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Phylogeny of the family Spongicolidae (Crustacea: Stenopodidea): evolutionary trend from shallow-water free-living to deep-water sponge-associated habitat

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The phylogenetic relationships within the family Spongicolidae were examined based on a cladistic analysis of 38 adult morphological characters with reference to two outgroup species of the family Stenopodidae. The strict consensus tree identified *Microprosthema* as the most basal genus, followed by *Paraspongicola*, *Spongicola* and the remaining genera. The *Spongicoloides* represents the most derived genus among spongicolids. The genera *Spongicola, Spongicoloides* and *Spongiocaris* should be redefined, because they formed paraphyletic clades. The cladogram indicates that symbiosis with the hexactinellid sponges is coincident with the loss of gills, exopods on maxillipeds 2 and 3, and with the loss of spination on carapace, pereopods, abdomen, tail fan etc. These losses in the spongicolids are thought to be secondarily derived in relation to their sponge-associated habitat.

INTRODUCTION

The family Spongicolidae is a relatively small group of marine decapod crustaceans. A total of 28 species and two subspecies are recognized and at present assigned to the following five genera: *Microprosthema* Stimpson, *Paraspongicola* de Saint Laurent and Cleva, *Spongicola* de Haan, *Spongicoloides* Hansen, and *Spongiocaris* Bruce & Baba (see de Saint Laurent & Cleva, 1981; Holthuis, 1994). The *Microprosthema* shrimps are free-living in shallow-water, but the others are well known for living as a sexual pair entrapped in an internal cavity of deep-water hexactinellid sponges. In spite of the attention of many workers, a taxonomic grouping of the spongicolids has never been tested by a comprehensive analysis of the relationships among all genera or species.

It is difficult to characterize these shrimps, ranging from those with well-developed mouthparts and a carapace with scattered spinules to those with reduced mouthparts and a soft, relatively uncalcified carapace without spines. Spongicolid genera are still identified by characters of maxillipeds 2 and 3. However, a detailed look at morphological features such as gills reveals even more diversity in the species of *Spongicoloides* and *Spongiocaris* than in the other genera. This case is similar to that of the pinnotherid crabs (Pohle & Marques, 1998), which is known for symbiosis with other invertebrates, mainly bivalve shells.

The present paper deals with evolutionary trends in the morphological characters of shallow-water free-living to deep-water sponge-associated habitat and the phylogenetic relationships among the species of the Spongicolidae, with special reference to biogeography, larval development and host association.

MATERIALS AND METHODS

Data on external characters, gill formulae, biogeographical and bathymetrical distributions, egg size, larval development and host association were obtained from published sources, museum collection records and examination of specimens, which are listed in Table 1. Comparative specimens were loaned from the following natural history museums: Natural History Museum and Institute, Chiba (CBM), Muséum National d'Histoire Naturelle, Paris (MNHN), Te Papa National Museum of New Zealand (NMNZ), National Science Museum, Tokyo (NSMT), Northern Territory Museum of Arts & Sciences (NTM), Port of Nagoya Public Aquarium (PNPA), Nationaal Natuurhistorisch Museum, Leiden (RMNH), Seto Marine Biological Laboratory, Kyoto University (SMBL), Tokyo University of Fisheries (TUFIL), the University Museum, University of Tokyo (UMUTZ), National Museum of Natural History, Smithsonian Institution (USNM), Zoologisches Museum, Christian–Albrechts–Universität Zu Kiel (ZMK), Zoologisk Museum, Copenhagen (ZMUC).

The relationships of all known spongicolids were analysed and evaluated by PAUP 4.0b8 (Swofford, 2000). Thirty-eight characters were used, all unordered and unweighted (Tables 6 & 7). Polarization decisions were made using the outgroup method as laid out by Maddison et al. (1984). Character states are indicated in the text by numbers, giving the character and character state where 0=presumed plesiomorphy; N>0=presumed apomorphy. For maximum parsimony, default settings included ACCTRAN, and multistate taxa were treated as uncertainties. Full heuristic searches were performed with starting trees obtained by stepwise random addition. Tree bisection-reconnection branch swapping was performed with the MULTREES option to save all minimum-length trees.

The strict consensus tree calculated from the 208 equally parsimonious trees obtained from a heuristic analysis of the data matrix is shown in Figure 3. Two outgroup taxa 2 genera, *Odontozona* and *Stenopus*, were drawn from the family Stenopodidae as the putative sister taxa of the

Table 1. *List of examined species, number, size range (mm), and source of specimens.*

Species	N	CL range (mm)	Source
Genus *Microprosthema* Stimpson, 1860			
Microprosthema emmiltum Goy, 1987	2	3.8–5.2	[Goy, 1987; USNM]
Microprosthema granatense Criales, 1997	1	3.5	[Criales, 1997; USNM]
Microprosthema inornatum Manning & Chace, 1990	1	1.8	[Manning & Chace, 1990; USNM]
Microprosthema looensis Goy & Felder, 1988	1	4.3	[Goy & Felder, 1988; USNM]
Microprosthema manningi Goy & Felder, 1988	9	2.9–5.9	[Goy & Felder, 1988; USNM]
Microprosthema plumicorne (Richters, 1880)	–	–	[Richters, 1880]
Microprosthema scabricaudatum (Richters, 1880)	4	2.0–3.5	[Richters, 1880; CBM, PNPA, ZMK]
Microprosthema semilaeve (von Martens, 1872)	4	3.8–4.5	[von Martens, 1872; USNM]
Microprosthema validum Stimpson, 1860 TYPE SPECIES	26	1.8–4.9	[Stimpson, 1860; Holthuis, 1946; Baba et al., 1968; de Saint Laurent & Cleva, 1981; CBM, NSMT, NTM, USNM, ZMK]
Genus *Paraspongicola* de Saint Laurent & Cleva, 1981			
Paraspongicola pusilla de Saint Laurent & Cleva, 1981 TYPE SPECIES	2	3.1–3.2	[MNHN]
Genus *Spongicola* de Haan, 1844			
Spongicola andamanica Alcock, 1901	–	–	[Alcock, 1901]
Spongicola cubanica Ortiz, Gfimez & Lalana, 1994	–	–	[Ortiz, Gómez & Lalana, 1994]
Spongicola henshawi henshawi Rathbun, 1906	4	2.4–6.6	[Rathbun, 1906; de Saint Laurent & Cleva, 1981; NTM, UMUTZ, USNM]
Spongicola henshawi spinigera de Saint Laurent & Cleva, 1981	8	2.2–4.3	[de Saint Laurent & Cleva, 1981; CBM, MNHN, USNM]
Spongicola holthuisi de Saint Laurent & Cleva, 1981	3	3.0–5.6	[de Saint Laurent & Cleva, 1981; CBM, MNHN]
Spongicola inflata de Saint Laurent & Cleva, 1981	2	1.6–2.5	[de Saint Laurent & Cleva, 1981; MNHN]
Spongicola japonica Kubo, 1942	443	1.6–8.8	[Kubo, 1942; PNPA, TUFIL]
Spongicola levigata Hayashi & Ogawa, 1987	12	2.3–3.2	[Hayashi & Ogawa, 1987; USNM]
Spongicola parvispina Zarenkov, 1990	–	–	[Zarenkov, 1990]
Spongicola venusta de Haan, 1844 TYPE SPECIES	56	2.0–10.5	[de Haan, 1844; Bate, 1888; Holthuis, 1946; de Saint Laurent & Cleva, 1981; MNHN, NSMT, PNPA, SMBL, TUFIL, UMUTZ]
Genus *Spongicoloides* Hansen, 1908			
Spongicoloides evolutus (Bouvier, 1905)	2	6.2–6.9	[Bouvier, 1905a; MNHN]
Spongicoloides galapagensis Goy, 1980	–	–	[Goy, 1980]
Spongicoloides hawaiiensis Baba, 1983	–	–	[Baba, 1983]
Spongicoloides inermis (Bouvier, 1905)	–	–	[Bouvier, 1905b]
Spongicoloides koehleri (Caullery, 1896)	–	–	[Caullery, 1896; Kemp, 1910]
Spongicoloides novaezelandiae Baba, 1979	4	7.7–12.7	[Baba, 1979; NMNZ, USNM]
Spongicoloides profundus Hansen, 1908 TYPE SPECIES	3	5.0–7.0	[Hansen, 1908; ZMUC]
Genus *Spongiocaris* Bruce & Baba, 1973			
Spongiocaris hexactinellicola Berggren, 1993	3	5.8–8.9	[Berggren, 1993; RMNH, USNM]
Spongiocaris semiteres Bruce & Baba, 1973 TYPE SPECIES	2	5.3–6.2	[Bruce & Baba, 1973; RMNH, NMNZ, USNM]
Spongiocaris yaldwyni Bruce & Baba, 1973	5	6.3–9.9	[Bruce & Baba, 1973; NMNZ, USNM]

