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CRETACEOUS APORRHAIDAE FROM CALIFORNIA: APORRHAINAE AND ARRHOGINAE

WILLIS PARKISON POPENOE[1]
Department of Earth and Space Sciences, University of California, Los Angeles 90024

ABSTRACT—Six species of aporrhaid gastropods from the California Cretaceous are described and discussed. These are: *Gymnarus manubriatus* (Gabb), the American representative of a genus widely distributed in the Indo-Pacific Cretaceous; *Arrhoges californicus* (Gabb), here referred to the subgenus *Latiala* Sohl, known widely in both Eastern and Western hemispheres in Cretaceous time; and *Pyktes* Popenoe, new genus found in Turonian beds in the Rocky Mountains and in Turonian to Maestrichtian in California. New species of *Pyktes* here described are *Pyktes daiphron* Popenoe (Turonian); *P. aspris* Popenoe (Coniacian); and *P. triphyllon* Popenoe (Santonian), which with *P. hamulus* (Gabb) are considered to form a genetic sequence. The evolutionary changes shown by this sequence include: 1) increase in apical angle producing stouter forms; 2) development of tabulation toward a biangled whorl profile; 3) progressively earlier appearance of tabulation in ontogeny; and 4) progressive onset of nodose spiral ornament on the whorl shoulder.

Gymnarus, Pyktes, Aporrhais, and *Tephlon,* new genus from South America, are grouped in the subfamily Aporrhainae. *Pugnellus, Arrhoges,* and *Latiala* are similarly grouped in the subfamily Arrhoginae. All are considered to be aporrhaid rather than strombid gastropods. Ecologically, *Arrhoges* (*Latiala*) *californicus* is probably normal marine deeper-water neritic. *Gymnarus* and *Pyktes* are probably of shallow-water, normal marine, sandy-bottom habitat.

INTRODUCTION

THIS paper is devoted to a study of the Cretaceous aporrhaid species described by William More Gabb (1864, p. 124–125, 128) as *Pugnellus, Aporrhais,* and *Arrhoges.* The species assigned to *Pugnellus* by Gabb are here referred to three different genera, and *Pugnellus* is restricted to the southeastern American-West African Cretaceous forms typified by *Strombus densatus* Conrad, 1858. Three new species are described and referred to the new genus *Pyktes,* which also includes the Gabbian species *Pugnellus hamulus.*

The geologic occurrence, geologic range, and taxonomic relations of *Aporrhais californica* (Gabb) are presented. This species is considered to belong to the genus *Arrhoges,* after Stewart, and to the subgenus *Latiala* Sohl, 1960. New information is given on the distribution and geologic range of all species and genera discussed, together with a revision of the classification of these animals.

The subfamilies Aporrhainae and Arrhoginae (new) are erected to include the species discussed here, and suggestions as to the ecology of the forms are presented.

Letter abbreviations used for the catalog and locality numbers are:

ANSP = Academy of Natural Sciences of Philadelphia
UCLA = University of California, Los Angeles
CIT = California Institute of Technology
UCBMP = University of California, Berkeley Museum of Paleontology
UCM = University of Colorado Museum
USNM = United States National Museum of Natural History

HISTORICAL REVIEW

In 1864, W. M. Gabb described, among others, three new species of California Cretaceous gastropods that he named *Pugnellus manubriatus, P. hamulus* and *Aporrhais cal-*

[1] Deceased. W. P. Popenoe sent this manuscript revising part of the family Aporrhaidae to the *Journal* shortly before his final illness. That this is only part of his proposed study of California Cretaceous aporrhaids is apparent from the omission of the genera *Anchura* and *Tessarolax.* He had carefully prepared representatives of both of these genera and evidently would have discussed them had he had the time. The manuscript has received invaluable reviewing by P. U. Rodda and N. F. Sohl. Nevertheless, it is, in all scientific respects, essentially as Popenoe wrote it. We wish to thank LouElla Saul for a very large investment of her time in shepherding the manuscript through the review process.—the Editors.

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ifornica. The genus *Pugnellus* had been established by T. A. Conrad (1860, p. 284) to include four species: *Strombus densatus* Conrad, 1858; *S. uncatus* Forbes, 1846; *S. contortus* Sowerby, 1846; and an undescribed South American species later named *Pugnellus tumidus* by Gabb (1860, p. 197). These four species would now be placed in as many different genera—*S. densatus* in *Pugnellus, S. uncatus* in *Arrhoges* (*Latiala*), *S. contortus* in *Gymnarus,* and *Pugnellus tumidus* in *Tephlon* (new genus, this paper). Conrad did not designate type-species for his new genus—an omission that was partly remedied by Gabb (1877, p. 298) who named *Pugnellus typicus* as type of *Pugnellus* by subsequent designation. *P. typicus* has been determined by Sohl (1960, p. 112) to be a very large example of *P. densatus* (Conrad) which is now generally accepted to be the type of *Pugnellus,* and which has almost universally been put in the Strombidae.

Since Conrad's and Gabb's time, new species from many different parts of the world have been referred to *Pugnellus,* which has thus been considered to be of practically cosmopolitan distribution with geologic range throughout the later Cretaceous.

Gabb (1868, p. 139) proposed the subgenus *Gymnarus* to accommodate *Pugnellus manubriatus* on the basis that 1) the anterior canal of that species is straight—an inference that has since proved untrue; 2) that the shell has a hooklike process on the posterior outer lip—a character that is present in many genera and hence is not distinctive; and 3) that the shell is only partially covered by callus in the adult stages—a character that represents a growth stage. However, *Gymnarus* has other definitive characters that Gabb did not mention. It is here treated as a a separate full genus widely dispersed in both space and time.

Later authors have generally accepted the placement of *P. manubriatus* and *P. hamulus* as valid species under *Pugnellus,* and some have even considered *Pugnellus* and *Gymnarus* to be exact synonyms (Fischer, 1887, p. 670; Zittel, 1881–85, p. 259; Cossmann, 1904, p. 36; Wenz, 1940, p. 940). R. B. Stewart (1927, p. 358) placed both species in the Struthiolariidae and recognized *P. manubriatus* as type of the subgenus *Gymnarus.* Anderson (1958, p. 157) and Sohl (1960, p. 115) have followed this classification but have referred the two species to the Strombidae.

SUMMARY OF CONCLUSIONS

In the following study, I have had available excellent examples of *P. manubriatus* and *P. hamulus* from collections at U.C.L.A., and *P. fusiformis* from the Codell Sandstone Member of the Carlile Shale of Colorado; of *Pugnellus densatus* from the Ripleyan (Maestrichtian) of the southeastern United States; and of *Pugnellus tumidus* Gabb from the Quiriquina beds of coastal Chile. Study of this material has indicated differences in these species that justify the taxonomic changes proposed below.

1) "*Pugnellus*" *manubriatus* Gabb and "*Pugnellus*" *hamulus* Gabb cannot be included in the genus *Pugnellus* Conrad, 1860, but represent two distinct genera, not closely related to *Pugnellus,* which with two exceptions have not been recognized outside of the Indo-Pacific faunal area.

2) "*Pugnellus*" *manubriatus* Gabb is referred to the genus *Gymnarus* Gabb, originally proposed as a new subgenus of *Pugnellus* but here raised to generic rank. Species tentatively referred to *Gymnarus* are found in beds of the Indo-Pacific region from California to South Africa, and in time from Cenomanian to Maestrichtian. With one dubious exception from a deep well core in Mississippi (Stephenson, 1947, p. 183 and pl. 33, figs. 25–32), it has not been found elsewhere in the globe.

3) "*Pugnellus*" *hamulus* Gabb does not belong in the genera *Pugnellus* Conrad, *Gymnarus* Gabb, or *Conchothyra* Hutton, to which it has been referred at one time or another. *P. hamulus* is here referred to the new genus *Pyktes,* in which are placed three new West Coast Cretaceous species: *P. daiphron* (Turonian); *P. aspris* (Coniacian); and *P. triphyllon* (Santonian). "*Pugnellus*" *fusiformis* (Meek) from the Codell Sandstone Member of the Carlile Formation (Turonian) is also a *Pyktes.* "*Pugnellus*" *tumidus* Gabb from the west South American Quiriquina beds of Chile (Gabb, 1860, p. 197, pl. 3, figs. 13, 14) is a probably closely related but distinct new genus here named *Tephlon* (Figure 5G, H). The geologic range of *Pyktes* as at present

known is from Turonian to Maestrichtian. It has not as yet been reported from the eastern United States or from Europe.

4) The genera *Gymnarus, Pyktes, Aporrhais* and *Tephlon* show considerable similarity to one another in certain persistent structural features that are lacking or transitory in nearly all other described Cretaceous aporrhaid genera. They are here placed in the subfamily Aporrhainae Gabb, 1868, which is placed in the family Aporrhaidae.

5) The genus *Pugnellus* Conrad is not found in the Pacific Coast Cretaceous beds, but occurs in the Cretaceous of the southeastern United States, in Mexico, and probably in western Africa. It is not closely related to *Gymnarus* and *Pyktes,* but is closely related to *Arrhoges,* with which it is included in the new aporrhaid subfamily Arrhoginae.

6) The genus *Arrhoges,* subgenus *Latiala* Sohl, 1960, is present in Turonian beds of the Pacific Coast, where it is represented by *Arrhoges californicus* (Gabb).

ACKNOWLEDGMENTS

The study of later Cretaceous formations and faunas of the Pacific Coast, of which this report is a small part, has been supported by grants-in-aid from the Penrose fund of the Geological Society of America, from the National Science Foundation, and from research funds of the Academic Senate, University of California, Los Angeles campus. In preparation of this report, I have been greatly aided by Takeo Susuki, Senior Museum Paleontologist, U.C.L.A., who has prepared the photographic illustrations and has expertly prepared a part of the Cretaceous collections for detailed study. LouElla Saul, Senior Museum Paleontologist, U.C.L.A., has helped at all stages of the work with discussions of the systematic and ecologic problems involved and with aid in the location of pertinent references. The charts and maps included in the report were skillfully prepared by Julie Guenther and Vicki Doyle-Jones. I have benefitted from the loan of essential comparative material by Norman Sohl, U.S. Geological Survey; Judith van Couvering, University of Colorado Geology Museum; Joseph Peck, Museum of Paleontology, Berkeley, California; Peter Rodda, California Academy of Sciences; Michael A. Murphy, University of California, Riverside campus; and Daniel Frassinetti, Museo Nacional de Historia Natural, Santiago, Chile. Robert Drachuk, Huntington Beach, California, collected the fine specimen of *Pyktes daiphron* illustrated here, and presented it to the paleontological collections of the University of California. The land owners of the regions I have visited have been uniformly kind in giving me access to their property and permission to collect there. I greatly appreciate the effective aid I have had from these sources.

