



## Phylogenetic analysis of the Paulsoni species (Decapoda: Alpheidae) from the American Pacific, with implications for the phylogenetic classification of the genus *Synalpheus*

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### Abstract

A cladistic analysis of 22 species of *Synalpheus*, represented primarily by species of the Paulsoni species group from the American Pacific and selected species from the Gambarelloides, Neomeris, Brevicarpus, and Biunguiculatus species groups was undertaken, based on 51 morphological characters. The Paulsoni species group proved to be paraphyletic, because species of the Neomeris, Brevicarpus, and Biunguiculatus species groups nested within it. It is proposed herein that in order to achieve a more natural classification, only two groups should be maintained within *Synalpheus*: Gambarelloides and Paulsoni, the latter in its broadest sense, treating the remaining species groups as synonyms.

**Key words:** American Pacific, Alpheidae, Caridea, *Synalpheus*, Phylogenetics

### Introduction

*Synalpheus* Bate, 1888 is one of the most diverse genera of Alpheidae, with species widely distributed along all the oceans. These shrimps constitute an important component of the cryptofauna from the intertidal zone. Many species live in symbiotic associations with corals, sponges and crinoids (Bruce, 1984; Chace, 1988). Approximately 115 species of *Synalpheus* are common in reef substrates from tropical and subtropical zones (Chace, 1988). Species of *Synalpheus* are known as snapping shrimps and pistol shrimps, because of the noise they produce by closing swiftly the disproportionately large and powerful fighting claw, apparently to indicate homeland defense (Duffy *et al.*, 2002; Anker *et al.*, 2006).

The systematic study of the genus *Synalpheus* has proven to be difficult (Chace, 1972, 1988; Banner and Banner, 1975; Dardeau, 1984; Hermoso Salazar *et al.*, 2005; Anker, 2001). There are many taxonomic problems, mainly because there are several morphologically similar and broadly distributed species. The apparent intraspecific variation and ambiguous morphological characters do not allow a clear identification of the species.

Coutière (1908, 1909) divided the genus *Synalpheus* into the Comatularum, Neomeris, Paulsoni, Brevicarpus, Laevimanus, and Biunguiculatus species groups, based on morphological features. Banner (1953) renamed the Biunguiculatus species group as Coutierei species group, due to confusion regarding the morphological, taxonomic and geographical distribution of *S. biunguiculatus* (Stimpson, 1860). Holthuis and Gottlieb (1958) renamed the Laevimanus species group as Gambarelloides species group, because *S. laevimanus* (Heller, 1862) was a junior synonym of *S. gambarelloides* (Nardo, 1847). Banner and Banner (1975) analyzed

Coutière's species groups and were unable to find diagnostic morphological characters for each group, noting that great modifications of the definition of the groups were necessary due to the description of new species, and concluded that only the Comatularum, Brevicarpus and Gambarelloides species groups were taxonomically valid. Chace (1972) and Dardeau (1984) also doubted the naturalness of Coutière's species groups.

At present, an analysis of all of the species of *Synalpheus* is beyond our capability. There are more than 130 species (Banner and Banner, 1975; Dardeau, 1988; Chace, 1988), many of which are poorly described and there may be several synonyms. There are few clear morphologically distinct characters for many species and intraspecific variation is imperfectly known. Although color patterns have proven useful in identification of alpheidids, the color of many species of *Synalpheus* has not been reported. Many species are found only in the Indo-Pacific region, where traveling to collecting sites and finding new fresh specimens may be difficult and expensive.

In the American Pacific, there are 22 species of *Synalpheus* (Wicksten and Hendrickx, 2003; Hermoso and Álvarez, 2005; Hermoso Salazar *et al.*, 2005; Hermoso Salazar and Hendrickx, 2005), basically belonging to the Paulsoni species group. As a start in analyzing the phylogenetic relationships within *Synalpheus*, we undertook an analysis of these species and some similar western Atlantic species.

## Methods

We analyzed 22 species of *Synalpheus* from the East Pacific (including one undescribed species) and five within the Paulsoni species group from the West Atlantic. Species belonging to other species groups were used as outgroups. *Potamalpheops stygicola* (Hobbs, 1973) and *Alpheus paracrinitus* Miers, 1881 were used to root the cladograms.

