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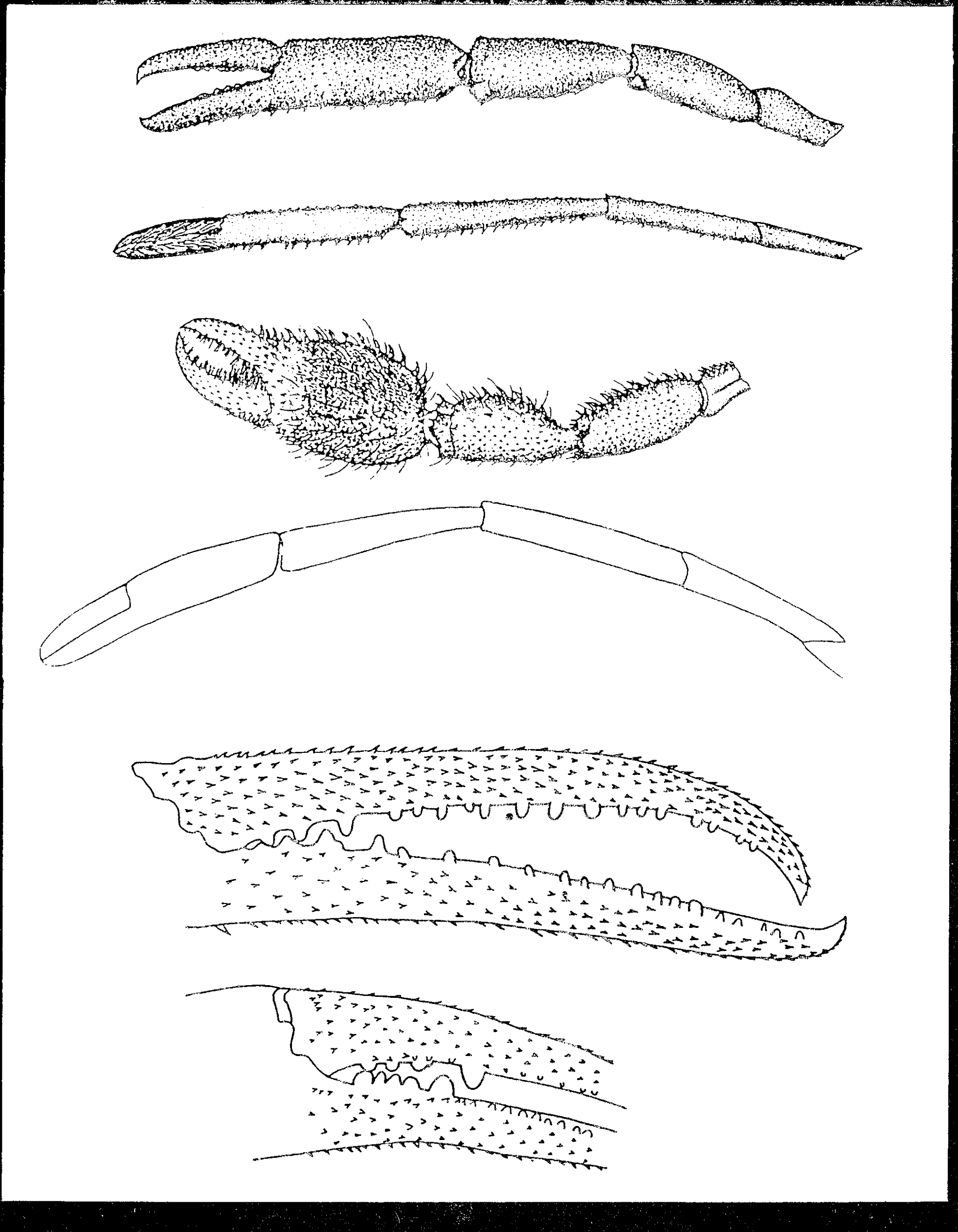

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Pearsall, N. H. 1950. Mountains and moorlands. London, Collins Publ., 375 pp.

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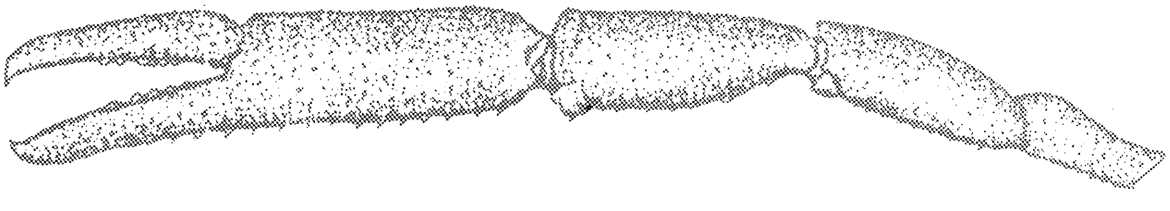

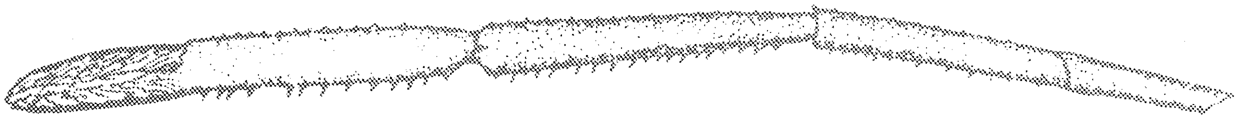

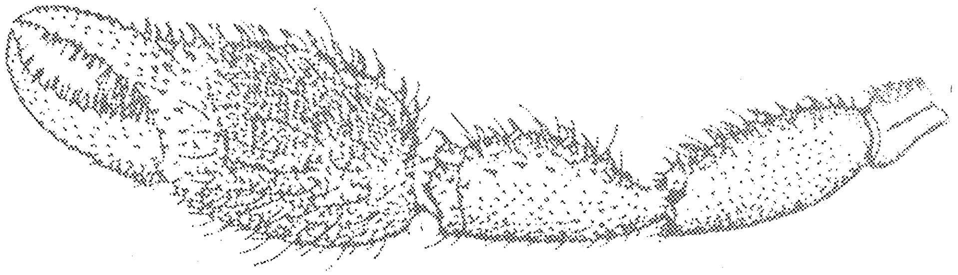

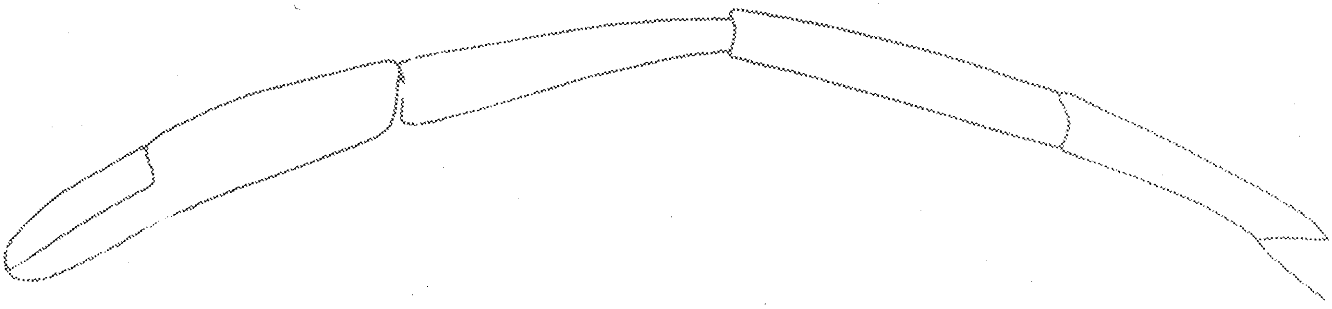

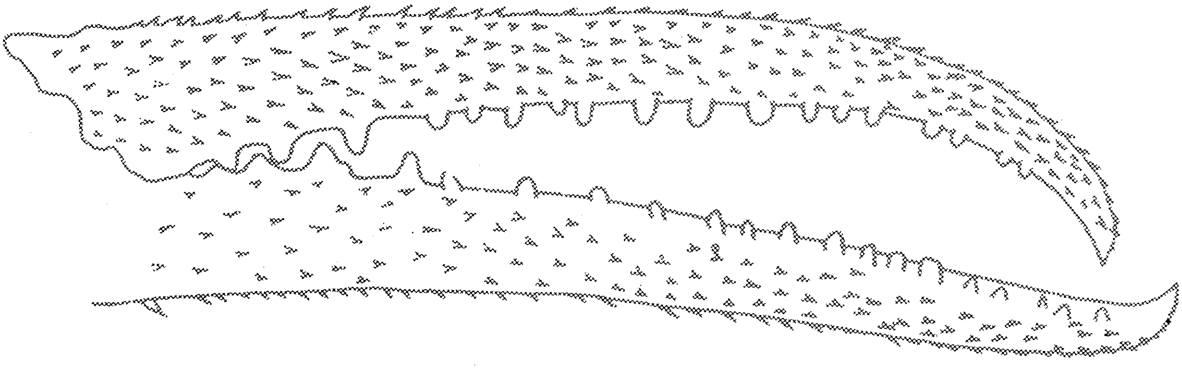

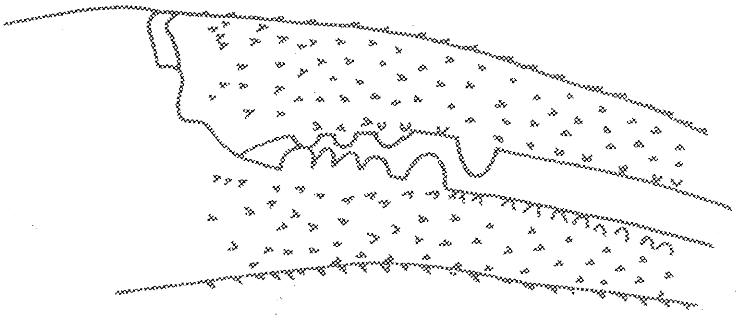

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Con aprecio
Guido Pereira

A CLADISTIC ANALYSIS OF THE FRESHWATER SHRIMPS OF THE FAMILY PALAEMONIDAE (CRUSTACEA, DECAPODA, CARIDEA)

ANALISIS CLADISTICO DE LOS CAMARONES DE AGUA DULCE DE LA FAMILIA PALAEMONIDAE (CRUSTACEA,DECAPODA,CARIDEA)

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ABSTRACT

The palaemonid shrimps represent one of the few groups of decapod crustaceans which have successfully radiated in freshwater, estuarine, and marine environments throughout the tropics and subtropics. The biology and ecology of the group is diverse and complex, probably as a consequence of its adaptation to various environments during the course of its evolutionary history. Before an understanding of the causal processes that gave rise to this important group can be gained, it is essential to erect a phylogenetic hypothesis. This is the main objective of the present work. A cladistic analysis of morphological characters was performed in which 81 characters exhibited by 172 species were used to provide a total of 397 character states. Due to the fact that taxa within the Palaemonidae have previously been defined without considering character polarity or evolutionary change, the monophyletic status of the group can not be assumed. Thus, several taxa distant from the Palaemonidae were simultaneously included in the data in order to perform an unrestricted overall parsimony analysis (in which restrictions of monophyly are loosened; Maddison *et al.*, 1984, modified by Clark and Curran, 1986; Mitter and Silverfine, 1988). The tree was rooted to the species *Procaris ascensionis* (Procaridoidea), which is considered to be primitive to the whole infraorder Caridea (Felgenhauer and Abele, 1983). The most parsimonious tree has 606 steps and a CI of 0.525. Results suggest that the superfamily Palaemonoidea and the family Palaemonidae (*sensu* Chace, 1992) represent monophyletic groups. The Palaemonidae however is comprised by several major lineages whose arrangement below family rank is paraphyletic at several levels in the clasification.

RESUMEN

Los camarones de la familia Palaemonidae, representan uno de los pocos grupos de crustáceos decápodos que han radiado exitosamente en el agua dulce, los estuarios y ambientes marinos tropicales y subtropicales. La biología reproductiva y ecología del grupo es muy diversa y compleja, probablemente como una consecuencia de su adaptación a los diferentes ambientes durante el desarrollo de su historia evolutiva. Antes de que podamos comprender los procesos causales que dierom origen a este grupo tan importante, es fundamental el contar con una hipótesis filogenética. Este es el principal objetivo de este trabajo. Se desarrolló un análisis cladístico empleando 81 carácteres morfológicos sobre 172 especies para un total de 397 estados de caracteres. Debido a que la clasificación actual de este grupo no está basada en su filogenia, no es posible suponer de entrada la monofilia del grupo. Así, varios taxa, distantes taxonomicamente de los palaemónidos fueron incluidos en el análisis para poder desarrollar un análisis de parsimonia total sin restricción de grupo de referencia (Maddison *et al.*, 1984, modificado por Clark y Curran, 1986; Mitter y Silverfine, 1988). El arbol filogenético final es enraizado a la especie *Procaris ascensionis* (Procaridoidea), la cual es considerada primitiva para todo el Orden Caridea (Felgenhauer and Abele, 1983); este arbol final tiene 606 pasos, y un índice de consistencia de 0.525. Los resultados sugieren que la Superfamilia Palaemonoidea y la Familia Palaemonidae (*sensu* Chace, 1992) son grupos monofiléticos. Sin embargo, la familia Palaemonidae está compuesta de varios linajes cuyo arreglo por debajo del nivel de familia y otros niveles inferiores son parafiléticos según la clasificación actual.

Palabras clave: Crustacea, Palemonidae, Sistemática, Cladística, *Macrobrachium, Palaemon, Palaemonetes,* camarones de agua dulce.

Keywords: Crustacea, Palemonidae, Systematics, Cladistics, *Macrobrachium, Palaemon, Palaemonetes,* freshwater shrimps.

INTRODUCTION

Natural classifications that accurately reflect an evolutionary pattern are desirable for evolutionary research and comparative biology (Eldredge and Cracraft, 1980; Ridley, 1983; Felsenstein, 1985a). Phylogenetic systematics (Hennig, 1966) purports that phylogenetic relationships should consider only synapomorphic characters when building phylogenetic trees in order to exclude the possibility of paraphyletic groupings. It is argued that a phylogeny generated this way provides a better estimate of the evolutionary history of a group than does one based upon traditional evolutionary systematic methods. After Hennig's publication (1966), steady development of this methodology gave rise to cladistic analysis (Farris *et al*, 1970), which relies upon the parsimony criterion (Camin and Sokal, 1965; Farris, 1970) as the most objective way to determine a cladistic pattern of characters. This pattern consists of a hierarchically arranged set of synapomorphies that summarizes most efficiently the information content of a natural classification and can be considered to be the tentative phylogenetic hypothesis for the group under study. Cladistic methods have formalized phylogenetic reconstruction (Kluge and Farris, 1969; Farris, 1970; 1980), have promoted theoretical research towards validation and reliability of the most parsimonious phylogeny, or have placed it in a statistical framework (Farris, 1969; Felsenstein, 1983; Penny and Hendy, 1986). Today, cladistic analysis is widely used among systematists as the basis for biological classification.

The family Palaemonidae (Crustacea: Decapoda) includes a large group of shrimp-like decapod crustaceans with marine, estuarine, and freshwater species. The Palaemonidae has a long taxonomic history, with early records dating from 1648. Linnaeus (1758) included the species now known as *Macrobrachium carcinus* in the genus *Cancer*. *Cancer* was later divided by many authors into a large number of different genera (cited in Holthuis, 1951a). Later revisions improved the classification of the Crustacea (Pennant, 1777; Lamarck, 1801; Leach, 1815; Milne-Edwards, 1840). Based on the type of appendages, branchial formulae, and general divisions and morphology of the body, Calman (1904, 1909) defined the Order Decapoda. His classification is essentially the one used today at the ordinal level. Holthuis (1950b, 1952a,b) established a classification of the family Palaemonidae that is widely used in literature (Table 1).

Table 1. Classification of the Family Palaemoninae, proposed by Holthuis (1950b, 1952a,b)

- Phylum Arthropoda
  - Subphylum Crustacea
    - Class Malacostraca
      - Order Decapoda
        - Infraorder Caridea
          - Superfamily Palaemonoidea
            - Family Palaemonidae
              - Subfamily Palaemoninae
              - Subfamily Pontoniinae
              - Subfamily Euryrhynchinae
              - Subfamily Typhlocaridinae

One objection to Holthuis' classification is that the genera within the family are defined by morphological structures with little regard for their evolutionary polarity. Although useful for practical purposes, this scheme has not proved valuable in establishing phylogenetic relationships within the subfamily and has been criticized because the combinations of characters used to define higher taxa may vary and do not reflect relationships (Chace, 1972; Hobbs, 1973); also the clasification of Chace (1992) agrees that his treatment does not necessarily indicate relationships. Since most widely used classifications are Holthuis (1950;52) for the palaemonid family level and Chace and Manning (1972) for Carideans (Table 2), I will use their scheme in order to keep consistency throughout the paper.

Although different subfamilies are now recognized (Palaemoninae, Pontoniinae, Euryrhynchinae, Typhlocaridinae, and Desmocaridinae). Desmocaridinae is not generally accepted and some authors consider the Pontoniinae to be included within the Gnathophyllidae (Bruce, 1986).

The subfamily Palaemoninae is composed of approximately 279 species that inhabit freshwater, estuarine, and marine environments divided into 17 genera and subgenera, from which *Desmocaris* So-

Table 2. Classification of the Suborder Caridea by Chace and Manning (1972). Palaemonids in boldface.

- SUPERFAMILY PASIPHAEOIDEA
  - FAMILY PASIPHAEIDAE
- SUPERFAMILY STYLODACTYLOIDEA
  - FAMILY STYLODACTYLIDAE
- SUPERFAMILY PSALIDOPOIDEA
  - FAMILY PSALIDOPODIDAE
- SUPERFAMILY BRESILOIDEA
  - FAMILY BRESILIDAE
  - FAMILY DISCIADIDAE
  - FAMILY EUGONATONOTIDAE
  - FAMILY RHYNCHOCINETIDAE
- SUPERFAMILY OPLOPHOROIDEA
  - FAMILY OPLOPHORIDAE
  - FAMILY NEMATOCARCINIDAE
  - FAMILY ATYIDAE
- SUPERFAMILY PANDALOIDEA
  - FAMILY PANDALIDAE
  - FAMILY THALASSOCARIDIDAE
  - FAMILY PHYSETOCARIDIDAE
- SUPERFAMILY **PALAEMONOIDEA**
  - FAMILY **PALAEMONIDAE**
  - FAMILY **CAMPYLONOTIDAE**
  - FAMILY **GNATHOPHYLLIDAE**
- SUPERFAMILY ALPHEOIDEA
  - FAMILY ALPHEIDAE
  - FAMILY HYPPOLYTIDAE
  - FAMILY OGYRIDAE
- SUPERFAMILY PROCARIDOIDEA
  - FAMILY PROCARIDIDAE
- SUPERFAMILY CRANGONOIDEA
  - FAMILY CRANGONIDAE
  - FAMILY GLYPHOCRANGONIDAE

llaud has recently been excluded (Powell, 1976).

The subfamily Pontoniinae, with approximately 345 species, has 57 genera. All of the species are marine. There is a tendency for species in the group to live as commensals with other organisms such as corals, clams, sponges, and sea anemones.

The subfamily Euryrhynchinae represents a homogeneous group of 6 species in 3 genera. All are strictly confined to freshwater and have abbreviated larval development (Tiefenbacher, 1978; Powell, 1979; Pereira, 1985; Magalhaes, 1988). *Euryrhynchus* Miers, 1877 is the most diverse genus, with 4 species that are all endemic to the Amazon-Orinoco river basins. The monotypic genera *Euryrhynchina* Powell, 1976 and *Euryrhyncoides* Powell, 1976 are restricted to Western Africa. Because of its distribution in freshwater in both South America and Africa (Fig. 1), it has been suggested that this subfamily originated before these continents separated (Powell, 1976).

The subfamily Typhlocaridinae includes 3 species in a single genus. All of the species are troglobitic, inhabiting freshwater caves in the Mediterranean and West Africa.

The family, Desmocarididae contains 2 very similar but allopatric species (one recently described by Powell, 1976) that inhabit freshwater environments in Western Africa. The taxonomic position of this peculiar genus has been debated by

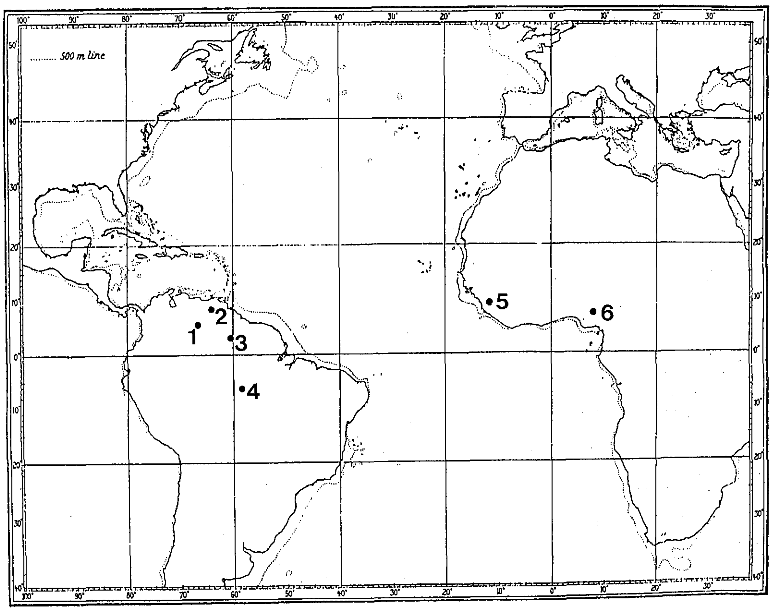

Figure 1. Map showing the distribution of the species in the subfamily Euryrhynchinae: 1. *Euryrhynchus amazoniensis*; 2. *E. pemoni*; 3. *E. burchelli*; 4. *E. wrzesniowskii*; 5. *Euryrhynchoides holthuisi*; 6. *Euryrhynchina edingtonae*.

carcinologists. Aurivillius (1898) described it for the first time as a member of the subfamily Palaemoninae in the genus *Palaemonetes*. Later Sollaud (1927) placed it in its own family, the Desmocaridae, and argued that this species possessed characters that should be regarded as ancestral to the Palaemoninae and Pontoniinae. Holthuis (1950b) synonymized it with the subfamily Palaemoninae in the monotypic genus, *Desmocaris*. Powell (1977) described a second species in the genus; based on adult and larval characters, he reestablished the genus in its own subfamily, the Desmocaridinae, arguing that the species possessed several unique characteristics not present in any other group of the family but Chace (1992) considered a family rank. Since the taxon Desmocaridinae is based only on autapomorphies that provide no evidence for relationship, *Desmocaris* is considered as a genus within the Palaemoninae in the present work.

As a major group of freshwater shrimps with a worldwide distribution, the Palaemonidae have been the subject of research in aquaculture, genetics, physiology, and ecology. Some authors have suggested that the group is actively migrating from the sea to the freshwater environment, while others have adopted the opposite view. The establishment of a hypothesis concerning the phylogenetic relatedness of the members of the Palaemonoidea, may provide a frame of reference for research on their comparative biology and to evaluate trends of evolution in the group. Additionally, the availability of extensive data on the alpha-taxonomy of the group makes a cladistic analysis based on morphological data feasible.

The monophiletic status of the Palaemonidae and outgroup comparisons

The family Palaemonidae belongs to a large group of shrimps placed in the Suborder Caridea of the Order Decapoda. Despite controversies over subordinal groupings within the Order Decapoda, shrimps of the Suborder Caridea have been considered to be monophyletic in all revisions (Dana, 1852; Boas, 1880; Bate, 1888; Ortmann, 1891; Borradaile, 1907; Felgenhauer and Abele, 1983). The synapomorphies linking members of the Suborder Caridea are: phyllobranchiate gills, second abdominal segmental pleuron that overlaps those of the first and third segments, and possession (with a few exceptions) of an appendix interna and masculina. These synapomorphic characters are remarkably consistent within the group.

Within the Suborder Caridea, the systematic position of the groups are more controversial and revisions show some disagreement. Traditionally, superfamilies have been used to define major groups within the Caridea, but these are believed to be rather arbitrary, and some authors suggest that classification at the superfamily level should not be used until the families have been better defined (Kemp, 1910; Chace and Manning, 1972).

An early clasification of the Suborder Caridea (Borradaile, 1907) include 6 Superfamilies (Table 3); later, Holthuis (1955) and Chace and Manning (1972) reviewed the clasification and increased the number of Superfamilies to 10, this classification is widely used today even though Chace (1992) suggested a new classification in which the number of Superfamilies is increased to 16 (Table 4). Although the classification have become more informative regarding the diversity of morphological patterns within the Suborder, they lack phylogenetic information and probably include paraphyletic groups (Forest, 1977; Carvacho, 1978; Christoffersen, 1988, present work). This is evident in the Superfamily Palaemonoidea in which the taxa assigned vary according to the emphasis placed on different characters that the taxonomists used (Borradaile, 1917; Balss, 1927; Holthuis, 1955).

Regarding the phylogenetic status of the family Palaemonidae, it may be contained in a larger unnamed monophyletic taxon within the Caridea. This group is defined by the following synapomorphic characters: second maxilliped with broad distal joint applied to the end of the sixth joint which also is broader distally; first and second pair of legs possessing well developed claws with carpus entire (not segmented), and an unjointed rostrum continuous with carapace. This definition encompasses the families Oplophoridae (Dana, 1852) (54 sps.), Atyidae (De Haan, 1849) (137 sps.), Nematocarcinidae (Smith, 1884) (17 sps.), Campylonotidae (Sollaud, 1913) (6 sps.), and Palaemonidae (Rafinesque, 1815) (664 sps.) (*sensu* Chace and Manning, 1972). Since these characters are synapomorphies, they define a large monophyletic group in which the su-

Table 3. Classification of the Suborder Caridea proposed by Borradaile (1907). Palaemonids in boldface.

- SUPERFAMILY PASIPHAEOIDEA
  - FAMILY PASIPHAEIDAE
  - FAMILY BRESILIIDAE
- SUPERFAMILY STYLODACTYLOIDEA
  - FAMILY STYLODACTYLIDAE
- SUPERFAMILY OPLOPHOROIDEA
  - FAMILY OPLOHORIDAE
  - FAMILY NEMATOCARCINIDAE
  - FAMILY ATYIDAE
- SUPERFAMILY PANDALOIDEA
  - FAMILY PANDALIDAE
- SUPERFAMILY **PALAEMONOIDEA**
  - FAMILY **PALAEMONIDAE**
  - FAMILY **HIPPOLYTIDAE**
  - FAMILY **RHYNCHOCINETIDAE**
  - FAMILY **ALPHEIDAE**
- SUPERFAMILY CRANGONOIDEA
  - FAMILY CRANGONIDAE
  - FAMILY AUTONOMAEIDAE
  - FAMILY GNATHOPHYLLIDAE
  - FAMILY PROCESSIDAE
  - FAMILY GLYPHOCRANGONIDAE

Table 4. Classification of the Suborder Caridea proposed by Chace (1992). Palaemonids in boldface.

- SUPERFAMILY PROCARIDOIDEA
  - FAMILY PROCARIDIDAE
- SUPERFAMILY PASIPHAEOIDEA
  - FAMILY PASIPHAEIDAE
- SUPERFAMILY OPLOPHOROIDEA
  - FAMILY OPLOPHORIDAE
- SUPERFAMILY PSALIDOPOIDEA
  - FAMILY PSALIDOPODIDAE
- SUPERFAMILY ATYOIDEA
  - FAMILY ATYIDAE
- SUPERFAMILY BRESILIOIDEA
  - FAMILY BRESILIDAE
- SUPERFAMILY NEMATOCARCINIDEA
  - FAMILY EUGONATONOTIDAE
  - FAMILY NEMATOCARCINIDAE
  - FAMILY RHYNCHOCINETIDAE
  - FAMILY XIPHOCARIDIDAE
- SUPERFAMILY PSALIDOPOIDEA
  - FAMILY PSALIDOPODIDAE
- SUPERFAMILY STYLODACTYLOIDEA
  - FAMILY STYLODACTYLIDAE
- SUPERFAMILY CAMPYLONOTIDEA
  - FAMILY BATHYPALAEMONOLLIDAE
  - FAMILY CAMPYLONOTIDAE
- SUPERFAMILY **PALAEMONOIDEA**
  - FAMILY **ANCHISTIODIDAE**
  - FAMILY **DESMOCARIDIDAE**
  - FAMILY **GNATHOPHYLLIDAE**
  - FAMILY **HYMENOCERIDAE**
  - FAMILY **PALAEMONIDAE**
    - SUBFAMILY **PALAEMONINAE**
    - SUBFAMILY **PONTONINAE**
  - FAMILY **TYPHLOCARIDIDAE**
    - SUBFAMILY **EURYRHYNCHINAE**
    - SUBFAMILY **TYPHLOCARIDINAE**
- SUPERFAMILY PHYSETOCARIDIDEA
  - FAMILY PHYSETOCARIDIDAE
- SUPERFAMILY PROCESSOIDEA
  - FAMILY PROCESSIDAE
- SUPERFAMILY ALPHEOIDEA
  - FAMILY ALPHEIDAE
  - FAMILY HIPPOLITYDAE
  - FAMILY OGYRIDAE
- SUPERFAMILY **PANDALOIDA**
  - FAMILY PANDALIDAE
  - FAMILY THALASSOCARIDIDAE
- SUPERFAMILY CRANGONOIDEA
  - FAMILY CRANGONIDAE
  - FAMILY GLYPHOCRANGONIDAE

perfamily Palaemonoidea is included. The structure of the second maxilliped is unique to this group; the primitive condition of this character is seen in the Procaridoidea in which the second maxilliped is nearly cylindrical distally, with the distal joint as wide as the previous one. This condition is similar to that of species in the suborder Penaeidea, a group with a Jurassic fossil history (Glaessner, 1969) that is considered to be the sister group of the Caridea (Felgenhauer and Abele, 1983). The possession of well developed claws on the first and second legs is another derived feature that characterizes this large group. Claws are absent in Procaridoidea. However, claw morphology is diverse among the superfamilies of the Caridea. Conditions range from no claws in the primitive Procaridoidea, 2 well developed claws on the first and second pairs of legs, subchelated claws (as in the Crangonoidea), to minuscule scissor-like claws in the Psalidopodidea. The characteristics of this trait provide important synapomorphies that define major groups within the Caridea as well as for the group that contains the Palaemonidae. An entire or segmented carpus of the second leg has been used to cladistically define another large monophyletic group within the Caridea (Christoffersen, 1988). This feature excludes the Palaemonoidea and related superfamilies. All of these considerations support the assertion that the families Oplophoridae, Atyidae, Nematocarcinidae, Campylonotydae, and

Palaemonidae form a natural group within the Caridea.

