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SPONGE-INHABITING BARNACLES OF THE AMERICAS:
A NEW SPECIES OF *ACASTA* (CIRRIPEDIA, ARCHAEOBALANIDAE),
FIRST RECORD FROM THE EASTERN PACIFIC, INCLUDING
DISCUSSION OF THE EVOLUTION OF CIRRAL MORPHOLOGY

BY

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ABSTRACT

Acasta newmani n. sp. from the Gulf of California, Mexico is described. This is the first report of *Acasta* from the eastern Pacific. Hypotheses are discussed concerning the correlation of cirral morphology with feeding methods and host specificity. The similarities between *A. newmani* and *Acasta cyathus* Darwin, 1854 indicate that they are examples of the common pattern of trans-isthmian sibling taxa in the Caribbean and eastern tropical Pacific. A key to the seven sponge-inhabiting barnacle species of the Americas is presented with citations noting their host sponge species and known ranges in the Americas. The range of *Membranobalanus nebras* (Zullo & Beach, 1973) is extended from the Galapagos Islands to the Gulf of California.

RESUMEN

Se describe *Acasta newmani* n. sp. del Golfo de California. Esta es la primera cita de *Acasta* en el Pacífico oriental. Se discuten las hipótesis sobre la correlación entre morfología cirral y los métodos de alimentación y especificidad de huéspedes. Las similitudes, entre *A. newmani* y *A. cyathus* Darwin, 1854 indican que son un ejemplo del patrón común entre especies hermanas a ambos lados del istmo de Panamá, en el Caribe y Pacífico oriental tropical. Se incluye una clave de las siete especies americanas de cirrípedos que viven en esponjas, indicando la especie huésped y sus distribuciones. El rango de distribución de *Membranobalanus nebras* (Zullo & Beach, 1973) se extiende desde las islas Galápagos hasta el Golfo de California.

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INTRODUCTION

Members of the barnacle genus *Acasta* are obligate symbionts of either Porifera, Alcyonaria, Octocorallia, or Antipatharia. Porifera is by far the most common host taxon. Fifty-one of the 73 previously described extant species and 2 subspecies are known to be sponge symbionts. Eight are symbionts of various coelenterates. Hosts for the remainder have not been recorded in the literature. *Acasta* species are not generally host species-specific; a single species may be found in more than one species of sponge.

Species of another archaeobalanid genus, *Membranobalanus*, are obligate symbionts of Porifera. The two genera are closely allied within the family Archaeobalanidae, differing principally in basis type: membranous (*Membranobalanus*) or calcareous (*Acasta*). In addition, the rostrum of *Membranobalanus* is often rounded at the bottom and extended beyond the bottom of the other compartmental plates. However, some *Acasta* have been described with membranous bases and some *Membranobalanus* have rostra the same length as other wall plates. This obviously may create a confusing situation for those attempting to identify sponge-inhabiting barnacles. However, for the sponge-inhabiting barnacles of the Americas, the membranous basis may be used as a diagnostic character for the genus *Membranobalanus*.

The systematics of *Acasta* and *Membranobalanus* are not well developed. Concerning only *Acasta*, Kolbasov (1993) erected four new genera within a new subfamily, Acastinae, in addition to *Acasta* s.s. Unfortunately, that author did not use cladistic methodology. In fact, while using traditional systematics methods, he did not present consistent sets of diagnostic features for these five genera. We could not conclusively assign our species to any of Kolbasov's (1993) new genera. Therefore, we provisionally assign *Acasta newmani* new species to the genus *Acasta* Leach. A taxonomic revision of the sponge-inhabiting barnacles would require a full-scale cladistic phylogenetic analysis. Such a complete revision is beyond the scope of this paper.

Acasta is found in nearly all tropical and warm temperate seas, but it has not been reported in the eastern Pacific Ocean. *A. newmani* is described from the Gulf of California, Mexico, symbiotic to the pachastrellid sponge *Poecillastra tenuilaminaris* (Sollas, 1888).

The geographically closest congener of *A. newmani* is *Acasta cyathus* Darwin, 1854 a Caribbean and western Atlantic species. These are the only species of *Acasta* known from the Americas. *A. newmani* and *A. cyathus* constitute an example of the common pattern of trans-isthmian sibling taxa in the Caribbean and eastern tropical Pacific. They show great similarity in morphology differing

in only a few characters. *A. cyathus* has a pink shell, a well-defined scutal adductor ridge, and hooks on cirrus IV.

Armature on cirrus IV occurs in several of the genera in the family Archaeobalanidae which we consider to be sister taxa and close outgroups to *Acasta*. Therefore, we consider this armature to be plesiomorphic in *A. cyathus*, having been lost in *A. newmani* and a few other species of *Acasta*. Cirral morphology in other cirriped taxa tends to be strongly correlated with feeding ecology. We discuss this as one potential adaptive advantage of cirral armature retention in *Acasta*.

A. newmani is also compared to five Indo-West Pacific species: *Acasta apertura* Rosell, 1991, *Acasta crassa* Broch, 1931, *Acasta denticulata* Hiro, 1931, *Acasta spinifera* Utinomi, 1967, and *Acasta spinitergum* Broch, 1931. These species share two obvious morphological characters with *A. newmani*. They all lack armature on cirrus IV and possess wall plates with calcareous spines. *A. newmani* is easily differentiated from these five species by the shape of bases and opercular plates.

Shell growth-forms in *A. newmani* include globose and tulipiform. Characters associated with these shapes (e.g., radii width and opercular valve shape) are commonly used to separate species of archaeobalanids. However, in *A. newmani*, shell shape is not consistently correlated with variation in opercular valve morphology. Therefore, we attribute these differences among individuals of *A. newmani* to intraspecific variation and plasticity rather than interspecific autapomorphies.

Membranobalanus nebrias (Zullo & Beach, 1973) is recorded from the Gulf of California in *Delaubenfelsia raromicrosclera* (Dickinson, 1945). It was previously found only in the Galapagos Islands.

Four other species of *Membranobalanus* are known from the Americas. *Membranobalanus costatus* Zullo & Standing, 1983 is restricted to the Atlantic coast of North America. *Membranobalanus declivis* (Darwin, 1854) lives in the Atlantic along the coast of North America, the Gulf of Mexico, and the eastern Caribbean. *Membranobalanus robinae* Van Syoc, 1988 is known only from the Gulf of California. *Membranobalanus orcutti* (Pilsbry, 1916) ranges from southern California to the Pacific Ocean coast of Baja California. All of these possess armature on cirrus IV.

METHODS

Holotype (CASIZ 88810) and paratype (CASIZ 88809) were drawn whole and the paratype then dissected. The appendages were mounted on glass slides in glycerine jelly for illustration. The figures were drawn using camera lucida.