N, number of examined specimens.

Table 2. *Egg sizes and hatched larvae in the Spongicolidae.*

Species	Hatched larva	Egg size (mm long axis)	Egg number	CL of ovigerous female (mm)
Microprosthema emmiltum	zoea (?)	0.5	37–82	3.8–5.2
Microprosthema looensis	?	large	20	4.3
Microprosthema manningi	zoea (?)	0.5	1592	5.9
Microprosthema scabricaudatum	zoea (?)	0.6	22	2.0–2.7
Microprosthema semilaeve	zoea	0.5	828	3.9–4.1
Paraspongicola pusilla	zoea	0.7–1.0	?	3.1
Spongicola henshawi henshawi	zoea (?)	0.6–0.7	631	6.2–6.6
Spongicola henshawi spinigera	zoea (?)	0.6	?	3.2
Spongicola holthuisi	zoea (?)	0.8	?	3.0
Spongicola japonica	1st juvenile	1.9	3–46	5.8–8.8
Spongicola levigata	zoea or postlarva (?)	0.4–0.6	few	2.3–2.9
Spongicola parvispina	zoea (?)	0.6–0.7	?	?
Spongicola venusta	zoea	0.9	240	7.5
Spongicoloides galapagensis	postlarva or 1st juvenile (?)	2.0	20	?
Spongicoloides koehleri	1st juvenile	2.0	62	?
Spongicoloides novaezelandiae	postlarva or 1st juvenile (?)	2.2–2.4	23	9.4
Spongicoloides profundus	postlarva or 1st juvenile (?)	1.5	few	7.0
Spongiocaris hexactinellicola	postlarva or 1st juvenile (?)	2.5	30–33	7.6–8.5
Spongiocaris semiteres	postlarva or 1st juvenile (?)	1.7	8	6.5
Spongiocaris yaldwyni	postlarva or 1st juvenile (?)	2.4	97	9.9

CL, carapace length.

Table 3. *Geographical distribution of the Spongicolidae.*

	Japan	Indo-West Pacific	East Pacific	West Atlantic	East Atlantic
Genus *Microprosthema*					
emmiltum			✓		
granatense				✓	
inornatum					✓
looensis				✓	
manningi				✓	
plumicorne		✓			
scabricaudatum	✓	✓			
semilaeve				✓	
validum	✓	✓			
Genus *Paraspongicola*					
pusilla		✓			
Genus *Spongicola*					
andamanica		✓			
cubanica				✓	
henshawi henshawi		✓			
henshawi spinigera		✓			
holthuisi		✓			
inflata		✓			
japonica	✓	✓			
levigata	✓	✓			
parvispina			✓		
venusta	✓	✓			
Genus *Spongiocaris*					
hexactinellicola				✓	
semiteres		✓			
yaldwyni		✓			
Genus *Spongicoloides*					
evolutus					✓
galapagensis			✓		
hawaiiensis		✓			
inermis				✓	
koehleri					✓
novaezelandiae		✓			
profundus					✓

✓, observed.

Table 4. *Vertical distribution of the Spongicolidae.*

Depth (m)	0–100	100–200	200–500	500–1000	1000–
Genus *Microprosthema*					
emmiltum	✓				
granatense	✓				
inornatum	✓				
looensis	✓				
manningi	✓				
plumicorne	✓				
scabricaudatum	✓				
semilaeve	✓				
validum	✓				
Genus *Paraspongicola*					
pusilla		✓			
Genus *Spongicola*					
andamanica			✓	✓	
cubanica			✓		
henshawi henshawi			✓	✓	
henshawi spinigera		✓	✓		
holthuisi		✓			
inflata		✓	✓		
japonica			✓		
levigata		✓			
parvispina			✓		
venusta	✓	✓	✓		
Genus *Spongiocaris*					
hexactinellicola				✓	
semiteres			✓		
yaldwyni				✓	
Genus *Spongicoloides*					
evolutus				✓	✓
galapagensis				✓	
hawaiiensis				✓	
inermis				✓	
koehleri				✓	✓
novaezelandiae				✓	✓
profundus					✓

✓, observed.

Spongicolidae (Holthuis, 1946; Dounas & Koukouras, 1989). Nine of 32 taxa in this analysis have incomplete data sets (Table 7), and therefore many of the contentious taxa also fall into this category. The average percentage of missing data in the matrix is only 3.5%, but in some species this percentage is as high as 31.6%. The placement of taxa with high proportions of missing data should be viewed with some reservation.