The monophyly of the 2 major groups within the Palaemonidae, the Palaemoninae and the Pontoniinae, has been subject to debate. Borradaile (1898) argued that the decrease in number of gills in the Pontoniinae (a unique characteristic of the group) depends on the activity of the organism and thus the environment. He suggested that in general, deep water shrimps have greater numbers of gills because they live in low oxygen conditions. More sedentary shrimps such as the symbiotic pontoniins tend to have reduced gill numbers. Borradaile (1898) argued that loss of gills could have occurred several times in the evolution of the Palaemoninae giving rise to pontoniins. On the other hand, the opposite situation, in which ancestral pontoniins gained gills as a consequence of increased activity could have given rise to palaemonins. Consequently, Borradaile (**o.c.**) suggested that both groups were paraphyletic. However, he did not consider telson morphology, which is consistently different between the 2 subfamilies and can be considered synapomorphic for the Pontoniinae (see below). Additionally, although gill number may vary in relation to the environment, this is not always the case. For instance, the number of gills varies independently in several littoral and freshwater shrimps; suggesting historical rather than ecological factors. Sollaud (1910) argued for a monophyletic origin of the palaemonids. Although he suggested that the distinction between pontoniins (*sensu* Holthuis, 1952b) and palaemonins was not clear and that some taxa like *Urocaris*, *Palaemonella*, and *Periclimenes* may represent a transition between the 2 subfamilies, consideration of characters such as telson morphology and gill arrangement led him to the conclusion that both groups represent different evolutionary lines that shared a common ancestor, suggesting monophyletic status for each subfamily. Holthuis (1950b, 1951a, 1952a) accepted the monophyletic status of the group. His classification was a great improvement at the species level due to the large number of species reviewed and the exhaustive synonyms compiled, but information on higher level relationships was very limited or absent.

It has been assumed by all subsequent workers that both subfamilies form monophyletic groups. Characteristics such as the presence of 2 pairs of spines at the posterior end of the telson with feathered setae between them and the presence of a pleurobranchia on the third maxilliped define the subfamily Palaemoninae. The possession of 3 pairs of spines at the posterior end of the telson, the absence of pleurobranchia, and a reduced or absent arthrobranchia from the third maxilliped define the subfamily Pontoniinae. From a phylogenetic point of view, the Pontoniinae certainly are defined by autapomorphies. The trend towards reduction of the gills is a unique derived characteristic; the ancestral condition is typified by the possesion of a full set of gills (present in primitive Caridea). The possesion of 3 pairs of distal spines on the posterior border of the telson is a further unique derived feature. More primitive carideans like procaridids have a larger numbers of spines. Regarding the Palaemoninae, the presence of pleurobranchia on the third maxillipeds may be considered a synapomorphic feature, since allegedly primitive members of the family do not have it. However, outside the Palaemonidae, some related families possess a complete set of gills that includes a pleurobranchia on the third maxilliped. Thus, this character could be symplesiomorphic rather than synapomorphic. On the other hand,, characters like 2 pairs of distal spines on the telson and the presence of plumose setae between the inner spines are unique and can be considered to be a derived condition of the entire family rather than of only the subfamily Palaemoninae. Thus, although the Palaemoninae *sensu stricto* seems to be a paraphyletic group, the taxa included belong naturally to the family Palaemonidae. Although earlier workers like Ortmann (1891) and Sollaud (1923) recognized that there were several lineages within the Palaemoninae, they were unable to establish relationships among them. A phylogenetic analysis in which this group is included together with the rest of the Palaemonidae and taxa from other related families will permit a rigorous test of the monophyly of the family and will provide the basis for an accurate assessment of the relationships of the major groups.

In order to perform the phylogenetic analysis using unrestricted parsimony analysis, representative species of the families Atyidae, Oplophoridae, Campylonotidae and Procarididae were used to simultaneously generate a cladogram. These families are not as diverse as the Palaemonidae and in general represent very homogenous morphological groups. Thus, the species examined represent a good sample of the morphological heterogeneity of these groups supposedly outside the Palaemonidae. The species *Procaris ascensionis* Chace and Manning, from the family Procarididae (Superfamily Procaridoidea) was chosen to root the tree. The Procaridoidea differ from the other superfamilies in that the first and second pairs of legs are not chelate, and in general possess morphological characters that are considered primitive to the whole suborder (Chace and Manning, 1972; Felgenhauer and Abele, 1983). Thus the tree is rooted to a taxon which apparently is totally outside the major monophyletic group in which the family Palaemonidae is included.

The present analysis is done using overall unrestricted parsimony, providing simultaneous resolution for ingroup-outgroup data sets (Maddison *et a*l., 1984, modified by Clark and Curran, 1986; Mitter and Silverfine, 1988; Mitter pers. comm.). Therefore, in case some taxa within the Palaemonidae are paraphyletic, relationships among the possible monophyletic subgroups may still be considered.

MATERIAL AND METHODS

Most of the species examined belong to the National Museum of Natural History, U.S.A. (USNM). Additional material was borrowed from the following institutions: British Museum Natural History, London (BMNH); Rijksmuseum van Natuurlijke Historie, Leiden, Holland (RMNH); Western Australian Museum, Australia (WAM); Instituto Nacional de Pesquizas Amazonicas, Brazil (INPA); Museu de Zoologia, Universidad de Sao Paulo, Brazil (MZUSP); Museo de Historia Natural, Lima, Peru (MHNLP); Museo de Historia Natural de Paraguay, Paraguay (MHNPA); Museo de Biología de la Universidad Central de Venezuela, Venezuela (MBUCV). A list of all the species of Palaemoninae can be seen on table 5, and a summary of the species examined is shown in table 6. No special criterion was used to select species for scoring except availability. Most species in each genus and subgenus of the subfamilies Palaemoninae, Euryrhynchinae and Typhlocaridinae were examined; for species in the genus *Macrobrachium*, only 40% of the species were examined. Taxa in the subfamily Pontoniinae tend to exhibit very derived and unique morphology due to their specialized habits (most are symbionts); thus, taxa examined were chosen from those genera which share the most characters with the typical palaemonids. Taxa from the families Oplophoridae, Campylonotidae, Atyidae, and Procarididae were chosen based on their availability. These families show less morphological diversity than the palaemonids. Thus, although only 1 or 2 representatives of these families were scored, they represent a good general view of the characters used to compare higher taxa in Caridea.

The scoring of characters started using a few species of each genus within the subfamily Palaemoninae, then more species were added. A total of 172 different species within the suborder Caridea were scored over a period of 3 years (Pereira, 1989). The reviews of Holthuis (1950b, 1952a, 1955) are used as the main taxonomic manuals and guide for terminology.

In general, the examination procedure was standardized by selecting large adult males from the best preserved samples. Unless fewer were available, a minimum of 10 individuals per species was examined under a dissecting microscope. Only discrete morphological characters were used in the analysis. Their definition was based on comparisons between taxa of the supposed homologous structures, and only those characters in which these comparisons yielded reliable (definable) discrete differences were used.

The scored characters were drawn using a camera lucida for most of the species examined, especially in those taxa where little information was available from the literature. Scanning Electron Microscope photographs (SEM) were made from well preserved individuals. The parts to be used were dissected, followed by preliminary cleaning with a pipette, thin brush and sonication for 30 seconds. Dirty samples were transferred from 70% alcohol to increasingly diluted solutions series to distilled water, and then immersed in a solution of 0.1% soap (Cargon) and sonicated for 30 seconds. Samples were transferred through a series of increasing alcohol concentrations to 100%. All samples were lyophilized using a critical point dryer. Samples were coated with platinum-palladium (20 nm thick),

Table 5.- Summary of the genera and species examined.

GENUS	SPECIES	SPS. EXAMINED	USED IN ANALYSIS
PALAEMONIDAE			
PALAEMONINAE			
MACROBRACHIUM	170	66	44
PALAEMON	34	24	21
PALAEMONETES	32	28	28
EXOPALAEMON	7	4	1
PSEUDOPALAEMON	5	5	5
TROGLOCUBANUS	6	6	6
NEMATOPALAEMON	4	3	1
LEANDER	4	3	1
LEANDRITES	3	2	1
LEPTOCARPUS	2	2	1
CRYPHIOPS	2	2	2
BITHYNOPS	2	1	1
DESMOCARIS	2	1	1
BRACHYCARPUS	2	1	1
NEOPALAEMON	1	1	1
TROGLINDICUS	1	1	1
CREASERIA	1	1	1
TOTAL	279	152	117
PONTONIINAE			
PERICLIMENES	132	4	2
PALAEMONELLA	11	1	1
GNATHOPHYLLUM	8	1	1
ANCHISTIOIDES	3	1	1
EURYRHYNCHINAE			
EURYRHYNCHUS	4	4	1
EURYRHYNCHINA	1	1	1
EURYRHYNCHOIDES	1	1	1
TYPHLOCARIDINAE			
TYPHLOCARIS	3	2	1
CAMPYLONOTIDAE			
CAMPYLONOTUS	5	1	1
ATYIDAE			
POTIMIRIN	5	1	1
OPLOPHORIDAE			
ACANTHEPHYRA	14	1	1
PROCARIDIDAE			
PROCARIS	3	1	1
VETERICARIS	1	1	1
TOTAL	192	17	14

stored, and observed within the next week by SEM. All SEM work was conducted at the Electron Microscope Laboratory of the Smithsonian Institution. A total of 81 characters were used in the final analysis (characters 68 and 83, Larval development and Habitat respectively were exclude in present aṇnalysis since they will be treated on a separate paper). The first state scored for each character was named state A; different states of this character were coded as states B C D E F G H J K L M N O P Q 9 8 7 6 5 4 3 2 1 0. Procedures for phylogenetic reconstruction assume that the characters are independent and not correlated. For this reason characters such as body length and in general morphometric characters with continuous distri-butions were avoided; otherwise, character coding included any character normally used in the taxo-nomy of the group (Holthuis, 1950b, 1952a) and any morphological feature that could be consistently defined. Some degree of subjectivity is involved, since there are few practical rules when comparing supposedly homologous characters. When doing morphological analysis, more experienced taxono-mists may find more characters to compare than inexperienced observers. In general, cladistics enhances the objectivity of this process.

The procedure of finding and coding characters was to: 1) score taxa until at least 2 states were identified; 2) draw and compare these states and assign a code to each; 3) continue scoring taxa and compare with the states already assigned; 4) include the data in an incipient data matrix (taxa x charac-ters) and do a preliminary test using the unordered option; 5) continue adding data; 6) if new character states appear, make general comparisons, assign new codes and test the data matrix again; and 7) continue until all taxa are added and perform final analysis.

The entire set of states for any character ranged from 2-22 and the total number of states in data matrix was of 397. Character states that were impossible to score because of too little material were scored as "?", meaning that the most parsimonious state was assigned by the computer program. With these data, a matrix of taxa by alpha-numeric characters was constructed for the phylogenetic computer program (Table 7). No transformation series was assigned to any character. Thus, all states were considered unordered. The phylogenetic computer packages used were PAUP version 3.1.1 and MacClade version 3.01 for Apple microcomputers, they were run on a Macintosh Quadra 800, 8 Mb RAM memory.

The total number of taxa scored was 172. However, only 129 were used in the final analysis because closely related species tend to have the same character states (repetitive taxa) so their inclusion in the data matrix therefore adds no new information. Also, when we did not have large adult males to properly record the states.

Due to the large number of taxa it is imposible to perform and exhaustive search for the shortest tree. So, the data was run using heuristic search (HSEARCH) with different search strategies: (1) adding sequence closest, holding 20 trees at each step, then branch swapping using tree bissection and reconection and retaining multiple most parsimonious trees. The maximum number of trees retained was equal to 100; once branch swapping was finish, we use the trees in memory to branch swapp again but this time increasing the number of trees automatically by 100 until the computer ran out of memory when reaching 400 trees, then let the computer finish branch swapping on all 400 trees. Another procedure (2) was repeating the HSEARCH with CLOSEST addition sequence but varying the number of trees to be retain (HOLD=) at each step from 4, 20, 50, 100, then continue as previous procedure. Procedure 3, consists of using the strict consensus as a topological constraint while repeating procedures 1 and 2 . Finally as procedure 4, we ran 25 times HSEARCH as in procedure 1 but using ramdom addition sequence of taxa. At the end of each procedure the strict and majority rule consensus, and several trees were printed and descriptions examined. The time each procedure took varies from 3 to 15 hours. The program MacClade was use to interact with PAUP files in order to manipulate shorthest tree by hand, to do local branch swapping and also to print trees. Bootstrapping procedure (Felsenstein, 1985b) was not performed because of the computing time it takes. The minimum search time in order to get the shortest tree leaving a minimum of 100 tree in memory was of 3 h and ussually the machine colapse during the procedure. However, although this procedure was originally intended as a method to place confidence limits on an estimated phylogeny, it presents several limitations. A phylogenetic tree consists of a complex multivariate identity with an associated topology. The degree of independence of the characters that define the tree is not obvious, and the technique assumes independence of the characters (Felsenstein, 1985b). Finally, since generation of these trees requires a lot of computer time, there is a practical limitation to the number of bootstraps that are feasible. Felsenstein (**o.c.**) arbitrarily recommended 50 trees. These problems limit the ability of this procedure to reliably place confidence limits on a phylogeny. Altough recent papers suggest that the bootstrap technique migth be a promissory statistical technique specially for nucleotide base phylogenies (Zarhiki, 1995), so far it can not be used for trees based on morphlogical data as more theoretical support is needed.

RESULTS

Characters And Codification

Description of each state and the consistency index of each character follows. Minimum steps, Tree steps and statistics for each character are on table 8.

1) Carapace Surface: smooth (A); spiny (B) (Fig. 2J). (CI= 1.00)

The carapace is smooth in most species, and all juvenile Palaemoninae have a smooth carapace. The outgroups have a smooth carapace too, so this is assumed to be the primitive state. Spiny refers to some species in which the anterolateral borders of the carapace are covered with minute spines.

2) Antennal Spine: present (A) (Fig. 2B); absent (B); present possessing a prominent carina (C). (CI= 0.50).

This character is present in all the Palaemonidae except in one species of *Troglocubanus* (Villalobos, 1971) and in the subfamily Typhlocaridinae (Calman, 1909; Caroli, 1924). The absence of this spine in the former is explained as a secondary loss.

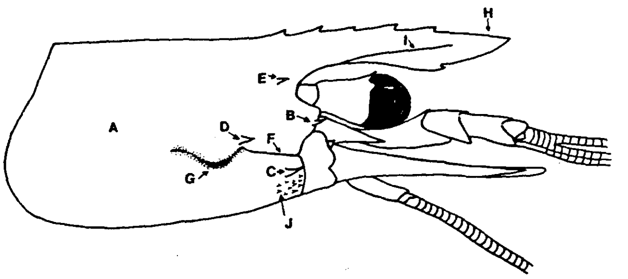

Figure 2. Composite drawing of the cephalotorax of Palaemoninae. A. carapace; B. antennal spine; C. branchiostegal spine; D hepatic spine; E. supraorbital spine; F. branchiostegal suture; G. branchiostegal groove; H. rostrum; I. rostrum keel; J. spinules.

3) Branchiostegal Spine: present (A) (Fig. 2C); absent (B); present with prominent carina (C); present located very high in the anterolateral border of the carapace just underneath the antennal spine (D). (CI= 0.60).

This spine is present in a large group of species, specifically in the genera *Palaemon* and *Palaemonetes*. This character is considered to be a derived character and an autapomorphy for the natural group that includes these two genera. The branchiostegal spine appears during early development, usually on larval state II or III. It arises as a small projection in the anterolateral angle of carapace (Sollaud, 1923: 541). Later it will migrate toward its position underneath the branchiostegal suture in the adult. The branchiostegal spine is usually associated with the branchiostegal suture just below it. However, the branchiostegal spine often is mistakenly defined as the one located beneath the branchiostegal groove, independent of the existence of the branchiostegal suture.

The branchiostegal spine, as defined here, originally develops (in early larval states) in a pterygostomian position and it migrates later towards the anterior part of the branchiostegite. Sollaud (1923: 541, 586) clearly distinguished 2 different origins for the hepatic and branchiostegal spines. Unfortunately, Sollaud's remarks have received very little attention and in the literature on larval development the future branchiostegal or hepatic spines are commonly described simply as a spine on the anterolateral border of the carapace. In earlier stages of development it is difficult to distinguish the spines, especially for species with complete larval development. Although this character could be codified as a set of independent variables, this in general was not done to avoid linking species by absence rather than presence of characters and to prevent the creation of sets of correlated characters.

4) Hepatic Spine: present (B)(Fig. 2D); absent (A); present with a prominent carina (C). (CI = 0.333.

The hepatic spine is located above the branchiostegal groove in the adult. There is some confusion about this, since some species do not have either a branchiostegal groove or a branchiostegal suture, but they do posses spines. Taxonomists tend to use a positional criterion. The hepatic spine and the branchiostegal spine have different origins (Sollaud, 1923; Gurney and Lebour, 1941; Williamson, 1969), and it is not clear during development which of the postembryonic spines would represent either one. Comparison of several descriptions on larval development (Pereira, 1989) suggest to me that the hepatic spine appears in branchiostegal position at late larval states (usually 3 or 4 in species with complete development). Then it migrates toward the he-patic position later during larval development (see figures in Holthuis, 1950b: 131; and discussion in Williamson, 1969), but sometimes it fails to reach a typical hepatic location. It is not associated with a branchiostegal suture but some authors still call it a branchiostegal spine. That there is some confusion about this is reflected in the fact that Stimpson (1860) described *Leander intermedium* in this genus because it has a branchiostegal spine. This identification was accepted until Holthuis (1952c) used the positional criteria to identify the hepatic spine and transferred the species to the genus *Macrobrachium*. During the present analysis it was found that *M. intermedium* showed characters that relate it to *Leander* and *Brachycarpus*. This interpretation is additionally supported by larval development (see Williamson, 1972).

5) Branchiostegal Suture: present (A) (Fig. 2F); absent (B). (CI = 1.0)

This feature constitutes a synapomorphy for *Palaemon* and *Palaemonetes*. There has been confusion in the literature between the branchiostegal groove and the branchiostegal suture. In general, authors refer to the branchiostegal groove as the furrow-like depression in the carapace that lies at some distance behind the antennal spine but make no comment about the branchiostegal suture. The branchiostegal suture is defined here as a sharp suture that continues from the branchiostegal groove towards the anterolateral border of the carapace. It probably results from differential growth of plates in the cephalothorax. Although clearly visible in

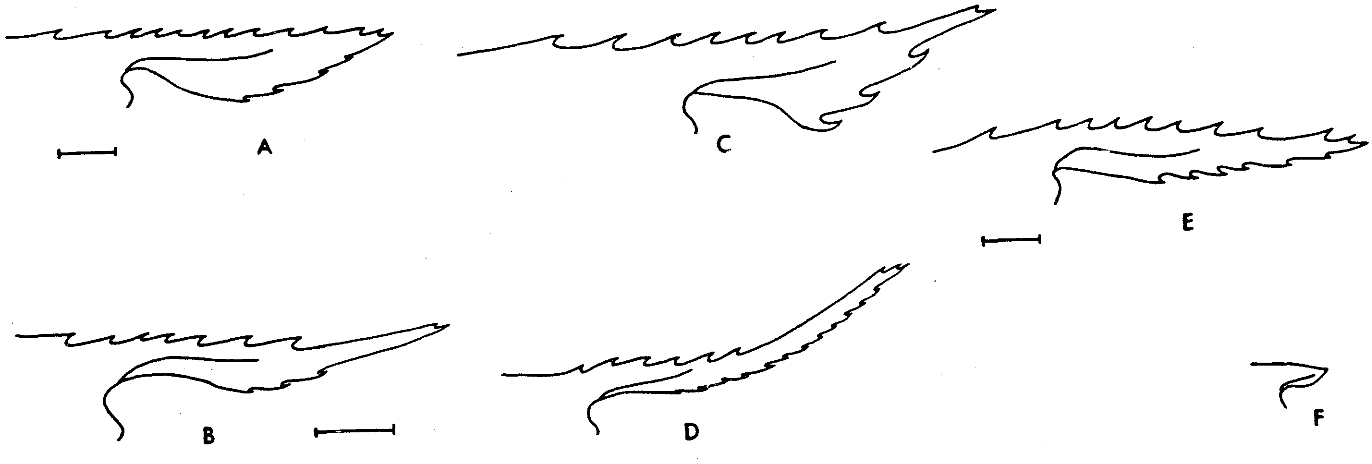

Figure 3. Details of rostrum in some Palaemoninae. A. *Palaemon serrifer*. B. *P. maculatus;* C. *P. macrodactylus*; D. *P. hancocki*; E. *Macrobrachium acanthurus*; F. *Troglocubanus inermis*. (scales A,C,D,F = 1 mm; B = 2 mm; E = 3 mm)

drawings, this distinction is often not stated precisely in written descriptions. The branchiostegal groove marks the origin of the branchiostegite and the point of attachment of masticatory muscles. It is present in a more or less defined form in all species of the family. Additionally, some species have a clear branchiostegal suture than runs just below this groove and continues towards the anterior border of the carapace, the branchiostegal suture.

6) **Supraorbital Spine:** absent (A) (Fig. 2E); present, not tubercle-like (B); present, tubercle-like (C).(CI = 0.667).

Most species do not have the supraorbital spine. the spine is modified as a tubercle on *A. antiguensis.*

Rostrum morphology is very diverse and has been extensively used in taxonomy at the specific level. Several characters were scored.

7) **Rostrum Shape:** compressed, straight (A) (Fig. 3A); distal 1/2 projected upwards (B) (Fig. 3B,D); compressed, tip of the rostrum projected upwards (C); arched over the eyes (D); depressed, very short, arising as a small prominence from the carapace (E); depressed at base, then compressed, short (F); compressed, more than distal 1/2 projected upwards (G). (CI = 0.545).

8) **Rostrum Length:** rostrum reaches distally between the third segment of the antennular peduncle and the distal end of the scaphocerite (A); longer than scaphocerite (C); reaching only the distal end of first segment of antennular peduncle (D); rostrum as a small prominence of carapace (E); Rostrum in subadults long as C, but adult males with shorter rostrum as in A (F).(CI = 0.571).

9) **Rostrum Lower Keel:** present (A); absent (B). (CI = 0.333).

10) **Shape of Rostrum Lower Border on Basal 1/3:** uniform, not diferent from the rest of the rostrum (A); lower border progressively projected until reaching the first tooth (B) (Fig. 3C); lower border projected, abruptly forming an angle before the first tooth (C); lower border not obvious since the rostrum arises as a conical projection from the carapace; cylindrical in cross section (D).(CI = 0.429).

11) **Teeth on Carapace:** 1-3 teeth situated on anterior 1/3 of carapace (A); 4-5 teeth on anterior 1/3 (B); no teeth present on carapace (C); 2 teeth of which the posterior one reaches distal 1/3 of carapace (D); 7 teeth on carapace situated on anterior 1/2 (E); teeth arising at the level of the orbital margin or anteriorly (F).(CI = 0.714).

12) **First Rostral Tooth Position:** not distant from others (A); distant from others by a larger space than among the other teeth (B); widely separated from the following teeth, which are in turn widely separated from the rest of the rostral teeth (C); absent (D).(CI = 0.30).

Troglobitic species show a trend for reduction in the number of teeth on the rostrum. In the absence of teeth, the character was declared unknown in troglobitic species (? in data matrix) and the most parsimonious character was assigned by the computer program.

13) **Teeth on Lower Border of Rostrum:** no teeth (A); 1-4 teeth (B); > 5 teeth (C); a single large conical tooth (D).(CI = 0.429).

14) **Distribution of Rostral Teeth on Distal Dorsal Border:** teeth uniformly spaced (A) (Fig. 3A); teeth not uniformly spaced, leaving a distal naked space of about 1/3 to < 1/2 the length of the rostrum (B)(Fig. 3B,C); distal naked portion ≥ 1/2 than rostral length (D)(Fig. 3D); no distal naked portion, but the teeth of the rostrum are not uniformly spaced and have larger than usual gaps between them (E)(Fig. 3E); no teeth (F)(Fig. 3F); similar to state E but the gaps between teeth are larger (G). (CI = 0.385).

The distribution of teeth on the rostrum is uniform in the majority of species in *Macrobrachium, Palaemon* and *Palaemonetes* and most probably is the plesiomorphic condition. States B, C and D appear to arise independently by either lengthening of the rostrum or widening of the distance between the teeth, together with elongation of the rostrum.

15) **Rostrum Tip:** ending in a straigth, sharp point with one subapical spine (A) (Fig. 2H, 3B,C,D); ending in a sharp point tip pointing upwards (B); ending in 2 well defined subapical

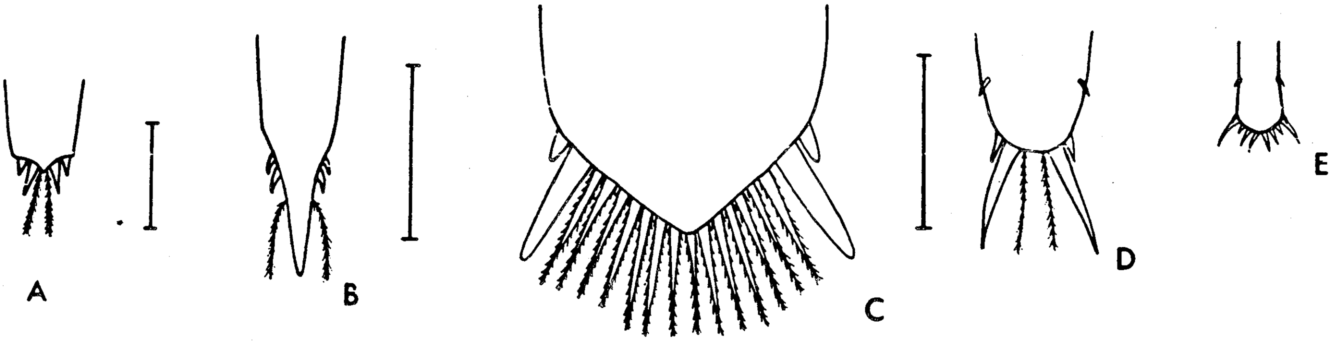

Figure 4. Detail of posterior part of telson in Palaemoninids. A. *Palaemonetes ivonicus;* B. *Palaemon hancocki*; C. *Macrobrachium cortezi*; D. *Palamonetes antrorum*; E. *P. holthuisi.* (scales: A-E = 1mm)

spines (C) (Fig. 3D); ending straight with no subapical spine (D). (CI = 0.50).

16) **Feathered Setae on Telson:** 2-20, thin distributed tigth as a bunch on distal telson (A) (Fig. 4A,B,D); > 30, straight and thicker than A(D); 2 strong feathered setae (E); no setae present (F); 2-4 hairlike setae (not feathered) (G); 14-30 thick, arrange well aligned on distal telson (H) (Fig. 4C). (CI. = 0.556).

This character refers to the number of feathered setae present between the inner spines of the posterior border of the telson. In general *Palaemon* and *Palaemonetes* are characterized by having a smaller number of setae than *Macrobrachium*. State E characterized a few taxa in which these posterior setae were strong (with a spine-like appearance) but plumose.

17) **Telson Tip:** Ending abruptly in a sharp triangular tip (A)(Fig. 4A); becoming progressively more slender toward a conical tip (B) (Fig.4B); ending abruptly, broad distal end with a less pronounced triangular point than A (C); becoming progressively more slender towards a thin end with depressed rather than conical shape (D); with a broad distal end and uniform distal border or a small median tip (E) (Fig. 4C); broad distall end, distal border nearly straight (F); distal end broader than anterior border (G) (Fig. 4E); distal end straight, not broader than anterior border with rectangular appearance (H); distal end broad, prominent and oval in shape, about the same width as anterior end (9) (Fig. 5A); ending sharply straight with two longitudinal dorsal ridges (K); broad distal end, similar to 9, but posterior end not projected (L); typical shape for *C. rathbunae* (M) ; typical shape *Ac. media* (N); typical shape for *P. glabra* (L). (CI. = 0.818).

18) **Telson Inner Spines:** larger than distal end of telson and about 2 times larger than outer spines (A) (Fig. 5C,D; 6A,B,D); about same size as distal end of telson (B)(Fig. 4B; 5A,6C); the spines are more than 2 times larger than outer spines and distally bent (C) (Fig. 5B); located in a different plane than outer spines (D). (CI. = 0.273).