The opercular and wall plates were cleaned in sodium hypochlorite, washed in distilled water, dried, and glued to stubs for the scanning electron microscope (SEM). Whole shells of paratypes CASIZ 106291 and 106737 were cleaned carefully and briefly with sodium hypochlorite to keep the plates from disarticulating. The shells were then washed, dried, and glued to stubs for SEM. Host sponge tissues are retained with cataloged barnacle specimens rather than removed to separate containers.

SYSTEMATIC ACCOUNT

Subclass Cirripedia Burmeister, 1834

Order Thoracica Darwin, 1854

Suborder Balanomorpha Pilsbry, 1916

Superfamily BALANOIDEA Leach, 1817

Family ARCHAEOBALANIDAE Newman & Ross, 1976

Subfamily ARCHAEOBALANINAE Newman & Ross, 1976

Acasta Leach, 1817

Acasta newmani new species (figs. 1-9)

Holotype. — Complete, intact specimen, partially imbedded in sponge, deposited at California Academy of Sciences, Invertebrate Zoology, CASIZ 88810.

Type locality. — Station MB-6904-5, TR#150, 28°57.0'N 112°35.0'W to 28°58.0'N 112°34.0'W, 82-100 meters deep, 6.4 km north of Punta Willard, off Isla Tiburon, Gulf of California, Mexico, 25 April 1969, collected by Geoffrey Moser, U.S. S.W. Fisheries Center.

Material examined. — Paratypes deposited at California Academy of Sciences, Invertebrate Zoology (CASIZ); 1 specimen, scuta only, on SEM stub, CASIZ 57814; 1 complete specimen, shell and opercular plates dry on SEM stubs, CASIZ 57815; 1 complete intact specimen, CASIZ 57816; 1 complete specimen, cirri and mouthparts mounted on microscope slide, shell dry on SEM stub, CASIZ 88809; 1 complete specimen, cirri and mouthparts mounted on microscope slide, CASIZ 106291; 1 specimen, disarticulated shell, opercular plates, cirri, and mouthparts mounted on microscope slide, CASIZ 106294; 1 specimen, cirri and mouthparts mounted on microscope slide, shell dry, CASIZ 106735; 1 specimen, dry shell only, CASIZ 106736; 1 specimen, dry shell only, CASIZ 106756; 4 whole specimens and fragments, CASIZ 106775; dry shell fragments from several specimens, CASIZ 106776.

Whole specimen paratypes deposited at United States Museum of Natural History, Smithsonian Institution, Washington, D.C.; USNM 261333, and Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA; SIO C-9978.

Diagnosis. — Shell thin, white, shape variable from globose to tulipiform; wall plates of mature individuals with spines; calcareous basis nearly flat with

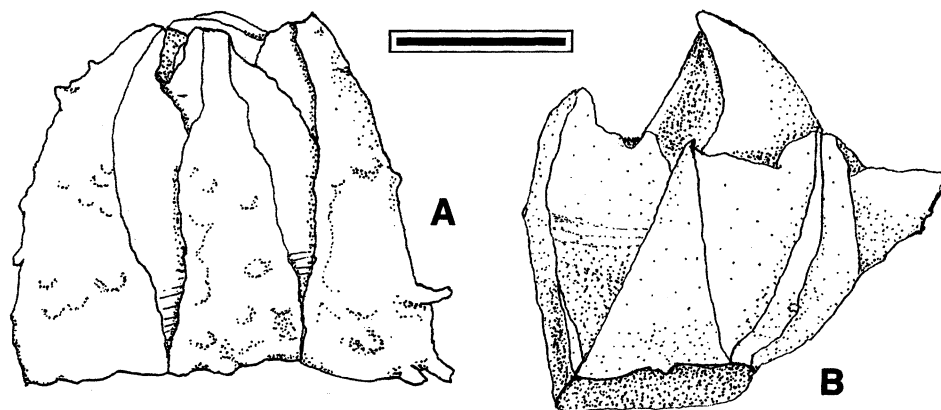


Fig. 1. *Acasta newmani* n. sp. a, CASIZ 88810, holotype, whole shell, globose, most spines broken off; b, CASIZ 88809, paratype, whole shell, tulipiform, most spines broken off. Scale bar equals 3 mm.

concentric ridges; scutum exterior with strong longitudinal striations and growth ridges, adductor pit shallow and indistinct; adductor ridge incipient or lacking; cirri, including cirrus IV, without curved hooks or “teeth”.

Description. — Shell (fig. 1a, b) globose to tulipiform, orifice as wide as or wider than basis, white, orifice toothed, radii present, transparietal (radius extends across ala throughout most of its length, sutural edge denticulate; see Zullo & Perreault, 1989), broadening near orifice; all wall plates about same height, carina may be slightly longer; orifice toothed; hollow, calcareous, upward curving spines present on parietes of all six compartmental plates in larger specimens, may be small or absent on some plates in smaller individuals; individuals exhibit variation in position and number of spines on parietes; spines on rostrum and carino-latera are usually down center of parietes, but spines below sheath on these plates may be near lateral margins of parietes; spines near lateral margins of parietes on carina (fig. 2a) and latus (fig. 3a); all plates fragile and thin, easily broken or disarticulated; alae thinner than parietes or radii; growth striations on outer surfaces, most common on radii and parietes, only occasionally on alae; carino-latera (fig. 2b) narrowest of compartmental plates, with ala slightly narrower than basal part of paries; latera (fig. 3a, b) about same width as rostrum; carina (fig. 2a) narrower than rostrum (fig. 2c), but about twice as wide as the second carino-latera. Inner surface of plates with basal margin of sheath adhering, longitudinal ribs below sheath, terminating in rounded tips at basal margin of plates (see latus interior, fig. 3b), smaller specimens with only two ribs, one each near lateral margins of plates, larger specimens with several ribs per plate, except on the narrow second carino-latera which may have only two marginal ribs, inner ribs generally shorter and less robust. Rounded tips of ribs rest

