MORPHOLOGICAL TRENDS IN THE GENUS
HEPTACARPUS (DECAPODA, CARIDEA) AND
THEIR PHYLOGENETIC SIGNIFICANCE

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ABSTRACT

Morphological trends or clines in a variety of morphometric, meristic, and two-state characters are described and analysed for the caridean shrimp genus *Heptacarpus*. One objective of this study was to determine the evolutionary polarity (ancestral to derived) in these various morphoclines. Evidence from functional morphology and out-group comparison strongly support the hypothesis that a high epipod (epipod-setobranch complex) number is primitive in *Heptacarpus* and related genera and that a lower number represents the derived or advanced condition (epipod loss). The evolutionary polarity in epipod number is used to hypothesize the direction of evolution in morphoclines that are significantly correlated with epipod number. Using this criterion, *Heptacarpus* species with high epipod number, a short high caparace, short and high abdominal segments, a short rostrum, large first chelae, a high number of antennular spinules, and a branchiostegal setal fringe are considered primitive with respect to these characters. *Heptacarpus* species which are farthest from the hypothesized ancestral form show a reduced epipod number, a slender or elongate carapace shape, elongate abdominal segments, a proportionately long rostrum, small first chelae, a reduced number of antennular spinules, and no branchiostegal setal fringe.

Species groups are formed on the basis of morphological similarity from the 16 *Heptacarpus* species examined in detail. An index of affinity, based on 17 characters, was calculated for all possible pairs of species. A group is formed by species which show a significant morphological similarity (index of affinity greater than 0.5) to all other members of the group. The phylogenetic validity of species groups formed by this phenetic method was tested by examining the concordance in epipod number among members of a particular group. Evidence is given that epipod number is an indicator of phylogenetic relationships.

Phylogenetic studies on the crustacean order Decapoda have chiefly dealt with relationships among the higher taxa, i.e., families, sections, orders (e.g., Burkenroad, 1963; Glaessner, 1969; Guinot, 1978; Rice, 1980; Števčić, 1969; Thompson, 1965, 1966). The classification and hypothesized phylogenetic relationships of decapod higher taxa continue to be unstable (e.g., compare Burkenroad, 1963 and 1981). This instability in classification and phylogeny may result from the lack of detailed studies needed for the determination of ancestral and derived states of characters used in phylogenetic construction. Perhaps advances in phylogenetic studies of higher decapod taxa would be made if there were a better basis for character analysis and a better knowledge of phylogeny at lower taxonomic levels. Studies on the phylogenetic relationships of lower taxonomic levels (e.g., species of a genus) are rare. One such investigation is that of Judkins (1978) who used phenetic similarities of petasma structure to hypothesize affinities within the *Sergestes edwardsii* species group.

The caridean shrimp genus *Heptacarpus* (Hippolytidae) is composed of 29 species from the North Pacific Ocean which are chiefly found in shallow water habitats. Holmes (1900) proposed the genus *Heptacarpus*; however, *Heptacarpus* species were later included in the genus *Spirontocaris sensu lato* by Rathbun (1904), Schmitt (1921), and several other authors. Holthuis (1947) split *Spirontocaris s.l.* into five genera: *Spirontocaris sensu stricto, Lebbeus, Eualus, Birulia,* and *Heptacarpus*; this view has been accepted by carcinologists. Holmes (1900), Rathbun (1904), Schmitt (1921), Holthuis (1947), Hayashi (1979), and Butler (1980) are important taxonomic references for *Heptacarpus*.

In this report, I document and analyse morphological trends in the genus *Heptacarpus*. One objective of the analysis is an attempt to determine ancestral and derived states for certain characters. The variation of epipod number and structure in *Heptacarpus* (and in the closely related genera *Eualus* and *Spirontocaris*) is described, and evidence from functional morphology is reviewed in order to hypothesize the primitive and derived condition of this character. Another goal of this investigation is to document the qualitatively observed morphocline in carapace shape: the two extremes for that character in *Heptacarpus* are short and high (stout) and long and low (slender). Correlations of several other morphological characters with epipod number and carapace shape are described and analysed in order to hypothesize ancestral and derived character states, parallelism, and reversals in these various morphoclines. A further objective of this study is to determine whether species groups in the genus *Heptacarpus*, formed on the basis of morphological similarity, are supported by phylogenetic evidence obtained from the study of *Heptacarpus* morphoclines.

METHODS

Measurement of body parts and counts of meristic characters were made on 16 species of *Heptacarpus* (Tables 1 and 2). Most material was from the crustacean collection of the National Museum of Natural History (Smithsonian Institution) which I examined during my tenure as a Postdoctoral Fellow (1980–81). The median number of specimens per species on which measurements and counts were taken was 20 (range, 11–30). Measurements recorded were the carapace length and height; length and height of the tergum of the second abdominal segment, length and height of abdominal segments 5 and 6, length of pereiopod 3 (sum of lengths of ischium, merus, carpus, propodus, and dactyl); eye length (eyestalk plus cornea length); chela 1 palm (propodus) length and breadth; rostral length and height. Measurements on the carapace and abdomen were made to determine the validity of a qualitatively observed trend in carapace and abdomen shape. Characters which showed obvious sexual dimorphism (e.g., pleura of the second abdominal segment, enlarged in breeding females) were avoided. Measurements were made on the third pereiopod, first chela, rostrum, and eye because preliminary observations indicated variation in these characters which might be useful in grouping species by either a phenetic or phylogenetic method.

Body and appendage structure of these small shrimps was recorded by means of drawings made with the aid of a camera lucida and dissecting binocular microscope. Measurements were later taken from the drawings and converted to actual size (mm) by multiplication with conversion constants appropriate for given magnifications. Drawings were made of the carapace, abdominal segments, and rostrum of specimens held in profile with insect pins. One of the first chelae, third pereiopods, and eyes were removed from the specimens and drawn in a consistent position. The highest magnification which included all of a particular structure was generally used.

The conventions for each measurement are as follows: carapace length, distance from posterior edge of orbit to middorsal posterior edge of carapace; carapace height, distance from edge of branchiostegite just above coxa of pereiopod 2 to middorsal surface of caparace (measured perpendicular to middorsal surface); length of abdominal segments 2 and 5, distance between anterior and posterior condyles; length of abdominal segment 6, distance from anterior condyle to tip of posterior spine which lies along side of telson; height of each abdominal segment, distance from ventral to dorsal edge of segment drawn perpendicular to midpoint of its length; rostral length, distance from posterior edge of orbit to tip of rostrum; rostral height, greatest vertical span of rostral blade (including spines); lengths of segments of pereiopod 3, eye, and palm of first chela measured between fixed points; breadth of first chela, distance from upper to lower side of palm measured perpendicular to palm length at its midpoint.

A number of meristic and presence-absence characters were recorded. These characters were chosen because they are often used in taxonomic studies on *Heptacarpus* and other caridean shrimp. Meristic characters observed and reported here are the number of: spinules on distal edge of first segment of antennular peduncle; epipods (mastigobranchs); setobranchs; meral spines of third pereiopod; dorsolateral and posterior telson spines. Presence or absence of the following characters was recorded: pterygostomial spine; fringe of setae along ventral edge of branchiostegite; posteroventral spine of fourth abdominal pleuron. Condition of the dactyl on the third pereiopod (bifid or simple) was recorded.

Morphometric (continuous) characters are reported in the form of ratios to give values which approximately describe the general shape (Hills, 1978) or relative size of a body part. The y-intercept of the allometric growth equation (used by Kuris and Carlton, 1977, to describe relative growth in *Crangon*) might have been used to give a value for each morphometric character of each species in

Table 1. *Heptacarpus* species examined, National Museum of Natural History (USNM) catalog numbers of collections from which material was taken, total number of individuals examined (in parentheses), and sexual composition of the total sample of a species.

Species	USNM catalog number and (*N*) number of individuals examined
H. brevirostris (Dana, 1852)	183194 (7); 183161 (6); 183036 (7); 8 ♂, 12 ♀
H. camtschaticus (Stimpson, 1860)	183073 (15); 183019 (5); 7 ♂, 13 ♀
H. carinatus Holmes, 1900	87433 (20); 16 ♂, 4 ♀
H. flexus (Rathbun, 1902)	27616 (1); 27626 (1); 27622 (1); 27620 (1); 27615 (1); 27621 (1); 27624 (2); 27627 (1); 27628 (3); 183367 (3); 183146 (1); 183478 (2); 183100 (1); 183390 (1); 2 ♂, 17 ♀, 1 juvenile
H. grebnitzkii (Rathbun, 1902)	183575 (30); 15 ♂, 15 ♀
H. maxillipes (Rathbun, 1902)	183004 (15); 183048 (12); 16 ♂, 11 ♀
H. moseri (Rathbun, 1902)	27640 (20); 6 ♂, 14 ♀
H. palpator (Owen, 1839)	16988 (22); 3 ♂, 15 ♀, 4 juveniles
H. paludicola Holmes, 1900	Collected by author at Morro Bay, California, October, 1978; 2 ♂, 12 ♀, 6 juveniles
H. pictus (Stimpson, 1871)	Collected by author at Cayucos, California, November, 1978; 4 ♂, 10 ♀, 6 juveniles
H. sitchensis (Brandt, 1851)	183156 (19); 4 ♂, 15 ♀
H. stimpsoni Holthuis, 1947	55522 (20); 4 ♂, 16 ♀
H. stylus (Stimpson, 1864)	27592 (15); 15 ♀
H. taylori (Stimpson, 1857)	7632 (20); 9 ♂, 9 ♀, 2 juveniles
H. tridens (Rathbun, 1902)	31820 (8); 27611 (8); 63112 (4); 3 ♂, 16 ♀, 1 juvenile
H. tenuissimus Holmes, 1900	27599 (1); 27600 (4); 55516 (6); 3 ♂, 8 ♀

order to describe general shape or relative length. However, unless regression lines for a given character of the various species are more or less parallel (similar slopes), the y-intercepts cannot be consistently used to order a morphocline (required in this study) from, for example, stout to slender or short to long (e.g., Abele *et al.*, 1981). The ratios reported here are not intended for use in discriminating between morphologically similar species for identification but rather to describe morphoclines and to indicate their possible correlation with other morphoclines. In addition, the use of ratios allows tentative comparisons of various morphometric characters with those of other *Heptacarpus*, *Eualus*, and *Spirontocaris* species not examined or measured in this study (values from the literature). The possible effect of sexual dimorphism and size (allometry) on ratios and their use for illustrating morphoclines and morphological similarity are investigated in two species for which the data are considered adequate to do so.

