (plate 411B) . . . . *Milneria minima*

LIST OF SPECIES

Yonge 1969, Proc. Malac. Soc. London 38: 493–527 (functional morphology); Coan 1977, Veliger 19: 375–386 (systematic review).

**Cyclocardia ventricosa* (Gould, 1850) (plate 411D). This is the most common carditid found offshore on soft bottoms. Coan et al. 2000: 302–304.

Glans carpenteri (Lamy, 1922). Attains only about 10 mm in length and attaches by a byssus to the undersurfaces of rocks on open coast; broods young. Coan et al. 2000: 305–306; Yonge 1969: 505–509.

Milneria minima (Dall, 1871). Reaches about 8 mm and also attaches with a byssus to rocks from the low intertidal zone to 50 m. Ventral margin is folded inward in the female to form a brood pouch. Coan 1974, Veliger 17: 183–184; Coan et al. 2000: 306–307.

Milneria kelseyi Dall, 1916. Reaches about 18 mm, this southern species occasionally gets as far north as Monterey Bay. Also with brood pouch in female. Coan 1974: 183–184; Coan et al. 2000: 306–307; Yonge 1969: 517.

CHAMIDAE

KEY TO CHAMIDAE

1. Attached by left valve; growth counter-clockwise, markedly foliose (plate 411E) . . . . *Chama arcana*
— Attached by right valve; growth clockwise, valves scaly, but not markedly foliose (plate 411F). . . . . *Pseudochama exogyra*

LIST OF SPECIES

Yonge 1967, Phil. Trans. Roy. Soc. London (B) 252: 49–105 (functional morphology); Bernard 1976, Contrib. Sci., Los Angeles Co. Mus. 278: 43 pp. (systematic review).

Chama arcana Bernard, 1976. Long misidentified as *C. pellucida* Broderip, 1835, a South American species. Cemented to protected surfaces of mid-intertidal rocks; on pilings. Yonge 1967; Bernard 1976: 14–15; Coan et al. 2000: 309–311; Hamada and Matsukuma 1995, Kyushu Univ., Dept. Earth and Planetary Sci., Sci. Repts. 19: 93–102 (shell structure).

Pseudochama exogyra (Conrad, 1837). Cemented to algae-covered rocks on open coast from mid- to low intertidal zone. Yonge 1967; Bernard 1976: 26–27; Coan et al. 2000: 310–311.

**Pseudochama granti* Strong, 1934 (plate 411G). An offshore species that has been confused with *P. exogyra*. Coan et al. 2000: 301–311.

GALEOMMATOIDEA

KEY TO GALEOMMATOIDEA

1. Hinge without teeth; shell entirely internal (plates 396C, 412A, 413A) . . . . *Chlamydoconcha orcutti*
— Cardinal teeth developed in at least one valve; animal fitting within shell . . . . Lasaeidae 2
2. Beaks near posterior end. 3
— Beaks subcentral 5
3. Left valve without teeth; right valve with a long anterior cardinal tooth and a short posterior cardinal; teeth not serrate (plate 413B) . . . . *Mysella pedroana*
— Left valve without teeth; right valve with subequal cardinal teeth; teeth not serrate . . . . *Rochefortia* 4
— Both valves with a long posterior cardinal and a short, ventrally directed anterior cardinal; teeth serrate (plate 413C) . . . . *Pristes oblongus*
4. Shell thin, subovate (plate 413D). . . . . . . *Rochefortia coani*
— Shell thick, subtrigonal to subquadrate (plate 413E). . . . . *Rochefortia tumida*
5. Hinge with cardinal teeth only; no lateral teeth; shell quadrangular, yellow; on abdomen of *Upogebia* (plate 414A). . . . . *Neaeromya rugifera*
— Hinge with lateral teeth or lamellae. 6

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* = Not in key.

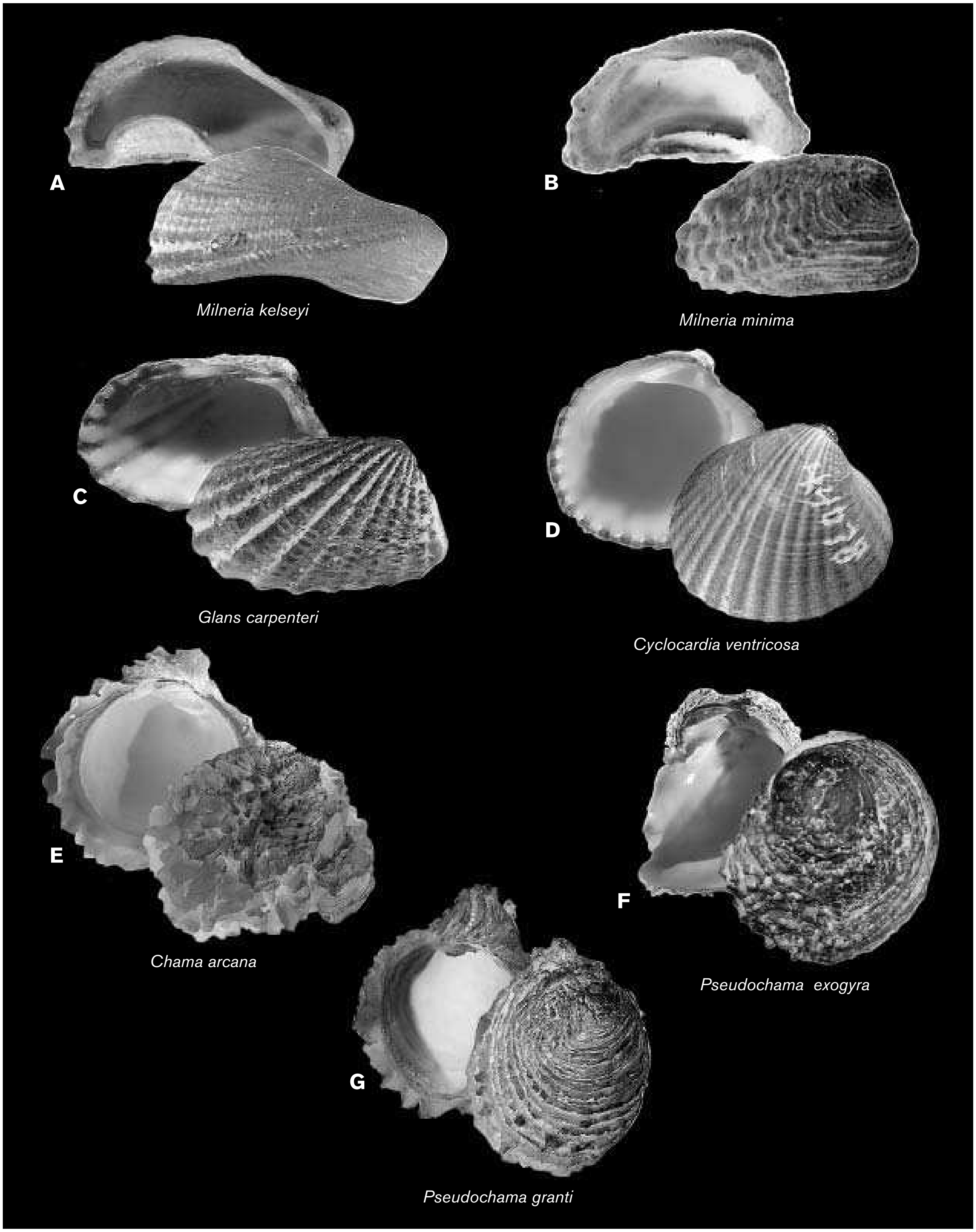

PLATE 411 A, *Milneria kelseyi,* length 5 mm; B, *Milneria minima,* length 4 mm; C, *Glans carpenteri,* length 9 mm; D, *Cyclocardia ventricosa,* length 15 mm; E, *Chama arcana,* height 57 mm; F, *Pseudochama exogyra,* height 56 mm; G, *Pseudochama granti*, height 17 mm.

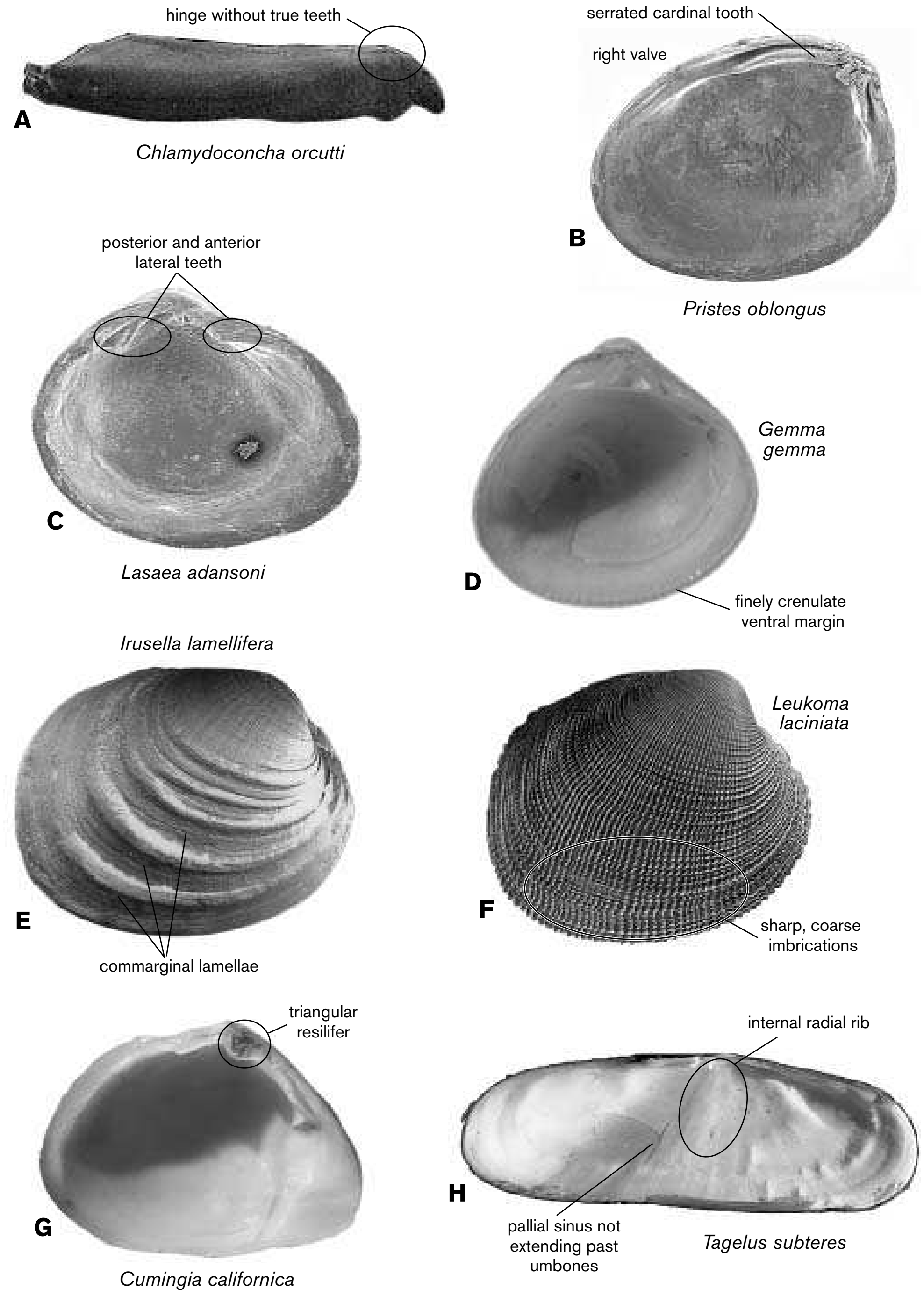

PLATE 412 A, *Chlamydoconcha orcutti,* length 7 mm; B, *Pristes oblongus,* length 4.1 mm; C, *Lasaea adansoni,* length 3.2 mm; D, *Gemma gemma,* length 2.5 mm; E, *Irusella lamellifera,* length 28 mm; F, *Leukoma laciniata,* length 69 mm; G, *Cumingia californica,* length 28 mm; H, *Tagelus subteres,* length 34 mm.

6. Hinge with posterior lateral teeth, no anterior laterals; shell nearly round to elliptical; with fine, commarginal, growth lines and thin, smooth, yellowish periostracum; length to 25 mm (plate 414C) . . . . *Kellia suborbicularis*
— Hinge with posterior and anterior lateral teeth; shell reddish; periostracum wavy, wrinkled; length to 3 mm (plates 412C, 414D) . . . . *Lasaea adansoni*
— Hinge with only thin lateral lamellae on each side of beaks (plate 414E) . . . . *Rhamphidonta retifera*

LIST OF SPECIES

Popham 1940, J. Mar. Biol. Assoc. U.K. 24: 549–587 (functional morphology of British species).

GALEOMMATIDAE

Chlamydoconcha orcutti Dall, 1884. Appearing more like a nudibranch than a clam, this species is rarely observed. Rocky

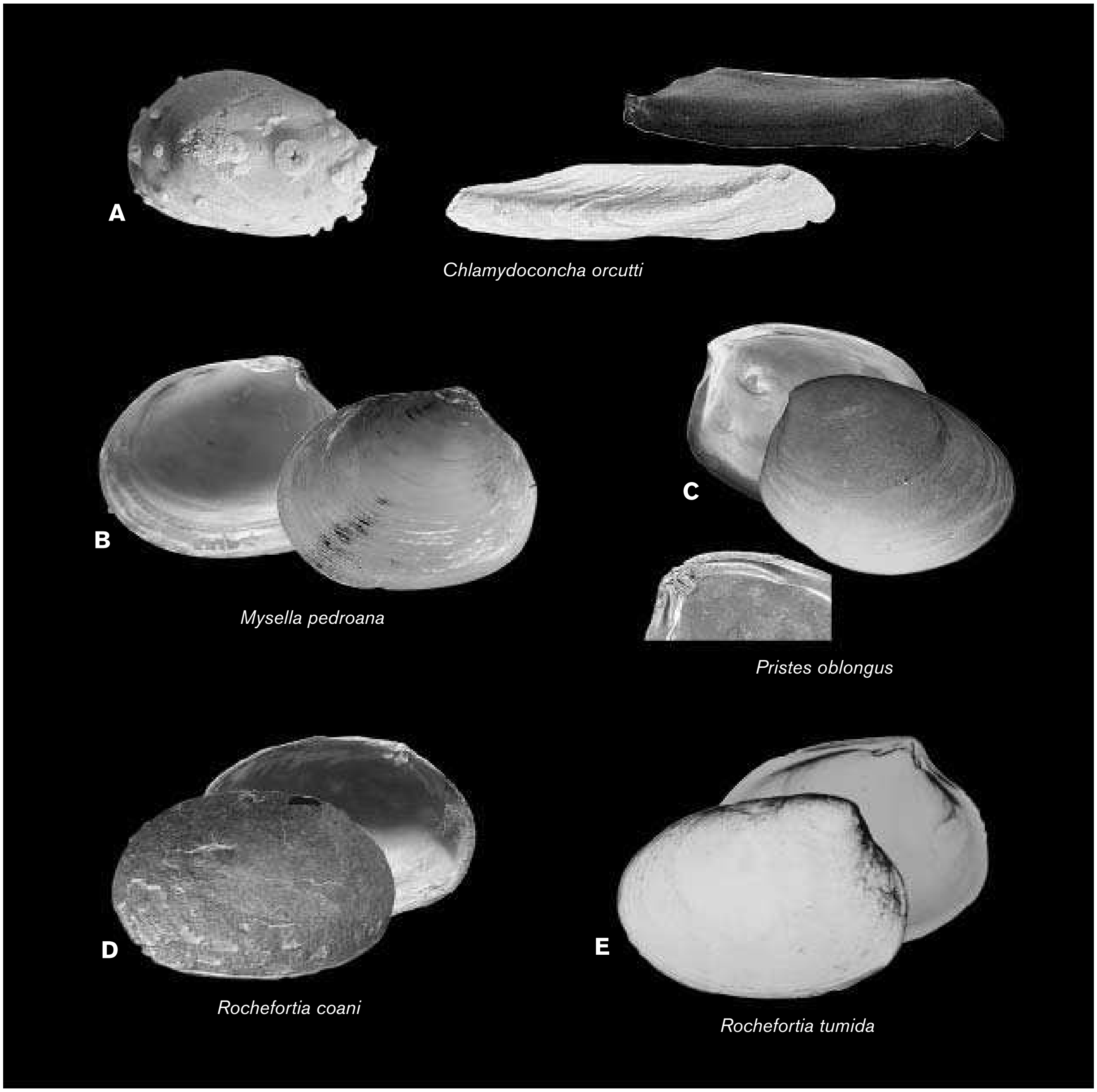

PLATE 413 A, *Chlamydoconcha orcutti,* (left) mantle completely covering shells, length 8 mm, (right) internal shells, length 7 mm; B, *Mysella pedroana,* length 6 mm; C, *Pristes oblongus,* length 4.1 mm; D, *Rochefortia coani,* holotype, length 5.1 mm; E, *Rochefortia tumida,* length 2.8 mm.

low intertidal and subtidal. Coan et al. 2000: 313, 315; Carlton 1979, Veliger 21: 375–378.

LASAEIDAE

Lasaea adansoni (Gmelin, 1791) (=*L. rubra* [Montagu, 1803], *L. cistula* Keen, 1938). In algal holdfasts and among byssal threads of mussels, abundant, on open and semiprotected rocky coast. These strange little bivalves are now known to represent hermaphroditic, polyploid clones ranging from 3°N to 6°N, which brood their young. Coan et al. 2000: 317, 320–321, with additional references to the now substantial literature; Ballentine and Morton 1956, J. Mar. Biol. Assoc. U.K. 35: 241–274 (filtering, feeding, digestion); Ó Foighil and Smith 1996, Evolution 49: 140–150 (genetics).

Kellia suborbicularis (Montagu, 1803) (=*K. laperousii* [Deshayes, 1839]). There is evidence that Pacific material may represent a separate species. Often abundant, nestling on pilings and rocks and in mussel beds, empty barnacles, bottles, and pholad holes; a common fouler in seawater systems of marine laboratories. This species broods its young in the suprabranchial chamber, with dwarf males occurring in the infrabranchial chamber. Coan et al. 2000: 321, 323; Yonge 1952, Univ. Calif. Publ. in Zool. 55: 451–454 (functional morphology); Howard 1953, Wasmann J. Biol. 11: 233–240 (larvae); Kamenev 2004, Malacologia 46: 57–71 (taxonomy); Oldfield 1961, Proc. Malac. Soc. London 34: 255–295 (functional morphology); Oldfield 1964, Proc. Malac. Soc. London 36: 79–120 (reproduction, development).