RESULTS

Egg size and larval development

There is little information available about the larval development of the family Spongicolidae. Table 2 shows the egg size and type of hatched larvae of selected species in the Spongicolidae and outgroups. *Stenopus hispidus* is known to bear an abundance of eggs that hatch as zoea with over nine developmental stages (Lebour, 1941). Most of *Microprosthema* have a large number of small sized eggs that hatch as zoea with over four stages (Raje & Ranade, 1978). *Paraspongicola pusilla* and *Spongicola venusta, S. henshawi h., S. h. spinigera, S. holthuisi* and *S. parvispina* are also considered to be a similar pattern (Bate, 1888; de Saint Laurent & Cleva, 1981; Zarenkov, 1990). Larvae in this group have extended larval development and presumably wide dispersal. On the other hand, *Spongicola japonica*, *Spongiocaris* and *Spongicoloides* bear a comparably small number of large eggs that hatch as postlarvae or decapodids without wide dispersal (Bruce & Baba, 1973; Goy, 1980; Berggren, 1993; Saito & Konishi, 1999).

Geographical and vertical distribution

Tables 3 and 4 show the geographical and vertical distributions of the Spongicolidae, respectively. Even though their occurrence is concentrated in deep water, the distribution of the Spongicolidae is restricted to tropical and temperate waters. The northernmost and deepest record for this family is that of *Spongicoloides profundus* from a depth of 1480 m off Iceland (Hansen, 1908).

Except for the *Paraspongicola*, for which little distribution data are available, the widely distributed species are found

Table 5. *Gill formulae of the Spongicolidae and outgroup.*

	Pleurobranch								Arthrobranch								Podobranch								Epipod								Exopod								
	Maxilliped			Pereopod					Maxilliped			Pereopod					Maxilliped			Pereopod					Maxilliped			Pereopod					Maxilliped			Pereopod					Gill formula (excluding exopod)
Taxa	1	2	3	1	2	3	4	5	1	2	3	1	2	3	4	5	1	2	3	1	2	3	4	5	1	2	3	1	2	3	4	5	1	2	3	1	2	3	4	5	
M. emmiltum, M. granatense, M. inornatum, M. looensis, M. manningi, M. plumicorne, M. scabricaudatum, M. semilaeve, M. validum, P. pusilla, S. inflata, St. hispidus	–	–	1	1	1	1	1	1	1	1	2	2	2	2	2	–	–	1	–	–	–	–	–	–	1	1	1	1	1	1	1	–	1	1	1	–	–	–	–	–	[19+7e]
S. andamanica, S. henshawi henshawi, S. henshawi spinigera, S. holthuisi, S. venusta, S. levigata	–	–	1	1	1	1	1	1	1	1	2	2	2	2	2	–	–	1	–	–	–	–	–	–	1	1	1	1	1	1	1	–	1	1	r	–	–	–	–	–	[19+7e]
S. japonica	–	–	1	1	1	1	1	1	1	1	2	2	2	2	2	–	–	1	–	–	–	–	–	–	1	1	1	1	1	1	1	–	1	r	–	–	–	–	–	–	[19+7e]
Sa. semiteres	–	–	1	1	1	1	1	1	1	1	2	2	2	2	2	–	–	1	–	–	–	–	–	–	1	1	1	1	1	1	1	–	1	1	–	–	–	–	–	–	[19+7e]
Sa. hexactinellicola	–	–	1	1	1	1	1	1	1	1	2	2	2	2	2	–	–	1	–	–	–	–	–	–	1	1	1	1	1	1	–	–	1	1	–	–	–	–	–	–	[19+6e]
Sa. yaldwyni	–	–	1	1	1	1	1	1	1	1	2	2	2	2	2	–	–	1	–	–	–	–	–	–	1	1	–	–	–	–	–	–	1	1	–	–	–	–	–	–	[19+2e]
So. evolutus	–	–	1	1	1	1	1	1	1	1	1	2	2	2	2	–	–	1	–	–	–	–	–	–	1	1	1	–	–	–	–	–	1	–	–	–	–	–	–	–	[18+3e]
So. galapagensis	–	–	1	1	1	1	1	1	–	–	1	1	1	1	1	–	–	1	–	–	–	–	–	–	1	1	1	–	–	–	–	–	1	–	–	–	–	–	–	–	[12+3e]
So. hawaiiensis	–	–	1	1	1	1	1	1	1	1	2	2	2	2	2	–	–	r	–	–	–	–	–	–	1	1	1	–	–	–	–	–	1	–	–	–	–	–	–	–	[19+3e]
So. inermis	–	–	1	1	1	1	1	1	–	1	1	1	1	1	r	–	–	r	–	–	–	–	–	–	1	1	1	–	–	–	–	–	1	–	–	–	–	–	–	–	[13+3e]
So. koehleri	–	–	1	1	1	1	1	1	1	1	2	2	2	2	2	–	–	1	–	–	–	–	–	–	1	1	1	1	1	1	1	–	1	–	–	–	–	–	–	–	[19+7e]
So. novaezelandiae	–	–	1	1	1	1	1	1	1	1	2	2	2	2	2	–	–	1	–	–	–	–	–	–	1	1	1	–	–	–	–	–	1	–	–	–	–	–	–	–	[19+3e]
So. profundus	–	–	1	1	1	1	1	1	r	r	1	1	1	1	1	–	–	r	–	–	–	–	–	–	1	1	1	–	–	–	–	–	1	–	–	–	–	–	–	–	[14+3e]

M, Microprosthema; *P, Paraspongicola*; *S, Spongicola*; *Sa, Spongiocaris*; *So, Spongicoloides*; *St, Stenopous*; e, epipods; r, rudimentary form; –, not observed.

Table 6. *List of characters and their states used in the parsimony analysis. Numeric character labels correspond with those in Table 7.*

