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CRUSTACEAN PHYLOGENY

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PHYLOGENETIC RELATIONSHIPS AMONG SHRIMP-LIKE DECAPODS

ABSTRACT

Early classifications involving peneids, stenopodids, carideans, and procaridids are reviewed. These shrimp-like decapods have at various times been placed together in one suborder or in three separate suborders. The morphological characteristics of these groups are reviewed with particular reference to the gills, protocephalic skeleton, and foregut. We conclude that Dendrobranchiata (Peneoidea and Sergestoidea), Stenopodidea, and Procaridoidea represent independent evolutionary lines. We suggest that the Caridea is a heterogeneous group that should be re-examined.

1 INTRODUCTION

There is tremendous morphological diversity among decapod crustaceans. In size they range from pontoniid shrimp of a few millimeters to the giant Japanese spider crab, which can exceed 3 m with the legs extended. The shape of a decapod can vary from that of the coconut crab to that of planktonic sergestid shrimp. Despite this diversity there is a basic unity to the Decapoda that may be defined as follows: eucarid crustaceans with carapace fused dorsally to all thoracic segments and extending laterally to form a branchial chamber; exopod of the second maxilla with large lamellar expansion, the scaphognathite; eight pairs of thoracic appendages, the first three modified as maxillipeds; branchiae typically arranged in a series, (a) podobranchiae arise from epipodite with coxal insertion, (b) arthrobranchiae often in pairs and arise from body wall above coxae, and (c) pleurobranchiae arise above arthrobranchiae and never paired (Calman 1909; see Burkenroad 1981, for comments on homologies).

Although the group Decapoda has been relatively well-defined since Latreille the internal classification of the decapods remains a matter of some controversy (see Abele & Felgenhauer 1982, Bowman & Abele 1982). In this report, we will review earlier classifications and discuss the characters upon which they were based; and review the morphological diversity of decapods with special reference to four groups, the Peneoidea, Procaridoidea, Caridea, and Stenopodidea.

2 THE HISTORICAL DEVELOPMENT OF CLASSIFICATIONS

The very early classifications of the Decapoda are reviewed by Bate (1888), Calman (1909), Balss (1957a), and Glaessner (1969). Briefly, the early classifications (1700's, early 1800's)

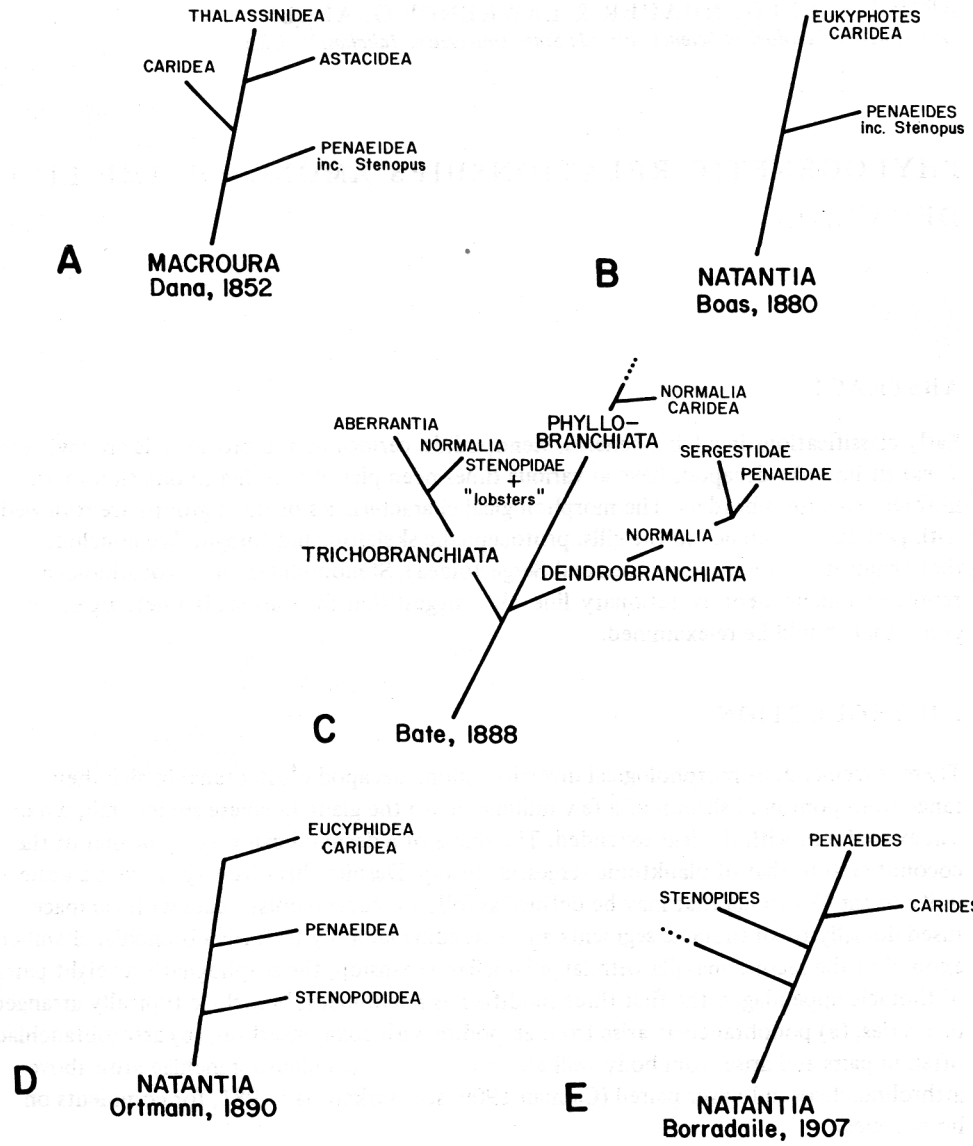

Figure 1. Phylogenetic relationships suggested by various authors within the shrimp-like Decapoda. Original spelling of taxa used by the various authors retained.

recognized two morphological types, a macrurous form with an elongated, subcylindrical body; and a brachyurous form with the cephalothorax greatly expanded and the abdomen reduced and folded beneath the cephalothorax. In Figures 1 and 2, we present the phylogenetic relationships suggested explicitly or implicitly by a number of authors representative of the various classifications that have been proposed. We have shown only those sections of the phylogenetic trees that deal with the groups under consideration here.

