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PHYLOGENETIC SYSTEMATICS OF THE EUCARIDA (CRUSTACEA MALACOSTRACA)

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ABSTRACT. *Ninety-four morphological characters belonging to particular ontogenetic sequences within the Eucarida were used to produce a hierarchy of 128 evolutionary novelties (73 synapomorphies and 55 homoplasies) and to delimit 15 monophyletic taxa. The following combined Recent-fossil sequenced phylogenetic classification is proposed: Superorder Eucarida; Order Euphausiacea; Family Bentheuphausiidae; Family Euphausiidae; Order Amphionidacea; Order Decapoda; Suborder Penaeidea; Suborder Pleocyemata; Infraorder Stenopodidea; Infraorder Reptantia; Infraorder Procarididea; Infraorder Caridea. The position of the Amphionidacea as the sister-group of the Decapoda is corroborated, while the Reptantia are proposed to be the sister-group of the Procarididea + Caridea for the first time. The fossil groups* ***Uncina*** *Quenstedt, 1850, and* ***Palaeopalaemon*** *Whitfield, 1880, are included as* ***incertae sedis*** *taxa within the Reptantia, which establishes the minimum ages of all the higher taxa of Eucarida except the Procarididea and Caridea in the Upper Devonian. The fossil group "Pygocephalomorpha" Beurlen, 1930, of uncertain status as a monophyletic taxon, is provisionally considered to belong to the "stem-group" of the Reptantia. Among the more important characters hypothesized to have evolved in the stem-lineage of each eucaridan monophyletic taxon are: (1) in Eucarida, attachement of post-zoeal carapace to all thoracic somites; (2) in Euphausiacea, reduction of endopod of eighth thoracopod; (3) in Bentheuphausiidae, compound eyes vestigial, associated with abyssal life; (4) in Euphausiidae, loss of endopod of eighth thoracopod and development of specialized luminescent organs; (5) in Amphionidacea + Decapoda, ambulatory ability of thoracic exopods*

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reduced, scaphognathite, one pair of maxillipedes, pleurobranch gill series and carapace covering gills, associated with loss of pelagic life; (6) in Amphionidacea, unique thoracic brood pouch in females formed by inflated carapace and specialized first pleopod, eclosion in zoea phase, body dorsoventrally depressed, thoracopods reduced and antennular statocyst lost, associated with planktonic life; (7) in Decapoda, double series of arthrobranchiae, laminar rostrum, acute stylocerite, two additional pairs of maxillipedes, three pairs of chelipedes and two pairs of walking legs, associated with nekto-benthonic life; (8) in Penaeidea, dendrobranchiae and post-larval mandibular palp expanded; (9) in Pleocyemata, pleopodal incubation of eggs and eclosion in zoea phase; (10) in Stenopodidea, pereiopodal exopods lost in adults and massive third chelipedes, associated with benthonic life; (11) in Reptantia + Procarididea + Caridea, pleura of second abdominal somite overlapping first and specialized setal brushes on propodus of fourth and fifth pereiopods; (12) in Reptantia, hypertrophied first chelipede, associated with benthonic life; (13) in Procarididea + Caridea, chela lost from third pereiopod and epipod-setobranch complexes for gill cleaning; (14) in Procarididea, chelae lost from first and second pereiopods; and (15) in Caridea, ocellus on ocular peduncle.

Introduction

The cladistic structure of the Articulata has been reasonably well established at several hierarchical levels, so that it is now possible to follow the main phylogenetic line – with some unknown gaps – from the Articulata to the Eucarida. The relative hierarchy of higher articulatan taxa is shown in the following sequence: Superphylum Articulata; Phylum Arthropoda; Subphylum Euarthropoda; Infraphylum Mandibulata; Superclass Crustacea; Class Malacostraca; Subclass Eumalacostraca; Cohort Caridoida; Superorder Eucarida. Major irresolutions in this sequence refer to the relationships of the Malacostraca to the remaining Crustacea (see Hessler, 1982) and of the Eucarida to the remaining Caridoida (see Schram, 1984).

Synapomorphies for the first three taxa in the above hierarchy may be obtained from Lauterbach (1973, 1980) and Boudreaux (1979); those for the Mandibulata and Crustacea were considered by Boudreaux (1979), Lauterbach (1980, 1983) and Hennig (1981); those for the Malacostraca, Eumalacostraca and Caridoida were discussed by Hessler (1983); and those for the Eucarida were suggested by Burkenroad (1963) and Schram (1984).

Many of the so-called alternative views on arthropod phylogeny, for example the polyphyletic interpretation of Manton (1977), do not rely on synapomorphies to establish relationships and thus do not reflect genealogy (Hennig, 1966). I do not consider such views valid phylogenetic reconstructions of the Arthropoda.

The hierarchy of taxa established above is based on the higher level phylogenetic hypothesis under which I have chosen to conduct the cladistic analysis of the Eucarida. Such preliminary hypotheses about relationships outside of the Eucarida are necessary for establishing the generalities of wide-ranging characters (my use of the term generality follows, among others, Nelson & Platnick, 1981). On the other hand, the Linnean categories in which these taxa have been included area considered irrelevant for the purposes of this paper. The traditional class concepts (categories) could be substituted for a series of age classes (Historical Classification), but it is felt that more information on the systematic structure of living organisms is needed before this can profitably be accomplished.

The available literature provides rather scarce information on the genealogical relationships of the Eucarida. Burkenroad (1963) suggested the monophyly of the eucaridan taxa Euphausiacea and Decapoda, of the decapod taxa Dendrobranchiata (= Penaeidea) and Pleocyemata, and of the pleocyematan taxon Reptantia. Williamson (1973) suggested that the genus *Amphionides* Zimmer, 1904 should be excluded fron the Decapoda *sensu* Calman (1909). Burkenroad (1981) indicated the monophyly of the Euzygida (= Stenopodidea) and Eukyphida (= Caridea) and published a cladogram reflecting his views on decapod relationships, but the proposed formal classification did not reflect the phylogeny. Burkenroad (1983) also presented a dendrogram of presumed phylogenetic relationships within the Dendrobranchiata (= Penaeidea), but did not provide derived characters to support the phylogenetic hypothesis. Felgenhauer & Abele (1983) exclused the genus *Procaris* Chace & Manning, 1972 from the Caridea and questioned the monophyletic status of the latter taxon. In their suggested dendrogram of relationships of the shrimp-like decapods, they avoided the controversial question of how the Reptantia should be related to the remaining decapods. Casanova (1984) attempted to establish the phylogenetic relationships of the genera of Euphausiacea using a gradistic approach.