Mysella pedroana Dall, 1899. In the gill chambers or externally attached to the sand crab *Blepharipoda occidentalis*. Coan

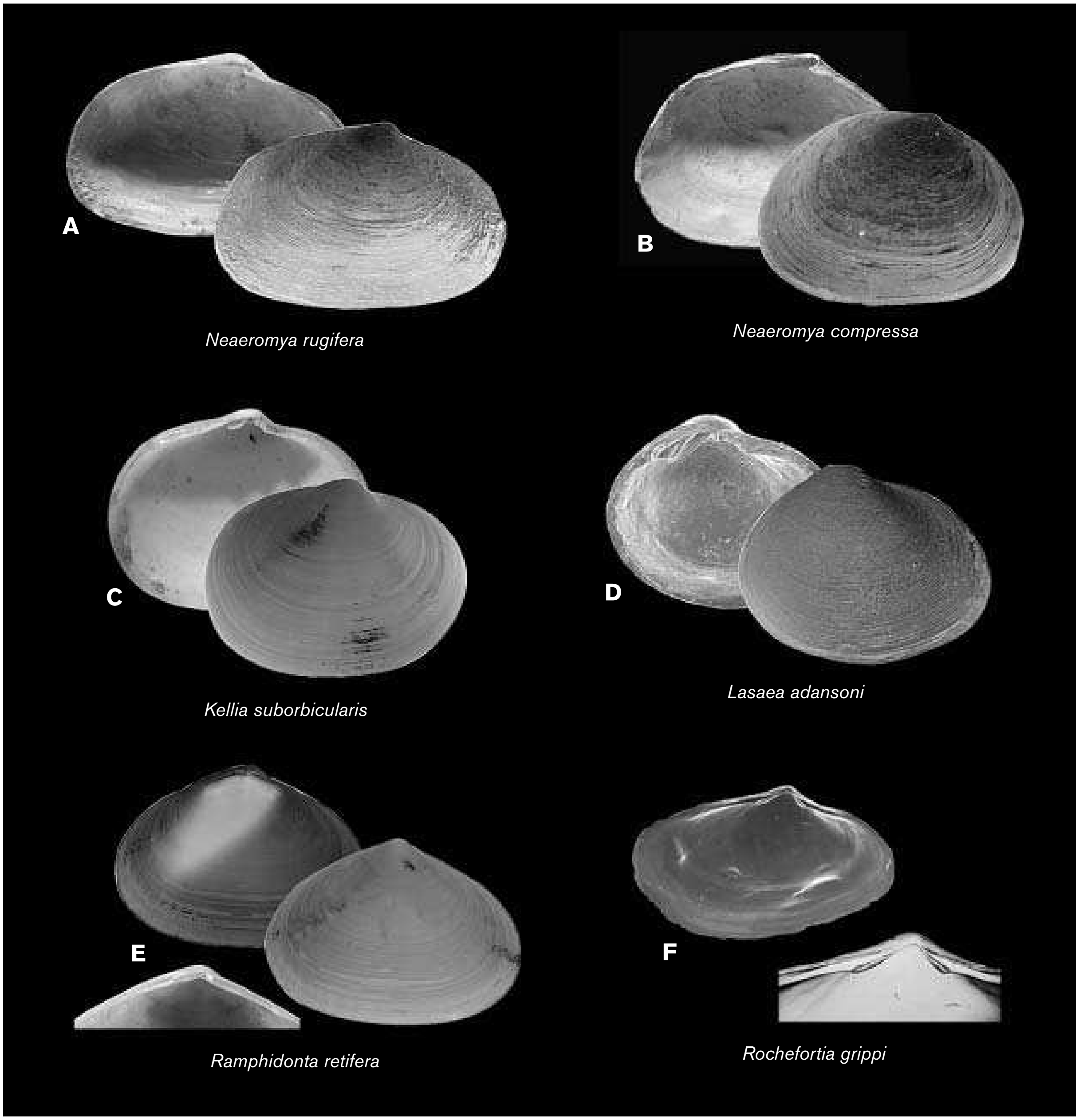

PLATE 414 A, *Neaeromya rugifera,* length 9.5 mm; B, *Neaeromya compressa,* length 13 mm; C, *Kellia suborbicularis,* length 26 mm; D, *Lasaea adansoni,* length 3.2 mm; E, *Ramphidonta retifera,* length 10 mm, detail of hinge (holotype); F, *Rochefortia grippi,* length 3.8 mm, detail of hinge.

et al. 2000: 321, 323–324; Boyko and Mikkelsen 2002, Zoologischer Anzeiger 241: 149–160 (anatomy, biology, commensal relationship with crab).

**Neaeromya compressa* (Dall, 1899) (plate 414B). An offshore species, possibly commensal with the sea urchin *Brisaster latifrons*. Coan et al. 2000: 324, 326.

Neaeromya rugifera (Carpenter, 1864) (=*Pseudopythina rugifera*). Intertidal, attached by byssus to abdomen of *Upogebia* and in the setae of the polychaete *Aphrodita*. Coan et al. 2000: 325–326; Narchi 1969, Veliger 12: 43–52 (morphology); Ó Foighil 1985, Veliger 27: 245–252 (reproduction).

Pristes oblongus Carpenter, 1864. Commensal with chiton *Stenoplax heathiana*, Monterey south. Coan et al. 2000: 326–327.

Rhamphidonta retifera (Dall, 1899). Possibly associated with enteropneusts. Coan et al. 2000: 326–327; Bernard 1975, J. Conchyl. 112: 105–115 (morphology).

Rochefortia coani Valentich-Scott 1998. Uncommon, mostly offshore. Coan et al. 2000: 328–329.

**Rochefortia grippi* Dall, 1912 (plate 414F). Just offshore. Coan et al. 2000: 328–329.

Rochefortia tumida (Carpenter, 1864). In bays and offshore. Coan et al. 2000: 329–330; Maurer 1967, Veliger 9: 305–309, 10: 72–76; 1969, Veliger 11: 243–249 (filtering, feeding, ecology); Ó Foighil 1985, Biol. Bull. 169: 602–614 (reproduction); Ó Foighil 1985, Zoomorph. 105: 125–135 (reproduction).

* = Not in key.

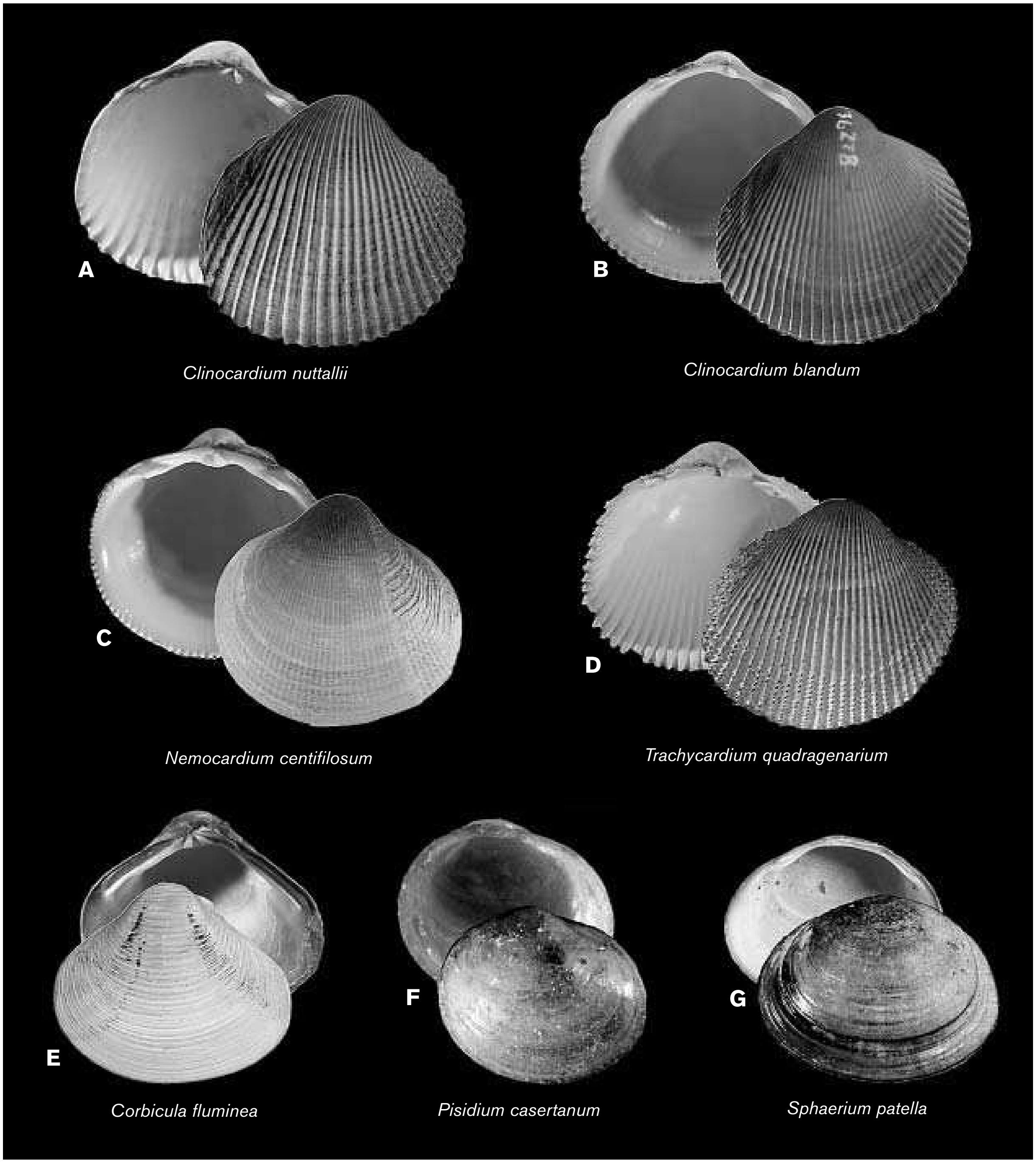

PLATE 415 A, *Clinocardium nuttallii,* length 56 mm; B, *Clinocardium blandum,* length 24 mm; C, *Nemocardium centifilosum,* length 13 mm; D, *Trachycardium quadragenarium,* length 72 mm; E, *Corbicula fluminea,* length 37 mm; F, *Pisidium casertanum,* length 4.5 mm; G, *Sphaerium patella,* length 7 mm.

CARDIIDAE

Schneider 1995, Zool. Scripta 24: 321–346 (evolution).

Clinocardium nuttallii (Conrad, 1837) (plate 415A). Midintertidal to offshore in sandy areas of bays. Coan et al. 2000: 351–354; Cooke 1975, Phycologia 14: 35–39 (endozoic green algae); Evans 1972, Science 176: 416–417 (growth); Fraser 1931, Trans. Roy. Soc. Can. Sec. 5, 25: 59–72 (ecology); Gallucci and Gallucci 1982, Mar. Ecol. Prog. Ser. 7: 138–145 (reproduction, ecology); Kafanov 1998, Bull. Mizunami Fossil Mus. 25: 30–35 (taxonomy, distribution); Schneider 1994, Veliger 37: 36–42 (anatomy); Weymouth and Thompson 1931, Bull. Bur. Fish. 46: 633–641 (age, growth).

**Clinocardium blandum* (Gould, 1850) (plate 415B). A more northerly species that is found just offshore as far south as Sonoma County. Coan et al. 2000: 353–354.

**Nemocardium centifilosum* (Carpenter, 1864) (plate 415C). Offshore in fairly shallow water. Coan et al. 2000: 358, 361.

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* = Not in key.

**Trachycardium quadragenarium* (Conrad, 1837) (plate 415D). More characteristic of southern California, but has been recorded at Monterey in association with El Niño years. Coan et al. 2000: 358, 362.

PISIDIIDAE

The small, freshwater fingernail clams are occasionally encountered in deltas or at river mouths. *Pisidium casertanum* (Poli, 1791) (plate 415F), with an exhalant siphon and anterior end much longer than posterior, is common in springs, ponds, and slow creeks, whereas *Sphaerium patella* (Gould, 1850) (plate 415G), with the posterior end longer than the anterior and with exhalant and inhalant siphons, is common in such streams as Salmon Creek (Sonoma County). Herrington 1962, Univ. Mich. Mus. Zool. Misc. Pub. 118 (systematic review). Burch 1972, U.S. Environmental Protection Agency, Biota of Freshwater Ecosystems, Identification Manual 3, 33 pp.

CORBICULIDAE

The introduced Asian *Corbicula fluminea* (Müller, 1774) (plates 398B, 415E) has a thick, trigonal shell with low commarginal ridges covered by a heavy black-brown periostracum. Sometimes encountered on bay and ocean beaches as discarded fish bait, it is abundant in freshwater canals and irrigation channels, and large aggregations have locally clogged canal systems and water pipes. Coan et al. 2000: 349; Britton 1986, Proceedings of the Second International *Corbicula* Symposium, American Malacological Bulletin, Special Ed. 2: 239 pp.; Britton and Morton 1982, A dissection guide, field and laboratory manual for the introduced bivalve *Corbicula fluminea*, Malacological Review, Suppl. 3: 82 pp.

NEOLEPTONIDAE

KEY TO NEOLEPTONIDAE

1. Shell with strong commarginal ribs (plate 416A) . . . . *Bernardina bakeri*
— Shell with commarginal striae only 2
2. With an anterior lateral tooth in the left valve (plate 416B) . . . . *Neolepton salmoneum*
— Without such a tooth (plate 416C) . . . . *Neolepton subtrigoneum*

LIST OF SPECIES

Coan 1984, Veliger 27: 227–237 (systematic account). Formerly known on this coast as the Bernardinidae, this family may represent neotenous derivatives of the Veneridae. All species are very small-size nestlers in rubble from the intertidal zone to just offshore.

Bernardina bakeri Dall, 1910. Coan et al. 2000: 326–327; Coan 1984: 345–346.

Neolepton salmoneum (Carpenter, 1864). Coan et al. 2000: 346–347; Coan 1984: 231–233.

Neolepton subtrigonum (Carpenter, 1857). Coan et al. 2000: 346–347; Coan 1984: 231.

VENERIDAE

KEY TO VENERIDAE

1. Adult shell small, <10 mm in length. 2
— Adult shell >10 mm in length 4
2. Shell no longer than high, triangular; inner ventral margin finely crenulate; pallial sinus directed sharply upward; maximum length 5 mm (plates 412D, 416D) . . . . *Gemma gemma*
— Shell elongate to oval; inner ventral margin with obscure, oblique striae only; pallial sinus directed anteriorly . . . . *Nutricola* 3
3. Shell uniform white to cream; siphons fused nearly to tips; anterior lateral tooth relatively weak (plate 416E). . . . . *Nutricola tantilla*
— Shell light to deep purple; siphons with prominent cleft; anterior lateral tooth strong (plate 416F) . . . . . . *Nutricola confusa*
4. Shell smooth, with a shiny, adherent periostracum; large, trigonal (plate 417A) . . . . *Tivela stultorum*
— Shell sculptured; without a shiny periostracum 5
5. Sculpture commarginal, some with very fine radial striae 6
— Sculpture radial and commarginal, the commarginal sculpture not predominating and occasionally obsolete 10
6. Shell short; pronounced, widely spaced, commarginal lamellae (see note in species list); nestling among rocks or in borer holes (plates 412E, 417B). . . . . *Irusella lamellifera*
— Shell elongate or ovate, without prominent commarginal lamellae 7
7. Hinge without anterior lateral teeth; valves not gaping. 8
— Hinge with short anterior lateral tooth, close to cardinals; valves with narrow gape posteriorly. 9
8. Shell trigonal; valves convex, somewhat inflated; commarginal sculpture fine; beaks prominent; lunule deep (plate 417C) . . . . *Mercenaria mercenaria*
— Shell elongate-ovate; valves flattened; sculpture of thin, sharp, widely spaced commarginal ribs and very fine radial striae; beaks not prominent; lunule shallow (plate 417D) . . . . *Callithaca tenerrima*
9. Commarginal ribs heavy, conspicuous, well spaced, frequently stronger posteriorly; shell elongate, thinner than *S. gigantea*; lunule absent, escutcheon narrow (plate 417E) . . . . *Saxidomus nuttalli*
— Commarginal ribs thin, low, and closely spaced, giving shell a relatively smooth appearance; shell ovate, more rounded than *S. nuttalli*; lunule and escutcheon absent (plate 417F) . . . . *Saxidomus giganteus*
10. Inner ventral margin smooth; ligament prominent, elevated above dorsal margin; siphons separate at tips (plate 418A) . . . . *Venerupis philippinarum*
— Inner ventral margin crenulate; ligament sunken, not markedly elevated above dorsal margin; siphons fused for entire length 11
11. Radiating ribs numerous, fine; commarginal ridges faint to lacking in some specimens (see note in species list) (plate 418B). . . . . *Leukoma staminea*
— Radiating ribs and commarginal ribs both predominant, forming a sharp, coarse imbrications (plate 418C) . . . . *Leukoma laciniata*

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* = Not in key.

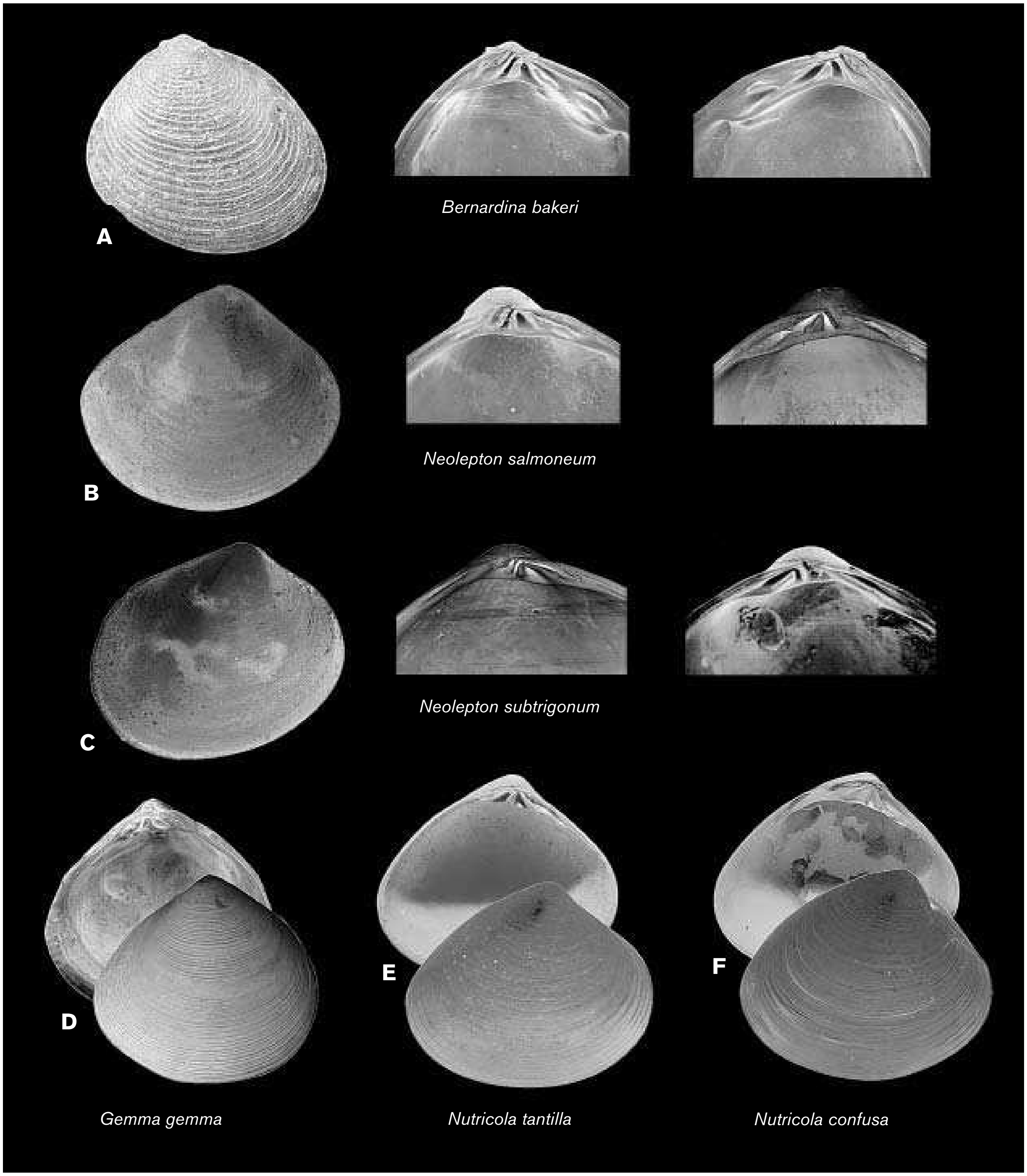

PLATE 416 A, *Bernardina bakeri,* length 2 mm; B, *Neolepton salmoneum,* length 2.5 mm; C, *Neolepton subtrigonum,* length 3 mm; D, *Gemma gemma,* length 2.5 mm; E, *Nutricola tantilla,* length 6 mm; F, *Nutricola confusa,* length 7 mm.

