

A new anchialine shrimp of the genus *Procaris* (Crustacea: Decapoda: Procarididae) from the Yucatan Peninsula

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Abstract.—A fourth species of the anchialine shrimp genus *Procaris* is described from Cozumel Island, Quintana Roo, México. The combination of character states observed for the abdomen, antennal scale/stylocerite, second antennular segment, carapace, eyes, rostrum, and telson is unique in the genus. The new species appears to be morphologically most closely related to *P. ascensionis* from Ascension Island. Cladistic analysis of differentiating character states supports a sister group relationship between *P. ascensionis* and the Mexican species, in two out of three most parsimonious hypotheses. In addition, the Bermudan *P. chacei* and Hawaiian *P. hawaiiiana* are positioned as sister taxa in all minimal length trees. While the discovery of a new *Procaris* species adds to our biogeographical knowledge of the genus, it has pointed to the possibility that the Atlantic taxa may be a paraphyletic assemblage.

Shrimps of the family Procarididae are restricted to anchialine habitats, and occupy an unclear position within the Decapoda relative to the Caridea (Christoffersen 1988, 1990; Felgenhauer & Abele 1983; Kensley & Williams 1986; Schram 1986). The Procarididae contains two genera, *Procaris* and *Vetericaris* Kensley & Williams, 1986. *Procaris* has perhaps the most interesting distribution of any anchialine decapod: *P. ascensionis* Chace & Manning, 1972 is restricted to Ascension Island in the mid-south Atlantic, *P. chacei* Hart & Manning, 1986 is endemic to Bermuda, and *P. hawaiiiana* Holthuis, 1973 is found on the Hawaiian archipelago. [A photograph of an undescribed "Procarid sp." from Christmas Island in the Indian Ocean has been published (Jones & Morgan 2002), although the habitus of the pictured specimen looks more atyid than procaridid.]

What is even more remarkable is the conservative morphology of *Procaris* species, considering the disjunct biogeography of

the taxa, as the three species differ in only a few characters (Hart & Manning 1986). *Vetericaris* is monotypic with the Hawaiian *V. chaceorum* Kensley & Williams, 1986 separated from any *Procaris* species by a plethora of character states. Despite the distinctiveness of *Procaris* and *Vetericaris*, the monophyly of the family has not been questioned. A recently described family for a genus of abyssal shrimp, the Galatheacarididae Vereshchaka, 1997, overlaps with the Procarididae in several key (albeit plesiomorphic) character states, indicating that the hypothesized connection between anchialine and abyssal caridean taxa of Hart et al. (1985) may not be entirely without merit. Interrelationships aside, an open question is how many additional anchialine and submerged cavernicolous carideans await discovery that could, potentially, complete the known biogeographical gaps.

Here we describe a fourth species of *Procaris*, from the Yucatan Peninsula. The discovery of this new species adds consider-