Schram (1984) presented for the first time objective cladograms which included the Eucarida Twelve characters were hypothesized to indicate the monophyly and relationships of seven eucaridan taxa Two alternative cladograms were offered for the pleocyematan section of the Decapoda one in which the Euzygida (= Stenopodidea) are more clo sely related to the Reptantia than to the Eukyphida (= Caridea + Proca rididea) and the other in which the Euzygida are more closely related to

the Eukyphida than to the Reptantia The former is a more traditional ar rangement while the latter corresponds to Burkenroad s (1981) clado gram However Schram *(op. cit)* apparently felt that the cladistic relationships within the caridoid eumalacostracans were not sufficiently corroborated to justify a formal phylogenetic classification for this group.

Fossil taxa sometimes posses morphological characters which can be directly compared with those of extant groups. This permits a combined analysis of both modern and fossil groups, with the assignment of fossil taxa to those levels of the hierarchy where their relationships with living taxa are best understood. Some ancient caridoid fossils are of particular interest for the present levels of cladistic analysis: The Lower Jurassic fossil *Uncina* Quenstedt, 1850, which Burkenroad (1963) suggested to be a reptant, but which is sometimes still classified in a distinct pleocyematan infraorder Uncinidea (Glaessner, 1969); the Paleozoic pygocephalomorphs, whose individual taxa have been variously treated as eucarids, peracarids and eocarids, before being reassigned to the Peracarida (Schram, 1974 a,b, 1984); and the Late Devonian Early Mississippian fossil *Palaeopalaemon* Whitfield, 1880, which has been recognized as a pleocyematan decapod (Schram, Feldmann & Copeland, 1978).

The purposes of this paper are to (1) perform a cladistic analysis of the higher taxa of Eucarida based on the available descriptive information; (2) present a formal phylogenetic classification of taxa which strictly reflects the monophyletic groups and sister-group relationships obtained in the cladogram; and (3) reassign some of the older fossils to more restrictive positions within the system of the Eucarida, establishing at the same time minimum ages for different levels of the phylogeny.

Material and Methods

The characters analysed were obtained mainly from the literature. I have examined specimens of *Euphausia* Dana, 1852, *Penaeus* Fabricius, 1798, *Stenopus* Latreille, 1819, *Axiopsis* Borradaile, 1903, *Parastacus* Huxley, 1878 and several carideans (my earthly connections with descriptive systematics within the Eucarida). At the higher levels of cladistic analysis such inspections of included semaphoronts *(sensu* Hennig, 1966) are not indispensable, but can sometimes be useful for the establishment of homologies, for the discovery of additional characters and for the suppression of erroneous judgments based on incomplete or incorrect statements in the literature. Characters have been described, as far as possible, as ontogenetic transformations within life cycles *(sensu* Nelson, 1985).

For the cladistic analysis of characters I have relied on pencil, paper and the human brain, rather than computers. To determine the presumed generalities of characters I have used both ontogenetic sequences of character transformations and out-group comparisons. Sets of characters whose generalities were easily perceived and could be readily ranked without much apparent conflict with each other – that is, cladistically reliable characters showing hierarchic correlation (Farris, 1969) – were used first to group taxa, while sets of characters showing apparent homoplasies – that is, cladistically unreliable characters that are random with respect to the branching pattern determined by the hierarchically correlated characters (Farris, 1969) – were incorporated only gradually into the cladogram. Several additional characters which obviously have different expressions within each of the subordinate taxa of Eucarida have not had their generalities determined and were not included in the cladistic analysis.

The parsimony principle represents the basic methodological tool which has been used throughout the cladistic analysis. Despite being the only objective method available for such analysis, decisions using parsimony are often subjective. This is because different characters are presently not directly comparable between themselves on any real metric base. The use of simple parsimony techniques (Maddison, Donoghue & Maddison, 1984), in cases where several characters seem to conflict, would only appear to permit confident choices between cladograms if one were able to recognize in characters true units of modification. However, the decoding of phenotypic structures into genotypic units of modification is still not possible in practice. Perceived characters may actually represent one or more than one evolutionary novelty (individual mutation or genetic recombination), or even bear no relation to evolutionary novelties. Thus a cladogram based on a single complex character – subjectively perceived or metrically defined – may be more parsimonious than an alternative cladogram based on several simple characters.

The proposed phylogenetic classification has the same cladistic information content as the cladogram. In order to provisionally maintain the names of taxa and categories closest to traditional use, the sequencing convention has been associated with subordination of taxa. In this convention each taxon is always the sister-group of all the following taxa of equal rank listed in the classification.

As a result of the sequencing convention, many monophyletic taxa remain unnamed in the classification. To refer to these unnamed taxa I have used the convention "taxon M^{+}" (Amorim, 1982), which indicates the monophyletic taxon M plus its sister-group.

Results

The general survey of articulatan descriptive information has provided several morphological characters whose generalities within the Eucarida could be reasonably postulated from the available evidence. These characters were ranked to produce a cladogram (Fig. 1) and a phylogenetic classification.

List of characters believed to be apomorphic and used to support the higher taxa of Eucarida in the cladogram of Fig. 1

1. Carapace attached to all thoracic somites in post-zoeal stages. Remarks: This character was used by Burkenroad (1963) and Schram (1984) to establish the monophyly of the Eucarida. In the remaining Eumalacostraca the carapace remains free from at least the four posterior thoracic somites. During eucarid ontogeny the carapace frequently remains free from the posterior one or two thoracomeres, from its appearance in the later (metanaupliar) stages of the nauplius phase or in the earlier (protozoeal) stages of the zoea phase, until the end of the zoea phase (Williamson, 1982). The status of the attached carapace of adults as an eucaridan synapomorphy thus seems secure (see also Newman & Knight, 1984). On the other hand, this character would appear to be very difficult to establish in fossil eumalacostracans. For example, all "Eocarida" were supposed to have a free carapace (Brooks, 1969), but this condition has apparently only been clearly described and illustrated for *Anthracophausia* Peach, 1908 (Burkenroad, 1963; Hessler, 1969). It may not be possible, based on this character alone, to exclude several Paleozoic caridoids from the Eucarida.

2. Free-swimming nauplius phase without masticatory spines at base of antennae and mandible (Gurney, 1942). Remarks: In some, if not all cases, the free-swimming nauplius of Eucarida is dependent upon internal yolk, the mouth being closed until the end of the nauplius phase (Gurney, 1942).

3. Mandibular endopod temporarily suppressed from most or all of zoeal phase of development. Remarks: The mandibular endopod is present both in the naupliar and in the post-zoeal stages of the Eucarida (Gurney, 1942). Another possible, but less parsimonious interpretation for this character would be to consider the post-zoeal mandibular palp of Eucarida as a new acquisition, not homologous to the naupliar endopod. However, the retention of a mandibular endopod throughout free developmental stages in the Mystacocarida and in at least some Ostracoda and Copepoda (Williamson, 1982) provides the ontogenetic evidence for deriving an adult mandibular palp from a naupliar mandibular endopod within the Crustacea. Available evidence thus seems to favor the chosen hypothesis.