In 1852 Dana (Fig.1a) recognized Peneidea (including the genera *Stenopus* and *Spongicola*), Caridea, Astacidea, and Thalassinidea as the four major subdivisions of the Macroura. He considered the Peneidea as exhibiting the greatest amount of 'degradation', and placed them as the Macroura Inferiora. Dana based his classification on the form of the pereopods, the condition of the pleuron of the second abdominal somite and the form of the mandibular palp. Dana's search for the 'perfect' taxon may have been the result of his having undergone a deep religious conversion just prior to leaving on the Wilkes Expedition (Stanton 1975).

Boas (1880), in a major review, subdivided the decapods into the Natantia and Reptantia, and placed the Peneidea (still including *Stenopus*) and the Eukyphotes (Caridea) into the Natantia (Fig.1b). In the view of Boas, both the Natantia and Reptantia formed natural groups. In addition, Boas suggested that the peneid gill type (dendrobranchiae of Bate) gave rise to both the trichobranchiae and phyllobranchiae.

Huxley (1878) proposed a radical departure from earlier classifications based on an examination of gill structure. [Bate (1888) and others cite a classification of Huxley's (1883) but we have been unable to locate this reference.] He subdivided the decapods into the Trichobranchiata and the Phyllobranchiata. In the former group he created the Caridomorpha, containing the Peneidae, Stenopodidae, and Euphausiidae as independent taxa. The carideans were placed in the Phyllobranchiata. This classification represents the first rejection of the Natantia as a natural unit, but it was not widely followed (see Calman 1909).

In the *Challenger* report on the Macrura, Bate (1888) extended Huxley's use of the decapod gills as a basis for classification (Fig.1c). He recognized the gill of peneids as different from those of the other decapods and proposed the term Dendrobranchiata to include, under the subgroup Normalia, the Peneidae and Sergestidae. Bate also commented on the variability of the dendrobranchiate gill, and suggested that the trichobranchiate gill may have given rise to both the dendrobranchiate and phyllobranchiate gill types. Bate placed the Stenopidea as a tribe under the Trichobranchiata Normalia, which also included the Scyllaridae, Palinuridae, Eryonidae, Homaridae, and Astacidae. The Caridea (although the term was not used) were placed as a series of tribes under the Phyllobranchiata, subgroup Normalia. Bate, therefore, believed that the natantians were unrelated, and placed them in three separate divisions of Macrura.

Bates' classification was not followed by Ortmann (1890), who largely followed Boas (1880), placing the Stenopidea, Peneidea, and Eucyphidea (= Caridea) as three tribes within the Macrura Natantia (Fig.1d).

Borradaile (1907) published a widely cited and accepted scheme (Fig.1e). He recognized two suborders, the Natantia, containing three tribes (Penaeides, Carides, and Stenopides), and the Reptantia, containing all the other decapods. This classification doesn't follow Borradaile's own discussion of phylogeny where he suggests that Caridea and Reptantia arose independently from an early peneid stem. In fact Borradaile questions whether or not Natantia is a natural group. The position of the Stenopides is 'extremely doubtful' but is related to lower reptantians because 'it is trichobranchiate, has a curved mandibular palp and short endopodite to the first maxilliped, and lacks the copulatory apparatus of the male peneids and the spine (stylocerite) on the stalk of the antennule which is so characteristic of the Peneidea and Caridea'. However, some carideans have a curved mandibular palp and short endopod of the first maxilliped and a stylocerite is present in *Stenopus* and other stenopodidean genera (see de Saint Laurent & Cleva 1981, Holthuis 1946).

The classifications discussed thus far were proposed by neozoologists, and rarely con-