SOURCE OF THE MATERIAL STUDIED

The Pacific Coast specimens studied are derived almost entirely from localities along the borders of the Sacramento and San Joaquin valleys in California; from the Hornbrook Formation, Siskiyou County, California and from the Ashland-Medford region, Oregon; from the valley of Chico Creek, Butte County; from the Asuncion Formation, Santa Lucia Range, San Luis Obispo and Monterey counties; from the Moreno Formation, east slope of the Diablo Range; and from the Santa Ana Mountains, Orange and Riverside counties, California. The fossils are found in medium-to-coarse grained sandstone, in places almost conglomeratic, and in finer grained sandy silt or silty sand.

Gymnarus manubriatus occurs commonly in great numbers in Turonian strata cropping out in the valley of Churn Creek, north of Redding, and in the valley of Little Cow Creek, northeast of Redding; in the Hornbrook Formation of Sisikiyou County, California, and in the vicinity of Ashland, Josephine County, Oregon; and in isolated outcrops on the west side of the Sacramento Valley, as far south as Carquinez Strait. Strangely, it has not been found in the Turonian beds of the Santa Ana Mountains, southern California. In Little Cow Creek Valley, northeast of Redding, the species is represented locally by phenomenal numbers of individuals which literally compose beds of rock five or six inches thick that extend for distances of hundreds of yards along the line of outcrop. *Gymnarus manubriatus* appears to be confined to beds of middle-to-late Turonian age, being associated in northern California and southern Oregon with the ammonite *Tragodesmoceras ashlandicum* (Anderson) and *Subprionocyclus* spp.

Pyktes daiphron n. sp. is represented by less

than one dozen individuals from the Turonian Baker Canyon Member of the Ladd Formation, Santa Ana Mountains, and by about 100 questionably identified and dwarfed specimens from an inexactly described locality in southern Oregon ("four miles from Ashland"). Nearly all of the specimens in this latter lot are imperfect, dwarfed, or represented by internal molds. Two or three specimens from the Santa Ana Mountains are well-preserved and are figured here. The species occurs in finer grained matrix than is usual with the later species of this genus, and may represent a different habitat.

P. aspris n. sp. is found sporadically but locally abundant in Oak Run Valley, 15 mi east of Redding. The principal occurrence is in a coarse sandy lens with associated pebbles in the midst of Member IV (Popenoe, 1943), where it is associated with the ammonite *Peroniceras shastense* Anderson and hence is probably Coniacian in age. The species has also been found in the Ponderosa Way Member, Chico Formation, in Chico Creek, California by L. R. Saul (1959, p. 125–126) where it ranges from 200–670 ft above the base of the Cretaceous beds.

P. triphyllon n. sp. is found at Redding in a sandstone member (Member V of Popenoe, 1943) cropping out on the south side of Oak Run Valley and in sandstones of probably the same age in Clover Creek, Old Cow Creek, and South Cow Creek valleys to the south. It also has been found in the "Musty Buck Member," Chico Formation, Chico Creek, by L. R. Saul (1959, p. 127). Its age is probably early Santonian.

P. hamulus (Gabb) is widely distributed in beds of the "Moreno Formation" (Maestrichtian) cropping out on the eastward slopes of the Diablo Range, and in the Asuncion Formation, valley of the Nacimiento River, Monterey and San Luis Obispo counties, California. In general, individuals of the species are not abundant locally and the specimens are poorly preserved, though widespread. The matrix enclosing the shells is commonly firmly cemented, and the shell material is recrystallized, making extraction difficult.

Arrhoges (*Latiala*) *californicus* is found in fine-grained muddy sandstone or siltstone beds of Turonian age cropping out in the Redding region (Members II–III), Shasta County, and in the Baker Canyon Sandstone Member of the Ladd Formation, Santa Ana Mountains, Orange and Riverside counties. In the two northern occurrences it is found in the same sections as *Gymnarus manubriatus* but not in the same beds. In the Santa Ana Mountains it is found in the same beds with *Pyktes daiphron.* Murphy and Rodda (1960) identified *Arrhoges californicus* in Cenomanian and early Turonian parts of the Budden Canyon Formation of the Bald Hills area, southwestern Shasta County. Most of these specimens have slightly coarser ribbing on the spire than do those of later Turonian age.

Figure 1 lists the localities, stratigraphy, and position in the Cretaceous sections of the aporrhaid species described in this paper. Additional stratigraphic information may be found in the following sources: column A, Siskiyou Mountains, Peck, Imlay and Popenoe (1956); column B, Redding area, Murphy, Peterson and Rodda (1964), Popenoe (1943) and Jones, Sliter and Popenoe (1978); column C, Chico Creek, Saul (1959) and Matsumoto (1960); column D, Martinez Weaver (1949); column E, the Diablo Range, Matsumoto (1960) and Page (1966); column F, Santa Lucia Range, Taliaferro (1944) and Howell and Vedder (1978); and column G, Santa Ana Mountains, Popenoe (1942) and Schoellhamer et al. (1981).

GROWTH CHARACTERS OF APORRHAID GASTROPODS

Aporrhaid gastropods are peculiar in their shell-secreting habits in the adult stage. Adolescent shell growth in these groups is generally similar to that found in the majority of Streptoneura; it takes place by shell deposition around the entire margin of the aperture, is spiral in pattern, and shows growthlines and other sculptural elements resulting from variation in shell deposition in time, in place, or in both, producing patterns that are axial, spiral, or a combination of the two. With cessation of spiral growth—a stage that is interpreted as the beginning of maturity (Fretter and Graham, 1962, p. 65)—the shell develops a thickened and expanded outer lip modified by various lateral outgrowth from the labral margin, and by basal sinuses similar to those found in *Aporrhais.* The labral modifications may take the form of spines, hooks, knobs, and fan-like or bolster-like ex-

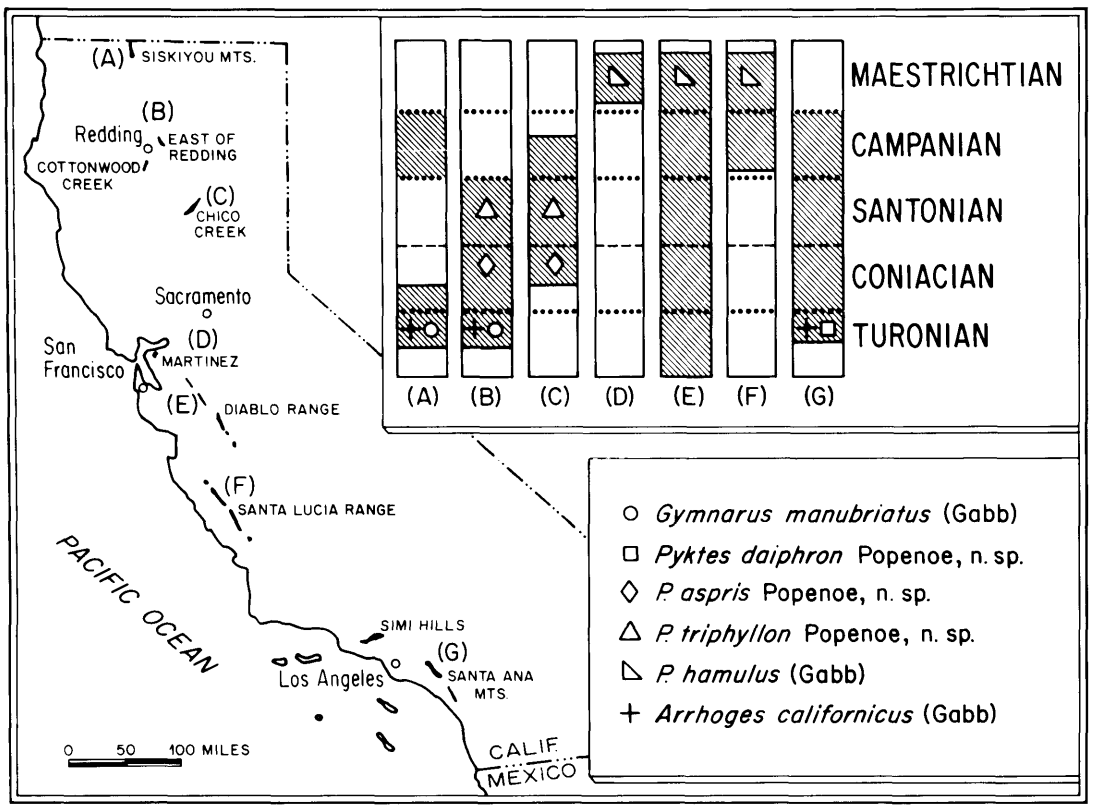


FIGURE 1—Sketch map of California showing location of Cretaceous sections, their stratigraphic content, and the approximate horizons of aporrhaid occurrences.

tensions, usually grooved internally by canals that probably served as incurrent and/or excurrent waterways to or from the mantle chamber. For convenience, the stage during which shell growth is spiral will be called adolescent; the stage during which the snail begins and finishes formation of the terminal outer lip will be called the young-adult stage. This latter stage was apparently short in time for the transition from the unornamented and thin outer lip to completion of the labral outgrowths takes only about one-third of a whorl. Immediately following the end of the young-adult stage, the mantle may spread over the margin of the aperture in all directions, progressively depositing callus over the surface of the helicocone (=coiled cone of the young-adult shell), obscuring the adolescent sculpture, filling in the lateral and anterior canals, capping the apex, and modifying spire and labral margin to ultimately form a smooth, bulbous, more-or-less amorphous and irregularly protuberant surface of the shell. This stage of callus deposition over the previously formed shell will be called the late-adult stage. The abapertural shoulder of the last whorl is apparently the last part of the shell submerged by the mantle and is the least obscured by the callus layer, for here a small area is visible in which the larger features of the adolescent and young-adult sculpture can be seen. The net effect of the callus deposit is to obscure or hide adolescent features of taxonomic importance and to produce bizarre specimens that are superficially similar. It has been possible in the present study to find late-adolescent and young-adult specimens in good condition showing the sculpture of the helicocone, and these have aided in working out the generic and specific relationships. Unfortunately, most of the extant diagnoses and descriptions of Cretaceous aporrhaids have been based upon study of the characters of the late-adult, callus-covered shell. Thus, any attempt to place described species in their proper relationships

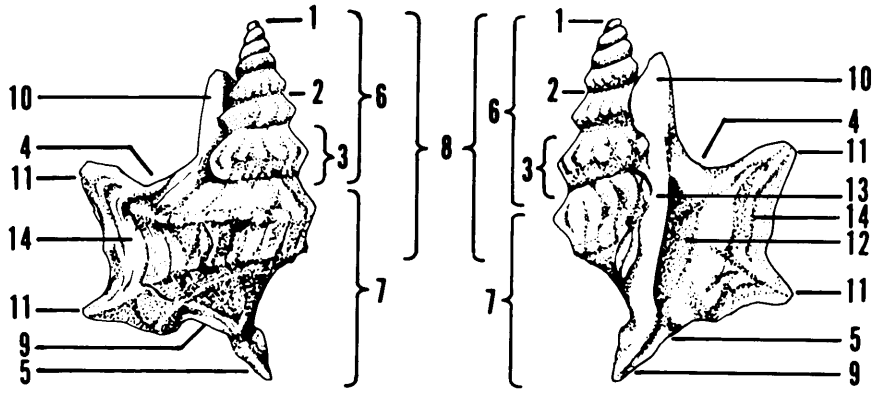


FIGURE 2—*Aporrhais pespelicani* (Linnaeus). Sketch of the shell (UCLA 59078) showing the location and character of the detailed parts. 1, apex; 2, whorl suture; 3, whorl; 4, posterior sinus; 5, anterior sinus; 6, spire; 7, last whorl; 8, helicocone; 9, rostrum and anterior process; 10, posterior labral process; 11, lateral labral processes; 12, aperture; 13, inner lip; 14, outer lip or labrum.

and taxonomic divisions is hampered from the beginning by ignorance of the shell ontogeny.