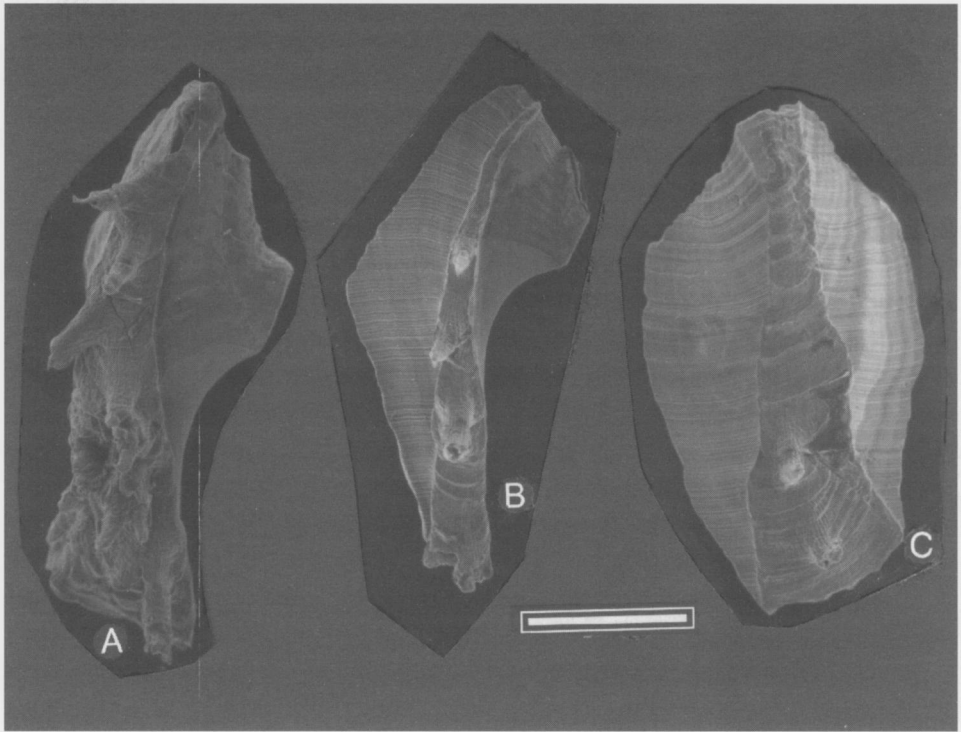


Fig. 2. *Acasta newmani* n. sp., CASIZ 57814, paratype. a, carina exterior; b, carino-latus exterior; c, rostrum exterior. Scale bar equals 600 μm .

in pits around margin of basis (fig. 3c), resulting in intervening gaps between basis and basal margins of compartmental plates; pits (and gaps) less numerous in smaller specimens. Basis (fig. 3c), calcareous, nearly flat but often uneven with concentric ridges, irregularly mushroom-shaped or shallow saucer-shaped in cross section, relatively small.

Scutum (figs. 4a, b; 5a, b) thick, convex, white; basal margin 3/4 length of tergal margin; tergal margin greatly curved; exterior with prominent growth ridges, forming small "teeth" at occludent margin; longitudinal ridges or striations present, becoming nodose where crossing growth ridges, small pits on longitudinal ridges just below growth ridges; chitinous lamellae; adductor muscle pit shallow and indistinct in specimens with globose shell, deeper and more defined in some individuals with tulipiform shells (fig. 5b), deepens at an angle into the plane of the scutum as it extends in direction of apex; adductor ridge low and faint, represented by slightly raised margin of adductor muscle pit; articular ridge prominent, triangular, perpendicular to plane of scutum; height about 1/4 width of basal margin; length about 1/2 of tergal margin; articular furrow prominent but narrow, width about 1/8 to 1/10 of basal margin, extending

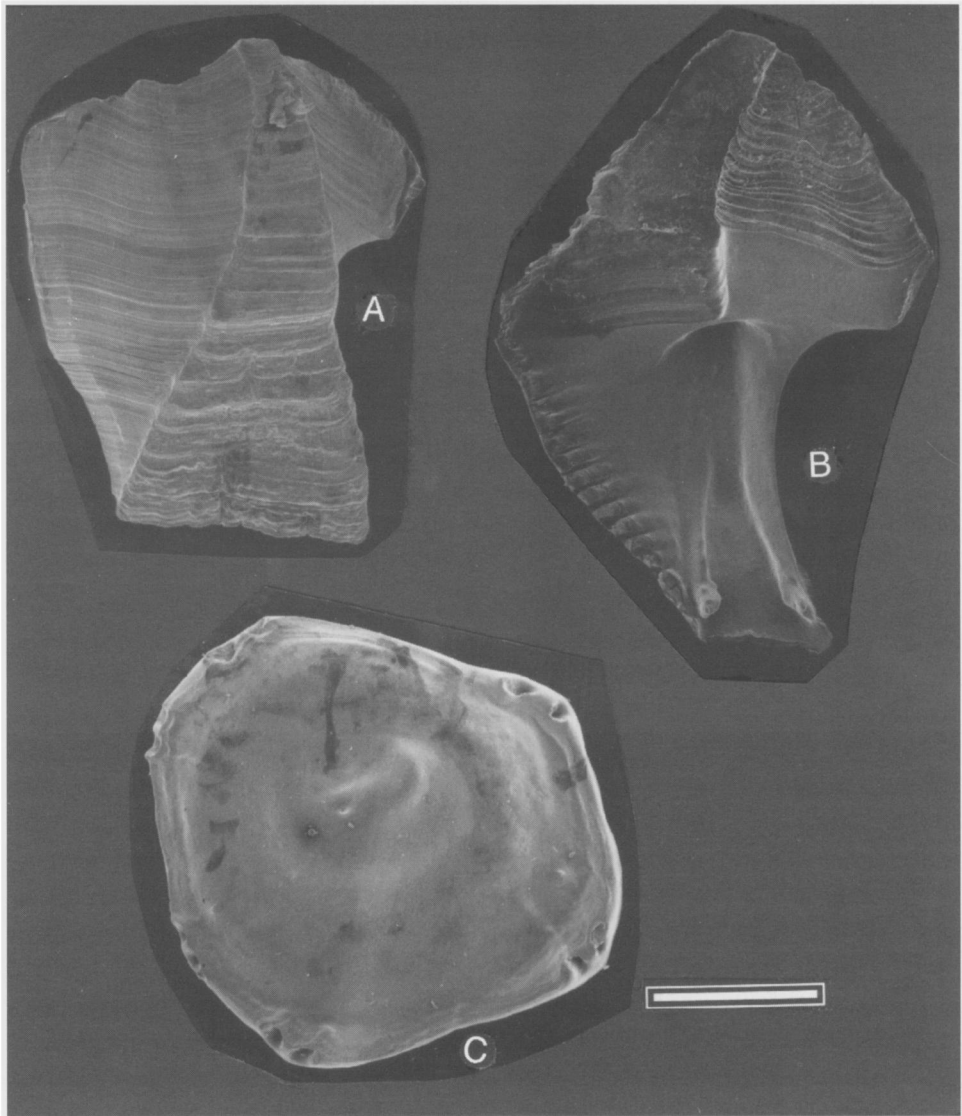


Fig. 3. *Acasta newmani* n. sp., CASIZ 88809, paratype. a, latus exterior; b, latus interior; c, basis interior. Scale bars equal 1 mm (a), 750 μm (b, c).

about 7/8 length of tergal margin; lateral depressor pit semi-circular and deep in larger specimens, especially prominent in some individuals with tulipiform shell (fig. 5b), diameter about 1/4 to 1/5 length of tergal margin.