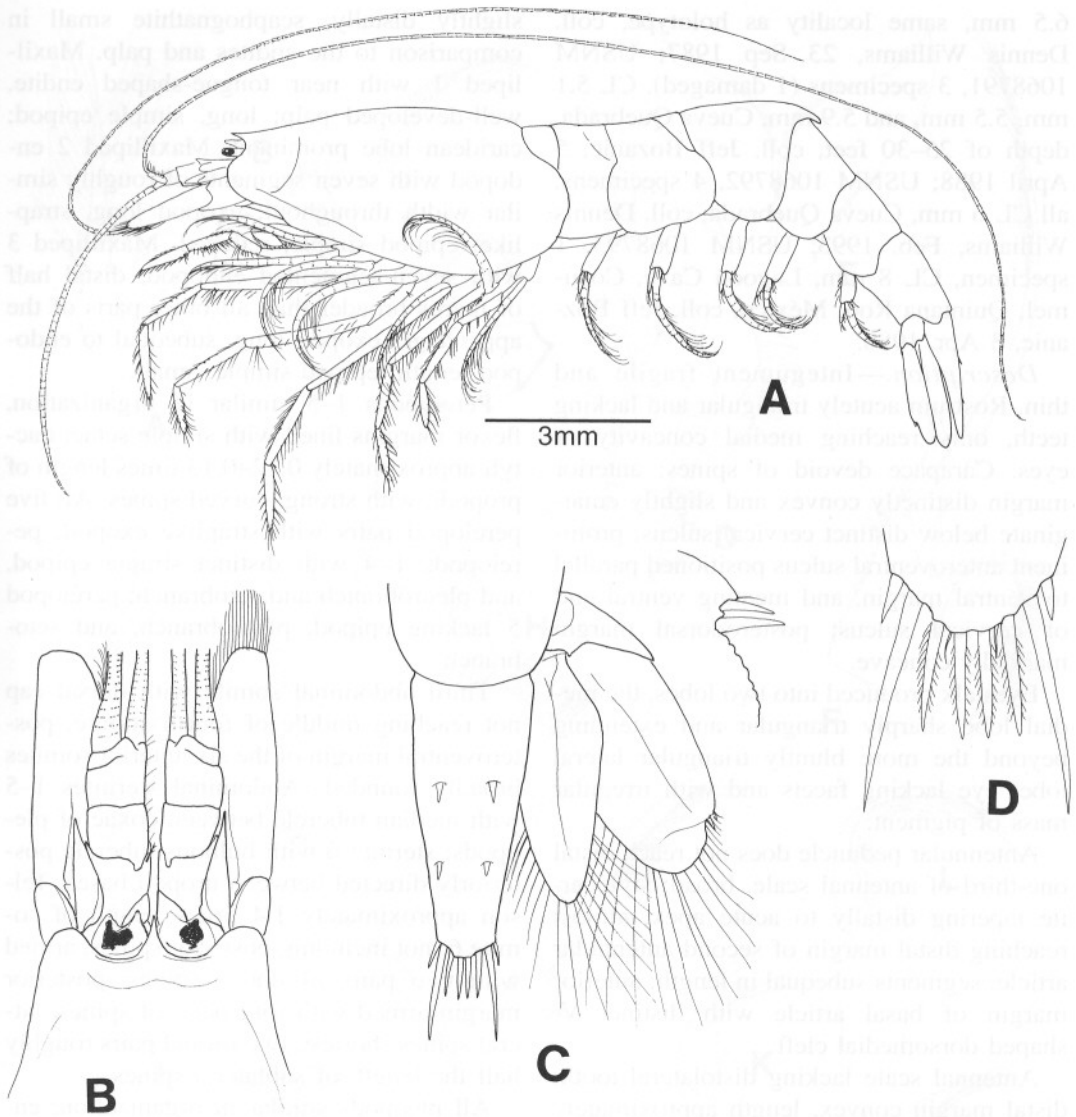


Fig. 1. *Procaris mexicana*, n. sp. A, habitus, lateral view; B, anterior region; C, telson and uropods; D, apex of telson.

ably to our biogeographic knowledge of the genus. The new *Procaris* material was collected by Drs. Dennis Williams and Jeff Bozanic who during the years 1988, 1989, and 1995 collected them from the cenotes of Quintana Roo, México. CL numbers refer to carapace length; USNM numbers denote catalog numbers in the National Museum of Natural History, Smithsonian Institution.

Procarididae Chace & Manning, 1972

Procaris mexicana, new species

Figs. 1–3, Table 1

Procaris sp. Kensley, 1988:688.

Material.—Holotype (USNM 1068789): México, Cueva Quebrada, Chankanaab Park, Cozumel, Quintana Roo, 25 September 1987, coll. Dennis Williams, CL 8 mm. Paratypes: USNM 1068790, 1 specimen, CL

6.5 mm, same locality as holotype, coll. Dennis Williams, 23 Sep 1987; USNM 1068791, 3 specimens (1 damaged), CL 5.1 mm, 5.5 mm, and 5.9 mm, Cueva Quebrada, depth of 25–30 feet, coll. Jeff Bozanic, 5 April 1988; USNM 1068792, 4 specimens, all CL 6 mm, Cueva Quebrada, coll. Dennis Williams, Feb. 1993; USNM 1068793, 1 specimen, CL 8 mm, Lagoon Cave, Cozumel, Quintana Roo, México, coll. Jeff Bozanic, 3 Apr. 1988.

Description.—Integument fragile and thin. Rostrum acutely triangular and lacking teeth, only reaching medial concavity of eyes. Carapace devoid of spines; anterior margin distinctly convex and slightly emarginate below distinct cervical sulcus; prominent anteroventral sulcus positioned parallel to ventral margin, and meeting ventral end of cervical sulcus; posterodorsal margin markedly concave.

Eyestalk produced into two lobes, the medial lobe sharply triangular and extending beyond the more bluntly triangular lateral lobe; eye lacking facets and with irregular mass of pigment.