C. M. Yonge (1937, p. 687–703) showed the importance in living *Aporrhais* of two sinuses in the outer lip, one just anterior to the posterior part of the lip, the other just posterior to the anterior end of the lip. These two sinuses serve as the bases of sand tubes built to the surface when the animal is buried in the substrate and are important in directing currents of water entering anteriorly through the mantle cavity and exiting posteriorly; they probably serve similar functions when the animal is crawling about on the sea-bottom. Each sand tube extends from its corresponding sinus in the snail's shell to the sea bottom, thus forming channels by which the animal can circulate water through its mantle cavity while buried.

The author recently examined a considerable number of specimens of different aporrhaid species in the fossil collections of the Academy of Natural Sciences of Philadelphia and the United States National Museum of Natural History, and a few smaller museums, with the uniform result that these specimens showed the two sinuses on the outer lip, suggesting that these structures are largely or even generally features of the aporrhaid shell.

The posterior sinus is usually by far the larger, and is thus more easily seen; it is concave aperturally and anteriorly and has an invariably thickened border. In this, it is somewhat similar to the struthiolariids, the strombids, and a few other related groups. The anterior sinus, conversely, is generally smaller and shallower, but may be distinguished by a different structure of the shell on either side. This distinction may be indicated by a greater shell thickness, smoother surface because of a thin deposit of callus, coarsening of the lamination at the shell-edge, outward turning of the shell edge, difference in the profile of the shell edge, or by being bounded on one or both ends by a small, low knob or tubercle. The two sinuses taken together form a character that is distinctive of the Aporrhaidae.

Additional characters equally distinctive but less easily visible are that the basal profile is concave in its columellar part, and that the layer on the inner lip extends considerably farther to the left than it does on the parietal part of the shell. Neither of these characters shows well in figures of the shell; therefore, their presence must be corroborated by examination of actual specimens. I am indebted to LouElla Saul for calling my attention to these last two characters.

Figure 2 shows the parts of the aporrhaid shell as used in this paper, exemplified by Recent *Aporrhais*.

CLASSIFICATION

The classification of the fossil Aporrhaidae and in particular the question whether a given form should be placed in Aporrhaidae or

Strombidae is one that has troubled systematists for more than one hundred years. Some workers believe the two families to be related groups diverging from a common stem probably in Mid-Cretaceous time. This view was expressed by Wenz (1940, p. 928) and has many current adherents. An alternative hypothesis is that Aporrhaidae and Strombidae represent unrelated stocks that have developed certain rather superficially similar features through convergent evolution. This view is stated by Davies (1935, p. 263) and more nearly represents my own opinion; however, some of Davies' criteria for separation of the two families appear not to do so. In mature strombids, there is present in most genera a distinct notch or sulcus developed in the outer lip above the base of the shell. This so-called "stromboid notch" serves as a kind of peep-hole for the right eye (Abbott, 1960, p. 09-831). A somewhat similar notch, generally broader and shallower and adjacent to the rostrum, is present in nearly all aporrhaid genera. Yonge (1937, p. 691) showed that this notch serves as the proximal opening to a mucus-cemented sand tube leading from the water-matrix interface to the mantle cavity of the animal when it is buried in the bottom sediment and which serves to conduct a current of water into the mantle cavity. The function of this notch, then, is completely different from that of the stromboid notch and probably denotes no relationship.

Conrad (1860, p. 330), without explanation, placed his new genus *Pugnellus* in the Strombidae. Most subsequent authors have accepted this placement without giving reasons for such acceptance. Cossmann (1904, p. 37) indeed referred to the "double sinuosité basale" in *Pugnellus* as indicating a morphological position for the genus between *Dientomocheilus* and *Rimella* in his taxonomic table of the Strombidae (Cossmann, 1904, p. 4), but this double basal sinuosity occurs not in an example of *Pugnellus densatus* (Conrad), type-species of the genus, but in an example of "*Pugnellus*" *hamulus* Gabb from California, supplied to him by T. W. Stanton of the United States Geological Survey. Furthermore, Cossmann placed *Gymnarus* Gabb, which has no "double sinuosité basale" in exact synonymy with *Pugnellus*. The "double sinuosité basale" can scarcely be other than the true basal sinuosity of *Pyktes* ("*Pugnellus*") *hamulus* plus the labral interval between the anterior and posterior projections on the outer lip of *Pyktes*, shown in Figure 5D–F. These "sinuosities" have no functional or structural relationship to one another, but their appearance, altered by a thick callus covering, doubtless gave rise to Stewart's (1927, p. 358) observation that "this species (*P. hamulus* is closely related to *Conchothyra tumida* (Gabb) from the Cretaceous of Peru, *but has a sinus in the outer lip* (italics mine) which is absent in that species."

"*Pugnellus*" *hamulus* Gabb has been treated in nearly every citation as a valid species of *Pugnellus*, and has been listed by authors as a representative species of the genus (see the synonymy of *P. hamulus* in this paper, particularly the exhaustive discussion by Cossmann). Stewart (1927, p. 358), to be sure, referred "*P.*" *hamulus* to *Conchothyra* McCoy in Hutton, 1877, family Struthiolariidae. Reasons for disregarding this placement are given by Olsson (1944, p. 93), and by Sohl (1960, p. 111) and are accepted here.

The classification offered here differs considerably from those used by previous workers. *Gymnarus, Pyktes,* and *Pugnellus* have usually been placed in the family Strombidae. This placement seems inadmissible, for these genera differ markedly from undoubted fossil strombids. *Gymnarus* and *Pyktes,* stripped of their calcareous surcoats are very close to *Aporrhais*; and *Pugnellus,* while only distantly allied with *Aporrhais,* is closely related to *Arrhoges* Gabb. This confusion arises in part from the habit of these Cretaceous genera of secreting a thick layer of callus over the entire shell, thus hiding features of systematic value. The dead hand of the past is also apparent in the classification. Conrad (1860) classified *Pugnellus* as a strombid, which appeared reasonable to those who came after and who were more concerned in citing the genera in fossil check-lists than in revising them.

The genera discussed in this paper are all considered to be members of the family Aporrhaidae. Two subfamilies are recognized—Aporrhainae and Arrhoginae. The Aporrhainae includes the genera *Aporrhais, Pyktes, Gymnarus* and the new genus of Chilean fossils, *Tephlon,* for "*Pugnellus*" *tumidus* Gabb (Figure 5G, H). The second subfamily, Arrhoginae, contains the Recent and fossil

members of the genus *Arrhoges,* s.l.; *Pugnellus* of the southeastern North American and West African Cretaceous faunas; and possibly the Indian species *Pugnellus uncatus* (Forbes), described by Stoliczka (1867, p. 22, Pl. III, figs. 9–11). This latter species while probably neither *Arrhoges* nor *Pugnellus* appears to be related to both and is hence a member of the same subfamily.

Aporrhais, the only living genus of the Aporrhainae, is represented in the Recent seas by the two northeastern Atlantic species *A. pespelicani* (Linnaeus) and *A. serresiana* (Michaud, 1828). The latter is considered only a variant of the former by some authors, but Yonge (1937, p. 698) has given good reasons to consider it as a separate species. *A. pespelicani* is the type-species of *Aporrhais,* and most of the characters hereafter quoted as being distinctive of the genus are taken from studies of this species.

A. pespelicani is a spindle-shaped shell with seven or eight noded tabulate whorls in the adult. The outer lip of the last whorl is greatly expanded and bears four extensions or prongs that extend beyond the general margin of the lip. One prong extends posteriorly along the spire of the shell and is affixed thereto except for the distal tip which is generally but not always free. The second and third prongs terminate laterally upon the labrum. The fourth extends anteriorly to form the rostrum. All prongs are primarily channeled internally, the anterior one possibly for an incoming current of water, the two lateral (?) and the posterior prongs for outgoing currents. The two lateral prongs are directly continuous with two prominent ridges on the last whorl, while a third, less prominent ridge immediately anterior to them is developed but usually without an extension in the form of a prong. Secondary ornamentation consists of fine, regular, close-set spiral riblets covering the entire external surface of the shell, numbering about 20 between the posterior external lateral ridge and the adjacent last whorl suture. Increase of riblets upon the mature, expanded labrum takes place by intercalation and by development of wider interspaces separating the riblets.

On the proximal part of the rostrum the callus deposit of the inner lip is folded back to the left, viewed from the aperture, over the wall of the rostrum.

The growth line of *Aporrhais* is broadly and rather deeply concave posteriorly with the apex of concavity situated between the two posterior whorl ridges. This concavity ends at the middle ridge of the last whorl; anterior to this, the growth line is nearly straight or very broadly convex aperturally to the anterior tip of the shell.

If the species listed above that are ranked in the Aporrhainae, be compared to Recent *Aporrhais,* these similarities are apparent: all have rostra that are bent in the middle with distal ends directed ventrally; all have a short, spine-like projection on the shoulder of the last whorl bent or curved with the tip pointing posteriorly; all have concave profiles at the base of the last whorl; all have well-marked posterior and anterior sinuses on the outer lip; three of the four genera have tabulate whorls with spiral ornamentation dominant. *Gymnarus* differs from the remainder of the genera placed in the Aporrhainae in having a deep, narrow anterior labral sinus and axial sculpture. This genus appears to be present over much of the Indo-Pacific Cretaceous faunal province. It may belong to an unrecognized subfamily of Aporrhaidae.