Tergum (fig. 5c, d) thin, white, about same width as scutum; apex beaked; basal margin slightly shorter than scutal margin; exterior growth ridges prominent, but shallower than those of scutum; chitinous lamellae; no longitudinal striations;

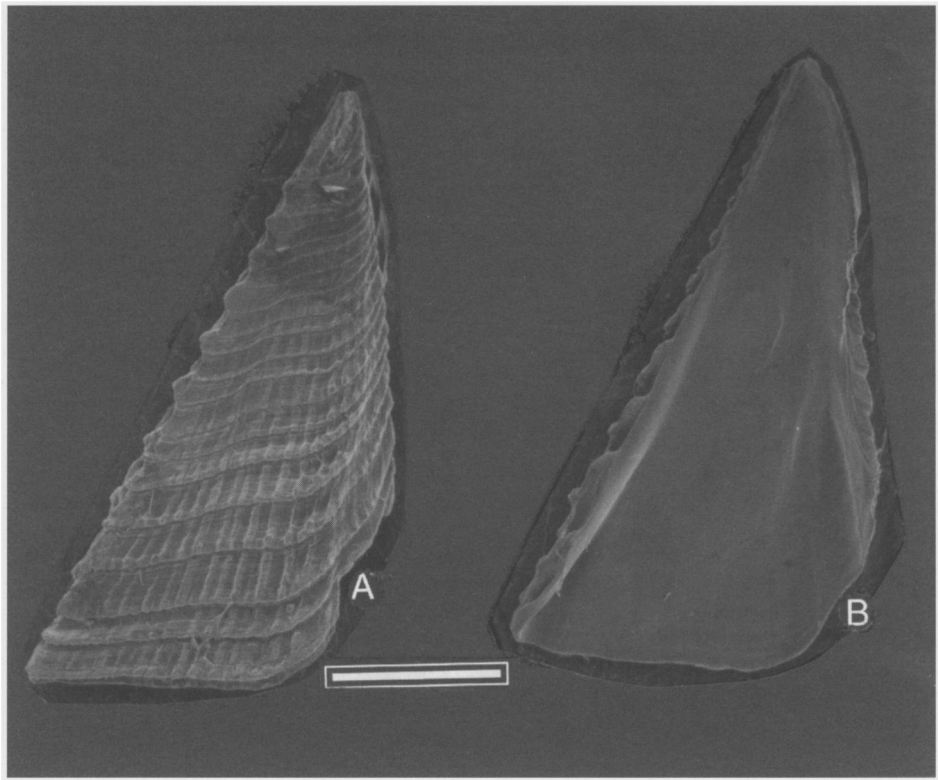


Fig. 4. *Acasta newmani* n. sp., CASIZ 57815, paratype. a, scutum exterior; b, scutum interior. Scale bar equals 600 μm .

tergal spur about 1/2 width of basal margin; about 1/2 length of basal margin, articular ridge gently sloping from high point nearest basal margin toward curved apex, depressor muscle crests well-defined in mature specimens; spur furrow shallow and open; distinct multiple low articular ridges; articular furrow about 1/2 length of scutal margin; 3 or 4 depressor crests prominent on larger specimens.

Labrum (fig. 6a) with deep notch at apex of crest; three teeth present on each side of notch.

Palp (fig. 6b) with superior margin straight, densely setose on inferior margin.

Mandible (fig. 6c) quadridentate, with a few smaller teeth below fourth tooth; first tooth more robust, but about same length as second tooth; second tooth located near center of cutting edge; third tooth about 2/3 length of first and second teeth; fourth tooth about 2/3 length of third tooth; remaining small teeth diminish in length to inferior margin; inferior and superior margins setose.

Maxilla I (fig. 6d) with straight edge; apical spine largest, but following spines nearly as long; inferior angle with several short spines; superior margin setose.

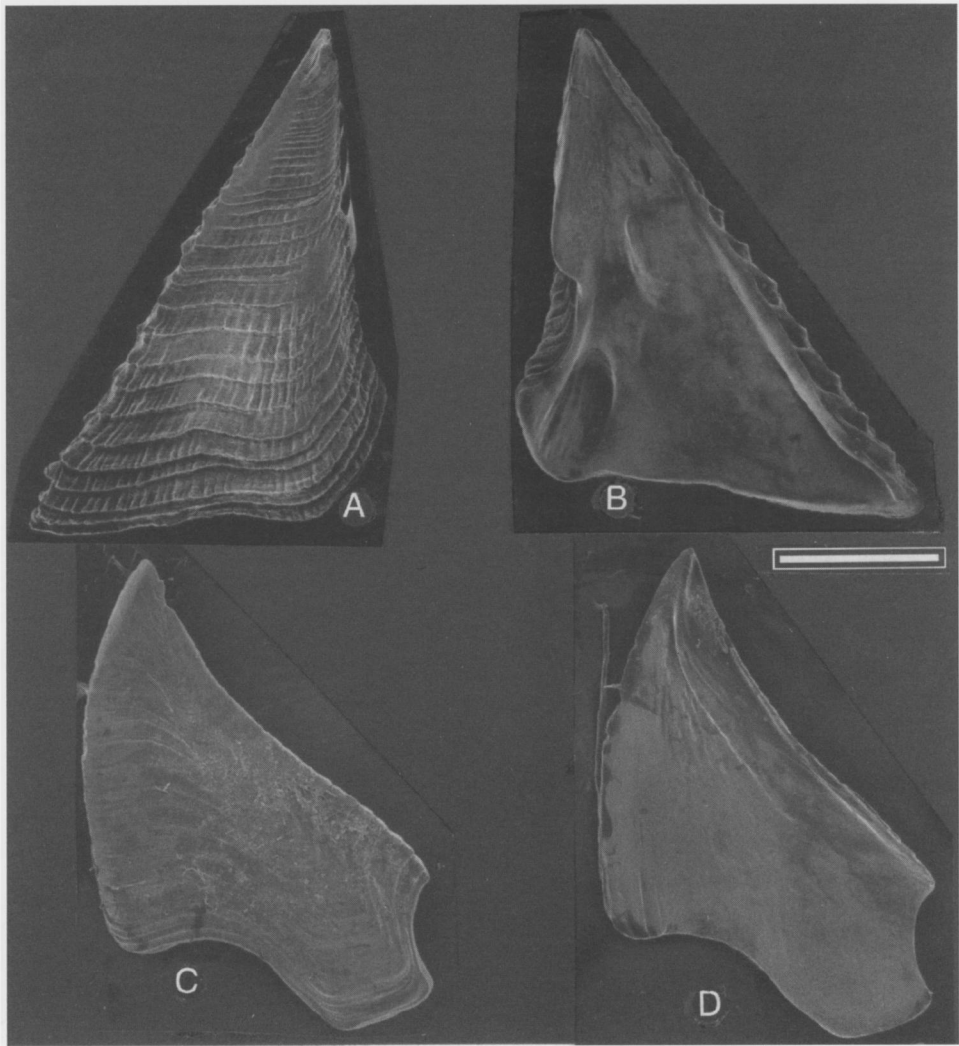


Fig. 5. *Acasta newmani* n. sp., CASIZ 88809, paratype. a, scutum exterior; b, scutum interior; c, tergum exterior; d, tergum interior. Scale bar equals 750 μm .

Maxilla II (fig. 6e) ovate, densely setose.