LIST OF SPECIES

Callithaca tenerrima (Carpenter, 1857) (=*Protothaca tenerrima*). Uncommon, in semiprotected areas of bays and offshore in sandy mud. Coan et al. 2000: 375–377.

**Compsomyax subdiaphana* (Carpenter, 1864) (plate 418D). Shell with weak commarginal striae; on soft offshore substrata. Coan et al. 2000: 375, 377.

Gemma gemma (Totten, 1834). Gem clam; introduced from Atlantic; common to abundant in mud of bays. Coan et al. 2000: 378, 380, with references to many additional biological papers; Sellmer 1967, Malacologia 5: 137–223 (functional morphology, ecology, life history); Narchi 1972, Bull. Mar. Sci. 21: 866–885 (anatomy).

**Globivenus fordii* (Yates, 1890) (plate 418E). A southern species occasionally found just offshore in rubble areas, particularly in warm-water years. Coan et al. 2000: 370–371.

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* = Not in key.

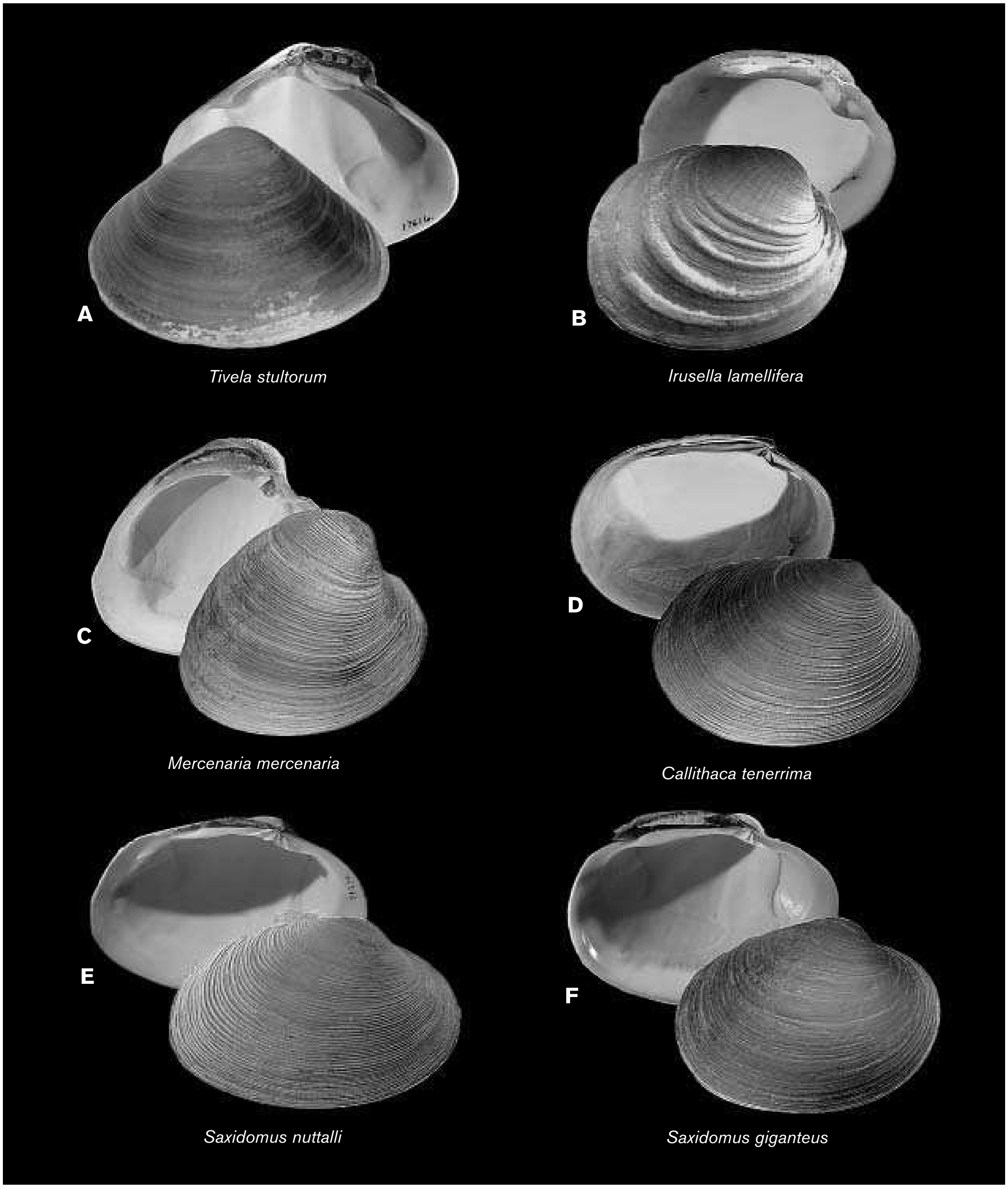

PLATE 417 A, *Tivela stultorum*, length 93 mm; B, *Irusella lamellifera,* length 28 mm; C, *Mercenaria mercenaria,* length 115 mm; D, *Callithaca tenerrima,* length 90 mm; E, *Saxidomus nuttalli,* length 113 mm; F, *Saxidomus giganteus,* length 76 mm.

**Humilaria kennerleyi* (Reeve, 1863) (plate 418F). A northern species found offshore on soft bottoms. Coan et al. 2000: 370–372.

Irusella lamellifera (Conrad, 1837) (=*Irus lamellifer*). Nestling among rocks and in pholad burrows along outer coast; on pilings, in fouling. In bays. See note under *Leukoma staminea*. Coan et al. 2000: 370, 372.

Leukoma laciniata (Carpenter, 1864) (=*Protothaca laciniata*). Less common than *L. staminea*, in sandy mud of bays. Coan et al. 2000: 374–375.

†*Leukoma staminea* (Conrad, 1837) (= *Protothaca staminea;* = *Protothaca restorationensis* [Frizzell, 1930], once thought to be a hybrid). The Pacific littleneck is common both in sand of bays and nestling among rocks (often in empty pholad holes) on outer coast. Coan et al. 2000: 374–376, with references to many

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* = Not in key.

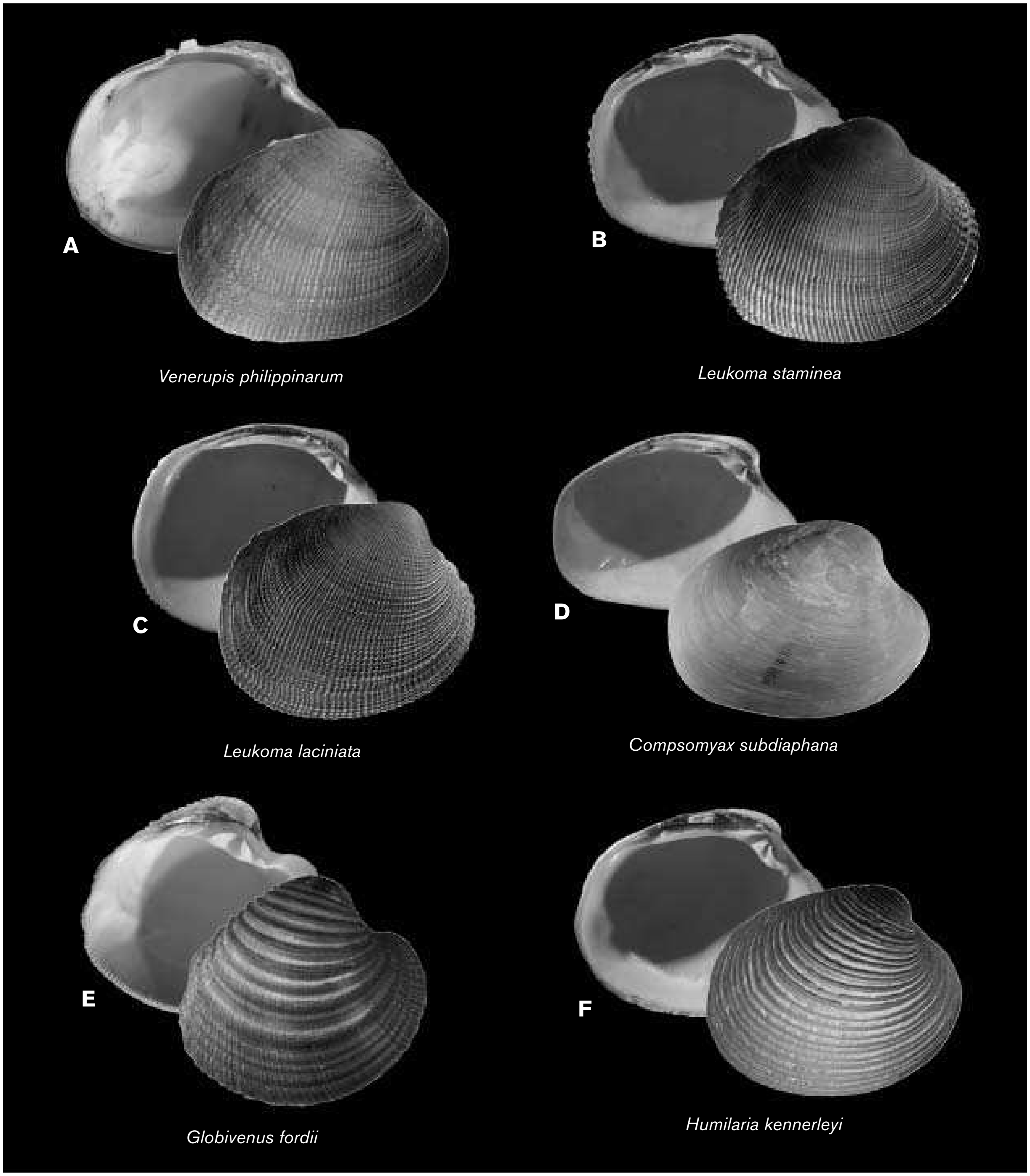

PLATE 418 A, *Venerupis philippinarum,* length 41 mm; B, *Leukoma staminea,* length 60 mm; C, *Leukoma laciniata,* length 69 mm; D, *Compsomyax subdiaphana,* length 49 mm; E, *Globivenus fordii,* length 46 mm; F, *Humilaria kennerleyi,* length 73 mm.

other biological papers; Fraser and Smith 1928, Trans. Roy. Soc. Canada (3) 22: 249–269 (ecology); Harrington 1987, Veliger 30: 148–158 (growth); Peterson 1982, Ecol. Mono. 52: 437–475 (ecology); Peterson 1983, J. Exper. Mar. Biol. Ecol. 68: 145–158 (ecology); Peterson and Ambrose 1985, Lethaia 18: 257–260 (growth); Schmidt and Warme 1969, Veliger 12: 193–199 (population characteristics); Boulding and Labarbera 1986 Biol. Bull. 171: 538–547 (crab predation by fatigue damage). A nestling form of this species may have raised, commarginal lamellae like *Irusella* but can be distinguished by its more prominent radial sculpture.

[†] Our recent review of many of the species that have been placed in the New World genus *Protothaca*, most of which are tropical, demonstrates that the several subgenera proposed for this genus are not helpful, being based on minor sculptural difference. Moreover, one of those subgenera, *Leukoma* Römer, 1857, is older than *Protothaca* Dall, 1902, and is therefore the genus to be used for the whole group. Further, we have concluded that *Callithaca* Dall, 1902, is sufficiently different to be regarded as a separable genus.

Mercenaria mercenaria (Linnaeus, 1758). The quahog; introduced from Atlantic, reproducing populations present in southern California and in southern British Columbia; in mud in bays; not common. Coan et al. 2000: 373–375; Kraeuter and Castagna 2001, Biology of the hard clam. New York (Elsevier), 732 pp., both with many references.

Nutricola confusa (Gray, 1982) (=*Transennella confusa*). In muddy sand of bays. Coan et al. 2000: 381–382; Gray 1982, Malac. Rev. 15: 107–117 (description, anatomy).

**Nutricola lordi* (Baird, 1862) and *N. ovalis* (Dall, 1902) (both formerly in *Psephidia*). Just offshore on soft bottoms. Coan et al. 2000: 382–383, plate 79.

Nutricola tantilla (Gould, 1853) (=*Transennella tantilla*). Common in sand or sandy mud in semiprotected situations in bays as well as offshore. Coan et al. 2000: 382, 384, with references to additional biological papers; Asson-Batres 1986, Veliger 30: 257–266 (reproduction, growth); Hansen 1953, Vidensk. Medd. Dansk. Naturh. Foren. 115: 313–324 (brood protection, sex ratio); Kabat 1985, J. Exp. Mar. Biol. Ecol. 91: 271–279 (brooding); Narchi 1972, Bull. Mar. Sci. 21: 866–885 (anatomy); Pamatmat 1969, Amer. Zool. 9: 419–426 (respiration).

Saxidomus gigantea (Deshayes, 1839). Uncommon in central California, a more northern species, in same habitat as *S. nuttalli*. Coan et al. 2000: 3384–3385, with many references to biological literature; Fraser and Smith 1928, Trans. Roy. Soc. Canada (3) 22: 271–277 (ecology).

Saxidomus nuttalli Conrad, 1837. California butter clam; common in bays and lagoons in mud or sand; also on outer coast in sand among rocks. Coan et al. 2000: 385–386; Peterson 1977, Mar. Biol. 43: 343–359 (ecology).

Tivela stultorum (Mawe, 1823). Pismo clam; on exposed sandy beaches from Half Moon Bay south. Coan et al. 2000: 379–380; Weymouth 1923, Calif. Fish Game Fish Bull. 7: 120 pp. (life history and growth); Herrington 1930, ibid. 18: 67 pp. (growth, populations); Coe and Fitch 1950, J. Mar. Res. 9: 188–210 (growth, reproduction); Fitch 1950, Calif. Fish Game 36: 285–312.

Venerupis philippinarum (A. Adams and Reeve, 1850) (=*V. semidecussata* and *V. japonica*; variously placed in *Paphia, Tapes, Protothaca,* and *Ruditapes,* the latter now used as a subgenus). Japanese littleneck, introduced from Asia; common in mud of bays. Coan et al. 2000: 385, 387–388, with references to the considerable biological literature.

PETRICOLIDAE

KEY TO PETRICOLIDAE

1. Shell with moderate to heavy radial sculpture 2
— Shell smooth, without heavy radial sculpture 3
2. With moderate radial sculpture, strongest anteriorly; nestling in crevices (plate 419A) . . . . *Petricola californiensis*
— With heavy radial sculpture, strongest on anterior end; shell elongate; burrowing in mud (plate 419B) . . . . *Petricolaria pholadiformis*
3. Periostracum adherent, shiny or with satin sheen (plate 419C). . . . . *Cooperella subdiaphana*
— Periostracum eroded, shell dull; with very fine radial striae, may be eroded; shell shape extremely variable; nestling in rock crevices (plate 419D) . . . . *Petricola carditoides*

* = Not in key.

LIST OF SPECIES

Coan 1997, Veliger 40: 298–340 (systematic account).

Cooperella subdiaphana (Carpenter, 1864). A thin, fragile species more common offshore, but occasionally found on low tidal mudflats. Often found living in mucus-lined "mud-balls." Coan et al. 2000: 391, 393–394; Morton 1995, Veliger 38: 162–170 (functional morphology); Hertz 2004, Festivus 36: 60–62 (habitat).

Petricola carditoides (Conrad, 1837). Common in rocky intertidal, nestling in rock crevices and in pholad holes, which it can enlarge by limited boring. Coan 1997: 302–307; Coan et al. 2000: 390–392; Yonge 1958, Proc. Malac. Soc. London 33: 25–31 (functional morphology).

Petricola californiensis Pilsbry and Lowe, 1832. A southern species that occasionally reaches central California in warm-water years. Coan 1997: 311–312; Coan et al. 2000: 391–392.

Petricolaria pholadiformis (Lamarck, 1818). Burrowing in mud; introduced from Atlantic coast in San Francisco Bay, although living populations have not been confirmed there in recent decades; remains established in Willapa Bay, WA. Coan 1997: 391, 394; Coan et al. 2000: 372, 375, both with references to a number of biological papers.

TELLINOIDEA

KEY TO TELLINOIDEA

1. Part of ligament internal, seated in a resilifer, either below beaks or in a posteriorly directed furrow (plate 420A). . . . . Semelidae 2
— Ligament entirely external 5
2. Shell smooth, shiny; in mud of bays (plate 419E). . . . . *Theora lubrica*
— Shell with conspicuous sculpture 3
3. Resilifer triangular, projecting below beaks; conspicuous commarginal sculpture; shell white internally (plates 412G, 419F) . . . . *Cumingia californica*
— Resilifer elongate, a posteriorly directed furrow . . . . *Semele* 4
4. Pallial sinus extending well past beaks; shell with heavy, frequently irregular, commarginal undulations; posterior end truncate (plate 420A). . . . . *Semele decisa*
— Pallial sinus not extending past beaks; shell with fine to medium commarginal sculpture and growth checks; posterior end not truncate, usually rounded (plate 420B). . . . . *Semele rupicola*
5. Shell elongate, cylindrical (plate 420C). . . . Solecurtidae 6
— Shell ovate, not cylindrical 7
6. Shell with weak internal radial strengthening rib extending ventrally from beaks; light purple to white in color; pallial sinus never extending to umbones (plates 412H, 420C) . . . . *Tagelus subteres*
— Shell white, without radial strengthening rib; pallial sinus never extending to umbones (plate 420D). . . . . *Tagelus californianus*
— Shell white, without radial strengthening rib; pallial sinus usually extending to or past umbones (plate 420E) . . . . *Tagelus affinis*
7. External ligament seated on a particularly conspicuous nymph (buttress for the external ligament); conspicuously colored with rays or purple color; without lateral teeth

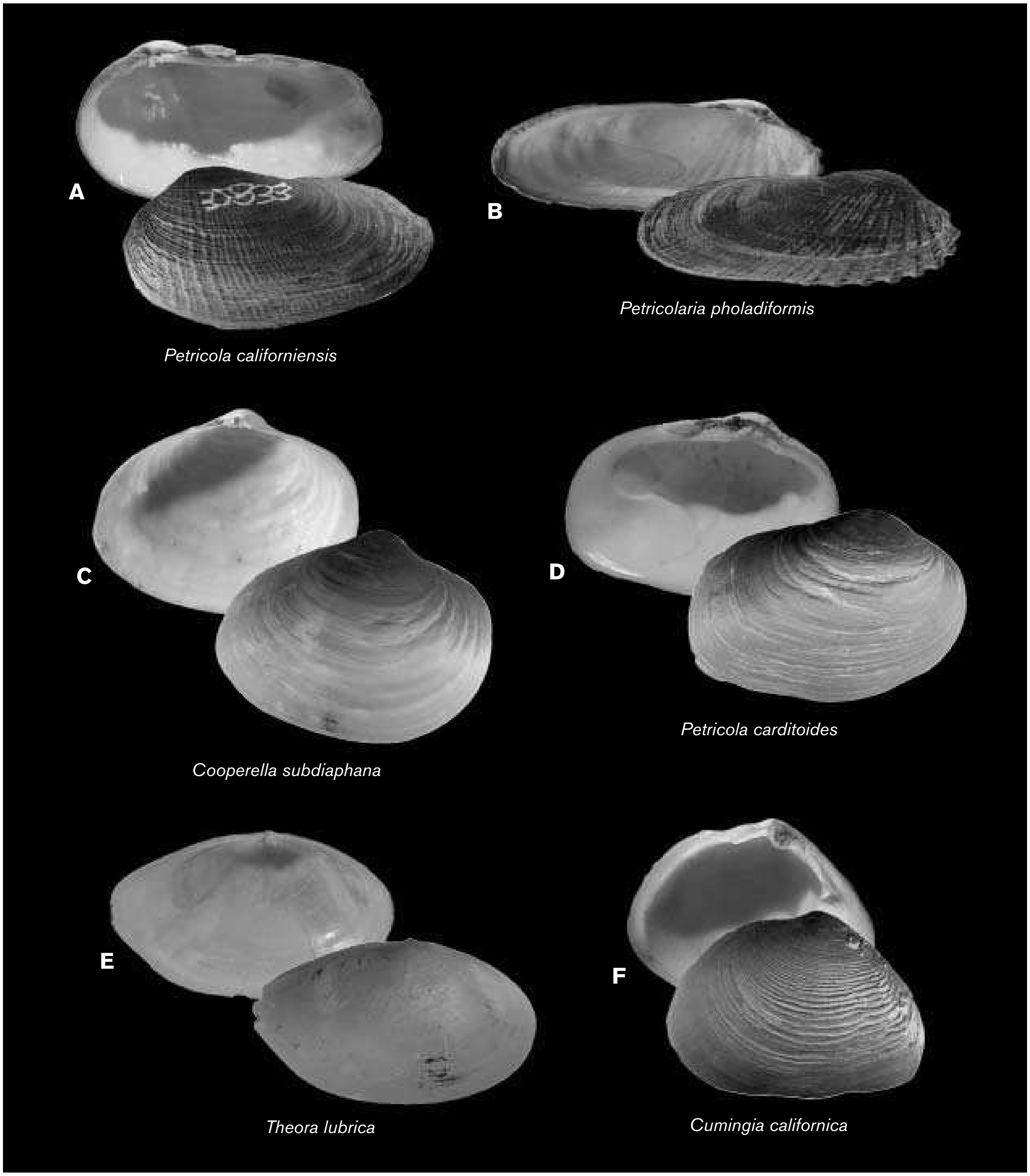

PLATE 419 A, *Petricola californiensis,* length 32 mm; B, *Petricolaria pholadiformis,* length 45 mm; C, *Cooperella subdiaphana,* length 13 mm; D, *Petricola carditoides,* length 32 mm; E, *Theora lubrica,* length 9 mm; F, *Cumingia californica,* length 28 mm.

