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PHYLOGENETIC RELATIONSHIPS BETWEEN OPLOPHORIDAE, ATYIDAE, PASIPHAEIDAE, ALVINOCARIDIDAE **FAM. N.**, BRESILIIDAE, PSALIDOPODIDAE AND DISCIADIDAE (CRUSTACEA CARIDEA ATYOIDEA)

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RESUMO - Os Pasiphaeoidea **syn.n.**, Psalidopodoidea **syn.n.** e Bresilioidea **syn.n.** foram incluídos nos Atyoidea (mais correntemente conhecidos como Oplophoroidea), para se obter um conceito natural deste táxon. A monofilia do táxon Atyoidea emendado é indicado pelo exópodo reduzido do primeiro maxilípede. Uma hierarquia de 20 subgrupos monofiléticos, delimitados por 42 novidades evolutivas hipotéticas, é sintetizada num cladograma. A seguinte classificação filogenética sequenciada é proposta: Superfamília Atyoidea; Família Oplophoridae; Família Atyidae; Subfamília Xiphocaridinae; Gênero **Xiphocaris**; Subfamília Atyinae; Família Pasiphaeidae; Família Alvinocarididae **fam.n.**; Gênero **Alvinocaris**; Família Bresiliidae; Gênero **Bresilia**; Família Psalidopodidae; Gênero **Psalidopus**; Família Disciadidae; Gênero **Pseudocheles**; Gênero **Lucaya**; Gênero **Tridiscias**; Gênero **Discias**.

ABSTRACT - The Pasiphaeoidea **syn.n.**, Psalidopodoidea **syn.n.**, and Bresilioidea **syn.n.** have been included under the Atyoidea (more currently known as Oplophoroidea), in order to obtain a natural concept for this taxon. The monophyly of the amended Atyoidea is indicated by the reduced exopod on the first maxilliped. A hierarchy of 20 included monophyletic taxa, delimited by 42 hypothetical evolutionary novelties, is summarized in a cladogram. The following sequenced phylogenetic classification is proposed: Superfamily Atyoidea; Family Oplophoridae; Family Atyidae; Subfamily Xiphocaridinae; Genus **Xiphocaris**; Subfamily Atyinae; Family Pasiphaeidae; Family Alvinocarididae **fam. n.**; Genus **Alvinocaris**; Family Bresiliidae; Genus **Bresilia**; Family Psalidopodidae; Genus **Psalidopus**; Family Disciadidae; Genus **Pseudocheles**; Genus **Lucaya**; Genus **Tridiscias**; Genus **Discias**.

INTRODUCTION

Present knowledge on phylogenetic relationships within the Caridea is far from satisfactory. Contrary to avowed beliefs, this state of affairs is not due to the inadequate nature of the fossil record, to the lack of clear limits between certain taxa, or even to a supposed general inadequacy of available empirical information. The problem lies rather in the inapropriatness of several traditional taxonomic practices for the reconstruction of phylogeny and for the production of phylogenetic classifications.

The most debated issue regarding the system of the Caridea generally accepted by carcinologists today refers to the limits of taxon Atyoidea De Haan, 1849, more currently known under the name Oplophoroidea Dana, 1852.