4. Eighth thoracopod reduced in size, with endopod containing only four segments in adults (Casanova, 1984). Remarks: In the plesiomorphic state of this character the eighth thoracopod is similar to the preceeding thoracopod and the endopod contains five segments.

5. First thoracopod of adult with large specialized masticatory lobe (endite) on coxa (Calman, 1909).

6. Compound eyes vestigial, associated with abyssal life (Hessler, 1969).

7. Endopod of eighth thoracopod absent in adults (Casanova, 1984).

8. Prominent luminescent organ present on coxa of seventh thoracopod in adults. Remarks: Possibly those photophores located in the stalks of the compound eyes, coxae of the second thoracopods and sternites of the first four abdominal somites (Calman, 1909) also evolved in the stem-lineage of this taxon.

9. First pleopod modified into a complex copulatory structure (petasma). Remarks: I consider the modified endopod of the first pleopod for copulation a malacostracan synapomorphy (see character 87). In both the Euphausiidae and the Penaeidea not only the endopod but the entire first pleopod has become strongly modified for copulation (petasma). Burkenroad (1963) considers the petasma of the Euphausiidae to result from the modification of the appendix interna, whereas in the Penaeidea it is the corpus of the endopod which is supposed to have become modified and to have shifted proximally from the tip of the protopod.

10. First thoracic appendage of adult modified into a functional maxillipede. Remarks: The most conspicuous change in the first thoracopod is the shortening and attenuation of the endopod. Many of the remaining characteristics of the first maxillipede of the Amphionidacea^{+} (a two-segmented exopod with a broadened proximal segment, a five-segmented endopod and a two-segmented protopod provided with masticatory endites) are primitive features.

11. Exopods of second to eighth thoracopods tapering throughout, without proximal swelling for swimming, apparently associated with loss of pelagic life. Remarks: In plesiomorphic state of this character the basal article of all thoracopods is large, flattened and conspicuously broadened, apparently an adaptation for swimming. The exopod of the first maxillipede remains proximally enlarged in *Amphionides* Zimmer, 1904, in several Penaeidea, in several Reptantia, in *Procaris* Chace & Manning, 1972 and in the Caridea. This basal lobe has been called the

"caridean" lobe in the latter two groups, being used by Schram (1984) to define the Procarididea+. However, from the above considerations it would appear that the "caridean" lobe is actually a primitive feature for the Procarididea.+

12. Maxilla with well developed scaphognathite from zoeal stages to adult, composed of both dorsal lobe (exopod) and ventral lobe (pseudexopod) fused to external lobe of basis (Heegaard, 1957). Remarks: The "scaphognathite" which can be recognized in some later juvenile stages of Stomatopoda (Williamson, 1982) is apparently not homologous to the scaphognathite of Amphionidacea+, because of the absence of the ventral lobe (*e.g.*, Provenzano & Manning, 1978). Schram (1984) has mistakenly restricted the generality of this character to the Decapoda.

13. Carapace well developed laterally in adults, covering gills in a branchial chamber. Remarks: In the pygocephalomorphs the carapace is also produced laterally, suggestive of a branchial chamber.

14. A series of zoeal stages present during development, distinguished from preceeding and succeeding stages by distinct metamorphosis, the only effective swimming appendages being thoracic. Remarks: A zoeal phase in which the only swimming appendages are thoracic also occurs in the Anostraca (Williamson, 1982), but here the development is gradual, without distinct metamorphosis. Schram (1984) considered the presence of zoeae to be a derived character for the Eucarida. However, if zoeae are simply defined to include stages in which thoracic swimming appendages are present, independently of whether the antennae are still used for swimming, then similar homologous larval phases are found throughout the Crustacea (Williamson, 1982).

15. A supraorbital spine present on each side of carapace, from second zoeal stage (protozoea II) onwards. Remarks: This spine frequently disappears at the metamorphosis to the megalopa phase.

16. Outer lobe (pseudexopod) absent from basis of maxillule in post-larval stages. Remarks: In the plesiomorphic state of this character an outer lobe is present on the basis of the maxillule of adults, usually being termed a pseudexopod to distinguish it from the more distal exite present in the larva, considered to represent the true exopod (Heegaard, 1957).

17. Endopod of first pleopod reduced, not more than half as long as exopod. Remarks: In the plesiomorphic state of this character the endopod appears to be at least three-fourths as long as the exopod.

18. Trichobranchiate pleurobranchiae present on third to eighth thoracopods, appearing in late zoeal stages.

19. Epipod and respective podobranch gill absent from eighth thoracopod.

20. Carapace greatly inflated in adult female. Remarks: This character may be related with the hypothetical brooding of eggs under the thorax.

21. First pleopod of mature female very long, leaf-like, unjointed and umbranched. Remarks: The female pleopod is supposedly modified to retain eggs under the thorax.

22. Dorsal lobe of scaphognathite of maxilla expanded laterally in adult, particularly in female.

23. Presence of large gap between first and second thoracopods throughout free developmental stages.

24. Second to eighth thoracopods with elongate basis throughout development, possibly associated with planktonic life.

25. Second to fourth and sixth to eighth thoracopods reduced in size. Remarks: The endopods of the second to third and seventh to eighth thoracopods contain four articles in the adult male (ischium fuses to merus) and usually fewer articles in the adult female (endopod undivided in second thoracopod, with 3 articles in third thoracopod, with 4 articles in seventh thoracopod and absent in eighth thoracopod).

26. Eighth thoracopod and associated pleurobranch gill absent in female.

27. Mandible and maxillule vestigial in post-larval stages.

28. Antennal scale enlarged in adults, almost circular in females.

29. Hepatopancreas lobulated and multi-sectioned during larval stages (Heegaard, 1969).

30. Second thoracopod modified into functional maxillipede in post-larval stages, with permanent flexion at propodo-carpal joint of endopod.

31. Third thoracopod modified into functional maxillipede in post-larval stages, the endopod being provided with row of serrate setae for grooming of antennular flagella (Bauer, 1981). Remarks: Other than tending to be directed forwards rather than downwards, the third thoracopod is not conspicuously modified and remains pediform. It is doubtful whether the specializations of the third maxillipede can be recognized in fossils. The Paleozoic pygocephalomorphs possibly had the first three thoracopods adapted as maxillipedes (Brooks, 1969), rather than only the first two, as interpreted by Schram (1974a, b) and would in this case appear to belong to the Decapoda.