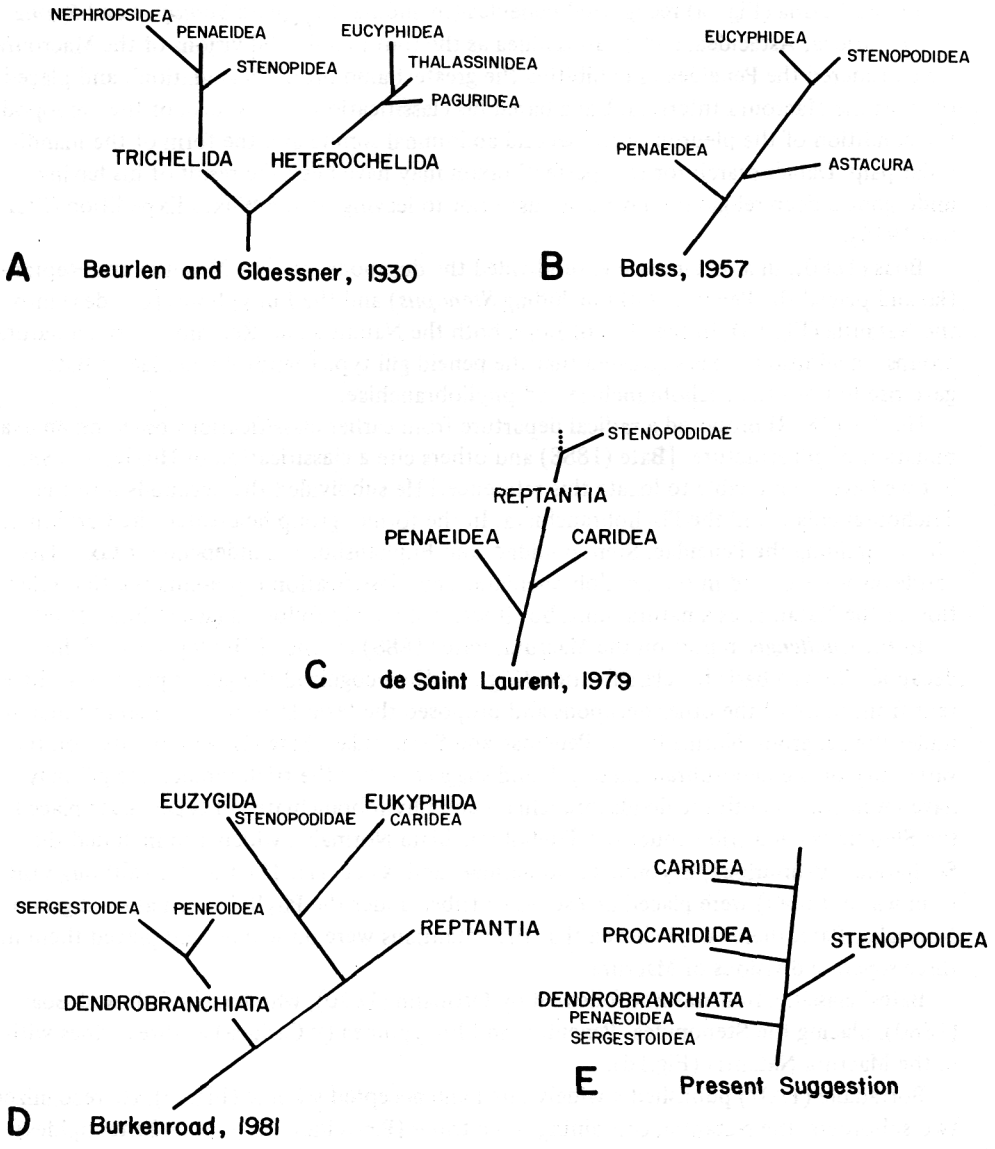

Figure 2. Phylogenetic relationships suggested by various authors within the shrimp-like Decapoda. Original spelling of taxa used by the various authors retained.

sidered fossils in any detail. Beurlen & Glaessner (1930, see also Glaessner 1960, 1969) proposed a classification (Fig.2a) that considered the known fossil record and the order of appearance of the various groups. They subdivided the Decapoda into two suborders, the Trichelida containing in one division (Nectochelida) the tribes Peneidea and Stenopidea, and in two additional divisions the fossil Paranephropsidea and the Recent Nephropsidea. The second suborder, Heterochelida, contained the remaining decapods, including the

tribes Thalassinidea, Paguridea, and Eucyphidea (Caridea) in the division Anomocarida. The Caridea were derived from ancestral thalassinoids during the Jurassic. It was suggested that phyllobranchiate gills, variability of chelae, the main articulation of the pereopods being between merus and carpus, and the presence of appendix internae on the pleopods all supported this interpretation. Their classification of the Trichelida differs from their phylogeny which shows the Peneidea and Nephropsidea coming off together and later than the Stenopidea (Fig.2a). This classification suggests that Peneidea, Stenopodidea, and Astacidea had a common origin, and Beurlen & Glaessner suggested that the ancestor was probably trichelate with trichobranchiate gills. The above views were not widely accepted among neozoologists.

While Gurney (1924, see also 1936, 1942) did not review all aspects of decapod classification he did propose that the Stenopidea be placed as a separate section in the Macrura Reptantia. This placement was based on similarities between stenopodid larvae and certain Thalassinidea (e.g. Laomediidae). Gurney (1942) also pointed out that one stenopodid larva collected off Bermuda had a maxillule, which suggested a primitive condition.

In a major review of decapod systematics, Balss (1957a) utilized the concept of Natantia with three tribes, Peneidea, Stenopodidea, and Eucyphidea (Caridea) and the remaining decapods in the Reptantia. This is inconsistent with his suggested phylogeny (1957b, p.1801) which has Peneidea (Fig.2b) coming off a main stem followed by Astacura, and a third branch which bifurcates into the Eucyphidea (Caridea) and Stenopodidea. Balss apparently felt, as did Borradaile, that a practical classification and taxonomy were not necessarily congruent with phylogenetic relationships.

Burkenroad (1963) considered the evolution of the Eucarida in relation to the fossil record. He proposed that there were two major lines of decapod evolution, the suborder Dendrobranchiata, containing the Peneidea and Sergestidea, and the suborder Pleocyemata, containing the remaining decapods. Burkenroad recognized within the suborder Pleocyemata the supersection Natantia containing the Stenopodidea and Eukyphida (Caridea).

Burkenroad's recognition of the Dendrobranchiata as a distinct evolutionary line was accepted by de Saint Laurent (1979) in her revision of the classification of the Decapoda (Fig.2c). However, de Saint Laurent recognized three suborders of the decapods, the Peneidea (= Dendrobranchiata), the Caridea, and the Reptantia which include the Stenopodidea. She also listed 12 morphological features that, in various combinations, characterized the three suborders.

In 1981 Burkenroad revised his earlier (1963) classification proposing that four suborders of Decapoda be recognized: Dendrobranchiata, Euzygida (= Stenopodidea), Eukyphida (= Caridea), and Reptantia, apparently dropping the suborder Pleocyemata. This classification is somewhat inconsistent with Burkenroad's cladogram (Fig.2d), which indicates an independent origin for the Dendrobranchiata and Reptantia but a common origin for the Euzygida (Stenopodidea) and Eukyphida (Caridea), which would suggest that these latter two groups should be in the same suborder.

Neither Burkenroad (1981) nor de Saint Laurent (1979) dealt with the interesting shrimp genus *Procaris* described in 1972 by Chace & Manning. There are two known species, *P.ascensionis* from Ascension Island and *P.hawaiana* from Hawaii (Holthuis 1973). Chace & Manning (1972) erected a new superfamily Procaridoidea and family Procarididae for this shrimp, and included it in the Caridea. As discussed below we believe the procaridids represent an independent evolutionary line similar to both peneids and carideans (Fig.2e).

3 MATERIALS AND METHODS

The many decapod species examined in this study were selected from the authors' personal collections or obtained from private sources. Specimens were dissected either fresh or after preservation in various fixatives. Drawings and photographs of the endoskeletal system were prepared with the aid of a Wild-Heerbrugg camera lucida in addition to scanning electron micrographs.

3.1 *Preparation of endoskeleton*

Selected specimens were freed of as much muscle and membrane as possible without causing damage to the delicate endoskeleton. For removal of remaining adhering tissues, dissected specimens were placed in 15 % KOH at room temperature overnight. Each specimen was then placed in 5 % KOH and heated for approximately 15 minutes to complete the clearing process. After clearing, the endoskeletons were rinsed in distilled water for 5 minutes and then dehydrated to final storage in acid alcohol. Exuviae sometimes proved extremely useful in the study of the branchiae and complex endoskeleton features. Drawings were made from unstained endoskeletons using uneven illumination.

3.2 *Preparation of specimens for scanning electron microscopy*

The endoskeletons and foreguts examined with the scanning electron microscope (SEM) were cleared in KOH as described above. Before dehydration the specimens were postfixed in 2 % osmium tetroxide (in distilled H_2O) for two hours. Following fixation, endoskeletons were rinsed thoroughly in distilled water (3 changes five minutes each), dehydrated in a graded series of ETOH, and critical-point dried. Specimens were then mounted on stubs and coated with 20 nm of gold palladium for observation in a Cambridge S4-10 SEM at accelerating voltages of 5-30 kV using secondary and backscattered mode.