One-way analysis of variance (ANOVA) was used to determine whether means of a particular morphometric character differed among species and to compare means of particular characters between sexes (*Heptacarpus grebnitzkii*) and size groups (*H. maxillipes*). The ANOVA tests were performed with untransformed as well as log transformed data. F values from both sets of data were similar and probabilities associated with the F values were the same, indicating that these data are highly homoscedastic (having equal standard deviation) and that for these data the log transformation is unnecessary. The Student Newman-Keuls test was used to test for specific differences in means among species for a given character.

Possible correlations between various characters and both epipod number and carapace shape (carapace length/height) were investigated by calculation of the Spearman rank correlation coefficient (r_s). The one-sided hypothesis of either no direct correlation or no inverse correlation between x and y was tested for possible rejection. For a particular morphometric character, species were grouped and given the same rank when the means for that character were not significantly different (as determined by the Student Newman-Keuls test). A problem in grouping resulted when results of the Student Newman-Keuls test gave overlapping sets of means, i.e., where there were no clear gaps between groups of statistically similar means (e.g., $\bar{x}_a = \bar{x}_b$; $\bar{x}_b = \bar{x}_c$; but $\bar{x}_a \neq \bar{x}_c$). In the character carapace length/height, there were no such overlapping groups of similar means. Overlaps between groups of means in other characters ranged from slight (abdominal segment 6 length/height) to extensive (abdominal segment 2 length/height). My policy was to overgroup means, i.e., to group means of species so as to produce more extensive ties in ranking for a particular character. I felt that this was a more conservative approach. To determine the effect of this conservative ranking procedure, I first calculated the correlation coefficient r_s for the various correlations without using *any* ties resulting from grouping

Table 2. Summary data on morphological characters examined for 16 *Heptacarpus* species. Continuous data are given as mean and standard error (in parentheses). Counts are given as median with range in parentheses. For presence (+) and absence (~) characters, (±) indicates variation in a species; symbol outside of the parentheses represents most frequent condition. ABD = abdominal segment; Per. 3 = pereiopod 3.

Species	N	x̄ carapace length, mm	Carapace length/height	Number of epipods	Branchiostegal setal fringe	Rostral length/carapace length	Rostral length/height	ABD 6 length/height	ABD 5 length/height	ABD 2 length/height
H. palpator	22	3.8 (0.16)	0.87 (0.01)	4 (0)	+	0.55 (0.02)	3.7 (0.10)	1.63 (0.03)	0.70 (0.02)	1.00 (0.02)
H. brevirostris	20	6.9 (0.60)	0.92 (0.01)	4 (0)	+	0.43 (0.02)	3.9 (0.21)	1.67 (0.03)	0.70 (0.01)	1.07 (0.03)
H. taylori	20	5.3 (0.30)	0.94 (0.01)	4 (0)	+	0.22 (0.002)	2.0 (0.13)	1.61 (0.03)	0.69 (0.03)	1.04 (0.03)
H. pictus	20	2.9 (0.18)	0.97 (0.01)	2 (0)	−	0.98 (0.02)	5.1 (0.07)	1.86 (0.03)	0.82 (0.03)	1.01 (0.04)
H. paludicola	20	3.3 (0.18)	1.02 (0.01)	2 (0)	−	1.36 (0.03)	5.5 (0.11)	1.94 (0.03)	0.85 (0.02)	1.06 (0.02)
H. sitchensis	19	4.3 (0.18)	1.03 (0.01)	2 (0)	−	0.91 (0.02)	5.4 (0.15)	2.02 (0.03)	0.92 (0.02)	1.18 (0.03)
H. stimpsoni	20	5.2 (0.21)	1.08 (0.01)	4 (0)	+	0.69 (0.02)	4.3 (0.11)	1.88 (0.02)	0.83 (0.02)	1.14 (0.02)
H. maxillipes	27	6.3 (0.31)	1.20 (0.01)	1 (0)	−	0.85 (0.02)	7.0 (0.22)	2.70 (0.04)	1.08 (0.02)	1.08 (0.02)
H. moseri	20	6.9 (0.32)	1.20 (0.01)	2 (0)	−	1.16 (0.03)	5.7 (0.13)	2.74 (0.02)	1.04 (0.02)	1.17 (0.03)
H. camtschaticus	20	6.0 (0.31)	1.30 (0.02)	1 (0)	−	1.41 (0.02)	6.0 (0.17)	2.35 (0.03)	0.97 (0.01)	1.01 (0.02)
H. tridens	20	8.1 (0.34)	1.31 (0.02)	1 (0)	−	1.41 (0.02)	7.8 (0.21)	2.63 (0.03)	1.03 (0.02)	1.06 (0.03)
H. carinatus	20	9.7 (0.37)	1.46 (0.02)	4 (0)	−	1.24 (0.03)	4.6 (0.11)	2.23 (0.03)	0.86 (0.02)	1.20 (0.02)
H. grebnitzkii	30	6.5 (0.29)	1.47 (0.02)	4 (0)	+	1.11 (0.02)	5.9 (0.15)	2.04 (0.02)	0.81 (0.01)	1.27 (0.04)
H. tenuissimus	11	5.3 (0.39)	1.55 (0.03)	0.5 (0–1)	−	1.53 (0.02)	11.9 (0.44)	2.93 (0.05)	1.15 (0.05)	1.15 (0.05)
H. flexus	20	8.5 (0.37)	1.60 (0.01)	3 (0)	−	1.40 (0.03)	11.2 (0.27)	2.93 (0.04)	1.09 (0.03)	1.08 (0.02)
H. stylus	15	8.0 (0.16)	1.63 (0.03)	1 (0)	−	1.45 (0.02)	7.2 (0.19)	2.22 (0.03)	1.91 (0.02)	1.05 (0.02)

Table 2. Continued.

Species	Per. 3 length/carapace length	Eye length/carapace length	Chela 1 palm area/carapace length	Number of antennular spinules	Pterygostomial spine (+ or −)	Per. 3 dactyl. simple (1) or bifid (2)	Number of Per. 3 meral spines	ABD 4 pleuron spine	Number of pairs of dorsolateral telson spines	Number of pairs of posterior telson spines
H. palpator	2.36 (0.04)	0.43 (0.01)	0.36 (0.02)	4 (1–4)	+ (±)	2 (0)	2 (2–3)	+	4 (0)	5 (3–6)
H. brevirostris	2.32 (0.04)	0.31 (0.01)	0.64 (0.06)	4 (3–4)	+ (±)	1 (0)	1 (0)	+	4 (0)	5.5 (4–7)
H. taylori	2.12 (0.02)	0.31 (0.01)	0.40 (0.03)	1 (0)	+ (±)	2 (1–2)	2 (1–2)		4 (3–4)	3 (3–4)
H. pictus	2.47 (0.05)	0.45 (0.01)	0.16 (0.01)	1 (0)	+	2 (0)	4 (2–5)	+ (±)	4 (0)	3 (0)
H. paludicola	2.49 (0.05)	0.44 (0.02)	0.15 (0.01)	1 (0)	+ (+)	2 (0)	5 (3–6)	+ (±)	4 (3–4)	3 (0)
H. sitchensis	2.08 (0.05)	0.35 (0.01)	0.15 (0.01)	1 (0)	+ (+)	2 (0)	4 (3–5)	+	4 (3–5)	3 (0)
H. stimpsoni	2.16 (0.03)	0.34 (0.02)	0.25 (0.01)	3 (2–3)	+ (+)	1 (0)	4 (3–6)	+	3 (3–4)	3 (2–3)
H. maxillipes	2.51 (0.04)	0.34 (0.01)	0.35 (0.02)	0 (0)	+ (+)	2 (0)	3 (2–5)	+ (±)	4 (3–4)	3 (0)
H. moseri	2.53 (0.06)	0.36 (0.01)	0.22 (0.01)	0 (0)	+	2 (0)	3 (3–5)	+ (±)	4 (4–5)	3 (0)
H. camtschaticus	1.98 (0.03)	0.33 (0.01)	0.14 (0.01)	0 (0)	+ (±)	2 (0)	5 (3–6)	−	4 (4–5)	3 (0)
H. tridens	1.87 (0.02)	0.30 (0.01)	0.18 (0.01)	0 (0)	+ (±)	2 (1–2)	4 (3–6)	−	3 (3–4)	3 (0)
H. carinatus	1.24 (0.06)	0.18 (0.01)	0.15 (0.01)	0 (0)	−	3 (2–3)	4 (3–4)		4 (3–5)	3 (2–3)
H. grebnitzkii	1.51 (0.03)	0.24 (0.01)	0.25 (0.02)	2 (1–2)	− (±)	2 (0)	3 (1–4)		4 (3–5)	3 (3–4)
H. tenuissimus	1.89 (0.03)	0.34 (0.01)	0.11 (0.01)	0 (0)	+ (±)	2 (0)	2 (1–3)		5.5 (5–7)	3 (0)
H. flexus	1.73 (0.05)	0.27 (0.01)	0.20 (0.03)	0 (0)	+ (±)	2 (1–2)	3 (3–4)		4 (3–4)	3 (0)
H. stylus	1.37 (0.02)	0.24 (0.01)	0.14 (0.004)	0 (0)	−	2 (0)	4 (3–5)		3 (0)	3 (0)

of statistically similar species means for a particular character and then I recalculated r_s using rankings with extensive ties from conservative grouping of means. There was little change in the outcome of the correlations using these two extremes. The absolute value of r_s was usually (but not always) slightly depressed in correlations done with extensive ties. However, out of the 20 correlations, in only two cases was there a difference in statistical significance (at the 0.05 confidence level). In these two correlations, the change was from just significant to nonsignificant. Therefore, even extensive ties in ranking of species for a particular morphometric character made little difference in the outcome of the various correlations. Tate and Clelland (1957) noted that extensive ties in ranking generally produce little effect on the outcome of statistical significance of the Spearman rank correlation coefficient.