Antennular peduncle does not reach distal one-third of antennal scale, broad; stylocerite tapering distally to acute apex, almost reaching distal margin of second antennular article; segments subequal in length; anterior margin of basal article with distinct V-shaped dorsomedial cleft.

Antennal scale lacking distolateral tooth, distal margin convex, length approximately 2.5 times the width; distal margin of scale reached by antennal peduncle.

Mandible pronouncedly developed, with three-segmented palp, molar and incisor processes forming one piece; incisor process subtrapezoidal, lacking distinct marginal teeth except for the two angular regions, scooplike. Paragnath sinuous, surrounding incompletely mandibular bases, distal end pointed, broadest around midlength. Endites of first maxilla well-developed, broad; palp simple. Second maxilla with two endites, distal endite with deep incision, palp pronounced and broader proximally, tapering

slightly distally, scaphognathite small in comparison to the endites and palp. Maxilliped 1 with near tongue-shaped endite, well-developed palp; long, simple epipod; caridean lobe prominent. Maxilliped 2 endopod with seven segments of roughly similar width throughout; exopod long, straplike; epipod simple, reduced. Maxilliped 3 with seven-segmented endopod, distal half of merus broader than all other parts of the appendage; exopod long, subequal to endopod length; epipod simple, small.

Pereiopods 1–5 similar in organization, flexor margins lined with simple setae; dactyli approximately 0.12–0.13 times length of propodi, with strong, curved spines. All five pereiopod pairs with straplike exopod; pereiopods 1–4 with distinct simple epipod, and pleurobranch and setobranch; pereiopod 5 lacking epipod, pleurobranch, and setobranch.

Third abdominal somite with dorsal cap not reaching middle of fourth somite; posteroventral margin of the six anterior somites broadly rounded. Abdominal sternites 1–5 with median tubercle between coxae of pleopods; sternite 6 with bulbous tubercle posteriorly directed between uropod bases. Telson approximately 1.4 times length of somite 6, not including posterior spines, armed with two pairs of dorsal spines; posterior margin armed with four pairs of spines, lateral spines shortest, two mesial pairs roughly half the length of sublateral spines.

All pleopods similar in organization; endopods short and weakly developed; appendices internae and masculinae absent from all pleopods.

Distribution.—Known only from anchialine habitats of Cozumel, Quintana Roo, Yucatan Peninsula, México.

Remarks.—All *Procaris* species are remarkably similar in morphology, differing slightly but specifically in a set of characters (Table 1; Hart & Manning 1986). This is significant given the immense distances separating all four taxa, especially *P. hawaiiiana* vis-à-vis the three Atlantic species. On the basis of biogeography, one might expect the