4 COMPARATIVE MORPHOLOGY

In Table 1, we have listed some morphological conditions that previous authors have indicated were important in characterizing the various groups. Although it is frustrating to state that the condition is 'unknown' or 'variable', the facts of the matter are that certain data are unavailable and that certain features are variable. Below we discuss each one of these characteristics in so far as data are available.

4.1 *Incubation of eggs and the first larval stage*

A basic difference among decapods is incubation of the eggs. Dendrobranchiate decapods release eggs into the water (although *Lucifer* carries them briefly on the pereopods, Burkenroad 1981), while all other decapods for which data are available carry the eggs on pleopodal setae. Nothing is known of the Procarididea.

The Dendrobranchiata hatch from the egg in the naupliar or protozoeal stage. Nothing is known of development in the Procarididea.

Table 1. Comparative morphological features among some Decapoda.

Character	Dendro-branchiata	Procaridida	Stenopodida	Caridea
Incubation of eggs	None	Unknown	Pleopodal	Pleopodal
Eclosion from egg	Naupliar	Unknown	Zoeal	Zoeal
Gill type	Dendro-branchiate	Phyllo-branchiate	Tricho-branchiate	Phyllobranchiate
Epistomal condition	Membranous, articulated	Membranous, articulated	Membranous, articulated	Membranous, articulated
Cervical groove	Present	Present, weak	Present	Variable (present in *Glypho-crangon*)
Pleuron of second abdominal somite overlapping first and third	Never	Always	Never	Variable (not in some Psali-dopidae, Glyphocrangoni-dae)
Pleonic hinges	Pleomeres 1-2, 2-3, 4-5, 5-6	Pleomeres 1-2, 2-3, 4-5, 5-6	Pleomeres 4-5, 5-6	Variable, usually Pleomeres 1-2, 2-3, 4-5, 5-6 (all hinged in *Glyphocrangon*)
Form of telson	Narrowly tri-angular, uropods with-out diaresis	Subrectangular, lateral branch with diaresis	Subrectangular, uropods with-out diaresis	Subrectangular, uropods variable
Appendix internae	Absent	Absent	Absent	Usually present on pl.2-5
Appendix masculinae	Absent	Absent	Absent	Present, sometimes reduced or absent, e.g. *Euryrhynchus, Synalpheus*
Form of first maxilli-ped (presence of caridean lobe)	No lobe on exopod	Very slight lobe on exopod	No lobe on exopod	Variable but usually with lobe
Form of third maxil-liped	7 segments, pediform	7 segments, pediform	7 segments, pediform	3-5 segments, not pediform
Form of pereopods	1-3 chelate, 4, 5 achelate	1-5 achelate	1-3 chelate, 4, 5 achelate	Variable (e.g. *Pseudocheles*), usually 1-2 chelae
Form of gastric mill	Well developed	Well developed	Developed	Usually reduced

The development of some stenopodids has been described by Gurney (1924, 1936, 1942) and Williamson (1976). Based on development of *Stenopus* Gurney (1924) suggested that stenopodids are closely related to the Laeomediidae among the Reptantia. However, there are many unique features of stenopodid development according to Gurney (1924). The larva of *Stenopus* is unique among the decapods in hatching with four pairs of natatory limbs, while carideans hatch with three and reptants usually two. The uropods do not appear until stage IV and the last pair of pereopods do not develop until stage VI. In general the larval facies is distinct.

The larval development of carideans was reviewed by Gurney (1942 and citations therein). Williamson (1982) provides a more recent literature review as well as a key for the identification of crustacean larvae. Although larvae from most caridean families have been described, 'no concise definition which will be applicable to the whole group can be framed' (Gurney 1942). A review similar to that provided for the Brachyura by Rice (1980) is needed for the carideans.

4.2 *Branchiae*

Various authors (e.g. Huxley 1878, Bate 1888, Burkenroad 1963, 1981) have utilized the form and number of decapod gills as a basis for classification. Early authors (e.g. Milne Edwards 1837) recognized two basic gill morphologies: a trichobranchiate gill (Fig.4a,b) with a series of rather filamentous lateral branches arising from the main stem or branchial axis, and a phyllobranchiate gill (Fig.5) with paired lamellar branches arising from the branchial axis (see Huxley 1878). Bate (1888) pointed out that the so-called trichobranchiate gill actually included a rather distinct morphological type that is characteristic of peneids (Fig.4c,d) and sergestids (Fig.4f). This dendrobranchiate gill has paired lateral branches arising from the branchial axis with a series of subdivided secondary rami coming off each lateral branch. Examination of a relatively few species has convinced us that only the dendrobranchiate form is distinct. Trichobranchiate gills occur in a number of apparently unrelated taxa (e.g. *Stenopus, Aeglea, Palinura,* some Paguroidea), and we have had difficulty in distinguishing 'trichobranchiate' gills with paired flattened branches from phyllobranchiate gills. For example, the gills of *Upogebia* and axiids seem to us to be phyllobranchiate (see also Burkenroad 1963). Bouvier (1940) illustrated a series of gills from the dromiid genus *Dicranodromia* that appear to be transitional between trichobranchiae and phyllobranchiae. A re-evaluation of the morphologies and terms is necessary before a complete evaluation is possible.

Huxley (1878) and Bate (1888) suggested that the trichobranchiate type gave rise to both the dendrobranchiate and phyllobranchiate gills. As Bate considered the Dendrobranchiata to be the most primitive decapods, it would then follow that some ancestral decapod must have been trichobranchiate. However, it is not clear to us how a trichobranchiate form could give rise to a dendrobranchiate gill. Boas (1880) and Burkenroad (1981) both suggested that the dendrobranchiate gill could have given rise to the trichobranchiate and phyllobranchiate gills (Fig.3). An expansion of the two lateral branches of the dendrobranchiate gill results in a phyllobranchiate gill while loss of the secondary rami of the lateral branches would form a basic type of trichobranchiate gill. However, trichobranchiate gills usually have a large number of lateral branches rather than pairs, as would be the situation resulting from the loss of the secondary rami of a dendrobranchiate gill. The large amount of variation in dendrobranchiate gills (Bate 1888) suggests that reduction of the lateral branches and expansion of the secondary rami would result in a typical trichobranchiate gill. Whichever is correct, there is little doubt that phyllobranchiate gills represent a derived condition.