Cirri lacking hooks or "teeth"; articles of both rami slightly protuberant. Cirrus I (fig. 7a) with unequal rami; anterior ramus about twice length of posterior ramus; both rami setose; setae not hooked or pectinate; setae are found on distal half of each article. Cirrus II shorter than other cirri; anterior ramus about 3/4 the length of the posterior ramus; both rami setose. Cirrus III longer than cirri I and II; anterior ramus slightly shorter than posterior ramus; form and distribution of setae similar to those of cirri I and II. Cirrus IV (fig. 7b) longer than cirrus III;

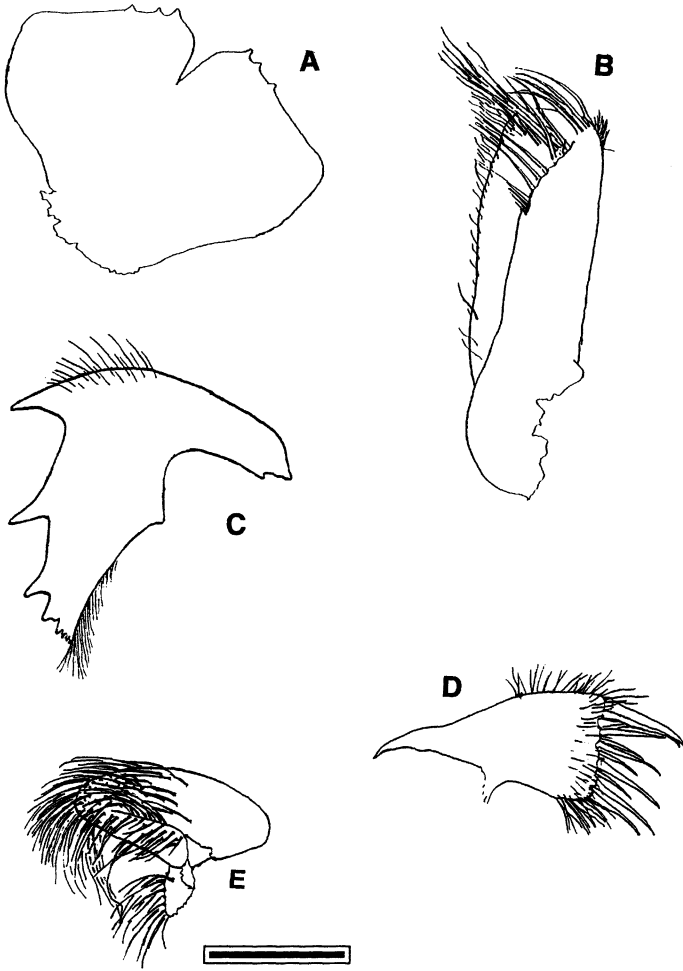


Fig. 6. *Acasta newmani* n. sp., CASIZ 106735, paratype. a, labrum; b, palp; c, mandible; d, maxilla 1; e, maxilla 2. Scale bar equals 75 μ m.

TABLE I
Counts of cirri articles of *Acasta newmani* n. sp.

		Cirrus					
		I	II	III	IV	V	VI
CASIZ 106294, paratype							
Right cirri	anterior ramus	8	6	8	21	24	24
	posterior ramus	12	9	8	24	24	26
CASIZ 88809, paratype							
Left cirri	anterior ramus	9	9	11	14	18	21
	posterior ramus	7	7	9	15	19	23

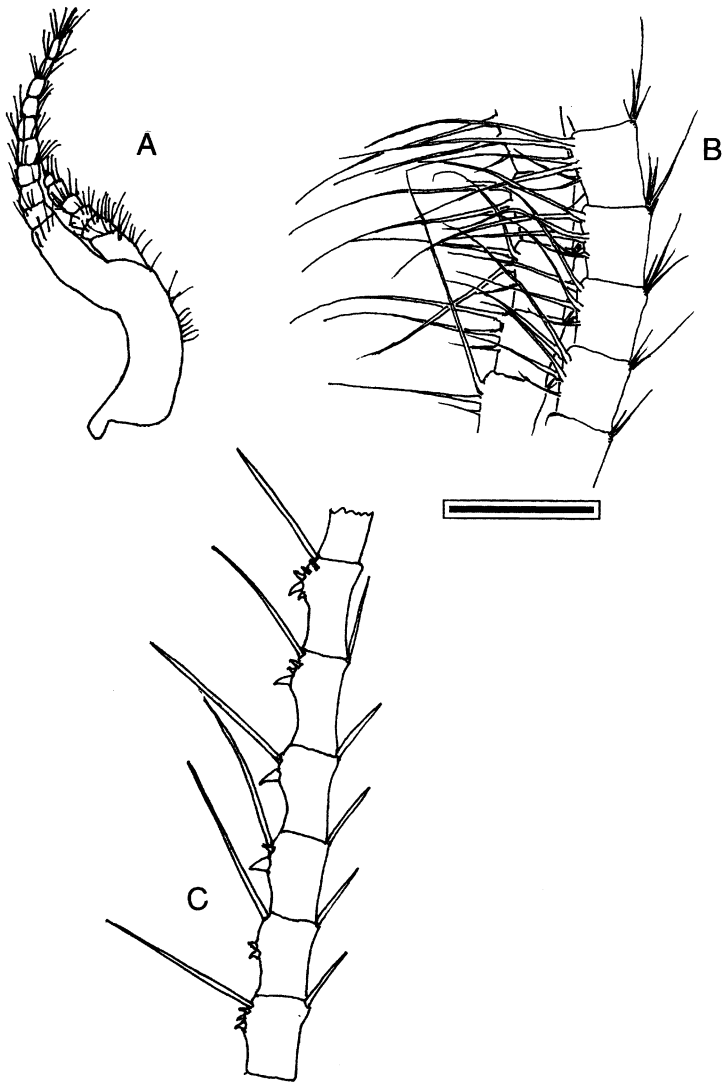


Fig. 7. a-b, *Acasta newmani* n. sp., CASIZ 106735, paratype. a, cirrus I; b, cirrus IV. c, *A. cyathus* Darwin, 1854, USNM 195295, cirrus IV. Scale bars equal 75 μm (a), 300 μm (b, c).

rami of equal length and diameter; anterior margin of each article with 1 or 2 long setae near distal margin and with 2 or more shorter setae proximally and almost evenly spaced along the distal half of the article; on posterior side 2-4 setae on distal margin of each article; pedicle about 1/5 the length of rami. Cirrus V longer than IV but shorter than VI; form and distribution of setae similar to those of IV. Cirrus VI longest; form and distribution of setae similar to those of IV.

Penis annulated, short setae around distal end and sparsely along length.

Etymology. — We name this species in honor of Prof. William A. Newman, Scripps Institution of Oceanography, for his prominent contributions to the systematics and biogeography of the Cirripedia.

Memranobalanus Hoek, 1913

Memranobalanus nebris (Zullo & Beach, 1973)

Balanus (*Memranobalanus*) *nebris* Zullo & Beach, 1973: 2.