CARAPACE	
1	Scattered spinules on surface: (0=p, 1=a).
2	Antennal spine: (0=p, 1=a).
3	Spines on hepatic region: (0=p, 1=a).
4	Postmarginal spines on pterygostomial angle: (0=p, 1=a).
5	Spines on rostral base: (0=p, 1=a).
6	Rostral length to distal end of segment 2 of antennular peduncle: (0=overreaching, 1=short).
EYES & ANTENNA	
7	Stalk length against cornea: (0=larger, 1=smaller or nearly equal).
8	Spinules on ophthalmic peduncle: (0=p, 1=a).
9	Shape of scaphocerite: (0=lance shaped, 1=semicircular, 2=quadrangular, 3=small & narrow).
ABDOMEN	
10	Scattered spinules on surface: (0=p, 1=a).
11	Posterior dorsal margin of segment 3: (0=covers most of dorsal forth segment, 1=not elongate).
GILLS	
12	Arthrobranchs on maxilliped 1: (0=1, 1=rudimentary, 2=a).
13	Arthrobranchs on maxilliped 2: (0=1, 1=rudimentary, 2=a).
14	Arthrobranchs on maxilliped 3: (0=2, 1=1, 2=a).
15	Arthrobranchs on pereopod 1: (0=2, 1=1, 2=a).
16	Arthrobranchs on pereopod 2: (0=2, 1=1, 2=a).
17	Arthrobranchs on pereopod 3: (0=2, 1=1, 2=a).
18	Arthrobranchs on pereopod 4: (0=2, 1=1, 2=rudimentary).
19	Podobranchs on maxilliped 2: (0=1, 1=rudimentary).
20	Epipod on pereopod 1: (0=p, 1=a).
21	Epipod on pereopod 2: (0=p, 1=a).
22	Epipod on pereopod 3: (0=p, 1=a).
23	Epipod on pereopod 4: (0=p, 1=a).
MOUTHPARTS	
24	Exopod on maxilliped 2: (0=well developed, 1=rudimentary, 2=a).
25	Exopod on maxilliped 3: (0=well developed, 1=rudimentary, 2=a).
26	Spines on ischium of maxilliped 3: (0=many, 1=few, 2=a).
27	Spines on merus of maxilliped 3: (0=p, 1=a).
28	M3-P brush: (0=definite, 1=rudimentary or absent).
PEREOPODS	
29	P1–CP brush: (0=definite, 1=rudimentary or absent).
30	Spines on merus of pereopod 2: (0=p, 1=a).
31	Dorsal margin of palm of pereopod 3: (0=spinous with crista, 1=spinous, 2=grained or setae, 3=a).
32	Ventral margin of palm of pereopod 3: (0=spinous or denticlate, 1=grained or setae, 2=a).
33	Carpi of pereopods 4 and 5: (0=distinctly more than 6-segmented, 1=sometimes faintly below 6-segmented, 2=not segmented).
34	Propodi of pereopods 4 and 5: (0=distinctly more than 3-segmented, 1=sometimes faintly below 3-segmented, 2=not segmented).
35	Dactyli of pereopods 4 and 5: (0=bifid, 1=bifid with teeth or trifid).
TELSON & UROPODS	
36	Shape of telson: (0=lance shaped, 1=triangular, 2=quadrangular).
37	Spines on outer margin of uropodal exopod: (0=1–9, 1=more than 10).
38	Spines on outer margin of uropodal endopod: (0=p, 1=a).

a, absent; p, present.

in *Microprosthema* and *Spongicola*, especially *Spongicola venusta*, which is known from several areas of the Indo-West Pacific waters (de Haan, 1844; Bate, 1888; Holthuis, 1946; de Saint Laurent & Cleva, 1981). *Spongiocaris* and *Spongicoloides* are widely distributed as genera, but each of their species is endemic to a specific region with no overlap in geographical ranges.

Distributions of the Spongicolidae seem strictly limited by the presence of suitable temperature ranges and substrate habitats within available current regimes. The latter ensures that their larvae do not disperse far on their own but are highly dependent on where the currents take them. Schram (1986) estimated that the Spongicolidae is a very old group, which originated in the tropical Tethys and highly specialized to comply with particular requirements.

The vertical distribution of the Spongicolidae is also interesting. The shallowest genus is the *Microprosthema*. The average habitat depth of spongicolids then becomes deeper in *Paraspongicola*, followed by *Spongicola*, *Spongiocaris* and finally *Spongicoloides*, the genus recorded from the deepest bottom for the family at 500–1500 m.

Morphological characters

Table 6 shows the characters and their states for 32 taxa used in the phylogenetic analysis, and Table 7 shows

Table 7. *Data matrix.*

Character number #0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3
Character number 0#	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8
Microprosthema emmiltum	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	2	0	1	1	0
Microprosthema granatense	1	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0
Microprosthema inornatum	1	0	0	0	0	1	0	0	2	1	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0
Microprosthema looensis	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	2	1	2	2	0	1	0	0
Microprosthema manningi	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	1	0	0
Microprosthema plumicorne	0	0	0	0	0	0	0	?	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	?	?	1	1	2	0	0	0	2	0	0
Microprosthema scabricaudatum	0	0	0	0	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	1	?	2	2	0	1	0	0
Microprosthema semilaeve	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	2	0	1	1	0
Microprosthema validum	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0
Paraspongicola pusilla	1	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	2	2	1	1	1	0
Spongicola andamanica	1	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	?	?	0	1	?	0	2	2	0	1	1	0
Spongicola cubanica	1	1	1	1	1	1	0	0	1	1	1	?	?	?	?	?	?	?	0	?	?	?	?	0	2	2	1	?	1	1	3	2	2	2	0	2	0	0
Spongicola henshawi henshawi	1	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	2	1	1	1	0
Spongicola henshawi spinigera	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	2	1	1	1	0
Spongicola holthuisi	1	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	1	0	1	2	1	1	1	0
Spongicola inflata	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	2	2	1	1	1	0
Spongicola japonica	1	1	1	0	1	1	1	1	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	2	2	1	1	1	1	3	1	2	2	1	2	1	1
Spongicola levigata	1	0	1	1	1	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	1	1	1	1	0	1	2	0	1	0	0
Spongicola parvispina	1	0	0	0	1	0	0	0	1	1	1	?	?	?	?	?	?	?	0	?	?	?	?	0	1	2	1	?	1	1	1	0	2	2	0	1	0	1
Spongicola venusta	1	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	1	1	1	1	1	0	2	2	1	1	1	0
Spongicoloides evolutus	1	1	1	0	0	1	0	0	2	1	1	0	0	1	0	0	0	0	0	1	1	1	1	2	2	2	1	1	1	1	3	2	2	2	1	2	0	1
Spongicoloides galapagensis	1	0	0	0	0	1	0	1	2	1	1	2	2	1	1	1	1	1	0	1	1	1	1	2	2	1	1	1	1	1	3	1	2	2	1	2	1	1
Spongicoloides hawaiiensis	1	1	1	1	1	?	1	1	2	1	1	0	0	0	0	0	0	0	1	1	1	1	1	2	2	2	1	1	1	1	3	2	2	2	?	2	1	1
Spongicoloides inermis	1	0	1	1	1	1	1	1	2	1	1	2	1	1	1	1	1	2	1	1	1	1	1	2	2	2	1	1	1	1	3	2	2	2	1	2	0	1
Spongicoloides koehleri	1	1	1	0	1	1	0	1	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	2	2	1	?	1	1	3	2	2	2	1	2	?	?
Spongicoloides novaezelandiae	1	0	0	0	1	1	0	1	2	1	1	0	0	0	0	0	0	0	0	1	1	1	1	2	2	2	1	1	1	1	3	2	2	2	1	2	1	1
Spongicoloides profundus	1	1	1	0	0	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	1	1	1	1	3	2	2	2	0	2	1	1
Spongiocaris hexactinellicola	1	0	1	0	1	1	1	1	2	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	2	2	0	1	1	1	3	1	2	2	1	2	1	1
Spongiocaris semiteres	1	1	1	1	1	1	1	1	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	1	1	1	1	3	2	2	2	1	2	1	0
Spongiocaris yaldwyni	1	0	0	0	1	0	1	1	2	1	1	0	0	0	0	0	0	0	0	1	1	1	1	0	2	2	1	1	1	1	3	2	2	2	1	2	1	1
Odontozona minoica	1	0	0	0	0	0	1	0	0	1	0	0	1	2	?	?	?	?	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Stenopus hispidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0

the data matrix, summarizing the character states. This includes characters 1–6 related to carapace, characters 7–9 related to eyes and antenna, characters 10 and 11 related to abdomen, and characters 12–23 related to the gill formula. Additional characters 24–28 are related to mouthparts, and characters 29–35 to pereopods. Finally, three characters listed as 36–38 related to telson and uropods are analysed.