Specimens analyzed are deposited in the following collections: National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A. (USNM); Natural History Museum of Los Angeles, California, U.S.A. (LACM); Texas A&M University, College Station, Texas, U.S.A. (TAMU); Muséum National d'Histoire Naturelle, Paris, France (MNHN); National Collection of Crustaceans, Instituto de Biología, UNAM, Mexico (CNC); Laboratory of Ecology and Biodiversity of Marine Invertebrates, Instituto de Ciencias del Mar y Limnología, UNAM, Mexico (CPICML); Collection of Invertebrates, Mazatlán, Instituto de Ciencias del Mar y Limnología, UNAM, Mexico (EMU); and Universidad Autónoma de Baja California Sur (CCUABCS) (Table 1). We examined approximately 30 or more specimens of some species (*S. bannerorum* Abele, 1975, *S. biunguiculatus*, *S. charon* [Heller, 1861], *S. digueti* Coutière, 1909, *S. mexicanus* Coutière, 1909, *S. nobilii* Coutière, 1909, *S. occidentalis* Coutière, 1909, *S. peruvianus* Rathbun, 1910, *S. sanjosei* Coutière, 1909, *S. superus* Abele and Kim, 1989, *S. stylopleuron* Hermoso Salazar and Hendrickx, 2005, *S. scaphoceris* Coutière, 1910, *S. apioceros* Coutière, 1909, *S. wickstenae* Hermoso Salazar and Hendrickx, 2005, and *Synalpheus* sp, an undescribed species from western Mexico in our collections); of others, we examined more or less 10 specimens (*S. brevispinis* Coutière, 1909, *S. fritzmulleri* Coutière, 1909, *S. lani* Hermoso and Álvarez, 2005, *S. lockingtoni* Coutière, 1909, *S. paulsonoides* Coutière, 1909, and *S. spinifrons* [H. Milne-Edwards, 1837]). We analyzed only type material of four species (*S. arostris* Wicksten, 1989, *S. sanlucasi* Coutière, 1909, *S. townsendi productus* Coutière, 1909, and *S. apioceros mayaguensis* Coutière, 1909). When no specimens were available, we used data from the literature (*S. mulegensis* Ríos, 1992) (Table 1). The specimens of each species were examined to assess their degree of variation. Specimens were stained with methylene blue, examined under dissecting and compound microscopes, and measured using an ocular reticule calibrated to a stage micrometer.

We identified 51 morphological characters for the phylogenetic analysis (Table 2; Figs. 1–3). Multistate characters 17 and 26 were treated as non-additive, and the remaining as additive. Characters with no information available were assigned a missing code (?). The analysis of the data matrix (Table 3) was performed with Nona 2.0 (Goloboff, 1999) and WinClada 1.00.08 (Nixon, 2002).

**TABLE 1.** Taxa included in the analysis, with indication of the sources of the specimens and the type material analyzed. Atl.= Atlantic Ocean; H= holotype; L= lectotype; P= paratypes; N= neotype; O= other material.

Taxon	Coutière's species groups	Material examined or source
<i>A. paracrinitus</i>		O (CNC)
<i>P. stygicola</i>		O (CNC)
<i>S. arostris</i>	-	H (AHF)
<i>S. bannerorum</i>	Neomeris (?)	H, P, O (USNM, CNC, CPICML)
<i>S. biunguiculatus</i>	Biunguiculatus (= <i>Couti_rei</i> )	N, O (USNM, CNC, EMU, CPICML, CCUABCS)
<i>S. brevispinis</i>	Paulsoni	O (TAMU, CNC, CPICML)
<i>S. charon</i>	Neomeris	O (CNC, EMU, CPICML, CCUABCS)
<i>S. digueti</i>	Brevicarpus	O (USNM, CNC, EMU, CPICML, CCUABCS)
<i>S. fritzmuelleri</i>	Neomeris	L, O (USNM, CNC)
<i>S. lani</i>	Paulsoni	H, P, O (CNC)
<i>S. lockingtoni</i>	Paulsoni	H, O (USNM, CPICML)
<i>S. mexicanus</i>	Paulsoni	H, O (USNM, CNC, CPICML)
<i>S. mulegensis</i>	Gambarelloides (= <i>Laevimanus</i> )	Ríos (1992)
<i>S. nobilii</i>	Neomeris	H, O (USNM, CNC, EMU, CPICML, CCUABCS)
<i>S. occidentalis</i>	Gambarelloides (= <i>Laevimanus</i> )	O (CPICML)
<i>S. paulsonoides</i>	Paulsoni	Coutière, 1909
<i>S. peruvianus</i>	Paulsoni	H, O (USNM, EMU)
<i>S. sanjosei</i>	Paulsoni	H, O (MNHN, CNC, EMU, CPICML, CCUABCS)
<i>S. sanlucasi</i>	Paulsoni	H (USNM)
<i>S. spinifrons</i>	Neomeris	O (USNM)
<i>S. superus</i>	Paulsoni	H, P (USNM)
<i>S. stylopleuron</i>	Paulsoni	H, P, O (EMU)
<i>S. wickstenae</i>	Paulsoni	H, P, O (EMU)
<i>Synalpheus</i> sp	Brevicarpus	O (USNM, CNC, CPICML, CCUABCS)
<i>S. townsendi</i> Atl.	Paulsoni	H, O (USNM, CNC)
<i>S. t. productus</i> Atl.	Paulsoni	H (USNM)
<i>S. scaphoceris</i> Atl.	Paulsoni	H, O (USNM, CNC)
<i>S. apioceros</i> Atl.	Paulsoni	H, O (USNM, CNC)
<i>S. a. mayaguensis</i> Atl.	Paulsoni	H (USNM)