32. Fourth to sixth thoracopods with endopods strong and chelate, developing gradually from zoeal phase. Remarks: The chelipedes are of similar size and structure, being used mainly in food handling and general body cleaning. The carpus and propodus of the fourth thoracopod

have specialized setae for cleaning the flagellum of the antenna (Bauer, 1981). Burkenroad (1963, 1981, 1983) considered the chelae as evolving independently in the various decapod groups. It is more parsimonious to consider the presence of three pairs of chelae to have evolved only once in the ancestor of the Decapoda, with subsequent losses of chelae in several groups. Only the chelae sometimes present on the fourth and fifth pereiopods of some Reptantia and the specialized chelae on the third to the fifth pereiopod in the caridean genus *Pseudocheles* Chace & Brown, 1978 are here considered to be independent acquisitions.

33. Seventh and eighth thoracopods with endopods strong and specialized as walking legs, which develop gradually from the zoeal phase, associated with nekto-benthonic life.

34. Basal masticatory endite of first maxillipede expanded dorsally into very large masticatory plate in post-larval stages. Remarks: Schram (1984) also considered this character a derived condition for the Penaeidea^{+}. The traditional name Decapoda turns out to be quite handy in referring to this large monophyletic group.

35. Well developed stylocerite covering statocyst slit on first segment of antennular peduncle in post-larval stages.

36. Large dorsolaterally compressed rostrum, usually armed with series of dorsal and ventral teeth, developing gradually from zoeal phase.

37. One arthrobranch gill present on first maxillipede and two arthrobranch gills present from second maxillipede to fourth pereiopod, appearing in late zoeal stages, before development of pleurobranch gills of second maxillipede to fourth pereiopod (Gurney, 1942). Remarks: In the lophogastrid and eucopiid mysidaceans there is a gill series attached to the articular membranes between the coxa and the body wall of the second to the eighth thoracopods (Calman, 1904; McLaughlin, 1980), but their relations to decapod gills are unclear. Calman (1909) tentatively homologues these gills to the podobranchiae of Eucarida, despite their articular position, while Burkenroad (1963) homologues these gills with the arthrobranchs of decapods. In this phylogenetic hypothesis I am assuming that the mysidacean gills are not homologous to the decapod arthrobranchs. Another difficulty refers to the interpretation of the dorsal body gill of the second maxillipede, which Burkenroad (1981) considers to be a pleurobranch in the Dendrobranchiata (= Penaeidea) and an arthrobranch in the Reptantia. I have called this gill an arthrobranch throughout the Decapoda.

38. All gills differentiated as dendrobranchiae. Remarks: In the plesiomorphic state of this character gills are of the trichobranchiate type, as Huxley (1878), Bate (1888) and Burkenroad (1963, 1981, 1983)

have already recognized. Considering that dendrobranchiae are only known to occur in Penaeidea, while trichobranchiae occur both inside and outside the taxon Decapoda, there is no genealogical support for Felgenhauer & Abele's (1983) view that trichobranchiae are derived from dendrobranchiae.

39. First pleopod of adult male with specialized copulatory structure (petasma) attached to proximal portion of protopod. Remarks: Burkenroad (1963) considers the petasma of the Penaeidea and Euphausiidae as non-homologous structures (see character 9).

40. Appendices internae absent from pleopods, except for vestiges in male first and second pleopod (Burkenroad, 1981) Remarks: Appendices internae are present in Phyllocarida and Stomatopoda (Brooks, 1969), so these structures should be considered a malacostracan synapomorphy. Independent losses of the appendices internae from all pleopods have occurred in Stenopodidea and Procarididea (see character 90).

41. Post-larval mandibular palp expanded and lamellar, apparently taking part in enclosing the respiratory passages (Calman, 1909). Remarks: When there are three articles on the mandibular palp, it is the middle one that is expanded, but when there are only two articles, it may be the distal article that is expanded (*e.g., Penaeopsis* Bate, 1881, in which the third article may have been lost) or the proximal article that is expanded (*e.g., Benthesicymus* Bate, 1881 and *Sergia* Stimpson, 1860, in which the first and second articles may have fused).

42. Eggs in mature female incubated attached to protopod of pleopods by ovigerous setae. Remarks: Burkenroad (1981) and Schram (1984) have considered this character a derived condition for the Stenopodidea^{+}. Once acquired by the ancestral species of this group the character appears not to have been lost or modified in the almost 10.000 known descendant species of Stenopodidea^{+}, although eggs have not yet been observed in the Procarididea. The available name Pleocyemata seems very handy to refer to this large bulk of eucarid evolution. It is not clear to me wy Burkenroad (1981) abandoned this taxon in his more recent formal classification of the Decapoda.

43. Chelae of first and second pereiopods of adults with thick brushes of multiscaled or serrate setae for gill cleaning (Bauer, 1981).

44. Post-larval mandibular palp strongly curved, the segments being articulated at an angle to each other and forming semi-circle when all three joints are present. Remarks: In the plesiomorphic state of this character the post-larval mandibular palp is straight.

45. Third abdominal somite with pronounced bend and dorsal hump in larval and post-larval stages.

46. Endopod of first maxillipede with no more than three segments in post-larval stages. Remarks: In the plesiomorphic state of this character there are 5 segments in the endopod of the first maxillipede.

47. Third pair of chelipedes much stronger than remaining pereiopods.

48. Pleonic hinges on abdominal somites restricted to somites IV-V and V-VI (Felgenhauer & Abele, 1983). Remarks: In the plesiomorphic state of this character there are pleonic hinges between all abdominal somites.

49. Basal swelling ("caridean lobe") absent from exopod of first maxillipede.

50. First abdominal somite somewhat reduced in adults. Remarks: Reduction of the first abdominal somite has occurred independently within the Reptantia; in several thalassinids the first abdominal somite may be just as long as the second somite.

51. Pleura of second abdominal somite of adults large and overlapping pleura of first somite. Remarks: In Stenopodidea, Penaeidea, Euphausiacea and several other caridoid out-groups it is the first pleura which overlaps the second, so this latter condition cannot be considered a derived character of Penaeidea, as suggested by Burkenroad (1981, 1983).

52. Propodus of fourth and fifth pereiopod of adults with brushes of serrate setae for general body grooming (Bauer, 1981).

53. Pleurobranch gill absent from third maxillipede.

54. Foliaceous epipods of third maxillipede to third pereiopod of adults with hooks on medial faces which clamp around setobranch tufts on coxae of first to fourth pereiopods, for gill cleaning (Bauer, 1979). Remarks: The compound setae (denticulate or serrate) on the thoracic appendages for gill cleaning are also present in lophogastrid Mysidacea (Borradaile, 1907), so the generality of these setae must be established within the Caridoida.

55. Chela absent from third pereiopod.

56. One of the two arthrobranch gills absent from second maxillipede and from first to fourth pereiopod.

57. Brushes of serrate setae, used for general body grooming, absent from propodus of fourth pereiopod (Bauer, 1978). Remarks: The presence of these brushes on both the fourth and the fifth pereiopods is considered a synapomorphy of the Reptantia+ (see character 52). Independent losses of these setae have also occurred within the Reptantia.