Borradaile (1907) tried to group the caridean family-level taxa into superfamily-level taxa, three of which are pertinent to the present discussion: The Hoplophoroida (containing the Hoplophoridae, Atyidae and Nematocarcinidae) , the PASIPHAEOIDA (with the Pasiphaeidae and Bresiliidae) and the Psalidopodoida (containing only the Psalidopodidae) Borradaile did not include the Disciadidae in his classification. Balls (1927) added the Disciadidae and Campylonotidae to the Hoplophoroida and Burkenroad (1939) added the Rhynchocinetidae and Eugonatonotidae to this same taxon Holthuis (1955) erected a new taxon Bresilioida (for the Bresiliidae, Disciadidae, Eugonatonotidae and Rhynchocinetidae), retaining Borradaile's concept for his taxon Oplophoroida and restricting Borradaile's concept for his taxon Pasiphaeoida (to contain only the Pasiphaeidae) Balls (1957) did not accept the taxon Bresilioida, following Burkenroad's concept for his Hoplophoroida, except for the exclusion of the Eugonatonotidae, and retaining Borradaile's concept for his Pasiphaeoida. Thompson (1966, 1967) rearranged the concepts of the Oplophoroidea (to contain the Oplophoridae, Atyidae and Eugonatonotidae), of the Pasiphaeoidea (to contain only the Pasiphaeidae) and of the resurrected Bresilioidea (to contain the Bresiliidae, Disciadidae and Nematocarcinidae). Forest (1977) once again rejected the concept of the Bresilioida and tentatively rearranged the Oplophoroida (to contain the Oplophoridae, Atyidae, Nematocarcinidae, Bresiliidae and Disciadidae). Chace & Brown (1978) synonymized the Disciadidae under the Bresiliidae. Bowman & Abele (1982) reestablished Borradaile's concept of the Hoplophoroida, but with the name corrected to Atyoidea De Haan, 1849, because of the priority of the family-group name Atyadea De Haan 1849 over the family-group name Oplophorinae Dana, 1852;they also reestablished Holthuis concept of the Bresilioida(with the Bresiliidae **sensu** Chace & Brown, Eugonatonotidae and Rhynchocinetidae), but with the name corrected to Rhynchocinetoidea Ortmann, 1890, because of the priority of the family-group name Rhynchocinetidae Ortmann, 1890 over the family-group name Bresiliidae Calman, 1896.

In this paper I will apply consistent methods (1) to resolve the limits of the Atyoidea and (2) to resolve the phylogenetic relationships of its included higher taxa.

MATERIAL, PRINCIPLES AND METHODS

All published descriptive information available on the Atyoidea and closely related taxa has been carefully scrutinized for pertinent data on phylogenetic relationships. Examination of a few species of Atyidae and Pasiphaeidae accessible to me did not provide additional relevant information.

To reconstruct phylogenetic relationships between extant supraspecific taxa and to incorporate such information into biological classification I have followed principles and manual methods current among phylogenetic systematists (Hennig, 1966; Eldredge & Cracraft, 1980; Nelson & Platnick, 1981; Wiley, 1981) As points of view sometimes differ on particulars, I furnish a very brief statement of my own understanding of phylogenetics pertinent to this paper

Evolution is the result of speciation - the phyletic subdivision of species - and descent with modification. Speciation events disrupt the otherwise continuous lineages of ancestor-descendant populations through time, producing the branching structure of real phylogenies. Character modification may accompany or proceed independently of speciation.

Biological classification is intended to group organisms, but such ordering cannot be based on all kinds of knowledge about organisms. There can be no optimal classification for all possible purposes. A general reference classification should be based on phylogenetic (genealogical) relationships between organisms because genealogy expresses the historical course of evolution and it is only through history that all other relationships between organisms may be readily understood. Consequently, direct relations extend from a phylogenetic system to all other possible biological systems, whereas there are often no such direct relations between these other systems.

Phylogenetic trees represent the historical course of speciation. Species are unique lineages of ancestor-descendant populations (evolutionary species), while supraspecific taxa include an ancestral species and all of its descendants (monophyletic taxa) All taxa thus denote historical groups, being determined by parentage rather than by definitions or diagnoses of shared attributes. This does not mean that in practice systematics has to do without morphological aids in determining the limits of taxa. Monophyletic taxa may be recognized in a precise way, at least in principle, and to the extent that the rate of speciation does not proceed faster than the rate of character evolution, by attributes hypothesized to have evolved in the ancestral species of each taxon.