State A is the rule throughout the subfamily Palaemoninae, but state B appears in some *Palaemon, Palaemonetes,* and especially in some *Macrobrachium.*

19) **First Dorsal (Anterior) Pair of Spines on Telson:** located between 1/2 and 2/3 of its length from the anterior border of telson (A) (Fig. 6A,B); at about 4/5 of its length from the anterior border of telson (C)(Fig. 6D); at 1/3 of its length from the anterior border of telson (D)(Fig. 5A); located at about 3/4 of its length from anterior border of telson (E); spines absent (F). (CI. = 0.800).

Although it seems clear that this character occurs as several states, sometimes these are difficult to separate. This codification reflects the major states. A finer separation may still be possible without overlap.

20) **Second (Posterior) Dorsal Pair of Spines on Telson:** located about 1/6 of the length of the telson from the distal border (A)(Fig. 6D); located > 1/6 (usually 1/3) the length of the telson from the distal border (B) (Fig. 6B); no spines (C); located at 1/2 or slightly > 1/2 the length of the

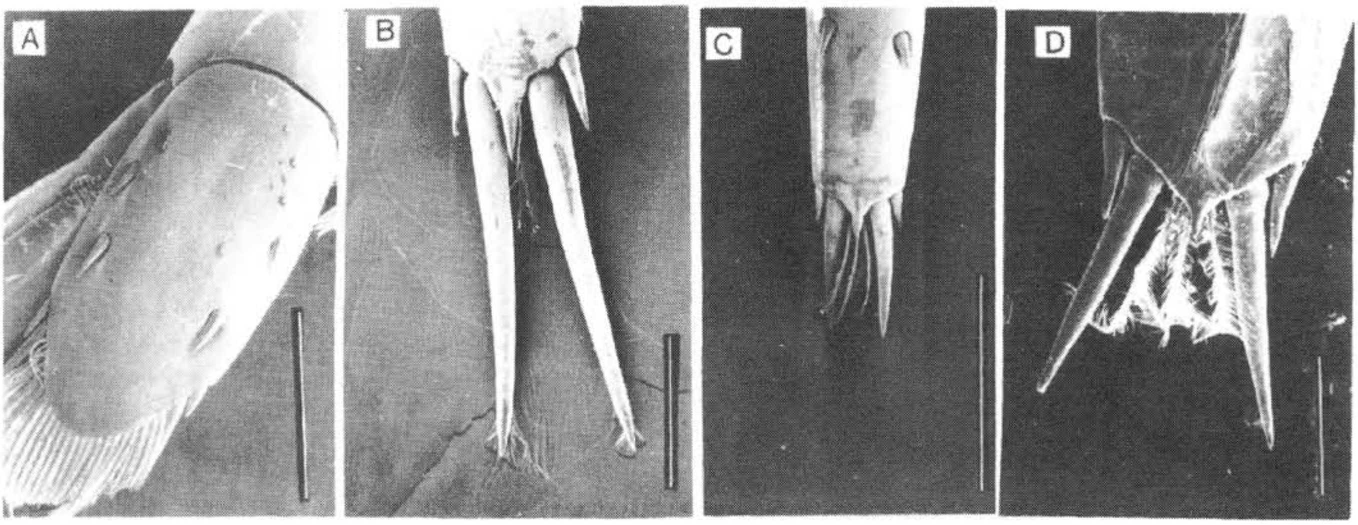

Figure 5. Details of telson. A. *Euryrhynchus amazonensis*; B. *Leander tenuicornis*; C. *Pseudopalaemon amazonensis*; D. *Palaemonetes antrorum*. (scales A,C = 1mm; B = 0.5 mm; D = 0.2mm)

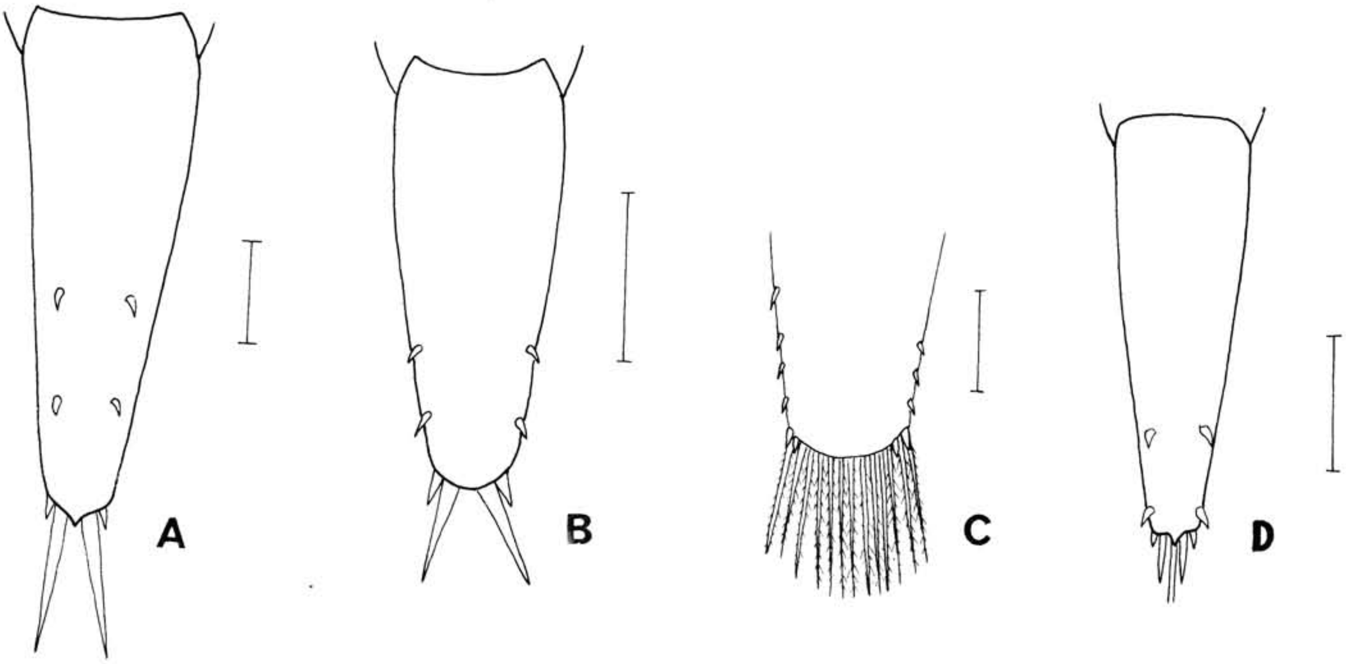

Figure 6. Detail of telson in some Palaemoninae. A. *Palaemonetes pugio*; B. *P antrorum*; C. *Troglocubanus perezfarfantae* (redrawn from Villalobos, 1971); D. *P. kadiakensis*. (sacales A,B = 1 mm; D = 2 mm)

telson from the distal border (D) (Fig. 5A); located at < 1/2 the length of the telson from the distal border but never located < 1/3 from the distal border (E).(CI. = 0.556).

21) **Location of Dorsal Spines:** center-dorsal position (A) (Fig. 6A); dorsal position but located more towards the lateral border than in state A (B) (Fig. 6B); located on the edge of lateral borders of the telson (C) (Fig. 6C); located distally but over the distal margin of telson (D). (CI. = 0.429).

Category A is the most common state of this character. These spines are moved conspicuously laterally in some species of *Palaemonetes* (B). Some *Troglocubanus* typically have the spines on the lateral borders of the telson (C).

22) **Ratio Between Lengths of Sixth and Fifth Abdominal Segments:** larger than 1.5 (A); ≤1.1 (B). (CI. = 0.250).

The values range from 0.7 to 2.5, with most species falling between 1.5 and 2.0.

23) **Number of Fused Segments in the Upper Flagella of Antenna I:** 4-9 (A) (Fig. 7A,B); > 10 (B)(Fig. 7C) none (C). (CI. = 1.0).

This character shows large variation but the code used avoids overlap. Most of the species fall in state B.

24) **Ratio of Number of Free Segments to Number of Fused Segments in Upper Flagella of Antenna I:** 2.5-3.3 (A); 0.8-1.9 (B); 0.20-0.50 (C); 4.5-7.1 (D); 0.16 (E); no fusion (F); flagella undivided (G); 0.07 (H) (Fig. 7). (CI. = 0.269).

This character is frequently used in the taxonomy of the group. The ratio is easy to score and shows considerably less overlap than when each trait is treated independently.

25) **External Spine of Uropods:** 1 (A) (Fig. 8C); absent (B)(Fig. 8A); 3-7 (C); 2 (D); > 10 (E). (CI. = 0.667).

A single spine is the rule. Some groups inside the subfamily Palaemoninae have lost the spine. Outside the subfamily it may be present in numbers greater than 1.

26) **Scaphocerite Shape:** oval, ratio of length to width about 2.5:1-3.0:1 (A)(Fig. 9A,B); more slender than state A, outer border subparallel to the inner border, ratio > than 3.5:1 (C)(Fig. 9C); shorter and stouter than previous stages, outer border subspherical, ratio <= 2.0 (D)(Fig. 9D); conspicuously slender and thin distally (E). (CI. = 0.214).

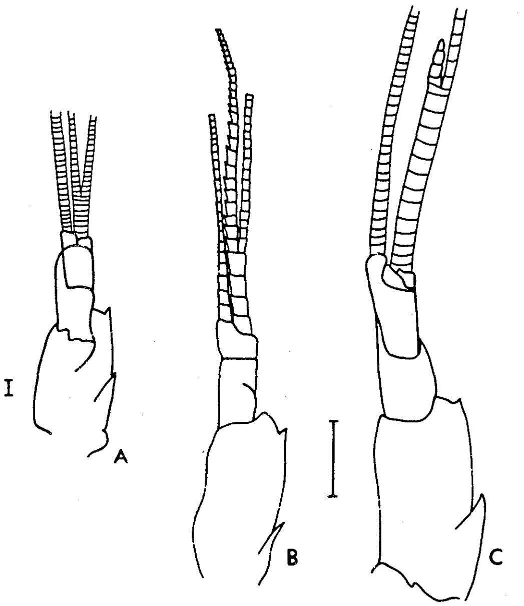

Figure 7. Antennular peduncle in the Palaemoninae. A. *Macrobrachium carcinus*; B. *Palaemonetes carteri*; C. *P. mesogenitor* (scale 1 mm)

Most of the species share state A, and C is the next most common state. State C is clearly detectable, since the entire scaphocerite tends to be more elongated, slender and tapering towards the distal border. In state D the scaphocerite tends to be broad and more spherical.

The mouth parts among Palaemoninae are sufficiently diverse that Paulucci Maccagno and Cucchiari (1955) developed a key to genera and species based mainly on characteristics of the mouth parts.

27) **Maxilla I, Shape of *Lacinia Mobilis*:** slender, rectangular in shape (A)(Fig. 10A); lower border expanded into an oval shape (B) (Fig. 10B); spherical shape (C); distal margin expanded (D). (CI. = 1.0).

This character refers to the general appearance of the maxillae: slender (A) represents a lobed lacinia, not very different in size from the inner and upper lacinia. This is the common shape of the lacinia mobilis in the subfamily. The broad shape

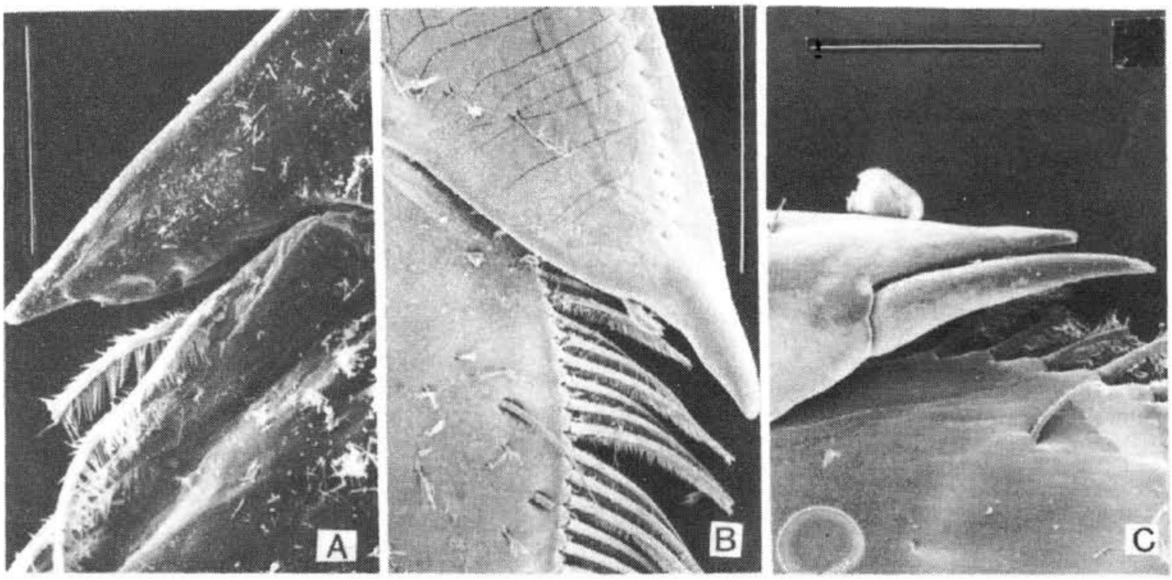

Figure 8. Detail of telson showing the external spine of the exo-uropods. A. *Palaemonetes antrorum*; B. *Creaseria morleyi*; C. *Pseudopalaemon amazonensis*. (scales A = 0.1mm; B = 0.5 mm; C = 0.2mm).

is present in a few species; it may be associated with filter feeding or detritivory.

28) **Maxilla I, Inner Lacinia Spines:** 1-5 twisted, not well aligned (A) (Fig. 11A,B,C); > 5 straigth (C) (Fig. 11D); absent (D). (CI. = 0.40).

29) **Maxilla I, Front of the Inner Lacinia:** curved (A)(12A); elongated (B) (Fig. 12C); broad (C)(Fig. 12B); sinuous (D) (Fig. 12D); prominent with straight front (E)(Fig. 12E); absent (F). (CI. = 0.556).

The most common state (A) refers to an inner lacinia which is about the same size as the upper lacinia, outer border of inner lacinia smoothly curved. Some species have the inner lacinia noticeably longer than in the previous state (B), other species have the outer border considerably broadened (C), while among some species of *Macrobrachium* the outer border is without any curvature, ending sharply straight (E).

30) **Maxilla I, Number of Spines on Upper Lacinia:** smooth (A) (Fig. 13A); 1-5 spines (B) (Fig. 13B); > 6 spines (H). (CI. = 0.182).

31) **Maxilla I, Shape of the Upper Lacinia:** finger-like, bent (A) (Fig. 13A); as A, but reduced by about 1/2 in size (B); broad and conspicuously bound to the inner lacinia (C) (Fig. 13C); elongated more than in state A (D); conical in shape and ending abruptly straight (E); conical ending in attenuated into an acute tip (G); slender and sharply bent toward the lower lacinia (H); aproximately rectangular in shape and situated parallel to the upper border of the lower lacinia (I). (CI. = 0.875).

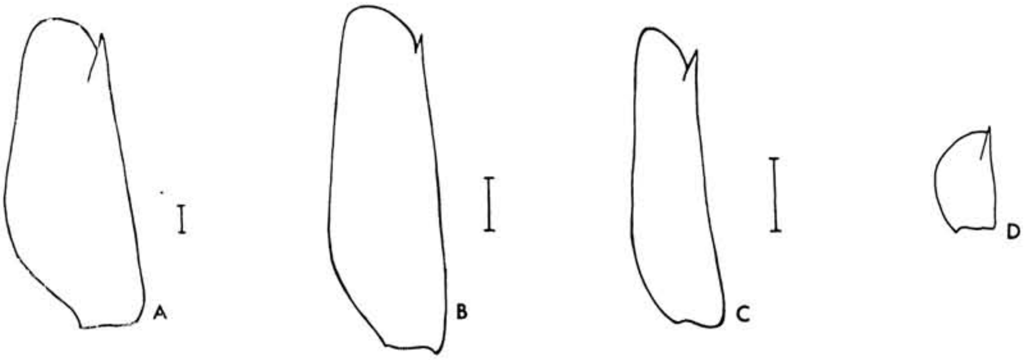

Figure 9. Scaphocerite shape variation in differente species in the Palaemonidae. A. *M. nattereri*; B. *P. gladiator*; C. *M intermedius*; D. *E. pemoni* (sclaes A = 1mm, B = 3 mm.; C,D = 2 mm).

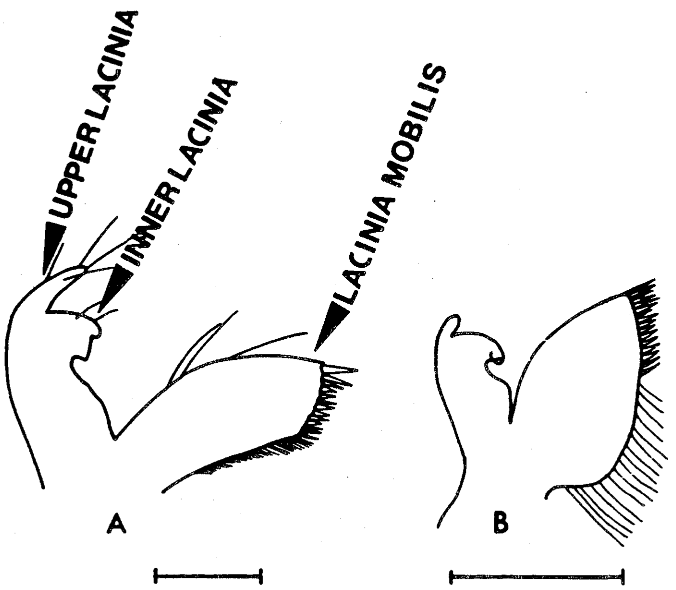

Figure 10. First maxillae. A. *Macrobrachium nattereri*; B. *Palaemonetes tonkinensis* (scales A = 1mm; B = 0.5 mm).

32) **Maxilla II, Endites:** cleaved into 2 endites (A) (Fig. 14A,B); single endite (B) (Fig. 14C); absent (C); 2 endites, one of them cleft (D); 2 endites, both cleft (E). (CI. = 0.667).

33) **Molar:** slender as compared to B, about 3 times longer than wide, dorsal surface with large teeth and tubercles (A)(Fig. 15A,B); shorter and stronger than A, about 1.5 times longer than wide, dorsal surface with large teeth and a few rows of spines between teeth (B)(Fig. 15E,F); similar in shape and dorsal surface to B, but the area covered by spines is larger, teeth present but not prominent (C); slender, dorsal surface with larger area covered with spines, teeth large and prominent (D)(Fig. 15C,D); with ridges on dorsal surface (E); dorsal surface totally covered with spines, teeth unnoticeable (F); dorsal surfaces with 4 prominent ridges (G).(CI. = 0.667).

Holthuis (1952b) acknowledged that this character could be important in the taxonomy of the subfamily Pontoniinae, but it has not been used in taxonomy at the generic or specific levels in any group of the family. It is very characteristic in *Desmocaris*. Fujino and Miyake (1968) suggest that it can be used for identification of species in the genus *Palaemon*. Other characters like the surface of the lateral borders of the molar show some interesting spinulation patterns. Unfortunately, this trait was difficult to score in all taxa, since the best way to observe it is using SEM. Consequently, it was not included in the analysis.

34) **Shape of the Incisor:** slender, about 3 times longer than wide (A) (Fig. 15A); short and strong as compared to A, about 1.5 or less times longer than wide (B) (Fig. 15E); reduced to a small prominence (C); laminar shape, broad and fused to the molar (D); absent (E); expanded distally (F). (CI. = 0.833).

States A and B are difficult to discern in small species, so slender was used only to refer to *Euryrhynchus* and some cave shrimps such as *Troglocubanus*.

The pereiopods, especially the first and second pairs of adult males are very important in the taxonomy of the group.

35) **Size of Second Pair of Legs:** equal (A); subequal (B); unequal (C). (CI. = 0.286).

Subequal indicates that one leg is slightly shorter than the other but both have the same shape. Unequal is used when one leg is different, usually stouter and larger than the other.

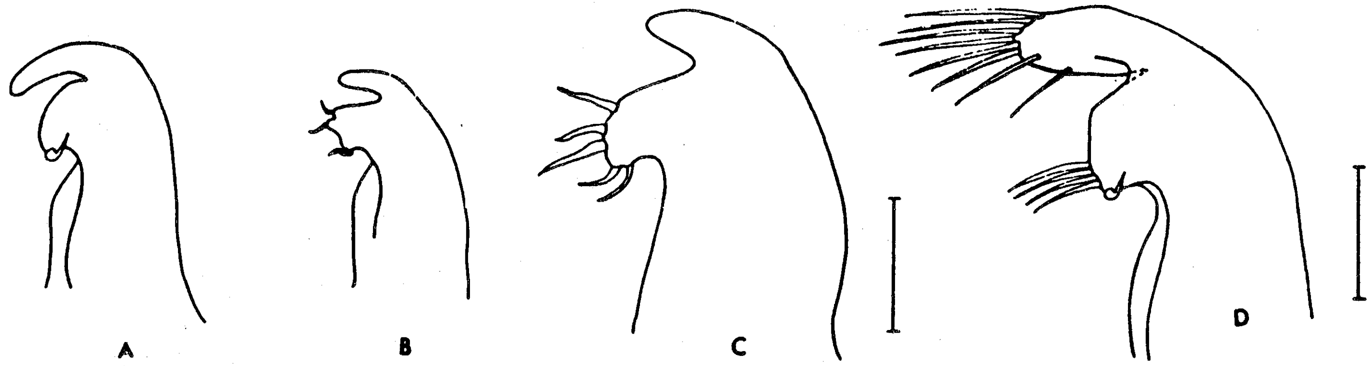

Figure 11. Spines of the inner lacinia in some Palaemoninae. A. *Macrobrachium praecox*; B. *Palaemonetes kadiakensis*; C. *P. varians*; D. *M brasiliense*. (scales A-C = 0.5 mm; D = 1 mm)

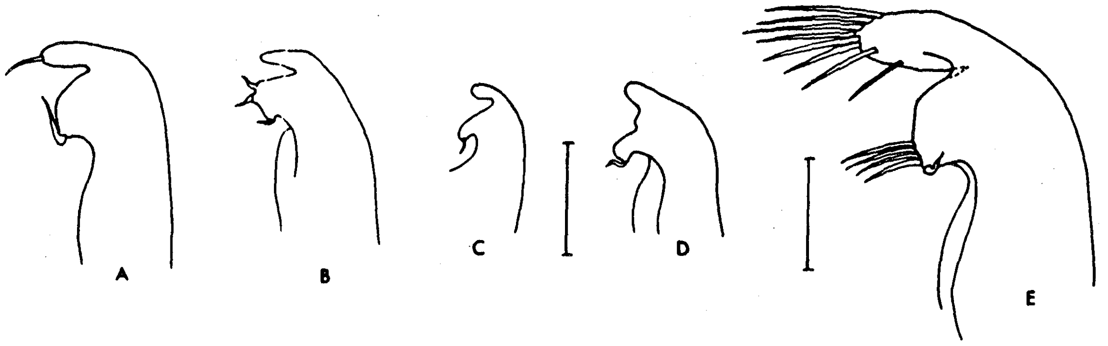

Figure 12. Inner lacinia in some Palaemoninae. A. *Palaemon pandalliformis*; B. *Palaemonetes kadiakensis*; C. *P. ivonicus*; D. *P. mesopotamicus*; E. *Macrobrachium brasiliense*. (scales A-D = 0.5 mm; E = 1mm)

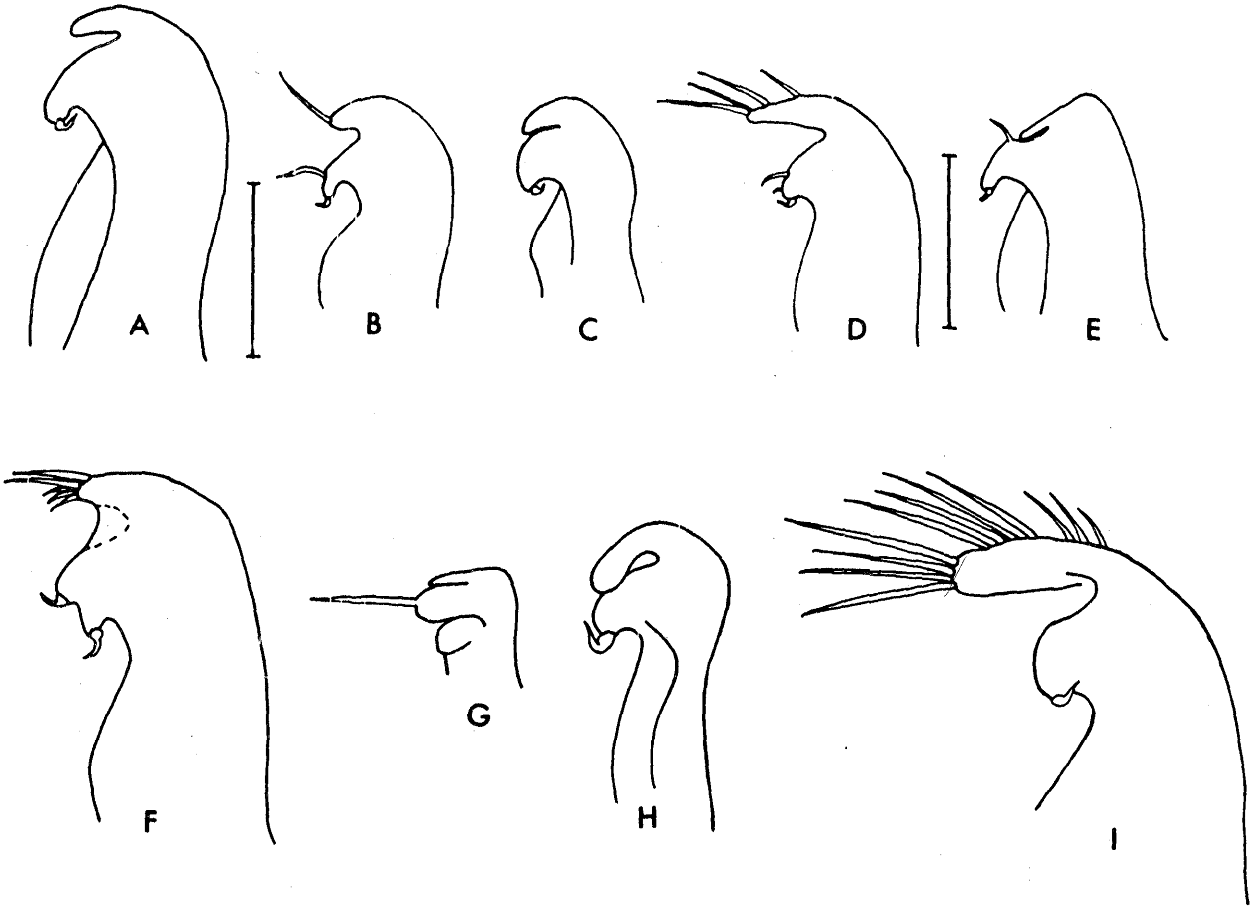

Figure 13. Shape and spines on upper lacinia in several Palaemoninae. A. *Palaemon hancocki*; B. *P. macrodactylus*; C. *P. concinnus*; D. *P. xiphias*; E. *P. gracilis*; F. *Leptocarpus flumicola*; G. *Desmocaris trispinosus*; H. *Macrobrachium pectinatum*; I. *M. acanthurus*. (scales A-C, E,F,H = 0.5 mm; D,G,I = 1mm).