Several characters that have been used in the diagnosis of the genus *Heptacarpus* (Holmes, 1900; Hayashi, 1979) were examined. Presence or absence of the following characters was recorded: incisor process of mandible; antennal spine; exopod of third maxilliped; and supraorbital spines. The number of segments in the mandibular palp, carpal segments of the second cheliped, and pleurobranchs were recorded. (Mandibles of only three individuals per species were examined to avoid damage to specimens.) No discrepancies from the generic diagnosis were found for these characters, and they are not included in the following analyses because they do not vary. Another nonvarying character was the presence of a grooming brush (Bauer, 1978) on the fifth pereiopod.

Attempts were made to record: presence or absence of an anterior spiniform rostral process; keel on mesial side of eyestalk (Butler, 1980); thickness or "strength" or rostral midrib; condition of carinae on abdominal segments. This group of characters was examined because they are often included in taxonomic works on the genus *Heptacarpus*; they are not included in this analysis because they could not be objectively recorded in a consistent fashion.

Data on the number of epipods, the ratio carapace length/height, and the relative rostral length were taken from the literature for 9 *Heptacarpus* spp., 17 *Eualus* spp., and 13 *Spirontocaris* spp. not examined directly by the author. Morphometric data were taken from publications such as Butler (1980), Hayashi (1977, 1979), and others from illustrations which were judged to be well executed. These values (Table 3) should be considered approximations. However, such values provide useful information on the relationships of epipod number, carapace shape, and relative rostral length.

The abbreviations used in the following text and tables are: ABD 2, 5, 6 = second, fifth, sixth abdominal segments, respectively; CH = carapace height; CL = carapace length; EL = eye length; H = height; L = length; LL = leg length (length of pereiopod 3); PA = palm area; RH = rostral height; RL = rostral length.

Results

Epipods

In caridean shrimp, epipods are hooked processes on the coxae of the third maxillipeds and pereiopods 1–4 which are functionally associated with setose papillae, the setobranchs. The epipod of one appendage is always linked with the setobranch of the limb just posterior to it. For example, the epipod of pereiopod 1 hooks around the bristlelike setobranch-setae of pereiopod 2 (Fig. 1). The maximum number of such epipod-setobranch complexes possible in carideans is five (epipods on maxilliped 3, pereiopods 1–4; setobranchs on pereiopods 1–5). Bauer (1979, 1981) has shown that the epipod-setobranch complexes function as gill-cleaning mechanisms. Both the epipod hook and the setobranch-setae are necessary for gill cleaning. Evidence was presented to support the hypothesis that reduction of epipods and setobranchs is a derived character state. Additional supporting evidence is presented here.

The distribution of epipods (=epipod-setobranch complexes) in the 16 *Heptacarpus* species examined in detail is presented in Table 2. Values of epipod number from the literature for various other *Heptacarpus* spp., *Eualus* spp., and *Spirontocaris* spp. are presented in Table 3. Except for *Heptacarpus tenuissimus*, all specimens of *Heptacarpus* observed (Table 2) possessed epipods which were coupled with setobranchs. There was considerable variation in the only epipod (third maxilliped) observed in *H. tenuissimus*. The epipod was lacking in one specimen, it lacked a hook in two others, and in all specimens there were no setobranch-setae on the first pereiopod, the expected location. All epipods in this

Table 3. Carapace shape (carapace length/height), relative rostral length (rostral length/carapace length), and epipod number for several *Heptacarpus, Eualus,* and *Spirontocaris* species, values taken from the literature. An asterisk by the epipod number indicates that I observed at least one specimen of the species and that my observations agree with those of the literature source. Fractional epipod numbers are discussed in "Results."

Species	Epipod number	Carapace length/ height	Rostral length/ carapace length	source
Heptacarpus rectirostris (Stimpson, 1860)	4	0.9	1.0	Miyake and Hayashi, 1968a
H. futilirostris (Bate, 1888)	4*	1.0	0.7	Miyake and Hayashi, 1968a
H. commensalis Hayashi, 1979	4	1.0	1.0	Hayashi, 1979
H. pugettensis Jensen, 1983	3*	1.0	0.4	Jensen, 1983
H. littoralis Butler, 1980	2	1.2	0.9	Butler, 1980
H. kincaidi (Rathbun, 1902)	1	1.2	1.2	Butler, 1980
H. geniculatus (Stimpson, 1860)	1*	1.3	1.5	Hayashi and Miyake, 1968
H. decorus (Rathbun, 1902)	1	1.6	1.1	Butler, 1980
H. pandaloides (Stimpson, 1860)	1	1.6	1.4	Hayashi and Miyake, 1968
Eualus kikuchii Miyake and Hayashi, 1967	4	1.0	0.6	Miyake and Hayashi, 1967
E. sinensis (Yu, 1931)	3*	1.1	0.6	Hayashi and Miyake, 1968
E. pusiolus (Krøyer, 1841)	4*	1.1	0.4	Butler, 1980
E. leptognathus (Stimpson, 1860)	4*	1.1	1.2	Miyake and Hayashi, 1967
E. berkeleyorum Butler, 1971	4	1.2	0.4	Butler, 1980
E. avinus (Rathbun, 1899)	4*	1.3	0.6	Butler, 1980
E. drachi Noel, 1978	4	1.3	0.8	Noel, 1978
E. townsendi (Rathbun, 1902)	3*	1.3	1.3	Butler, 1980
E. suckleyi (Stimpson, 1864)	2.5*	1.3	1.1	Butler, 1980
E. fabricii (Krøyer, 1841)	2.5*	1.4	1.3	Butler, 1980
E. herdmani (Walker, 1898)	4	1.4	0.6	Butler, 1980
E. middendorffi (Brashnikov, 1907)	0.5	1.5	1.5	Brashnikov, 1907, for measurements; author's observations on epipods.
E. spathulirostris (Yokoya, 1933)	4	1.6	0.6	Miyake and Hayashi, 1968b
E. barbatus (Rathbun, 1899)	1*	1.6	1.2	Butler, 1980
E. kuratai Miyake and Hayashi, 1967	0*	1.7	1.1	Miyake and Hayashi, 1967
E. biungus (Rathbun, 1902)	1*	1.7	1.3	Butler, 1980
E. macrophthalmus (Rathbun, 1902)	1	1.7	0.8	Butler, 1980
Spirontocaris pectinifera (Stimpson, 1860)	4*	0.9	0.6	Hayashi, 1977
S. prionata (Stimpson, 1864)	4*	0.9	0.8	Butler, 1980
S. arcuatoides Kobjakova, 1962	4	1.0	0.7	Hayashi, 1977
S. ochotensis (Brandt, 1851)	4*	1.0	0.9	Butler, 1980
S. lamellicornis (Dana, 1852)	4	1.0	0.9	Butler, 1980
S. truncata (Rathbun, 1902)	4	1.1	0.6	Butler, 1980
S. spinus (Sowerby, 1805)	4	1.2	0.7	Hayashi, 1977
S. brashnikovi Kobjakova, 1936	4*	1.2	0.9	Brashnikov, 1907, for measurements (as *S. dalli*); Hayashi, 1977, for epipods.
S. lilljeborgii (Danielssen, 1859)	4	1.2	0.8	Hayashi, 1977
S. snyderi (Rathbun, 1902)	3	1.2	0.8	Butler, 1980
S. murdochi (Rathbun, 1902)	4*	1.4	0.8	Hayashi, 1977
S. sica (Rathbun, 1902)	2	1.4	1.1	Butler, 1980
S. holmesi (Holthuis, 1947)	3	1.5	1.2	Butler, 1980
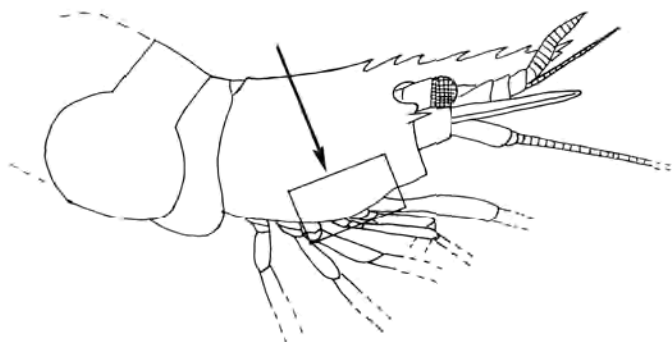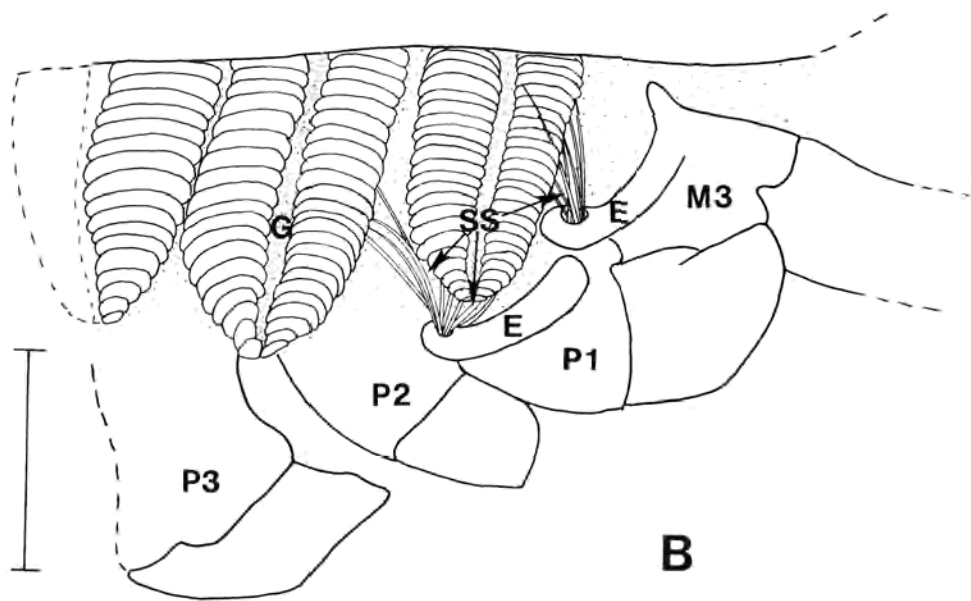
Fig. 1. Epipod-setobranch complexes of *Heptacarpus paludicola*. A, rectangle (arrow) showing area of branchial chamber uncovered and illustrated in B; B, lower half of anterior branchial chamber (branchiostegite partially cut away) showing two epipod-setobranch complexes; E, epipod; G, gill; M3, P1, P2, P3, coxae of third maxilliped, pereiopods 1–3, respectively; SS, setobranch-setae. Scale = 1 mm.