Our traditional Linnean classification is only appropriate to express a hierarchical arrangement of taxa. Phylogenetic trees, which depict ancestral-descendant relationships between evolutionary species, are not adequate for direct translation into hierarchical classifications,because ancestral species do not form part of the hierarchy of the nested sets of monophyletic taxa. Cladograms are more general concepts derived from real phylogenies, in which phylogenetic relationships and monophyletic taxa can be expressed without the actual recognition of ancestral species. Hence cladograms depict relative recency of common ancestry between taxa, as determined by their nested pattern of evolutionary novelties. The task of phylogenetic systematists is therefore to discover the relative generalities of characters and to transcribe the resultant branching structure of cladograms into biological classification.

In order to establish a classification of the Atyoidea consistent with phylogenetic relationships, I have presently attempted to introduce only minimal changes in the current taxonomy of the Caridea, retaining monophyletic taxa in their traditional ranks as far as possible. This aim has been accomplished using the phyletic sequencing convention of Nelson (1972, 1974) Under this convention taxa forming as asymmetrical part of a cladogram are maintained at the same categorial rank and sequenced in phylogenetic order of origin. Thus the first taxon is the sister-group of all subsequent taxa and so on for each subsequent taxon in the list.

RESULTS

From the mosaic of atyoidean descriptive attributes accumulated in the literature during the last two centuries, I have been able to establish a hierarchy of 21 monophyletic taxa, delimited by 43 hypothetical evolutionary novelties (Fig. 1)

The following sequenced classification is proposed for the Atyoidea:

Superfamily Atyoidea De Haan, 1849
- Family Oplophoridae Dana, 1852
- Family Atyidae De Haan, 1849
  - Subfamily Xiphocaridinae Ortmann, 1895
    - Genus **Xiphocaris** Von Martens, 1872
  - Subfamily Atyinae De Haan, 1849
- Family Pasiphaeidae Dana, 1852
- Family Alvinocarididae **fam.n.**
    - Genus **Alvinocaris** Wiliams & Chace, 1982
- Family Bresiliidae Calman, 1896
    - Genus **Bresilia** Calman, 1896
- Family Psalidopodidae Wood Mason & Alcock, 1892
    - Genus **Psalidopus** Wood Mason & Alcock, 1892
- Family Disciadidae Rathbun, 1902
    - Genus **Pseudocheles** Chace & Brown, 1978
    - Genus **Lucaya** Chace, 1939
    - Genus **Tridiscias** Kensley, 1983
    - Genus **Discias** Rathbun, 1902

DISCUSSION

My main purpose has not been to provide a final word on atyoidean classification - that is, to name all possible monophyletic taxa and to group these taxa into logically defined class concepts (categories) - but to furnish a minimally novel classification which reflects the phylogeny of the group more closely than present schemes. My argumentation scheme is thus the cladogram, not the resultant idiosyncratic classification. It is through the characters in the cladogram that I summarize clearly and objectively my reasons for accepting and delimiting each particular taxon. My plea is that in subsequent attempts to improve the proposed scheme particular evolutionary novelties (Fig. 1, characters 1-43) be rejected in favor of more likely individual hypothesis, rather than overlooked or summarily disregarded. Continuing comparative studies will undoubtedly provide much additional knowledge on phylogenetic relationships within the Atyoidea.