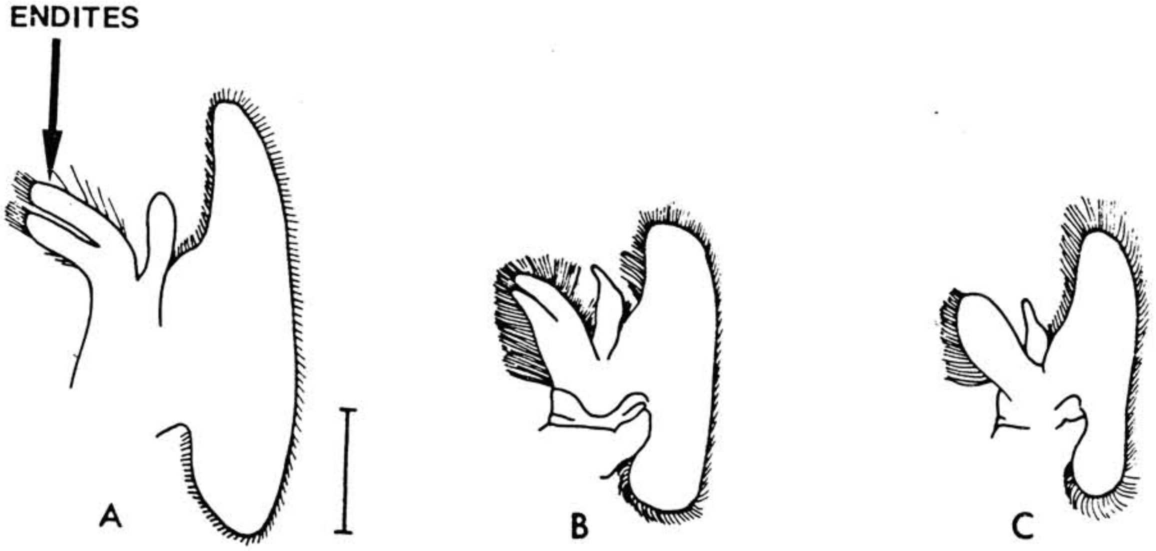

Figure 14. Maxilla II. A. *Macrobrachium nattereri*; B. *Palaemonetes tonkinensis*; C. *Desmocaris trispinosus*. (scales A,B,D = 2 mm)

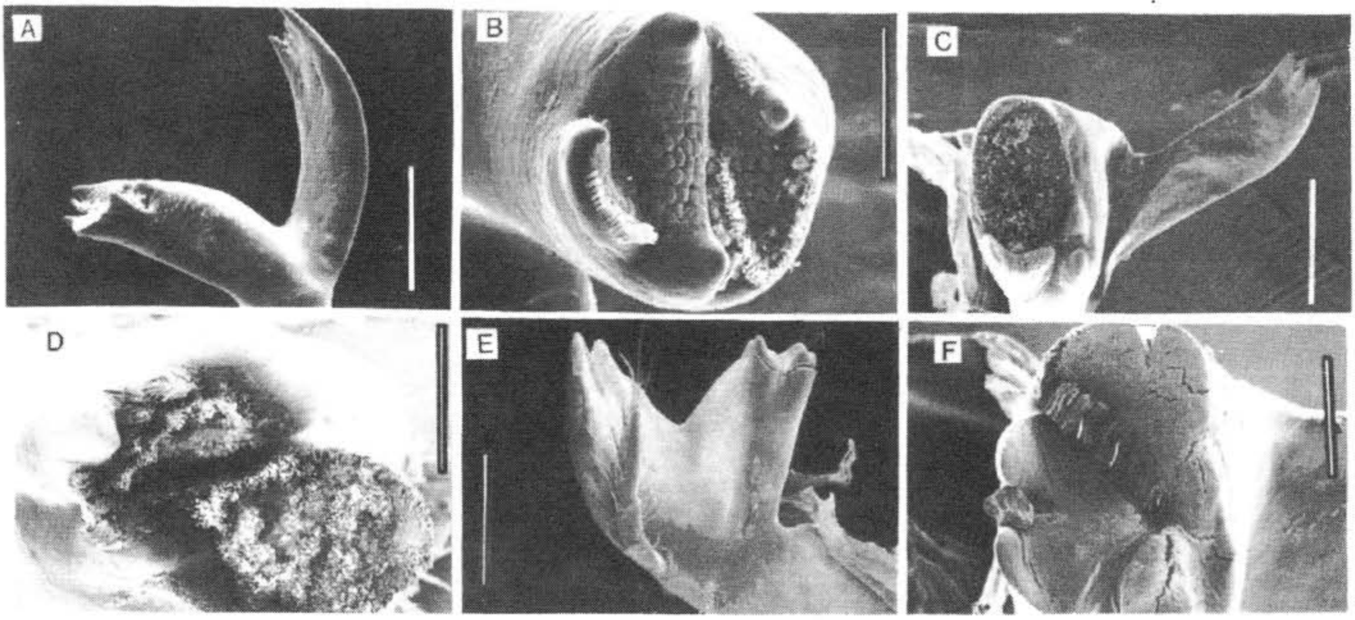

Figure 15. Mandible. A. *Euryrhynchus amazonensis*; B. detail of dorsal surface of molar; C. *Palaemonetes antrorum*; D. *Troglocubanus inermis* detail of dorsal surface; E. *Macrobrachium nattereri*, mandible lateral view showing the 3-jointed mandibular palp; F. *Palaemonetes pugio*, detail of dorsal surface of molar. (scales A,C,D,F = 0.2mm; B = 0.1 mm; E = 1 mm)

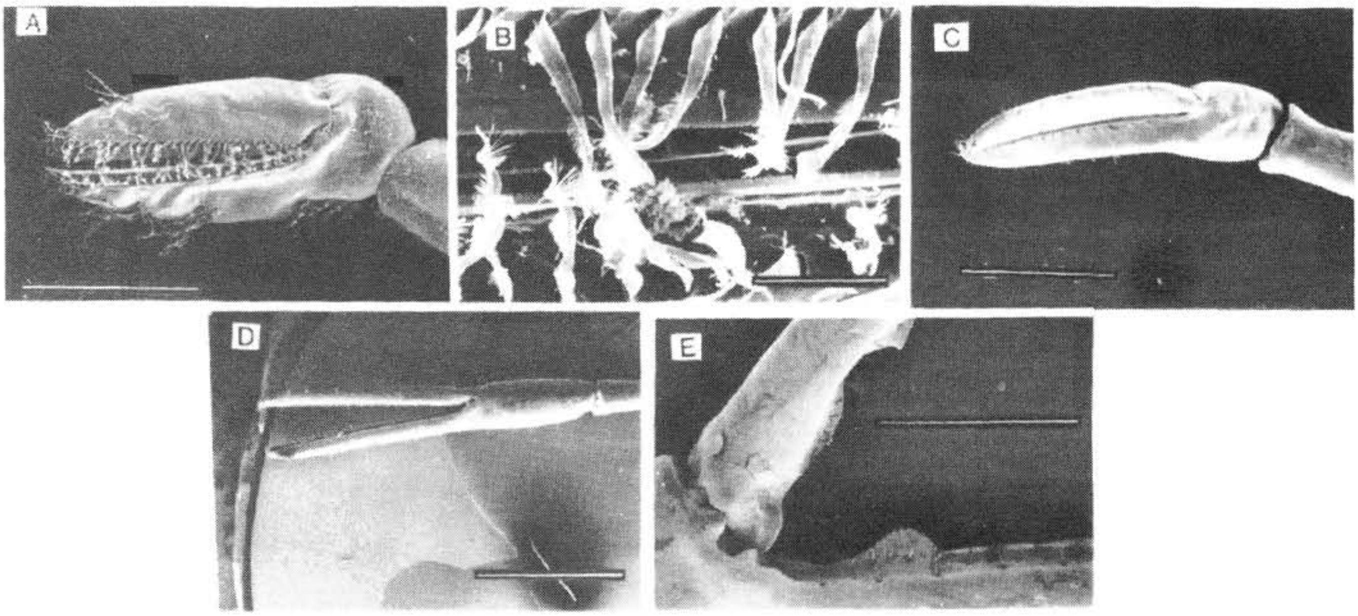

Figure 16. Finger of the second pair of legs. A. *Palaemonetes antrorum*; B. Detail of cutting edge; C. *Troglocubanus inermis*; D. *Euryrhynchus amazonensis*; E. *Creaseria morleyi*, detail of cutting edge of fingers. (scales A = 0.5mm; B = 0.05 mm; C = 1mm; D, E = 2mm).

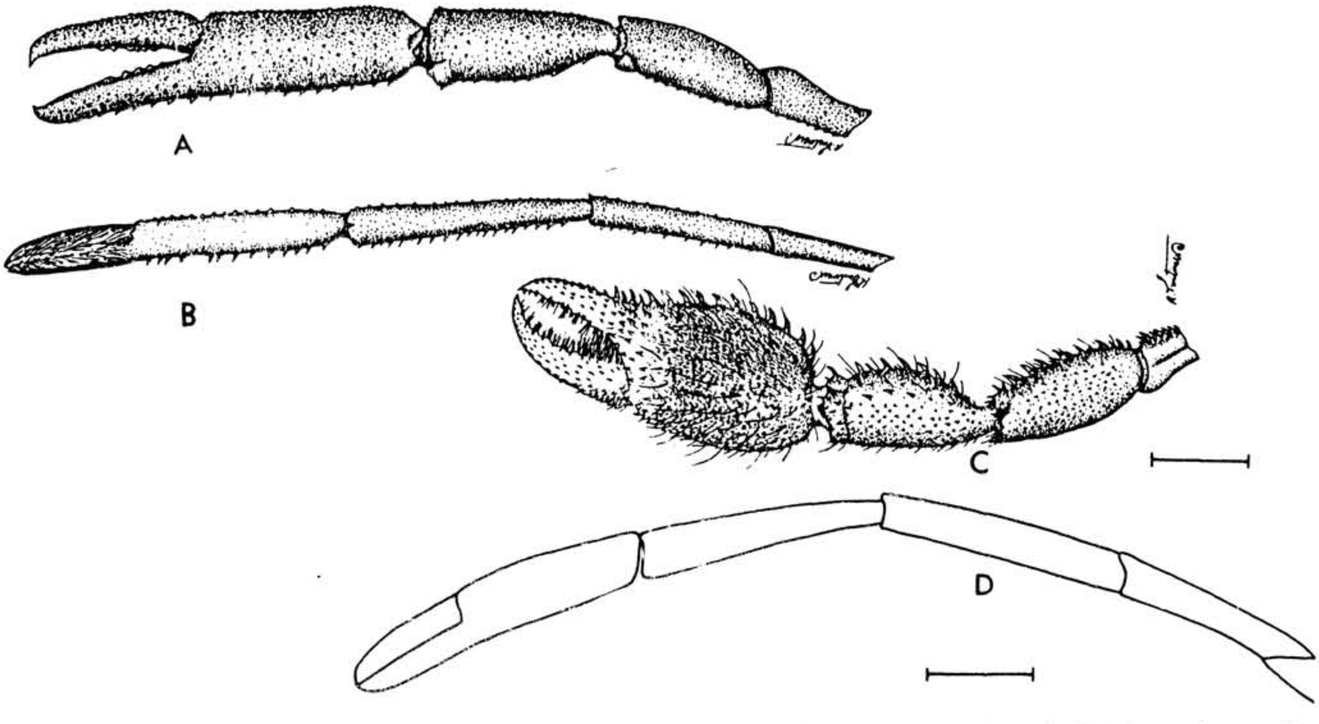

Figure 17 Second pereiopod in Palaemoninae. A *Macrobrachium heterochirus*, larger leg of a male, B. *M. acanthurus*, right leg (both legs equal); C. *M. olfersi*, larger leg of male; D. *Palaemon serrifer*, right leg of female (both legs equal). (scale A,B,C = 10mm; D = 2 mm)

36) **Shape of First and Second Legs:** both extending beyond the scaphocerite and equal in length (A); extending beyond the scaphocerite but second pair longer and more robust (B); not extending beyond the scaphocerite and equal (C); extending beyond scaphocerite, legs similar to each other but not ending in claw (D). (CI. = 0.60).

In the great majority of the Palaemonidae, the first pair of legs are smaller and more slender than the second pair. Only in a few species are both of legs the same size and shape.

37) **Shape of the Propodus of the Second Pair of Legs:** as long as wide, spherical shape (A) (Fig. 16A); cylindrical, sometimes slightly compressed, 2.5-3.5 times as long as wide (B) (Fig. 17A); cylindrical, 4-10 times longer than wide (C) (Fig. 17B); swollen in middle section, 1.0-1.5 times longer than wide (D) (Fig. 17C); cylindrical with no modification to form a claw (E); palm very reduced, fixed finger comprising most of the propodus (F); swollen, but less than 2.0-1.5 longer than wide, also sligthly compressed (G).(CI. = 0.60).

The ratio between the length and width of the palm and its overall morphology give a general idea of this character. The palm of *Palaemonetes antrorum* was considered typical and a different state from D, even though they have about the same ratios. State D is spiny and more robust than A (compare Figs. 16A with 17C).

38) **Shape of the Fingers of the Second Pair of Legs:** straight (A) (Fig. 16D); gaping (B) (Fig. 17C); bent in such a way that the claw forms a spoon-like structure (C) (Fig. 16A); both fingers slightly bent inwards laterally (D) (Fig. 16C); fingers gaping only at distal end (E); single finger not very different from the dactyl of other pereiopods (F); fingers straight, fixed finger with a groove to accommodate dactyl (G). (CI. = 0.750).

Most Palaemoninae have the fingers of the claw straight. In some species of *Macrobrachium* the fingers gape, ie, they leave a clear space between them. The fingers of some species of *Macrobrachium* and *Troglocubanus* are bent laterally. Hollow means that the internal border has a spoon shape. Finally, *M. potiuna* has bent fingers which also bend distally. This typical shape apparently is derived from state D, but is sufficiently different to be considered a different state.

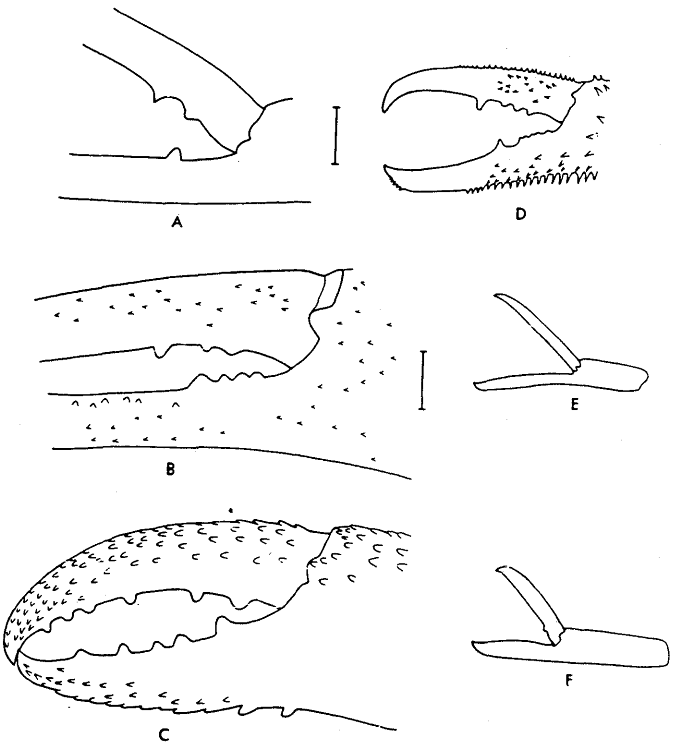

Figure 18. Finger of the second pair of legs. A. *M. weberi*; B. *Cryphiops brasiliensis*; C. *C. caementarius*; D. *M. cortezi*; E. *Exopalaemon orientis*; F. *Leptocarpus potamiscus* (scales A,C-E = 2 mm; B, F = 1 mm).

39) **Cover of the Fingers of the Claw in the Second Pair of Legs:** smooth (A) (Fig. 17D); spiny (B) (Fig. 22B,C,D); velvety-like pubescence (C) (Fig. 17B); with large tuft of hairs distally (D); smooth with thick short hairs (E). (CI. = 0.80).

Smooth refers to not having any spines although the fingers may possess setae. Felt refers to the presence of velvety pubescence on the finger, whether spines are present or not.

40) **Formula of Teeth of the Fingers of the Claw on the Second Pair of Legs:** smooth cutting edge entire (A) (Fig. 18E); formula 1/1 or 1/0 (B) (Fig. 18F); pectinate cutting edge (C) (Fig. 16A,B); 1+3/2+3 (D) (Fig. 19A,B); 5/5 (E) (Fig. 18C); 1+2/1+2 (F); 2/1 and prominent tubercle (G) (Fig. 18A); 1 + crest (H); 2/1 with socket on fixed finger (9); pectinate with larger and more widely spaced denticles than C (J); smooth, no obvious cutting edge (K); smooth, cutting edge broad with longitudinal groove (L). (CI. = 0.379).

Most of the variation in number of teeth is found in *Macrobrachium*; other genera have states A or B. Assigning formulae to the teeth proved to

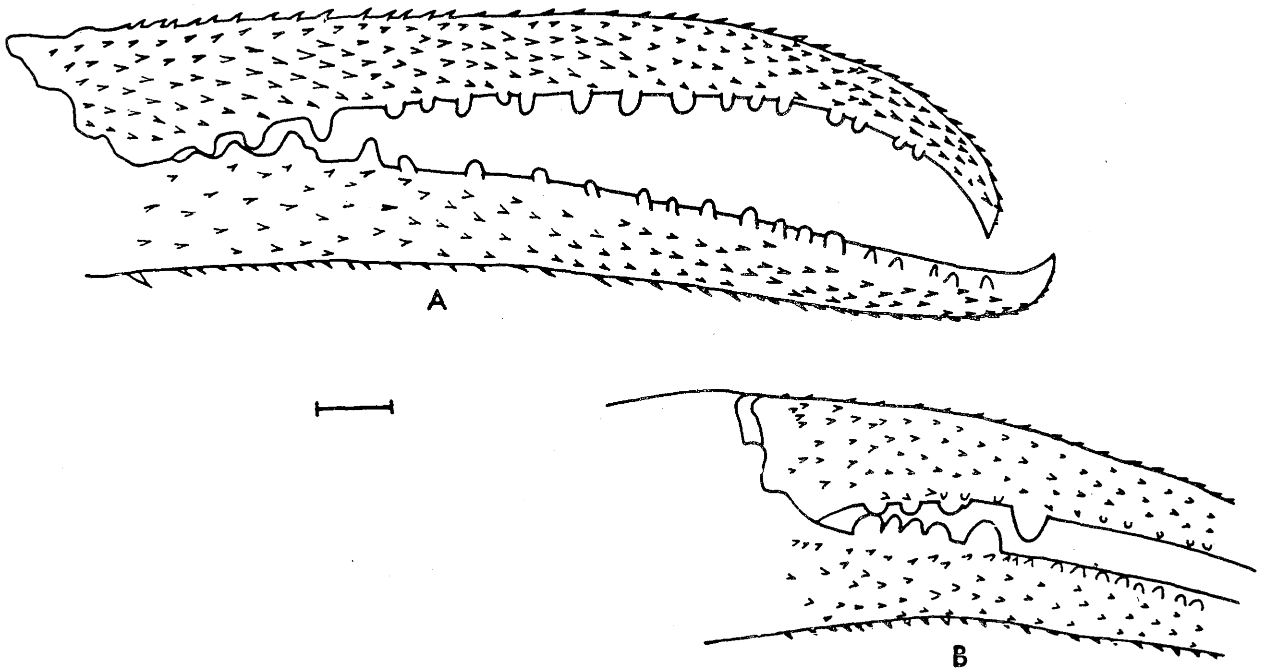

Figure 19. Finger tubercles A. *Macrobrachium dux* ; B. *Macrobrachium iheringi*. (scales A, B = 3 mm)

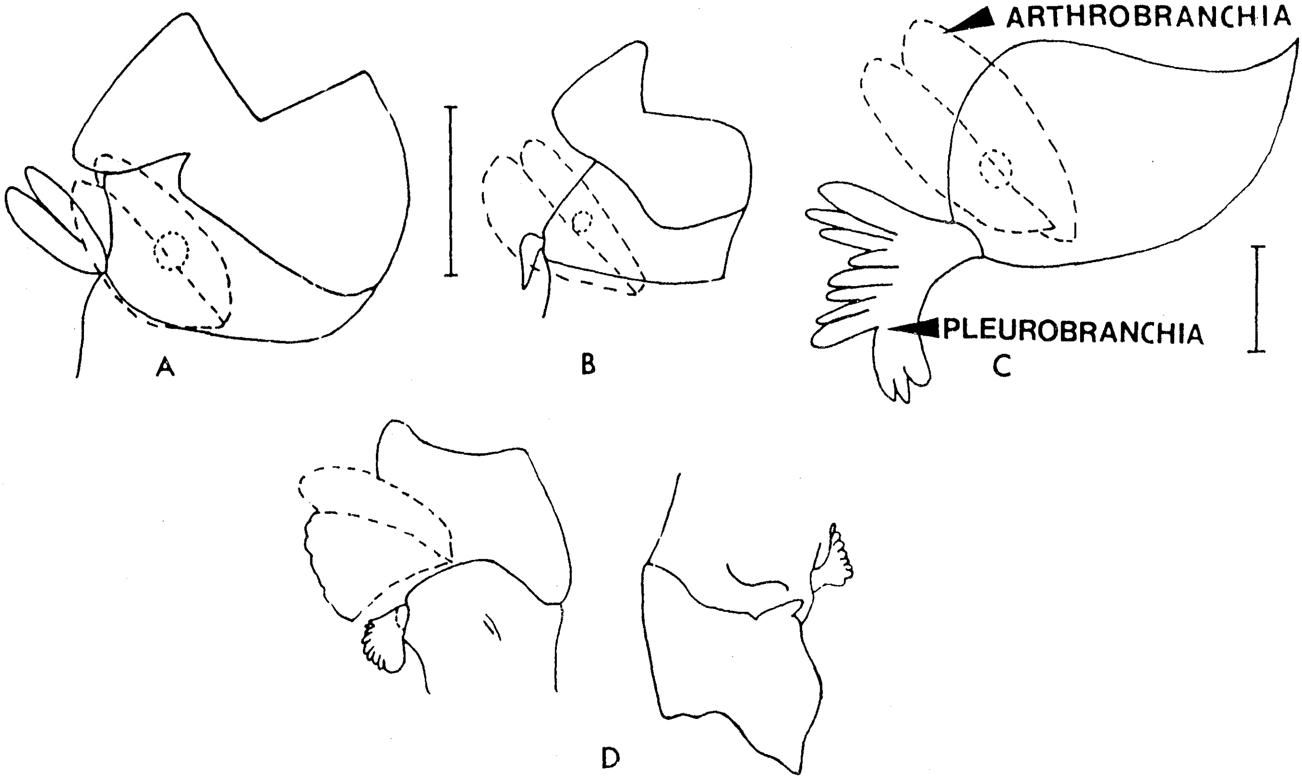

Figure 20. Branchiae of third maxilliped. A. *Palaemon hancocki*; B. *Palaemonetes tonkinensis*; C. *P. varians*; D. *Desmocaris trispinosus*. Doted line refers to Arthrobranchiae and entire line to Pleurobranchia (scales A,B,D = 0.5 mm; C = 1mm)

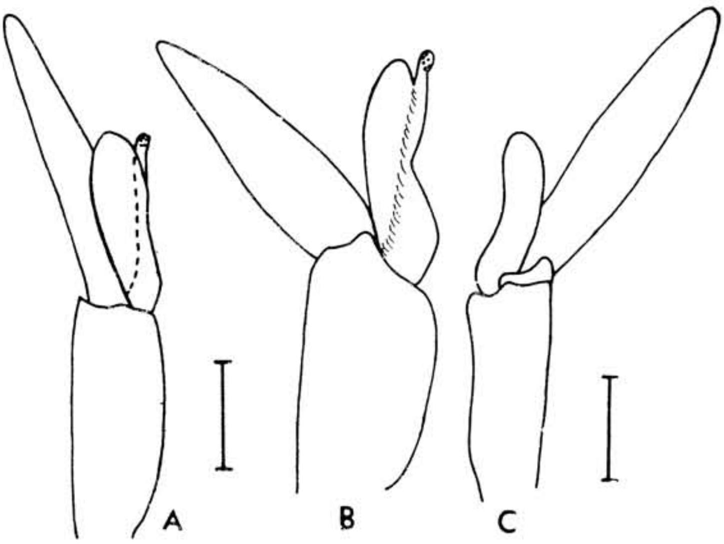

Figure 21. First pleopod and apendix interna. A. *Leander tenuicornis*; B. *Brachycarpus biunguiculatus*; C. *Macrobrachium amazonicum* (scales A,B = 1mm; C = 2mm).

be rather difficult because of their diversity and small size. Broad ranges were used, smooth referring to those with no noticeable teeth. Those with 1 tooth on each finger or 1 over 0 to 2 over 2 were considered to be a single state (B). Large variation was found among the species in the genus *Macrobrachium*. The state 1+3/1+3 refers to many species of *Macrobrachium* and other genera in which the teeth may have some degree of fusion. In some species, like *M. heterochirus*, the teeth are numerous and regularly spaced (State D). Some other species of *Macrobrachium* show a large basal tooth with a few smaller distal teeth (state G). Finally, some species have small separate teeth (state H).

43) **Legs 3-5:** about same size (A); third pereiopod the most robust (C); pereiopods 3-5 very thin and long (D). (CI. = 1.0).

44) **Eye Stalk and Cornea:** elongate eye stalk, cornea broad and pigmented (A); reduced eye stalk and cornea without pigment (B); reduced eyestalk, no cornea but a knob (C); reduced eye stalk, cornea with well formed ocelli (D); reduced eyestalk and cornea, trace of pigments and a conical process on interior margin of eye stalk (E).(CI. = 0.571).

The eyestalk and eye facets of some cavernicolous species are reduced (B); other species have no facets and a single knob is found distally on the eye stalk (*Troglocubanus*, see Chace, 1942, 1943) (C); in other epigean species the area of the eye facets are considerably reduced compared to those of typical species of *Macrobrachium*.

45) **Mandibular Palp:** absent (A); with 2 joints (B); with 3 joints (C) (Fig. 15E); 3 joints but segments are noticeably broader than B (D).(CI. = 0.250).

The mandibular palp is a character to which taxonomists have given much importance. It has been used to define genera in the subfamily, although several authors have raised questions about its validity, since they found wide variation of the trait within certain species (Chace, 1972; Bray, 1976; Carvacho, 1978). The approach used here was simply to code for the different states. States B or C were assigned when there was no evidence of variation (from the literature or from the analysis). For species that showed variation in the number of joints, the character was declared unknown.

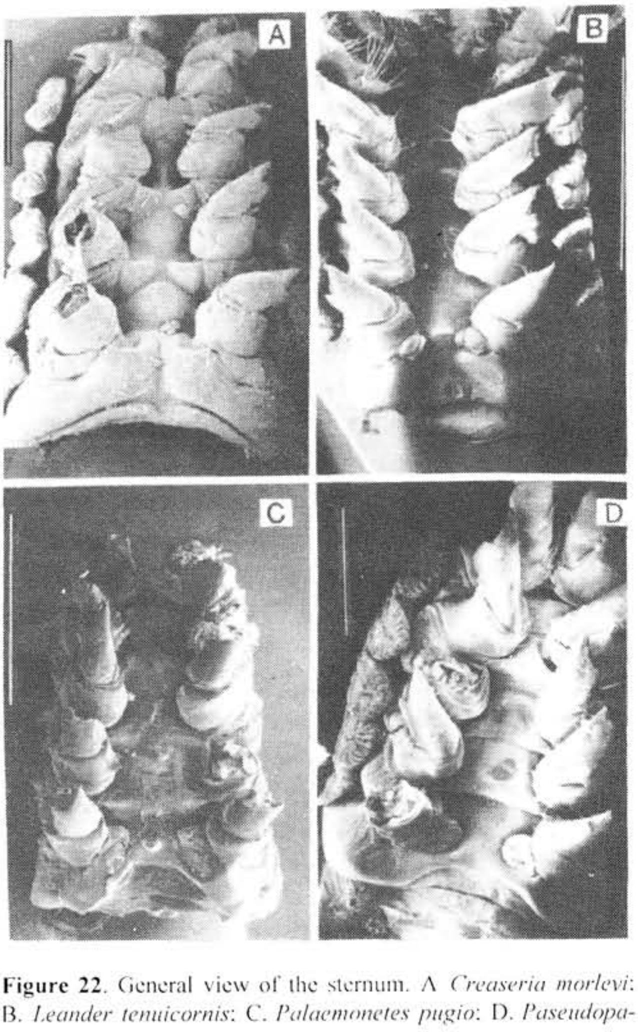

Figure 22. General view of the sternum. A *Creaseria morleyi*; B. *Leander tenuicornis*; C. *Palaemonetes pugio*; D. *Paseudopalaemon amazonensis*. (scales A-C = 2mm; D = 1mm).

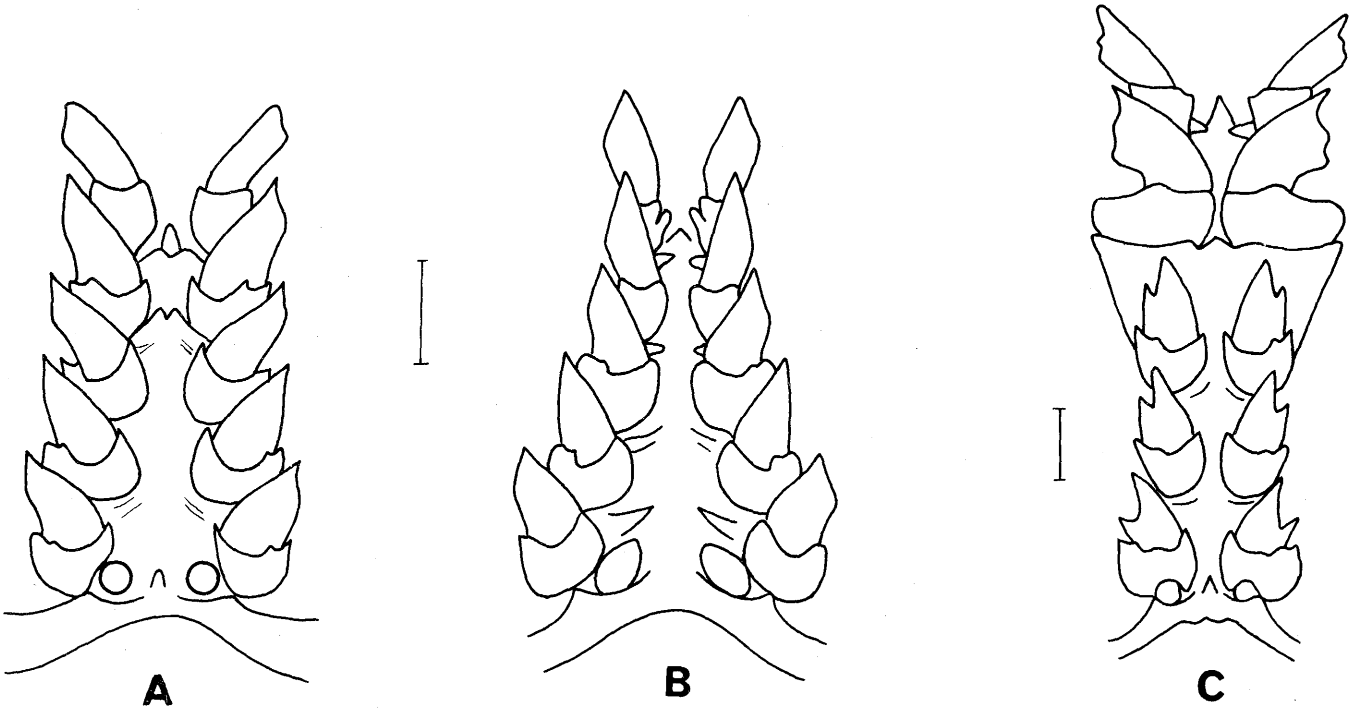

Figure 23. General view of the sternum. A. *Palaemon adspersus*; B. *P. schmitti*; C. *Troglocubanus calcis*. (sclaes A=2mm; B,C=1mm)

46) **Gills of the Third Maxilliped:** with both arthrobranchia and pleurobranchia well developed (A) (Fig. 20A); with arthrobranchia developed and pleurobranchia reduced to a knob (B) (Fig. 20B); with arthrobranchia developed and pleurobranchia reduced to a few disorganized leaflets (C) (Fig. 20C); with arthrobranchia developed and pleurobranchia surrounded by a folded invagination of the coxa (D) (Fig. 20D); with arthrobranchia only (E); with a single reduced arthrobranchia (F); with 2 arthrobranchia plus pleurobranchia (G); with no branchia (H). (CI. = 0.583).