species, complete in structure or not, were very small and could have been easily overlooked. This may explain observations (Rathbun, 1904; Butler, 1980) that this species lacks epipods completely. The epipod of *H. tenuissimus* is clearly reduced and nonfunctional as a gill-cleaning device. In view of the variation in this character, I assigned a value of 0.5 for epipod number for *H. tenuissimus* in the rankings of epipod number for correlations (below) because this species is clearly intermediate between a value of 0 (epipods completely absent) and 1 (present and apparently functional). In a similar manner, I assigned epipod values of 2.5 for *H. pictus* and *H. paludicola*. The *H. pictus* examined in this study had
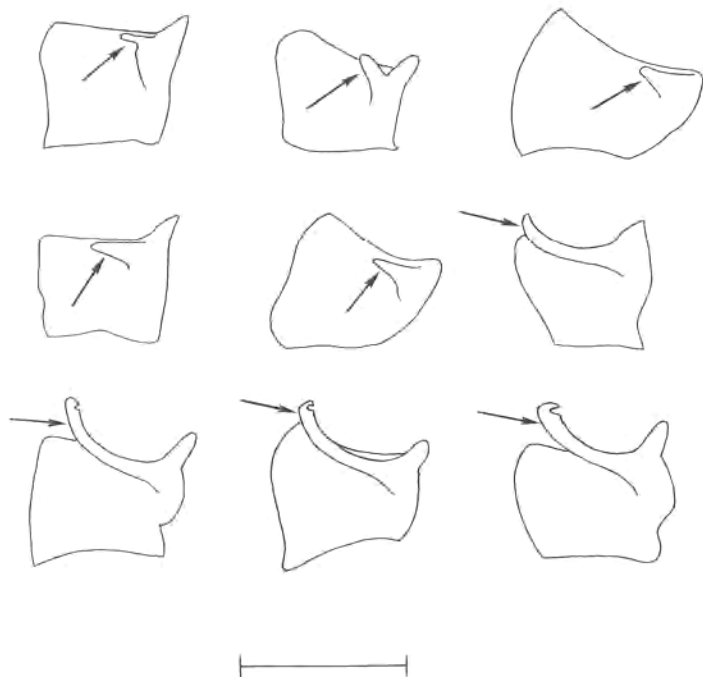
Fig. 2.   Variation in morphology of epipod of third maxilliped of *Eualus middendorffi*. Coxae of third maxilliped (right side, lateral view) of nine different individuals are illustrated. Arrows indicate epipod or epipod vestige. Scale = 1 mm.

2 functional epipods, but some members of a population from another location (Bauer, 1979) had an additional but nonfunctional epipod on pereiopod 2. *Heptacarpus paludicola* from Morro Bay, California, show only 2 functional epipods (Table 2), but Butler (1980) reported that individuals from more northern localities had 3 epipods. Epipod values of 2.5 were assigned to these species in the correlation calculations to reflect this variation.

Three *Eualus* species reported in Table 3 show variation in epipod number. *Eualus middendorffi* from *Albatross* 1906 Expedition station 4999 clearly illustrates how epipod structure can vary within a species. In *E. middendorffi* (Fig. 2), the third maxilliped varies from a small nub to fully structured with a hook; none of these individuals showed setobranch-setae on the following limb. This epipod appears to be nonfunctional with respect to gill cleaning. Some individuals from other localities did show a small but complete epipod-setobranch complex on the third maxilliped-pereiopod 1. The epipod value assigned to *E. middendorffi* was 0.5, which reflects this variation within the species. In *E. suckleyi*, similar variation was observed in the most posterior of its 3 epipods. Rathbun (1904) and Butler (1980) also reported variation in this epipod. *Eualus suckleyi* was given an epipod number of 2.5 in the correlation calculations. Similarly, I gave an epipod number of 2.5 to *E. fabricii* because both Rathbun (1904) and Butler (1980) reported the variable presence of a third epipod in this species. The complete absence of epipods in *E. kuratai* (Miyake and Hayashi, 1967) was confirmed by examination of 26 specimens from 11 *Albatross* 1906 Expedition stations; a small nub, possibly
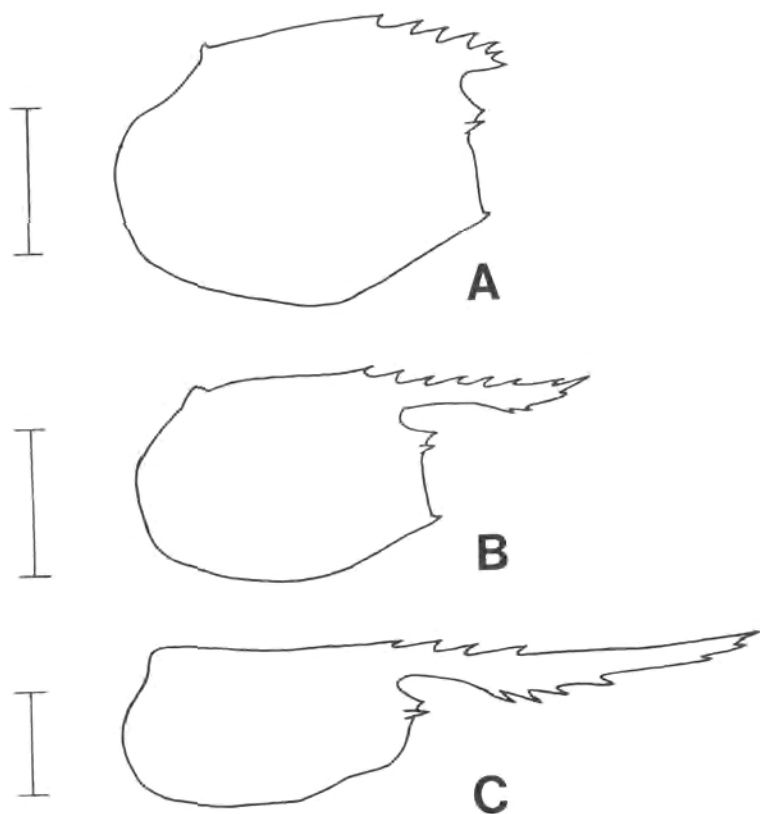
Fig. 3. Morphocline in carapace shape and relative rostral length as illustrated by A, *Heptacarpus taylori*; B. *H. sitchensis*; and C. *H. stylus*. All scales = 3 mm.

representing an epipod vestige, was seen on the coxa of the third maxilliped of most specimens.

General Carapace Shape and Epipod Number

The general shape of the carapace, measured here as the ratio of carapace length (CL) to carapace height (CH), shows considerable variation among species of the genus *Heptacarpus* (Tables 2 and 3; Fig. 3). Stout or robust species show low CL/CH values which represent a short and high carapace; high CL/CH values are exhibited by species with a more slender or elongate carapace shape.

Heptacarpus species with short, high carapaces tend to have high epipod numbers, while slender species have reduced epipod number (Tables 2 and 3; Fig. 4). The possible inverse correlation between carapace shape (CL/CH) and epipod number is not significant for the 16 species reported in Table 2 ($r_s = -0.385$; $0.10 > P > 0.05$). However, when values for the 9 additional species taken from the literature (Table 3) are included, the inverse correlation between carapace shape and epipod number is highly significant ($r_s = -0.543$; $0.005 > P > 0.001$). The initial sample of 16 species contained the three species which deviate most
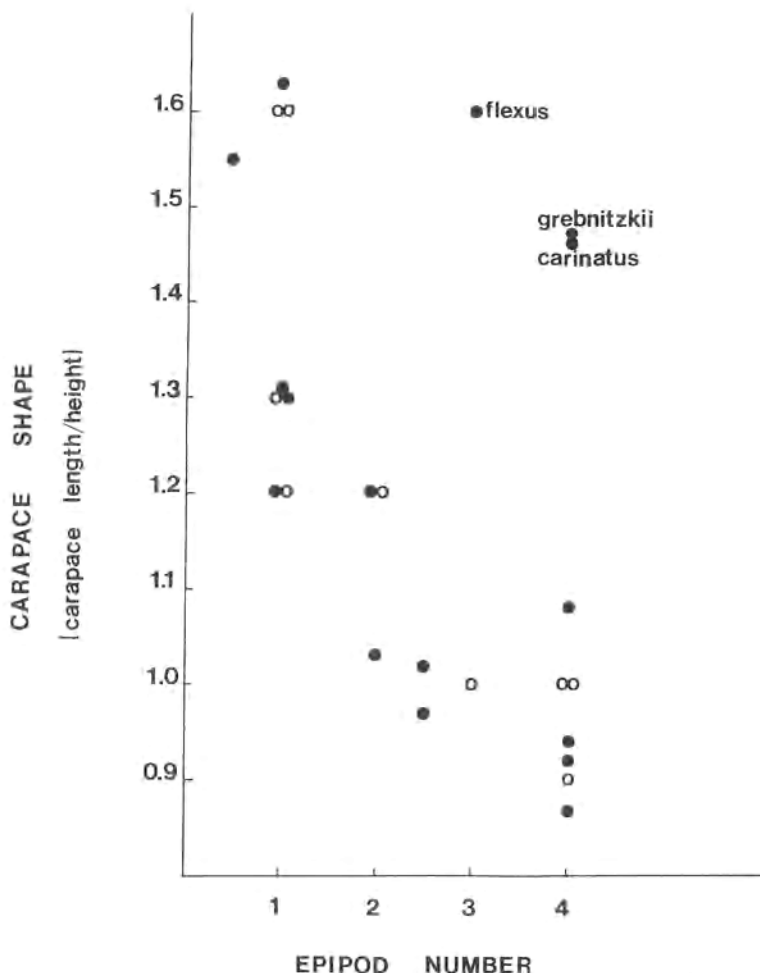
Fig. 4. Variation of general carapace shape (carapace length/height) with epipod number in *Hepta-carpus*. Dots represents values (means) for species examined in detail (Table 2); open circles represent values taken from literature (Table 3). Data points are labeled for three species which deviate markedly from the general trend between carapace shape and epipod number.