Material examined. — One complete voucher specimen, CAS 106289. Cirri and mouthparts dissected and mounted on microscope slide. Collected by Linda Ball, 7 April 1975; Mexico, Gulf of California, Sonora, Guaymas, Bahia San Carlos; depth 4.6-18.3 m; in sponge *Delaubenfelsia raromicrosclera* (Dickinson, 1945).

DISCUSSION

Systematics

Acasta newmani n. sp. is unusual among the 73 extant species and 2 subspecies of *Acasta* Leach in the lack of prominent “teeth” or thick hooks on basal segments of cirrus IV. This lack of cirral armature is shared by only nine other species in the genus. The presence of spines on the shell exterior is typical of most species of *Acasta*. Only *A. apertura*, *A. crassa*, *A. denticulata*, *A. spinifera*, and *A. spinitergum* share the combination of these two characters with *A. newmani*.

A. apertura is distinct from *A. newmani* in having uncalcified gaps along the basal portion of sutural margins between compartmental plates. These gaps form slit-like fenestrae in *A. apertura*. It also has an indistinct articular ridge on the scutum and a deep cup-shaped basis. The terga are similar. However, the angle between the basi-carinal margin and the spur is well-defined and almost perpendicular in *A. apertura*. In *A. newmani* the angle between the basi-carinal margin and spur is shallow, thereby forming a short basi-carinal margin (fig. 5c, d).

A. newmani lacks a well-defined scutal adductor muscle pit, whereas *A. apertura*, *A. crassa*, and *A. denticulata* have prominent pits. *A. crassa* further differs from *A. newmani* in lacking tergal depressor crests and having a deep tergal furrow. *A. denticulata*, unlike *A. newmani*, has a feeble scutal articular ridge, a straight articular edge on the terga, two “teeth” on the tergal spur, and a cup-shaped basis.

A. spinifera is similar to *A. newmani* in the possession of a small flat basis; and scutum with prominent articular ridge, longitudinal ridges crossing growth ridges, lack of distinct adductor and lateral depressor muscle pits. The two species differ, however, in tergal morphology. The tergum of *A. spinifera* has a narrow spur with prominent open furrow and lacks depressor muscle crests.

The shape of the opercular plates of *A. newmani* show similarity to those of *A. spinitergum*. However, the former has a prominent scutal articular ridge, a deep articular furrow and usually has a clearly delimited lateral depressor muscle pit; the depressor crests in the tergum are also more distinct than those of *A. spinitergum*.

A. newmani is known only from the Gulf of California, whereas the five species of *Acasta* compared above are all found in the western Pacific Ocean. Published localities and hosts for these five species follow:

A. apertura: Philippines, in “calcareous” sponge (Rosell, 1991);

A. crassa: Indonesia in *Agelas* sp. (Kolbasov, 1993) and Madagascar (Broch, 1931);

A. denticulata: Sagami Bay, Honshu, Japan in “monaxon sponge growing on a fish” (Hiro, 1931: 154);

A. spinifera: Tokyo Bay, Japan in *Phakellia foliacea* (Thiele, 1898) (Utinomi, 1967);

A. spinitergum: Indonesia in gorgonian (Broch, 1931).

Cirral hooks as a plesiomorphy

Prominent cirral hooks or “teeth” are present on the anterior margin of cirrus IV in many species of *Acasta* as well as three other genera within the Archaeobalanidae: *Armatobalanus*, *Membranobalanus*, and *Conopea*. Two of these, *Membranobalanus* and *Conopea*, also contain species with “unarmed” cirrus IV.

Considering the presence of cirral hooks on most species in three other related genera, and the lack of hooks on some species in only two of them, we conclude, through out-group comparison, that cirral hooks are plesiomorphic in the *Armatobalanus-Acasta-Membranobalanus-Conopea* branch of the Archaeobalanidae. Therefore, cirral hooks or “teeth” are plesiomorphic within *Acasta*, having been lost by species in several lineages in the genus.

Ecological explanations for cirral morphology

There is some independent evidence from other barnacle lineages suggesting that cirral morphology is driven more by ecology than by genealogy. Yamaguchi & Newman (1997) note that cirripeds associated with hydrothermal vents (e.g.,

Neolepas, *Neoverruca*, and *Eochionelasmus*) universally possess finely setose cirri, presumably evolved for feeding on drifting clots of vent-dwelling sulfide-reducing bacteria. This cirral morphology is homoplastic, not dependent on ancestry, present in several disparate lineages and clearly adapted for specialized feeding requirements. Similarly, cirripeds that are more “raptorial”, feeding on large prey, generally possess armature of hooks or “teeth” on cirri, e.g., species in the genera *Paralepas* and *Heteralepas*. In these cases, the cirri are used more as accessory mouth parts to rip apart large prey items than as a cirral net to gather small planktonic food particles.

Adaptational reasons for retention of hooks in *Acasta* are that they function to remove fast-growing, tough sponge tissue from the opercular area and they aid in feeding on sponge tissues. In such an adaptational argument, loss of hooks would presumably be correlated with slow-growing, soft tissue sponge hosts and/or lack of reliance on scraping sponge tissues for food. A non-adaptational explanation is that the cirral armature no longer serves a function in *Acasta* and is retained only in those species where the loss of cirral hooks has not occurred by chance, as a product of random genetic drift and fixation.

We are unable to fully explore the potential explanations for retention of cirral hooks in all relevant barnacle species. However, we can address the issue of removal of sponge tissue overgrowing the opercular opening in *A. cyathus* and *A. newmani*. *A. cyathus* is known from nine different sponge species, *A. newmani* from only a single species, *Poecillastra tenuilaminaris*. The latter is relatively soft, with loosely aggregated tissues that are easily broken apart. The sponges inhabited by *A. cyathus* possess various tissue types from tough and elastic to hard and crumbly, but they are generally more tightly organized than *P. tenuilaminaris* tissues. Therefore, *A. cyathus* may require hooked cirri IV to scrape tougher/harder sponge tissue away from the barnacle’s opercular area. Clearly, a larger scale analysis of sponge-inhabiting barnacle genera, *Acasta* and *Membranobalanus*, will offer more data with regard to this question.

According to Kolbasov (1993: 420): “No sponge-inhabiting barnacle eats the tissues of the host sponge”. Kolbasov (1993: 420-421), citing Tabachnik, notes that sponge spicules are not a primary item in gut contents of *Acasta sulcata* Lamarck, 1818, *Acasta laevigata* Gray, 1825 and *Acasta pertusa* Kolbasov, 1991. *A. sulcata* has prominent hooks on cirri IV. The other two species lack prominent hooks on the cirri. Therefore, this is some evidence that the presence of hooks is not strongly correlated with feeding on host sponge tissues. However, since the gut contents of only one species of “armed” *Acasta* have been examined, we hesitate to concur with Kolbasov’s unequivocal statement regarding the absence of sponge feeding by all *Acasta*.