Carapace. Figure 1A–C shows the spongicolid carapace, which is distinctive in spination, and the taxonomy of various genera is mostly based on its appearance (Hansen, 1908; Bruce & Baba, 1973; de Saint Laurent & Cleva, 1981; Holthuis, 1994). In the present study, six characters are found to be phylogenetically informative, with an outgroup comparison suggesting the presence of each of these characters to be plesiomorphic. Scattered spinules on the carapace surface (1) are observed in *Stenopus* and most of *Microprosthema*, while they are not present in *M. granatense*, *M. inornatum* and the others. The numbers of spines associated with some specific parts of the carapace are also useful and polarized by comparison to the outgroup as shown in Table 6: antennal spine (2), spines on the hepatic region (3), postmarginal spines on the pterygostmial angle (4), and spines on the rostral base (5). For the Stenopodidea, almost all free-living shrimp have scattered spinules on the body, such as on the carapace and abdomen. Thus, those spongicolids with sponge associations represent derived taxa. The carapace multistate character is left unordered, since it is uncertain whether evolution to a membranous carapace proceeded through an intermediate stage with a less pliant carapace in all taxa. Rostral length to distal end of second segment of antennular peduncle (6) is overreaching in the outgroup (i.e. all *Microprosthema* except for *M. inornatum*, *Paraspongicola pusilla, S. inflata, S. henshawi h., S. h. spinigera, S. parvispina* and *Spongiocaris yaldwyni*), but is short in all *Spongicoloides* and the others.

Eyes and antenna. The characters 7–9 relating to the state of eyes and antenna are also phylogenetically informative. Stalk length against cornea (7) is related to visual ability, and spinules on the ophthalmic peduncle (8) are also found to be useful. The outgroup comparison suggests

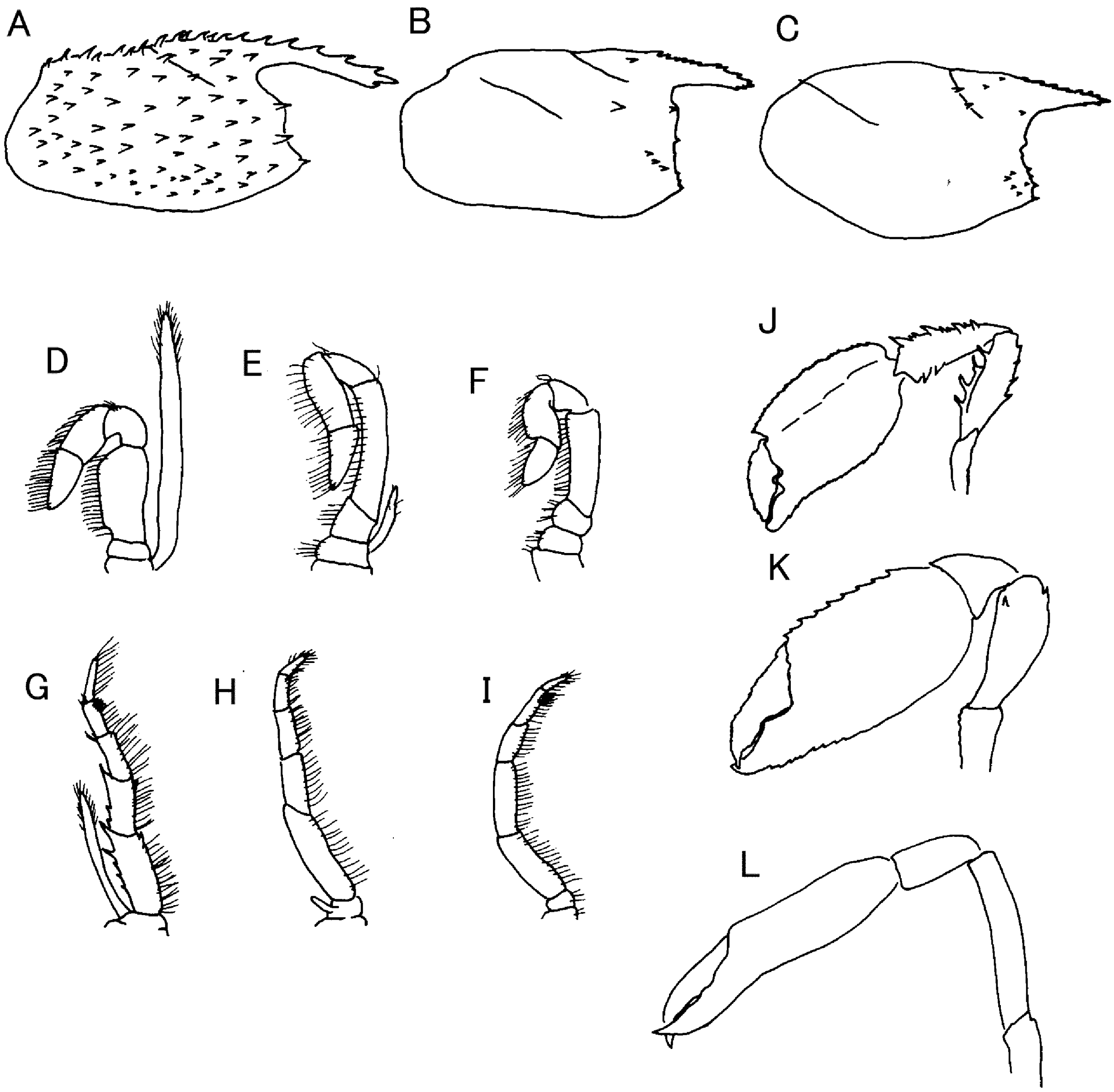

Figure 1. Schematic representations of *Microprosthema validum* (A, D, G, J), *Spongicola venusta* (B, H, K), *S. japonica* (C, E), and *Spongicoloides profundus* (F, I, L). A–C, Carapace; D–F, exopod of maxilliped 2; G–I, exopod of maxilliped 3; J–L, pereopod 3.

that the larger cornea and presence of spinules on a stalk are plesiomorphic states. The shape of the scaphocerite (9) is informative, lance shaped in the outgroup, semicircular in most *Microprosthema* and *Spongicola*. However, it is quadrangular in *M. granatense*, *M. inornatum*, *M. plumicorne*, *S. japonica*, *Spongiocaris* and *Spongicoloides*.