Burkenroad (1981) based his classification, in part, on the ontogenetic development of gills and the formulae of the adults. Briefly, pleurobranchs appear later in ontogeny than arthrobranchs in Dendrobranchiata, while pleurobranchs appear earlier than arthrobranchs in carideans and stenopodideans. The gills apparently appear simultaneously in Reptantia. Reptants also are unique in lacking a pleurobranch on the first pereonal somite even when one is found on the posterior somites. Comparison of gill formulae is, as Burkenroad points out, sometimes difficult because homologies are not immediately apparent when some of the gills are absent.

4.3 *The protocephalon*

In her discussion of decapod classification de Saint Laurent (1979) suggested that the form of the protocephalon is a major distinguishing feature among the suborders of the Deca-

poda. The protocephalon is the anterior portion of the endophragmal skeleton, consisting of the eyes, antennules, antennae, and associated skeletal elements (Snodgrass 1951, Young 1959). De Saint Laurent points out that a free ophthalmic segment is present within the Reptantia and that this is represented by an unpaired cavity in the protocephalon of this group. In addition, the epistome of peneids and carideans is said to be divided by a membranous invagination into two portions that move against each other. In Reptantia (except stenopodids, which de Saint Laurent includes in this group), the epistome is solid, without any subdivisions formed by membranes. We consider the epistome to be the skeletal elements that begin posteriorly at the site of attachment to the labrum. The epistome continues laterally and anteriorly as the skeletal elements forming the basal regions of the antennae, antennules, and ophthalmic area.

The morphology of the protocephalon is complex and requires numerous illustrations and photographs for an adequate description. Here we can only present a brief description of the following groups that are examined: Dendrobranchiata (e.g. *Peneus, Sicyonia*), Procarididea (*Procaris*), Stenopodidea (*Stenopus*), Caridea (e.g. *Atya, Potimirim, Palaemonetes, Macrobrachium, Oplophorus, Alpheus*), Reptantia Astacidea (*Cambarus*) [for a complete list, see Appendix I]. De Saint Laurent is essentially correct in her descriptions, but the variation within groups is much greater than perhaps she anticipated. In Figure 6a, the epistome of *Peneus* is shown. The mandibular palps have been removed from Figure 6a for clarity. The episome is membranous with a deep median invagination and membranes along the lateral extensions (Fig.6a). In *Peneus* then, the epistome consists of a series of medial and lateral skeletal elements separated by membranes (see Young 1959, fig.28). This morphology seems characteristic of all members of the Dendrobranchiata we examined.

The epistomal region of carideans is variable. In *Palaemonetes* (Fig.6d), there is a medial and, anteriorly, a lateral membranous region while in *Oplophorus* (Fig.6e) there is only a weak medial invagination suggesting a membranous region. The situation in large species of *Macrobrachium* is quite different and suggests that fusion of skeletal elements may be, in part, a function of size. In *Macrobrachium americanum* the epistome is rigid, heavily chitinized with no indication of membranes. Although the presence and degree of membranes in the epistome of carideans is variable all that we have examined have the epistome anterior to the base of the antennae.

The epistome of *Stenopus* is membranous, articulates with itself and is rather complex. It consists of a heavily armed anterior portion that is semicircular and to which the labrum attaches. Anterior to this portion ('ep' in Fig.6b) is a deeply recessed membrane that attaches to the anterior portion of the epistome that projects clearly between the antennal bases and the two lateral spines of the posterior portion of the epistome. This arrangement differs from anything we have seen in dendrobranchiates, carideans, or reptantians.

The epistomal region of *Procaris* (Fig.6f) has an anterior medial invagination that permits movement of the two lateral portions similar to both *Peneus* and some carideans.

In the reptantians that we have examined the epistomal region differs from that of the dendrobranchiates, carideans, procaridids, and stenopodids. In astacids (Fig.6c) the epistome is a large plate that is located between the mandibles and the antennae; it extends anteriorly between the bases of the antennae. The large posterior portion between the mandibles and antennae is always heavily sclerotized with no membranes present. However, even within a single family (e.g. Cambaridae) some species have a membrane separating the anterior from the posterior portion (Fig.6c) while in other species the entire epistome

is a continuous plate. In general, reptantians (excluding stenopodids, which we do not consider reptantians) have the largest portion of the epistome as an extensive plate between the mandibles and the antennae. Perhaps the most extreme situation is found in the only extant representative of the Mesozoic Glypheoidea, *Neoglyphea inopinata,* where the epistome is extremely elongated, being almost twice as long as wide (Forest & de Saint Laurent 1981, Fig.9).

4.4 *The cervical groove*

Several authors have suggested that a cervical groove is absent in carideans, but it is present in some forms (e.g. alpheids, see Coutiere 1899) and is particularly well-developed in the genus *Glyphocrangon* (see Holthius 1971). A cervical groove is present in the other groups as noted in Table 1.

4.5 *Pleura*

A feature considered characteristic of carideans is the expanded pleura of the second abdominal somite which overlap those of the first and third (e.g. Holthius 1955). However, in some species of Psalidopodidae (see Chace & Holthuis 1978, *Psalidopus barbouri*) and Glyphocrangonidae (see Holthius 1971, *Glyphocrangon neglecta*) the pleura of the second abdominal somite are not expanded and do not appear to overlap those of the first and third somites. However, even in these groups the second pleuron overlaps the first when the abdomen is flexed. In dendrobranchiates and stenopodids the pleura never overlap while in procaridids it does (see Chace & Manning 1972).