58. Brushes of serrate setae, used for general body grooming, absent from propodus of fifth pereiopod (Bauer, 1978). Remarks: Independent losses of these setae have also occurred within the Caridea.

59. Chelae absent from first and second pereiopods.

60. Arthrobranchiae absent from first maxillipede and from first to fourth pereiopods.

61. Both arthrobranchiae absent from third maxillipede.

62. Pleurobranch gill absent from fifth pereiopod.

63. Epipods of third maxillipede to fourth pereiopod of adults developed into narrow laminae which clamp around setobranch tufts on first to fifth pereiopod, forming fully developed epipod-setobranch complexes for gill cleaning.

64. Ocellus present on ocular peduncle of adult, partly or totally separated from cornea.

65. Endopod of third maxillipede composed of no more than three segments in post-larvae (dactyl fused to propodus and merus fused to ischium). Remarks: Females of *Amphionides* Zimmer, 1904 also appear to have only three segments in the endopod of the third thoracopod, but there are four segments in males. The occasional presence of four or five segments in the maxillipedal endopod of some advanced Caridea may be due to an evolutionary reversal of this character.

66. Dorsal vesicular portion of epipod absent from fourth pereiopod. Remarks: This structure apparently represents a modified podobranch (see remarks for characters 85 and 86).

67. First chelipede enlarged in adults, specialized mainly for crushing of food and defense. Remarks: One of the chelipede specializations seems to be the development of a second propodo-carpal hinge, which restricts the movement of the chela to a single plane (Burkenroad, 1981).

68. Ischium of third maxillipede of adults with a dentate ridge (crista dentata).

69. One of transversal grooves of carapace (post-cervical ?) very conspicuous in adults. Remarks: The generalities and homologies of the carapace grooves have not been satisfactorily established within the Eumalacostraca, despite the great attention which these structures have received, particularly in the Reptantia (Glaessner, 1969).

70. Serrate setae for cleaning flagellum of antenna absent from opposite sides of propodo-carpal joint of first pereiopod (Bauer, 1981). Remarks: The presence of these specialized grooming setae is considered a decapod synapomorphy (see remarks for character 32).

71. Dorsal hump and bend on third abdominal somite absent. Remarks: The presence of a dorsal hump and a pronounced bend on the third abdominal somite is considered a pleocyematan synapomorphy (see character 45).

72. Pleurobranch gill absent from first pereiopod (Burkenroad, 1963, 1981).

73. Larval antennal scale unsegmented (Burkenroad, 1981). Remarks: This may be due to an eclosion of the Reptantia in a more advanced zoeal stage (mysis) (Gurney, 1942).

74. Exopods absent from pereiopods in post-larval stages, associated with benthonic life. Remarks: In two of his alternative cladograms of the caridoid eumalacostracans, Schram (1984) considered the loss of exopods from the thoracopods as a synapomorphy for the Stenopodidea^{+}, and then postulated a new acquisition of exopods in the Procarididea^{+}. He obviously did not consider the ontogeny of decapods, in which exopods appear on the thoracopods of the larvae and are reduced or disappear in the post-larval stages. His polarity decision for this character can thus be dismissed as contrary to facts. Exopods have also been lost independently in several malacostracan lineages.

75. First pleopod without exopod in adults of both sexes and appearing later than posterior pleopods during individual development. Remarks: A loss of the exopod and a delay in the development of the first pleopod appear to have occurred independently also within other caridoid lineages.

76. Stylocerite strongly reduced. Remarks: The stylocerite has also been reduced independently in several caridean lineages.

77. Arthrobranchiae appear later than pleurobranchiae during ontogenesis. Remarks: Arthrobranchiae occur together with pleurobranchiae for the first time in Penaeidea, the arthrobranchiae developing first (see character 37). It is most parsimonious to consider this developmental sequence also to have occurred in the ancestral decapod, so this character state must be considered plesiomorphic for the Penaeidea (*cf.* Burkenroad, 1981, 1983). The gradual loss of importance of the arthrobranchiae during the evolution of the Decapoda has also occurred independently within the reptant line leading to the Brachyura (Burkenroad, 1981). Nothing is know n of the ontogeny of the Procarididea.

78. One of the two arthrobranchiae absent from second maxillipede. Remarks: Independent losses of one arthrobranch gill from second maxillipede have also occurred within the Penaeidea and the Reptantia.

79. Development abbreviated, with loss of free nauplius phase and eclosion in zoea phase, in stages in which the antennae are no longer used for locomotion.

80. Trichobranchiate gills modified into phyllobranchiate gills. Remarks: The gills were apparently modified independently into phyllobranchiae also within the Reptantia.

81. Distal coxal endite of maxilla reduced or absent throughout free developmental stages.

82. Body, including rostrum, depressed dorsoventrally throughout free developmental stages. Remarks: In the plesiomorphic state of this character both the body and the rostrum are distinctly compressed laterally, which is partly responsible for the shrimp-like aspect of many caridoids.

83. Podobranch gill absent from first maxillipede. Remarks: This gill is also absent in almost ali Reptantia and Caridea.

84. Podobranch gill absent from second maxillipede. Remarks: This gill has been lost independently within Penaeidea, Caridea and Reptantia.

85. Podobranch gill of fourth pereiopod absent or modified. Remarks: The dorsal vesicular portion of the epipods of the third maxillipede to the fourth pereiopod in the Procarididea and in some Reptantia, and which is also present in some Caridea up to the third pereiopod apparently represents a modified podobranch (see remarks for characters 66 and 86). The podobranch gill has also been lostw ithin the Reptantia.

86. Podobranch gills from third maxillipede to third pereiopod absent or modified. Remarks: In the Procarididea, some Caridea and some Reptantia the podobranch of the third maxillipede and of the anterior pereiopods is apparently modified into a dorsal sac-like projection of the epipod (see remarks for character 85). The podobranch gills have also been lost within the Penaeidea and Reptantia.

87. Male copulatory structure (modified endopod) absent from first pleopod. Remarks: I have assumed that the modified endopods of the male first pleopod found in some Leptostraca, Stomatopoda, Anaspidacea, Euphausiacea, Penaeidea and Reptantia are homologous, which would indicate that this modification is a malacostracan synapomorphy. The more complex copulatory structures of the Euphausiidae and Penaeidea represent subsequent and independent specializations (see remarks for characters 9 and 39). Schram (1984), in some of his alternative cladograms of caridoid eumalacostracans, considered the possibility of at least the anaspidacean and eucaridan male copulatory structures being homologous.

88. Female seminal receptacle (thelycum) absent from between posterior thoracic appendages. Remarks: The thelycum of the Euphausiacea and Penaeidea may be homologous to the seminal receptacles

found in some Reptantia, Isopoda, Syncarida and "Eocarida", so the generality of this structure must still be established within the Caridoida.