(plate 398E)........................ Psammobiidae 8

— Nymph not conspicuous; some with reddish tinge (not rays); some with lateral teeth 10

8\. Shell subquadrate, heavy, white internally; periostracum dull; with pink to purple radial rays externally (plate 420F) .... *Gari californica*

— Shell ovate, thin, purple internally; periostracum, shiny brown .... *Nuttallia* 9

9\. Posterior end tapered; left valve more inflated than right; white to light purple internally (plate 421A)........... .... *Nuttallia nuttallii*

— Posterior end rounded; equivalve; color always deep purple internally (plate 421B)........... *Nuttallia obscurata*

10\. Shell with fine radial sculpture (plate 421C) .... *Donax gouldii*

— Shell with commarginal ribs or striae only .... Tellinidae 11

11\. Hinge with lateral teeth, especially evident in right valve .... *Tellina* 12

— Hinge without lateral teeth .... *Macoma* 14

12\. Shell with regular, strong commarginal sculpture; to 60 mm in length (plate 421D) .... *Tellina bodegensis*

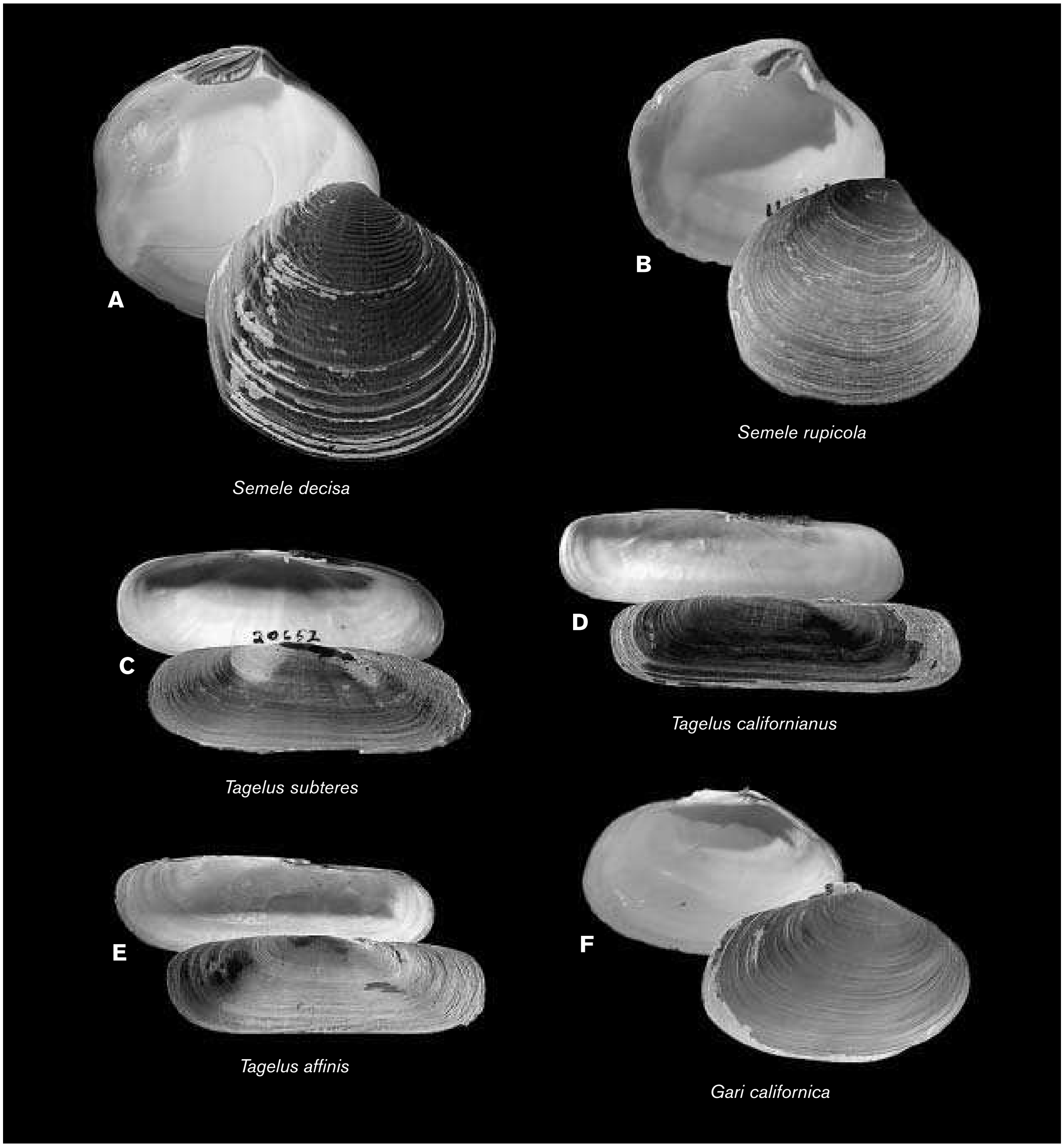

PLATE 420 A, *Semele decisa,* length 92 mm; B, *Semele rupicola,* length 24 mm; C, *Tagelus subteres,* length 38 mm; D, *Tagelus californianus,* length 114 mm; E, *Tagelus affinis,* length 41 mm; F, *Gari californica,* length 112 mm.

— Shell smooth externally or weak commarginal sculpture or growth lines; to 20 mm in length 13

13. Shell ovate-elongate, thin; color white; periostracum inconspicuous; with internal strengthening rib anteriorly (plate 421E) . . . . *Tellina modesta*

— Shell ovate-trigonal, heavy; color pink to white; often with olive periostracum; without internal strengthening rib (plate 421F) . . . . *Tellina nuculoides*

14. With a tendency to produce a posterordorsal flange from posterior end to ligament (plate 422A) 15

— Without a posterior dorsal flange 16

15. Posterior end truncate (plates 422A, 423A) . . . . *Macoma secta*

— Posterior end produced, pointed; posteroventral margin often flexed (plate 423B) . . . . *Macoma indentata*

16. Anterior ventral edge of pallial sinus detached for at least one-quarter distance to posterior adductor muscle scar and more or less paralleling pallial line (true of both valves); length <30 mm (plate 422B) 17

— Anterior ventral end of pallial sinus not detached from pallial line for a substantial distance, although it may overlap slightly near point of juncture (usually only in one valve); length to 110 mm (plate 422D) 18

17. Pointed to produced posteriorly (plates 422B, 423C) . . . . *Macoma yoldiformis*

— Broadly rounded posteriorly (plates 422C, 423D) . . . .

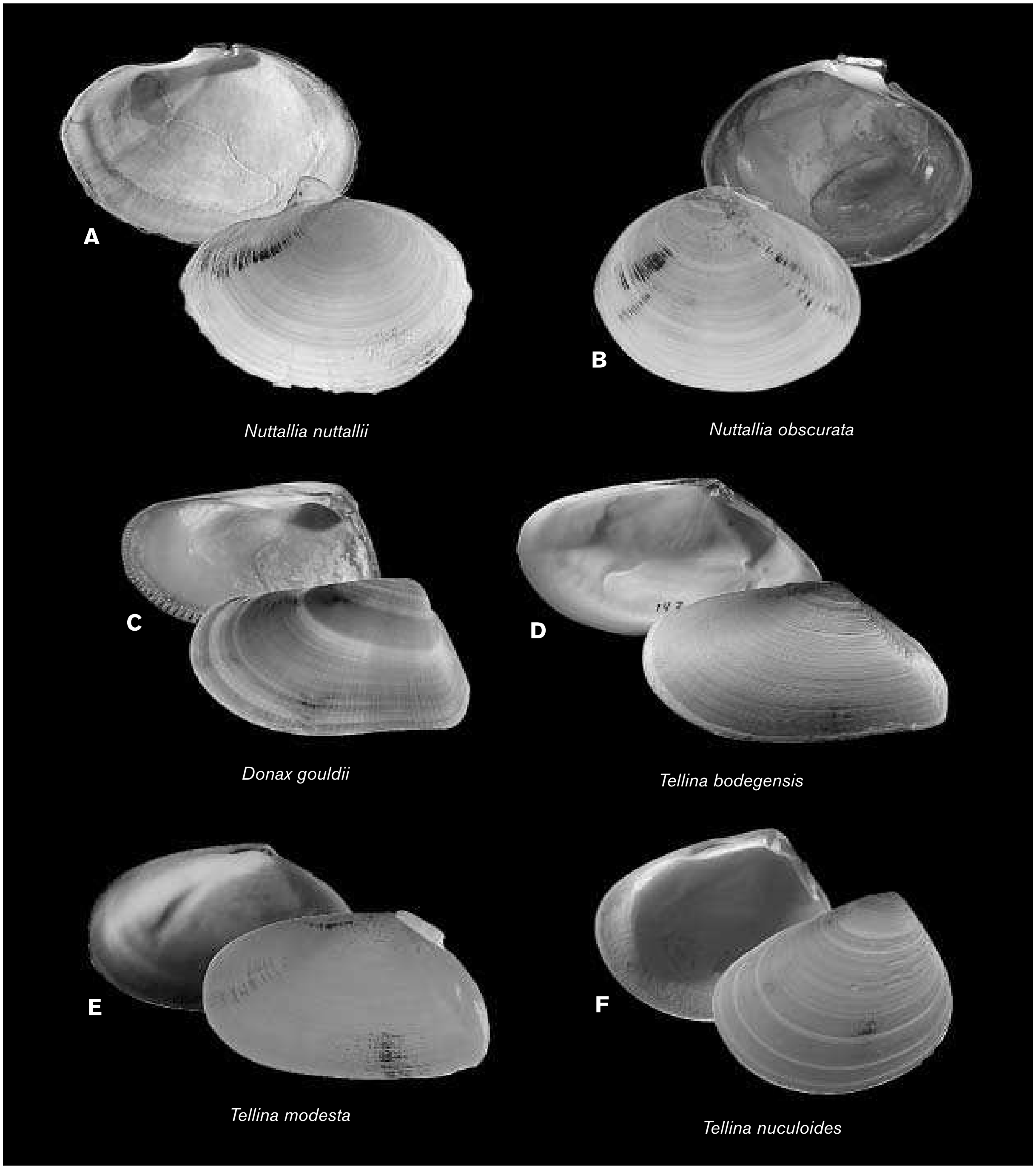

PLATE 421 A, *Nuttallia nuttallii,* length 84 mm; B, *Nuttallia obscurata,* length 44 mm; C, *Donax gouldii,* length 18 mm; D, *Tellina bodegensis,* 59 mm; E, *Tellina modesta,* length 14 mm; F, *Tellina nuculoides,* length 13 mm.

. . . . *Macoma acolasta*

18. Pallial sinus terminating only one-quarter of way to anterior adductor muscle scar; often with pinkish tinge (plates 422D, 423E) . . . . *Macoma balthica/M. petalum*

Note: (see species list)

— Pallial sinus reaching to or almost to anterior adductor muscle scar in one or both valves; whitish 19

19. Pallial sinus in left valve nearly always reaching anterior adductor muscle scar and fusing with it; shell bent to right posteriorly (plates 422E, 423F) . . . . *Macoma nasuta*

— Pallial sinus not quite reaching ventral end of anterior adductor muscle scar; equivalve, not bent posteriorly (plates 422F, 424A) . . . . *Macoma inquinata*

LIST OF SPECIES

Yonge 1949, Phil. Trans. Roy. Soc. London (B) 234: 29–76; Pohlo 1969, Proc. Malac. Soc. London 38: 361–364 (both functional morphology).

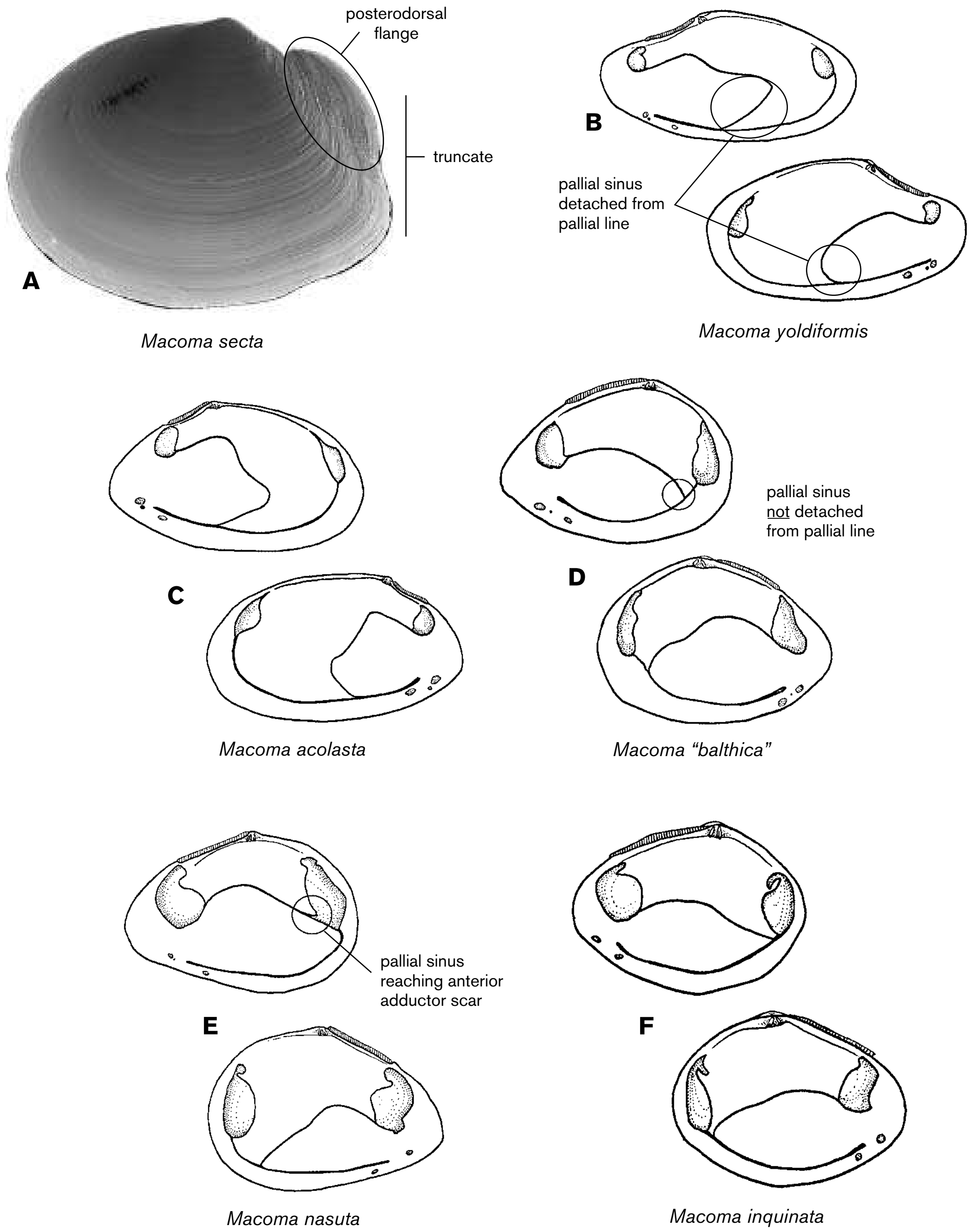

PLATE 422 A, *Macoma secta,* length 51 mm; B–F, diagrammatic sketches of adductor muscle scars, pallial line, and pallial sinus of member of the genus *Macoma*.

DONACIDAE

Coan 1983, Veliger 25: 273–298 (systematic account).

Donax gouldii Dall, 1921. Coan 1983: 290–291; Coan et al. 2000: 423, with references to additional biological papers; Pohlo 1967, Veliger 9: 330–337 (functional morphology). Normally not north of Pismo Beach, but sporadically to Santa Cruz in warm-water periods.

PSAMMOBIIDAE

Coan 1973, Veliger 16: 40–57; Coan 2000, Malacologia 42: 1–29 (systematic accounts).

Gari californica (Conrad, 1837). Among rubble, low intertidal zone. Coan 1973: 42–43; Coan 2000, Malacologia 42: 3–7; Coan et al. 2000: 426–427.