Some disagreement exists in the literature about the name of the pleurobranchia on the third maxilliped of the Palaemoninae. Calman (1909) called both pleurobranchia. Kemp (1917) and Patwardhan (1958) mentioned both as arthrobranchia. Holthuis (1950b) referred to it as a pleurobranchia and arthro-branchia, and Powell (1976) termed those of *Desmo-caris* as two arthrobranchiae. As judged by this analysis, both branchia are located over and on the internal proximal border of the arthrodial membrane of the coxa. Although some folding of this membrane is noticeable, the branchia itself arises from the articulation between the arthrodial membrane and the pleuron. Thus it should be named an arthrobranchia rather than a pleurobranchia. I agree with Calman's suggestion that the difference between arthrobranchia and pleurobranchia is merely positional and they have the same origin. Thus the Palaemoninae possess 2 arthrobranchiae, one reduced compared to the other; for convenience the name pleurobranchia is used here to differentiate the reduced one.

Previous taxonomic work considered this character to be homogeneous in the whole Palaemoninae. However, I found that in some species the pleuro-branchia was reduced to a knob or to small projec-tions which were quite different from the leaflets in the vast majority of the Palaemoninae. Finally, because of the folding of the arthrodial membrane around the pleurobranchia, a different state was given to *Desmocaris*.

47) **Distal Setae of Leg 5:** present (A); absent (B). (CI. = 0.250).

This character is very constant among the Palaemoninae, being absent only in *Brachycarpus*, *Leander, Leandrites,* and *Neopalaemon*.

48) **Appendix Interna:** on endopods 2-5 (A) (Fig.21C); on endopods 1-5 (B) (Fig. 21A,B); on endopods 3-5 (C); absent (D). (CI. = 0.429).

This character has approximately the same distribution as the previous one. State B occurs in *Brachycarpus, Leander* spp., and *Leandrites* spp.

The sternal side of the thoracic segments has not been used previously in the classification of the family, even though some conspicuous characters are present. The basic structure of the sternum is seen in Figs. 22 through 26. Characters have been scored starting from the first thoracic sterna, the one associated with the first pair of pereiopods. Only the first, second, fourth, and fifth sterna showed characters that could be scored.

49) **Frontal Spine of First Sternum:** present with thin blunt tip (A) (Fig. 23A,C); absent (B); present, ending in a rather thick conical tip (C).(CI. = 0.176).

This character refers to a large spine located anteriorly on the sternum in front of the lateral ridges that border the first pair of legs. The shape of this spine varies somewhat when comparing different species. its absence, presence and extreme difference were scored. State C is present only in *Troglindicus phreaticus*.

50) **Lateral Ridges of First Sternum**: present with triangular shape (A) (Fig. 23A); absent (B) (Fig. 23B); fused (C); present, rectangular in shape (D); prominent and spine-like (E); socket-like, supporting coxa (F). (CI. = 0.714).

The lateral ridges arise from the base of the coxa of the first pair of legs and run transversely toward the center of the sternum.

51) **Lateral Ridge Spine of First Sternum:** present (A); absent (B); present but very massive (C); present and fused with the sternal ridge (D).(CI. = 0.50).

When there is some fusion between the lateral ridges, a spine sometimes is present between them. This may be the same spine as the frontal spine because they are never present simultaneously. However in the absence of any other evidence, it was scored as a different character.

52) **Shape of the Fifth Sternum:** with a middle folding that forms a superficial groove (A) (Fig. 24A,B,E,F); sternum is wider than A and

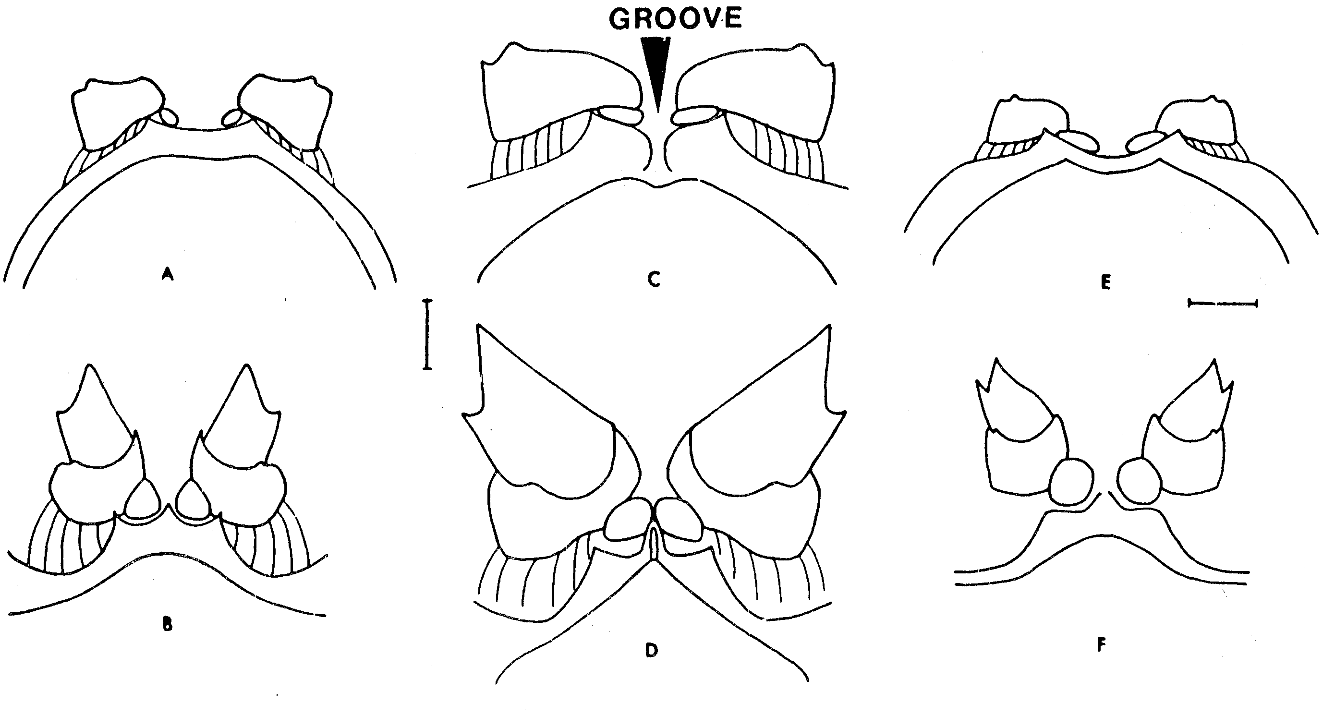

Figure 24. Detail of ventral view of fifth sternite. *Macrobrahium weberi* A. posterior view; B. dorsal view;. *M. acanthurus*. C. posterior view; D. dorsal view; *M. jelskii* E. posterior view; F. dorsal view. (scale A-D = 2mm; E,F = 1 mm).

there is no groove (B); coxae very close together and the groove remains as a small suture (C); coxae close together and groove is conspicuous and deep (D) (Fig. 24C,D); coxae separated, sternum wide and groove very superficial, with an acute pro-minence facing the anterior end (E); sternum wide and groove absent, with spine in middle of the sternum (F); sternum concealed by coxa of fifth pereiopod (G). (CI. = 0.462).

The fifth sternum shows several modifications. The groove is a narrow longitudinal trench in the posterior mid part of the sternum, formed apparently by the folding of the lateral borders.

53) **Coxa of the Fifth Leg:** not expanded over the sternum (A) (Fig. 25A-F); expanded over the sternum (B) (Fig. 26A-F). (CI. = 1.0).

The coxa of the fifth pair of legs usually is not different from that of other legs, but in the males of certain species of *Macrobrachium* the coxa is expanded, almost concealing the sternum.

54) **Spine of Fifth Sternum:** present, sharp (A) (Fig. 23C, 22C); absent (B) (Fig. 22A, 23B); present but thicker than A and ending not sharply but conical (C); reduced to a small bump (D). (CI. = 0.231).

This is a very conspicuous character in the males. The spine varies in size and shape in some species, but may be totally absent in others.

55) **Lateral Ridges of Second Sternum:** triangular shape, without fusion between them (A) (Fig. 23A); triangular shape not very pronounced and with some degree of fusion between them (B); ridge-like and failing to reach each other (C); pronounced rectangular shape and not fused (D); pronounced rectangular shape with a large degree of fusion to coxae (E)(Fig. 23C); rectangular but not pronounced, and clearly separated (F); forming a tubular projection (G); concealed by the coxae of the second pereiopod (H); semifused with the coxa of the second pereiopod, leaving 2 basal holes on each side (9); semifused, spine-like with distal end bent (J); typical, a small triangle in the middle of the sternum (K). (CI. = 0.750).

56) **Fourth Sternum:** with small lateral ridges and a bump in middle (A)(Fig. 22A); small lateral ridges and smooth in the middle (B)(Fig. 22C,D); very prominent fused ridges (C); ridges undistinguishable, smooth in the middle (D); both lateral sides prominent, forming a groove in the middle (E); concealed by prominent ridges (F); socket-like, supporting the coxa (G). (CI. = 0.375).

The fourth sternum is usually smooth (B); some species show a broad prominence in the middle (A), while in others the sternum is flat and transversely crossed by lateral ridges arising from the coxae of the fourth pair of legs. These ridges may be prominent (C) or absent (D).

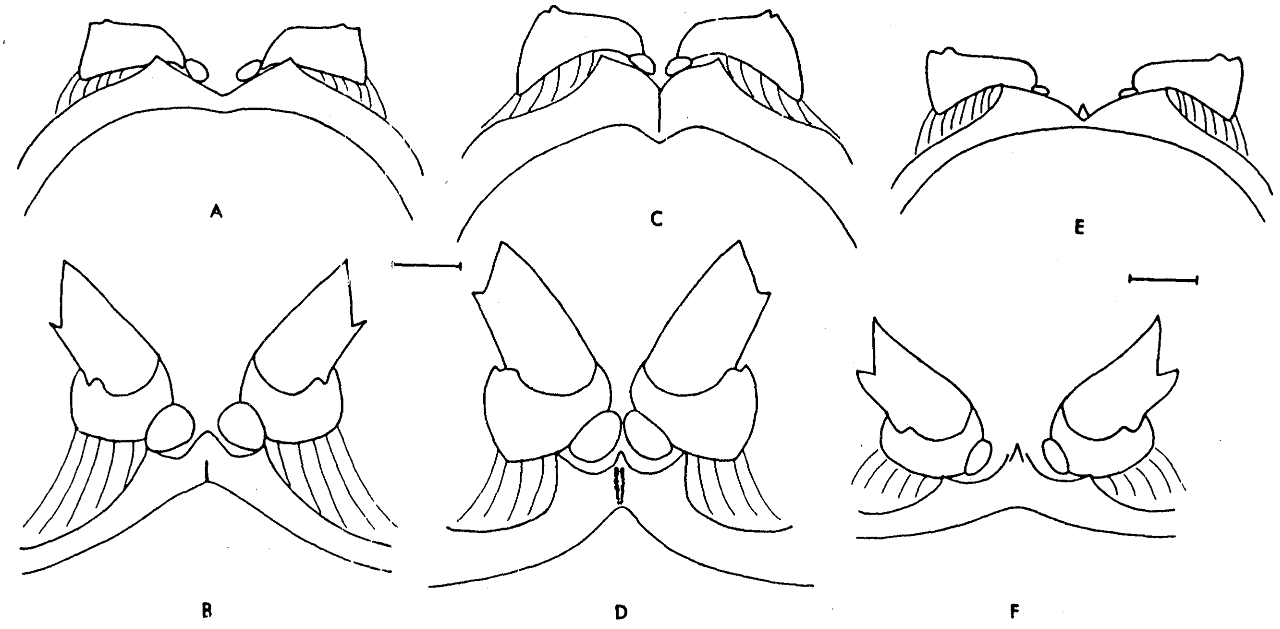

Figure 25. Detail of ventral view of fifth sternite. *Macrobrachium surinamicum,* A. posterior view B. dorsal view. *M. ferrierai,* C. posterior view; D. dorsal view. *Palaemon sundaicus*, E. posterior view; F. dorsal view (scales A-D = 1mm; E,F, = 2mm).

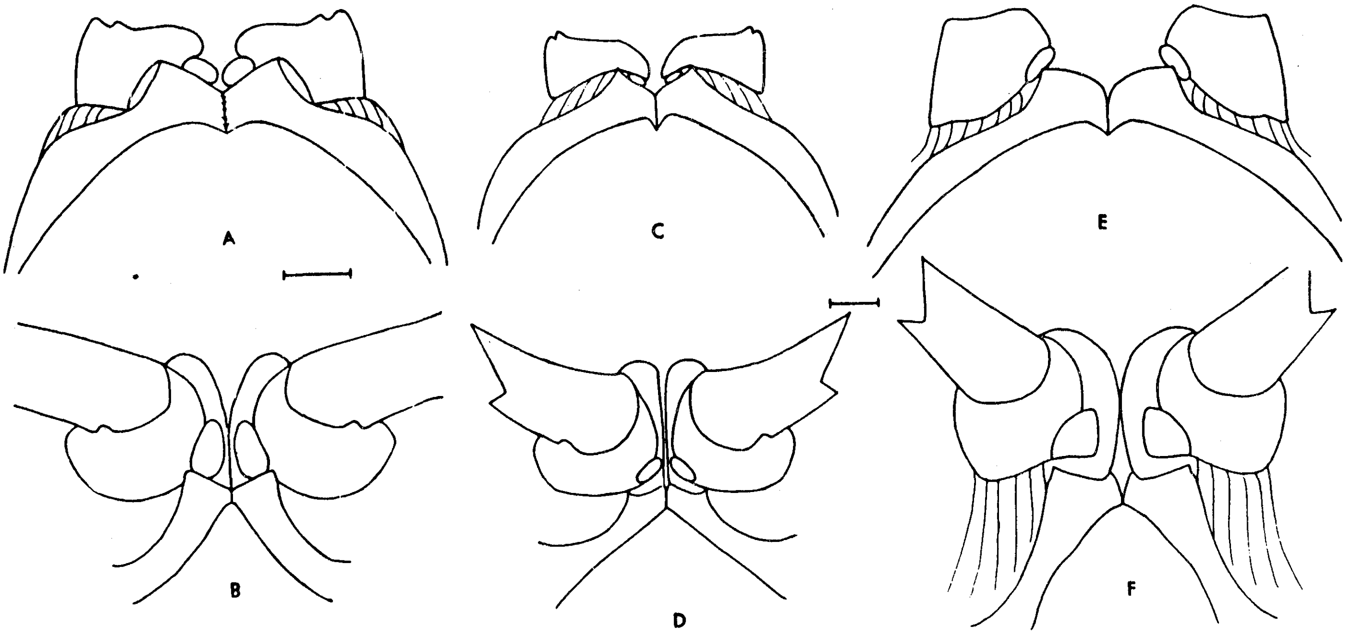

Figure 26. Detail of the coxa in fifth sternite. *Macrobrachium olfersi*, A. posterior view B. dorsal view. *M. heterochirus*, C. posterior view; D. dorsal view. *M. vollenhovenii*, E. posterior view; F. dorsal view. (scales A,B = 2mm; C-F = 3mm).

57) **Anal Plate:** with a spine (A) (Fig. 27B); smooth (B) (Fig. 27A); with a keel (C) (Fig. 27C); with a hump (E); with a tubercle bearing a spine at the top (F). (CI. = 0.267).

The anal plate has not been used previously in the taxonomy of the group.

58) **Shape of the Gill Lamellae:** finger-like (A) (Fig. 28C); cylindrical but relatively broader than A (B); flat upper margin (C) (Fig. 28A,B); cylindrical, distal end with a small crest (D); cylindrical, ending bifurcated distally (E).(CI. = 0.571).

The shape of the gill lamellae was always scored by comparing the lamella located in the middle of the pleurobranchia of the second pair of legs. The shape of the gill lamellae in *Nematopalaemon* spp. is cylindrical, but the distal end has a small crest on the inner border (D); the lamellae of *Desmocaris trispinosus* are cylindrically shaped but the distal end has a small bifurcated projection on the inner border (E).

59) **Epipod of the Third Maxilliped:** oval, sides not prŏnounced (A)(Fig. 29A); oval with inner side pronounced (B)(Fig. 29B,C); square shaped (C) (Fig. 29H); round shaped (D) (Fig. 29D); square shaped, but borders sharply defined (E) (Fig. 29E); inner side longer than outer one, ending sharply and slightly curved (F) (Fig. 29G); elongated (G) (Fig. 29F); typical, outer side bent, with an acute lateral projection (9) (Fig. 29I); typical, square shaped, with strong spines over the upper surface (J); tube-like (K); noticeably large with a projection that runs parallel to the body surface (L). (CI. = 0.692).

Although taxonomists have never used this character in the taxonomy of the family, the epipod has a very diverse array of shapes over the species examined (Fig. 29).

60) **Epipod of the First Maxilliped:** round, not bilobated (A) (Fig. 30C); round and bilobated (B) (Fig. 30A); round and bilobated, lower lobe smaller than upper one (C) (Fig. 30D); only one triangular lobe (D) (Fig. 30P); single oval lobe (E) (Fig. 30E); 2 lobes partially fused, upper part is broad and angular (F) (Fig. 30F); 2 lobes, upper one triangular, lower one rounded and clearly smaller than the upper one and overlapping about half of its surface (G) (Fig. 30G); single lobe, oval, like state E but upper part thinner and acute distally (H) (Fig. 30H); 2 lobes, upper one triangular, lower one rounded and larger, overlapping the upper one with < 1/3 of its surface (9) (Fig. 30J); similar to state 9 but the 2 lobes are fused (J) (Fig. 30K); similar to state J, but lower lobe is less prominent and does not overlap upper lobe (K) (Fig. 30L); lower border fused and convex (L) (Fig. 30M); only one oval lobe which is relatively reduced in size (M) (Fig. 30I); a single, relatively large lobe

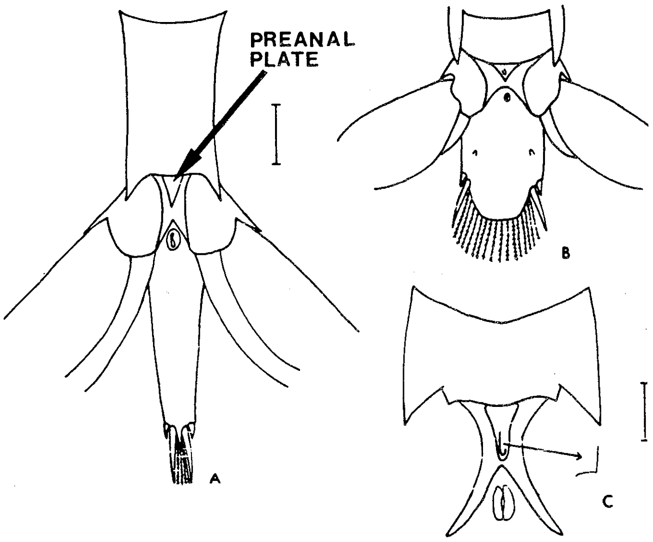

Figure 27. Preanal plate. A. *Pseudopalaemon amazonensis*; B. *Euryrhynchus amazonensis*; C. *Macrobrachium olfersi*. (scale A,B, = 1mm; C = 2 mm).

similar to state F, but upper border is rounded (N) (Fig. 30N); similar to state N, but upper and lower borders are angular and relatively larger compared to N (O) (Fig. 30O); simple lobe with round shape and a small commissure on external border (P); bilobed, upper lobe rounded, lower one with an acute pro-jection on upper border that defines an angular margin (7); similar to 7 but lobes fused, relatively larger lower border straight rather than curved (6); lobes fused, with outer border convex (4); 2 elongated tubular shaped lobes (2); fused, square in shape with a very prominent lower border (1); reduced to a very small lobe (0). (CI. = 0.645).

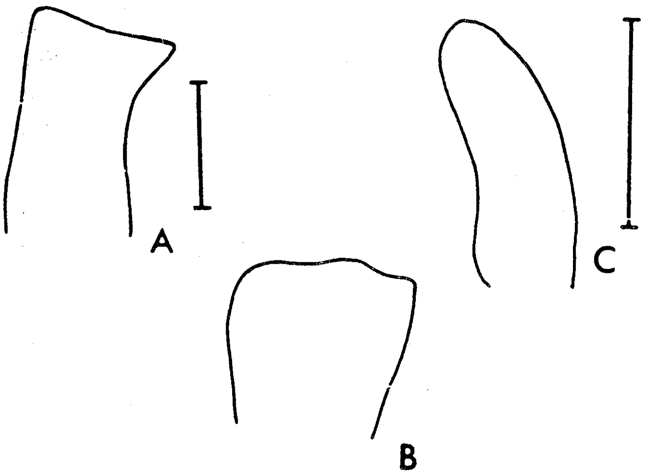

Figure 28. Shape of the gill lamellae. A. *Macrobrachium nattereri*; B. *Creaseria morleyi*; C. *Palaemon longirostris*. (scale A,B = 1mm; C = 0.5mm).

This character shows considerable diversity of shapes as partially summarized in Fig. 30.

61) **Endites of the First Maxilliped:** upper endite about the same size as the lower one, internal borders at the same level (A) (Fig. 31A); upper endite larger than the lower one, upper one with internal border projected about 30° (B) (Fig. 31B); both endites very different in shape, upper rather elongated and projected almost at 40° (C) (Fig. 31C); upper endite larger than the lower one, with a prominent basal notch (D) (Fig. 31D); upper endite very large and lamelliform, almost concealing the lower endite which is very inconspicuous (E) (Fig. 31E); upper endite larger than the lower, internal border continuous (F) (Fig. 31F); upper endite larger, typically with a convex internal border (G) (Fig. 31G); upper endite slightly larger than the lower one distal inner portion in both endites are projected innerly, distal border of lower endite angular (H) (Fig. 31H); single segment (9); upper endite larger than lower one which is reduced to a small band (J); single prominent endite, oval in shape and projected leaving a wide gap between the endite and the palp (K).(CI. = 0.769).

This character shows several character states, some of them seen in Fig. 31.

62) **Mesial Border of Endite of Maxilla II:** smooth (A), with setose hairs (B) (Fig. 14B,C). (CI. = 0.50).

63) **Posterior Border of Pleura of the Fifth Abdominal Segment:** acute (A) (Fig. 32A); lobe-like (B) (Fig. 32B); typical shape for *C. rathbunae* (C).(CI. = 1.0).

Some taxonomists also distinguish between acute and round ends of the fifth pleura. I found this difficult, and consequently both (acute and round) are considered to be the same state A.

64) **Mastigobranchia of Third Maxilliped:** thin (A)(Fig. 33A); thick (B)(Fig. 33B). (CI. = 1.0).

The mastigobranchia is uniform in most of the species, except in a small group of *Macrobrachium* in which it is considerably thicker (see Fig. 33).

65) **Appendix Masculina:** with a single row of lateral spines from the base to the tip (A) (Fig. 34A, 35A,B); the lateral spines are reduced in

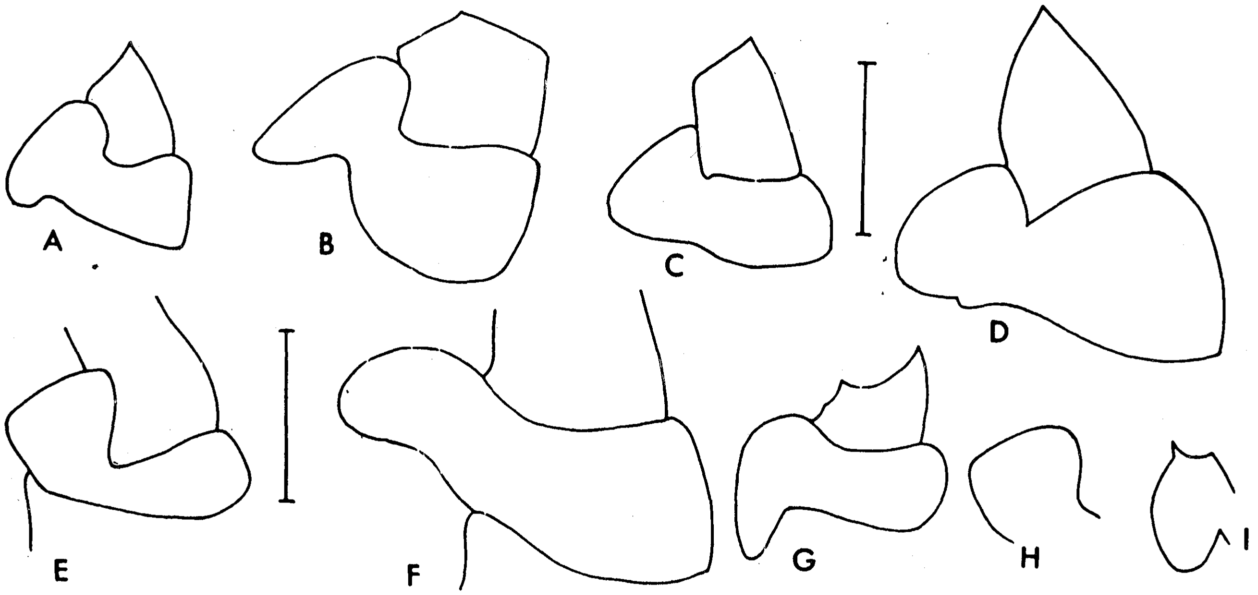

Figure 29. Epipod of the third maxilliped. A. *Palaemon maculatus*; B. *P. floridanus* ; C. *P. concinnus*; D. *P. gracilis*; E. *Palaemonetes mecedae*; F. *P. antrorum*; G. *Leander tenuicornis*; H. *Euryrhynchus amazonensis*; I. *Desmocaris trispinosus*. (scale A-D, G-I = 1mm; E,F = 0.5mm).

number in the basal half, usually without spines (B) (Fig. 34B,E); like A, in addition, with several small distal spinules (C) (Fig. 34C); distal 1/3 slightly bent, spines smooth and relatively long only on the distal 1/3 (D) (Fig. 34D); tip with 1 large strong spine plus 2 smaller spines (F) (Fig. 34F,G); spines all about the same size, appendix ending in 4 spines (G) (Fig. 34H,I); few small lateral spines on distal 1/3 and tip with 4 or 5 strong spines (9) (Fig. 34K,L,N); distal end of gonopod noticeably smaller and acute than G (J) (Fig. 34J); short gonopod smaller than appendix interna, 2 or 3 large spines at tip covered with minute strong spinules (K) (Fig. 36A); tip with 3-4 strong spines, one of them noticeably longer than the others and bent (L) (Fig. 34M); less than 1/3 the length of the appendix interna, broad distally with several rows of spines of about the same size, typical of *Desmocaris* (M); with several longitudinal rows of spines (3-5) along the main axis and a lateral longitudinal groove (N) (Fig. 35C); general shape as N, but only 2 rows of longitudinal spines, no longitudinal groove (O) (Fig. 36B); with endopod fused to the gonopod (P); typical of *Typhlocaris galilea*, noticeably shorter than the appendix interna and possesses several long and strong spines distally (Q); shorter than appendix interna, with 2 longitudinal rows of lateral spines, all about the same length (8); 1/4 longer than the appendix interna, upper end thicker than basal part, with 8-12 large spines on the tip (7); about 2/3 longer than the appendix interna, distal half covered by minute spinules, with a single, large, and strong spine on the tip, flanked by 2 smaller ones (6); same size as appendix interna, relatively flat and 2 rows of strong spines on each lateral border (5); laminar shape (4); absent (3).(CI. = 0.833).

66) **Statocyst:** statocyst open, statolith of sand grains (A); statocyst closed, statolith secreted (B) (Fig. 37); statocyst closed, statolith fluid-like, probably a drop of oil (C); absent (D).(CI. = 0.750).

Statocysts have been reported in a large number of physiological papers (Prentis, 1901, and references therein; Shen, 1934), but have never been used for classification purposes and few papers show drawings (Calman, 1909). It is my view that the 3 states reflect complex morphological and physiological differences between species. The statocyst chamber is open in most species but concealed by a projection of the lateral basal spine on the first segment of the antennular peduncle. Inside the otocyst there is a row of sensory hairs that are attached to sand grains. In the other state, the otocyst is closed, the lateral spine is not expanded, and the otolith consists of a secreted structure that rests on the circular row of sensory hairs whose tips are inserted in the otolith.

67) **Ocellus:** present (A); absent (B).(CI. = 0.250).