**TABLE 2.** List of the characters and character states analyzed.

1. Epipod on pereopods: (0) present; (1) absent.
2. Eyes: (0) exposed dorsally; (1) covered dorsally.
3. Rostrum: (0) present; (1) absent.
4. Ocular teeth: (0) absent; (1) present.
5. Ocular process: (0) present; (1) absent.
6. Rostrum, direction: (0) distally not upturned; (1) distally upturned.
7. Length of rostrum compared to length of ocular teeth: (0) subequal (Figs. 1A-C); (1) clearly longer (Figs. 1A, D).
8. Width of rostrum compared to width of ocular teeth: (0) narrower; (1) subequal.
9. Space of anterior margin of carapace between ocular teeth and base of rostrum: (0) rostrum or ocular teeth absent; (1) reduced (Fig. 1A); (2) concave (90°) (Fig. 1D); (3) concave (180°); (4) wide and straight (Figs. 1B, C).
10. Length vs. width of ocular teeth: (0) wider than long (Fig. 1A); (1) subequal (Figs. 1B-D); (2) longer than wide.
11. Shape of external margin of ocular hoods: (0) not notably convex (Figs. 1B-D); (1) notably convex (Fig. 1A).
12. Ventrorostral process: (0) absent or only dome; (1) present, not bilobed; (2) present, bilobed.
13. Length vs. width of antennular peduncle: (0) > 5 times (Fig. 1C); (1) approximately 4 times (Figs. 1A, B, D); (2) between 3-3.5 times; (3) < 3 times.
14. Extent of stylocerite compared to distal margin of first antennular segment: (0) shorter; (1) clearly longer.
15. Scaphocerite blade: (0) well-developed; (1) poorly developed; (3) absent.
16. Extent of lateral spine scaphocerite compared to distal margin of carapocerite: (0) clearly overreaching (Fig. 1D); (1) about the same length; (2) shorter (Figs. 1B, C).