4.6 *Pleonic hinges*

The pleural somites of many decapods are locked to each other by mid-lateral hinges. Each hinge is formed by an expansion of the pleuron into a knob-like structure that fits into a cavity formed by the adjacent pleuron. It is usually the posterior somite that locks into the anterior one. Burkenroad (1981) stated that pleural hinges are found on all somites of the Dendrobranchiata, but those of the junction 3 to 4 are hidden under the posterior margin of the third somite. We were unable to locate the hinge on the junction of 3 to 4 in specimens of *Solenocera.* In specimens of *Peneus* (and to a lesser extent *Solenocera*) there are muscle bundles under the margin of the third somite at the point where the hinge would be located but there are no obvious skeletal modifications that are so apparent on the other somites. In the Stenopodidea Burkenroad (1981) states that only the last three pleonic somites are hinged together, that is, hinges are present between somites 4 and 5, and 5 and 6. We have examined these in *Stenopus hispidus* and find them to be more ventral than in other groups, and they are not hinged in the same ball and socket morphology as in other groups. The hinges in most carideans are present on all somites but the junction of 3 to 4, presumably to permit greater flexing at that point. However, in *Glyphocrangon* (Holthius 1971), all somites appear to be hinged. Our single specimen of each species of *Procaris* has undergone some deterioration but hinges appear to be present on all somites except the junction of 3 to 4. Finally all somites are said to be hinged in Reptantia (Burkenroad 1981) and this was the case in those representatives that we examined although the morphology was variable. It seems clear that a much more detailed examination of these hinges is required before any strong phylogenetic conclusions can be drawn.

4.7 *Form of telson*

In their discussion of the systematic position of *Procaris* Chace & Manning noted that the telson of *Procaris* is more similar to that of carideans than to that of dendrobranchiates. In dendrobranchiates the telson tends to be narrowly triangular and the uropods lack a diaeresis, while in *Procaris* the telson is subrectangular and the lateral branch of the uropods has a diaeresis. However, as with other characters, carideans are variable in this regard. Some pontoniids have an almost oval telson (Holthuis 1951b) while *Psalidopus* has a narrowly triangular telson (Chace & Holthuis 1978).

4.8 *Appendices internae*

An appendix interna is absent from all pleopods in dendrobranchiates, procaridids, and stenopodids. The situation, however, is variable in carideans. An appendix interna is usually present on pleopods 2 through 5. However, the genus *Desmocaris* (usually in the family Palaemonidae, though we agree with Powell 1977, that it is probably a separate family) lacks appendices internae, and they are absent from the second pleopods in females of the palaemonid *Euryrhynchus* (Holthuis 1951b, Powell 1976).

4.9 *Appendix masculina and petasma*

The form of the male copulatory organ varies within the Decapoda. Dendrobranchiate males have the first pleopods modified as a petasma for sperm transfer (e.g. Farfante 1975). There is no major modification of male pleopods in stenopodids, though the first pleopod has some minor sexual modifications (Holthuis 1946), and though no one has sexed procaridids the pleopods are not modified (Chace & Manning 1972). In contrast, carideans usually have the second pleopod of the male with an appendix masculina which is involved in sperm transfer (Bauer 1976, Felgenhauer & Abele 1982). *Synalpheus* males lack an appendix masculina (Coutiere 1899). Holthuis (1951b) suggested that *Euryrhynchus* males lack an appendix masculina. However, Powell (1976) suggested that what has been called an endopod is actually an appendix masculina attached to a greatly reduced endopod. Powell (1976) also described a complex copulatory apparatus in the genus *Euryrhynchoides* that involves both the endopod and appendix masculina of the second pleopod. This structure appears to be unique among the carideans.

4.10 *Stylocerite*

As noted earlier, Borradaile (1907) suggested that stenopodids and reptantians lack stylocerites. However, a stylocerite is present in both of these groups as well as in peneids and carideans.

4.11 *Caridean lobe*

Numerous authors, including Burkenroad (1981), have stated that a lobe on the basal portion of the exopod of the first maxilliped is characteristic of carideans, hence its name, caridean lobe or α lobe of Boas (1880). This lobe is absent in dendrobranchiates and stenopodids. There is a weak, but distinct, lobe in *Procaris* and, again, its presence and development in carideans is variable. The most unusual first maxilliped is found among the Pasi-

phaeidae where it consists of a large, lamellar, 2-segmented appendage in *Pasiphaea semispinosa* (see Holthuis 1951a, fig.1). In another pasiphaeid, *Leptochela bermudensis,* the first maxilliped apparently consists of an endite, a small endopod, a club-like exopod with a distal indentation, and an epipod (Chace 1976, fig.6). In some crangonids (e.g. *Pontophilus bidens,* see Holthuis 1951a, fig.33) there is no obvious lobe present. Among hippolytids it is weakly developed in *Latreutes parvulus* but well-developed in *Bythocaris cosmetops* (see Holthuis 1951a, figs.20, 30). Among alpheids it is well-developed in some genera and weak in others (e.g. *Athanas,* see Coutiere 1899). In many families (e.g. Processidae, Palaemonidae, Oplophoridae, Physetocaridae) it appears to be well-developed in all members. Finally, there appears to be a 'caridean lobe' in some pagurids (see Kunze & Anderson 1979).

4.12 *Third maxillipeds*

The third maxillipeds in the Dendrobranchiata, Procarididea, and Stenopodidea are seven-segmented and pediform. The third maxillipeds in carideans never have seven segments and are often operculiform in shape. When the third maxillipeds are pediform they have five segments at most.

4.13 *Pereopods*

The form of the pereopods has been used as a basis for classification. The Dendrobranchiata and Stenopodidea have the first three pairs of pereopods chelate while the Procarididea are achelate. Among the carideans there are species with all five pereopods chelate, though the last three are modified chela (*Pseudocheles* in the family Bresiliidae, Chace & Brown 1978); or species with subchelate pereopods (e.g. *Glyphocrangon,* Holthuis 1971); and many species with the first two pereopods chelate. The chelae of carideans are extremely diverse.

4.14 *Morphology of the foregut*

A general decapod foregut (see Huxley 1880, Patwardhan 1935 and citations therein; Kaestner 1970, Schaefer 1970, Coombs & Allen 1978, Kunze & Anderson 1979) consists of two distinct regions. A J-shaped esophagus opens into a large anterior cardiac chamber and a smaller posterior pyloric region (Fig.7a, 8a) separated from the cardiac stomach by a ventral cardiopyloric valve of varying degrees of complexity. A ventral gland filter (ampulla) (Fig.8a) is present in the floor of the pyloric chamber. This structure accepts only the smallest of particles and leads directly to the hepatopancreas. In general, both the cardiac and pyloric stomachs are chitinous and form a complex series of ossicles (Mocquard 1883) and this is also true in *Atya* (Fig.7a). It is this chitinous, interior lining of the cardiac stomach that forms the gastric mill. The gastric mill typically consists of a large median tooth located on the urocardiac ossicle (Fig.7b,c) extending from the roof of the cardiac stomach, and a pair of lateral teeth borne on the zygocardiac ossicles (Fig.7d). Patwardhan (1935, 1936) (also Coombs & Allen 1978, de Saint Laurent 1979) suggested that the Stenopodidea and Peneidea have simple gastric mills, and from this condition two trends are apparent: a progressive reduction of the gastric mill in Caridea (said sometimes to be absent) from the Hippolytidae-Atyidae to the rest of the carideans, and, an increasing development of the gastric mill from the lower Reptantia-Astacura-Anomura to the Brachyura. The situation in reality, as might be expected, is much more complex.