89. Statocyst absent from basal segment of antennular peduncle. Remarks: A statocyst is also present in the Syncarida (Burkenroad, 1963), so the generality of this structure must be established within the Caridoida. A statocyst has occasionally been lost also within the Caridea.

90. Appendices internae absent from pleopods. Remarks: The presence of these structures is considered a malacostracan synapomorphy (see remarks for character 40).

91. Outer lobe (exopod ?) absent from maxillule of larvae. Remarks: An outer lobe, whose homology with the exopod is not definitively established throughout the Decapoda, is present in larvae of Euphausiacea, Penaeidea, some Caridea and one unidentified specimen of Stenopodidea (Williamson, 1982).

92. Palp of maxillule with no more than two segments in adults. Remarks: In the plesiomorphic state of this character there are 3 segments in the palp of the maxillule. The presence of 3-4 segments in some Penaeidea (Calman, 1909) appears to be quite exceptional for the Eucarida.

93. Diaeresis absent from outer ramus of uropod. Remarks: The outer ramus of the uropod is articulated in the Stomatopoda, which may indicate that a diaeresis is an eumalacostracan synapomorphy.

94. Appendix masculina absent from second pleopod of male. Remarks: Although larger, an appendix masculina of similar position and structure occurs in many male isopods. The generality of this character must thus be established within the Caridoida, rather than used to distinguish the Eucarida (*cf.* Burkenroad, 1963).

Combined Recent-fossil sequenced phylogenetic classification of the higher taxa of Eucarida, with indication of minimum ages of taxa for which fossils are known

Superorder Eucarida Calman, 1904. U. Dev. - Rec.
  Order Euphausiacea Boas, 1883. Rec.
    Family Bentheuphausiidae Colosi, 1917. Rec.
    Family Euphausiidae Dana, 1850. Rec.
  Order Amphionidacea Williamson, 1973. Rec.
  Order Decapoda Latreille, 1803. U. Dev. - Rec.
    Suborder Penaeidea Dana, 1852. Permotrias. - Rec.
    Suborder Pleocyemata Burkenroad, 1963. U. Dev. - Rec.
      Infraorder Stenopodidea Bate, 1888. Rec.
      Infraorder Reptantia Boas, 1880. U. Dev. - Rec.
        Reptantia "stem-group": "Pygocephalomorpha" Beurlen, 1930. L. Carb. - Perm.

Reptantia *incertae sedis:* Plesion *Uncina posidoniae* Quenstedt, 1850. L. Jur.

Reptantia *incertae sedis:* Plesion *Palaeopalaemon newberryi* Whitfield, 1880. U. Dev. - L. Miss.

Infraorder Procarididea Felgenhauer & Abele, 1983. Rec.

Infraorder Caridea Dana, 1852. M. Jur. - Rec.

Discussion

Remarks on the cladogram

The 94 characters analysed in the cladogram of Fig. 1 were interpreted as having provided 73 synapomorphies and 55 homoplasies, which gives a total of 128 derived characters and a homoplasy value of 42%. For a similar comparison, Schram (1984, fig. 1) indicates 34 characters (including evolutionary reversals) for one of his alternative cladograms on caridoid eumalacostracans, which provide 25 synapomorphies and 22 homoplasies, giving a total of 47 derived characters and a homoplasy value of 47%. On the other hand, Gosliner & Ghiselin (1984) believe 60 to 80% parallelism not to be uncommon in opisthobranchs, angiosperms, insects and vertebrates.

Although such high homoplasy values are certainly a challenge to phylogenetic reconstruction, it is important to realize that the nuclear point in phylogenetic methodology refers to the analysis of congruence of characters. In this sense, the discovery of a high number of cladistically correlated characters (Fig. 1, characters number 1-73) may be a significant contribution towards the resolution of the true phylogeny of the Eucarida. After all, even if it is acknowledged that "rampant parallelism, far from being a peculiarity of certain taxa, may be a general rule" (Gosliner & Ghiselin, 1984), it should not be overlooked that the cladistically unreliable characters responsible for these homoplasies may be hierarchically correlated only by chance (Farris, 1969). In fact, as will be discussed below, the homoplasies of Fig. 1 provide little margin for alternative interpretations of relationships, and most individual hypotheses are little affected by them.

Many of the homoplasies in Fig. 1 are based on characters which appear to recur so frequently in closely related taxa that very little confidence can be bestowed upon them as indicators of alternative views of relationships for the present levels of cladistic analysis. For example, characters 83-86 refer to losses of podobranch gills, which have also occurred independently within the remaining decapod taxa; characters 87-94 all refer to losses of structures, while the presence of these structures seem to have very wide generalitiesw ithin the Malacostraca, and seem to have been lost frequently also within the remaining eucaridan and non-eucaridan groups of malacostracans.