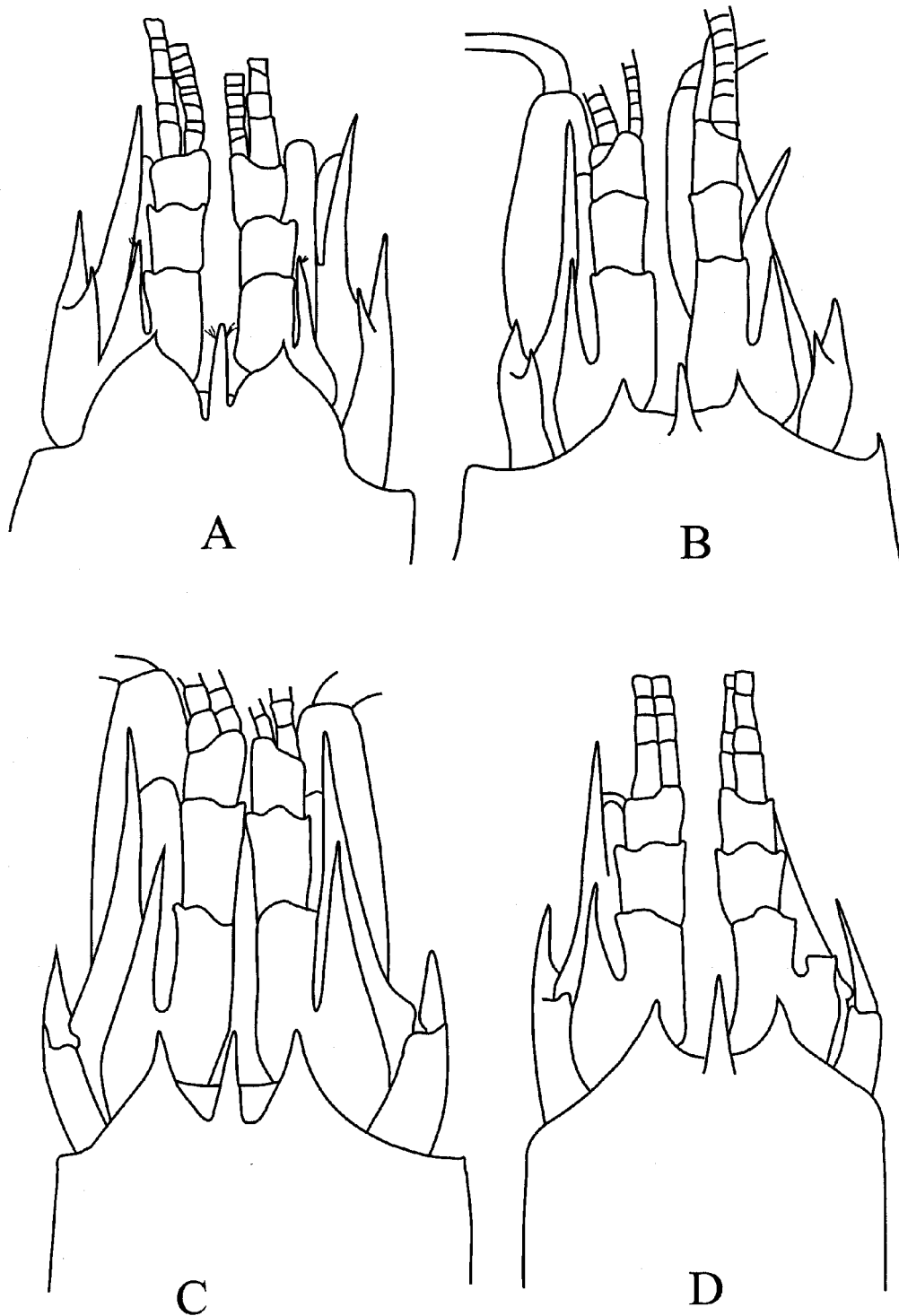
17. Extent of lateral spine scaphocerite compared to distal margin of antennular peduncle: (0) about the same length (Fig. 1C); (1) shorter; (2) clearly longer (Figs. 1A, B, D).
18. Length vs. width of carpoperite: (0) < 4 times; (1) ca. 4 times; (2) > 5 times.
19. Extent of carpoperite compared to distal margin of antennular peduncle: (0) shorter; (1) about the same length (Fig. 1D); (2) clearly longer (Figs. 1B, C).
20. Length of dorsal spine of basicerite: (0) absent (Fig. 1C); (1) present, very small (Fig. 1D); (2) present, short; (3) present, long (Figs. 1A, B).
21. Extent of lateral spine of basicerite compared to first segment of antennular peduncle: (0) clearly shorter (Figs. 1B, C); (1) about the same length (Fig. 1D); (2) longer (Fig. 1A).
22. Extent of lateral spine basicerite compared to stylocerite: (0) clearly shorter (Fig. 1B-D); (1) about the same length; (2) longer (Fig. 1A).
23. Spines on apex of third maxilliped: (0) present; (1) absent.
24. Length of fingers of major first pereopods compared to palm: (0) > 0.5; (1) < 0.5.
25. Length of fixed finger of major first pereopods compared to dactyl: (0) subequal; (1) clearly shorter.
26. Projection on dorsal distal margin of palm of major first pereopods: (0) absent; (1) tapering acute spine; (2) acute spine on basal tubercle; (3) tapering tubercle.
27. Lobe on dorsal distal margin next to spine of palm of major first pereopods: (0) both absent; (1) lobe absent and spine present; (2) both present.
28. Spine or projection on dorsal distal margin of merus of major first pereopods: (0) absent; (1) present.
29. Dorsal margin of merus of major first pereopods: (0) slightly convex (Fig. 2A); (1) convex (Fig. 2B); (2) strongly convex.
30. Spine on dorsal distal margin of palm of minor first pereopods: (0) absent; (1) present.
31. Transverse dorsal setal combs on dactyl of minor first pereopods: (0) absent; (1) present.
32. Length vs. width of carpus of minor first pereopods: (0) clearly longer than wide; (1) subequal.
33. Length of carpus of minor first pereopods compared to half length of palm: (0) clearly longer; (1) subequal; (2) clearly shorter.
34. Spine or projection on dorsal distal margin of merus of minor first pereopods: (0) absent; (1) present.
35. Spine of dorsal margin of merus of minor first pereopods: (0) absent; (1) present.
36. Width vs. length of dactyl of third pereopods: (0) < 0.33 (Fig. 2C); (1) approximately 0.33 (Fig. 2D); (2) > 0.33.
37. Prominence on dactyl of third pereopods: (0) absent; (1) present.
38. Dactyl of third pereopods: (0) not biunguiculate; (1) biunguiculate.
39. Relative size of unguis on dactyl of third pereopods: (0) subequal in length; (1) clearly unequal.
40. Width at base of unguis on dactyl of third pereopods: (0) subequal in length; (1) clearly unequal.
41. Unguis wider on dactyl of third pereopods: (0) dorsal; (1) ventral.
42. Direction of ventral unguis compared to dorsal unguis of third pereopods: (0) subparallel (Fig. 2C); (1) slightly curved (Fig. 2D).
43. Length vs. width of merus of third pereopods: (0) > 4 times (Fig. 2C); (1) between 3-4 times (Fig. 2D); (2) < 3 times.
44. Spines on ventral margin of merus of third pereopods: (0) absent; (1) present.
45. Internal appendix on second to fifth male pleopods: (0) present; (1) absent.
46. Posterior ventral margin of first abdominal pleura of male: (0) rounded; (1) scarcely produced; (2) produced; (3) strongly produced.
47. Third abdominal pleura of male: (0) not produced (Fig. 3A); (1) produced (Fig. 3B).
48. Number of fixed teeth on uropodal exopod: (0) one; (1) more than two.
49. Anterior width in relation to posterior width of telson: (0) more than twice wider than posterior; (1) approximately twice; (2) less than twice wider than posterior.
50. Dorsal spines on telson: (0) near lateral margin; (1) between lateral margin and median line (Figs. 3D, E); (2) near median line (Fig. 3C).
51. Distal margin of telson: (0) notably convex (Fig. 3C); (1) convex (Fig. 3D); (2) not convex (Fig. 3E).