4.14.1 *Dendrobranchiata.* The gastric mills of *Peneus* (Fig.9a), *Solenocera* (Fig.9b,c) and *Sergestes* (Fig.9d) exhibit striking similarities in their morphology. All have a well-developed median tooth (mt) armed with a series of teeth along their lateral margins (see Fig.9c). All three representatives also have strong lateral teeth arising from the zygocardiac ossicles.

4.14.2 *Stenopodidea.* The gastric mill of *Stenopus* (Fig.9e) has a moderately developed median tooth attached to a subcircular hastate plate. The teeth are knob-like and do not resemble those seen in other decapods. Well-developed peg-like lateral teeth are also present.

4.14.3 *Procarididea.* The foregut of *Procaris* has a well-developed median tooth (Fig.10a, b) armed with accessory teeth (Fig.10c). Large lateral teeth (Fig.10b,d) are also present. The floor of the cardiac chamber has the denticles guarding the entrance to the gland filter (gf) (Fig.10f).

4.14.4 *Caridea.* There is considerable diversity in the gastric mill of species referred to the Caridea. Perhaps one of the more unusual is found in the pasiphaeid genus *Leptochela* (Fig.11). The foregut itself is less than 1 mm in length with a well-developed gastric mill. The median tooth is magnificent and bifurcates medially into a large number of scaled teeth (Fig.11b). A large number of serrate petals surround the base of the median tooth (Fig.11f). Strong lateral teeth (Fig.11c,d) are present. The cardiopyloric valve is rather elaborate for a caridean (Fig.11e). (N.B. Fig.11e: cardiopyloric valve; X1500)

The chitinous foregut of *Atya* (Fig.7a) has a bifid, heavily armed median tooth (Fig.7b, c) with sharp teeth lining its interior (Fig.7c). A series of stout sclerotized teeth (lateral teeth) are present, arising from the broad zygocardiac ossicle (Fig.7d, arrow). A convoluted membrane borne on the median projection from the roof of the pyloric stomach (Fig.7e) is apparently unique to certain atyids.

The gastric mill of *Palaemonetes* (Fig.8b) consists of a very small median tooth with minute teeth (Fig.8c), extending from the roof of the cardiac chamber. There are no lateral teeth present; instead a lateral row of plumose setae is present (Fig.8b, arrow).

Saron (Fig.8a) lacks a gastric mill, the foregut consists of two sacs with no obvious chitinized regions. We also examined the foregut of *Crangon, Oplophorus, Gnathophyllum* and *Alpheus* and found no gastric mill present.

4.14.5 *Reptantia.* The massive gastric mill of *Cambarus* (Fig.9f) consists of a large, smooth bifid median tooth with strong lateral teeth.

The gastric mill region of *Upogebia* (Fig.8d,e,f) has a strong median tooth with approximately 16 stout lateral teeth present. The lateral teeth are robust, consisting of 20 or more movable plates (Fig.8d). The pyloric fingerlets are shown in Figure 8e, with a closeup in Figure 8f. Details of the morphology and function of the foregut of this species can be found in Powell (1974).

5 THE FOSSIL RECORD

The fossil record of the Decapoda has recently been reviewed by Glaessner (1960, 1969), Burkenroad (1963), and Schram (1982). The earliest decapod is *Palaeopalaemon newberryi,*

known from the Upper Devonian in central North America (Schram et al. 1978). The species is reptant in form and shares some characters with the Astacidea and the Glypheoidea. Although *Palaeopalaemon* tells us little about the groups under consideration here, it is significant because it is the earliest decapod recognized and it is 100 million years older than any other known form.

Burkenroad (1963), following Brooks (1962), suggested that the Permian genus *Palaeopemphix* is an early decapod, but Glaessner (1969) suggested that it needs re-examination before this can be accepted. The problems center around interpretation of the carapace furrows.

Other than *Palaeopalaemon* the earliest accepted decapods are Permo-Triassic, the rare Peneidae and the extinct family Erymidae in the Astacidea (Glaessner 1969, Förster 1966, 1967). Among the Permo-Triassic Peneidae is the genus *Antrimpos,* very similar if not identical to *Peneus* (see Burkenroad 1963). Since the Peneidae are rather advanced dendrobranchiates, the group as a whole must have been present earlier than the Permo-Triassic.

Although the familial status is uncertain, carideans are known from the Middle Jurassic (e.g. *Udora*). The genus *Oplophorus* (family Oplophoridae) is known from the Upper Jurassic (see Glaessner 1969). Another interesting caridean is *Udorella* (family Udorellidae) known only from the Upper Jurassic. As reconstructed *Udorella* has five subchelate pereopods, long exopods, and a pediform third maxilliped which ends in a long, thin terminal segment. If the third maxilliped of *Udorella* has seven segments, there would be some similarity to *Procaris.* For the most part, the available fossils tell us little about caridean evolution.

There are no known fossils of either the Stenopodidea or the Procarididea.

6 THE PROPOSED CLASSIFICATION

Examination of the material listed in Appendix I and a survey of the literature has convinced us that the Dendrobranchiata, Procarididea, and Stenopodidea are natural taxa and should stand alone. The Caridea consists of a large and diverse group of species that may have to be reorganized in some other way. We do not wish to indicate the taxonomic level (suborder, infraorder, etc.) for these groups until more is known concerning the features in table 1 for all the decapods. For the present we recognize the Caridea as a taxon but believe that a revision is needed. Below we provide diagnoses for these taxa and then discuss their relationships.

Dendrobranchiata Bate 1888

Eggs released free, hatch as nauplii or protozoeas. Gills consist of branchial axis, with paired lateral branches each with subdivided secondary rami (dendrobranchiate condition). Gastric mill well-developed, strong armed median tooth, well-developed lateral teeth. Protocephalon of an ocular plate and an epistomial region, the latter subdivided such that it can articulate with itself. Epistomal bars anterior to the labrum. Pleura of first abdominal somite overlap those of the second. Appendices internae and masculinae absent. First pleopod in males modified into a complex copulatory appendage, the petasma. Third maxillipeds pediform, with seven segments. First three pairs of pereopods chelate (Permo-Triassic to Recent).