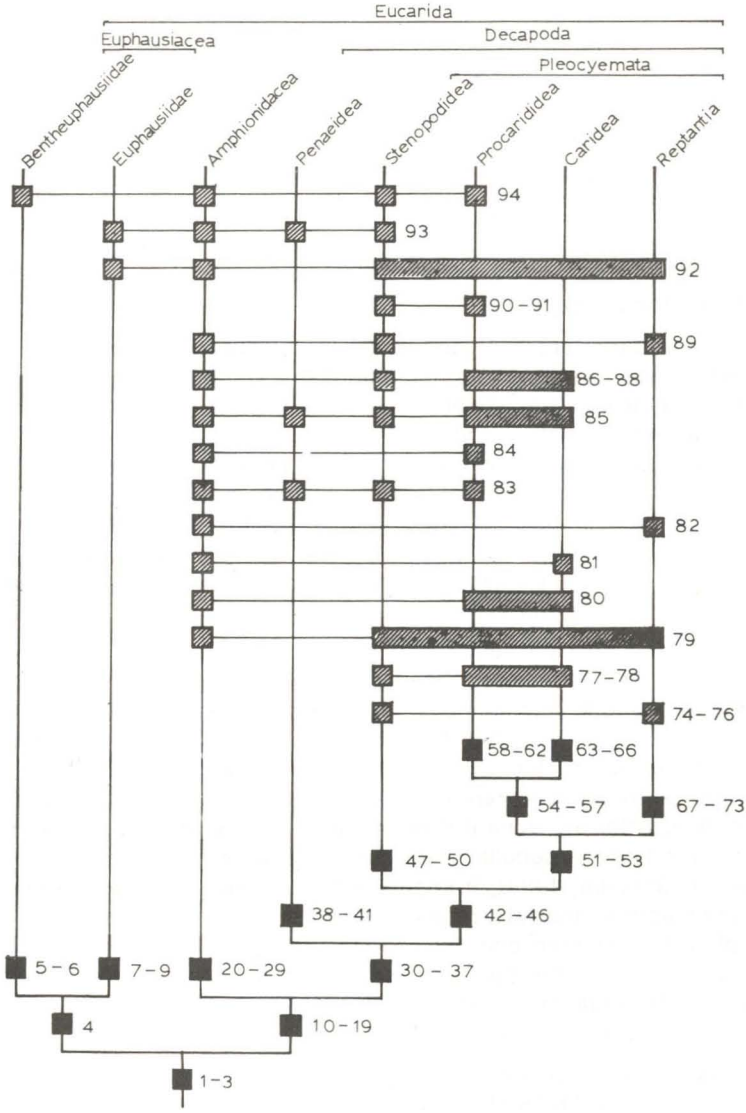


Fig. 1. – Cladogram of eucaridan higher taxa, showing hypothesized generalities of characters. Black bars represent derived characters interpreted as synapomorphies. Hatched bars represent derived characters interpreted as homoplasies. Characters are listed and commented in the text, under corresponding numbers. They may be grouped under the following topics: Carapace (1, 13, 15, 20, 36, 69, 82); branchiae

(18, 19, 26, 37, 38, 53, 56, 60-62, 72, 77, 78, 80, 83-86); eyestalk (6, 64); antennule (35, 76, 79, 89); antenna (2, 28, 73, 79); mandible (2, 3, 27, 41, 44); maxillule (16, 27, 91, 92); maxilla (12, 22, 81); first thoracopod (5, 10, 34, 46, 49); second thoracopod (11, 24, 25, 30); third thoracopod (11, 24, 25, 31, 54, 63, 65, 68); fourth thoracopod (11, 24, 25, 32, 43, 54, 59, 63, 67, 70, 74); fifth thoracopod (11, 24, 32, 43, 54, 59, 63, 74); sixth thoracopod (11, 24, 25, 32, 47, 54, 55, 63, 74); seventh thoracopod (8, 11, 24, 25, 33, 52, 54, 57, 63, 74); eighth thoracopod (7, 11, 19, 24-26, 33, 52, 58, 63, 74); other thoracic features (23, 29, 88); specializations of first and second pleopod (9, 17, 21, 39, 75, 87, 94); other abdominal features (40, 42, 45, 48, 50, 51, 71, 82, 93); larval developmental patterns (14, 79).

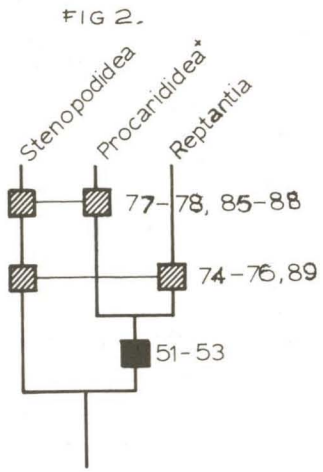
Amphionides reynaudii (H. Milne Edwards, 1832) shares several other homoplasies with different decapod groups (characters 79-82), which have been responsible for this taxon's previously unstable position within the system of the Eucarida. Character 79 would at first appear to unite *Amphionides* Zimmer, 1904 and the Pleocyemata, but in this case, although one could suggest that character 92 evolved independently only twice, instead of three times, characters 30-37 would have to be reinterpreted as homoplasies or evolutionary reversals. It seems more likely that abbreviated development (character 79) has evolved independently in *Amphionides*, in connection with its supposed thoracic brood pouch. Character 80 may at first appear to unite *Amphionides* with the Procarididea^{+}, but phyllobranchiae have also evolved independently within the Reptantia, and with present knowledge it is more parsimonious to consider this character a further homoplasy for the Amphionidacea. If character 80 were considered a synapomorphy uniting *Amphionides* and Procarididea^{+}, it would be possible to eliminate one homoplasy for each of characters 79, 85-88 and 92, but on the other hand characters 30-37, 42-46 and 51-53 would all have to be reconsidered as homoplasies or evolutionary reversals. Character 81 could be taken to represent a synapomorphy uniting *Amphionides* and the Caridea. However, even though in this case characters 79-80 would at first seem to corroborate this hypothesis, and there would be one homoplasy less for characters 85-88 and 92, this would require that each of characters 30-37, 42-46 and 51-57 be reinterpreted. It seems simpler to consider that the distal coxal endite of the maxilla was reduced independently in *Amphionides* and Caridea (character 81). Finally, character 82 may at first appear to unite *Amphionides* and Reptantia. However, although in this case characters 79, 89 and 92 could be taken to corroborate this view, all of characters 30-37, 42-46 and 51-53 would have to be reconsidered. The dorsoventral depression of the body (character 82) may be related to the benthonic life of the Reptantia, while this similar condition

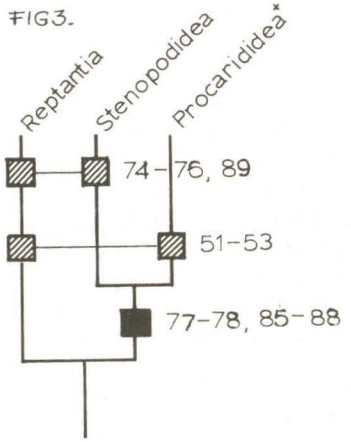
in *Amphionides* (lateral expansion of the body ?) could be an independent adaptation to planktonic life. The conclusion is that the position of the Amphionidacea as the sister-group of the Decapoda seems presently well corroborated, despite the large number of homoplasies with several decapod taxa.

The most controversial matter in eucaridan phylogeny refers to the definitive relationships of the Stenopodidea, Reptantia and Procaridi-dea^{+}. In the chosen solution the Reptantia are considered more closely related to the Procarididea^{+} than to the Stenopodidea, based on characters 51-53 (Fig. 1,2). Characters 74-76 and 89 are considered homoplasies for the Stenopodidea and Reptantia, while characters 77-78 and 85-88 are considered homoplasies for the Stenopodidea and Procaridi-dea^{+}. The two remaining possibilities of relationships between these three monophyletic taxa were considered by Burkenroad (1981) and Schram (1984). The Stenopodidea could be considered more closely related to the Procarididea^{+} than to the Reptantia, based on characters 77-78 and 85-88 (Fig. 3), or the Stenopodidea could be considered more closely related to the Reptantia than to the Procarididea^{+}, based on characters 74-76 and 89 (Fig. 4). Of the 13 characters considered in Fig. 2-4, only numbers 51-53 represent evolutionary acquisitions of structures. The remaining characters all represent simple evolutionary reductions of structures which have also occurred independently within several malacostracan taxa (see remarks for characters 74-78 and 85-88). As previously discussed, the more widely distributed and apparently highly homoplastic characters 85-88 are not considered very reliable for the present cladistic analysis. The evolutionary losses of characters 74-78 may be considered outweighted by the evolutionary gains of characters 51-53. However, in this case the most parsimonious solution is not as clear-cut as for the remaining levels of Eucarida here considered, and further evidence is needed for a reconsideration of the true relationships existing between the pleocyematan decapods.