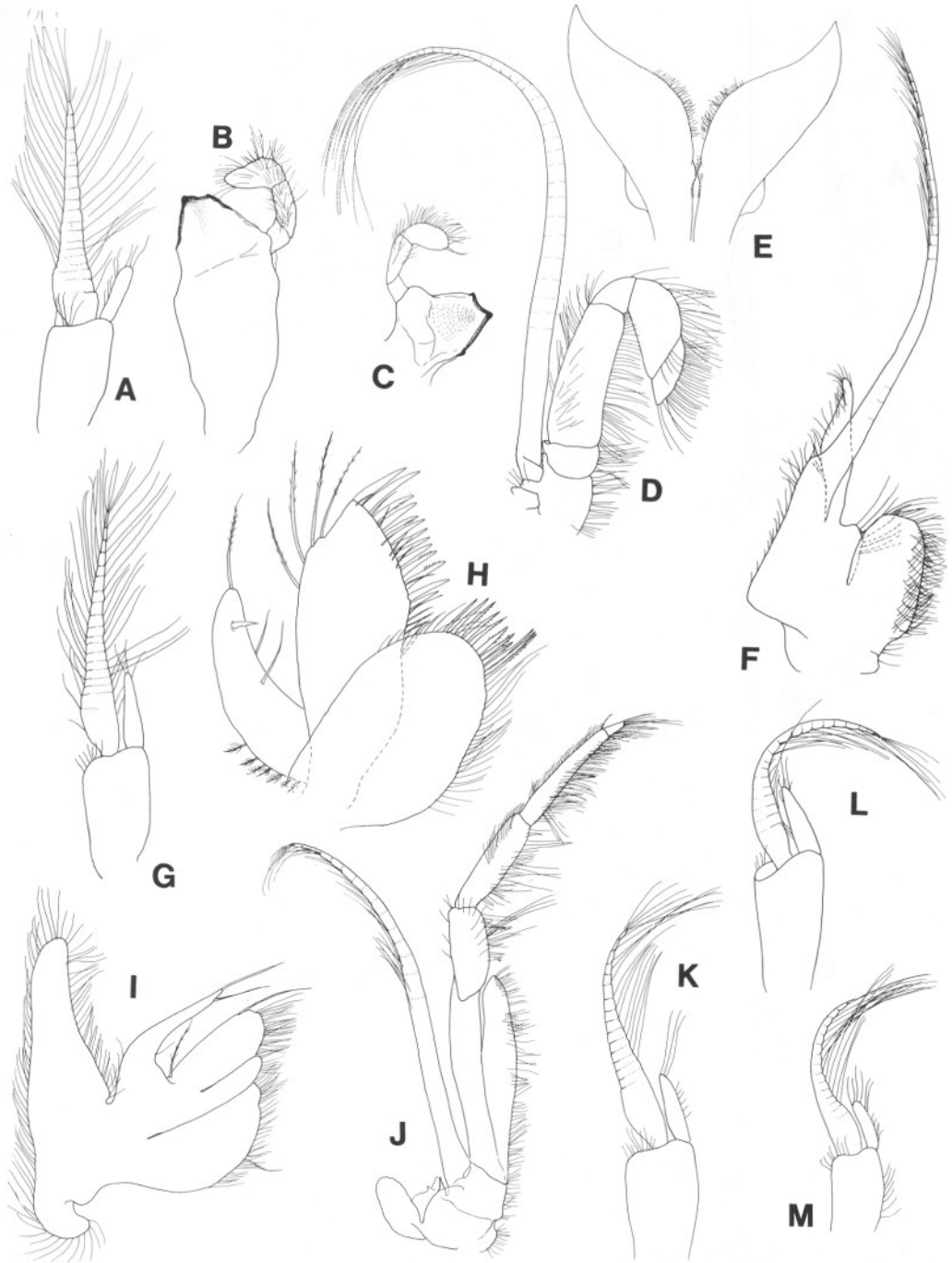


Fig. 2. *Procaris mexicana*: A, pleopod 4; B and C, mandible; D, second maxilliped; E, paragnaths; F, first maxilliped; G, pleopod 1; H, first maxilla; I, second maxilla; J, third maxilliped; K, pleopod 3; L, pleopod 2; M, pleopod 5.