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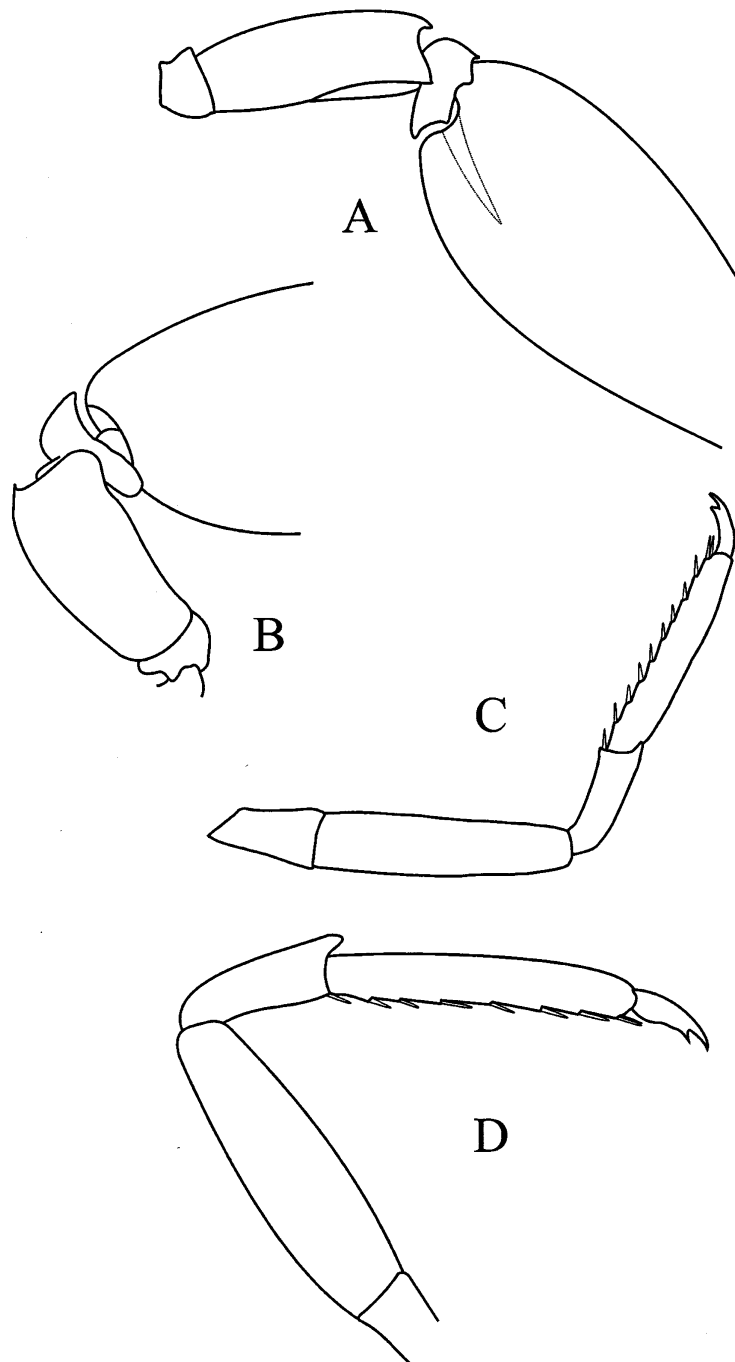
## Results and discussion

The analysis of the data matrix (Table 3) led to four equally parsimonious cladograms, with 241 steps, consistency index of 0.33 and retention index of 0.53. The strict consensus cladogram (Fig. 4) had 265 steps, a consistency index of 0.33 and a retention index of 0.59. According to our results, the Paulsoni species group does not represent a monophyletic group. The clade including *S. mulegensis* and *S. occidentalis*, which belong to

the Gambarelloides species group, is the sister taxon to the remaining species of *Synalpheus* analyzed herein. The remaining species constitute a large clade, with *S. charon* as the sister species to the remaining. Within it, three small subgroups are defined. The first includes *S. biunguiculatus*, *S. scaphoceris* and *S. brevispinis*; the second subgroup includes *S. fritzmuelleri*, *S. nobilii*, and *S. sanlucasi*; and the third subgroup includes *S. digueti* and *Synalpheus* sp.