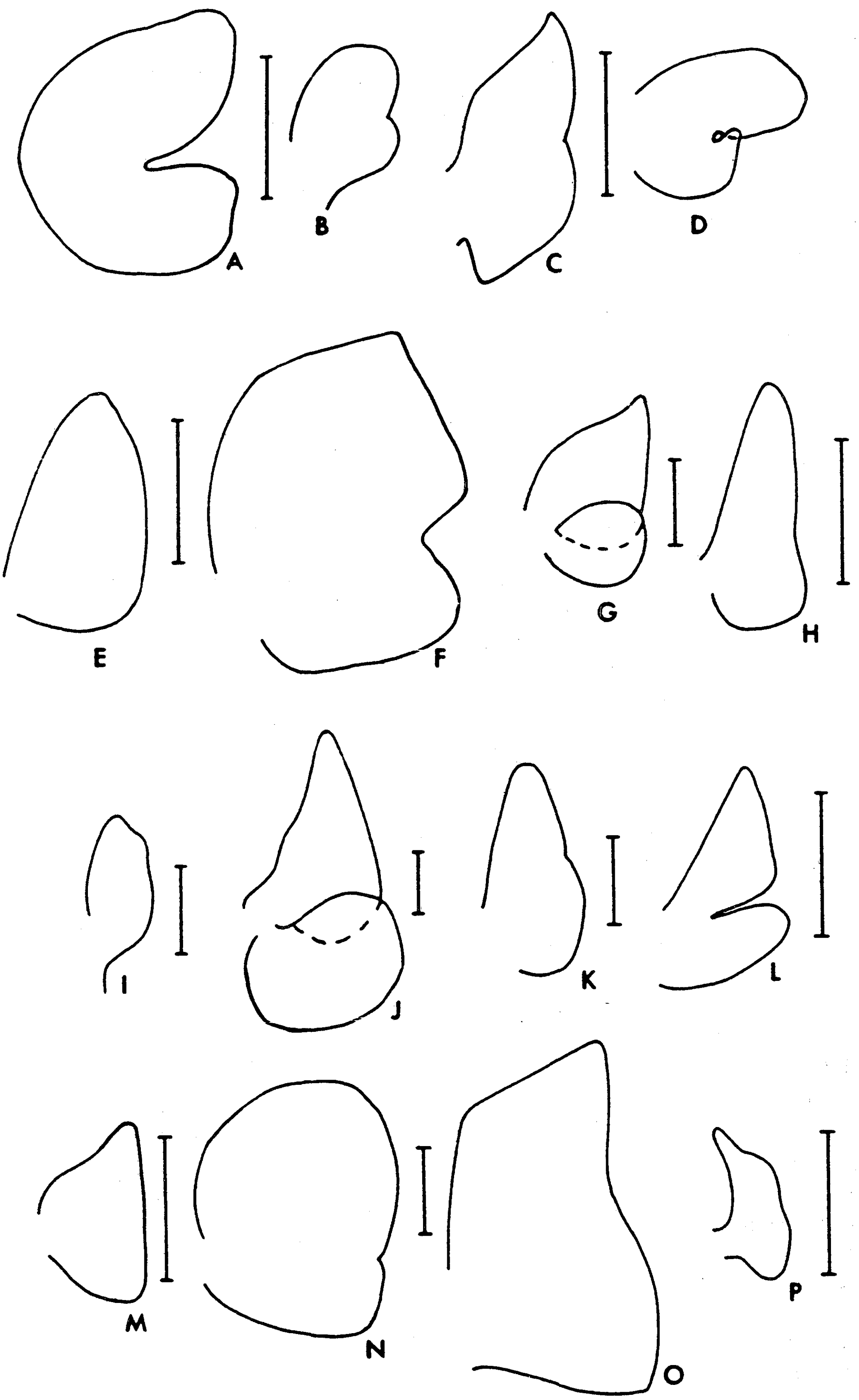

Figure 30. Epipod of the first maxilliped. A. *Palaemon ritteri*; B. *Palaemonetes sutkusi*; C. *P. kadiakensis* ; D. *Palaemon concinnus*; E. *P. gracilis*; F. *Nematopalaemon schmitti*; G. *Leptocarpus potamiscus*; H. *Palaemonetes mercedae*; I. *Desmocaris trispinosus*; J. *Macrobrachium carcinus*; K. *M. cortezi*; L. *M. dierthrum*; M. *M. pumilum*; N. *Creaseria morleyi*; O. *Troglocubanus calcis*; O. *Troglindicus phreaticus* (scales A-G,I,K-P = 1mm; H = 0.5mm; J = 3mm).

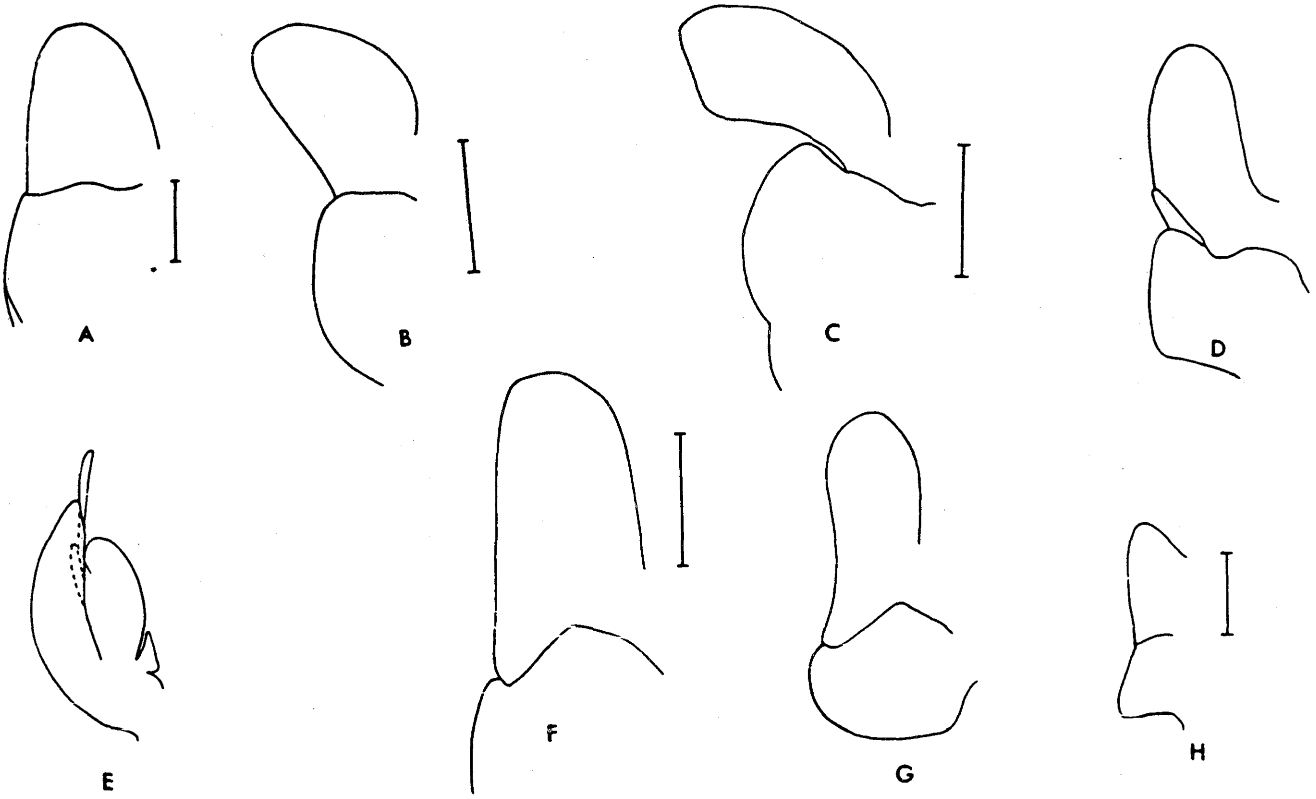

Figure 31. Endite of the first maxilliped. A. *Macrobrachium amazonicum*; B. *Palaemonetes kadiakensis*; C. *P. sinensis*; D. *P. tonkinensis*; E. *P. holthuisi* redraw from Holthuis, 1952); F. *Palaemon gracilis*; G. *Palaemonetes ivonicus*; H. *Desmocaris trispinosus*. (scale 1 mm).

The ocellus refers to a small commissure of unknown function along the dorsal internal border of the eye. It is present in all species of the subfamily except for members the genera *Nematopalaemon* and *Desmocaris*.

68) **Larval development:** abbreviated (A); complete (B). Not used in the annalysis.

There has been considerable research on larval development in the subfamily (Pereira, 1989; Pereira & Garcia, 1995). Species whose entire larval development has not been do-cumented were assigned as complete (B) if they produce a large number (usually > 300) of small eggs (0.4-0.7 mm in diameter). Species with a smaller number (ususaly < 200) of large eggs (1.0-2.8 mm in diameter) were classified as having abbreviated larval development (A), since they have no more than 6 larval stages and no planktonic stages.

69) **Shape of the Dactyl of Pereiopods 3-5:** simple (A); biunguiculate (B); with several conspicuous spines (D); with a row of spines forming a comb-like structure (E). (CI. = 0.5).

70) **Pattern of Distal Spines on the Telson:** 2 pairs, inner pair about the same thicknes as outer pair (A); 3 pairs of about same thickness (B); 3 pairs of about same thickness but the 2 inner pairs are the same size and about 2 times smaller than the outer pair (C); 2 pairs, inner pair about 2 times thicker at base than the outer pair (D); 2 pairs, each pair in a different dimensional plane (E); 7 pairs (F); 4 pairs (G); 2 pairs, outer pair located dorsally on telson (H). (CI. = 0.778).

71) **Number of Dorsal Spines on the Telson:** 2 pairs (A); 3 pairs (B); 5 pairs (C); 7-8 pairs (D); absent (E). (CI. = 1.0).

72) **Shape of the Lower Blade of Scaphognathite:** round, of about the same shape as upper blade (A); elongated compared to upper blade (B). (CI. = 0.50).

73) **Pleurobranchia on Pereiopods 4-8:** absent (A); present (B).(CI. = 1.0).

74) **Arthrobranchia on Pereiopods 4-8:** absent (A); present (B). (CI. = 1.0).

75) **Epipod on Pereiopods 4-8:** absent (A); present (B). (CI. = 0.5).

76) **Exopod on Pereiopods 4-8:** absent (A); present (B). (CI. = 0.5).

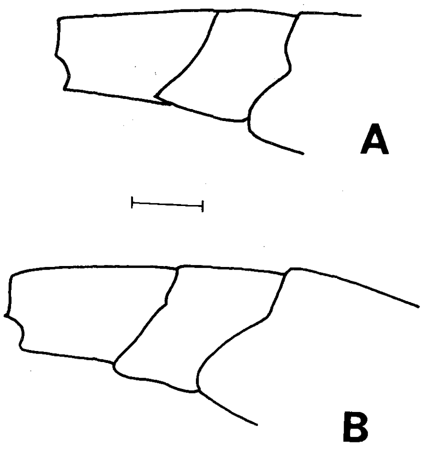

Figure 32. Detail of the pleuron of fifth abdominal segment. A. *Palaemon debilis*; B. *Exopalaemon orientis* (scale, 3 mm)

77) **Mastigobranchia on Maxilliped 2:** absent (A); present (B). (CI. = 1.0).

78) **Shape of the Lower Palp of Maxilla 1:** about same length as upper endite, cylindrical shape (A); larger than upper endite, distal end broader than basal part (B). (CI. = 1.0).

79) **Mastigobranchia on Maxilliped 1:** absent (A); present (B). (CI. = 1.0).

80) **Number of Segments of Maxilliped 3:** 7 (A); 6 (B). (CI. = 1.0).

81) **Shape of the Eye Facet:** typically square in all palaemonins (A), except in *Nematopalaemon schmitti*, where the eye facets are further subdivided into clusters of 4 and situated in a more perpendicular plane rather than tangential to the surface of the eye (B). This is a derived condition, as opposed to the single square facet found in other palaemonins or the hexagonal facet present in *Euryrhynchus* and *Typhlocaris* (Fig. 38) (C). This latter condition is considered to be more primitive since hexagonal facets are typical of apposition optics and the square facet of superposition optics (Fincham, 1980, 1984). Hexagonal facets usually are seen only during early larval stages in Caridea. Finally, the vestigial condition of the eyes of *Procaris ascensionis* and *Vetericaris chaceorum* was scored as a different state (D). (CI. = 1.0).

82) **Carapace Shape:** approximately cylindrical shape (A); oval shape, expanded appearance (B). (CI.= 1.0).

83) **Habitat:** strictly freshwater (F); Adults live on rivers but larvae develops in estuarine conditions (8); esturine species (E); litoral marine species (M). Not use in the annalysis.

Although characters 83 and 68 were scored, there were not used in the analysis.

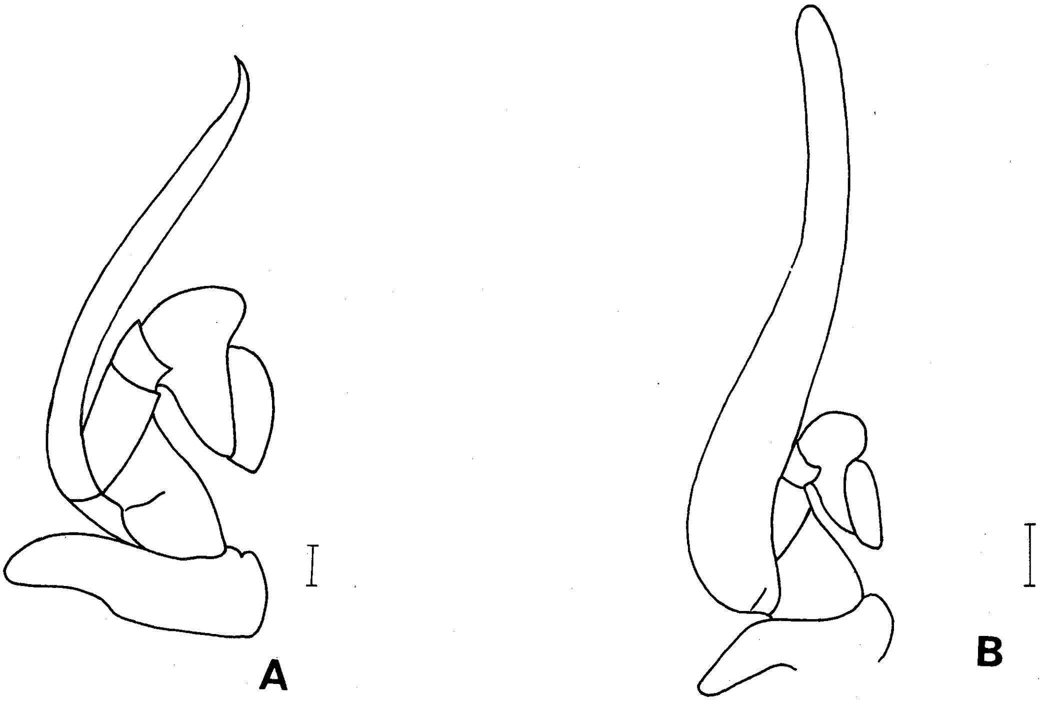

Figure 33. Comparison of the mastigobranchia on the third maxilliped. A. *Macrobrachioum carcinus*; B. *M. olfersi* (scale A = 1mm; B = 2mm)

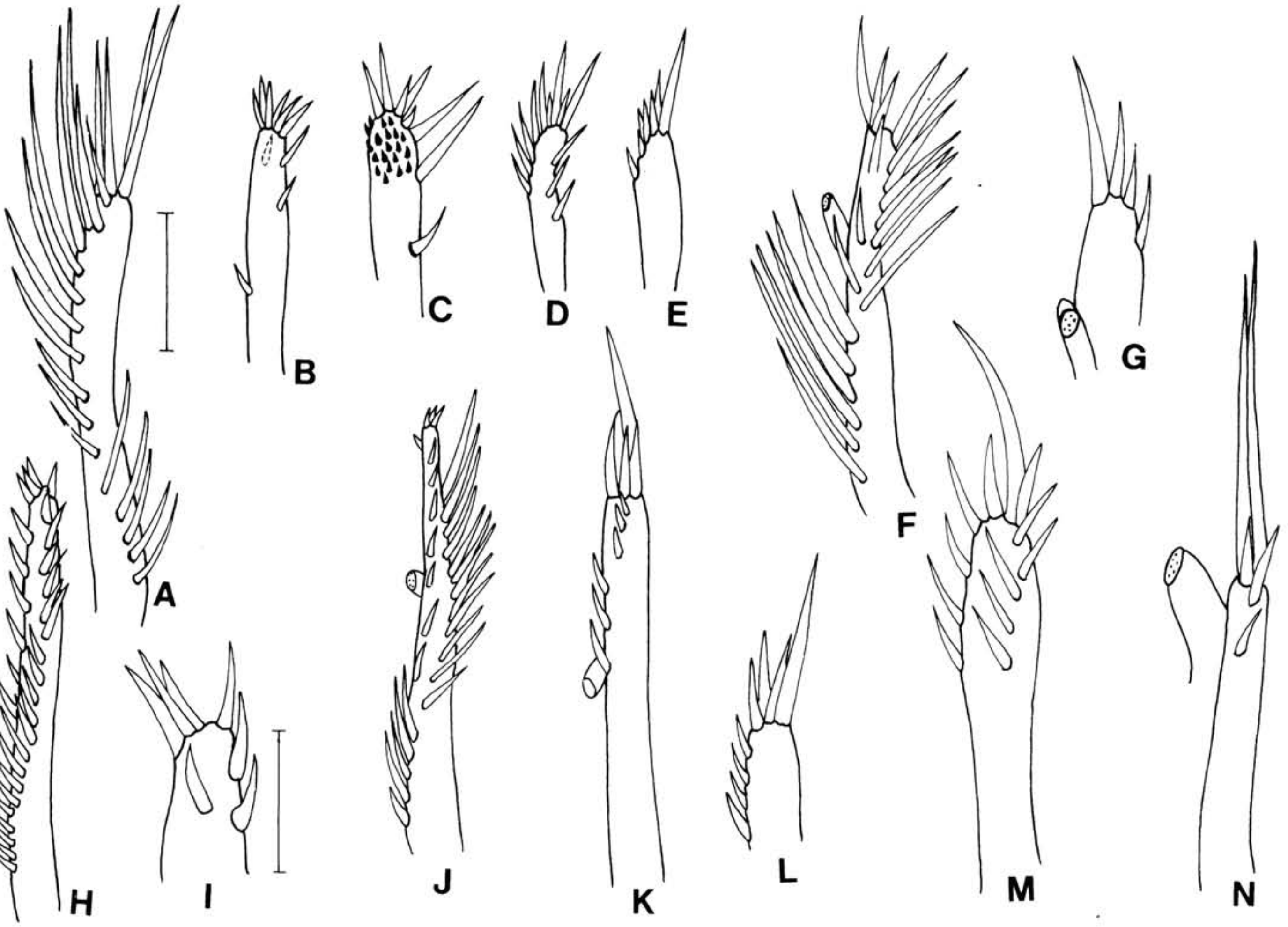

Figure 34. Apendix masculina. A. *Palaemon elegans*; B. *Palaemonetes texanus*; C. *P mesogenitor*; D. *P antrorum*; E. *P sinensis*; F. *Palaemon concinus*; G. detail of tip; H. *P paucidens*; I. detail of tip; J. *P semmelinki*; K. *P gracilis*; L. detail of tip; M. *Palaemonetes ivonicus*; N. *Exopalaemon orientis* (scales A,C,G,I-N = 0.5mm; B,D-F,H = 1mm)

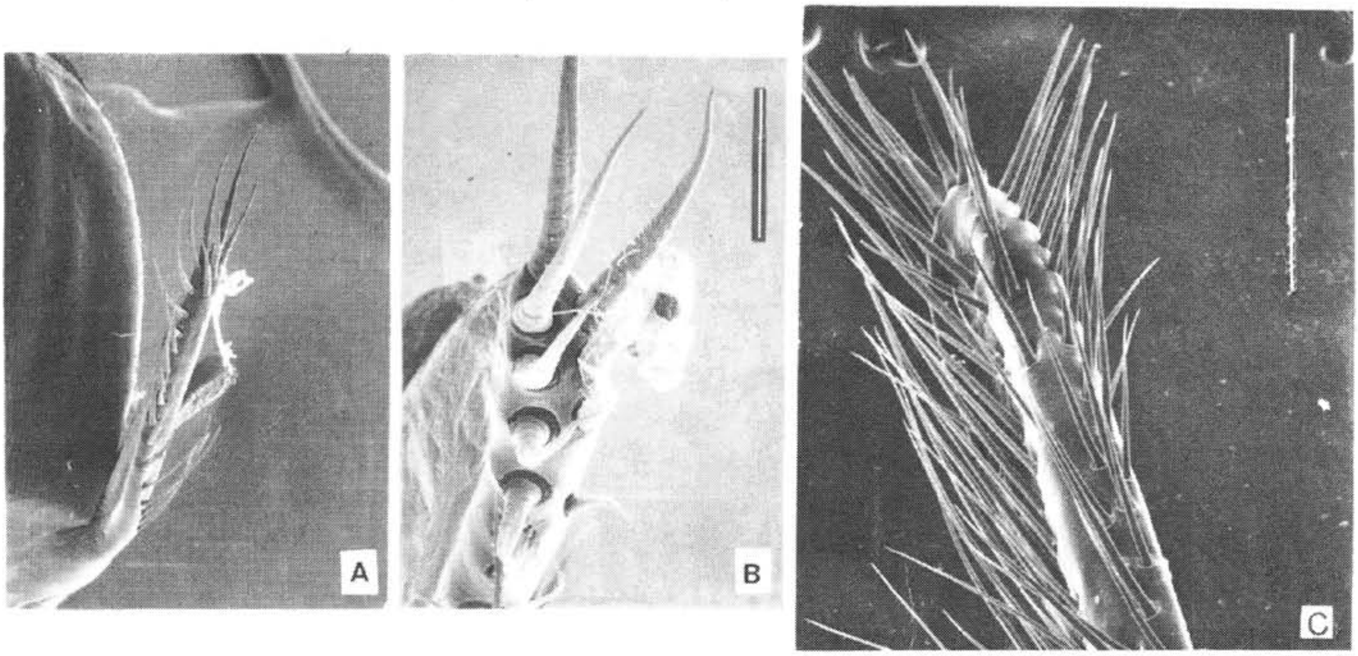

Figure 35. Apendix masculina. A. *Palaemonetes pugio*; B. detail of tip; C. *Macrobrachium acanthurus* (scale A,C=0.5mm; B=0.1mm)

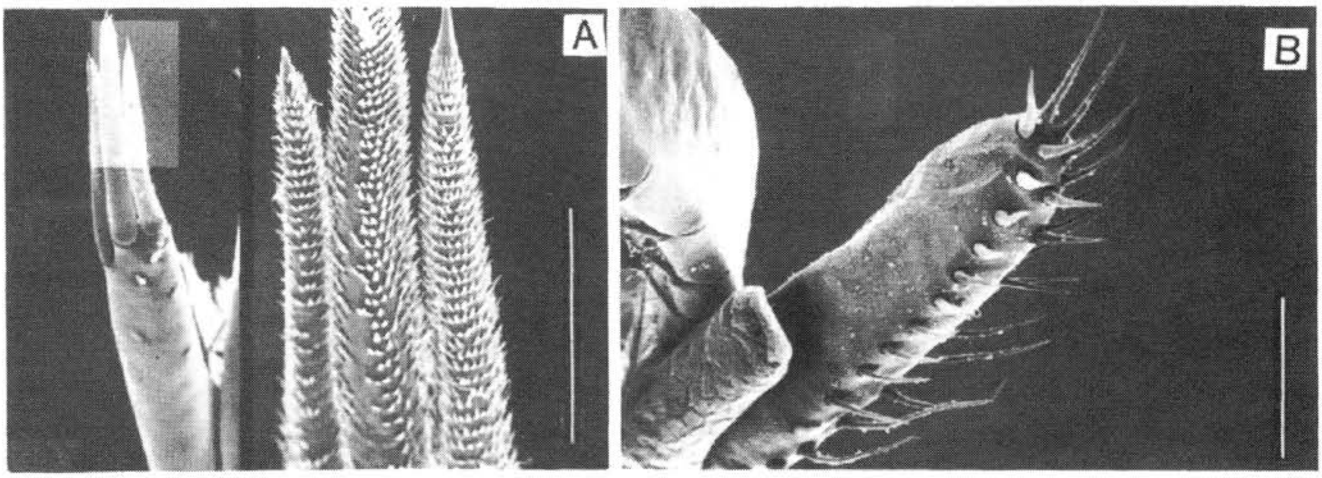

Figure 36. Apendix masculina A. *Brachycarpus biunguiculatus* with detail of the spines on the tip; B. *Pseudopalaemon amazonensis*. (scales A = 0.5mm; B = 0.2mm).

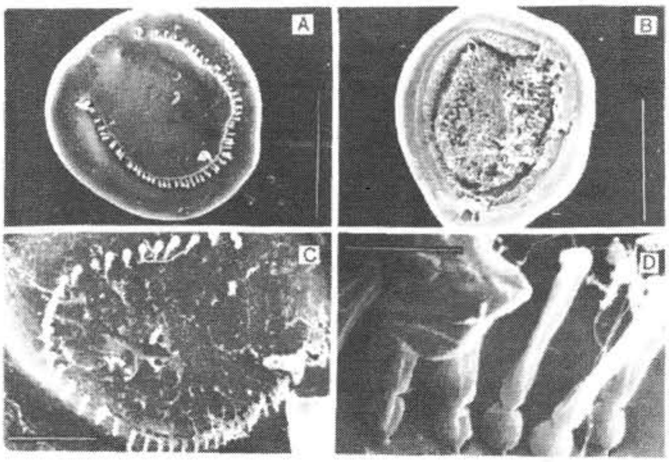

Figure 37. Statolith and statocyst. A. *B. biunguilatus*, view of the basal side of the statocyst showing the insertion points of the sensory organs; B. *L. tenuicornis*, secreted statolith same view as A; C. *P. floridanus*, surface of the statocyst showing the row of sensory organs; D. *P pugio*, detail of sensory organs (scale A,B,D = 0.2mm; C = 0.1mm)

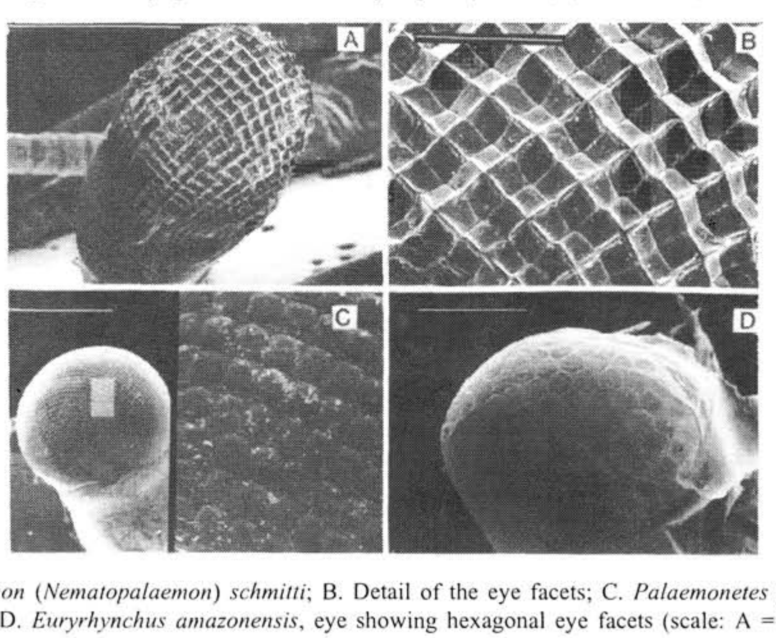

Figure 38. Eye. A. *Palaemon* (*Nematopalaemon*) *schmitti*; B. Detail of the eye facets; C. *Palaemonetes pugio*, eye and magnified detail of the eye facets; D. *Euryrhynchus amazonensis*, eye showing hexagonal eye facets (scale: A = 1mm; B-D = 0.2mm).

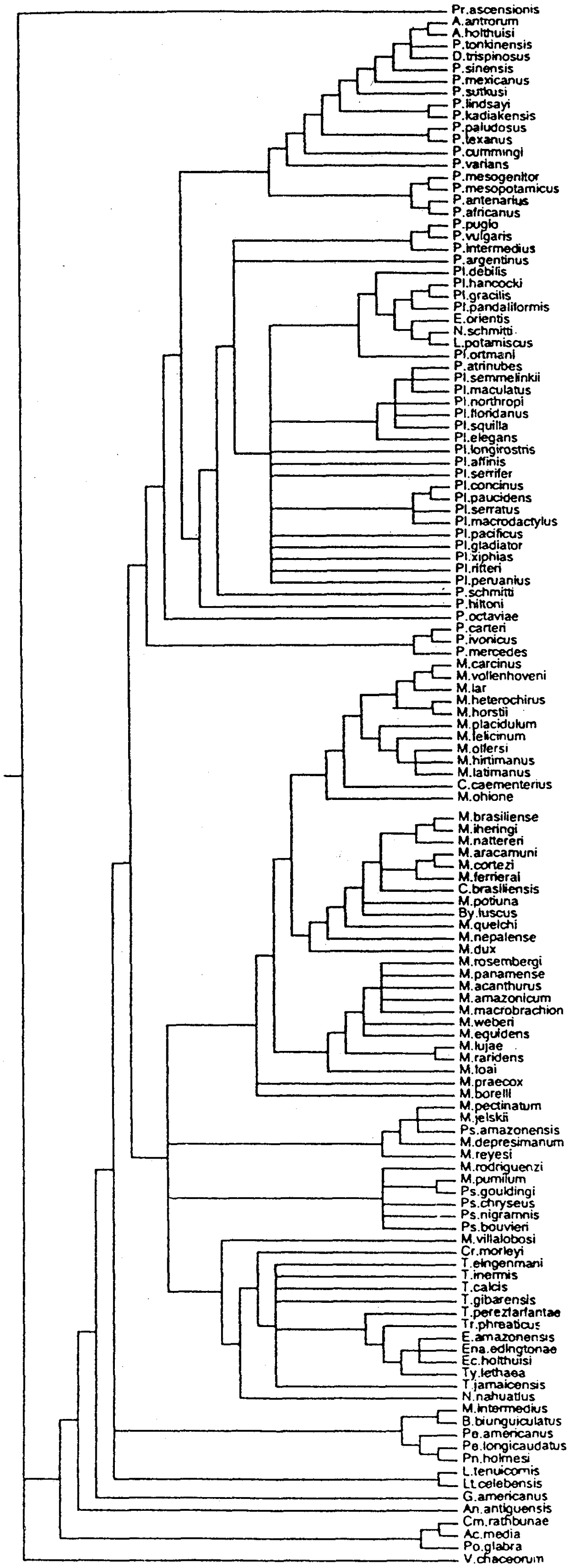

Figure 39.- Strict consensus tree from 400 trees retained in memory in final annalysis; tree length 606 steps. Name of taxa are based on Holthuis, 1950b, 1955.