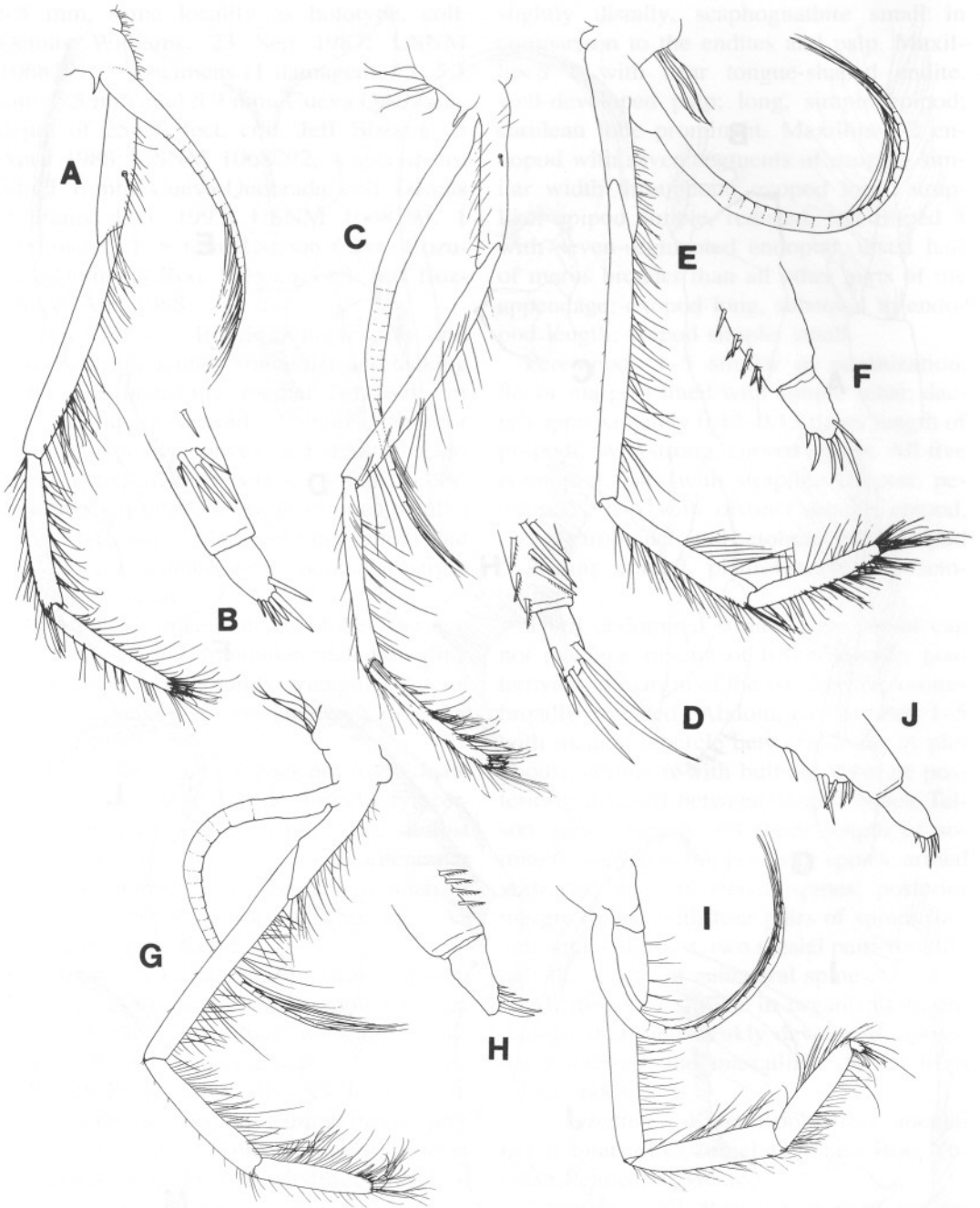


Fig. 3. *Procaris mexicana*: A, pleopod 1; B, same, dactyl; C, pereopod 2; D, same, dactyl; E, pereopod 3; F, same, dactyl; G, pereopod 4; H, same, dactyl; I, pereopod 5; J, same, dactyl.

Table 1.—Character state differences among the four species of *Procaris*. Plesiomorphic states = 0; apomorphies = 1, 2, and 3.

	<i>Vetericaris</i>	<i>P. ascensionis</i>	<i>P. chacei</i>	<i>P. hawaiiiana</i>	<i>P. mexicana</i>
1. Rostrum	not reaching medial concavity of eye (0)	reaches medial concavity (1)	overreaches medial concavity (2); reaches medial lobe	overreaches medial concavity (2); overreaches eyes	reaches medial concavity (1)
2. Eyes	median lobe longer (0)	median lobe longer (0)	lateral lobe equal to or longer than median lobe (1); lateral lobe longer	lobes equal (1)	median lobe longer (0)
3. Stylocerite	overreaching antennal segment 2 (0)	overreaching antennal segment 2 (0)	to end of antennal segment 2 or less (1); not reaching end of antennal segment 2	to end of antennal segment 2 (1)	almost to end of antennal segment 2 (1)
4. Antennal scale tooth	present (0)	absent (1)	present (0)	present (0)	absent (1)
5. Cervical sulcus	absent (0)	distinct (2)	weak (1)	weak (1)	distinct (2)
6. Third abdominal somite cap	absent (0)	to middle of fourth somite (2)	to middle of fourth somite (2)	beyond middle of fourth somite (3)	not reaching middle of fourth somite (1)
7. Posteroventral margin of fifth somite	narrowly rounded (0)	angular (2)	angular (2)	broadly rounded (1)	broadly rounded (1)
8. Length ratio: sixth abdomen somite to telson	~1.5 (0)	~1.75 (3)	~1.25 (2)	~1.4 (1)	~1.4 (1)