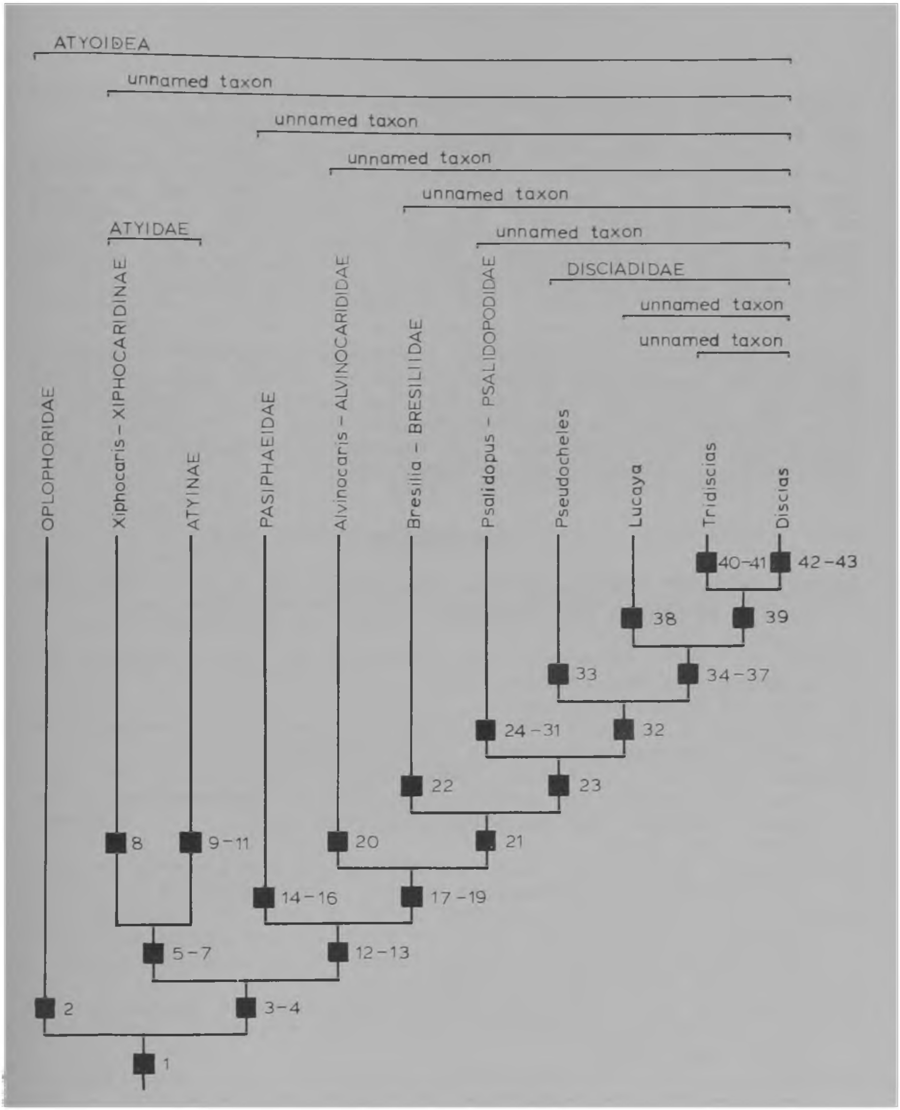
Remarks on nomenclatural changes

It has been necessary to propose a major rearrangement in our current classification of the Caridea at the superfamily level. The Pasiphaeidae, Psalidopodidae and Bresiliidae **sensu** Williams & Chace (1982) and Kensley (1983) are all descendants of the same ancestral species which also gave rise to the Oplophoridae and Atyidae. All these groups thus belong to the larger monophyletic taxon Atyoidea, and the concepts Oplophoroidea, Pasiphaeoidea, Bresilioidea and Psalidopodoidea must all be included under the synonymy of the amended taxon Atyoidea. In view of the highly unsatisfactory historical development of the superfamily-level classification within the Caridea, the present change will certainly not come as a surprise to caridean taxonomists.

A second innovation has been the introduction of the new family Alvinocarididae. An alternative decision, namely, to once again revise the scope of the Bresiliidae **sensu** Williams & Chace (1982) so as to include **Psalidopus**, would have been more conservative as regards nomenclature. However, for priority reasons this revised concept would have to be called Psalidopodidae. I judged that this action would so drastically change the traditional concept of the Psalidopodidae, which has always been firmly attached to the bizarre and highly modified members of the genus **Psalidopus**, that the former decision would result in less taxonomic confusion. Consequently the Alvinocarididae **fam.n.** has been erected to contain the well described species **Alvinocaris lusca** Williams & Chace, 1982, and may be delimited from other Caridea by the unique reduction of the exopod of the second maxilliped (Fig 1, character 20) I then use Bresiliidae and Disciadidae **sensu** **Forest** (1977), the latter taxon expanded to include the more **recently described** **Pseudocheles** Chace &