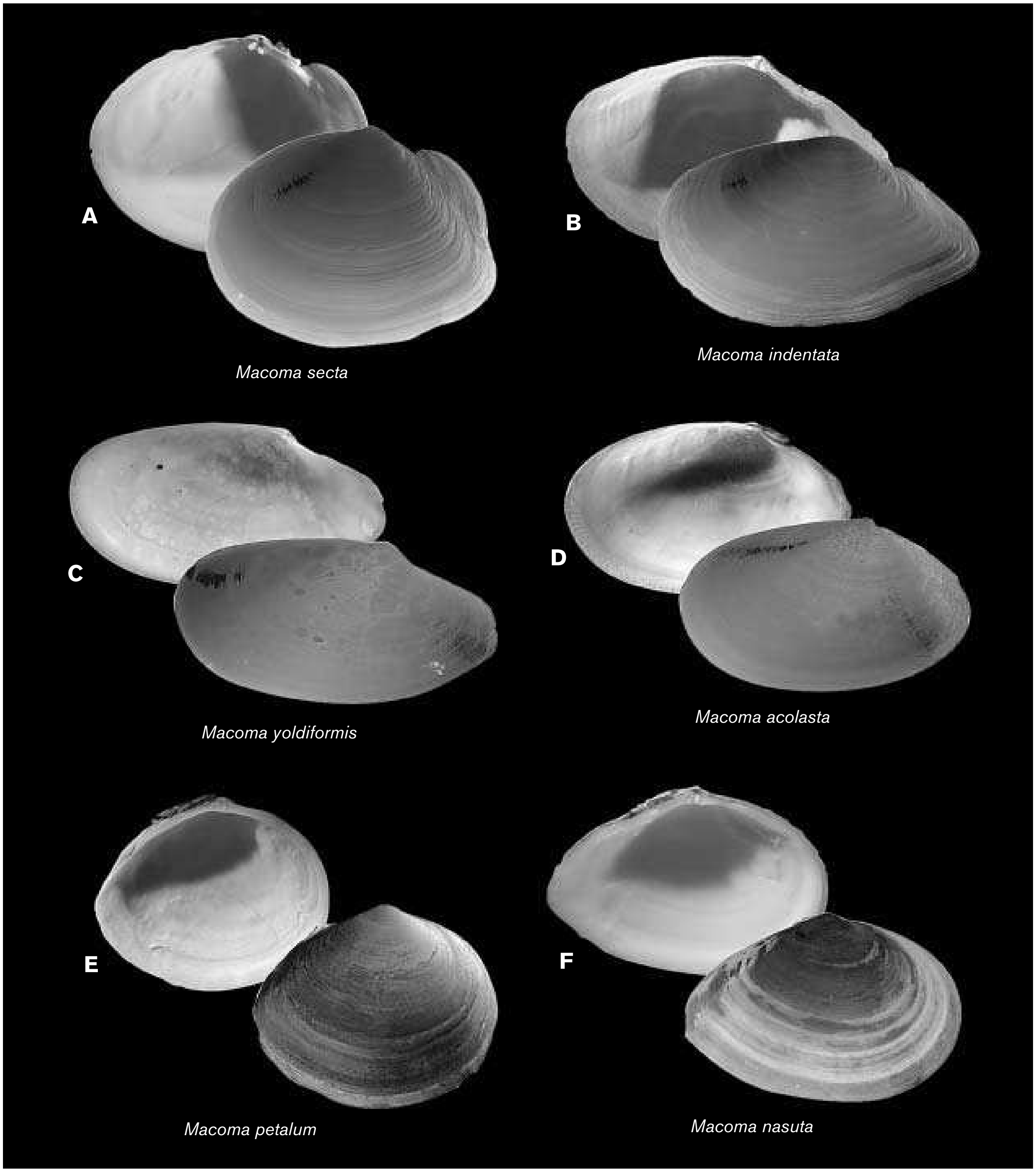

PLATE 423 A, *Macoma secta,* length 51 mm; B, *Macoma indentata,* length 43 mm; C, *Macoma yoldiformis,* length 14 mm; D, *Macoma acolasta,* length 11 mm; E, *Macoma petalum,* length 23 mm; F, *Macoma nasuta,* length 37 mm.

Nuttallia nuttallii (Conrad, 1837) (=*Sanguinolaria nuttallii*). In sand and sandy mud of low intertidal, protected bays. Reported as far north as Humboldt Bay (Yoshimoto 2004, Festivus 36: 128–129), and Coos Bay (J. Carlton, personal communication, 2004). Coan 1973: 48–49; Coan et al. 2000: 427, 429; Pohlo 1972, Veliger 14: 298–301 (feeding, associated morphology).

Nuttallia obscurata (Reeve, 1857). Introduced from Asia by ballast water. Coan et al. 2000: 427, 429.

SEMELIDAE

Coan 1973, Veliger 15: 314–329; Coan 1988, Veliger 31: 1–42 (systematic reviews).

Cumingia californica Conrad, 1837. Common nestler in rocky intertidal zone. Coan 1973: 323–325; Coan et al. 2000: 436–437.

Semele decisa (Conrad, 1837). A southern California species that occurs as far north as Point Arguello, nestling in rocky situations. Coan 1988: 6–7; Coan et al. 2000: 432–433.

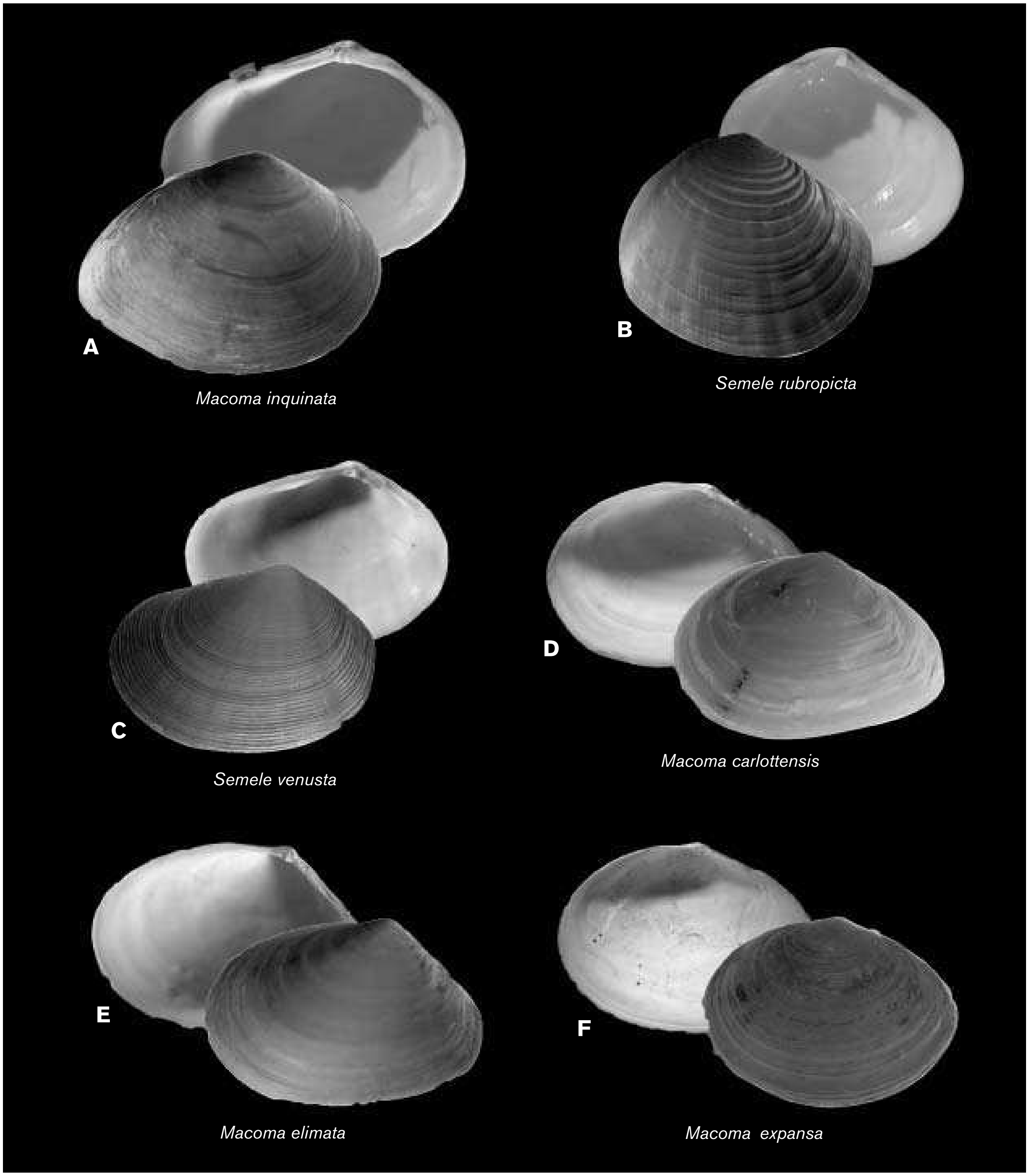

PLATE 424 A, *Macoma inquinata,* length 53 mm; B, *Semele rubropicta,* length 33 mm; C, *Semele venusta,* length 21 mm; D, *Macoma carlottensis,* length 18 mm; E, *Macoma elimata,* length 15 mm; F, *Macoma expansa,* length 43 mm.

**Semele rubropicta* Dall, 1871 (plate 424B). Uncommon, offshore species; valves occasionally wash ashore; characterized by conspicuous radial and commarginal sculpture and red radial rays. Coan 1988: 12–13; Coan et al. 2000: 432–434.

**Semele venusta* (Reeve, 1853) (plate 424C). An offshore species in mud bottoms. Coan 1988: 21–23; Coan et al. 2000: 433–434.

Semele rupicola Dall, 1915. Nestler in rocky intertidal; uncommon. Coan 1988: 23–24; Coan et al. 2000: 433–435.

Theora lubrica Gould, 1861. Introduced from Asia, this species occurs in several Californian bays, including San Francisco Bay. Coan et al. 2000: 4436, 438.

SOLECURTIDAE

Coan 1973, Veliger 16: 40–57 (systematic account).

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* = Not in key.

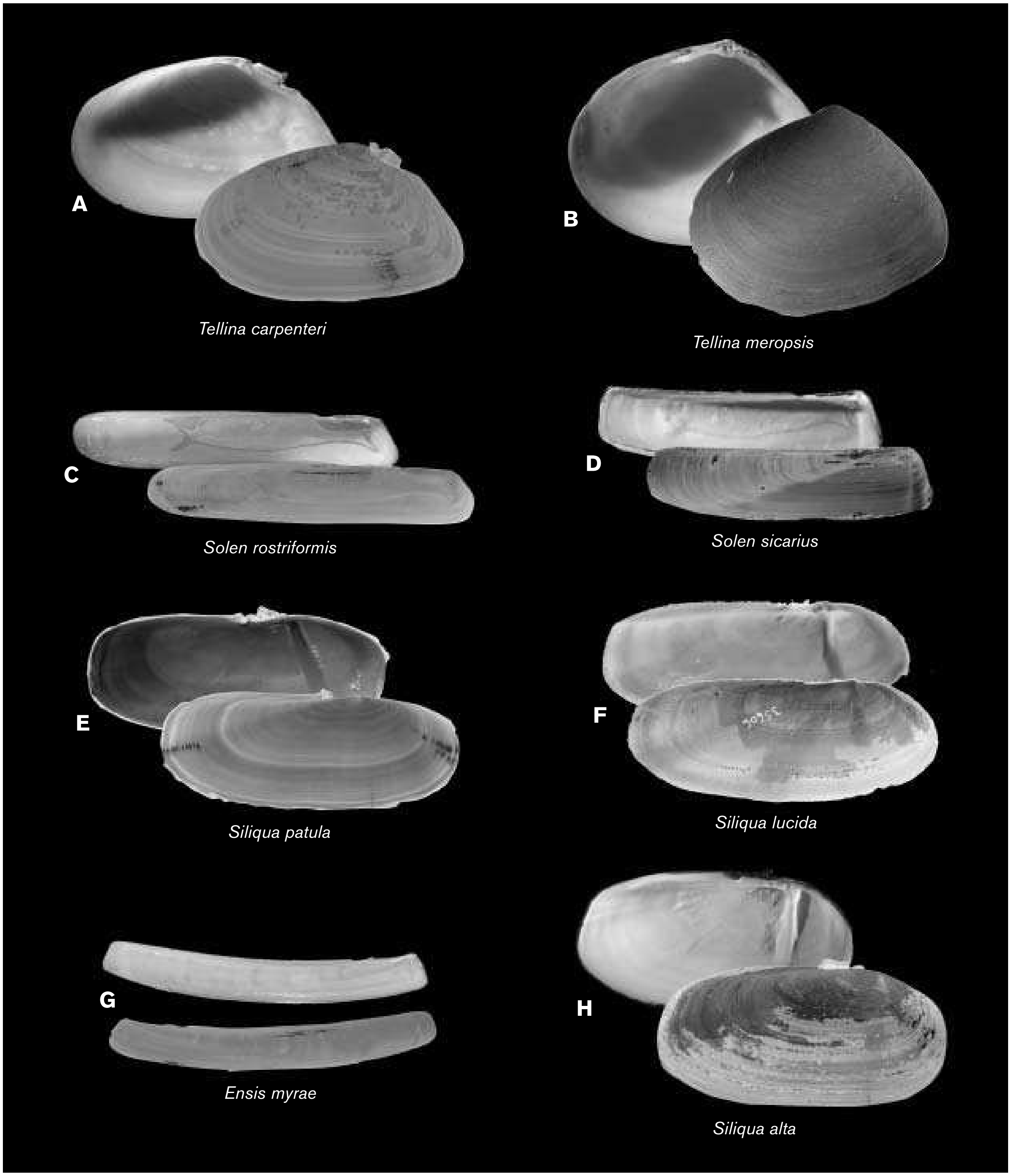

PLATE 425 A, *Tellina carpenteri,* length 10 mm; B, *Tellina meropsis,* length 16 mm, C, *Solen rostriformis,* length 57 mm; D, *Solen sicarius,* length 78 mm; E, *Siliqua patula,* length 125 mm; F, *Siliqua lucida,* length 52 mm; G, *Ensis myrae,* length 56 mm; H, *Siliqua alta,* length 120 mm.

Tagelus affinis (C. B. Adams, 1852). Low intertidal zone in sand and mud of protected bays; as far north as Morro Bay. Coan 1973: 50–51; Coan et al. 2000: 441–442.

Tagelus californianus (Conrad, 1837). Low intertidal zone in sand and mud of protected bays. Coan 1973: 51–52; Coan et al. 2000: 441–442; Pohlo 1966, Veliger 8: 225 (feeding).

Tagelus subteres (Conrad, 1837). Low intertidal zone in sand and mud of protected bays. Southern, occasionally north to Morro Bay. Coan 1973: 52–53; Coan et al. 2000: 442.

TELLINIDAE

Coan, 1971, Veliger 14 Suppl.: 63 pp. (systematic review); Dunnill and Ellis 1969, Veliger 12: 207–291 (*Macoma* ecology); Reid and Reid 1969, Can. J. Zool. 47: 64–57 (*Macoma* feeding).

Macoma acolasta Dall, 1921 . Protected bays in low intertidal zone in sand; uncommon. Coan 1971: 34–35; Coan et al. 2000: 414, 416.

Macoma balthica (Linnaeus, 1758) (=*Macoma inconspicua* [Broderip and G. B. Sowerby I, 1829]). The common brackish water macoma from at least Coos Bay, Oregon, north through the Arctic. See Vainola 2003 (above); Meehan et al. 1985, Mar. Biol. 102: 235–241 (genetics of San Francisco Bay and Coos Bay populations); Coan 1971: 44–46; Coan et al. 2000: 417–419, with references to the extensive biological literature. See also *Macoma petalum*.

**Macoma carlottensis* Whiteaves, 1880 (plate 424D). Offshore on soft bottoms. Coan 1971: 35–37; Coan et al. 2000: 414, 416.

**Macoma elimata* Dunnill and Coan, 1968 (plate 424E). Offshore on soft bottoms. Coan 1971: 22–23; Coan et al. 2000: 405, 410.

**Macoma expansa* Carpenter, 1864 (plate 424F). Of the same group as *M. secta* and *M. indentata,* but thinner, more inflated, with an only slightly developed posterior dorsal flange: rare, in sand offshore, in exposed areas; valves occasionally washed ashore. Coan 1971: 40–41; Coan et al. 2000: 415–416.

Macoma indentata Carpenter, 1864. In silt to sand of bays, uncommon. Coan 1971: 39–40; Coan et al. 2000: 415, 418.

Macoma inquinata (Deshayes, 1855). Common, in silt and mud in protected areas, most common in bays, but also below surf zone offshore. Coan 1971: 42–43; Coan et al. 2000: 418–419; Levinton 1991, Mar. Biol. 110: 375–383 (feeding).

Macoma nasuta (Conrad, 1837). Bent-nosed clam; common, in mud and muddy sand in protected areas, most common in bays at mid-tide, also below surf zone offshore. Coan 1971: 41–42; Coan et al. 2000: 418, 420; Gallucci and Hylleberg 1976, Veliger 19: 59–67 (growth); Hylleberg and Gallucci 1975, Mar. Biol. 32: 167–178 (feeding); Levinton 1991, Mar. Biol. 110: 375–383 (feeding); Rae 1978, Biol. Bull. 155: 207–291 (reproduction); Rae 1979, Veliger 21: 384–299 (population study).

Macoma petalum (Valenciennes, 1821) (=*Macoma balthica* of San Francisco Bay and other central California localities). Common in mud in upper intertidal of bays, especially in brackish water. The common small pink and white macoma of San Francisco Bay is the North American Atlantic coast species *M. petalum*, now recognized as genetically distinct from the boreal and European *M. balthica* (Vainola 2003, Mar. Biol. 143: 935–946). It was introduced with oysters.

Its range along the Pacific coast has not been determined. Morphological distinctions between *M. petalum* and *M. balthica* have not been worked out; they are keyed together here, and a specimen of *M. petalum* from Chesapeake Bay is shown in the plate. See Vassallo 1969, Veliger 11: 223–234; 1971, 13: 279–284 (ecology in San Francisco Bay).

Macoma secta (Conrad, 1837). Sand clam; common, intertidal in sand in semiprotected areas of bays and offshore of sandy beaches. Coan 1971: 37–39; Coan et al. 2000: 417–418; Levinton 1991, Mar. Biol. 110: 375–383 (feeding); Rae 1978, Biol. Bull. 155: 207–291 (reproduction); Rae 1979, Veliger 21: 384–299 (population study).

Macoma yoldiformis Carpenter, 1864. In silt to sand, in protected areas in low intertidal of bays; rare. Coan 1971: 33–34; Coan et al. 2000: 414, 416.

Tellina bodegensis Hinds, 1845. Low intertidal in sand of exposed beaches; in bays. Coan 1971: 10–11; Coan et al. 2000: 404–405.

**Tellina carpenteri*. Dall, 1900 (plate 425A). Similar to *T. modesta*, but light pink in color; below low tide on various bottoms. Coan 1971: 15–16; Coan et al. 2000: 400–401.

**Tellina meropsis* Dall, 1900 (plate 425B). A southern form that is sometimes transported northward in warm-water years; on soft bottoms just offshore. Coan 1971: 14–15; Coan et al. 2000: 401–402.

Tellina modesta (Carpenter, 1864). In sand to silty sand of bays, to well offshore. Coan 1971: 16–17; Coan et al. 2000: 401–402; Maurer 1967a–c, Veliger 9: 305–309, 376–381, 10: 72–76, 1969, Veliger 11: 243–249 (biology).

Tellina nuculoides (Reeve, 1854). On various bottoms in protected areas of bays. Coan 1971: 12–13; Coan et al. 2000: 401, 403; Maurer 1967a–c, Veliger 9: 305–309, 376–381, 10: 72–76, 1969, Veliger 11: 243–249 (aspects of biology).

SOLENIDAE

KEY TO SOLENIDAE

1. Shell thin, tapered; periostracum light olive to light brown (plate 425C) . . . . *Solen rostiformis*
— Shell thick, blunt posteriorly; periostracum dark brown (plate 425D) . . . . *Solen sicarius*

LIST OF SPECIES

Cosel 1990, Veliger 35: 366–380 (taxonomy).

Solen rostiformis Dunker, 1862 (=*Solen rosaceus* Carpenter, 1864). In mud in bays as far north as Morro Bay. Coan et al. 2000: 444–445; Cosel 1990, Veliger 35: 366–380 (taxonomy; with *S. rostiformis* and *S. rosaceus* regarded as separate species); Pohlo 1963, Veliger 6: 98–104 (functional morphology).