Recent *Arrhoges,* fossil *Arrhoges* subgenus *Latiala,* and *Pugnellus* are strikingly similar (see Figure 6D–I) as exemplified by the general form and sculpture of the three species, *Arrhoges occidentalis* (Beck), *A. californicus* Gabb and *Pugnellus densatus* Conrad. The differences between the two species of *Arrhoges* include shape of the outer lip, caliber of the spire whorls, comparative length of rostrum, and comparative length of axial ribs. In the fossil form, *A. (Latiala)* has a more quadrate shape and straighter lateral edge of the lip; the whorls have coarser ribbing, shorter in relation to the last whorl; the rostra are comparatively longer, and the whorls more tabulate. These differences are the basis for establishing the subgenus *Latiala* Sohl, 1960.

Resemblances between *Arrhoges* and *Pugnellus* are less obvious; but comparison between the two, especially the late-adolescent stages, shows that the relationship is close indeed. It is only in the late-adult stage of *Pugnellus* when the snail puts on its callus overcoat that the similarity with *Arrhoges* is obscured.

Sculptural features common to both genera

Maestrichtian *Pyktes—P. aspris, P. triphyllon* and *P. hamulus*—in coarser-grained sandstone with occasional pebble-beds in association with a fauna in which *Calva* is rare and *Cymbophora* is dominant. Such beds probably accumulated in a near-shore, normal marine, inner sublittoral location just below low-tide mark.

Arrhoges (*Latiala*) *californicus* (Gabb) and *P. daiphron* are found in muddy, fine-grained sandstone similar to the Frazier Silt Member (Jones, Sliter and Popenoe, 1978) of the Redding Turonian and similar beds elsewhere. Accumulation of such sediments probably took place in quieter water than did those containing *Gymnarus* and later *Pyktes*, whether because of protected environment or of deeper water remains uncertain.

SYSTEMATIC PALEONTOLOGY

Phylum MOLLUSCA Linnaeus, 1758
Class GASTROPODA Cuvier, 1797
Order MESOGASTROPODA Thiele, 1927
Family APORRHAIDAE Morch, 1852

Alate gastropods with immature whorls normally spirally coiled, last whorl with alate outer lip with margins commonly drawn out into finger-like, wing-like or bolster-like extensions; columella projected into a rostrum, more or less long, grooved, usually along right-front side; usually two labral sinuses situated at opposite proximal margins of outer lip; anterior part of basal shell concave in profile, covered with a thickened callus extending a considerable distance to left of columella viewed from aperture; sculpture commonly spiral with noded ribs along whorl shoulder, but less frequently with axial threads, bands or ribs; smooth or nodose; aperture small, narrow, without tubercles or folds.

Subfamily APORRHAINAE Gabb, 1868

Aporrhaid gastropods with (always ?) a prominent bent projection on outer lip whorl shoulder, usually bent medially with distal top posteriorly directed; additional labral projections developed in some genera; columella bent in middle, distal end directed ventrally; labral sinuses well developed; spire more or less high, whorl shape commonly convex, inflated.

The Aporrhainae include the genera *Aporrhais* da Costa, 1778; *Gymnarus* Gabb, 1868; *Pyktes* and *Tephlon* Popenoe, this paper.

Genus GYMNARUS Gabb, 1868

Type species.—*Pugnellus manubriatus* (Gabb), 1864 by monotypy.

Discussion.—Species which appear to be referable to *Gymnarus* are found in the Indo-Pacific Cretaceous in beds from Cenomanian to Maestrichtian ages, inclusive; and Stephenson (1947, p. 183) has described a new species from a deep well in Mississippi which may belong to this genus. In the Pacific Coast region of North America, *Gymnarus* is known only from the Turonian. The species from outside of the latter region more or less confidently referred to *Gymnarus* include: "*Pugnellus*" (*Gymnarus*) *yabei* Nagao; Cenomanian, Japan; (Nagao, 1939, p. 226, pl. 20, figs. 1–8). "*Strombus*" *contortus* Sowerby; ?Turonian, South India; (Stoliczka, 1867, p. 19, pl. 3, figs. 1–5). "*Pugnellus*" *granuliferus* Stoliczka; ?Turonian, South India; (Stoliczka, 1867, p. 21, pl. 3, figs. 6–8). "*Pugnellus*" *calcaris* Stephenson; ?Coniacian, Mississippi, USA; (Stevenson, 1947, p. 183, pl. 33, figs. 25–32). "*Pugnellus*" *auriculatus* Woods; Senonian, South Africa; (Woods, 1906, p. 319, pl. 38, fig. 15). "*Pugnellus*" *fraasi* Harbort; ?Campanian–?Maestrichtian, Kamerun, W. Africa; (Riedel, 1932, p. 96, pl. 19, figs. 1, 1a, 2–5; pl. 20, figs. 5, 7–8; pl. 21, figs. 7, 7a–c).

GYMNARUS MANUBRIATUS (Gabb, 1864)
Figure 4A–E

Pugnellus manubriatus GABB, 1864, p. 126, Pl. 29, fig. 229; GABB, 1868, p. 139, Pl. 13, figs. 4–5; TRYON, 1883, p. 190, Pl. 60, fig. 73; COSSMANN, 1904, p. 37; STEWART, 1927, p. 358, Pl. XX, figs. 10–12; ANDERSON, 1958, p. 167; SOHL, 1960, p. 112, 115.

Gymnarus manubriatus (Gabb). JONES, SLITER AND POPENOE, 1978, Pl. 1, fig. 11.

Description.—Shell of medium size with average height of 35 mm in adult, subfusiform in adolescent stages, with shape greatly modified in post-adolescence by callus deposition; helicocone shell material thin, fragile; spire of shell usually of six whorls, low, convex, twice as wide as high; first three whorls (nuclear ?) smooth; fourth whorl finely cancellate with about 25 fine axial lirae crossed by nine or ten fine revolving lirae which are suppressed on later whorls; fifth and sixth whorls showing increase in thickness and separation of axial sculpture which

develops into ribs, strong and almost nodose at suture; suture linear and impressed; whorl profile just anterior to suture narrowly tabulate; last whorl pyriform, bulbous and inflated in parietal part, rapidly narrowing with concave profile into thin and narrow anterior canal (rostrum ?) which is bent in a smooth ventrally directed curve in adolescent shells but modified in later adult stages by callus deposition into an almost right angle; last whorl ornamented by sigmoid axial ribbing, coarse posteriorly, diminishing anteriorly and disappearing at about midheight of whorl which is smooth below except for growth-lines; growth line slightly antecurrent at suture, thence proceeding in a broad curve concave aperturally to greatest diameter of whorl where lines turn forward in a broad curve convex aperturally which straightens out essentially parallel to columellar axis, thus to bend in the anterior canal; apertural margin thickened markedly at end of immature stage of helicocone, concave aperturally between suture and beginning of a lateral spur developed just below maximum diameter of body whorl; lateral spur broad proximally, narrowing distally and at about half-length bent so as to point posteriorly, externally thickened marginally, depressed medially, triangular in cross-section, grooved by a narrow canal on internal face; margin of outer lip thickened below (anterior) to spur and just before bend in anterior canal flexed into a deep U-shaped sinus; deposit of callus at beginning of mature stage immediately following development of lateral labral spur and anterior aporrahid notch, for very few specimens show these structures without callus deposition. Deposition beginning along apertural margins, extending over apertural face of entire shell from apex to columellar tip, filling in grooves of anterior and spur canals, and ultimately extending over exterior of shell from both inner and outer lips, meeting in a longitudinal line on abapertural part of body whorl. In earlier stages of callus deposition, about two-thirds of external surface of shell commonly covered; in advanced adult shells, whole shell sometimes thus "plastered" with smooth callus, generally thinnest along posterior part of abapertural part of body whorl between suture and greatest diameter of shell; this portion of shell seldom so deeply covered that coarser sculpture is not visible; interior surface of aperture without folds, teeth, or tubercles.

Lectotype.—ANSP 4278.

Paratypes.—ANSP 52488a, 52488b.

Hypotype.—UCLA 58439.

Dimensions of lectotype.—Height, 24.0 mm; diameter of last whorl, 11.3 mm; diameter including spur (incomplete) 20.5 mm.

Dimensions of hypotype.—(UCLA 58439) height, 33.2 mm; maximum diameter of last whorl, 16.0 mm; diameter including spur, 23.0 mm.

Type locality.—"Cottonwood Creek, Siskiyou County," California, (Gabb, 1864, p. 125; Stewart, 1927, p. 359).

Distribution.—Eastern foothills of the Coast Ranges north of Curry Canyon to Redding, Shasta County, California; Cretaceous of Little Cow Creek Valley and minor exposures north of Redding in Churn Creek Valley; beds of Hornbrook Formation in Siskiyou County, extending from the vicinity of Montague, north and west along the west side of Cottonwood Creek, Siskiyou County, across the Oregon line to the vicinity of Ashland, Jackson County, Oregon.

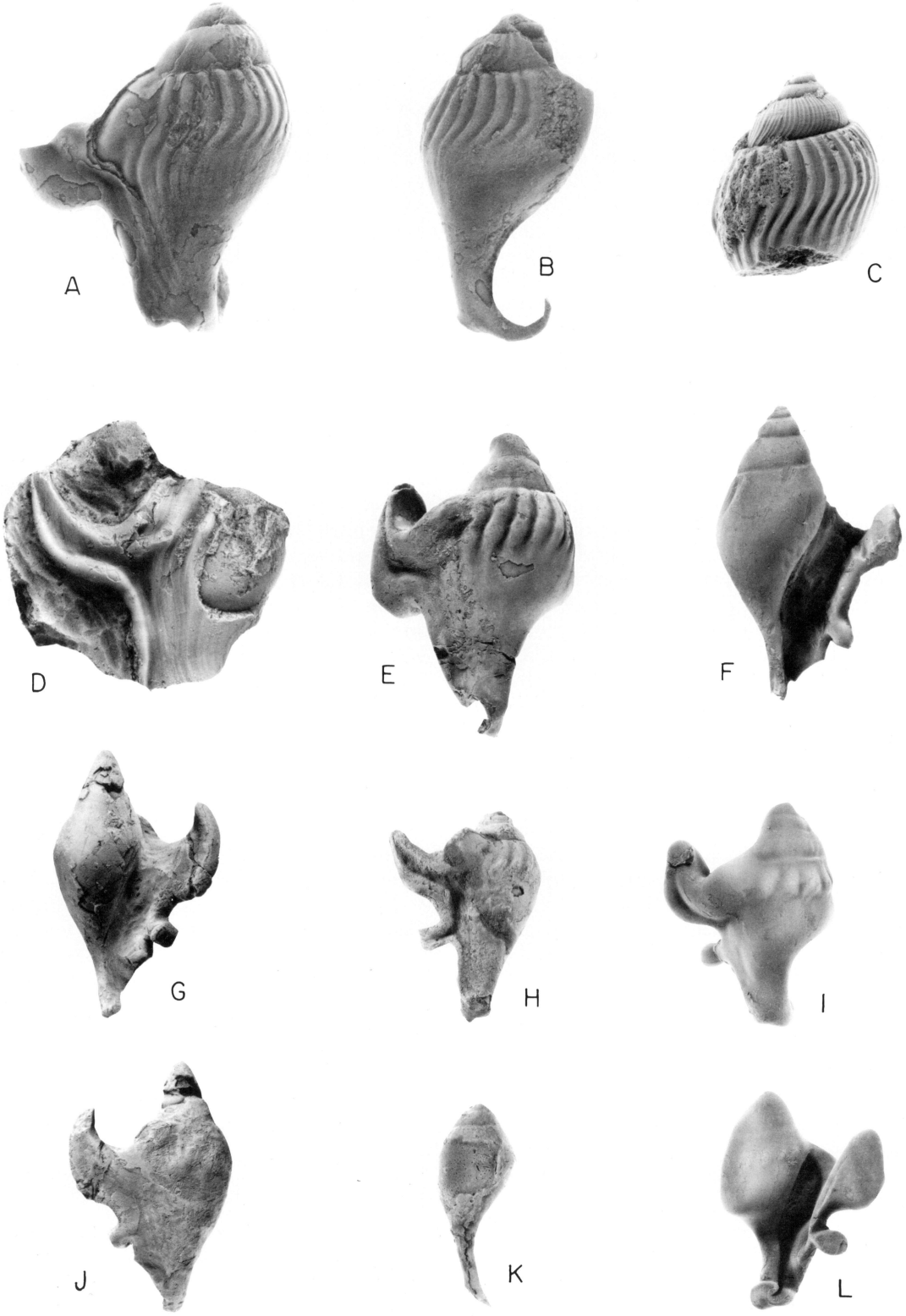
Geologic age.—Middle to upper Turonian; found below and in association with the horizon of *Tragodesmoceras ashlandicum* (Anderson) to the top of the section in Little Cow Creek Valley, where it is associated with *Subprionocyclus normalis* (Anderson).