from this trend; these species, *H. flexus*, *H. grebnitzkii*, and *H. carinatus*, are slender species which have a high, rather than the expected low, number of epipods.

In the closely related genus *Eualus*, a similar relationship between carapace shape and epipod number is apparent from published data (Table 3; Fig. 5). As in *Heptacarpus* species, the inverse correlation between carapace shape and epipod number is statistically significant ($r_s = -0.570$; $0.01 > P > 0.005$). In the *Spirontocaris* species reported here (Table 3), only 3 of the 13 species have reduced epipod numbers; therefore, the correlation between carapace shape and epipod number is not significant ($r_s = -0.183$; $P > 0.10$). The three *Spirontocaris* species which have reduced epipod numbers are slender species (high CL/CH) for the genus (Table 3).
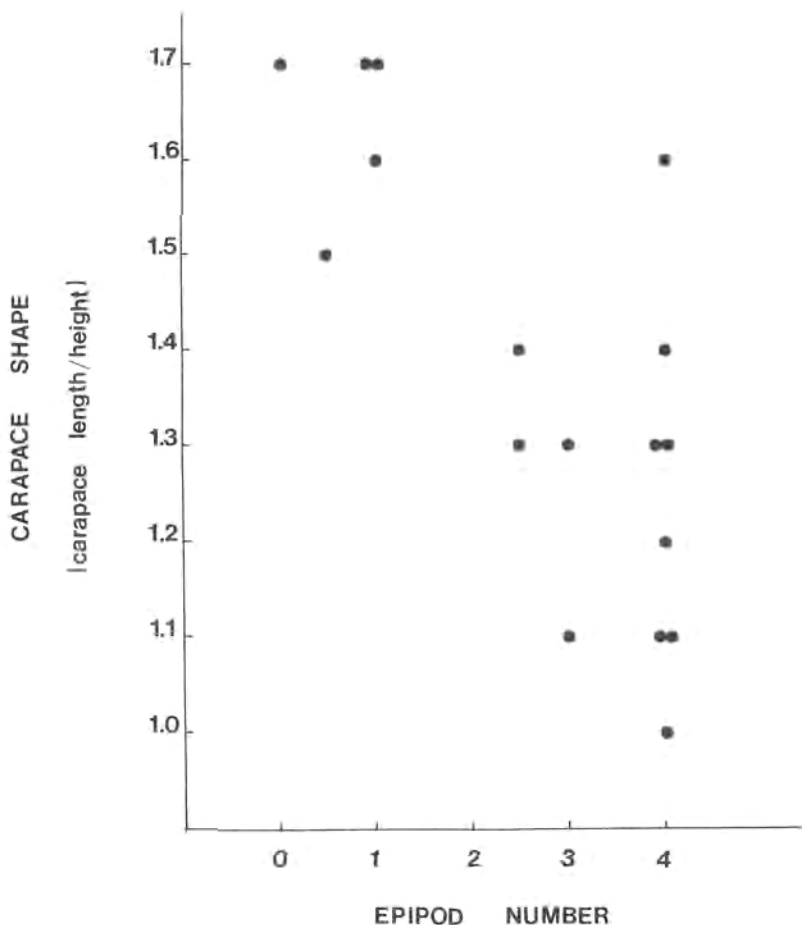
Fig. 5.   Variation of carapace shape (carapace length/height) with epipod number in *Eualus* species. Values taken from literature (Table 3).

Correlation of Various Morphological Characters with Epipod Number and Carapace Shape

Relative Rostral Length. — In the 16 *Heptacarpus* species examined here (Table 2), there is a significant inverse correlation between relative rostral length (rostral length/carapace length) and epipod number ($r_s = -0.579; 0.025 > P > 0.01$); when values taken from published illustrations of 9 additional species are included, the results of the correlation are similar ($r_s = -0.456; 0.025 > P > 0.01$). The results of these correlations indicate that species with a short rostrum are species with high epipod number, while species with a proportionately longer rostrum tend to have reduced epipod numbers. In the genus *Heptacarpus*, the relative rostral length is positively correlated with carapace shape (CL/CH); species with a short and high carapace tend to have a short rostrum, while more elongate species have a proportionately longer rostrum (for the 16 *Heptacarpus* spp. in Table 2, $r_s =$

+0.807, $P < 0.001$; for all 25 *Heptacarpus* spp. in Tables 2 and 3, $r_s = +0.770$; $P < 0.001$).

Using data taken from published illustrations (Table 3), tests of correlation between relative rostral length and epipod number were done for *Eualus* spp. and *Spirontocaris* spp. In *Eualus* species, relative rostral length is negatively associated with epipod number ($r_s = -0.564; 0.025 > P > 0.01$). There is not enough variation in epipod number in the *Spirontocaris* spp. reported here to determine if epipod number and relative rostral length are correlated in this genus. In both *Eualus* and *Spirontocaris*, species with a slender carapace shape tend to have a long rostrum, while stout species show, in general, a short rostrum (*Eualus* spp., $r_s = +0.597; 0.01 > P > 0.005$; *Spirontocaris* spp., $r_s = +0.508; 0.05 > P > 0.025$).

Relative Rostral Height.—The ratio of rostral length (RL) to rostral height (RH) is a measure of the general shape of the rostrum. Long and slender rostra have high RL/RH ratios, while comparatively short and high (deep) ones have lower values. In the 16 *Heptacarpus* species examined (Table 2), the correlation of rostral shape and epipod number is inverse, i.e., species with low epipod number tend to have a slender rostrum ($r_s = -0.671; 0.005 > P > 0.001$). Slender *Heptacarpus* species (high CL/CH) tend to have a slender rostrum, while more robust species (low CL/CH) generally have a less slender rostrum. The correlation between relative rostral height and carapace shape is highly significant ($r_s = +0.695; 0.005 > P > 0.001$).

Relative Length of Pereiopod 3.—Preliminary observations indicated a trend in the relative length of the walking legs with respect to carapace shape. Data on the relative length of pereiopod 3 (leg length/carapace length) (Table 2) and carapace shape (CL/CH) show a significant inverse correlation between these characters ($r_s = -0.651; 0.005 > P > 0.001$). Species with a slender carapace shape tend to have relatively short legs, while stout species tend to have proportionately longer ones. However, the correlation between relative length of pereiopod 3 and epipod number is *not* significant ($r_s = +0.047; P > 0.10$). In the previous characters described, the correlation of a given character with epipod number was opposite in direction to that of its correlation with carapace shape.

Abdominal Characters.—The length to height ratios of the second abdominal tergum, fifth abdominal segment, and sixth abdominal segment are indicators of the general shape of these body parts (stout versus slender). In the 16 *Heptacarpus* species examined (Table 2). the relative shape of both abdominal segments 5 and 6 show a significant correlation (inverse) with epipod number, i.e., species with slender abdominal segments 5 and 6 tend to have low epipod numbers, while those with stouter abdominal segments 5 and 6 generally have high epipod numbers (for abdominal segment 5, $r_s = 0.715; 0.005 > P > 0.001$; for abdominal segment 6, $r_s = -0.621; 0.01 > P > 0.005$). *Heptacarpus* species with a slender carapace shape tend to have relatively slender fifth and sixth abdominal segments, while stout species show the opposite tendency. Correlations between the length/height relationships of abdominal segments 5 and 6 and carapace shape (CL/CH) are highly significant (for abdominal segment 5, $r_s = +0.665; 0.005 > P > 0.001$; for abdominal segment 6, $r_s = +0.813; P < 0.001$). There is no significant correlation of the length/height ratio of the tergum of the second abdominal segment with either epipod number ($r_s = +0.201; P > 0.10$) or carapace shape ($r_s = +0.360; 0.10 > P > 0.05$).

Relative Palm Area of Chela 1.—The area (length × breadth) of the palm (propodus) of the first chela divided by the carapace length gives the relative palm area, a measure of the relative size of chela 1. Species with reduced epipod number (Table 2) generally show small first chelae, while species with higher epipod numbers tend to have larger ones ($r_s = +0.496$; $0.005 > P > 0.025$). The possible inverse correlation between carapace shape and relative palm area is not statistically significant ($r_s = -0.218$; $P > 0.10$).

Relative Eye Length.—In the 16 *Heptacarpus* species examined, there was no correlation between relative eye length (eye length/carapace length) and epipod number ($r_s = +0.145$; $P > 0.10$). However, there is a negative correlation between relative eye length and carapace shape (CL/CH) ($r_s = -0.446$; $0.05 > P > 0.01$). Slender species (high CL/CH) generally have smaller eyes than stouter (low CL/CH) species.