Phylogenetic Relationships of The Palaemonidae.

The shortest 'tree found was 606 steps length with a Consistency Index of 0.525 excluding uninformative characters; there is not a single tree, we end up with 400 trees before the computer ran out of memory. However, the strict consensus tree has a length of 638 steps and CI.= 0.502 (Fig. 39) single trees choosen ramdomly, are all very similar differing only in the position of some terminal taxa within otherwise invariate clades; the major branches of this tree have remained unchanged since the early stages of annalysis. The majority rule consensus (Fig.40) shows an almost fully resolved tree with a length of 606 so, it is one of the most parsimonious trees found. Polytomies, correspond mainly to ambiguity of character change from node to terminal taxa (Tabla 9). Otherwise, most clades appear 100% of the time and just few appear 76 % or more (Figure 40). This indicates that the tree is very stable and the cladistic pattern generated may be used as the first hypothesis of phylogenetic relationship of Palaemoninae shrimps and a working hypothesis to address questions of taxonomy and evolutionary history of the group (Figure 41).

Taxa in families other than the Palaemonidae were always located basally (Figure 41; below node 2) clustering outside. This can be interpreted as additional support for the monophyly of the family Palaemonidae (Farris, 1972; Clarke and Curran, 1986; Mitter and Silverfine, 1988), above node 1-2 with 22 apomorphies; Table 9 but certainly not for the superfamily Palaemonoidea. The representative of the superfamily Campylonotoidea (*Campylonotus rathbunae*) clustered closer to the representatives of the superfamily Oplophoroidea (*P. glabra* and *A. media*), in agreement with Balss (1927) early classification. This result corroborates Chace and Manning's (1972) assertion that the superfamilies among the Caridea are not well delimited. In this case similarities of mouth parts and gill formulae link the Campylonotidae with members of the superfamily Oplophoroidea. Taxa in the Procaridoidea remain the most basal in the tree; *P. ascensionis* and *V. chaceorum* cluster together as related taxa , then a small cluster formed by representatives of the families Oplophoridae, Atyidae and, as mentioned above, the Campylonotidae.

An. antiguensis is the most basal taxa that split along in a single branch (node 2) with 13 autapomorphies. It is considered by Chace (1992) as a monotypic family. Then follows *G. americanus* considered also as a distinct small familiy by Chace (1992). It is represented in a single branch node (3), with 10 apomorphies (Fig. 41, Table 9).

The clade above node 12, groups all taxa in the sub family Pontoniinae and some genera in the Palaemoninae; *Periclimenes, Palaemonella*, (Pontoniinae), *Brachycarpus, Leander* and *Leandrites* (Palaemoninae) with 2 apomorphies. *Ln. tenuicornis* and *Lt. celebensis* form a cluster together basally with 5 apomorphies (node 13), follows another branch (nodes 12-14) that include the species *B. biunguiculatus* and *M. intermedius* with 4 apomorphies. Finally the species *Pe. longicaudatus*, *Pn. holmesi* and *Pe. americanus* cluster with 6 apomorphies (node 14-15) .

From nodes 4-5 and above with 7 apomorphies, there is a major clade that comprises only species in the subfamily Palaemoninae, (excluding *Leander, Leandrites* and *Brachycarpus*). This major clade split into 2 major branches above node 5, one containing species in the genera *Macrobrachium, Pseudopalaemon, Bithynops, Cryphiops, Creaseria, Neopalaemon, Trglocubanus, Troglindicus, Eurhyrynchus, Eurhyrhynchoides, Euryrhynchina* and *Typhlocaris*; (nodes 5-18 and above) with 5 apomorphies, and the other major branch (nodes 5-6), with 2 autapomorphies, include the genera *Palaemonetes, Allaocaris, Desmocaris, Palaemon, Nematopalaemon, Exopalaemon,* and *Leptocarpus.*

The first cluster that arises from the former major clade is nodes 18-19 (with 2 apomorphies) containing all of the species in the genus *Pseudopalaemon* and some species of *Macrobrachium.* Then follows 2 cluster one containing a group of species of *Macrobrachium* (node 19-24 and above, with 2 apomorphies). The other cluster in cluding species in the genera *Pseudopalaemon* and *Macrobrachium* (node 19-20 and above, with 1 apomorphy). The major branch continues with another cluster of species (node 18-27 and above, with 3 apomorphies), that includes all taxa in the subfamily Euryrhynchinae, Typhlocaridinae, *Troglocubanus*, *Creaseria*, *Neopalaemon* and one species of *Macrobrachium.* Subfamilies Typhlocaridinae and Euryrhynchinidae are above

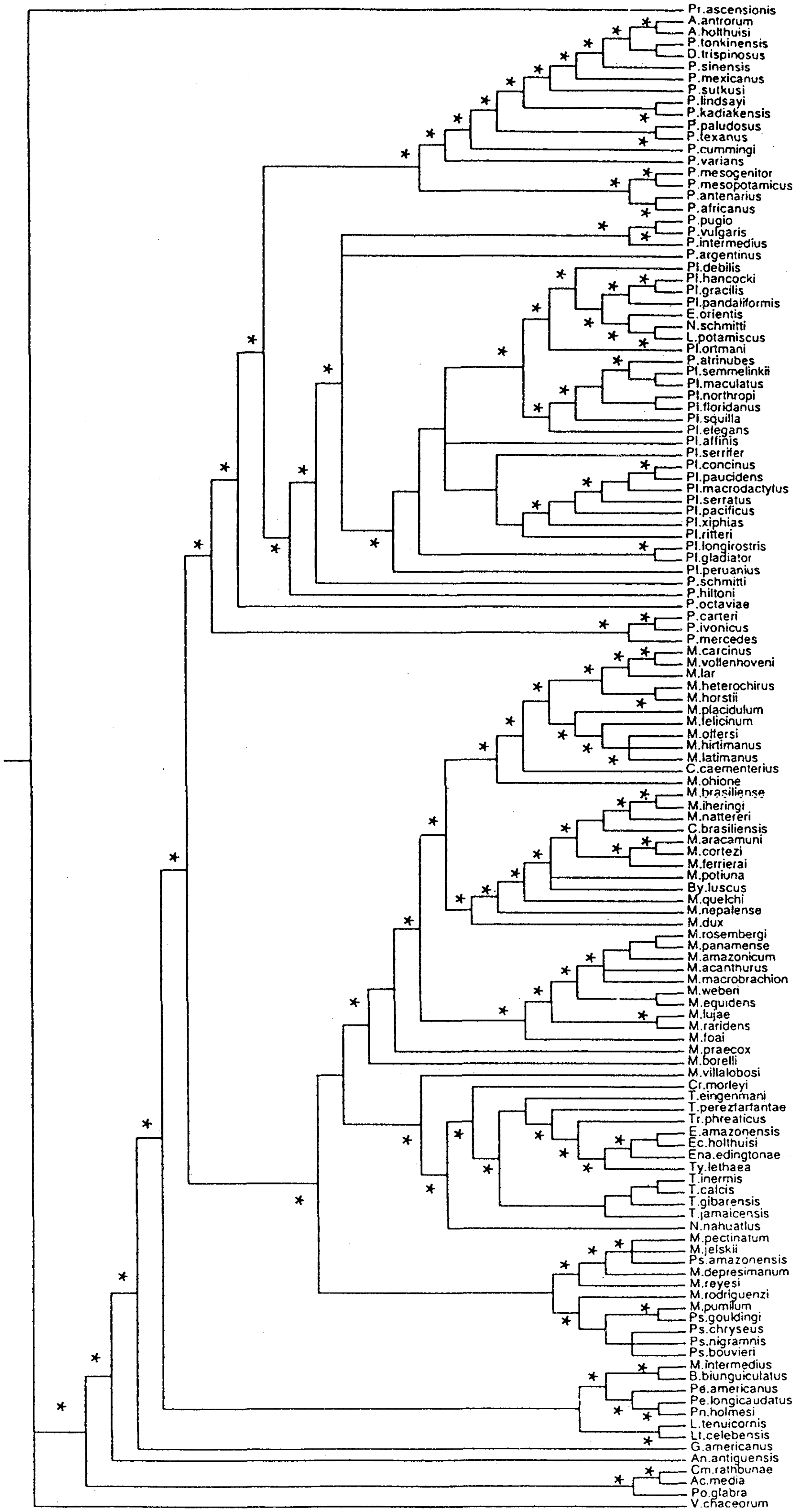

Figure 40.-Majority rule consensus tree from 400 trees retained in memory from final annalysis; * denote branches that appear 100% of the time.Tree length 606 steps. Name of taxa are based on Holthuis, 1950b, 1955.

nodes 37-38, with 9 autapomorphies; with the exception of the Eurhyrynchinae all other taxa in this clade are cave dwellers.

Then nodes 27-41 and above, with 4 apomorphies, cluster most of the species of *Macrobrachium* and the small genera *Bythinops* and *Cryphiops*. This clade contain 2 species of *Macrobrachium* that split sucessivelly from basal line (*borelli, praecox*) and 3 major clades, node 43-44 and above with 1 apomorphies contains a basal clade, and node 43-52 with 2 apomorphies hold the other 2 clades one with 1 apomorphy (nodes 52-53) and the oher one (nodes 52-63) with 2 autapomorphies.

The other major clade within the Palaemoninae (nodes 5-6 and above) contains all species in the genera *Palemon* and *Palemonetes*; the first clade contain 3 related species from South American (nodes 6-73) with 9 apomorphies. Then one species split apart *P. octaviae* with 1 apomorphy. It follows a major clade (nodes 8-9 and above) with 3 apomorphies that comprises most of the species of *Palaemonetes*, and all especies of *Allocaris* and *Desmocaris*, this last genus (with 2 very similar species) is morphologically distant from other correlatives since its node is defined by 21 apomorphies; however, it always cluster together with *P. sinensis* and *P. tonkinensis* with (nodes 116-118) with 4 autapomorphies. 4 species of *Palemonetes*: *mesogenitor, mesopotamicus, antenarius* and *africanus* form a small monophyletic group (nodes 9-105 and above) with 1 autapomorphy. Above nodes 8-77, split off sequentially 6 species of *Palaemonetes*: *hiltoni, schmitti, argentinus* and a monophyletic group (nodes 77-103) with 1 apomorphy, of closely morphologically related species *pugio, vulgaris* and *intermedius*. Above nodes (77-78) with 1 apomorphy split all the species in the genera *Palaemon, Exopalaemon, Nematopalaemon* and the monotypic genus *Leptocarpus*. The first that split apart is *Pl. peruvianus*, then follows *Pl. longirostris* and *Pl. gladiator* in a single group above nodes 78-80 with 1 apomorphy, follows a major clade above nodes 79-81 with 1 autapomorphie with other species left. This major clade split into 3 smaller clades; the first one, above nodes 81-82 with 1 apomorphy contains 7 the species of *Palaemon*: *ritteri, xiphias, pacificus, macrodactylus, serratus, paucidens* and *concinus*; then follows *P. affinis* with no clear relations to other clades because of having a 0 length branch; 2 major clades follow defined by 1 synapomorphy in node 81-89; the clade above nodes 89-90 with 1 apomorphy, contains 6 species of *Palaemon*: *elegans, squilla, floridanus, northropi, maculatus* and *semmelinkii* and the species *Palaemonetes atrinubes*. The other major clade (node 89-96 and above) with 4 apomorphies contain especies in the genera *Palaemon, Exopalaemon, Nematopalemon* and *Leptocarpus*. the species split off sequentially starting with *Pl. ortmani*, then *Pl. debilis*, then a clade with 3 species of *Palaemon*: *pandaliformis, hancocki* and *gracilis* and a sister clade with species *Exopalaemon orientis, Nematopalaemon schmitti* and *Leptocarpus potamiscus*.

DISCUSSION

Since early taxonomic reviews, most of the taxa that comprise the family Palaemonidae have been considered to be a natural group. Changes that occurred subsequently have improved our knowledge of the morphological diversity but failed to assess relationships among higher taxa, Chace (1992) clasification is a major improvement, but still more work has to be done (as he assert in the paper). The probable reason for this is that taxonomists have emphasized on unique characteristics, or unique combination of characters to define major groups rather than judging characters using the minimal assumption of descent with modification. Therefore, the genealogy is the best predictor of monophyletic groups (Wiley, 1979). Some conflicts emerge between this analysis and Holthuis (1950b;52) and Chace (1992) classification of Palaemonidae. For example, *Cr. brasiliensis* (node 60, Fig. 41) and *Cr. caementarius* (node 64, Fig.41) cluster in different clades, suggesting that the genus is polyphyletic. The species *M. intermedium* (node 17, Fig. 41) is outside of the major clades of Palaemoninae being a species more related to *Brachycarpus* than to any other species of *Macrobrachium* (Node 18 and above). The genus *Pseudopalaemon* (node 19 and above) is also paraphyletic sharing the clade with some species currently asigned to *Macrobrachium*. Most *Macrobrachium* species (node 18 and above) form several clades of species groups giving some support to earlier classification by Ortman (1891) who first considered this genus divided into several subgenera. Finally, the genera *Palaemon* and

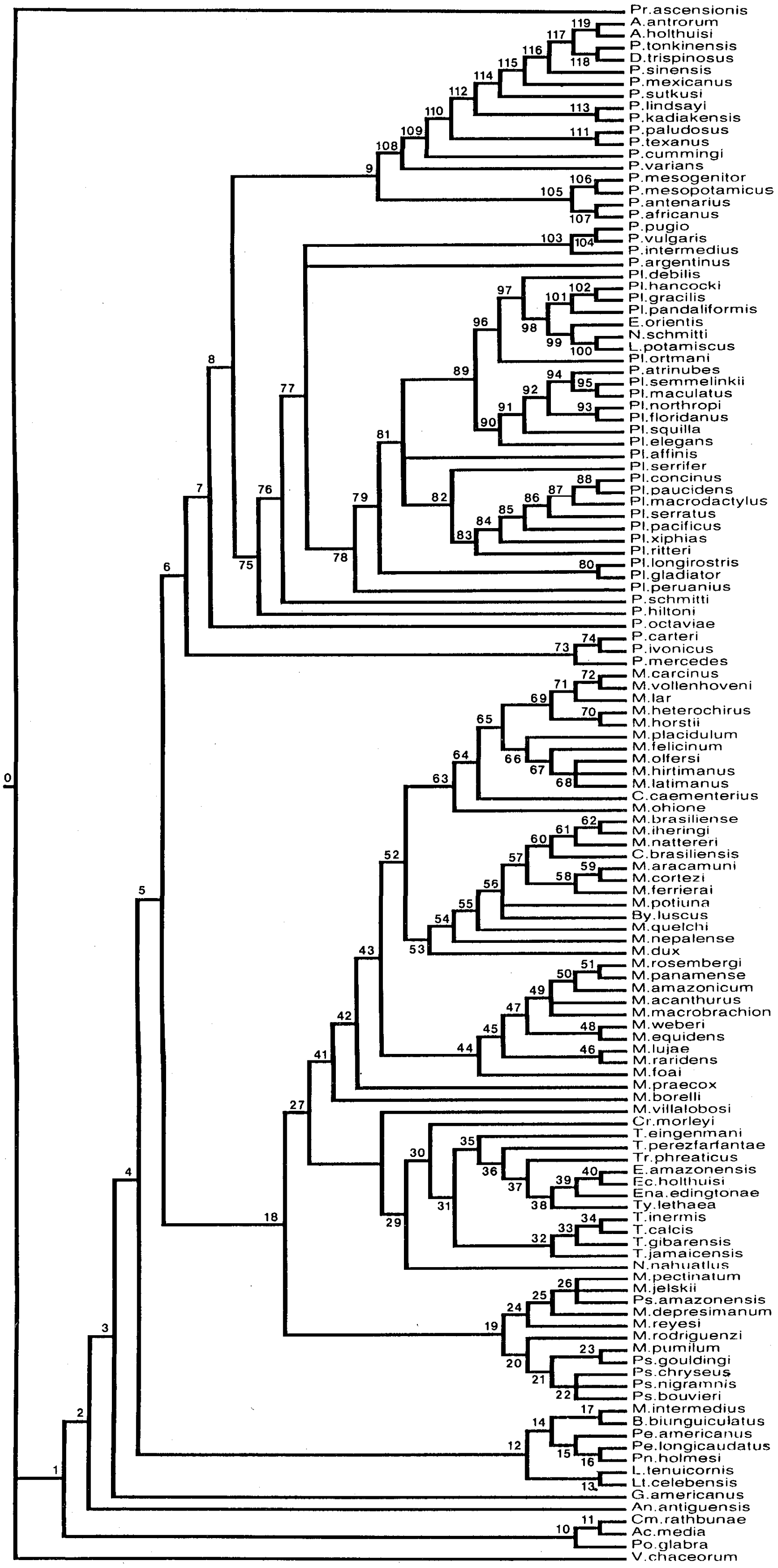

Figure 41.-Phylogenetic tree of the family Palaemonidae, numbers correspond to nodes for tree description as in table 9. Tree length 606 steps, Consistency Index 0.525 excluding uninformative characters. Name of taxa are based on Holthuis, 1950b, 1955.

Palaemonetes (above node 6) sensu Holthuis (1950) are paraphyletic, with the 2 genera spread into several smaller monophyletic groups. *Desmocaris* cluster as a taxa related to *Palaemonetes*, and do not deserve the current family status assign by Chace (1992). Thus, Holthuis (1950) and Chace (1992) classifications provides a frame of reference to sort out species and some natural groups but has minimal information on the relationships of the group.

All cave species in the *Macrobrachium* major clade (node 27 and above) cluster together with the subfamilies Typhlocaridinae and Euryrhynchinae these two subfamilies are considered as a monophyletic group by Chace (1992), this result support this conclusion independent of the rank assigned; Euryrhynchinae are also considered to be a very old group from Createaceous origin (Powell, 1976).

Regarding cave species, apparently they retained a large number of plesiomorphic characters, suggesting that they represent primitive species which persist today in archaic cave or ecologically isolated environments. The genus *Pseudopalaemon* and some species currently assigned to *Macrobrachium* seems to be very primitive also, sharing with former group the most basal position in the tree.

CONCLUSIONS

Present analysis provides additional support for the idea that the Superfamily Palaemonoidea and the family Palaemonidae represent a monophyletic group. However, it also suggests that an internal rearrangement of subgroups within the family would more accurately reflect their phylogenetic relationships. Above the superfamily level, the Campylonotidae should be excluded from the superfamily Palaemonoidea and replaced again in the superfamily Oplophoroidea. Chace (1992) did exclude the later family from palaemonoidea but assign them to its own superfamily with no obvious relationships. However, conclusions of present work above family level are limited. Within Palaemonidae our analysis suggests that *Gnathophyllum*, and *Anchistioides* (both monotypic) have several morphological apomorphies and should be considered related to the Pontoniinae, (see also Bruce 1986) but not within the same clade, Chace (1992) classification properly reflect this fact. The subfamily Pontoninae remains as a monophyletic taxon and should be considered the sister group of the Palaemoninae. However, the genera *Brachycharpus*, *Leander* and *Leandrites* should be included within the subfamily Pontoniinae and the genera *Palemonetes*, *Palaemon*, and *Macrobrachium* are paraphyletic.

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Table 6.- Listing of all the species in the subfamilies Palaemoninae, Euryrhynchinae, and Typhlocaridinae. Additionally, listed species examined in the Atyidae, Campylonotidae, Gnathophyllidae, Oplophoridae, Pontoniinae, and Procarididae. Those species followed by * have been examined directly during the present work; the others were documented through the literature. Species in bold face type were selected for use in the cladistic analysis. Authors and date for original descriptions are cited but not listed in literature cited. Classification used is based in Holthuis (1950;1952;1955). ANSP = Academy of Natural Science of Philadelphia, U. S. A.; BMNH = British Museum of Natural History, England; IN = Survey Nacional de Paraguay, Paraguay; INPA = Instituto de Pesquizas de Amazonas, Brasil; MBUCV = Museo de Biología Universidad Central de Venezuela; RMNH = Rijksmuseum van Natuurlijke Historie, Holland; USNM = National Museum of Natural History U.S.A.; WAM = Western Australian Museum.

FAMILY PALAEMONIDAE
SUBFAMILY PALAEMONINAE
***Bithynops luscus* Holthuis, 1973* paratypes, RMNH**
Bithynops perspicax Holthuis, 1977
***Brachycarpus biunguiculatus* (Lucas, 1849)* USNM 110985**
Brachycarpus holthuisi Fausto Filho, 1966
***Cryphiops brasiliensis* Correa, 1973* INPA**
***Cryphiops caementerius* (Molina, 1782)* USNM 84077**
***Creaseria morleyi* (Creaser, 1936)* USNM 213896**
Leander kempi Holthuis, 1950*
Leander paulensis (Ortmann, 1897)* USNM 354571,104111,104118
Leander tenuicornis (Say, 1818)* USNM 23598, 54167
Leander urocaridella (Borradaile, 1915)* USNM 54167
Leandrites celebensis (De Man, 1881)* USNM 57640
Leandrites cyrtorynchus Fujino and Miyake, 1969*
Leandrites indicus Holthuis, 1950
Leandrites stenopus Holthuis, 1950
Leptocarpus fluminicola (Kemp, 1917)* RMNH
***Leptocarpus potamiscus* (Kemp, 1917)* USNM 65523,65596, 65598, 65523-24; RMNH 33183**
***Macrobrachium acanthurus* (Wiegmann)* USNM 149810, MBUCV**
Macrobrachium acanthochirus Villalobos, 1966* USNM not in catalog
Macrobrachium acherontiun Holthuis, 1977* USNM Type 156257
Macrobrachium adscitum Riek, 1951
Macrobrachium aemulum (Nobili, 1906)
Macrobrachium altifrons (Henderson, 1893)
***Macrobrachium amazonicum* (Heller, 1862)* USNM;INPA; MBUCV**
Macrobrachium americanum Bate, 1868* USNM 84858
Macrobrachium andamanicum Tiwari, 1952
***Macrobrachium aracamuni* Rodriguez, 1982* USNM 231600 - 01**
Macrobrachium asperulum (Von Martens, 1868)
Macrobrachium assamensis Tiwari, 1955
Macrobrachium atabapense Pereira, 1986* USNM 228618
Macrobrachium atactum Riek, 1950
Macrobrachium australe (Guerin-Meneville, 1838)
Macrobrachium australiense (Ortmann, 1891)
Macrobrachium banjarae Tiwari, 1955
Macrobrachium bariense (De Man, 1892)
***Macrobrachium borelli* (Nobili, 1896)* USNM 8496672;**
***Macrobrachium brasiliense* (Heller, 1862)* USNM 78046, 191250; MBUCV**
Macrobrachium caledonicum (Roux, 1926)
Macrobrachium callirhoe (De Man, 1898)
Macrobrachium canarae Tiwari, 1955
Macrobrachium carcinus (Linnaeus, 1758)* ANSP 3133
Macrobrachium cavernicola (Kemp, 1924)
Macrobrachium chevalieri (Roux, 1935)* USNM 121426
Macrobrachium choprai Tiwari, 1947
Macrobrachium clymene (De Man, 1902)
Macrobrachium cocoense Abele and Kim, 1984* USNM type
***Macrobrachium cortezi* Rodriguez, 1982* USNM 231457; MBUCV 1738**
Macrobrachium cowlesi Holthuis

Table 6.- Listing of all the species in the subfamilies Palaemoninae, Euryrhynchinae, and Typhlocaridinae. (cont.)

Macrobrachium crenulatum Holthuis, 1950* USNM 126592; MBUCV 203,1771
Macrobrachium danae (Heller) 1865
Macrobrachium dayanum (Henderson, 1893)
***Macrobrachium dierythrum* Pereira, 1986* USNM 228323, 228324, MBUCV paratypes**
Macrobrachium digueti (Bouvier, 1895)* USNM 134780
***Macrobrachium dux* (Lenz, 1910)* USNM 57882**
Macrobrachium edentatum Liang. et al.,1987
***Macrobrachium equidens* (Dana, 1852)* USNM 65517, 65779**
Macrobrachium eriocheirum Day, 1984
Macrobrachium esculentum (Thallwitz, 1891)
Macrobrachium faustinum (De Saussure, 1857)* USNM 126603-18; MBUCV 1711, 0833
Macrobrachium felicinum Holthuis, 1951* USNM not in catalogue
***Macrobrachium ferrierai* Kensley and Walker, 1982* INPA**
***Macrobrachium foai* (Coutière, 1902)* USNM 57880**
Macrobrachium formosense Bate, 1868
Macrobrachium fukienense Liang et Yang, 1980
Macrobrachium gallus Holthuis, 1952
Macrobrachium geron Holthuis, 1950
Macrobrachium glypticum Riek, 1951
Macrobrachium gracilirostre (Miers, 1875)
Macrobrachium grandimanus (Randall, 1839)
Macrobrachium guangxiense Liang et Yan 1984
Macrobrachium hainanense (Parisi, 1919)
Macrobrachium hancocki Holthuis, 1950* USNM 171253, 204786
Macrobrachium hendersodayanus Tiwari, 1952
Macrobrachium hendersoni (De Man, 1906)
***Macrobrachium heterochirus* (Wiegmann)* USNM 21348; MBUCV 840, 1452**
Macrobrachium hildebrantii (Hilgendorf, 1893)
Macrobrachium hirsutimanus Tiwari, 1952
***Macrobrachium hirtimanus* (Olivier, 1811)* ANSP. 99; USNM 21358**
Macrobrachium holthuisi Genofre and Lobao, 1978* Paratypes
***Macrobrachium horstii* (De Man, 1892)* USNM 90872**
Macrobrachium idae (Heller, 1862)
Macrobrachium idela (Hilgendorf, 1898)
***Macrobrachium iheringi* (Ortmann, 1897)* USNM 84148, IN Paraguay**
Macrobrachium inca Holthuis, 1950* USNM
Macrobrachium indicum Jayachandran and Joseph, 1986
Macrobrachium insulare (Parisi, 1919)
***Macrobrachium intermedium* (Stimpson, 1860)* USNM 64583-4**
Macrobrachium jacobsoni Holthuis, 1950
Macrobrachium japonicum (De Haan, 1849)
Macrobrachium jaroense (Cowles, 1914)
Macrobrachium javanicum (Heller, 1862)
***Macrobrachium jelskii* (Miers, 1877)* MBUCV 1224, 1319**
Macrobrachium johnsoni Ravindranath, 1979
Macrobrachium joppae Holthuis, 1950
Macrobrachium kempi Tiwari, 1947
Macrobrachium kistnensis Tiwari, 1952
Macrobrachium kiukianense (Yu, 1931)
Macrobrachium lamarrei (Milne Edwards, 1837)
Macrobrachium lanceifrons (Cowles, 1914)
Macrobrachium lanchesteri (De Man, 1911)
***Macrobrachium lar (*Fabricius, 1798)* ANSP.181; USNM 3135, 23267**
Macrobrachium latidactylus (Thallwitz, 1891)* USNM 399
***Macrobrachium latimanus* (Von Martens, 1868)* USNM 67559**
Macrobrachium lepidactyloides (De Man, 1892)
Macrobrachium lepidactylus (Hilgendorf, 1879)* USNM
Macrobrachium longidigitum Day, 1984
Macrobrachium lorentzi (Roux, 1921)

Table 6.- Listing of all the species in the subfamilies Palaemoninae, Euryrhynchinae, and Typhlocaridinae. (cont.)