Genus PYKTES n. gen.

Type species.—*Pyktes aspris* n. sp.

Diagnosis.—Aporrhaid gastropods with two labral projections: one posterior, situated posterior to whorl periphery, broad and laterally directed proximally, bent posteriorly in the middle; anterior projection short, spatulate or plug-like, situated about midway between posterior projection and anterior end of last whorl; anterior sulcus of labrum broad and low; shell covered with callus in the adult; sculpture primitively nearly smooth, to markedly spiral, strongest on whorl shoulder.

Discussion.—*Pyktes* resembles *Gymnarus* Gabb in the general shape of the shell, the bent anterior canal (or rostrum), the shape and placement of the posterior labral spur, the posterior labral sinus, development of an anterior labral sinus, and in the habit of covering the adolescent shell with a layer of callus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in the adult stage. It differs from *Gymnarus* in developing an anterior plug-like or spatulate projection on the outer lip, in having dominantly spiral rather than axial sculpture, in having its anterior labral sinus broad and shallow, and in its more or less tabulate later whorls in the adult rather than evenly convex. These differences, together with the long range of the group in time, justify considering *Pyktes* as a full genus related to *Gymnarus,* but distinct from it. The resemblances of the two genera and their marked differences from other genera of Aporrhaids are acknowledged by placing them in the subfamily Aporrhainae.

Pyktes is represented in the California Cretaceous by four species: *P. daiphron* n. sp., Turonian; *P. aspris* n. sp., type-species of the genus, Coniacian; *P. triphyllon* n. sp., Santonian; *P. hamulus* (Gabb), Maestrichtian. "*Pugnellus*" *fusiformis* (Meek) (Figure 4H, K) from the Codell Sandstone Member of the Carlile Shale (Kauffman and Pope, 1961) of the Western Interior Cretaceous is a *Pyktes*; "*Pugnellus*" *tumidus* Gabb (Figure 5G, H) from the Cretaceous Quiriquina beds of Chile (Wilckens, 1904) is a closely related form, but as it lacks the anterior lip digitation is probably at least generically distinct from the species named above. It is herein assigned to the new genus *Tephlon.*

Specimens of the genus *Pyktes* have so far been found in California in rocks of ages from Turonian to Maestrichtian. Arranged in order of geologic age, inferred evolutionary changes in the character of the helicocone include alterations in the growth-line, outline, ornamentation and apical angle.

In two previous papers (Popenoe, 1957; Saul and Popenoe, 1962), I have pointed out that other members of the Pacific Coast Cretaceous molluscan faunas show similar evidence of gradual serial change; examination of numerous bivalves and gastropods not yet described in detail suggests that this is a phenomenon of fairly common occurrence.

Turonian examples of *Pyktes* are at present known from only a few specimens, but enough material is at hand to indicate the earliest known characters of the genus. *P. diaphron* is characterized by a relatively slender shell with apical angle of about 45°, an unornamented spire relative to all later members of the genus, a last whorl showing adjacent to the aperture four or five more pronounced transverse ridges agreeing in trend with the growth-line and which are continued with accentuated curvature upon the outer lip.

P. aspris of the succeeding Coniacian beds includes individuals of somewhat greater average size, with wider apical angle, with penultimate whorls showing a beginning of tab-

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FIGURE 4—All figures printed at height of 5–6 cm to facilitate comparison of common features. *A–E, Gymnarus manubriatus* (Gabb, 1868), Turonian. *A–D,* from "Cottonwood Creek," Siskiyou Co., Calif. *A, B,* lectotype, ANSP 4278. Height 24.0 mm; diameter with hook 20.8 mm; diameter of last whorl 11.4 mm. *A,* dorsal or abapertural view; *B,* lateral view showing profile, sculpture, and callus covering on lower half of base. *C, D,* paralectotypes. *C,* ANSP 52488a, fragment of shell showing protoconch and sculpture of early whorls. Height (incomplete) 15.7 mm; diameter without labrum 14.4 mm. *D,* ANSP 52488b, fragment showing shape and sculpture of lateral hook before callus deposition. *E,* hypotype, UCLA 58439 from CIT loc. 1197, Stinking Creek, Shasta Co., Calif. Height 33.6 mm; diameter of shell including hook 23.5 mm; diameter of last whorl 16.4 mm. Complete advanced-adult specimen showing dorsal sculpture, anterior sulcus and callus covering of shell except for dorsal posterior. *F, G, J, Pyktes daiphron* Popenoe n. gen., n. sp., Turonian. *F,* paratype, UCLA 59048 from CIT loc. 92, Harding Canyon, Santa Ana Mts., Orange Co., Calif. Height 14.0 mm; diameter including hook 14.0 mm; diameter of last whorl 9.5 mm. Apertural view showing small size, slender profile and smooth sculpture of the species. *G, J,* holotype, UCLA 59047 from CIT loc. 1164, Silverado Canyon, Santa Ana Mts., Orange Co., California. Height 38.8 mm; diameter with hook 24.9 mm; diameter of last whorl 20.8 mm. Apertural and abapertural views to show mature callus-covered form. *H, K, Pyktes fusiformis* (Meek, 1877), Turonian. Hypotypes, from Huerfano Park area, southern Colorado. *H,* UCM 29919. Height 31.0 mm; diameter including hook 23.9 mm; diameter of body whorl 14.2 mm? *K,* UCM 29928. *I, L, Pyktes aspris* Popenoe n. gen., n. sp., type species. Holotype, UCLA 59050 from UCLA loc. 4104, Oak Run Valley, Millville Quad., Shasta Co., Calif., Coniacian. Height 33.6 mm; diameter including hook 25.2 mm; diameter of last whorl 12.5 mm. Abapertural views to show general adult features.

ulation on the whorl shoulder adjacent to the posterior suture and of a spiral row of nodes developed upon the shoulder. The nodes number about 16 on the last whorl; the earlier whorls are smooth. The apical angle is about 50°.

P. triphyllon from the early Santonian strata shows an increase in the sculptural trends noted in *P. aspris*. The nodes on the whorl shoulder number about 20 on the last whorl, and are developed on the spire whorls to the protoconch; this is indeed the easiest way to descriminate *P. triphyllon* from *P. aspris*. The nodes are relatively smaller. The apical angle is about 50°. There is little change in the shape of the shell.

Campanian *Pyktes* are known from meager numbers of specimens and from questionably dated strata. Two localities that have been dated as uppermost Campanian or earliest Maestrichtian have yielded one specimen each, and in neither is the specimen well enough preserved to permit confidence about specific characters. One of these localities is in the vicinity of Carlsbad, near Oceanside; the other is from Pigeon Point, situated along the Pacific Coast about half-way between San Francisco Bay and Santa Cruz. The fauna from the Pigeon Point locality appears to be uppermost Campanian; the Carlsbad locality suggests probably the early Maestrichtian. Fossiliferous Campanian beds of the California region are generally of finer grained sediment than are the beds both earlier and later and may thus be of deeper water or at least quieter water origin than the coarser grained sediments containing *Pyktes*. *Pyktes* is known from Santonian strata underlying the Campanian and from overlying Maestrichtian beds. It seems probable that better representatives of the genus may yet be found in coarser grained Campanian beds in California.

P. hamulus, from Maestrichtian strata, represents the known culmination of the evolution of the genus. It is distinctly shouldered to the protoconch whorls, and its shoulder is ornamented by about 30 nodes—the greatest number of nodes present on any species. *P. hamulus* has also the widest apical angle.

The growth-line of *Pyktes* is fairly uniform throughout its range. It is practically normal to the suture posteriorly; from suture to periphery it is essentially straight and normal or gently concave aperturally; at the whorl periphery or slightly posterior to it, the growth-line passes into a broad curve convex aperturally to the anterior tip of the rostrum.

In summary, evolution in the genus *Pyktes* proceeds in the direction of increase of apical angle, tabulation of the whorls, earlier appearance of tabulation in ontogeny, and development of nodose spiral ornament on the whorl shoulder with at first smooth development of the geologically oldest whorls, followed by few and coarse nodules on the last whorl, then smaller and more numerous nodules in geologically younger forms, with spiral lirae appearing on the last whorl in the Maestrichtian.

Derivation of the generic name.—*Pyktes,* Greek, a boxer or pugilist.

PYKTES ASPRIS n. sp.
Figures 4I, L; 5J, L

Description.—Shell of medium size, usually 35 mm or less in height, with general characters of genus; shell material thin; helicocone consisting of six spire whorls and last whorl; protoconch of three smooth, regularly convex whorls about twice as broad as high; fourth to sixth whorls with obtuse bend in profile at about mid-height, and a sculpture of fine, close-set spiral lines on earlier whorl, becoming coarser and fewer with shell growth, and most strongly developed on posterior suture and periphery of whorl; axial sculpture of low, opisthocline, obscure, rather widely spaced riblets on earlier whorl, developing into distinct thickened welts extending from suture to periphery of last whorl, where these welts tend to become nodose; base of shell broadly convex posteriorly (parietally), nearly straight in profile viewed aperturally, without ornamentation except for irregularly and widely spaced, low, obscure spiral bands; posterior suture of earlier whorls situated above (posterior to) shell periphery, but advancing anteriorly with succeeding whorls, lying anterior to the periphery on penultimate and ultimate whorls; earlier sutures linear, later ones channeled; spiral angle, about 55°; growth-line nearly normal to suture posterior to shoulder, thence swinging forward (aperture-ward) in a broadly convex curve nearly to anterior tip of shell.