Abdomen. The abdomen in all taxa examined is invariant with no phylogenetic useful characters. Transverse ridges seen frequently in *Microprosthema* are not used in this study, as they are sometimes unusable in the deposited condition of specimens. Scattered spinules on surface (10) were recognized in only outgroup and *M. scabricaudatum*. Posterior dorsal margin of third abdominal segment (11) is elongated in outgroup, *M. granatense* and *M. inornatum*.

Gills. Characters 12–23 relating to the state of the gills are phylogenetically informative, with arthrobranchs on maxillipeds 1–3 (12–14) and pereopods 1–4 (15–18), podobranch on maxilliped 2 (19), and epipods on pereopods 1–4 (20–23), considered plesiomorphic from outgroup comparison. Particular gills also show a reduced state by lacking one of the usual states, or by being reduced to a rudimentary axis. The data for the three resulting character states provided ordered, developmental evidence (Hong, 1988), indicating that a loss of gills is preceded by reduction. Table 5 shows gill formulae among the Spongicolidae. *Microprosthema*, *Paraspongicola* and *Spongicola* represent the maximum number of gills. Gill formulae are relatively consistent within these genera, but there are slight variations in *Spongiocaris* and *Spongicoloides*, where some species have lost gills.

Mouthparts. The Spongicolidae possess a number of synapomorphies associated with the maxillipeds, which are distinctive, and taxonomy of various genera is based

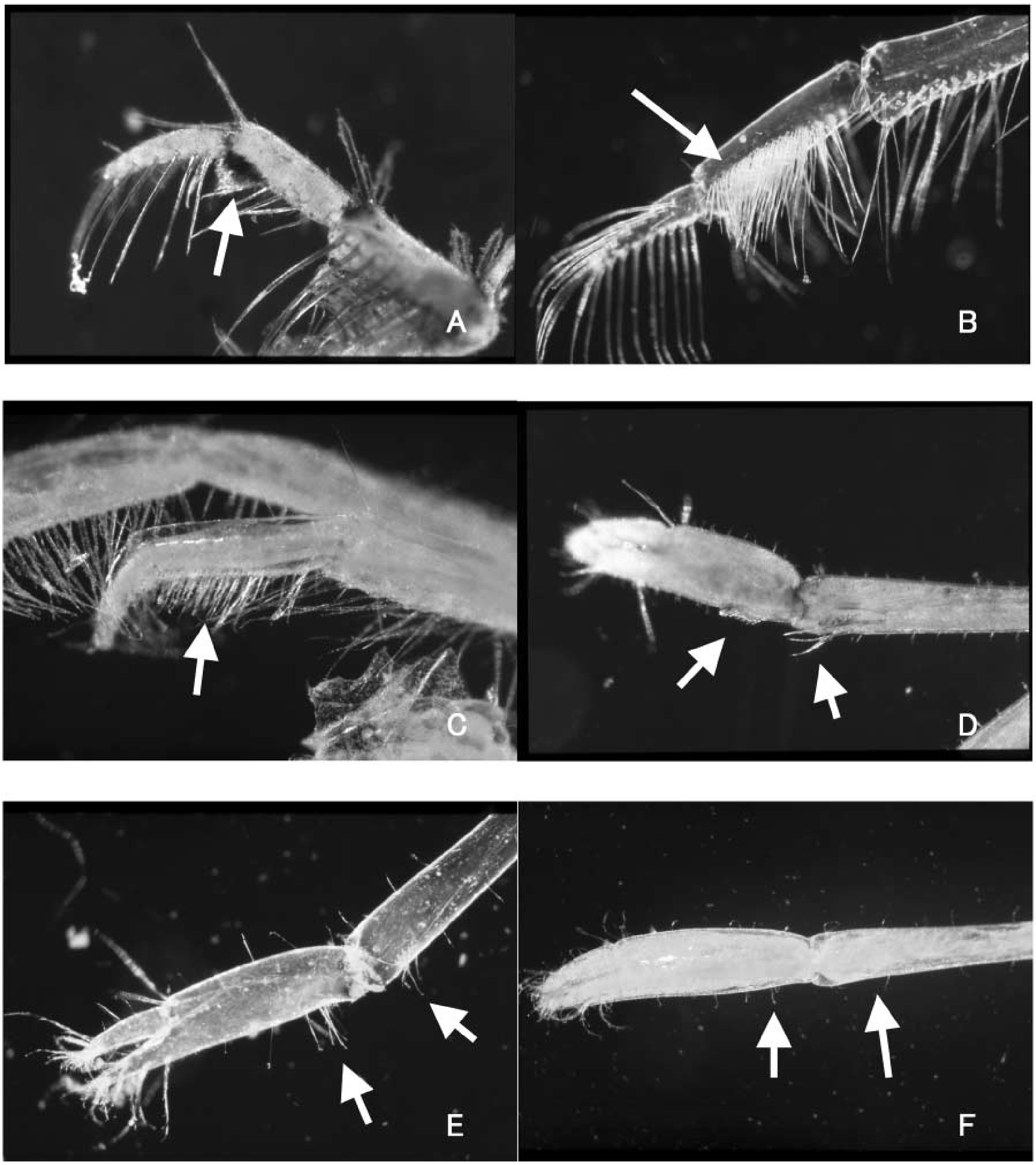

Figure 2. Schematic representations of *Microprosthema validum* (A, D), *Spongicola japonica* (B, E), and *Spongicoloides profundus* (C, F). A–C, Setiferous organ of maxilliped 3 (arrow); D–F, setiferous organ of pereopod 1 (arrow).

on their appearance (Figures 1D–I & 2A–F). Spongicolids except for *Microprosthema* differ from other stenopodideans in that some lack exopods on the maxillipeds. For this character, an outgroup polarization showed the presence of exopod on all maxillipeds to be in a plesiomorphic state. The states of exopods on maxillipeds 2 and 3 (24, 25) are consistent within genera; *Microprosthema* and *Paraspongicola* have well-developed ones on each maxilliped (Figure 1D, G). Most *Spongicola* members have a well-developed exopod on maxilliped 2, but a reduced one on maxilliped 3 (Figure 1H). *Spongicola japonica* has a reduced exopod on maxilliped 2 (Figure 1E), but lacks one on maxilliped 3. *Spongicola cubanica* represents the characteristics in maxillipeds 2 and 3 of *Spongiocaris*, showing a well-developed exopod on maxilliped 2, but lacking one on maxilliped 3. *Spongicoloides* lacks it on both maxillipeds 2 and 3 (Figure 1F, I). Spines on the ischium and merus of maxilliped 3 (26, 27) are informative, recognized mainly in the outgroup, *Microprosthema* and some species of *Spongicola*. The maxilliped 3 propodal brush (M3–P brush) (28)