Concerning the ontogeny of individual *Acasta*, it is unlikely that the presence of hooks on cirrus IV is a phenotypically plastic character which varies among populations of a particular species depending on the host sponge tissue type. *Acasta dofleini* (Krüger, 1911), for example, a species which has cirral hooks, inhabits several host sponge species of various tissue types (Kolbasov, 1993). We are not aware of any morphological analysis to specifically examine the relationship of cirral morphology with host type. We can only assume that since the specimens were identified as *A. dofleini*, they all possessed cirral armature.

Trans-isthmian sibling species hypothesis

The only other *Acasta* known from the Americas, *A. cyathus*, is closest to *A. newmani* geographically. It has been recorded in *Spongia tubulifera* (Lamarck, 1814) (= *S. officinalis* Linnaeus, 1759) from the Caribbean and western Atlantic (Darwin, 1854) as well as in *Dysidea* sp., haliclonid and stellettid sponges from the Indian Ocean (Seychelles; Kolbasov, 1993). The two species have a globose or tulipiform shell (both species exhibit variability) and possess a shell exterior ornamented with calcareous spines, a small flat basis and similar opercular plate morphology. However, the shell of *A. cyathus* is pink while that of *A. newmani* is white. In addition, *A. cyathus* possesses hooks on the anterior margin of cirrus IV and a prominent scutal adductor ridge, but these are lacking in *A. newmani*. As previously discussed, cirral hooks are plesiomorphic in *Acasta*. Thus, this character is not phylogenetically informative for these two species.

Therefore, relying on similarities in shell and opercular valve morphology, we propose a hypothesis that *A. cyathus* and *A. newmani* are closely related, perhaps even trans-isthmian sibling taxa in the Caribbean and eastern tropical Pacific. The rising Panama isthmus closed off the Panama seaway between the Caribbean and Pacific about 3 to 3.5 million years ago (Saito, 1976; Duque-Caro, 1990). This relatively recent geologic event produced an obvious vicariance event for populations of species living on both Caribbean and Pacific sides of the seaway. Sibling species have been noted in shrimp (Knowlton et al., 1993), fishes (Jordan, 1885; Rosenblatt, 1967), and barnacles (Laguna, 1988), as well as many other taxa. Our hypothesis can be tested by making genetic comparisons of the Caribbean and eastern Pacific *Acasta* species (*A. cyathus*, *A. newmani*), using either DNA sequences or allozyme electrophoresis, with other *Acasta* possessing similar morphology. These data would reveal the phylogenetic relationships among the species examined and either support or refute the trans-isthmian species hypothesis.

Intraspecific variation

As noted in the description, variation between individuals exists in general shell shape; globose (e.g., fig. 1a: holotype) to tulipiform (e.g., fig. 1b: paratype), with many intermediates (e.g., figs. 8 and 9: paratypes). Intraspecific variation

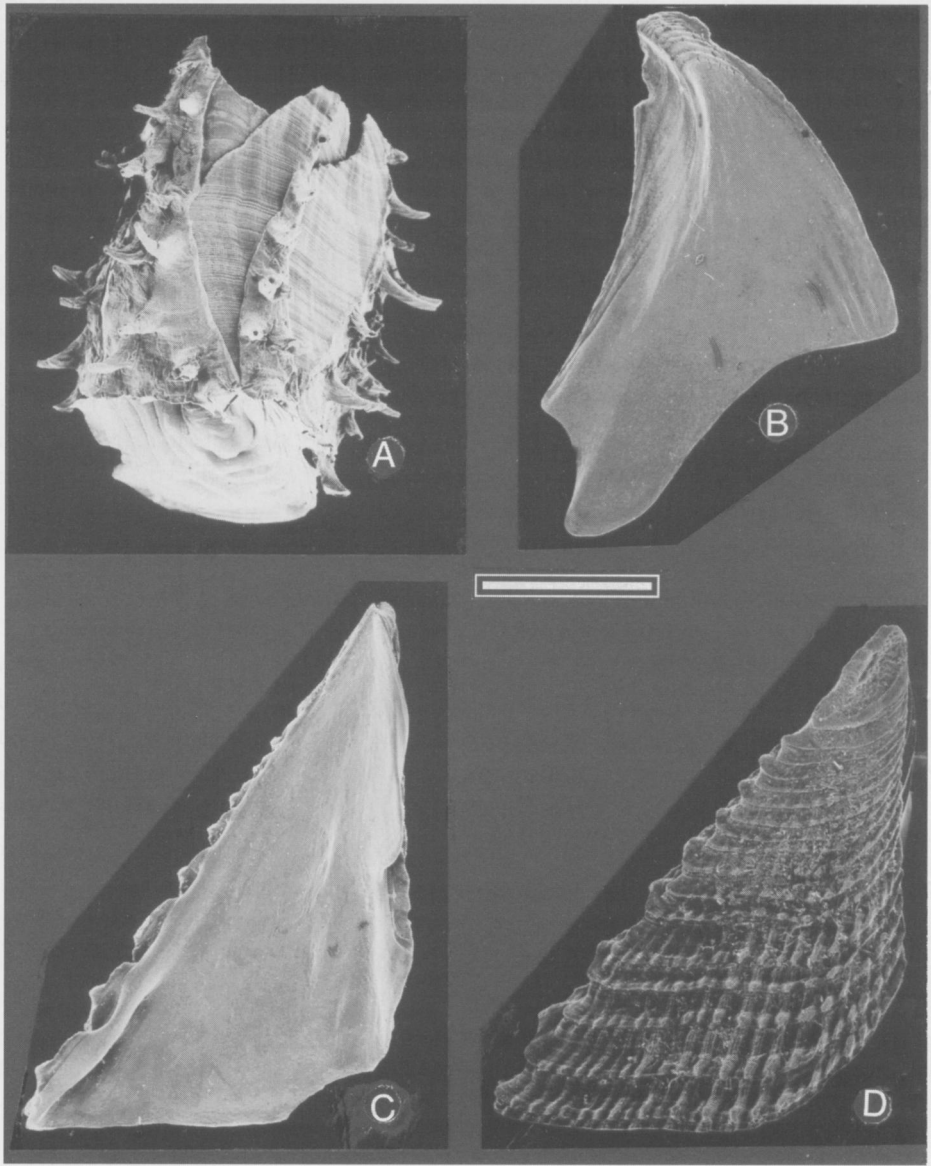


Fig. 8. *Acasta newmani* n. sp., CASIZ 106291, paratype. a, whole shell; b, tergum interior; c, scutum interior; d, scutum exterior. Scale bars equal 1 mm (a), 450 μ m (b), 430 μ m (c, d).

in shell shape due to crowding is well-known (see Newman & Ross, 1976, for explanation of various types of environmental influences on shell shape). However, the shell and scutal variation in *A. newmani* seems to be independent of crowding. That is, globose and tulipiform shells are found growing without contacting nearby individuals.