Holotype.—UCLA 59050.

Paratypes.—UCLA 59051, 59052.

Dimensions of holotype.—Height 33.6 mm; diameter including hook 25.2 mm; diameter of last whorl 12.5 mm.

Type locality.—UCLA locality no. 4104, ¼ mile north of the Oak Run Road opposite the Hathaway House, Oak Run Valley, Millville Quadrangle, Shasta County, California.

Distribution.—Member IV of Popenoe (1943), Redding area, Tehama County; lower 700′ of the section at Chico Creek, Butte Co. (Saul, 1960, p. 1527; Saul, 1959, p. 126); boulder in conglomerate, Panoche Fm., Garza Peak, Fresno Co., California.

Age.—Coniacian, associated with *Peroniceras* sp.

Discussion.—*Pyktes aspris* is confined in its occurrence to the coarser clastic beds of the Redding and Chico Creek Cretaceous areas, and is abundant in these localities. The individuals found in these prolific occurrences are generally advanced adults, and it is rare that one finds any adolescent specimens among them. Two or three fortunate finds have supplied all that we know of the earlier growth stages of this species. The nearly complete and well-preserved paratype (UCLA 59051) is the best of these. This pronounced segregation of specimens into adult callus-covered and adolescent non-callused individuals suggests a change of habitat at this ontogenetic boundary. This is the stage of formation of the outer lip with its characteristic labral processes and sinuses; for a brief period, the labral processes housed canals, inferred to be excurrent. Both growth stages are associated with assemblages of other fossils that do not show a similar segregation. Reasoning from the fact that immature specimens are thin-shelled, and that the adult specimens are robust because of their callus surcoats, it is suggested that the immature forms developed in deeper or quieter water and migrated into shallower and more turbulent habitats at maturity, and that the added bulk and structural strength of the mature forms was an adjustment to this change. Some support for this idea is found in the fact that some of the most prolific assemblages of adults occur in coarse, pebbly sandstone interlayered with pebble beds in the basal beds of transgressing seas. No modern analogues of the callus covering of *Pyktes* (and *Gymnarus*) are known in present day faunas; the controlling factors, therefore, are conjectural.

P. aspris has a wider apical angle than do *P. daiphron* and *P. triphyllon,* but narrower than does *P. hamulus.* It has a more angulate whorl profile than that of *P. daiphron.* The shoulder nodes of *P. aspris* are stronger than those of *P. daiphron* and *P. triphyllon* and more elongate than those of *P. hamulus.*

Derivation of the specific name.—*Aspris,* Greek, a type of oak, from Oak Run.

PYKTES DAIPHRON n. sp.
Figure 4F, G, J

Description.—Shell with general characters of genus, relatively small, with maximum height of adult shell generally less than 30 mm; spiral angle narrow, about 45–50°; spire consisting of four (?) smooth, gently convex whorls, somewhat wider than high, but increasing in relative height anteriorly; last whorl about ¾ the height of shell, regularly convex parietally, rostrally concave in profile viewed aperturally, ventrally curved distally; aperture elongate, narrow, oblique to shell axis; axial sculpture of spire whorls of growth-lines only, of last whorl of growth-lines for about first ¾ of whorl; last quarter of last whorl ornamented between suture and periphery by three to five strongly opisthocline, gently aperturally concave ribs, highest, widest, and somewhat angulate at periphery, fading out abruptly toward rostrum, more gradually posteriorly toward suture which they meet at nearly a right angle; a very faint sculpture of spiral lirae discernible on some spire whorls.

Holotype.—UCLA 59047.

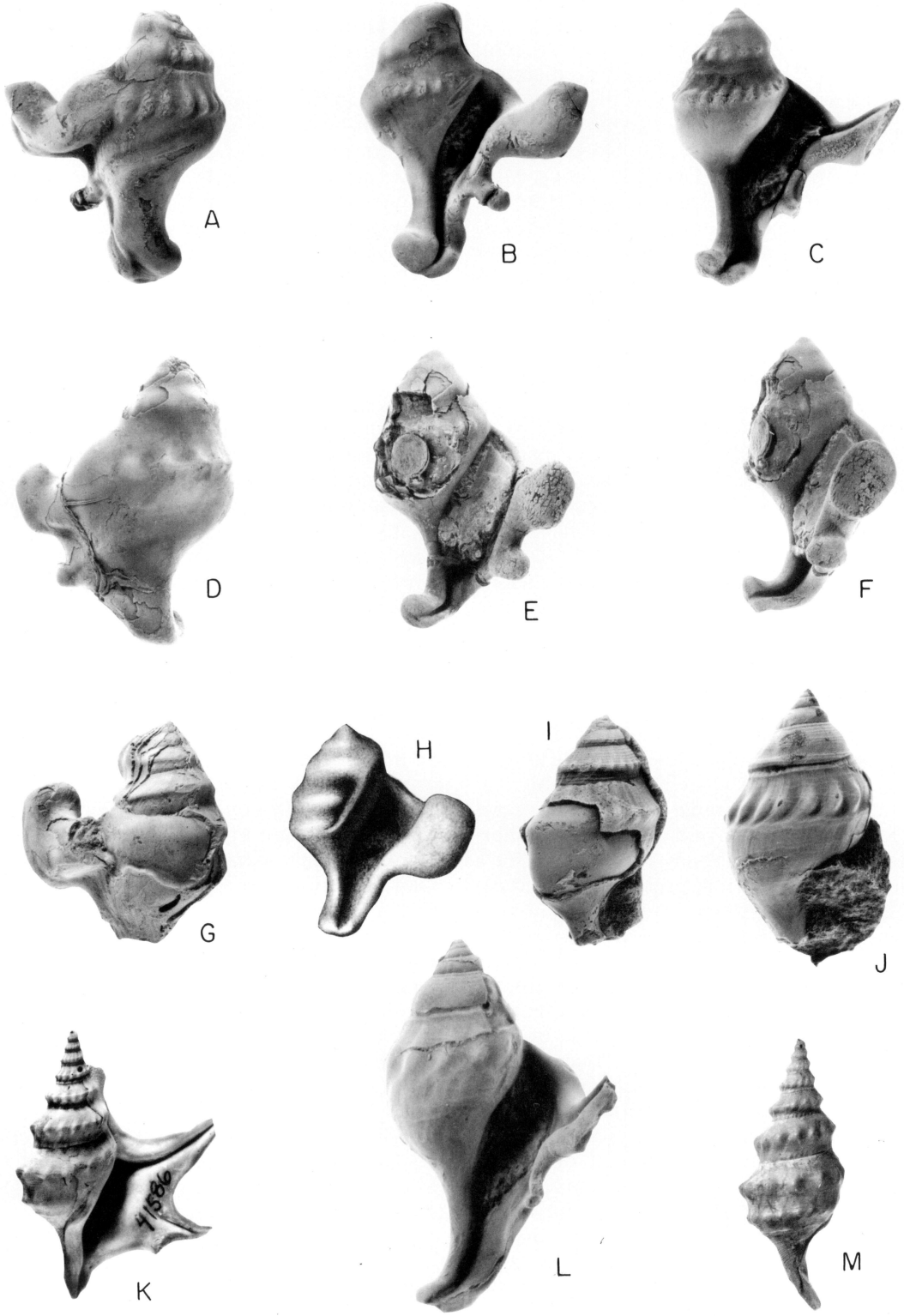
Paratype.—UCLA 59048.

Dimensions of the holotype.—Height 38.8 mm; diameter, including labral processes 24.9 mm; diameter at right angles to labral processes 20.9 mm.

Dimensions of paratype.—UCLA 59048; height 14.0 mm; diameter, including labral processes, 14.5 mm; diameter at right angle to labral processes 9.4 mm.

Type locality.—CIT loc. 1164: Silverado Canyon, El Toro Quadrangle, Santa Ana Mountains, Orange Co., Calif.

Distribution.—Hornbrook Fm., Jackson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Co., Oregon; Ladd Fm., lower Holz Shale Member, Orange Co., Calif.

Age.—Late Turonian—associated with *Subprionocyclus* spp.

Discussion.—*Pyktes daiphron* is distinguished among species of the new genus principally by its meager axial ornamentation, its relatively narrow and straight-sided spire, and its age, earliest of the known species of *Pyktes.* The specimens from Oregon appear to be slightly wider in apical angle than do those from southern California, but lack of well-preserved specimens leaves this comparison imprecise. *P. daiphron* resembles "*Pugnellus*" *fusiformis* (Meek) more nearly than do any other of the Pacific Coast species of *Pyktes,* the most obvious difference being that the rostrum of "*P.*" *fusiformis* is somewhat less strongly bent than are those of the California species; also, the "transverse costae" on the shoulder of "*P.*" *fusiformis,* mentioned by Stanton (1893, p. 149) are more numerous, irregular, and prominent than are those of *P. daiphron.*

Derivation of specific name.—*Daiphron,* Greek, warlike.