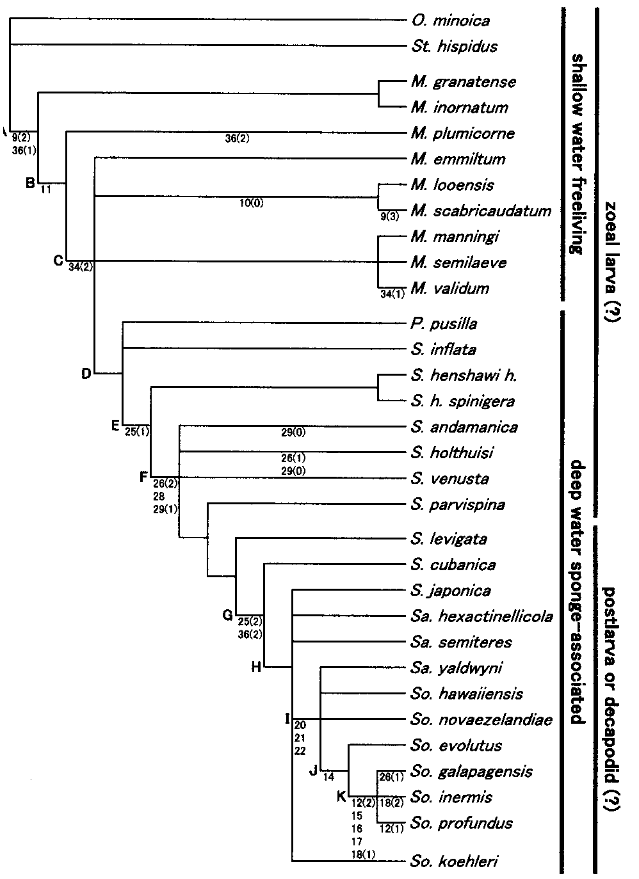

Figure 3. The strict consensus tree based on 38 characters of 30 spongicolid and 2 outgroup taxa. Tree length=114 steps, CI=0.4649, RC=0.3697. Synapomorphies are indicated below branches; characters 11, 14, 15, 16, 17, 20, 21, 22, and 28 are unique in the taxa examined and unreversed; character state numbers in parentheses are shown only for multi-state or reversed characters.

ranges from rudimentary or absent in *Spongiocaris* and *Spongicoloides* to well developed in the outgroup, *Microprosthema*, *Paraspongicola* and some *Spongicola* (Figure 2A–C). This character is used for grooming antennule in *Stenopus hispidus* (Bauer, 1989).

Pereopods. The form of the spongicolid pereopod is well documented. Variations in the pereopod 1 carpal-propodal joint brush (P1–CP brush) (29) are also found. It ranges from rudimentary or absent in *Spongiocaris* and *Spongicoloides* to well-developed in the others (Figure 2D–F). This character is also used for grooming the antenna in *Stenopus hispidus* (Bauer, 1989). Spines on the merus of pereopod 2 (30) are present in *Stenopus hispidus*, *M. manningi*, *M. semilaeve*, *M. validum*, and *P. pusilla*. Dorsal and ventral marginal states of pereopod 3 (31, 32) are also informative, ranging from spinous with crista, spinous, grained, with setae to absent (Figure 1J–L). Subdivisions of the carpi and propodi of pereopods 4 and 5 (33, 34) are of phylogenetic use, as outgroup comparison suggesting the subdivision to be plesiomorphic. In the outgroup, *M. granatense*, *M. inornatum* and *M. plumicorne*, these characters are distinct. However, they are equivocal in the

Table 8. *Records of host species and their spongicolid symbionts.*

Host species	*E. aspergillum*	*E. curvistellata*	*E. imperialis*	*E. jovis*	*E. marshalli*	*E. oweni*	*H. sieboldi*	*D. pumiceus*	*R. phoenix*	*R. okinoseana*
S. cubanica								✓		
S. japonica					✓	✓				
S. levigata						✓				
S. venusta	✓	✓	✓		✓	✓	✓			
Sa. hexactinellicola				✓						
Sa. yaldwyni										✓
So. koeleri									✓	

D, *Dactylocalyx*; *E*, *Euplectella*; *R*, *Regadrella*; *S*, *Spongicola*; *Sa*, *Spongiocaris*; *So*, *Spongicoloides*; ✓, observed.

other *Microprosthema* and some *Spongicola* species, and not at all divided in the rest of *Spongicola*, *Spongiocaris* and *Spongicoloides*. The dactyli of pereopods 4 and 5 (35) are bifid in the outgroup, *Microprosthema* and *Spongicola andamanica*, *S. cubanica, S. levigata* and *S. parvispina*, while they are bifid with accessory teeth or trifid in most *Spongiocaris* and *Spongicoloides*.

Telson and uropods. The forms of telson and uropods are used to distinguish spongicolid genera. However, a ridge on the surface used as definitive genera is not employed in this study, since it is sometimes unrecognizable due to the deposited condition of the specimens. Shape of the telson (36) ranges from lance-shaped in the outgroup to triangular in most *Microprosthema* and *Spongicola*, and to quadrangular in *M. plumicorne*, *S. cubanica*, *S. japonica*, *Spongiocaris* and *Spongicoloides*. Spines on the outer margins of uropodal exopod and endopod (37, 38) are informative. A trend seen in both characters is to be spinous in the outgroup, most *Microprosthema* and *Paraspongicola*, and absent in most *Spongicola*, *Spongiocaris* and *Spongicoloides*.

Host association

Others than *Microprosthema* occurring in tropical shallow-waters, the spongicolid genera are associated with deep-water hexactinellid sponges. The host species for each symbiont of *Spongicola*, *Spongiocaris* and *Spongicoloides* are given in Table 8. *Spongicola venusta* has a wide selection, being associated not only with *Euplectella* but also with *Hyalonema*, while the others are mostly reported only from the *Euplectella* species.

Phylogenetic analysis

The strict consensus of the 208 most parsimonious trees based on the analysis of 38 characters with a total of 94 character states (Table 7), is shown in Figure 3. Seventeen clades are apparent, but in the following section, selected clades necessary to our discussion are labelled in alphabetical order. Numbers below the branches correspond to characters in Table 6 and show where derived states evolved; character state numbers in brackets are shown only for multistate characters and characters with reversals.