Antennular Spinules.—The median number of antennular spinules (defined as the number of spinules on the dorsal edge of the first peduncular segment of the first antenna) varied from 0–4 in the *Heptacarpus* species examined (Table 2). There is a strong positive correlation between the median number of antennular spinules and epipod number ($r_s = +0.746$; $P < 0.001$). The correlation between antennular spinules and carapace shape is inverse ($r_s = -0.594$; $0.01 > P > 0.005$).

Meral Spines.—The median number of meral spines of pereiopod 3 varied from 1–5 (Table 2). There was no significant correlation of meral spine number with carapace shape ($r_s = +0.168$; $P > 0.10$) or epipod number ($r_s = -0.278$; $P > 0.10$).

Pleuron 4 Spine.—All species with a mean carapace length/height ratio of 1.2 or less have a spine on the posteroventral edge of the pleuron of the fourth abdominal segment (Table 2). Species with a more slender carapace shape (CL/CH > 1.2) lack this spine. As might be expected, the inverse correlation between the number of pleuron 4 spines (0 or 1) and carapace shape is highly significant ($r_s = +0.603$; $0.01 > P > 0.005$). There is no significant correlation between pleuron 4 spine number and epipod number ($r_s = +0.422$; $0.10 > P > 0.05$). Although Tate and Clelland (1957) state that even extensive ties in ranks make little difference in the value of the correlation coefficient (here, in the ranking of pleuron 4 spine number, 0 or 1, there are very extensive ties), an additional procedure, the 2×2 contingency table chi-square, was used to test the possible association between epipod number and the presence or absence of the pleuron 4 spine. The categories for epipods are maximum epipod number (4) or reduced epipods (3 or less); the null hypothesis of no association between epipod condition and presence or absence of a pleuron 4 spine is accepted ($\chi^2 = 0.423$; $0.75 > P > 0.50$).

Dorsolateral Telson Spines.—The median number of pairs of dorsolateral spines on the telson varied from 3–5.5 (Table 2). There is no correlation between dorsolateral spine number and carapace shape ($r_s = -0.150$; $P > 0.10$) or epipod number ($r_s = +0.212$; $P > 0.10$).

Branchiostegal Setal Fringe.—In several *Heptacarpus* species, plumose setae border the ventral edge of the branchiostegite (gill cover) (Fig. 6). The *Heptacarpus* species with an epipod number of 4 show, with the single exception of *H. carinatus*, this setal fringe on the branchiostegite (Table 2). All other species examined (with 3 epipods or fewer) lack the setal fringe. As expected, the test of association between epipod condition (full or reduced) and the presence or absence of the branchiostegal setal fringe is highly significant ($\chi^2 = 18.6$; $P < 0.005$). This character is
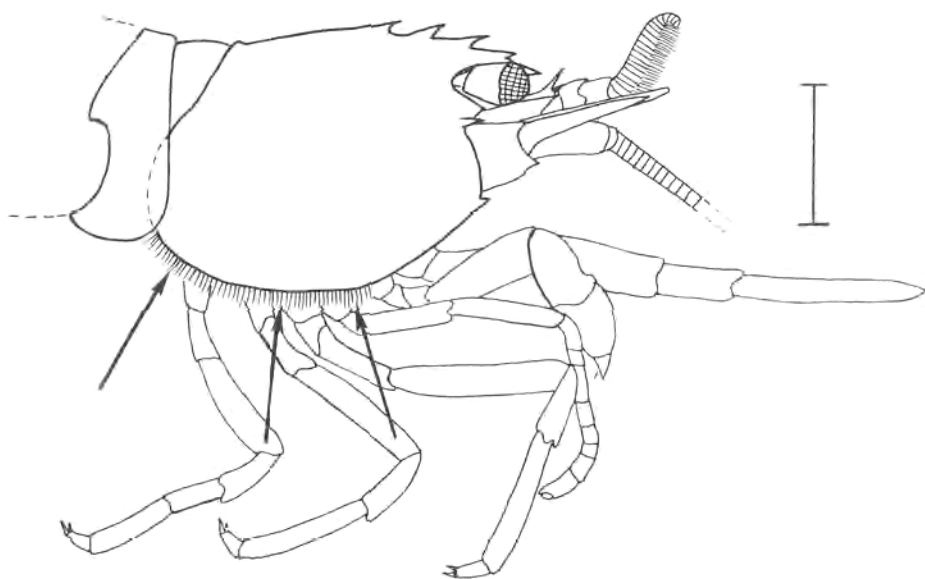
Fig. 6.   Branchiostegal setal fringe (arrows) in *Heptacarpus brevirostris*. Scale = 5 mm.

not one recorded in species descriptions. However, Jensen (1983) has recently described a new species, *H. pugettensis*, which is very similar morphologically to *H. brevirostris*, *H. taylori*, and *H. palpator*, all species with 4 epipods and a branchiostegal fringe. One major difference between *H. pugettensis* and these three species is that *H. pugettensis* has 3 instead of 4 epipods. As in other *Heptacarpus* species observed with 3 or fewer epipods, *H. pugettensis* lacks the branchiostegal setal fringe (personal observation on specimens sent to me by G. Jensen).

Effect of Sex and Size on Ratios

In *Heptacarpus grebnitzkii*, there was sufficient material to investigate the effect of sexual dimorphism on the various ratios used in calculating correlations (above) and in grouping species (below). Table 4 lists the mean values for each character for comparison. A one-way ANOVA was used with log transformed data to determine whether the means of each character were significantly different. The object of this analysis was to determine how the ratios used in the various correlations are affected by sexual dimorphism, i.e., is the ranking of a given ratio character for *H. grebnitzkii* among other *Heptacarpus* species greatly altered by the sexual composition of the sample? Table 4 shows those characters in which the means for males and females were significantly different. A comparison of the *H. grebnitzkii* values from Table 4 with those of other species (Table 2) shows that the rank of *H. grebnitzkii* among other species would not change as far as carapace length/height (CL/CH), rostral length/carapace length (RL/CL), abdominal segment 6 length/height (ABD 6 L/C), and leg length (pereiopod 3)/carapace length (LL/CL) are concerned. The position of *H. grebnitzkii* among other species would change by 1 rank at most in rostral length/height (RL/RH) and eye length/carapace length (EL/CL) if the sample was completely biased towards either males or females. In the assignment of character states for determining morphological

Table 4. Comparison of mean values of morphometric characters between male and female *Heptacarpus grebnitzkii*. Characters marked with an asterisk are those in which female and male means were statistically different ($P \leq 0.05$; one-way ANOVA). See key at end of "Methods" for character abbreviations.

Sex and sample size (N)	$\bar{x}$ size (CL, mm)	CL/CH*	RL/CL*	RL/RH*	ABD 6 L/H	ABD 5 L/H	ABD 2 L/H	PA/CL	LL/CL*	EL/CL*
Females (15)	7.6	1.42	1.17	5.6	1.99	0.81	1.27	0.23	1.44	0.22
Males (15)	5.5	1.51	1.07	6.3	2.09	0.81	1.27	0.28	1.57	0.27
Combined (30)	6.5	1.47	1.11	5.9	2.04	0.81	1.27	0.25	1.51	0.24

similarity (see below), only RL/CL and RL/RH ratios would be placed in a different character state (1 higher or lower) than the combined values if a predominantly male or female sample were used.

Two lots of *Heptacarpus maxillipes* were available and combined to provide a sample of 27 for this species. To look at the effect of size on ratios used in this study for this species, the combined sample was separated into two groups on the basis of size (Table 5) (the median carapace length, 5.8 mm, was used to divide the sample into two groups). Table 5 shows the mean values for each morphometric ratio for each size group along with the means of the combined sample for each character. For those characters in which the means between size groups were significantly different, a change in one rank in position among other *Heptacarpus* species could be possible with rostral length/height (RL/RH) and rostral length/carapace length (RL/CL) if the sample were highly biased to small or to large individuals. In the morphological similarity analysis (below), *Heptacarpus maxillipes* could change position in character state in abdominal segment 2 tergal length/height (ABD 2 L/H) and eye length/carapace length (EL/CL) if the sample was biased toward one size group or the other.

Morphological Similarity

Formation of species groups on the basis of morphological similarity was based on 17 meristic, two-state, and morphometric (continuous) characters (Table 6). For continuous characters, the range of variation of mean values of all the species was divided into evenly spaced intervals on a subjective basis to give character states for a particular character (Table 6). To form groups from the 16 *Heptacarpus* species investigated in detail here, an index of affinity between pairs of species was calculated. The index of affinity used by Judkins (1978) to form species groups in *Sergestes* spp., by Fleminger and Hulsemann (1974) for *Pontellina* spp. (calanoid copepods), and by Fager (1969) for flexibacteria was selected for calculation

Table 5. Comparison of mean values of morphometric characters between two size groups of *Heptacarpus maxillipes*; those individuals with carapace length >5.8 mm or with carapace length ≤5.8 mm. Characters marked with an asterisk indicate means that are significantly different ($P \leq 0.05$; one-way ANOVA). See key at end of "Methods" for character abbreviations.

Size group and sample size (N)	$\bar{x}$ size (CL, mm)	CL/CH	RL/CL*	RL/RH*	ABD 6* L/H	ABD 5* L/H	ABD 2 L/H	PA/CL	LL/CL	EL/CL*
CL > 5.8 mm (12)	7.8	1.20	0.93	6.2	2.59	1.11	1.04	0.32	2.46	0.29
CL ≤ 5.8 mm (15)	5.2	1.19	0.79	7.7	2.79	1.04	1.11	0.38	2.56	0.37
Combined (27)	6.3	1.20	0.85	7.0	2.70	1.08	1.08	0.35	2.51	0.34

Table 6. Character states used in computing indices of affinity between pairs of *Heptacarpus* species.