PYKTES TRIPHYLLON n. sp.
Figure 5A–C

Description.—Shell with general characters of genus, of medium-to-small size, with maximum height of adults about 32 mm, although most specimens at hand considerably shorter. Apical angle of helicocone about 45–50°. Shell consisting of six whorls; first three, probably representing the protoconch, smooth, convex, about twice as wide as high; fourth to sixth whorls rather strongly shouldered at a level about one-third height of whorl from anterior suture; whorl surface anterior to shoulder approximately parallel with shell axis; posterior to shoulder whorl, profile forming broad sloping ramp expanding anteriorly and at an angle of about 30° to shell axis; fourth and fifth whorls ornamented by seven or eight fine, revolving lines between shoulder and posterior suture, and by narrow sinuous peaked ridges aligned with growth lines, most prominent along whorl shoulder, becoming coarser and larger approaching shell maturity, numbering about 20 on last whorl. Growth-line of last whorl retrocurrent at suture, thence trending in a broad curve convex

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FIGURE 5—All figures printed at height of 5–6 cm to facilitate comparison of common features. *A–C, Pyktes triphyllon* Popenoe n. gen., n. sp., UCLA loc. 4106, Upper Clover Creek, Millville Quad., Shasta Co., Calif., Santonian. *A, B,* Holotype, UCLA 59053. Height 29.3 mm; diameter including hook 24.0 mm; diameter of last whorl 13.3 mm. Apertural and abapertural views to show semitabulate spire, noded whorls, and broad termiantion of rostrum. *C,* paratype, UCLA 59054. Height 30.1 mm; diameter of last whorl including hook 24.2 mm; diameter of last whorl 13.0 mm. Early-mature specimen showing character of noded whorls below nucleus. *D–F, I Pyktes hamulus* (Gabb, 1864), hypotypes. *D–F,* UCLA 59056 from CIT loc. 1572, Laguna Seca Quad., Merced Co., Calif., Maestrichtian. Height 42.3 mm; diameter including hook 32.2 mm; diameter of last whorl ca. 19.4 mm. Three views to show general features of shell. *I,* UCLA 59055 from UCLA loc. 3314, Deer Valley, Antioch South Quad., Contra Costa Co., Calif., Maestrichtian. Height (incomplete) 33.8 mm; diameter including hook ca. 31.2 mm; diameter of last whorl (incomplete) ca. 19.7 mm. Broken specimen to show strongly tabulate spire, small and numerous tubercles on whorl shoulder, and character of fine revolving sculpture. *G, H, Tephlon tumidus* (Gabb, 1860). *G,* plastohypotype, UCLA 58323 cast of specimen from Quiriquina Island, Chile, Maestrichtian. Height (incomplete) 32.7 mm; diameter of last whorl including hook 30.6 mm; diameter of last whorl (incomplete) 19.4 mm. Broken specimen showing the actual form of the hook and the tabulate spire. *H,* reproduction of illustration of hypotype (Wilckens, 1904, pl. 18, fig. 2b) from Quiriquina Island, Chile, Maestrichtian. Height 37 mm; diameter including outer lip (Wilckens) 27 mm. Showing characters of complete shell. *J, L, Pyktes aspris* Popenoe n. sp., paratypes. *J,* UCLA 59052 from CIT loc. 1225, north side of Oak Run Valley, Shasta Co., Calif., Coniacian. Fragment of specimen showing character of whorls and noding of shoulder of last whorl. *L,* UCLA 59051 from UCLA loc. 4104, ¼ mi north of Hathaway ranch house, Oak Run Valley, Shasta Co., Calif., Coniacian. Height 27.4 mm; diameter including hook (broken) 21.9 mm; diameter of last whorl 11.5 mm. Early-mature specimen showing nature of helicocone and noded shoulder of last whorl. *K, M, Aporrhais pespelicani* (Linnaeus, 1766). Hypotype, UCLA 41586 from Mediterranean Sea, Recent. Height 40.4 mm; diameter including hooks 34.0 mm; diameter of last whorl 14.5 mm. *K,* apertural view; *M,* lateral view showing curvature of rostrum.

aperturally, most prominent approximately opposite anterior labral plug, thence trending adapically to rostral tip. A spiral belt of extra-thick callus applied in advanced-adult stage to outer surface of helicocone at base of parietal area, giving a squarish profile to shell.

Holotype.—UCLA 59053.

Paratype.—UCLA 59054.

Dimensions of the holotype.—Height 29.3 mm; diameter including hook 24.0 mm; diameter of last whorl 13.3 mm.

Dimensions of paratype.—UCLA 59054; height 30.1 mm; diameter at right angles to posterior hook 13.3 mm; including posterior hook 24.2 mm.

Type locality.—UCLA loc. 4106, Member VI, north side Clover Creek Valley, 2,200 ft. W of NE corner sec. 23, T32N, R2W, Millville (1953) Quad., Shasta Co., Calif.

Distribution.—Member VI, Clover Creek, Old Cow Creek, and South Cow Creek valleys of the Redding area, Tehama Co; approx. 340–500 m above the base of the Chico Fm., Chico Creek, Butte Co., Calif.

Age.—Santonian.

Discussion.—*Pyktes triphyllon* has presently been recognized in two general regions on the east side of the Sacramento Valley: first from a number of localities in Clover Creek, Old Cow Creek, and South Cow Creek valleys; second from two localities in the "Musty Buck Member," Chico Formation, canyon of Chico Creek, Butte County (Saul, 1959, p. 126–127). Several hundred adolescent specimens at UCLA loc. 3618 were obtained by Saul from a single nodule jutting from the cliff face. Nearly all these specimens show the shape and characteristic shouldered profile well, but the surface layers of shell have been so leached that fine features of surface sculpture are lost. *P. triphyllon* is very similar to *P. aspris* from which it differs in having a narrower spiral angle and narrower colabral ridges which form finer nodes on the shoulder. *P. aspris* has a narrower apical angle and fewer nodes than has *P. hamulus.*

Derivation of specific name.—*Triphyllon,* Greek, trefoil, or clover, from Clover Creek.

PYKTES HAMULUS (Gabb, 1864)
Figure 5D–F, I

Pugnellus hamulus GABB, 1864, p. 124, Pl. 18, fig. 48, Pl. 20, fig. 81; GABB, 1868, p. 139, Pl. 13, figs. 1–3; GABB, 1869, p. 162, 225, Pl. 27, figs. 42–42a; TRYON, 1883, p. 190, Pl. 60, figs. 71–72; COSSMANN, 1904, p. 37, Pl. 7, fig. 3.

Conchothyra hamula (Gabb). STEWART, 1927, p. 358, Pl. 20, figs. 6–7.

Pugnellus (Gymnarus) hamulus Gabb. ANDERSON, 1958, p. 168.

Description.—Shell with general characters of genus, comparatively large with maximum height of studied material ca. 42 mm; spire consisting of six whorls, first three representing protoconch, low, smooth, regularly convex, approximately twice as wide as high; fourth whorl conspicuously ornamented with 9–10 narrow revolving lirae separated by interspaces twice as wide as lirae and showing beginning of a faint shoulder to whorl about one-third of whorl height above posterior suture; fifth and sixth whorls increasing in height relative to diameter and becoming more strongly shouldered in accordance with development of small close-set subconical nodes on whorl shoulder; nodes becoming larger, more widely spaced, and fewer with growth of shell, about 30 on penultimate whorl; spiral ornamentation conspicuous on spire whorls but decreasing anteriorly and becoming more widely-spaced and nearly obsolete on last whorl; spiral angle about 70°; parietal profile of last whorl nearly straight below shoulder and parallel with shell axis but indented below shoulder by a shallow revolving sulcus.

Holotype.—UCBMP 31395 (Stewart, 1927, p. 358).

Dimensions of holotype.—Height 39.3 mm; diameter 30.5 mm.

Type locality.—"Martinez" (Stewart, 1927), Contra Costa Co., Calif.

Distribution.—Great Valley Series, near Martinez and Mount Diablo, Contra Costa Co.; Moreno Fm., north and south of Garzas Creek, Merced and Stanislaus cos., Asuncion Fm., north side of Lake Nacimiento, San Luis Obispo Co., Calif.

Discussion.—The material at hand in this study consists of about 25 specimens from the Cretaceous beds south of Martinez, and in Deer Valley, about seven mi south of Antioch, Antioch South Quadrangle, Contra Costa County; at various localities in the Moreno Formation on the west slope of the Diablo Range as far south as Los Baños, Merced County; and in the Asuncion Group, Nacimiento River drainage, Monterey and

San Luis Obispo counties. Practically all of the study material is poorly preserved and fragmental. Details of the helicocone sculpture are obtained from a single incomplete specimen in which details of the spire sculpture have been revealed by peeling off the callus layer.

P. hamulus is distinctly shouldered to the protoconch whorls, is slightly constricted just anterior to the shoulder, has a spiral row of about 30 small and short nodes on the shoulder, and the last whorl is ornamented by rather widely spaced spiral lirae. The apical angle is about 65° and is thus the widest among the described species. In average size, specimens of this species are considerably larger than are those from earlier beds.

Genus TEPHLON n. gen.
Figure 5G, H

Type species.—*Pugnellus tumidus* Gabb, 1860.

Diagnosis.—Aporrhaid gastropods with noded tabulate whorls, dominantly spiral sculpture and with a single spur-shaped posterolateral labral spine bent posteriorly in the middle. Adult shells usually covered with heavy callus.

Discussion.—*Tephlon* is known presently only from the type-species and from the type-locality, the Maestrichtian beds cropping out on Quiriquina Island, opposite Concepcion, coastal Chile. The genus much resembles *Pyktes* but lacks the anterior spatulate process on the outer lip, characteristic of the latter genus; it is not closely related to *Pugnellus*.

Subfamily ARRHOGINAE n. subfam.

Diagnosis.—High-spired, round-whorled usually transversely sculptured aporrhaid gastropods; last whorl alate, with generally entire margin except for a prominent spine-like posteriorly directed process arising from the posterolateral border of the outer lip. Last whorl generally one-half or more the total height of the shell; columella one-half the body whorl height or less.

Typical genera.—*Arrhoges* Gabb; *Pugnellus* Conrad; *Drepanocheilus* Meek.

Genus ARRHOGES Gabb, 1868

Type species.—*Chenopus occidentalus* Beck, 1847, by original designation.

Subgenus LATIALA Sohl, 1960

Type species.—*Anchura lobata* Wade, 1926, by original designation.

ARRHOGES (LATIALA) CALIFORNICUS (Gabb, 1864)
Figure 6F, I

Aporrhais californicus GABB, 1864, p. 128, pl. 29, figs. 230a–b.
Anchura californica (Gabb). GABB, 1869, p. 226.
Arrhoges californicus (Gabb). STEWART, 1927, p. 363, Pl. 21, fig. 15; MURPHY AND RODDA, 1960, p. 841, Pl. 102, figs. 6–7; POPENOE, *in* JONES, SLITER AND POPENOE, 1978, Pl. 1, fig. 10.
Alaria nodosa PACKARD, 1922, p. 430, Pl. 36, figs. 5a–5b.

Description.—Shell of medium size, height about 31 mm (imperfect); spindle-shaped except for mature labrum which is expanded, subquadrate, thickened along internal lateral border; whorls about seven, twice as wide as high, ornamented with about 14 low ribs slightly oblique to suture and gently concave aperturally; last whorl approximately one-half height of shell, bulbous, inflated, expanded into a broad quadrate outer lip, thickened laterally, extended at posterolateral and anterolateral corners into short, more-or-less blunt projections; margin of outer lip slightly divergent to axis, thickened ventrally with a broadly concave ventral margin toward aperture, dorsal labral margin oblique, thinner and slightly emarginate adjacent to parietal wall of whorl; aperture long, narrow, straight-sided, without plaits or other complications; rostrum or anterior canal short, bent ventrally at midlength; axial sculpture persisting on shell up to beginning of extended outer lip, surface smooth therefrom to lip margin.

Lectotype.—ANSP 4272 (Murphy and Rodda, 1960, p. 841).