The monophyly of clade A is supported by two synapomorphies of multistate: the semicircular or quadrangular shape of the scaphocerite [9(2)] and the triangular shape of the telson [36(1)]. Clade B is supported by a unique and unreversed synapomorphy: not elongate posterior dorsal margin of the third abdominal segment (11). A polytomy at clade C is supported by a multistate synapomorphy: unsegmented propodi of the pereopods 4 and 5 [34(2)]. Although *Microprosthema* forms the most basal taxon within the Spongicolidae, it represents a paraphyletic clade. A polytomy at clade D consisting of *Paraspongicola*, *Spongicola* and the ancestor of the remaining taxa is poorly defined, and not supported by any synapomorphies. A monophyly at clade E is supported by only one synapomorphy of multistate, a rudimentary exopod on the maxilliped 3 [25(1)]. The polytomy at clade F is supported by three synapomorphies, one of which is unique and the others multistate: no spines on the ischium of the maxilliped 3 [26(2)], a rudimentary or no M3–P brush (28) and no P1–CP brush [29(1)]. The monophyly at clade G is supported by two synapomorphies, all of which multistate: no exopod on the maxilliped 3 [25(2)] and the quadrangular shape of the telson [36(2)]. Results from the strict consensus tree indicate that *Spongicola japonica*, *Spongiocaris hexactinellicola*, *S. semiteres* and *Spongicoloides koehleri* are sister taxa at clade H, which is, however, poorly defined and not supported by any synapomorphies. *Spongiocaris yaldwyni*, *Spongicoloides hawaiiensis* and *S. novaezelandiae* are sister taxa at clade I, which is supported by three unique and unreversed synapomorphies: the epipods on the pereopods 1–3 (20–22). The monophyly at clade J is supported by a unique and unreversed synapomorphy: arthrobranchs on the maxilliped 3 (14). The monophyly at clade K is supported by five synapomorphies, three of which are unique and the others multistate: no arthrobranchs on maxilliped 1 [12(2)] and arthrobranchs on pereopods 1–4 [15–17, 18(1)].

DISCUSSION

Decapod crustaceans spend much time and energy in grooming or cleaning their bodies using a variety of appendages and processes while under constant exposure to a variety of microbial and macroscopic fouling organisms that can interfere with feeding and locomotion if not removed. Many studies have indicated that various specialized setal areas, located on the posterior maxillipeds and pereopods, are used to brush, comb, scrape, and pick other appendages, gills, and general body surfaces, keeping them free of fouling organisms and debris. Numerous grooming structures and behaviours have evolved in decapod crustaceans in response to the selective pressure of fouling. Bauer (1989) reviewed the grooming behaviour and characteristics in many species of decapod crustaceans, and stated that the grooming characters might have contributed to our understanding of certain aspects of decapod phylogeny.

In the coral banded shrimp *Stenopus hispidus*, the long antennular flagellum is groomed by a cup-shaped setal brush located at the distal end of the maxilliped 3 propodus (M3–P brush). The specialized brushes of setae on either side of the carpal-propodal joint of pereopod 1 (P1–CP brush) are also used for grooming the long chemotactile antennal flagellum (Bauer, 1989). The spongicolids characteristically reveal diversity in such setiferous organs as those on maxilliped 3 and pereopod 1, and even in the exopods of maxillipeds 2 and 3, which are also used for gill grooming. Several caridean shrimps use the posterior pereopods for grooming the abdomen and posterior parts of cephalothoraxes. Stenopodidean shrimps have no setal brushes or combs on pereopods 4 and 5; however, a sub-division of each propodus and carpus on pereopods 4 and 5 provides flexibility, which may be related to cleaning the abdomen or the inside of the posterior carapace region.

The sponges have passive defence systems armed with poisons, and immune systems to protect themselves against fusion, overgrowth, and predation. The body wall of hexactinellid sponges makes a perfect mesh resembling a filtering system, which will strain out a variety of microbial and macroscopic fouling organisms from the seawater. Under those circumstances, the internal water of the gastral cavity of sponges is more clearly comparable to the outer water in physical or biological respects. In such environments, applying to the frequency of exploitation on sponges, all the characters about grooming behaviour are not necessary for sponge associates and have degenerated because of disuse. Thus, the authors of this study believe that variation of the grooming characters within a family will contribute to an understanding of Spongicolidae phylogeny.

Gill formulae are generally considered to be characteristic of major subgroups among decapods (Burkenroad, 1981) and are believed to be constant in the families (Hong, 1988). Some semi-terrestrial crabs such as ocypodids (Takeda et al., 1996) and the Pinnotheridae (Pohle & Marques, 1998) are known for having fewer gills. Gill reduction is also observed in the Spongicolidae, where gill formulae are more diverse than in the Stenopodidae.

A comparison of gill formulae (Table 5) with a proposed phylogenetic relationship shows the distribution of characters and indicates how the reduction of gills evolved. A reduction in the number of gills in the Spongicolidae might have resulted from the adaptation to sponge-associated habitats like the adaptation in pinnotherids with bivalves. The reduced gills are adequate to meet the respiratory requirements of an inactive sponge-associated shrimp, where space is at a premium. It is suggested that the reduction of gills was achieved during the evolution of spongicolid shrimps.

Reduction of gills in the Spongicolidae is related to the presence or absence of host sponges. The *Microprosthema* without symbiotic associations may have the same number of gills, while in genera with host sponges gill numbers vary. Generally, the selected characters were based upon the spiniform and gills in shrimps. These characters are considered to be variable due to their adaptation and reliance on the host sponge habitat. Thus, the reduction and loss of exopods started first on maxilliped 3, then on maxilliped 2, before the reduction or loss of gills on posterior pereopods. The loss of the gill grooming epipodite occurred subsequently, but before further reduction or loss of other gills on maxilliped 3.

The host sponges of each species of *Spongicola*, *Spongicoloides* and *Spongiocaris* are summarized in Table 8. Most species of the genera are associated with the *Euplectella* species. *Spongicola venusta* has a wide choice for host species, associating not only with *Euplectella* but also with *Hyalonema*, while the others were reported only from one or two species of *Euplectella*. The geographical distribution of these species is related to their larval life. Some ancestral *Spongicola* species probably led a free-swimming larval life in deep water, enabling them to distribute widely given the large selectivity for host species.

Glaessner (1969) placed *Uncina posidoniae*, a Jurassic species from Germany, in a separate infraorder between the Stenopodidea and Caridea, as *Uncina* shares several features with the stenopodideans. Recently, Schram et al. (2000) described a new genus and species of fossil stenopodidean, *Jilinocaris chinensis*, from the late Cretaceous of northern China. Although incompletely preserved, enough anatomy is discernible to suggest that this species represents the first fossil example of the Stenopodidea and is tentatively assigned to the Spongicolidae.

Tabachnick (1991) proposed two hypotheses for the recent habitats and palaeontological history of hexactinellid sponges. The first reason for the deep-water life of the Hexactinellida is to avoid genetic homogenization, and the second is the competition among sedimentary organisms for substrata. One can not give a definite answer, but a catastrophic faunal change at the Palaeozoic–Mesozoic boundary was observed in the Hexactinellida (Finks, 1960), a group with preference for deep-water regions with a low density of planktonic and macrobenthic organisms. The ancestral spongicolids emerged during the late Permian to the late Jurassic. At that time some members might be associated with hexactinellid sponges, which also flourished in shallow-water during this period. Until the late Jurassic era, spongicolid habitats had shifted from all vertical distribution to deep water accompanied by the transition in the host sponge habitat for some reason.

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