Procarididea Chace & Manning 1972
Nothing is known of the eggs or larvae. Gills phyllobranchiate, branchial axis with pairs of lateral lamellae (Fig.12f). Gastric mill well-developed, with strong, armed median tooth, large lateral teeth. Protocephalon, with an occular plate and a subdivided epistome that articulates against itself. Pleura of the second abdominal somite overlap those of the first and third. Appendices internae and masculinae absent. Third maxillipeds pediform, with seven segments (Fig.12b,c). All pereopods achelate (Fig.12a). First four pereopods with very large epipods at right angles, extending into branchial chambers (Fig.12f). All maxillipeds and pereopods with well-developed exopods (Recent).

Stenopodidea Bate 1888
Eggs attached to pleopodal setae, hatch as zoeas. Gills trichobranchiate, branchial axis bearing numerous filaments irregularly arranged. Gastric mill with median tooth attached to subcircular hastate plate, knob-like teeth on margins of median tooth, well-developed lateral teeth present. Protocephalon with ocular plate and epistome, latter with heavily armed subcircular narrow portion attached to labrum connecting by a membrane anteriorly to a narrow portion between antennae. Pleura of second abdominal somite do not overlap those of first and third. First pleopod in both sexes uniramous, appendices internae and masculinae absent. Third maxillipeds pediform, with seven segments. First 3 pairs of pereopods chelate, third enlarged (Recent).

Caridea Dana 1852
Eggs attached to pleopodal setae, hatch as zoeas. Gills phyllobranchiate, branchial axis with pairs of lateral lamellae. Gastric mill variable [well-developed in *Leptochela* (Pasiphaeidae) and *Atya* (Atyidae); greatly reduced to absent in Palaemonidae and Hippolytidae; absent in some members (at least all we examined) of Crangonidae, Alpheidae, Gnathophyllidae, and Oplophoridae]. Protocephalon of an occular plate and epistomal region, the latter usually subdivided so that it may articulate with itself (e.g. *Palaemonetes, Oplophorus*) or be as a solid plate (e.g. *Macrobrachium*). Pleura of second abdominal somite usually overlap those of the first and third (except in some species of *Glyphocrangon* and *Psalidopus*). Appendices internae and masculinae usually present (except *Desmocaris* lacks internae and *Euryrhynchus* may lack masculinae). First maxilliped usually with expansion of lateral border of exopod (absent in pasiphaeids and greatly reduced in many others). Third maxillipeds variable, with three to five segments. First and second pereopods usually chelate or achelate, but variable (Middle Jurassic-Recent).

A comment on nomenclature is probably in order as various names have been applied to the Dendrobranchiata, Caridea, and Stenopodidea. We agree with Burkenroad (1963) on the use of Dendrobranchiata Bate 1888 for the Peneidoidea and Sergestoidea. We believe that Caridea Dana 1852 was applied by Dana to families of shrimps that constitute this taxon today. We see no need to use the later terms of Boas (1880, Eukyphotes), Ortmann (1890, Eucyphidae) or Burkenroad's (1981) modification (Eukyphida) of Boas's term. Similarly we see no need to erect a new name for stenopodids in the manner of Burkenroad's (1981) Euzygida. We have cited Bate (1888) as the author of the higher taxon and Huxley (1878) as author of the family for stenopodids. Huxley (1878) included the stenopodids in the Trichobranchiata with peneids and it was Bate (1888) who separated the stenopodids as an independent group.

Finally, we believe that the evidence in favour of recognizing the Dendrobranchiata is overwhelming. The evidence in favor of other groups is not so decisive, but to include the procaridids with either the dendrobranchiates or the carideans would weaken the former and expand even more the already variable Caridea. We feel that until information becomes available on egg incubation and larval development in procaridids, it is best to separate them as an independent group. The taxonomic status of the stenopodids has changed several times in the past from a separate taxon to a subdivision of the Reptantia (Gurney 1924; de Saint Laurent 1979). However, we feel that inclusion of the stenopodids in the Reptantia would require too serious a modification of the definition of that group, especially in regard to the protocephalic region, pleonic hinges, and branchial formula.

7 DISCUSSION

It is now more than 100 years since Boas (1880) proposed a major revision of decapod classification. It would appear that interest in decapod phylogeny and classification has increased again. Guinot (1977, 1979) has proposed a reclassification of brachyurans. Rice (1980) re-examined brachyuran classification in light of larval characteristics. De Saint Laurent (1979) proposed a new higher classification of the decapods as well as some changes (1980a,b) in brachyuran classification. Burkenroad (1981) proposed a modification of his earlier (1963) classification, but emphasized modern rather than fossil forms. These studies and the present one are the result of both a renewed interest in comparative morphology and the discovery of important new species. A Recent representative of the previously thought to be extinct Glypheoidea, *Neoglyphea inopinata* (see Forest, de Saint Laurent, & Chace 1976, Forest & de Saint Laurent 1975) has stimulated a re-examination of the Reptantia, and the discovery of the shrimp *Procaris ascensionis* Chace & Manning 1972, has stimulated a study of the Caridea.

However, it is probably worthwhile to re-examine decapod morphology without any biases generated by previous classifications. As we have shown here, the concept of Caridea is based on a large number of variable characters. Similarly, the Reptantia is a diverse group of species that may not have enough shared derived characters to warrant unification as a single taxon.

The value of various characters in taxonomy should also be reconsidered. For example, the gills of axiids are often considered to be trichobranchiae, but some species have gills that appear to us to be phyllobranchiate. The presence and development of the caridean lobe is also a questionable character. It is absent in some pasiphaeids and little, if at all, developed in some alpheids. Additional characters that might have systematic value should also be evaluated and these are most likely to be discovered through extensive studies of comparative anatomy. For example, de Saint Laurent (1979) has called attention to the value of the endophragmal skeleton of the protocephalon as an important character, but very few species have been examined in this regard. We believe that an analysis of comparative morphology, internal and external, without attempting to fit species into any current classification would yield important results in sorting out the complexities of decapod evolution.

Finally, there is the problem of the fossil record. The oldest known decapod, *Palaeopalaemon newberryi,* may be characterized as follows (modified from Schram et al. 1978):