**FIGURE 1.** Dorsal view of frontal portion of caparace: A, *S. bannerorum* (holotype); B, *S. superus* (holotype); C, *S. peruvianus* (holotype); D, *S. mexicanus* (holotype).

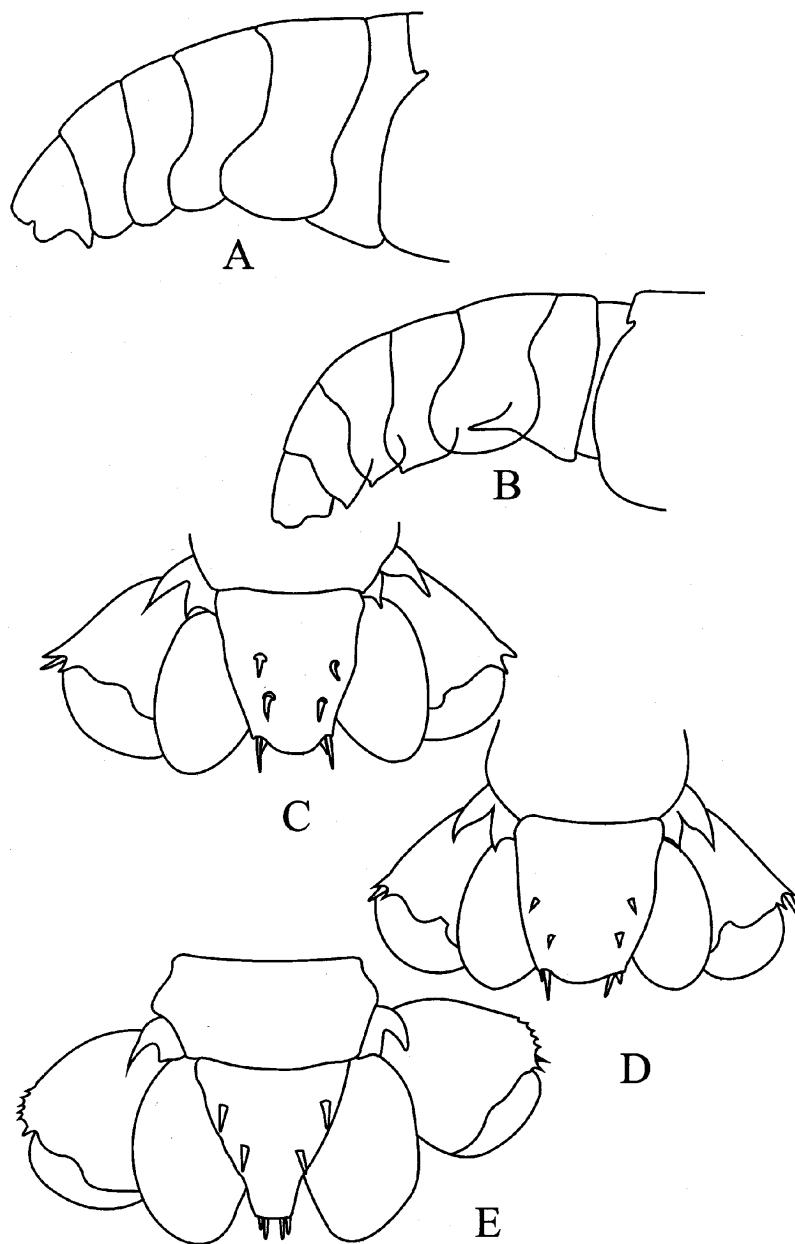


**FIGURE 2.** Major cheliped: A, *S. biunguiculatus* (neotype); B, *S. lockingtoni* (holotype). Third pereopod: C, *S. brevispinis*; D, *S. lockingtoni* (holotype).

Duffy *et al.* (2000) proposed a phylogeny for the Gambarelloides species group (13 species) from the American Atlantic, hypothesizing the monophyly of this group. Morrison *et al.* (2004) also agreed with this hypothesis when analyzing species from the same area, but included 31 species that are symbionts of sponges. They analyzed both molecular and morphological characters. Our results agree with Morrison's *et al.* (2004) conclusion. Our cladogram shows that the Gambarelloides species group (*S. mulegensis* and *S. occidentalis*) is a monophyletic clade, and appears as sister taxon to the remaining species of *Synalpheus*. The remaining species constitute a monophyletic group supported by three characters: stylocerite clearly overreaching distal margin of first segment of antennular, carpus of minor first pereopod as long as wide, and merus of third pereopod between 3-4 times as long as wide. This group includes the species of the Neomeris, Paulsoni,



Brevicarpus and Biunguiculatus species groups, and *S. arostris*. This latter species, which lacks a rostrum, was used to illustrate the difficulties in finding relationships among the species of *Synalpheus*, because it is difficult to place this species in any of Coutière's species groups (Wicksten, 1989).