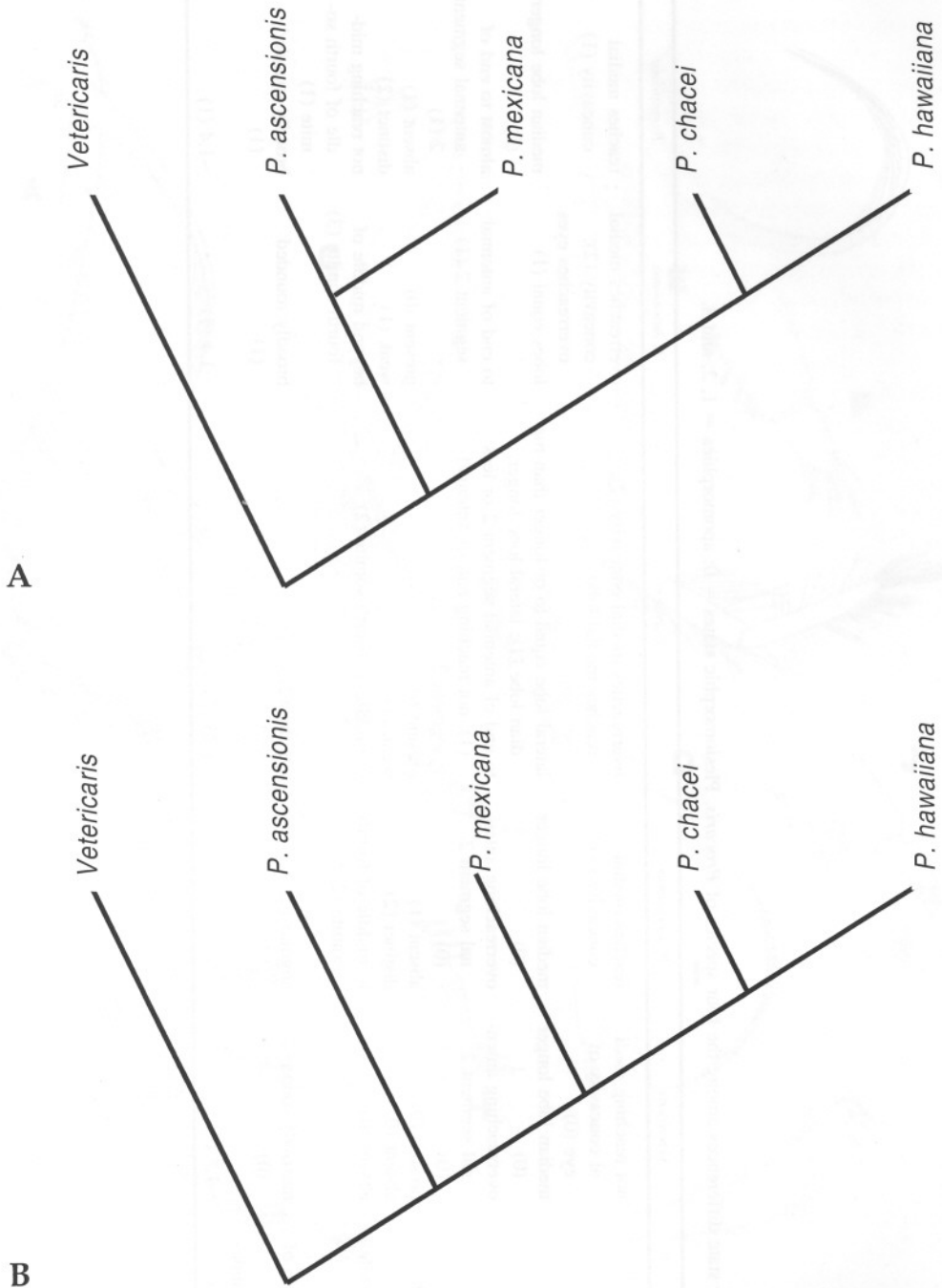


Fig. 4. Most parsimonious cladograms obtained with the data matrix in Table 2. A, single shortest length tree found with characters 1-7 ordered; B, one of two alternative minimal step topologies identified with all characters unordered (the other tree identical to A).

three Atlantic species to form a clade, with the Indo-Pacific *P. hawaiiiana* as the sister group of the lineage. However, a comparison of the character states presented in Table 1 affords no clear-cut separation between Atlantic and Pacific congeners. Each *Procaris* species instead appears to be a mosaic of character states found in the other taxa; species differences are due then to specific character state combinations as opposed to the presence of apomorphies. To test the possibility that *P. ascensionis*, *P. chacei*, and *P. mexicana* may be more closely related to each other than to *P. hawaiiiana*, a data matrix was prepared for parsimony analysis (Table 2), and *Vetericaris* was used as the outgroup for character state polarization (Table 1). The purpose of the cladistic test was twofold: to identify a parsimonious hierarchy of *Procaris* taxa, and to compare this hierarchy with biogeography.