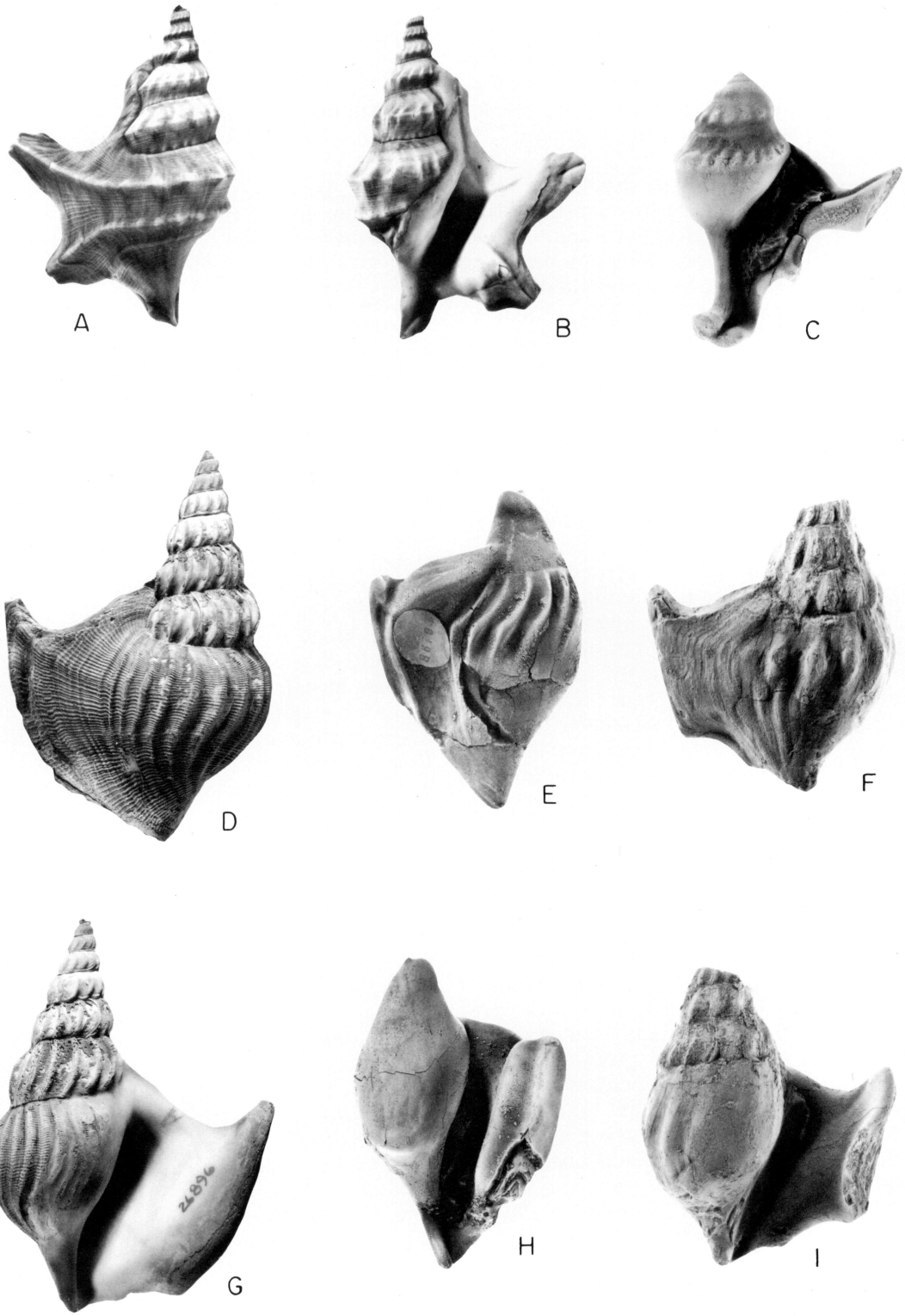
Dimensions of lectotype.—Height, 15 mm; width of last whorl and expanded lip, 10 mm (Stewart, 1927, p. 363).

Type locality.—"Siskiyou Mountains" (Stewart, 1927).

Hypotype.—UCLA 58438.

Locality of hypotype.—CIT loc. 1212, 2,500 ft N, 750 ft W of the SE corner sec. 4, T32N, R3W, Millville Quadrangle, Shasta Co., California.

Dimensions of hypotype (imperfect).—Height, 31.0 mm; width of last whorl and expanded lip, 28.3 mm.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Distribution.—Bald Hills Formation (Murphy and Rodda, 1960) = Budden Canyon Formation (Murphy, Rodda and Morton, 1969) west side and north end of the Sacramento Valley—specimens generally with somewhat coarser ribbing on the spire than is present on the typical form; Member II = Frazier Silt, and Member III = Melton Sandstone, Redding region, Shasta Co.; Hornbrook Formation, Siskiyou Co.; Ladd Fm., upper Baker Canyon Sandstone Member (*Cucullaea gravida* division), Santa Ana Mountains, Orange Co., California.

Age.—?Cenomanian—early Turonian (Murphy and Rodda, 1960; late Turonian, associated with the horizon of *Subprionocyclus.*

Discussion.—*Arrhoges californicus* (Gabb) is found in fine-grained, muddy sandstone and siltstone. At Redding and near Hornbrook, it occurs in the same section as *Gymnarus manubriatus,* but not in the same beds; in the Santa Ana Mountains, it is found in the same beds as *Pyktes daiphron.* This suggests that *P. daiphron* is of deeper, quieter water habitat in the Turonian and that the genus migrated into shallower water in Senonian and Maestrichtian time.

The subgenus *Latiala* was proposed by Sohl (1960, p. 101) for forms similar to *A. occidentalis* (type-species of *Arrhoges*) but is discriminated by an angulate outer lip, extended at both anterior and posterior lateral corners, with a longer and more pronounced anterior rostrum, and with fewer axial ribs in general. The time-range of *Latiala* is at least Turonian-Maestrichtian; its geographic distribution includes both Indo-Pacific and Atlantic provinces (Sohl, 1960).

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FIGURE 6—All figures printed at height of 5–6 cm to facilitate comparison of common features. *A, B, Aporrhais pespelicani* (Linnaeus, 1766). Hypotype, UCLA 59070 from Mediterranean Sea, Recent. Height 48.6 mm; diameter including hooks 36.0 mm; diameter of last whorl 17.4 mm. Apertural and abapertural views. *C, Pyktes triphyllon* Popenoe n. sp. Paratype. Duplication of Figure 5C to show similarities and differences with Figure 6A, B. *D, G, Arrhoges occidentalis* (Beck, 1836). Hypotype, UCLA 26896 from coast of Newfoundland, Recent. Height 59.6 mm; diameter including hook 42.7 mm; diameter of last whorl 24.2 mm. To show relationships with *Arrhoges californicus* Gabb and *Pugnellus densatus* (Conrad). *E, H, Pugnellus densatus* (Conrad, 1858). Hypotype, USNM 325026 from USGS loc. 10198, Coon Creek, McNairy Co., Tenn., Maestrichtian. Height 47.8 mm; diameter including hook 32.5 mm; diameter of last whorl ca. 17.8 mm. To show relationship with *Arrhoges occidentalis* (Beck) and *Arrhoges californicus* (Gabb). *F, I, Arrhoges* (*Latiala*) *californicus* (Gabb, 1864). Hypotype, UCLA 58438 from CIT loc. 1212, Little Cow Creek valley, Millville Quad., Calif., Turonian. Height (incomplete) 30.5 mm; diameter including hook 26.5 mm; diameter of last whorl 14.9 mm. To show relationships with *Arrhoges occidentalis* (Beck) and *Pugnellus densatus* (Conrad).

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APPENDIX: LOCALITIES CITED

92 CIT: Santiago Canyon, Santiago Peak Quad., Santa Ana Mts., Orange Co., Calif. Concretions in shale 100 ft above stream and near fence on north side of canyon. About ½ mile north of road fork in Santiago Canyon at Harding Canyon junction. Ladd Fm., Baker Canyon Member. Turonian.

1197 CIT: Little Cow Creek, Redding (1946) Quad., Shasta Co., Calif. Block of sandstone crowded with *Gymnarus manubriatus* found in stream bed of Stinking Creek just downstream from first fence across creek upstream from stream mouth, 4,050 ft N 44°W of SE corner sec. 6, T32N, R3W. Member I (Bellavista Sandstone). Turonian.

1164 CIT: South side of Silverado Canyon, El Toro Quad., Santa Ana Mts., Orange Co., Calif. Near mouth of small north-flowing gully and at top of lower fossiliferous sandstone series. About 400 ft SE of Holz ranch house in the SE corner of sec. 7, T5S, R7W. Ladd Fm., top of Baker Canyon Member. Turonian.

1212 CIT: Little Cow Creek Valley, Redding (1901) Quad., Shasta Co., Calif. About ¾ mi west of Alturas-Redding highway bridge (US 299) above Salt Creek and ¼ mi south of the highway, approximately 2 mi northeast of Frazier's Corners. Hard sandy concretions in shale banks of gullies in pasture, 3,870 S 49°W from the NE corner sec. 7, T32N, R3W. Frazier Siltstone. Late Turonian.

1225 CIT: North side Oak Run Valley, Redding Quad., Shasta Co., Calif. ½ mi north of Hathaway Bros. farmhouse. Just over the hill, north about 300–450 ft from CIT 1007. 3,635 ft N 20°35′E from NE corner of sec. 20, T32N, R2W. Member IV. Coniacian.

1572 CIT: Laguna Seca Quad., Merced Co., Calif. (Probable equivalent of USGS loc. 7006). 2,400 ft N and 6,400 ft W of SE corner of sec. 19, T12S, R11E. On north bank of canyon. Moreno Formation, Tierra Loma Member. Middle Maestrichtian.

3314 UCLA: Deer Valley, Mt. Diablo Quad., Contra Costa Co., Calif. Fine-grained slabby sandstone, float in bed of gully. About 2,100 ft S 28°W of NE corner of sec. 24, T1N, R1E, south side of valley. Deer Valley Formation. Maestrichtian.

3618 UCLA: Chico Creek, Paradise Quad., Butte Co., Calif. Concretion from west side Chico Creek about 10 ft up in sandstone cliff, 50 ft S of first fence line to south of bridge below Mickey's Place, approx. 425 ft S, 1,650 ft E of NW corner of sec. 12, T23N, R2E. Chico Formation. Santonian.

4104 UCLA: Valley of Oak Run, Millville Quad., Shasta Co., Calif. Hard-cemented sandstone slabs weathering out of siltstone in pasture a little west of north of the Hathaway ranch house and about 1,500 feet S and 600 ft E of the NW corner of sec. 16, T32N, R2W. Member IV. Coniacian.

4106 UCLA: Clover Creek valley, Millville Quad., Shasta Co., Calif. Fossiliferous sandstone slabs on hillside north of Clover Creek in small gully flowing south to creek. About 2,200 ft W of the NE corner of sec. 23, T32N, R3W. Member VI? Santonian.