**FIGURE 3.** Abdomen, lateral view: A, *S. lani* (holotype); B, *S. mexicanus* (holotype). Telson and uropods, dorsal view: C, *S. peruvianus* (holotype); D, *S. mexicanus* (holotype); E, *S. lani* (holotype).

Our results indicate that the Paulsoni species group is a paraphyletic group (Fig. 4). Its species have many taxonomic, and morphological problems, because the characters used to identify them are subtle and may lead to confusion. Coutière (1909) included 13 species from both of the American coasts, of which eight had subspecies. Some of them have been synonymized; and in others, subspecies have been elevated to species (Holthuis, 1952; Dardeau, 1984; Wicksten, 1994; Hermoso Salazar *et al.*, 2005). Five other species of the Paulsoni group have been described for the American Pacific (Rathbun, 1910; Abele and Kim, 1989; Hermoso and Álvarez, 2005; Hermoso Salazar and Hendrickx, 2005). Undoubtedly, there are more species yet to be described. According to Coutière (1909), all the species in the Paulsoni species group have the following features: ocular teeth always longer than wide, process ventrorostral bilobed, dactyl long and slender, unguis



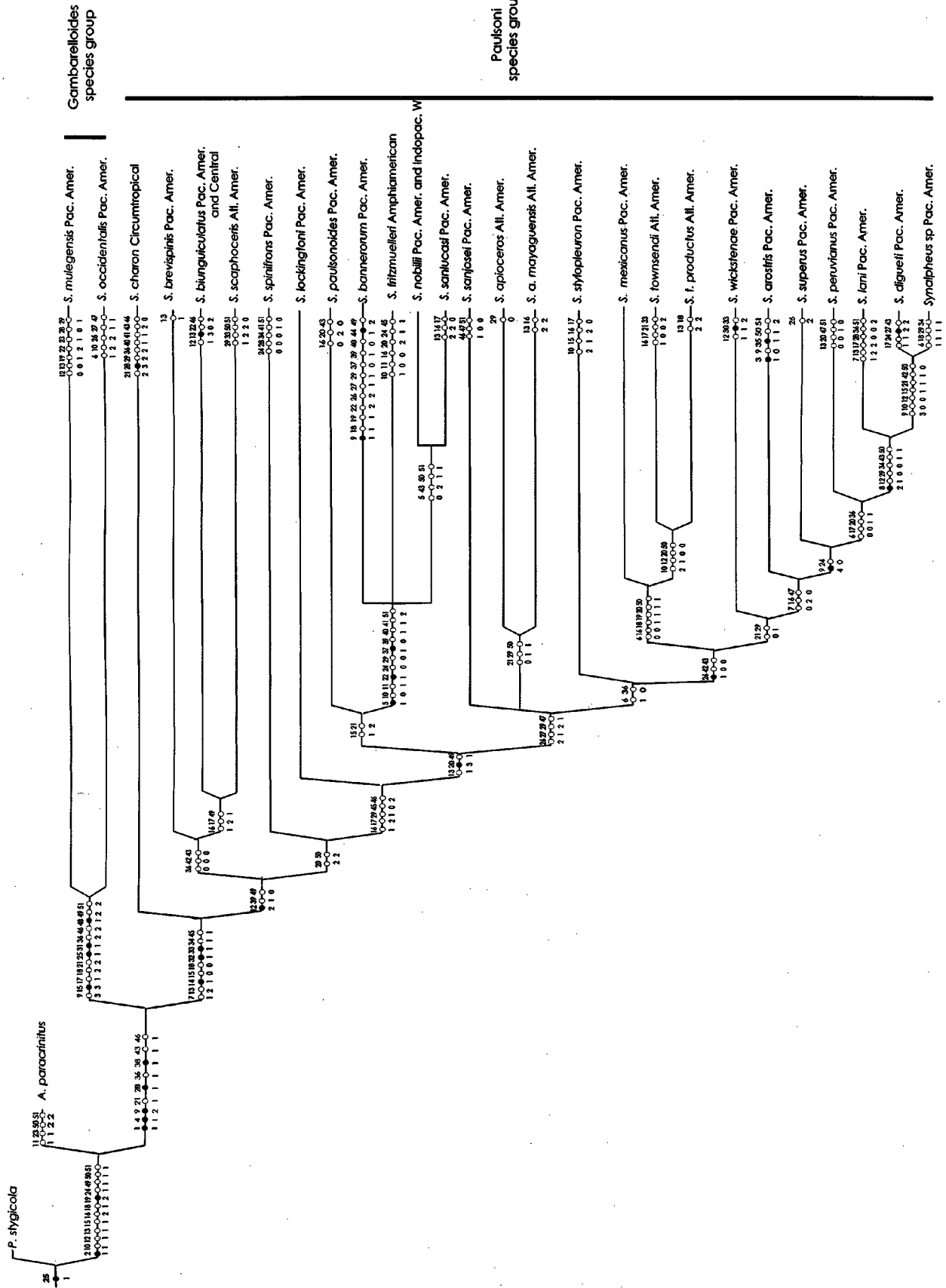


FIGURE 4. Strict consensus tree of four equally parsimonious trees obtained for the American Pacific species the *Synalpheus* based on 53 morphological characters.

equal in width, ventral unguis shorter than dorsal and little curved, without spines on merus of third pereopods. Our study detected some imprecision in these characters due to intraspecific variation. Banner and Banner (1975) arrived at a similar conclusion when reexamining Coutière's species groups.