When characters 1–7 were treated as ordered transformation series, one tree was obtained by Exhaustive Search using PAUP 3.1 software (Swofford 1993), with a length of 18 steps, consistency index (CI) value of 0.833, and a retention index (RI) number of 0.571 (Fig. 4A). This first hypothesis indicates that *P. ascensionis* and *P. mexicana* are sister species, with *P. chacei* and *P. hawaiiiana* forming a species pair. Placing the cladogram into the context of time and space, the split between Atlantic and Pacific *Procaris* species would have occurred after the emergence of two Atlantic clades: *P. ascensionis* and *P. mexicana* on the one hand, and the proto-*P. chacei*/*P. hawaiiiana* ancestor.

A second exhaustive search was performed though this time all characters were parameterized as unordered series. Two trees most parsimonious were found with lengths of 17 steps, CI = 0.882, and RI = 0.667. The topology of one of the cladograms is identical in structure to the one in Fig. 4A. The second hypothesis is also a resolved hierarchy, though with *P. ascensionis* branching off first, followed by *P. mexicana*, and

Table 2.—Data matrix used in the parsimony analysis. See Table 1 for explanation of character states.

Character	12345678
<i>Vetericaris</i>	00000000
<i>P. ascensionis</i>	10012223
<i>P. chacei</i>	21101222
<i>P. hawaiiiana</i>	21101311
<i>P. mexicana</i>	10112111

with *P. chacei* and *P. hawaiiiana* positioned as sister taxa (Fig. 4B).

Cladistic analysis of *Procaris* interrelationships indicates three things. First, *P. chacei* and *P. hawaiiiana* are more closely related to each other on morphological grounds than either is to any other *Procaris* species. Second, relationships between *P. ascensionis* and *P. mexicana* are ambiguous. Parsimony searches conducted with ordered and unordered characters support a sister group relationship between the two (Fig. 4A). Yet the hypothesis that *P. ascensionis* is basal to the remaining *Procaris* species (Fig. 4B) cannot be dismissed. Finally, the Atlantic species appear not to form a clade; i.e., they are a paraphyletic assemblage minus the inclusion of *P. hawaiiiana*.

One serious caveat of the parsimony study is the paucity of characters (eight) relative to the number of taxa (five). This reflects the extremely conservative morphology of *Procaris* species. Another caveat is the coding of character states (Table 1). Character states were coded to maximize hierarchical resolution given a limited number of characters. For instance, the rostrum character was divided into three character states: not reaching medial concavity of eyes (plesiomorphic); reaching medial concavity (apomorphic); overreaching medial concavity (also apomorphic). The way this character was coded for *Procaris* species, *P. chacei* and *P. hawaiiiana* have the same state. Yet the rostrum only reaches the median lobe in *P. chacei* although it overreaches the eyes in *P. hawaiiiana*. The same critique applies to character 2. Nevertheless, if characters are recoded to reflect all the differences seen,

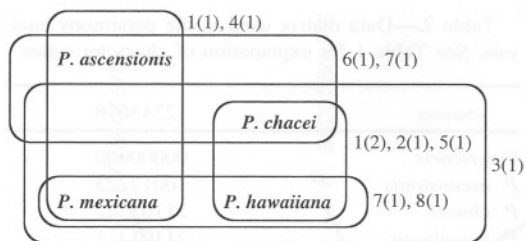


Fig. 5. Venn diagram of apomorphy-based groupings. Numbers to the right of a box denotes derived character states supporting a particular set of taxa.

the tree obtained is identical to that shown in Fig. 4A (unpublished results).

Figure 5 shows a Venn diagram of apomorphy-based relationships in *Procaris*, underscoring the polythetic nature of species differences.

Hart & Manning (1986) suggested that the remarkable similarity of *Procaris* species may be explained by the reduction of variability by natural selection. The "reduced variability" hypothesis appears rather weak considering that anchialine caridean taxa occurring with *Procaris* often exhibit considerable variability, morphs, and species-specific apomorphies (e.g., Kensley & Williams 1986, Smith & Williams 1981). It may be that the distribution of *Procaris* is much more extensive than currently known, with gene flow over great distances occurring via semi-continuous populations distributed among shallow submerged "crevicular" habitats (Hart et al. 1985, Maciolek 1983).

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