Solen sicarius Gould, 1850. Protected areas of bays in mud or muddy sand; forming permanent burrows in which it moves freely up and down. Coan et al. 2000: 445.

PHARIDAE

KEY TO PHARIDAE

1. Internal radial rib sloping anteriorly, relatively wide; posterior end tapered in specimens less than 55 mm; large, to 190 mm in length (plate 425E) . . . . *Siliqua patula*
— Internal radial rib vertical, narrow; posterior end truncate; not more than 55 mm in length (plate 425F) . . . . *Siliqua lucida*

LIST OF SPECIES

Cosel 1990, An introduction to the razor shells (Bivalvia: Solenacea), pp. 283–311, in B. Morton, ed., The Bivalvia, University of Hong Kong Press (systematics).

**Ensis myrae* Berry, 1953 (plate 425G). A long, thin, offshore species. Coan et al. 2000: 446–447, 449.

**Siliqua alta* (Broderip and G. B. Sowerby I, 1829) (=*S. sloati* Hertlein, 1961) (plate 425H). A northern species occurring offshore in central California, where it is smaller than in Alaska. Coan et al. 2000: 448–449.

Siliqua lucida (Conrad, 1837). Protected sandy areas of bays. Coan et al. 2000: 448–449; Hertlein 1961, Bull. So. Calif. Acad. Sci. 60: 12–18 (comparisons). Possibly only young of *S. patula;* more research needed.

Siliqua patula (Dixon, 1789). Razor clam; semiprotected, clean-sand beaches. Coan et al. 2000: 448–449, with references

* = Not in key.

to many additional biological and fisheries papers; Bourne and Quayle 1970, Fish. Res. Bd. Can. Tech. Report 232: 42 pp. (breeding, growth); Hertlein 1961, as above (comparisons); Lassuy and Simons 1989, U.S. Fish and Wildlife Serv. Biol. Rept. 82: 16 pp. (general review); LeClair and Phelps 1994, J. Shellfish Res. 13: 207–216 (genetics); Pohlo 1963, Veliger 6: 98–104 (morphology, burrowing); Taylor 1959, J. Conseil 25: 93–101 (growth); Weymouth and McMillin 1930, Bull. U.S. Bur. Fish. 46: 543–567 (growth); Weymouth et al. 1925, ibid. 41: 201–236 (growth); Weymouth et al. 1931, J. Exp. Biol. 8: 228–249 (growth); Yonge 1952, Univ. Calif. Publ. Zool. 55: 421–438 (aspects of morphology, reproduction, growth, biology, ecology).

MACTRIDAE

KEY TO MACTRIDAE

1\. Shell broadly gaping posteriorly .... *Tresus* 2

— Shell narrowly gaping or closed posteriorly........... 3

2\. Shell ovate-elongate; posterior end markedly longer than anterior (plate 426A) .... *Tresus nuttallii*

— Shell ovate to rhomboidal; posterior end not markedly longer than anterior (plate 426B) .... *Tresus capax*

3\. Chondrophore projecting ventrally (plate 427A) .... *Mactromeris* 4

— Chondrophore not projecting past hinge line, or projecting only slightly past it (plate 427B) 5

4\. Anterior end shorter than posterior, broad; anterodorsal margin straight (plate 426C) .... *Mactromeris catilliformis*

— Anterior end longer than or equal to posterior; anterodorsal margin concave (plates 426D, 427A) .... *Mactromeris hemphillii*

5\. Beaks with commarginal undulations (plate 426E)...... .... *Mactrotoma californica*

— Beaks without undulations .... *Simomactra* 6

6\. Shell longer anteriorly; pallial sinus of moderate depth; anterior lateral tooth long in left valve, aligned with anterior cardinal tooth (plate 426F) .... *Simomactra falcata*

— Shell subequilateral; pallial sinus shallow, narrow; anterior lateral tooth short in left valve, not aligned with cardinal (plates 426G, 427B).............. *Simomactra planulata*

LIST OF SPECIES

Mactromeris catilliformis (Conrad, 1867) (=*Spisula catilliformis*). On sand beaches on open coast, often washing ashore after large storms. Coan et al. 2000: 454–455.

Mactromeris hemphillii (Dall, 1894) (=*Mactra hemphillii*). Occurs in the same situations, only as far north as Cayucos. Coan et al. 2000: 454–455.

Mactrotoma californica (Conrad, 1837) (=*Mactra californica*). In sandy mud of bays. A southern species found north of Point Conception in warm-water years. Coan et al. 2000: 457.

Simomactra falcata (Gould, 1850) (=*Spisula falcata*). Uncommon in sandy areas, chiefly offshore. Coan et al. 2000: 458–459.

Simomactra planulata (Conrad, 1837) (=*Mactra planulata*). Occurs in similar situations. Coan et al. 2000: 458–459.

**Tresus allomyax* Coan and Valentich-Scott, 2000 (plate 426H). Offshore, northern California; occasionally washes ashore. Coan et al. 2000: 460–463.

Tresus capax (Gould, 1850) (=*Schizothaerus capax*). The fat gaper; a more northern species and uncommon in central California. Coan et al. 2000: 461, 463, with references to many additional biological papers; Bourne and Smith 1972, Proc. Natl. Shellfisheries Assn. 62: 35–37 (larvae); Bourne and Smith 1972, Proc. Natl. Shellfisheries Assn. 62: 38–46 (reproduction, growth); Breed-Willecke and Hancock 1980, Proc. Natl. Shellfisheries Assn. 70:1–13 (reproduction, growth); Campbell and Bourne 2001, J. Shellfish Res. 19: 933–942 (populations, growth); Machell and DeMartini 1971, Calif. Fish Game 57: 274–282 (reproduction); Pearce 1965, Veliger 7: 166–170 (ecology); Smith and Davis 1965, J. Exp. Biol. 43: 171–180 (physiology); Swan and Finucane 1952, Nautilus 66: 19–26 (distinctions between *T. capax* and *T. nuttallii*).

Tresus nuttallii (Conrad, 1837) (=*Schizothaerus nuttallii*). The Pacific gaper, in sand in bays. Coan et al. 2000: 461, 463–464; Campbell et al. 1990, J. Shellfish Res. 9: 273–278 (growth); Campbell and Bourne 2001, J. Shellfish Res. 19: 933–942 (populations, growth); Clark et al. 1975, Calif. Fish Game 61: 215–227 (life history); Pearce 1965, as above (ecology); Pohlo 1964, Malacologia 1: 321–330 (ontogeny, ecology); Illg 1949, Proc. U.S. Nat. Mus. 99: 391–428 (parasitic copepods); Smith and Davis 1965, as above (physiology); Stout 1970, Veliger 13: 67–70 (epizoics on siphonal plates). The two intertidal species of *Tresus* are further distinguished by the presence of a "visceral skirt" (a prolongation of the inner palp lamellae, which forms a curtain-like structure hanging from the dorsal extremities of and covering much of posterior of the visceral mass) in *T. capax* and its absence in *T. nuttallii* (see Pearce 1965, above).

MYIDAE

KEY TO MYIDAE

1\. Shell heavy, with wavy commarginal sculpture; anterior round, posterior truncate, gaping; periostracum thick at posterior end; boring into rock, hard clay (plate 428A) .... *Platyodon cancellatus*

— Shell thin; burrowing in mud or sand 2

2\. Pallial sinus deep; length to 120 mm or more (plates 395H, 428B) .... *Mya arenaria*

— Pallial sinus shallow, inconspicuous; length to 30 mm (plate 428C).................... *Cryptomya californica*

LIST OF SPECIES

Cryptomya californica (Conrad, 1837). In sand or mud in bays; using its very short siphons, *Cryptomya* "taps" the burrows of other invertebrates, particularly of *Urechis* and *Upogebia*; also on open coast in gravel, among rocks; Coan et al. 2000: 474–475; Lawry 1987, Veliger 30: 46–54 (various aspects of biology); Yonge 1951, Univ. Calif. Publ. Zool. 55: 395–400 (functional morphology).

Mya arenaria Linnaeus, 1758. Soft-shelled or long-necked clam; in mud and sand of bays, burrowing to 30 cm deep; introduced from Atlantic coast. Coan et al. 2000: 470, 472, with many references to the substantial biological and fisheries literature; Bernard 1979, Venus 38: 185–204 (taxonomy); Checa and Cadée 1995, J. Molluscan Studies 63: 157–171 (burrowing); MacNeil 1965, U.S. Geol. Surv. Prof. Paper 483G: 33–35 (taxonomy, evolution).

Platyodon cancellatus (Conrad, 1837). A rock borer, common in shale, also in sandstone and hard clay. Coan et al. 2000:

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* = Not in key.

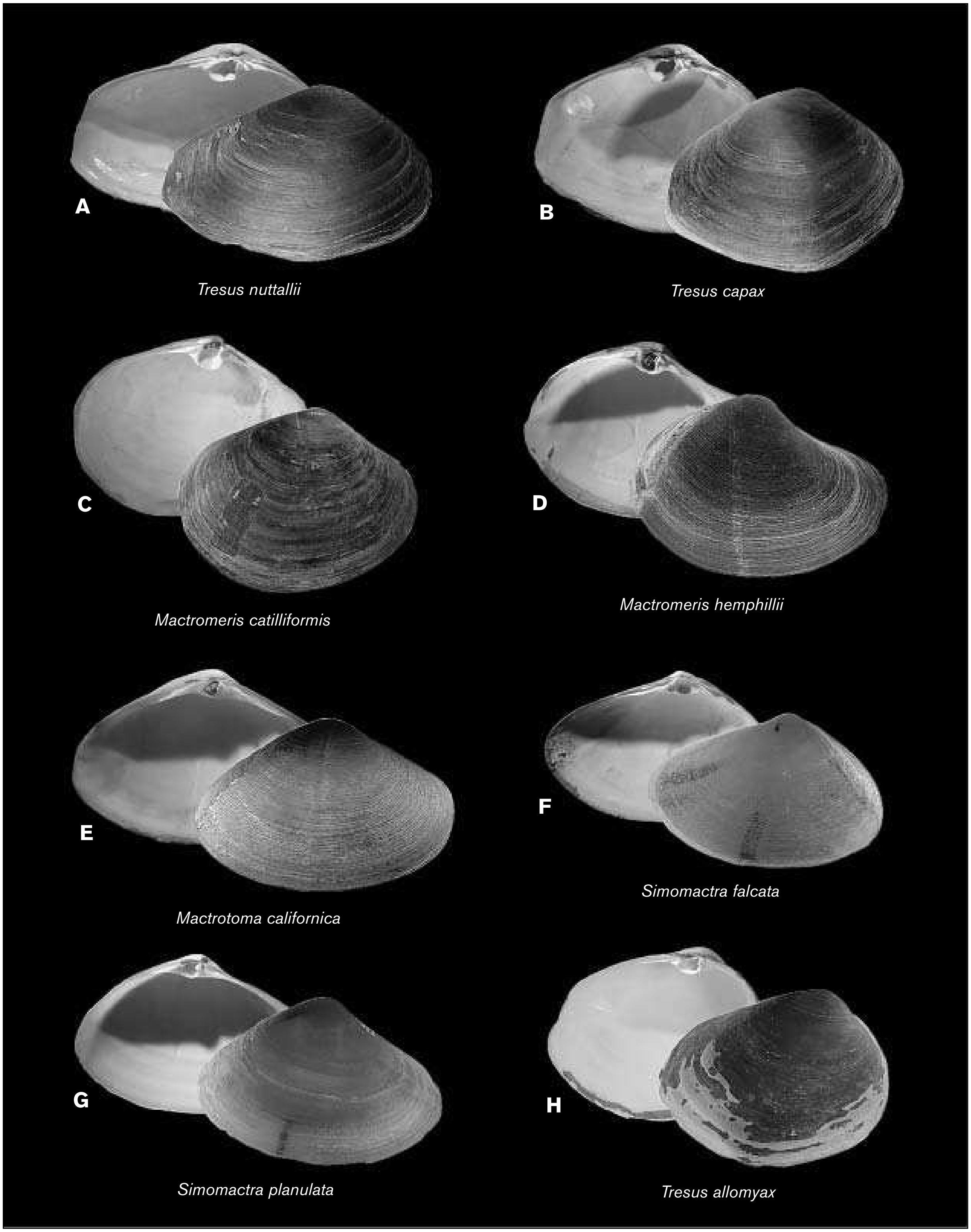

PLATE 426 A, *Tresus nuttallii*, length 142 mm; B, *Tresus capax*, length 120 mm; C, *Mactromeris catilliformis*, length 140 mm; D, *Mactromeris hemphillii*, length 87 mm; E, *Mactrotoma californica*, length 32 mm; F, *Simomactra falcata*, length 32 mm; G, *Simomactra planulata*, length 38 mm; H, *Tresus allomyax*, holotype, length 142 mm.

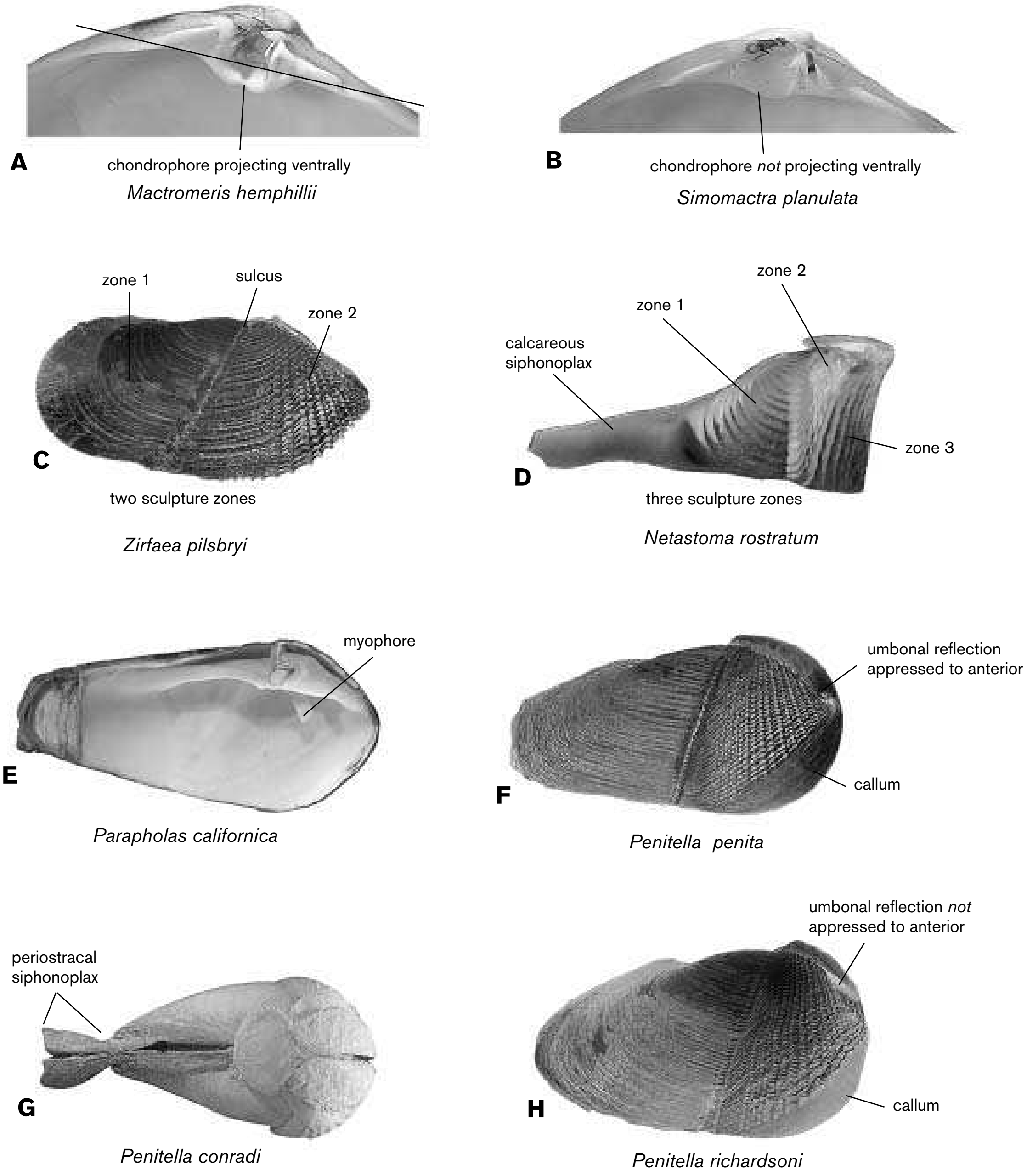

PLATE 427 A, ventrally projecting chondrophore of *Mactromeris hemphillii*; B, *Simomactra planulata* without vertically projecting chondrophore; C, sculpture zones of *Zirfaea pilsbryi,* length 92 mm; D, sculpture zones and siphonoplax of *Netastoma rostratum,* length 18 mm; E, projecting myophore of *Parapholas californica,* length 83 mm; F, appressed umbonal reflection of *Penitella penita,* length 50 mm; G, periostracal siphonoplax of *Penitella conradi,* length 20 mm; H, free umbonal reflection of *Penitella richardsoni,* length 46 mm.

472–473; Yonge 1951, Univ. Calif. Publ. Zool. 55: 401–418 (functional morphology).

**Sphenia luticola* (Valenciennes, 1846) (plate 428D). An offshore species nestling in rock cavities; occasionally washed ashore in rocks entwined in kelp holdfasts. Coan 1999, Nautilus 113: 112–115; Coan et al. 2000: 475–476.

CORBULIDAE

Coan 2002, Malacologia 44: 47–105 (systematic treatment).

**Corbula luteola* Carpenter, 1864 (plate 428E). A southern Californian species recorded in shallow water in Monterey Bay in warm-water years. Coan et al. 2000: 479–480; Coan 2002: 84–87.

Corbula amurensis Schrenck, 1861 (=*Potamocorbula amurensis*) (plate 428F). An Asian species introduced into San Francisco Bay, where it has occurred in vast numbers. Coan et al. 2000: 479–480; Coan 2002: 71–72; Carlton et al. 1990, Mar. Ecol. Prog. Ser. 66: 81–94 (introduction); Nichols et al. 1990, Mar. Ecol. Prog. Ser. 66: 95–101 (ecology).

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* = Not in key.