Of particular interest in the present study is the placement of *S. brevispinis* and *S. scaphoceris* within the Paulsoni species group. They are close to *S. biunguiculatus* in the first subgroup. The Biunguiculatus species group is characteristic of the Indo-Pacific, in the American Pacific being known only by *S. biunguiculatus*. In this phylogenetic analysis, we reviewed the neotype selected by Banner (1953) from the Hawaiian Islands. This specimen has different morphological characteristics from those in Coutière's description of the Biunguiculatus species group. Its stylocerite visibly overreaches the middle of the second segment of the antenular peduncle, the scaphocerite is broad and its tip reaches the end of the antennular peduncle, the lateral spine of the basicerite reaches the middle of the first segment of the antenular peduncle, the dactylus of the third pereopods is long and thin, and the ventral unguis is not clearly curved. According to Coutière (1909), in this group the stylocerite does not overreach the middle of the second segment antennular, the scaphocerite is narrow and does not reach beyond the end of the second segment antennular, the lateral spine of the basicerite is always longer than the first antennular segment, and the dactylus of the third pereopods is short, with the ventral unguis strongly curved. We agree with Banner and Banner (1975) that the Biunguiculatus species group cannot be accepted, because some species from Australia violate each characteristic as set forth by the definition.

**TABLE 4.** Morphological comparison between the *S. gambarelloides* and *S. paulsoni* species groups. Asterisks denote characters that may apply only to species of the Eastern Pacific.

	Gambarelloides species group	Paulsoni species group
Extent of stylocerite	Not overreaching distal margin of first antennular segment (except in <i>S. mcclendoni</i> and <i>S. paraneptunus</i> )	Clearly overreaching distal margin of first antennular segment
Scaphocerite blade	Frequently absent or reduced	Present
Length of fixed finger of major first pereopods	Clearly shorter than dactyl*	Subequal in length to dactyl
Transverse dorsal setal combs on dactyl of minor first pereopods	Present	Absent
Length vs. width of carpus of minor first pereopods	Clearly longer than wide	Subequal
Length of carpus of minor first pereopods	Clearly longer than half length of palm	Subequal in length or clearly shorter than half length of palm
Number of fixed teeth on uropodal exopod	More than two*	One
Distribution	West Atlantic (the best represented), East Atlantic, East Pacific and Indo-Pacific West	East Pacific (the best represented), Indo-Pacific West, East and West Atlantic

The species of the Neomeris species group do not constitute a monophyletic group. *S. charon* in this study appears to be separate from the remaining species: *S. fritzmulleri*, *S. nobilii* and *S. sanlucasi*. This latter subgroup is supported by two synapomorphies: the lateral spine basicerite reaching to the stylocerite and the prominence of the dactyl of the third pereopods obtuse or spinous.

The addition of new species, especially *S. bannerorum*, caused greater modifications of the definition of the species groups. Its placement in the Neomeris species group was mentioned by Morrison *et al.* (2004). For Coutière (1909), the characteristics of the Neomeris species group were the following: ventral unguis of the

third pereopods always stronger than dorsal and often accompanied by obtuse or spinous prominence, ocular teeth always longer than wide, and merus of third pereopods spinous. Of these characteristics, *S. bannerorum* only coincides in the presence of spines on the merus of the third pereopods. This suggests again that Coutière's species groups cannot be regarded as being of taxonomic use nor of systematic importance, except the Gambarelloides species group. In the present phylogenetic analysis *S. bannerorum* has two autapomorphies: the space on the anterior margin of the carapace between the ocular teeth and the base of rostrum is reduced and there are spines on the merus of the third pereopod. *S. dominicensis* Armstrong, 1949 from the Dominican Republic also has spines on the merus of third pereopods. In Morrison's *et al.* (2004) cladogram, both species are the sister clade of the Gambarelloides species group.

Based on our phylogenetic analysis and the findings of previous authors (Duffy *et al.*, 2000; Morrison *et al.*, 2004; Anker *et al.*, 2006), we postulate that a more natural classification may be achieved by considering that the genus *Synalpheus* is comprised of two species groups (Table 4): Gambarelloides and Paulsoni (in its broadest sense given herein, by treating all other groups as synonyms). Further studies and a more global sampling of taxa will allow to contrast our hypothesis and refine the relationships of smaller clades within *Synalpheus*.

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