Variation also exists in scutal morphology (figs. 4a, b; 5a, b). Opercular plate variability associated with general shell shape has been noted for *Balanus amphitrite* Darwin, 1854 (cf. Van Syoc, 1992). However, in several specimens with shell shapes ranging from globose to tulipiform we found that scutal morphology

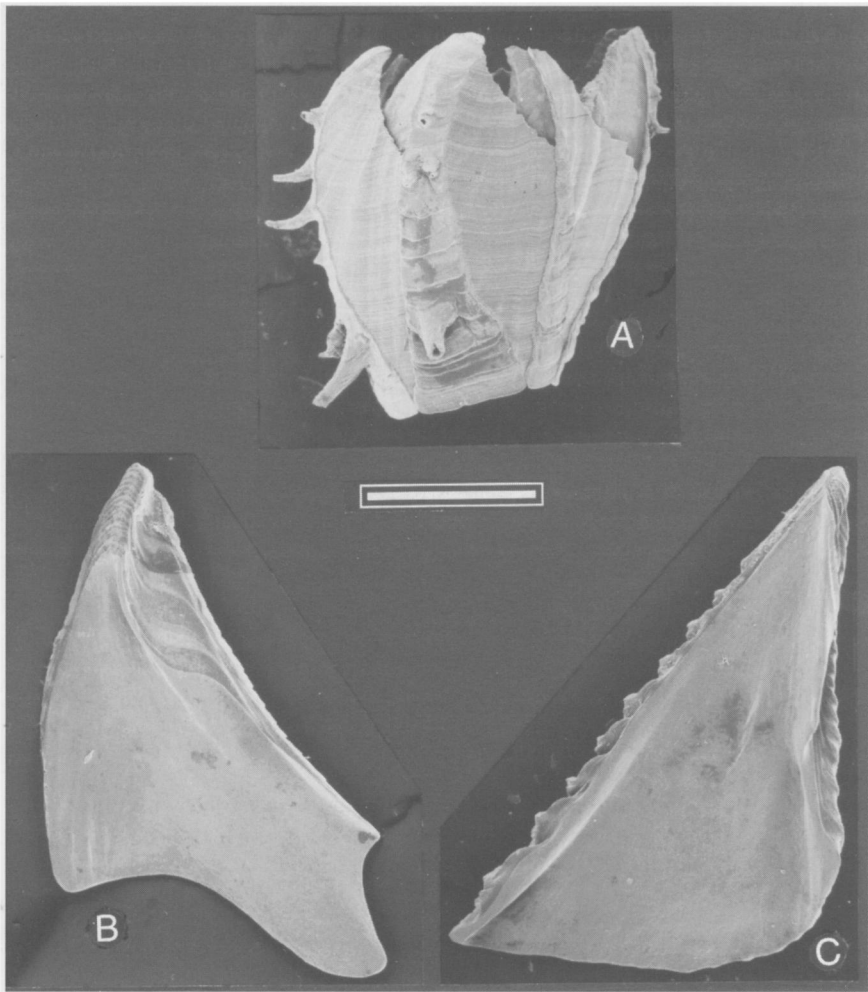


Fig. 9. *Acasta newmani* n. sp., CASIZ 106737, paratype. a, whole shell; b, tergum interior; c, scutum interior. Scale bars equal 1 mm (a), 430 μ m (b, c).

was not always correlated with shell shape. Indeed, no stable set of opercular plate, cirral, or trophi characters consistently correlated with shell shape. Therefore, we must conclude that the shell shape and scutal morphology variation is simply intraspecific variation and not indicative of a species level difference.

KEY TO SPONGE-INHABITING BARNACLES OF THE AMERICAS

1. Calcareous basis; shell with calcareous spines on exterior of parietes 2
 - Membranous basis; shell without calcareous spines on exterior of parietes 3
2. Shell pink, hooks on anterior margin of cirrus IV *A. cyathus* Darwin, 1854
 - Shell white, no hooks or “teeth” on cirrus IV *A. newmani* n. sp.
3. Rostrum longer than other compartmental plates 4
 - Rostrum shorter, or same length as, other compartmental plates 5
4. Radii present *M. declivis* (Darwin, 1854)
 - Radii lacking or very narrow *M. orcutti* (Pilsbry, 1916)
5. Basal margins of all compartmental plates rounded *M. robinae* Van Syoc, 1988
 - Not all compartmental plates with rounded basal margins 6
6. Parietes costate *M. costatus* Zullo & Standing, 1983
 - Parietes not costate *M. nebrias* Zullo & Beach, 1973

Published ranges and known hosts of sponge-inhabiting barnacles of the Americas are presented here. Records for *A. cyathus* and *M. orcutti* outside of the Americas are considered suspect and are therefore not listed.

A. cyathus Darwin, 1854:

- Darwin, 1854: 312, West Indies, in *Spongia tubulifera* (Lamarck, 1814), (= *S. officinalis* Linnaeus, 1759);
 Wells, 1966: 85, Gulf of Mexico (Florida), in *Spinosella* (= *Callyspongia*) *vaginalis* (Lamarck, 1814), *Ircinia felix* (Duchassaing & Michelotti, 1864), *Verongia* sp.;
 Zullo & Standing, 1983: 470, North Carolina, in unidentified mycalid, unidentified coppatiid, *Ircinia campana* (Lamarck, 1813), *Verongula ardis* (DeLaubenfels, 1950), *Cinachyrella kuekenthali* (Uliczka, 1929), *Erylus ministrongulus* (Hectel, 1965).

A. newmani n. sp.:

- Herein: Gulf of California, Mexico, in *Poecillastra tenuilaminaris* (Sollas, 1888).

M. declivis (Darwin, 1854):

- Darwin, 1854: 275, West Indies; Jamaica, no host given;
 Pearse, 1932: 119, Dry Tortugas, Florida, in *Spheciospongia vesparia* (Lamarck, 1814);
 Pilsbry, 1916: 230, off Cape Sable, Florida, no host given;
 Wells, 1966: 83, Gulf of Mexico (Florida), in *Spheciospongia vesparia*;
 Zullo & Standing, 1983: 471, North Carolina, in *Spheciospongia vesparia*.

M. orcutti (Pilsbry, 1916):

- Pilsbry, 1916: 233, San Ysidro, Baja California, in sponge;
 Jones, 1978: southern California, in *Spheciospongia confoederata* (DeLaubenfels, 1930), *Cliona celata californiana* DeLaubenfels, 1932.

M. robinae Van Syoc, 1988:

- Van Syoc, 1988: Gulf of California, in *Delaubenfelsia raromicroscлера* (Dickinson, 1945).

M. costatus Zullo & Standing, 1983:

Zullo & Standing, 1983: North Carolina, in *Anthosigmella varians* (Duchassaing & Michelotti, 1864).

M. nebrias (Zullo & Beach, 1973):

Zullo & Beach, 1973: Galapagos, in unidentified clionid;

Herein: Gulf of California, off Guaymas, Mexico, in *Delaubenfelsia raromicrosclera* (Dickinson, 1945).

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