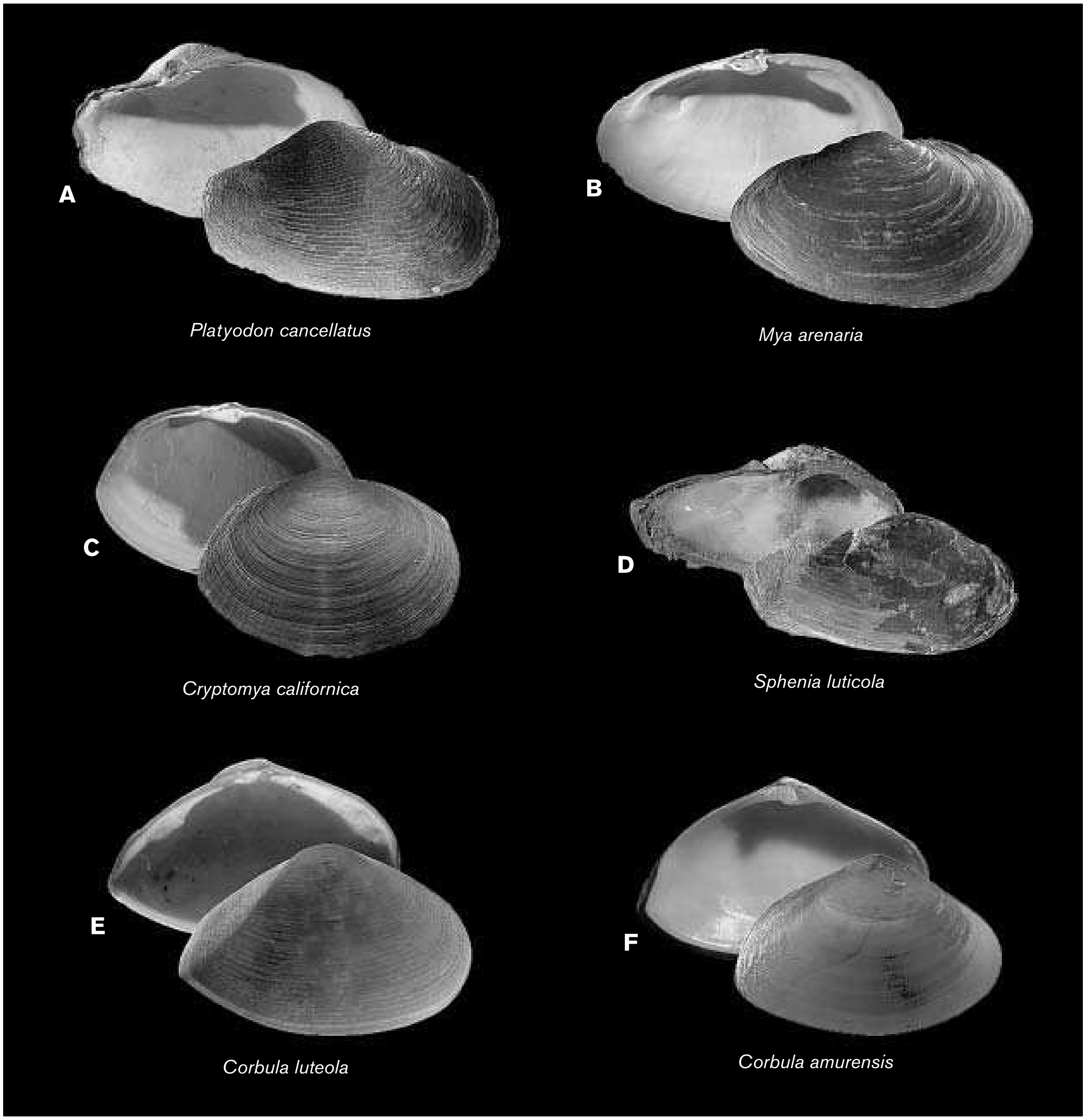

PLATE 428 A, *Platyodon cancellatus,* length 52 mm; B, *Mya arenaria,* length 78 mm; C, *Cryptomya californica,* length 27 mm; D, *Sphenia luticola,* length 15 mm; E, *Corbula luteola,* length 8 mm; F, *Corbula amurensis,* length 17 mm.

HIATELLIDAE

KEY TO HIATELLIDAE

1. Shell length to 200 mm, quadrate; pallial line entire, broad; posterior end broadly gaping; shell not distorted (plate 429A) . . . . *Panopea abrupta*

— Shell length to 78 mm, extremely variable shape, often distorted by boring or nestling habit pallial line faint, broken into irregular patches (plates 395D, 429B). . . . . *Hiatella arctica*

LIST OF SPECIES

Yonge 1971, Malacologia 11: 1–44 (functional morphology).

Hiatella arctica (Linnaeus, 1767). (=*Saxicava arctica*; other species names in occasional use include *H. pholadis* [Linnaeus, 1771] and *H. solida* [G. B. Sowerby I, 1834]). Attaches with a byssus but can also bore; in bays, on pilings, in fouling clumps, open coast in algal holdfasts, abandoned pholad holes, and *Mytilus* beds. This highly variable species is a dominant byssally attached bivalve of arctic and boreal regions. There may be more than one species in this genus: different spawning times, eggs of two colors (red and pinkish cream), two post-larval forms (oval and triangular), juvenile shell with or without spinose external radial ridges, animal with or without a byssus, position of the adductor muscles and their scars relative to the dorsal margin, and siphon tips of two colors (red and white). Unfortunately, these traits have not been correlated with each other or with type material. Full taxonomic understanding of

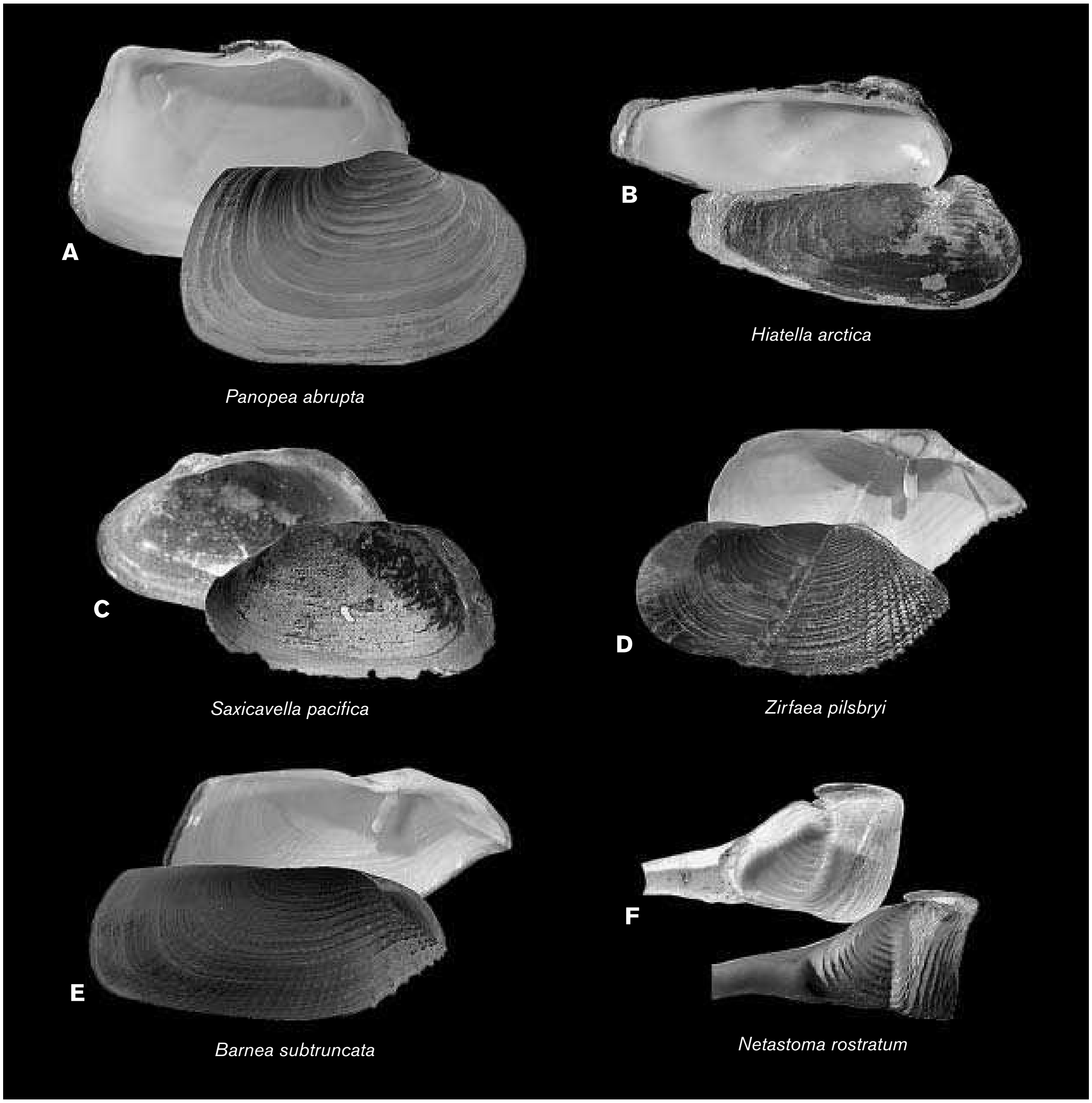

PLATE 429 A, *Panopea abrupta,* length 110 mm; B, *Hiatella arctica,* length 36 mm; C, *Saxicavella pacifica,* length 5.5 mm; D, *Zirfaea pilsbryi,* length 92 mm; E, *Barnea subtruncata,* length 59 mm; F, *Netastoma rostratum,* length 18 mm.

this genus is a problem that cries out for attention with modern methodologies grounded in sound nomenclature and with type specimens. One might expect that the situation will prove to be genetically complex as well, in part because of human introductions through shipping. Coan et al. 2000: 485–487; Beu 1971, New Zealand J. Geol. Geophysics 14: 64–6 (taxonomy); Narchi 1973, Mar. Biol. 332–337 (functional morphology of *H. "solida"*); Russell-Hunter 1949, Proc. Roy. Soc. Edinburgh (B) 43: 271–289 (morphology, biology of British material); Yonge 1971, Malacologia 11: 1–44 (functional morphology).

Panopea abrupta (Conrad, 1849). (*Panope* is an invalid emendation; =*P. generosa* Gould, 1850). The geoduck (several variant spellings, but usually pronounced gooey-duck, possibly from the Chinook *gweduc*); a very deep burrower in soft bottoms from low intertidal to offshore; siphons may be several feet long. Coan et al. 2000: 486, 490, with many additional references to the biological and fisheries literature; Goodwin 1977, Veliger 20: 155–158 (ecology); Illg 1949, Proc. U.S. Nat. Mus. 99: 391–428 (parasitic copepods); Shaul and Goodwin 1982, Can. J. Fish. Aquatic Sci. 39: 632–636 (growth); Yonge 1971, as above (functional morphology).

**Saxicavella pacifica* Dall, 1916 (plate 429C). A small species offshore on soft bottoms. Coan et al. 2000: 491.

PHOLADIDAE

KEY TO PHOLADIDAE

1. Burrowing into sand or mud; adult shell without a callum 2

* = Not in key.

— Boring into clay, shale, or shell; adult shell with a callum in form of a band or complete anterior covering (plate 427F) 3

2. Sculpture with two distinct zones, divided by a sulcus (plates 427C, 429D) . . . . *Zirfaea pilsbryi*

— Sculpture without two distinct zones or a dividing sulcus (plate 429E) . . . . *Barnea subtruncata*

3. Shell without myophores; callum present only as an anterior band (sculptured with high, thin flutes); adult with a long, tapering, calcareous siphonoplax; sculpture with three distinct zones; shell often irregular in shape (plate 429F) . . . . *Netastoma rostratum*

— Myophore present; callum present in adult as an anterior covering; siphonoplax never wholly calcareous (plate 427E) 4

4. Sculpture divided into three distinct zones; posterior end of shell with overlapping chitinous plates (plates 427E, 430A) . . . . *Parapholas californica*

— Sculpture divided into two distinct zones; posterior end without overlapping plates 5

5. Umbonal reflection appressed to anterior end (plate 427F) 6

— Umbonal reflection not appressed to anterior end (plate 427H) 7

6. Siphonoplax absent; callum complete (when present); siphons smooth (plate 430B) . . . . *Penitella turnerae*

— Siphonoplax heavy, laminate; callum (when present) with gap; siphons smooth (plate 430C) . . . . *Penitella fitchi*

— Siphonoplax heavy, flexible, chitinous flaps not lined with calcareous granules; siphons smooth (plates 427F, 430D) . . . . *Penitella penita*

— Siphonoplax heavy, not flexible, composed of a chitinous outer layer lined with coarse calcareous granules; callum complete (when present); siphons smooth (plates 427G, 430E) . . . . *Penitella conradi*

7. Callum in adult with gape; shell ovate; umbonal reflection only slightly appressed dorsally; siphons with conspicuous, orange, chitinous patches and warty tips that cannot be retracted into shell (plate 430F) . . . . *Chaceia ovoidea*

— Callum in adult complete (when present); shell ovate-elongate; umbonal reflection free anteriorly, appressed dorsally; siphonoplax absent; siphons pustulose (plates 427H, 430G) . . . . *Penitella richardsoni*

LIST OF SPECIES

Turner 1954–1955, Johnsonia 3: 1–160; Kennedy 1974, Mem. San Diego Soc. Nat. Hist. 8: 128 pp. (monographic treatments).

Barnea subtruncata (G. B. Sowerby I, 1834). Burrowing in mud or clay of well-protected bays. Coan et al. 2000: 497, 500; Turner 1954: 31–34.

Chaceia ovoidea (Gould, 1851). Boring into shale. Coan et al. 2000: 500, 503; Turner 1955: 66–70.

Netastoma rostratum (Valenciennes, 1846). Boring in shale at low tide and occurring offshore. Coan et al. 2000: 500, 502; Turner 1955: 143–145; Turner 1962, Mus. Comp. Zool., Occ. Papers Mollusks 2: 289–308.

Parapholas californica (Conrad, 1837). Boring into a variety of substrata from clay to rock; siphonoplax absent, instead, a thick tube ("chimney") of finely cemented particles is formed by the siphons as a result of boring activity. Coan et al. 2000: 500, 503; Turner 1955: 124–128.

Penitella conradi Valenciennes, 1846. Often found boring into such shells as *Mytilus* or *Haliotis* (forming "blister pearls" inside abalone shells); occasionally in shale or soft rock. Coan et al. 2000: 504–505; Hansen 1970, Veliger 13: 90–94 (habitat); Smith 1969, Amer. Zool. 9: 869–880 (functional morphology); Turner 1955: 75–80.

Penitella fitchi Turner, 1955. Found in rocks from the low intertidal zone to 25 m, rare. Coan et al. 2000: 504–505; Turner 1955: 71–74.

Penitella penita (Conrad, 1837). Boring into a variety of substrata from stiff clay to sandstone and cement; common. Coan et al. 2000: 505–506; Evans 1967, Veliger 10: 148–149 (ecology); Evans 1968, Ecology 49: 619–628 (growth rate); Evans 1968, Palaeogeo., Palaeoclim., Palaeoecol. 4: 271–278 (boring); Evans 1968, Proc. Malac. Soc. London 38: 111–119 (morphology); Evans 1968, Ecol. 49: 156–159 (ecology); Evans 1970, Can. J. Zool. 48: 625–627 (reproduction); Evans and LeMessurier 1972, Can. J. Zool. 50: 1251–1258 (functional morphology); Turner 1955: 80–85.

Penitella richardsoni Kennedy 1989 (=*P. gabbi*, of authors). Found along with *P. penita,* but much less common. Coan et al. 2000: 505–506; Kennedy 1989, Veliger 32: 313–319.

Penitella turnerae Evans and Fisher, 1966. In rocks, not common. Coan et al. 2000: 505, 507; Evans and Fisher 1966, Veliger 8: 222–224.

Zirfaea pilsbryi Lowe, 1931. In bays, burrowing into mud and clay. Coan et al. 2000: 500–501; MacGinitie 1935, Amer. Midl. Nat. 16: 731–735 (burrowing); Turner 1954: 58–62.

TEREDINIDAE

KEY TO TEREDINIDAE

1. Pallets with elongate blade, composed of distinct, cone-shaped segments (plates 394C 431A) . . . . . *Bankia setacea*

— Pallets not segmented 2

2. Distal half of pallet blade with dark colored periostracal cap overlapping calcareous base (plates 431B, 432A). . . . . *Lyrodus pedicellatus*

— Pallet almost entirely calcareous, periostracum covers less than half of blade (plates 431C, 432B). . . . . *Teredo navalis*

LIST OF SPECIES

All local species of shipworms occur in wood, such as wharf pilings, in bays and harbors. Because of their economic importance, there is a substantial literature. Key references include: Turner 1966, A Survey and Illustrated Catalogue of the Teredinidae (Mollusca: Bivalvia), Mus. Comp. Zool., Harvard, 265 pp.; C. L. Hill and C. A. Kofoid, eds. 1927, Marine Borers and their Relation to Marine Construction on the Pacific Coast, Final Report, San Francisco Bay Marine Piling Comm., San Francisco, 357 pp.

Bankia setacea (Tyron, 1863). Possesses external fertilization and planktonic larval stage. Coan et al. 2000: 515; Haderlie and Mellor 1973, Veliger 15: 265–286 (aspects of biology); Turner 1966: 38, 121, 248–249.

Lyrodus pedicellatus (Quatrefages, 1849). Introduced; young are retained to late veliger stage. Coan et al. 2000: 511, 513; Eckelbarger and Reish 1972, Bull. So. Calif. Acad. Sci. 71: 48–50 (self-fertilization); Turner 1966: 70–71, 116, 132–141.

Teredo navalis Linnaeus, 1758. Introduced; young are retained until veliger stage. Coan et al. 2000: 511–512; Miller et al. 1922–1924, Univ. Calif. Publ. Zool. 22 and 26: 41–80 (biology,

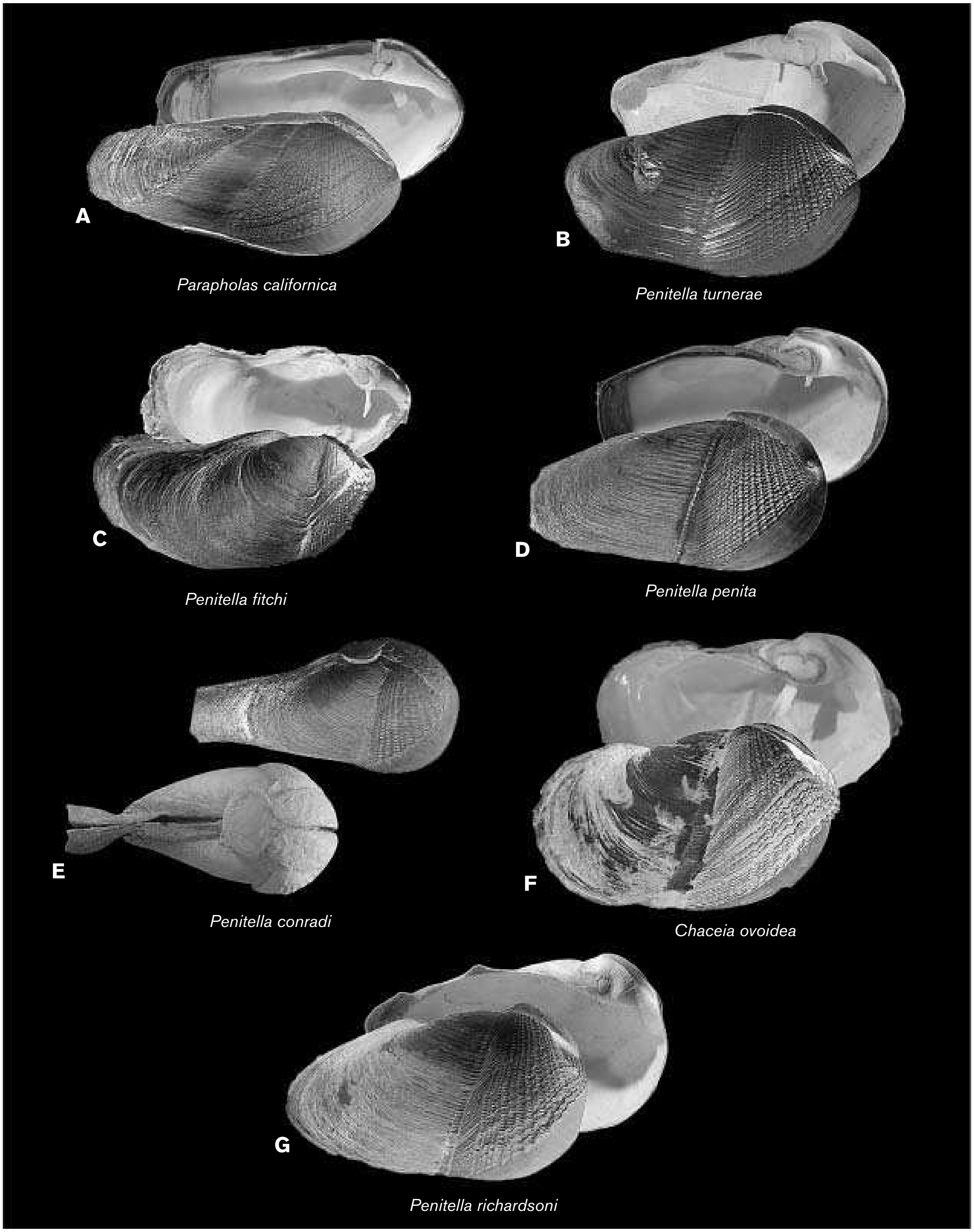

PLATE 430 A, *Parapholas californica,* length 83 mm; B, *Penitella turnerae,* length 60 mm; C, *Penitella fitchi,* length 26 mm; D, *Penitella penita,* length 50 mm; E, *Penitella conradi,* length 20 mm; F, *Chaceia ovoidea,* length 94 mm; G, *Penitella richardsoni*, length 46 mm.