LEGEND OF FIGURE 1

Cladogram of phylogenetic relationships within the Atyoidea. The following evolutionary novelties delimit the Atyoidea and each of its monophyletic subtaxa: 1 - Distal lash on exopod of first maxilliped reduced; 2 - Dactyl of fifth pereiopod reduced; 3 - Loss of distal segment from triarticulate mandibular palp; 4 - Loss of ocellus from base of cornea; 5 - Loss of mandibular palp; 6 - Adaptations for life in fresh-water; 7 - Epipod of first maxilliped rudimentary; 8 - Appendix masculina short, broad, and provided with numerous spine-like projections; 9 - Chelae of first and second pereiopods provided with unique pencils of long hairs on finger-tips; 10 - Arthrobranchs lost from second to fourth pereiopods; 11 - Carpus of first pereiopod deeply escavate anteriorly; 12 - Chelae of first and second pereiopods with fingers pectinate along opposable margins; 13 - Epipods lost from third maxilliped to fourth pereiopod; 14 - Loss of molar process from mandible; 15 - Third to fifth pereiopods reduced; 16 - Exopod of first maxilliped strongly inflated distally; 17 - First pereiopod more robust than second pereiopod, rather than subequal in strength; 18 - Podobranch lost from second maxilliped; 19 - Loss of one of the two arthrobranchs from third maxilliped; 20 - Exopod of second maxilliped strongly reduced; 21 - Arthrobranchs lost from third maxilliped to fourth pereiopod; 22 - Pleurobranch of fifth pereiopod rudimentary; 23 - Ischium and merus of first and second pereiopods fused; 24 - Exposed body parts covered by numerous spine-like teeth; 25 - Chela of first pereiopod with both fingers movable, forming a scissors-like structure; 26 - Dactyl of second pereiopod reduced to a nodular rudiment; 27 - Incisive process of mandible modified into a sharp and slightly recurved knife-like plate; 28 - Eye-stalk immovable; 29 - First abdominal somite with shallow lateral lobe forming secure sliding junction with submarginal ridge of carapace; 30 - Endopods and exopods of second to fifth pleopods elongate; 31 - Pleurobranch lost from fifth pereiopod; 32 - Development of a dorsal lobe on epipod of second maxilliped, which thus becomes bilobed; 33 - Propodus and dactyl of third to fifth pereiopods modified into functional chelae; 34 - Chela of first pereiopod with dactyl disc-like, the pectinate teeth being reduced to fine striae; 35 - Molar process of mandible foliaceous, rather than "molar-like"; 36 - Dorsal flagellum of first antenna with narrow distal portion shortened (with less than about 20 articles); 37 - Dactyl of second maxilliped inserted obliquely, rather than perpendicularly, to axis of propodus; 38 - Ultimate segment of third maxilliped obliquely truncate at apex, rather than being rectangular in shape; 39 - Rostrum flattened dorsoventrally, rather than laterally; 40 - Stylocerite strongly reduced; 41 - Loss of accessory teeth from incisive process of mandible; 42 - Dactyl and propodus of fifth pereiopod strongly twisted, being flexed in nearly opposite direction from those of third and fourth pereiopods; 43 - Ultimate segment of third maxilliped with distal portion lanceolate, rather than rectangular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ATYINAE
PASIPHAEIDAE
Alvinocaris - ALVINOCARIDIDAE
Bresilia - BRESILIIDAE
Psalidopus - PSALIDOPODIDAE
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Brown (1978) and **Tridiscias** Kensley (1983), and in this manner maintain the traditional concept Psalidopodidae.

A minor change has been the resurrection of the Xiphocaridinae Ortmann (1895) originally intended for **Xiphocaris** Von Martens, 1872, **Troglocaris** Dormitzier, 1853 and **Atyaephyra** De Brito Capello, 1867, but here restricted to contain only the taxon **Xiphocaris**. I have found this action desirable, because all diagnoses provided for the Atyidae contain characters which actually only apply to the Atyinae.

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