Character	Character states
1. $\bar{x}$ carapace length/height	(a) 0.80–0.99; (b) 1.00–1.19; (c) 1.20–1.39; (d) ≧ 1.40
2. epipod number	(a) 4; (b) 3; (c) 2, 2.5; (d) 1; (e) 0.5
3. branchiostegal setal fringe	(a) present; (b) absent
4. $\bar{x}$ rostral length/carapace length	(a) 0.20–0.69; (b) 0.70–1.19; (c) ≧ 1.20
5. $\bar{x}$ rostral length/height	(a) 2.0–3.9; (b) 4.0–5.9; (c) 6.0–7.9; (d) ≧ 8.0
6. $\bar{x}$ sixth abdominal segment length/height	(a) 1.50–1.99; (b) 2.00–2.49; (c) 2.50–2.99
7. $\bar{x}$ fifth abdominal segment length/height	(a) 0.60–0.79; (b) 0.80–0.99; (c) ≧ 1.0
8. $\bar{x}$ second abdominal segment length/height (values rounded to first decimal place)	(a) 1.0; (b) 1.1; (c) ≧ 1.2
9. $\bar{x}$ chela 1 palm area/carapace length	(a) 0.11–0.20; (b) 0.21–0.30; (c) 0.31–0.40; (d) ≧ 0.41
10. $\bar{x}$ pereiopod 3 length/carapace length	(a) < 2.00; (b) ≧ 2.00
11. $\bar{x}$ eye length/carapace length	(a) 0.30; (b) 0.30–0.39; (c) ≧ 0.40
12. median number of antennular spinules	(a) 0; (b) 1; (c) 2; (d) 3; (e) 4
13. median number of pereiopod 3 meral spines	(a) 1; (b) 2; (c) 3; (d) 4; (e) 5
14. pterygostomial spine	(a) present; (b) absent
15. median number of pairs of dorsolateral telson spines	(a) 3; (b) 4; (c) ≧ 5
16. median number of pairs of posterior telson spines	(a) 3; (b) ≧ 3
17. posteroventral spine on fourth abdominal pleuron	(a) present; (b) absent

of the degree of morphological similarity between pairs of species. Following Judkins (1978), the index of affinity is defined as $\dfrac{J}{C} - \dfrac{1}{2\sqrt{C}}$ where C is the number of characters in the analysis and J is the number of identical character states shared by a pair of species. A similarity matrix was constructed with the indices of affinity calculated for all possible pairs of species (Table 7). In the studies cited above, an index of affinity greater than 0.5 has been found to be useful in forming objective groupings of species, and this value is used here to signify a significant degree of morphological similarity between species.

Three distinct species groups, in which all members have an index of affinity greater than 0.5 for all other members of the group, are obvious from Table 7: (1) *H. brevirostris, H. palpator,* and *H. taylori,* (2) *H. sitchensis, H. pictus,* and *H. paludicola,* (3) *H. flexus, H. tridens,* and *H. tenuissimus.* Pairs of species which show a significant index of affinity are *H. moseri* and *H. maxillipes, H. tridens* and *H. camtschaticus, H. tridens* and *H. stylus, H. carinatus* and *H. grebnitzkii, H. flexus* and *H. carinatus,* and *H. stylus* and *H. carinatus.* The reliability of these morphological groupings as indicators of phylogenetic relationship is discussed below.

DISCUSSION

The number of epipod-setobranch complexes varies considerably in the genus *Heptacarpus* and in the closely related genus *Eualus* from a maximum of 4 to a minimum of 0. One purpose of this study was to determine the direction of evolution (evolutionary polarity) in epipod number in *Heptacarpus* and to use this information to determine the direction of evolution in other morphological trends in the genus. Bauer (1979, 1981) has already suggested that the epipod-

Table 7. Morphological similarity of *Heptacarpus* species estimated by the index of affinity. Phenetic groupings of species pairs are indicated by an index of affinity >0.5 (underlined).

Species	H. palpator	H. brevirostris	H. taylori	H. pictus	H. paludicola	H. sitchensis	H. stimpsoni	H. maxillipes	H. moseri	H. camtschaticus	H. tridens	H. carinatus	H. grebnitzkii	H. tenuissimus	H. flexus	H. stylus
H. palpator	—															
H. brevirostris	0.70	—														
H. taylori	0.59	0.59	—													
H. pictus	0.35	0.23	0.35	—												
H. paludicola	0.23	0.23	0.29	0.64	—											
H. sitchensis	0.12	0.17	0.29	0.64	0.59	—										
H. stimpsoni	0.29	0.35	0.47	0.35	0.29	0.41	—									
H. maxillipes	0.06	0.17	0.23	0.23	0.23	0.29	0.29	—								
H. moseri	0.12	0.23	0.23	0.41	0.41	0.47	0.35	0.64	—							
H. camtschaticus	0.12	0.12	0.23	0.35	0.41	0.41	0.17	0.41	0.35	—						
H. tridens	−0.06	0.06	0.06	0.17	0.23	0.23	0.17	0.53	0.35	0.53	—					
H. carinatus	0.06	0.06	0.12	0.29	0.35	0.41	0.17	0.17	0.29	0.47	0.35	—				
H. grebnitzkii	0.06	0.06	0.12	0.17	0.12	0.23	0.23	0.06	0.23	0.23	0.06	0.59	—			
H. tenuissimus	0	0.06	0.12	0.12	0.12	0.17	0.12	0.12	0.35	0.35	0.59	0.41	0.12	—		
H. flexus	0	0.06	0.06	0.17	0.29	0.17	0.06	0.35	0.41	0.35	0.53	0.59	0.29	0.64	—	
H. stylus	−0.12	−0.06	−0.06	0.17	0.23	0.23	0.17	0.29	0.12	0.47	0.59	0.53	0.35	0.41	0.47	—

setobranch complex is a primitive gill-cleaning mechanism which has been replaced by the more efficient cheliped brushing of gills in various decapod crustacean groups. In the Caridea, species which have the highest number of epipod-setobranch complexes (5) do not usually clean the gills by cheliped brushing. In other groups in which epipod-setobranchs are absent, gill brushing is generally well developed. However, in the family Hippolytidae, of which *Heptacarpus* is a member, there is considerable inter- and intrageneric variation in gill-cleaning methods. All hippolytids observed brush the gills with chelipeds to some degree, but gill brushing seems to be best developed in species with reduced epipod number (Bauer, 1979). Previous evidence from functional morphology, then, suggests that epipod-setobranchs are being reduced and lost in the Hippolytidae and, as in other decapod and caridean groups, are being replaced by cheliped brushing. Additional evidence from this study supports this view. In some *Heptacarpus* and *Eualus* species, the most posterior epipod is apparently nonfunctional with respect to gill cleaning. There may be no setobranch-setae associated with an epipod which has normal size and the usual hook (some *H. pictus, H. tenuissimus, Eualus middendorffi*). In addition, the epipod itself may be very small and/or without a hook, obviously vestigial in form and function (*Heptacarpus tenuissimus, Eualus suckleyi, E. middendorffi*). Solely on the basis of functional morphology, one can hypothesize that a low number or the absence of epipod-setobranchs is a true reduction (loss) from an ancestral condition of 4 (in *Heptacarpus* and *Eualus*) epipod-setobranch complexes.

One can also establish that a high epipod number is primitive, and a low number the derived condition, by comparison with other crustacean groups. It is generally accepted that thoracic epipods are a primitive malacostracan feature (Calman, 1909; Hessler and Newman, 1975). Therefore, loss of epipods (epipod-setobranchs of carideans) is a derived state. [Lebour (1936: 91) reviews evidence that both the hooked epipod (mastigobranch) and setobranch of one limb are derived from the same epipodial primordium, i.e., represent the epipod of that limb.] Within the Decapoda, the shrimp *Procaris* (Chace and Manning, 1972; Holthuis, 1973), with some of the most primitive characters of any natant decapod, shows an epipod-setobranch formula only slightly reduced (Bauer, 1979). In the thalassanid-anomalan (=anomuran) line, the axiid thalassanids, the most primitive within the group (macruran facies least modified), possess setobranchs for gill cleaning but in all other (more advanced) members of the group, setobranchs are lost and replaced by cheliped (pereiopod 5) brushing of the gills (Bauer, 1981).

The evidence from two different sources, functional morphology and out-group comparison with other crustacean groups, thus strongly indicates the evolutionary polarity in epipods (=epipod-setobranchs) in *Heptacarpus* and related groups: the highest number of epipods (4) is the ancestral character state and lower epipod number is the derived state. The evidence from functional morphology also shows that the chance of reversals (redevelopment of epipods and setobranchs after their loss) in this character is improbable. It is difficult to imagine how this complicated structure, consisting of a hooked process on one thoracic limb which functionally couples with another process on a different pereiopod, could evolve again after loss in a form so close to the original that an observer could not detect the difference.

A number of morphoclines (Maslin, 1952) or phenoclines (Ross, 1974) have been described in this study on *Heptacarpus*. The direction of evolution in epipod number has been relatively easy to establish, given the evidence available. However, functional morphology and out-group comparison cannot be used at this time for the other described morphoclines. No functional evidence is available

to determine the evolutionary polarity of trends in carapace shape, relative rostral length, etc. Out-group comparison (e.g., Watrous and Wheeler, 1981; Ross, 1974) is difficult to use with *Heptacarpus* because the various characters under consideration show the same high variability (two to several character states) in the potential out-group, the apparently closely related genus *Eualus*. Watrous and Wheeler (1981) emphasized that out-group comparison is very difficult to use in such a situation. I will use instead methods described by Maslin (1952), especially his "principle of paradromism." If morphocline "A" is correlated (parallel or paradromic) to morphocline "B," whose evolutionary polarity is already determined, then the direction of evolution (ancestral to derived) in morphocline "A" can be determined, i.e., is the same as that of morphocline "B." The morphological extreme of morphocline "A," correlated with the ancestral extreme of morphocline "B," is primitive; the other extreme of morphocline "A," correlated with the derived extreme of morphocline "B," is also derived. In this study, the polarity of the morphocline "epipod number" has been established and strongly supported by two independent kinds of evidence. I will attempt to hypothesize the ancestral and derived extremes of various morphoclines by comparing them to the morphocline in epipod number. Arnold (1981) does not believe that correlations between characters are as effective as out-group comparison or functional evidence (not feasible at this time for morphoclines other than epipod number in this study). However, Ross (1974) and Wagner (1980) support the basic idea of using correlation of characters of unknown polarity with other characters in which the direction of evolution is fairly well established in order to hypothesize evolutionary polarities.