Problems with the classification

The final cladogram (Fig. 1) indicates 14 monophyletic groups of Eucarida, of which 11 were named in the classification. There are many ways in which to provisionally translate the cladistic structure of a cladogram into a formal classification under the International Rules of Zoological Nomenclature. For example, the Euphausiacea could have been sequenced with the 6 remaining terminal taxa of Eucarida, in which case there would be no need to use the terms Decapoda and Pleocyemata, as preferred by Schram (1984), and all these taxa would be included in the same category. On the other extreme, a strictly subordinated classification could have been constructed, in which case it would be necessary





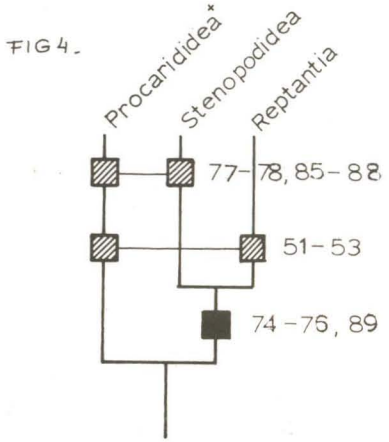


Fig. 2. – Proposed relationships for ther pleocyematan taxa Stenopodidea, Procarididea^{+} and Reptantia, based on cladogram of. Fig. 1, showing the conflicting characters involved.

Fig. 3. – An alternative possibility of relationships for the pleocyematan taxa Stenopodidea, Procarididea^{+} and Reptantia, showing the corresponding interpretation given to the conflicting characters of Fig. 2. Burkenroad (1981) indicated this possibility based on character 77 and Schram (1984) suggested this possibility based on character 87.

Fig. 4. – A third and last possibility of relationships for the three monophyletic taxa Stenopodidea, Procarididea^{+} and Reptantia, showing the corresponding interpretation given to the conflicting characters of Fig. 2. Schram (1984) suggested this possibility based on character 74.

to introduce new names for the taxa Amphionidacea^{+} Reptantia^{+}, and Procarididea^{+}, and the 7 pairs of sister-taxa would have to be included in 6 distinct categories.

In any case, there is little hope in fulfilling the stability ideal of classifications under the present rules of nomenclature. The main problem seems to lie in the inherent confusion between the concepts of systems and classes in the logic of our so-called Linnean system of classification (Griffiths, 1974). Besides not being based on any objective criteria, our traditional Linnean categories (which were intended as terms of Aristotelian logic) have been further built into group names in the form of suffices, and into binomial nomenclature, where the forename of a species at the same time belongs to a generic category.

One of the secondary objectives of phylogenetic systematics is to indicate the class structure of monophyletic taxa in terms of age of origin of these taxa (Historical Classification). But as knowledge on the history of living organisms will probably be obtained more slowly and less accurately than knowledge on the systems structure of these organisms, I believe that stability of nomenclature will best be served if these two concepts are completely separated in the construction of classifications. Thus the class structure of classifications should be reflected exclusively in the categories, the names of taxa should be ruled basically by the laws of priority and usage, the prescription of standard endings to indicate the categorial rank of taxa should be discontinued and the forenames of Quaternary species should coincide with generic names only by convention, while the forenames of species originating earlier than about the Miocene should have nothing to do with names of supraspecific taxa (Griffiths, 1976).

While the above suggestions are not generally agreed upon and incorporated into the rules of nomenclature, it may be preferable for the time being to compromise with present taxonomic procedures as far as possible. This is why I have not dropped the subjective Linnean categories altogether, and why I have subordinated the classification of the Eucarida only at points where collective taxon names were already available. As the present cladistic analysis provides strong evidence that both the named groups Decapoda and Pleocyemata are monophyletic, these names have also been incorporated into the final classification.

Analysis of fossils

Three fossil groups have been assigned to more restrictive positions within the system of the Caridoida, based on the generalities of characters of living forms which can be recognized in these fossils. They have been placed in the hierarchy at the level where their rela-

tionships are best understood, following conventions discussed in Wiley (1981) and Hennig (1981). *Uncina* Quenstedt, 1850 belongs to the Reptantia+, because of the enlarged second abdominal pleura overlapping the first somite (character 51) and to the Reptantia because of the enlarged first chelipede (character 67); furthermore, this taxon may be considered somewhat evolved along the reptant line, because of the reduced nature of the first pleomere (see remarks for character 50). *Palaeopalaemon* Whitfield, 1880 should also be considered a reptant, because of the hypertrophied first chelipede (character 67) and of the conspicuous transverse groove on the carapace (character 69); furthermore, this taxon may also be considered somewhat evolved along the reptant line, because of the absence of true chelae on the second and third pereiopods and because of the reduced nature of the first pleomere. The "Pygocephalomorpha" Beurlen, 1930, of uncertain status as a monophyletic group, cannot be definitively excluded from the Eucarida based on their supposedly free carapace (see remarks for character 1), appear to belong to the Amphionidacea+ because of the branchiostegal development of the carapace (see remarks for character 13), and may belong to the Decapoda because of the possible presence of three pairs of maxillipedes (see remarks for character 31). The only characters which would at first seem to exclude some of the pygocephalomorphs from the Reptantia are the presence of large imbricating endites on the thoracic appendages in the presumably mature females of *Pygocephalus* Huxley, 1857 and *Tealliocaris* Peach, 1908, and the presence of birramous thoracic appendages in these two taxa, as well as in *Anthracaris* Brooks, 1962 and *Mamayocaris* Brooks, 1962. If the pygocephalomorph thoracic endites are considered non-homologous to the peracarid oostegites, it is possible to provisionally consider these fossils as belonging to the "stemgroup" (*sensu* Hennig, 1981) of the Reptantia – that is, they may have diversified before the loss of exopods in the remaining reptants. It is of course hoped that further evidence will be presented for determining the exact relationships of each of the individual pygocephalomorph fossils.

The inclusion of *Palaeopalaemon* – the oldest eucarid fossil – in the Reptantia pushes the minimum age of this group back from the Upper Mississippian (Schram & Mapes, 1984) to the Upper Devonian. This same minimum age also becomes established for all of the remaining higher taxa of Eucarida except the Procaridídea and Caridea. The minimum age of these two younger taxa is presently established in the Middle Jurassic by fossils belonging to the taxon *Udora* Münster, 1839 (Glaessner, 1969). This taxon seems to belong to the Procaridídea+ because of the apparent absence of chelae on the third pereiopods (character 55) and is excluded from the Procaridídea by the presence of chelae on the first pereiopods.

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