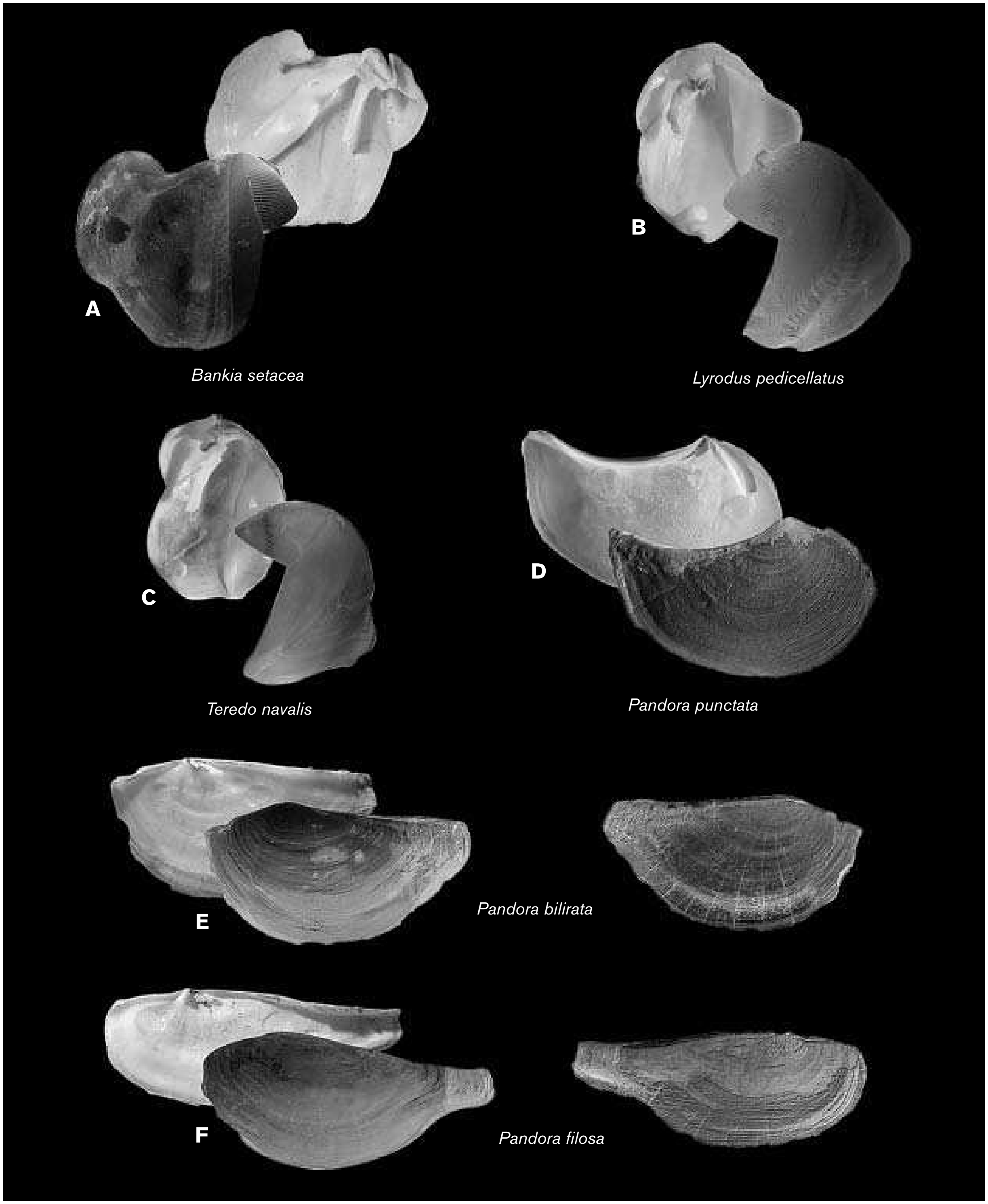

PLATE 431 A, *Bankia setacea,* length 11 mm; B, *Lyrodus pedicellatus,* length 4 mm; C, *Teredo navalis,* length 6 mm; D, *Pandora punctata,* length 42 mm; E, *Pandora bilirata,* length 12 mm; F, *Pandora filosa,* length 22 mm.

morphology, boring mechanism); Turner 1966: 112–113, 158–161.

PANDORIIDAE

This family occurs only offshore on soft sediments. The following three species may be dredged in fairly shallow water.

**Pandora punctata* Conrad, 1837 (plate 431D). Occasionally washed up on beaches. Coan et al. 2000: 520, 522.

**Pandora bilirata* Conrad, 1855 (plate 431E). Coan et al. 2000: 520, 522.

**Pandora filosa* (Carpenter, 1864) (plate 431F). Coan et al. 2000: 521–522.

* = Not in key.

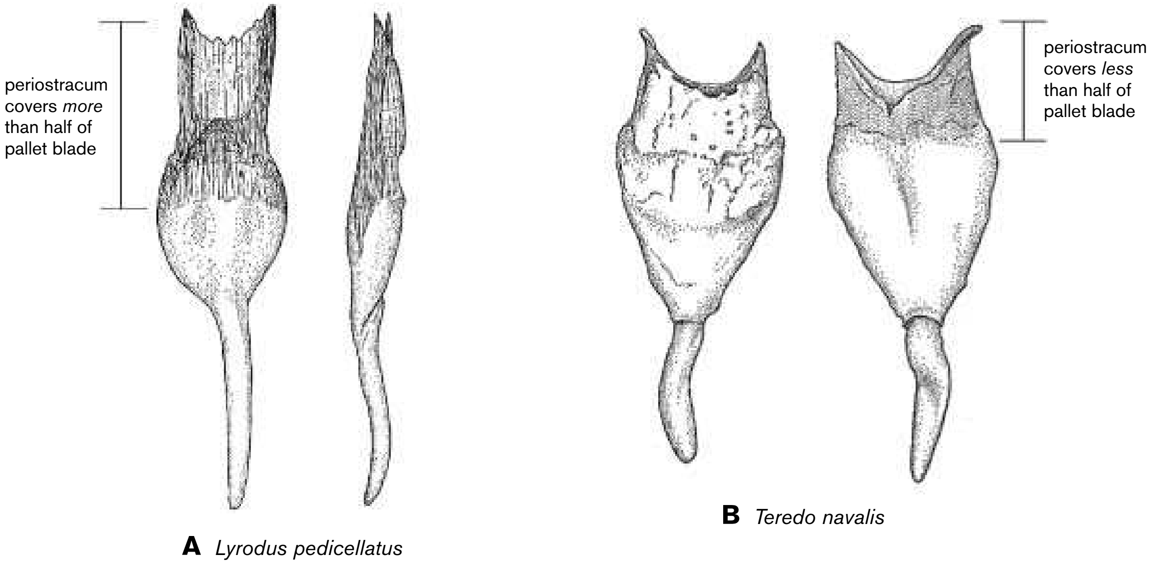

PLATE 432 A, pallets of *Lyrodus pedicellatus*; B, pallets of *Teredo navalis* (both from Turner 1966). For pallets of *Bankia*, see plate 394C.

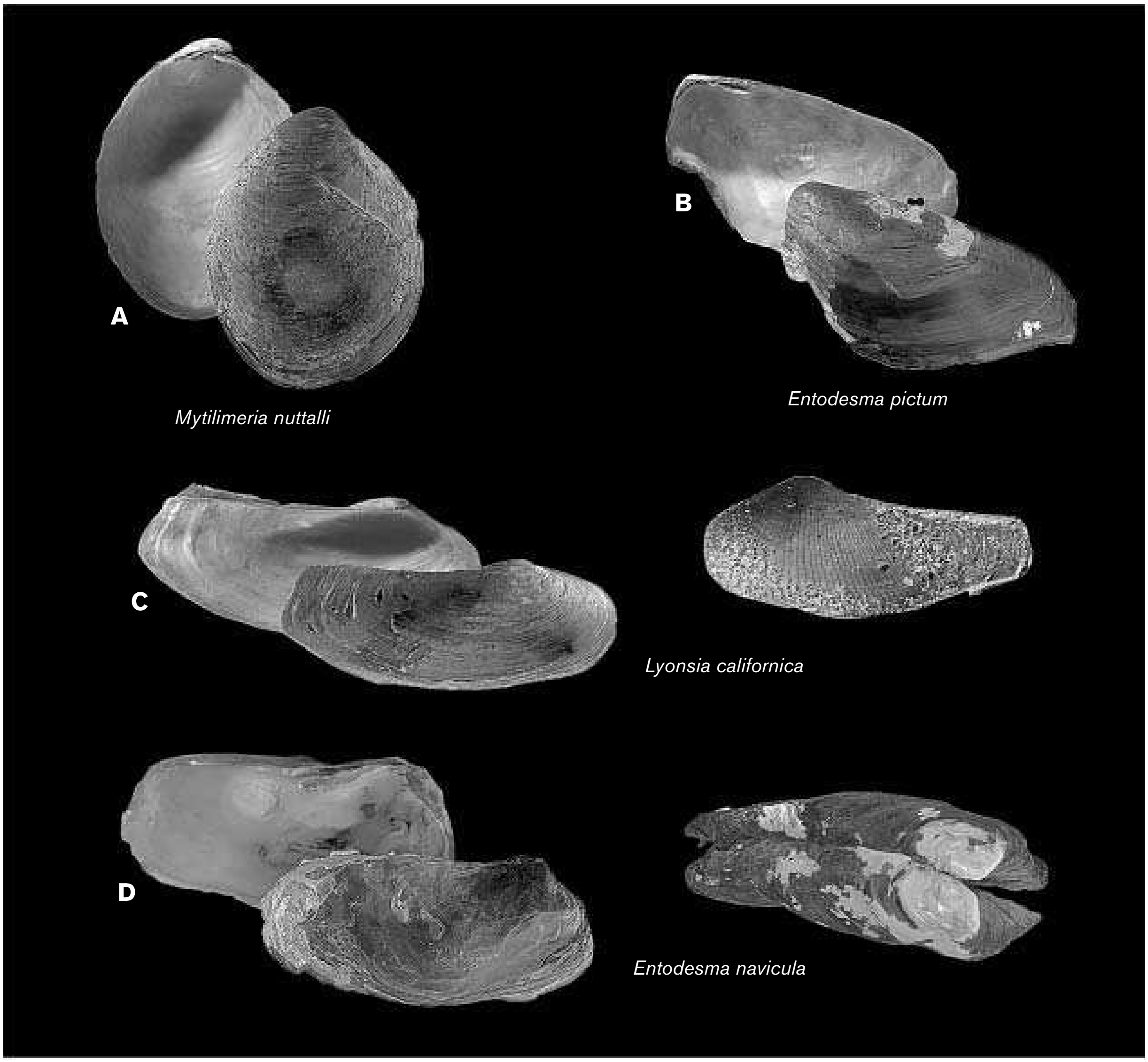

PLATE 433 A, *Mytilimeria nuttalli,* length 21 mm; B, *Entodesma pictum,* length 25 mm; C, *Lyonsia californica,* length (left pair) 32 mm, length (right valve with sand grains) 18 mm; D, *Entodesma navicula,* length (left pair) 112 mm, length (dorsal view) 80 mm.

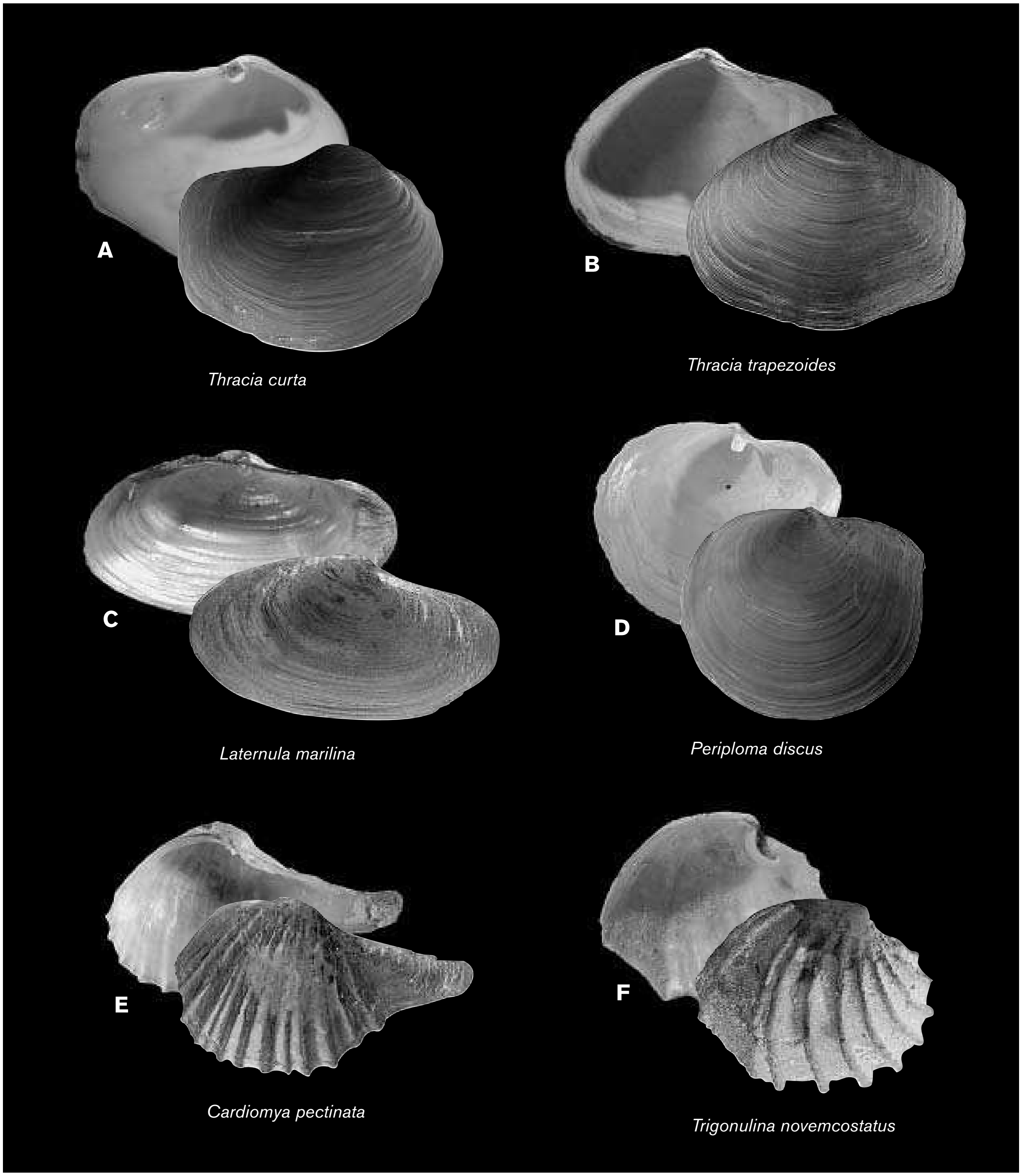

PLATE 434 A, *Thracia curta,* length 32 mm; B, *Thracia trapezoides,* length 48 mm; C, *Laternula marilina,* length 5.5 mm; D, *Periploma discus,* length 42 mm; E, *Cardiomya pectinata,* length 11 mm; F, *Trigonulina novemcostatus,* length 5 mm.

LYONSIIDAE

KEY TO LYONSIIDAE

1. Outline circular or ovate; beaks twisted; living in compound ascidians (plate 433A) .... *Mytilimeria nuttallii*
— Posterior end produced; beaks not twisted; free-living or byssally attached 2
2. Periostracum thin, striate; shell thin, elongate, pearly; in muddy substrata (plate 433C) .... *Lyonsia californica*
— Shell irregular in shape; nestling or attached to hard substrata .... *Entodesma* 3
3. Shell thick; anterior end one-third of length; periostracum heavy (plate 433D) .... *Entodesma navicula*
— Shell thin; anterior end much less than one-third of length; periostracum thin (plate 433B)........ *Entodesma pictum*

LIST OF SPECIES

Entodesma pictum (G. B. Sowerby I, 1834 (=*E. inflatum* [Conrad, 1837]). Small, lighter in color and more regular in shape than *E. navicula*; reported in sponges and compound ascidians. Coan et al. 2000: 526, 528; Morton 1987, J. Moll. Stud. 52: 139–151 (mantle).

Entodesma navicula (A. Adams and Reeve, 1850) (=*E. saxicola* Baird, 1863). Byssally attached under rocks in low intertidal, in fouling on wharf pilings. Coan et al. 2000: 526–527; Morgan and Allen 1976, Malacologia 15: 233–240 (functional morphology); Morton 1987, J. Moll. Stud. 52: 139–151 (mantle); Yonge 1952, Univ. Calif. Publ. Zool. 55: 439–450 (functional morphology); Yonge 1976, J. Moll. Stud. 42: 395–408 (ligament).

Lyonsia californica Conrad, 1837. In muddy substrata in protected areas of bays. Coan et al. 2000: 525–527; Narchi 1968, Veliger 10: 305–313 (functional morphology); Maurer 1967, Veliger 10: 72–76 (aspects of biology).

Mytilimeria nuttallii Conrad, 1837. In compound ascidians *Eudistoma* and *Distaplia* in rocky intertidal; commonly washed ashore (e.g., at Horseshoe Cove, Bodega Head) embedded in ascidians. Coan et al. 2000: 526, 528; Prezant and Carriker 1983,Veliger 24: 326–328 (lithodesma); Yonge 1952, Univ. Calif. Publ. Zool. 55: 439–450 (functional morphology).

THRACIIDAE

Thracia curta Conrad, 1837 (plate 434A). Nestling in rock crevices from the low intertidal zone to offshore. Coan et al. 2000: 533–534; Coan 1990, Veliger 33: 333–335.

**Thracia trapezoides* Conrad, 1849 (plate 434B). An offshore species on soft substrata. Coan et al. 2000: 523–533; Coan 1990, Veliger 33: 30–31.

LATERNULIDAE

Laternula marilina (Reeve, 1860) (plate 434C). Introduced from Asia in ballast water; in mud in Humboldt Bay. Coan et al. 2000: 539; Miller et al. 1999, Veliger 42: 282–284.

PERIPLOMATIDAE

**Periploma discus* Stearns, 1890 (plate 434D). Offshore on soft sediments. Coan et al. 2000: 542, 544.

CUSPIDARIIDAE

**Cardiomya pectinata* (Carpenter, 1864) (plate 434E). Offshore on soft sediments. Coan et al. 2000: 555–556.

VERTICORDIIDAE

**Trigonulina novemcostatus* (A. Adams and Reeve, 1850) (=T. *pacifica* Jung, 1996) (plate 434F). Offshore in mud. Coan et al. 2000: 563–564.

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See also general molluscan references.

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* = Not in key.

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