Epipod number is used as a phylogenetic marker in this study, i.e., it is used to establish the evolutionary polarity in other morphoclines. The extreme of a given morphocline associated with a high epipod number is considered ancestral or primitive, while the other end of the morphocline associated with low (reduced) epipod number is considered the derived character state. A measure or value for various morphometric (continuous), meristic, and two-state characters was assigned in each species. Correlations between the various character states of a particular morphocline and epipod number were calculated. The direction of evolution or polarity of a given morphocline is assigned (hypothesized) when the correlation is statistically significant.

There is considerable variation in the general shape of the carapace in *Heptacarpus* from short and high (stout or robust) to long and low (elongate or slender). There is no functional or out-group evidence to indicate the evolutionary polarity of this morphocline. Comparison of carapace shape and epipod number, however, does indicate the direction of evolution in this morphocline. The correlation between carapace shape and epipod number in the 16 *Heptacarpus* species studied in detail was not quite statistically significant. However, when data on carapace shape and epipod number of other *Heptacarpus* species taken from published illustrations were included, the correlation was quite significant. Stout or robust species tend to have high epipod number (primitive), while more slender species have reduced epipod number (derived). On this basis, stout species such as *H. palpator*, *H. brevirostris*, and *H. taylori* are considered primitive with respect to carapace shape, while slender species with reduced epipods, such as *H. stylus* and *H. tenuissimus*, are considered much more advanced or derived. *Heptacarpus flexus*, *H. grebnitzkii*, and *H. carinatus* are important deviations from these trends; they are species with high epipod number but relatively slender carapace shape. I believe that this is an example of parallelism, i.e., evolution of the slender carapace shape independent of the line leading to other slender species. Correlations of carapace shape (and other characters) with epipod number, the phy-

logenetic marker, would be nearly perfect given no parallelism or reversal and uniform rates of evolution. However, as Arnold (1981) has pointed out, parallelism and reversal in characters are quite common in low taxonomic categories. This certainly appears to be the case in *Heptacarpus* (see below).

Another morphocline significantly correlated with epipod number is relative rostral length. *Heptacarpus* species with primitive epipod number tend to have a short rostrum, while a proportionately longer rostrum is characteristic of species with reduced epipods.

Data on carapace shape (carapace length/height) and relative rostral length were taken from the literature for 17 *Eualus* species. The correlations of carapace shape and relative rostral length with epipod number are significant. As in *Heptacarpus*, high (ancestral) epipod numbers are associated with a stout carapace shape and a proportionately short rostrum, while reduced epipods are characteristic of slender species with a longer rostrum. *Eualus* is the genus most closely related to *Heptacarpus* (Holthuis, 1947). Maslin (1952) noted that similar morphoclines with the same evolutionary polarity should be expected and often appear in closely related groups. The appearance of similar correlated trends in *Eualus* and *Heptacarpus* with respect to carapace shape, rostral length, and epipod number is additional evidence that the direction of evolution in these trends is as hypothesized above.

In the 16 *Heptacarpus* species examined, there is a significant association between the presence of a dense fringe of setae along the edge of the branchiostegite (gill cover) and an epipod number of four. All species with four epipods (except *H. carinatus*) have a branchiostegal setal fringe, while all species with fewer epipods lack it. The presence of a branchiostegal setal fringe is thus considered primitive and its absence derived. The functional significance of this setal fringe is not known, although it may have something to do with the filtering or monitoring of the respiratory current as it enters the gill chamber. Species with reduced epipod number that have been observed alive have well-developed gill-cleaning behavior (cheliped brushing); perhaps the selective pressure to maintain the setal fringe (if it does filter debris from the respiratory current) has abated and thus the structure has been lost.

Statistically significant correlations between epipod number and the additional following characters were found in the 16 *Heptacarpus* species examined in this study: general rostral shape (rostral length/height) (inverse correlation); general shape of the fifth and sixth abdominal segments (inverse correlation); number of antennular spinules (positive correlation); and relative chela 1 palm area (palm area/carapace length) (positive correlation). Several characters examined showed no significant correlation with epipod number (general shape of the second abdominal segment, relative eye length, number of meral spines of the third pereiopod, presence or absence of a spine on the fourth abdominal pleuron, and number of pairs of dorsolateral telson spines).

Using the criterion that high epipod number establishes the primitive end, and reduced epipod number the derived end of morphoclines correlated with epipod number, the ancestral *Heptacarpus* were probably short, stout species (carapace and abdominal segments short and high) with a short rostrum, large first chelae, a high number of antennular spinules, and a branchiostegal setal fringe. Under these criteria, the most advanced or derived species examined in this study is *H. tenuissimus*, a slender species which has nearly lost the epipod-setobranch complex and which demonstrates well the various hypothesized derived features: long rostrum, small first chelae, antennular spinules, and lack of branchiostegal setal fringe.

Several characters correlated with epipod number were also correlated with general carapace shape (carapace length/height): relative rostral length, relative rostral shape, relative palm area of chela 1, general shape of abdominal segments 5 and 6, and number of antennular spinules. This is not surprising since epipod number and carapace shape are themselves highly (inversely) correlated. However, three characters (relative length of pereiopod 3, relative eye length, and presence or absence of a spine on pleuron 4) are highly correlated or associated with measures of carapace shape but *not* with epipod number. Shrimps with a short high carapace tend to have long walking legs, long (large) eyes, and a spine on the pleuron of the fourth abdominal segment, while more slender species show the opposite trends. The lack of correlation of these characters with epipod number, the phylogenetic marker, indicates that these characters are highly linked to carapace shape in a functional way and are not useful indicators of phylogenetic relationship. Although characters correlated with epipod number must certainly be subject to parallelisms and reversals, characters correlated only with carapace shape are apparently so strongly subject to parallel evolution that they are not useful in showing evolutionary relationships in *Heptacarpus*.

One approach to looking at phylogenetic relationships among species is to use morphological similarity as an indicator of genetic relationship (Adansonian methods, phenetic methods; Ross, 1974). Having attempted to analyse some morphological trends in *Heptacarpus* and to determine the evolutionary direction of these trends, it would be interesting to determine or assess the phylogenetic validity of species groupings formed on the basis of a morphological similarity method. The method used to assess morphological similarity between pairs of species was the index of affinity (Fager, 1969) which workers such as Judkins (1978) and Fleminger and Hulsemann (1974) have applied to crustaceans. The index of affinity was calculated for all possible pairs of the 16 *Heptacarpus* species examined in detail and was based on 17 characters. One group (*H. taylori, H. brevirostris, H. palpator*) is composed of species which represent the primitive or ancestral ends of several morphoclines. Another group (*H. pictus, H. paludicola, H. sitchensis*) shares similar derived epipod numbers and probably represents a natural grouping. On the other hand, the group formed by *H. flexus, H. tridens,* and *H. tenuissimus* is not in concordance with a phylogeny based on epipod number. *Heptacarpus tridens* and *H. tenuissimus* seem closely related on the basis of epipod number, but *H. flexus* is more primitive in this respect. Pairs of species which show a significant degree of morphological similarity (index of affinity greater than 0.5) and which agree in epipod number are *H. tridens* and *H. camtschaticus, H. tridens* and *H. stylus,* and *H. carinatus* and *H. grebnitzkii. Heptacarpus moseri* and *H. maxillipes,* and *H. flexus* and *H. carinatus* are two pairs of species with significant morphological similarity but which are one epipod number apart. *Heptacarpus stylus* and *H. carinatus* are a pair of species in which a significant phenetic similarity exists, but in this case morphological similarity is a misleading indicator of phylogenetic relationship. Based on epipod number, *H. carinatus* (4 epipods) is a much more primitive species than *H. stylus* (1 epipod). The high degree of morphological similarity between the two species probably results from parallelism in characters such as carapace shape, relative rostral length, and eye and leg length.

In summary, of three groups of three species formed by using the index of affinity employed in this study, only one species was far out of place with respect to hypothesized phylogenetic relationships. Three phenetically formed pairs of species were concordant in epipod number, two pairs of species were one epipod (one phylogenetic step) apart, and one pair was very discordant with respect to

epipod number. Overall, and as a first approximation, the index of affinity method used to form species groups from the 16 *Heptacarpus* species studied in detail here seems a fair indicator of phylogenetic relationships. Epipod number (epipod-setobranch complexes) indicates when overall morphological similarity is a false indicator of phylogenetic relationship.

Can any of the morphological trends discussed here be related to the ecology of the species studied? I have collected and observed alive *H. taylori, H. palpator, H. pictus, H. paludicola,* and *H. stylus.* The first two species are short stout shrimps which cling tightly to stones, algae, and sessile invertebrates; they appear to be rather sluggish and cryptic in their general behavior. *Heptacarpus pictus* and *H. paludicola* are active omnivorous shrimps in tidepool and shallow bay habitats, respectively. *Heptacarpus stylus,* a representative of an elongate species, appears much like a large "grass" shrimp, i.e., like a *Hippolyte* species, in its behavior of clinging or lying flat on algal blades. Observations are still too few to speculate on the functional significance of the various morphoclines described in this study. However, investigation on the functional or adaptive value of trends in carapace, abdomen, rostrum, eye, chela size and shape, and of various other (meristic, two-state) characters could reveal important information on their phylogenetic significance in the genus *Heptacarpus.*

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