Macrobrachium lucifugum Holthuis, 1977* USNM 151299-04
***Macrobrachium lujae* (De Man, 1912)* USNM 57881**
Macrobrachium macrobrachion (Herklots, 1851)* USNM 57879
Macrobrachium maculatum Liang et Yang, 1980
Macrobrachium malayanun (Roux, 1934)
Macrobrachium malcolnsonii (Milne Edwards, 1844)
Macrobrachium mamillodactylus (Thallwitz, 1892)
Macrobrachium manipurensis Tiwari, 1952
Macrobrachium microps Holthuis, 1978
Macrobrachium mieni Dang, 1975
Macrobrachium minutum (Roux, 1917)
Macrobrachium mirabile (Kemp, 1917)
Macrobrachium morei (Calman, 1899)
Macrobrachium naso (Kemp, 1918)
Macrobrachium nattereri (Heller, 1862)* MBUCV 1199, 1714
Macrobrachium natulorum Holthuis, 1984
Macrobrachium nepalense Kamita, 1974* USNM, not in catalog
Macrobrachium niloticum (Roux, 1833)
Macrobrachium nipponense (De Haan, 1849)
Macrobrachium novahollandiae (De Man, 1908)
Macrobrachium obtusifron Day, 1984
Macrobrachium occidentale Holthuis, 1950* USNM 210777
Macrobrachium oenone (De Man, 1902)
Macrobrachium ohione (Smith, 1874)* USNM 9909
Macrobrachium olfersi (Wiegmann, 1836)* USNM 77549; MBUCV 1030, 1481
Macrobrachium palaemonoides Holthuis, 1950
Macrobrachium palawanensis Johnson, 1962
Macrobrachium panamense Rathbun, 1912* USNM 85191
Macrobrachium patsa (Coutière, 1900)
Macrobrachium pectinatum Pereira, 1986* USNM 228620, 228763; MBUCV 1759-60
Macrobrachium peguensis Tiwari, 1952
Macrobrachium petersii (Hilgendorf, 1879)
Macrobrachium petiti (Roux, 1934)
Macrobrachium pilimanus (De Man, 1879)* USNM 65622
Macrobrachium pinguis Day, 1984
Macrobrachium placidulum (De Man, 1892)* USNM 105410-12
Macrobrachium placidum (De Man, 1892)
Macrobrachium poeti Holthuis, 1984
Macrobrachium potiuna (Muller, 1880)* USNM 50686
Macrobrachium praecox (Roux, 1928)* USNM 85245; MBUCV 1474
Macrobrachium pumilum Pereira, 1986* USNM 228319, 228320, Paratypes
Macrobrachium quelchi (De Man, 1902)* MBUCV; BMNH Paratypes
Macrobrachium raridens (Hilgendorf, 1893)* USNM 102049
Macrobrachium rathbunae Holthuis, 1950* USNM 58220
Macrobrachium reyesi Pereira, 1986* USNM 228619, Paratype; MBUCV
Macrobrachium rodriguezi Pereira, 1986* USNM 228321-22, Paratype; MBUCV
Macrobrachium rogersi Tiwari, 1952
Macrobrachium rosenbergii (De Man, 1879)* USNM 65486
Macrobrachium rude (Heller, 1862)
Macrobrachium scabriculum (Heller, 1862)
Macrobrachium scortecci Paulucci Maccagno, 1961
Macrobrachium shokitai Fujino and Baba, 1973
Macrobrachium sintangense (De Man, 1898)
Macrobrachium siwalikensis Tiwari, 1952
***Macrobrachium sollaudii* (De Man, 1912)* ANSP 2651**
***Macrobrachium depressimanum* Pereira in press.* USNM 228902, 228906-7**
Macrobrachium srilankense Costa, 1979
Macrobrachium sulcicarpale Holthuis, 1950
Macrobrachium superbum (Heller, 1862)

Table 6.- Listing of all the species in the subfamilies Palaemoninae, Euryrhynchinae, and Typhlocaridinae. (cont.)

Macrobrachium surinamicum **Holthuis, 1948* USNM 85277, MBUCV**
Macrobrachium tenellum (Smith, 1871)* USNM 108159
Macrobrachium therezieni Holthuis, 1965
Macrobrachium thysi **Powell, 1980**
Macrobrachium tolmerum Riek, 1951
Macrobrachium transandicum Holthuis, 1950* USNM 85322
Macrobrachium trompii (De Man, 1898)
Macrobrachium veliense Jayachandran and Joseph, 1986
Macrobrachium venustum (Parisi, 1919)
Macrobrachium villalobosi **Hobbs, 1973* USNM Type, 172615**
Macrobrachium villosimanus Tiwari, 1947
Macrobrachium vollenhoveni **(Herklots, 1857)* USNM 81793**
Macrobrachium weberi **(De Man, 1892)* USNM not in catalog**
Macrobrachium yeti Dang, 1975
Macrobrachium yui Holthuis, 1950
Macrobrachium zariqueyi Holthuis, 1951* USNM 121427
Macrobrachium inflatum Xiang-Qui and Shang-Liang, 1980
Macrobrachium jiangxiense Xiang-Qui and Shang-Liang 1985
Neopalaemon nahuatlus **Hobbs 1973* USNM Paratypes 143120, 143121**
Palaemon (Exopalaemon) annandalei (Kemp, 1917)* USNM 59150
Palaemon (Exopalaemon) carinicauda (Ortmann, 1890)* USNM 62144, 62058, 62059
Palaemon (Exopalaemon) macrogenitus (Yu, 1930)
Palaemon (Exopalaemon) mani (Sollaud, 1914)
Palaemon (Exopalaemon) modestus (Heller, 1862)
Palaemon (Exopalaemon) orientis **(Ortmann, 1890)* USNM 21461,28537**
Palaemon (Exopalaemon) styliferus (M-Edwards, 1840)* USNM 65605, 65544
Palaemon (Nematopalaemon) colombiensis Squires and Mora, 1971* USNM 128121-22 Paratypes
Palaemon (Nematopalaemon) hastatus Aurivillius, 1898* USNM 97840-43
Palaemon (Nematopalaemon) karnafuliense Khan, Fincham and Mahmood, 1980
Palaemon (Nematopalaemon) schmitti **Holthuis, 1950* USNM 231520, MBUCV**
Palaemon (Nematopalaemon) tenuipes (Henderson, 1893)
Palaemon (Palaemon) affinis Milne Edwards, 1837* USNM 18171, 98858
Palaemon (Palaemon) belindae (Kemp, 1925)
Palaemon (Palaemon) capensis (De Man, 1897)* USNM
Palaemon (Palaemon) concinnus **Dana, 1852* USNM 94989, 169673**
Palaemon (Palaemon) debilis **Dana, 1852* USNM 23938**
Palaemon (Palaemon) folirostris Phan, 1972
Palaemon (Palaemon) gladiator **Holthuis,1950* USNM 84385-86**
Palaemon (Palaemon) gracilis **(Smith, 1871)* USNM 43944, 20075**
Palaemon (Palaemon) gravieri (Yu, 1930)
Palaemon (Palaemon) hancocki **Holthuis, 1950* USNM 85310**
Palaemon (Palaemon) longirostris **Milne Edwards, 1837* USNM 20671, 105405**
Palaemon (Palaemon) macrodactylus **Rathbun, 1902* USNM 120107, 62129**
Palaemon (Palaemon) miyadii Kubo, 1938
Palaemon (Palaemon) ogasawarensis Kato and Takeda, 1981
Palaemon (Palaemon) ortmanni **Rathbun, 1902* USNM 28536**
Palaemon (Palaemon) pacificus **(Stimpson, 1860)* USNM 26311, 25420**
Palaemon (Palaemon) paivai Fausto Filho, 1967
Palaemon (Palaemon) pandaliformis **(Stimpson, 1871)* USNM 78039,85210**
Palaemon (Palaemon) paucidens **De Haan, 1841*USNM USNM 21355**
Palaemon (Palaemon) peruanus **Holthuis, 1950* USNM Type**
Palaemon (Palaemon) ritteri **Holmes, 1895* USNM 84059, 90984**
Palaemon (Palaemon) roscleri de La Cruz, 1965
Palaemon (Palaemon) serratus **(Pennant, 1777)* USNM 6778; ANSP 119**
Palaemon (Palaemon) serrifer **(Stimpson, 1860)* USNM 54573, 62139, 105260, 105266**
Palaemon (Palaemon) sewelli (Kemp, 1925)* USNM 57638
Palaemon (Palaemon) adspersus **(Linnaeus, 1758)* USNM 57387-88**
Palaemon (Palaemon) xiphias **Risso, 1826* USNM 57395**
Palaemon (Palaemon) yamashitai Fujino and Miyake, 1970

Table 6.- Listing of all the species in the subfamilies Palaemoninae, Euryrhynchinae, and Typhlocaridinae. (cont.)

Palaemon (Paleander) elegans Rathke, 1837* USNM 152086
Palaemon (Paleander) floridanus Chace, 1942* USNM 96617, 23623, 84960-64
Palaemon (Paleander) maculatus (Thallwitz, 1892)* USNM 57878
Palaemon (Paleander) northropi (Rankin, 1898)* USNM 135522
Palaemon (Paleander) semmelinkii (De Man, 1881)* USNM 64999, 105266
Palaemonetes (Alaocaris) antrorum Benedict, 1896* USNM 21849, 26125
Palaemonetes (Palaemonetes) holthuisi Strenth, 1976* USNM Type
Palaemonetes (Palaemonetes) africanus Balls, 1916* USNM 97847
Palaemonetes (Palaemonetes) antennarius (Milne-Edwards, 1837)* USNM 152094-5
Palaemonetes (Palaemonetes) argentinus Nobili, 1901* USNM 62330- 31, 81802, 84900-16
Palaemonetes (Palaemonetes) atrinubes Bray, 1976* USNM not in catalog
Palaemonetes (Palaemonetes) australis Dakin, 1915* WAM
Palaemonetes (Palaemonetes) carteri Gordon, 1935* USNM 92512; MBUCV 92517
Palaemonetes (Palaemonetes) cummingi Chace, 1954* USNM 102836, 102276, 142211, 143614
Palaemonetes (Palaemonetes) granulosus De la Cruz, 1965
Palaemonetes (Palaemonetes) hiltoni Schmitt, 1921* USNM 78047, 295100 (Acc)
Palaemonetes (Palaemonetes) intermedius Holthuis, 1949* USNM 84729
Palaemonetes (Palaemonetes) ivonicus Holthuis, 1950* USNM 231207; INPA- CR032
Palaemonetes (Palaemonetes) kadiakensis Rathbun, 1902* USNM 781100
Palaemonetes (Palaemonetes) karukera Carvacho, 1979
Palaemonetes (Palaemonetes) lindsayi Villalobos, 1974* USNM 149161-64
Palaemonetes (Palaemonetes) mercedae Pereira, 1986* USNM 228318, 231452
Palaemonetes (Palaemonetes) mesogenitor Sollaud, 1912* USNM not in catalog
Palaemonetes (Palaemonetes) mesopotamicus Pesta, 1913* USNM 100873
Palaemonetes (Palaemonetes) mexicanus Strenth, 1976* USNM 152394
Palaemonetes (Palaemonetes) octaviae Chace, 1972* USNM 169731
Palaemonetes (Palaemonetes) paludosus (Gibbes, 1850)* USNM 129693
Palaemonetes (Palaemonetes) pugio Holthuis, 1949* USNM 84845
Palaemonetes (Palaemonetes) schmitti Holthuis, 1950* USNM 85233, (82222-2)
Palaemonetes (Palaemonetes) sinensis (Sollaud, 1911)* USNM 62128A, 57641
Palaemonetes (Palaemonetes) sutkusi Smalley, 1964* USNM 113569
Palaemonetes (Palaemonetes) texanus Strenth, 1976* USNM 152395
Palaemonetes (Palaemonetes) tonkinensis (Sollaud, 1914)* USNM 62128B
Palaemonetes (Palaemonetes) turcorum Holthuis, 1961
Palaemonetes (Palaemonetes) varians (Leach, 1814)* USNM 119404, 190999, 156416
Palaemonetes (Palaemonetes) vulgaris (Say, 1818)* USNM 31305
Palaemonetes (Palaemonetes) zariquieyi Sollaud, 1939
Desmocaris trispinosus (Aurivillius, 1898)* USNM 171372-73
Desmocaris bislineata Powell, 1977
Pseudopalaemon amazonensis Ramos-Porto, 1975* USNM not in catalog, MBUCV
Pseudopalaemon bouvieri Sollaud, 1911* USNM 84182, 84862
Pseudopalaemon chryseus Kensley, 1982* USNM 184887-9
Pseudopalaemon gouldingi Kensley, 1982* USNM 228772
Pseudopalaemon nigramnis Kensley, 1982* USNM 184892
Troglindicus phreaticus Sankolly and Shakuntala,1979* USNM Paratype
Troglocubanus calcis (Rathbun, 1912)* USNM type
Troglocubanus eigenmanni (Hay, 1903)* USNM 26349, 66768, 44497
Troglocubanus gibarensis (Chace, 1943)* USNM Type
Troglocubanus inermis (Chace, 1943)* USNM 103357
Troglocubanus jamaicensis Holthuis, 1963* USNM 228744
Troglocubanus perezfarfantae Villalobos, 1971* USNM 139136

SUBFAMILY EURYRHYNCHINAE

Euryrhynchus pemoni Pereira 1984 * USNM paratypes
Euryrhynchus burchelli Calman 1907 * INPA; MBUCV
Euryrhynchus wrzesniowskii Miers 1877* USNM 77604, 73103, INPA
Euryrhynchus amazonensis Tiefenbacher, 1978* USNM 231210; MBUCV; INPA
Euryrhynchyna edingtonae Powell, 1976* USNM 171376
Eurhyrhyncoides holthuisi Powell, 1976

Table 6.- Listing of all the species in the subfamilies Palaemoninae, Euryrhynchinae, and Typhlocaridinae. (cont.)

SUBFAMILY TYPLHOCARIDINAE
***Typhlocaris lethaea* Parisi, 1920* USNM 54761**
Typhlocaris galilea Calman, 1909* USNM 46097
Typhlocaris salentina Caroli, 1923

SUBFAMILY PONTONIINAE
***Anchistioides antiguensis* (Schmitt, 1924)* USNM 89035-42**
Periclimenes anthophilus Holthuis and Eibl-Eibesfeldt, 1964* USNM 173101
***Periclimenes americanus* (Kingsley, 1868)* USNM 85340, 97631,8537, 31145, 82166, 85445-86, 82160**
***Periclimenes longicaudatus* Costa, 1844* USNM 135589-90**
Periclimenes yucatanicus (Yves, 1891)* USNM 151056-9
***Palaemonella holmesi* (Nobili, 1907)* USNM 90256-61**

FAMILY GNATHOPHYLLIDAE
***Gnatophyllum americanum* Guerin, 1856* USNM 105943, 135843, 235837**

FAMILY CAMPYLONOTIDAE
***Campilonotus rathbunae* Schmitt, 1926* USNM 56233**

FAMILY OPLOPHORIDAE
***Acantephyra media* Bate, 1888* USNM 195732, 195737**

FAMILY ATYIDAE
***Potimirin glabra* Kingsley, 1878* USNM 149805**

FAMILY PROCARIDAE
***Procaris ascensionis* Chace & Manning, 1972* USNM 139461-4**
***Vetericaris chaceorum* Kensley & Willians, 1986* USNM 205725**

Table 7.- Data matrix (Taxa by Alpha numeric characters) used in the annalysis. Characters 68 and 83 were scored but not used in final analysis.

Pr.ascensionis	ABBABAEEBACDAFAFAAABAADGDAADFAGDEDADEFAKABAEDHADAFAGABHGFCL1JAAA3DB?DGAAABAABAAADAM
A.antrorum	AAAAAAAAAABAAAAAAAAACAAABABAAAAADBAAACACABABABAAAACAADAABAGAABAADA?AAAAABBBBAAABAAF
A.holthuisi	AAAAAAAAAAAAAAAAGAABCAAABABAAAAA?CAABCAAABABABAABAAAADAABAGAEBAADA?AACAABBBBAAABAAF
P.sinensis	AAAAAAAAAAAABAAAAAABAAAAAABAAAAABBABBAAAABAAACAABAAAAAAABAAACBAABAAAACAABBBBAAABAAF
P.tonkinensis	AAAAAAAAAAAABAAAAAABAAAAAABAAAAABBABBCAAABAAABAABAAAAAAABAAADAAABAAAAAAABBBBAAABAAF
P.sutkusi	AAAAAAAAAAAABAAAAAABAAACBAAACAAABBABBAAAABAAABAABAAAAAABBAAAABAABAAAAAAABBBBAAABAAF
P.lindsayi	AAAAAAAAAAAABAAAAAABAAACBAAACAAABBABBAAAABAAABAABAAAAAABBBAABBAABAAAAAAABBBBAAABAAF
P.kadiakensis	AAAAAAAAAAAABAAAAAABAAACAAAACAAABBABBAAAABAAABAABAAAAAABBBADBBAABAAAAAAABBBBAAABAAF
P.paludosus	AAAAAAAAAAAABAAAAAABAAACAAAAAAAABBABBAAAABAAAAAABAAAAAABBAAABBAABAAAAAAABBBBAAABAAF
P.texanus	AAAAAAAAAAAABAAAAAABAAACAAAAAAAABBABBAAAABAAAAAABAAAAAABBAAABBAABAAAAAAABBBBAAABAAF
P.mexicanus	AAAAAAAAAAAABAAAAAAAAAACAAAAAAAABBABBAAAABAAABAABAAAAAABBAAAABAABAAAAAAABBBBAAABAAF
P.cummingi	AAAAAAAAAAAABAAAAAAAAAACAAAACAAABBABBAAAABAAAAAABAAAAAABBAADBBAAAA?AAAAABBBBAAABAAF
P.varians	AAAAAAAAAAAABAAAAAABAAACAAAACAAABBABBAAAABAAACAABAAAABABBAAABBAAAAABAAAABBBBAAABAAF
P.mesogenitor	AAAAAAAAAAAABAAAAAABAAACAAAADBAABBABBAAAABAAABAABAAAABABBAAABBAACAAAAAAABBBBAAABAAF
P.mesopotamicus	AAAAAAAAAAAABAAAAAABAAACAAAADAAABBABBAAAABAAABAABAAAABABBAAABBAACAAAAAAABBBBAAABAAF
P.antenarius	AAAAAAAAAAAABAAAAAABABACAAAAABAABBABBAAAABAAABAABAAAABABBAAABBAAAAAAAAAABBBBAAABAAF
P.octaviae	AAAAAAAAAAAABAAAAAABAAABAAAAAAAABBABBAAAABAAAAAABCAAABABBCABABAAAAABAAAABBBBAAABAAE
P.africanus	AAAAAAAAAAAABAAAAAABABABACAAAAABBBABBCAAABAAABAABAAAABABBAAABBAAAAA?AAAABBBBAAABAAF
P.pugio	AAAAAAAAAAABBAAAAAABAAABAAAAAABABBABBAABABAAAAAABAAAAAABBCABABAAAAABAAAABBBBAAABAAE
P.vulgaris	AAAAAAAAAAABBAAAAAABAAABAAAAAAAABBABBAABABAAAAAABAAAAAABBCABABAAAAABAAAABBBBAAABAAE
P.intermedius	AAAAAAAAAAABBAAAAAABAAABAAAAAAAABBABBAABABAAAAAABAAAAAABBAABABAAAAABAAAABBBBAAABAAE
P.schmitti	AAAAAAAAABABBAAAAAABAAABAAAAAAAABBABBAABABAAAAAABAAAABABBAABABAAAAABAAAABBBBAAABAAE
P.hiltoni	AAAAAAAAABAABAAAAAABAAABAAAAAAAABBABBAABABAAAAAABAAAABABBAABABAAAAABAAAABBBBAAABAAE
P.argentinus	AAAAAAAAABABBAAAAAABAAABAAAAAAAABBABBAAAABAAAAAABAAAAAABBAABABAAAAABAAAABBBBAAABAAE
Pl.debilis	AAAAAABCAAABCDCAAAABAAABAAAAAAAABBABBAAAABAA?AAABAAAAAABBAABABAAAAABAAAABBBBAAABAAM
P.atrinubes	AAAAAAAAAAABBBAAAAABAAABAAAAAAAABBABBAAAABAA?AAABAAAAAAAAAABABAAAAAAAAAABBBBAAABAAE
Pl.semmelinkii	AAAAAAAAAAABBBAAAAABAAABAAAAAAAABBABBAABABAABAAABAAAAAAABAACABAAJAABAAAABBBBAAABAAM
Pl.maculatus	AAAAAAAAAAABCBAAAAABAAABAAAAAAAABBABBAAAABAABAAABAAAAAAABAACABAAAAABAAAABBBBAAABAAE
Pl.northropi	AAAAAAAAABABBBAAAAABAAABAAAAAAAABBABBAABABAABAAABAAAAAAABABBABAAAAABAAAABBBBAAABAAM
Pl.longirostris	AAAAAAAAABABBAAAAAABAAABAAAAAAAABBABBAAAABAACAAABAAAAAABBABCABAAAAABAAAABBBBAAABAAE
Pl.elegans	AAAAAAAAABABBBAAAAABAAABAAAAAAAABBABBAABABAABAAABAAAAAABAABBABAAAAABAAABBBBBAAABAAM
Pl.affinis	AAAAAAAAABABBAAAAAABAAABAAAAAAAABBABBAABABAA?AAABAAAAAABAABBABAAAAABAAAABBBBAAABAAM
Pl.serrifer	AAAAAAAAABABBAAAAAABAAABAAAAABCABBABBAABABAACAAABAAAAAABAABBABAAFAABAAAABBBBAAABAAM
Pl.concinus	AAAAAAAAAAABBBAAAAABAAAAAAAAAABCABBABBAABABAA?AAABAAAAAABBABCABAAFAABAAAABBBBAAABAAE
Pl.paucidens	AAAAAAAAAAABBBAAAAABABAAAAAAABAABBABBAAAABAACAAABAAAAAABBABCABAAGAABAAAABBBBAAABAAE
Pl.ortmani	AAAAAABCABABCBCAAAABAAABACA?A??ABBABBAABABAACAAABAAAA?ABAAB??BAA?AABAAAABBBBAAABAAM
Pl.floridanus	AAAAAABAABABBBAAAAABAAABACAAAAAABBABBAABABAABAAABAAAAAAABABBABAAAAABAAAABBBBAAABAAM
Pl.pacificus	AAAAAABAABABBBAAAAABAAAAAAAAABAABBABBAABABAACAAAAAAAAAABAABBABAAAAABAAAABBBBAAABAAM
Pl.squilla	AAAAAAAAABABBBAAAAABAAAAAAAAAAAABBABBAABABAA?AAABAAAAAAAAABBABAAAAABAAAABBBBAAABAAM
Pl.gladiator	AAAAAAAAABABBAAAAAABAAAAAAAAAAAABBABBAAAABAA?AAABAAAAAABBABBABAAAAABAAAABBBBAAABAAM
Pl.xiphias	AAAAAAAAABABBBCAAAABAAADACAAABAABBABBAABABAACAAABAAAAAABAABBABAAAAABAAAABBBBAAABAAM
Pl.serratus	AAAAAAAAABABBBAAAAABAAAAAAAAABAABBABBAABABAA?AAABAAAAAABAABCABAAAAABAAAABBBBAAABAAM
Pl.macrodactylus	AAAAAAAABABBBAAAAABAAAAAAAAABAABBABBAABABAACAAABAAAAAAAAABCABAA?AABAAAABBBBAAABAAM
Pl.ritteri	AAAAAAAAABABBAAAAAABAAADAAAAABAABBABBAABABAACAAABAAAAAAABABBABAAAAABAAAABBBBAAABAAM
Pl.peruanius	AAAAAAAAABABBAAAAAABAAAAAAA?A??ABBABBAABABAACAAABAAAAAAABAAB?BAA?AABAAAABBBBAAABAAE
Pl.hancocki	AAAAAABCAAAACDCABBABAAADAAAAAAAABBABBAAAABAACAAABAAAABABBADEFBBA9AABAAAABBBBAAABAAE
Pl.gracilis	AAAAAABCAAAACDCABBABAAADAAAAAAHABBABBAAAABAACAAABAAAABABBADEFBBA9AABAAAABBBBAAABAAE
Pl.pandaliformis	AAAAAABCAAABCDCAABABAAADAAAAAAAABBABBAAAABAA?AAABAAAABABBABEABBA9AABAAAABBBBAAABAAE
E.orientis	AAAAAABCAAABCDCABBABAAAAACAAAAAABBABBAAAABBACAAABAAAAAABBABBABBA9AABAAAABBBBAAABAAE
N.schmitti	AAAAAABCAAAACDCABBABAAAAACAAABAABBABBAAAABDACAAABAAAAAABBDBFFBBA9ABBAAAABBBBAAABBAE
L.potamiscus	AABAAABCAAAACDCABAABAAAAACAAAAAABBABBAAAABAACAAABAAAAAABBABGABBA8AABAAAABBBBAAABAAE
P.carteri	AAAAAAAAAAAABBAAAAABAAABAAAABADACBABBAAAABAAAAAABAABABBABCEHGBAALAAAAAAABBBBAAABAAF
P.ivonicus	AAAAAAAAAAAABAAAAAABAAAAAAAABADACBABBAAAABAAAAAABCABABBABCEHGBAALAAAAAAABBBBAAABAAF
P.mercedes	AAAAAAAAAAAABAAABAFAAAAAAAAABAAACBABBAABABAAAAAAAAABABBABCEHGBAALAAAAAAABBBBAAABAAF
D.trispinosus	AAAAABAAAAAABAAAABFCBAAHACBAAA9BCBAABCACABAAADAABAACABAABE9MHAAAMABAAAEABBBBAAABAAF
M.carcinus	ABBBACAAABABABDABABAAADAAACAHAABBBBBABDAAAACAAAAABDBBDCCCA9ABAANAABAAAABBBBAAABAA9
M.vollenhoveni	AABBBACAAABABABDABABAAADAAACAHAABBBBBABDAAAACAAAAABDBBDCCCA9ABAANAABAAAABBBBAAABAA9
M.lar	AABBBACAAAABBADAABABAAADAAACAHAABBBBBABDAAAACAAAADBDBBDDCCA9ABAANAABAAAABBBBAAABAA9
M.heterochirus	AABBBAAAAABABADDABABAAADAAACAHAABBBBBABEAAAACAAAAAADBBDDCCA9ABAANAABAAAABBBBAAABAA9
M.horstii	AABBBAAAAABABADDABABAAADAAACAHAABBBBBABEACAACAAAAAADBBDDCCA9ABAANAABAAAABBBBAAABAA9
M.placidulum	AABBBAAAAABABADDABABAAADAAAAAHAABBCBBABDACAACAAAAAADBBDDCCA9ABAANAABAAAABBBBAAABAA9
M.felicinum	AABBBAAAAABABADDABABAAADAAAAAHAABBCBDBBFACAACAAABAADBBDDCCA9ABABNAABAAAABBBBAAABAA9
M.olfersi	AABBBAAAAABABADDABABAAADAAAAAHAABBCBDBBFACAACAAAAABDBBDCCCA9ABABNAABAAAABBBBAAABAA9
M.hirtimanus	AABBBAAAAABABADDABABAAADAAAAAHAABBCBDBBFACAACAAAAABDBBDCCCA9ABABNAABAAAABBBBAAABAA9
M.latimanus	AABBBAAAAABABADDABABAAADAAAAAHAABBCBDBBFACAACAAAAABDBBDCCCA9ABABNAABAAAABBBBAAABAA9

Table 7.- Data matrix (Taxa by Alpha numeric characters) used in the annalysis. Characters 68 and 83 were scored but not used in final analysis.

C.caementerius	AABABAAAAAAABADDABABAAADAAAAAHAABBCBDABEAAAACAAABCADABDDCCA9ABAANAABAAAABBBBAAABAA9
M.ohione	AABBBACAAAAABABAABABAAADAAAAAHAABBBBBABDAAAACAAABAADABDDCCA9ABAANAABAAAABBBBAAABAA9
M.rosembergi	AABBBAAFAAABCEAADBABAAADAAACAHAABBABCACDAAAACAAABAAAAADDACA9ABAANAABAAAABBBBAAABAA9
M.panamense	AABBBAAFAAABCEAADBABAAADAAAAAHAABBABCACDAAAACAAABAAAABDDBCA9ABAANAABAAAABBBBAAABAA9
M.acanthurus	AABBBAAFAAABCEAAABABAAADAAAAAHAABBABCACDAAAACAAABAADABDDBCA9ABAANAABAAAABBBBAAABAA9
M.amazonicum	AABBBAAFAAABCEAADBABAAADAAAAAHAABBABCACDAAAACAAAAAADABADBCA9ABAANAABAAAABBBBAAABAA9
M.macrobrachion	AABBBAAFAAABCEAAABABAAADAAAAAHAABBABCACDAAAACAAABAADABDDBCA9ABAANAABAAAABBBBAAABAA9
M.weberi	AABBBAAAAAABBEAAABABAAADAAAAABAABBABCACDAAAACAAABAAAABDDBCA9ABAANAABAAAABBBBAAABAA9
M.lujae	AABBBAAAAAABBEAAABABAAADAAAAABAABBBBCABDBAAACAAAAAADABDDBCA9ABAANAABAAAABBBBAAABAA9
M.equidens	AABBBAAAAAABBAAAABABAAADAAAAAHAABBABCACDAAAACAAABAAAABDDBCA9ABAANAABAAAABBBBAAABAA9
M.foai	AABBBAAAAAAABAAAABABAAADAAAAABAABBABCABDAAAACAAABAADABDDBCA9ABAANAABAAAABBBBAAABAAF
M.raridens	AABBBAAAAAABBAAAABABAAADAAAAABAABBABCABDBAAACAAAAAADABDDBCA9ABAANAABAAAABBBBAAABAA?
M.brasiliense	BABBBAAAAAAABADDABABAAAAAAACEHAABBBBBABDBAAACAAABAADABDDBCAJABAANAAAAAAABBBBAAABAAF
M.iheringi	BABBBAAAAAAABADDABABAAADAAACAHAABBBBGABDBAAACAAABAADABDDCCAJABAANAAAAAAABBBBAAABAAF
M.nattereri	BABBBAAAAAAABADDABABAAAAAAAAAABAABBBBBABDBAAACAAABAADABDDBCAJABAANAAAAAAABBBBAAABAAF
M.nepalense	AABBBAAAAAAABADDABABAAADAAAAABAABBBBBAEDAAAACAAABAADABDDBCAJABAANAAAAAAABBBBAAABAAF
M.potiuna	AABBBAAAAAAABADDEBABAAADAAAAEBAABBBBGEBDBAAACAAABAADABDDBCAJABAANAAAAAAABBBBAAABAAF
M.aracamuni	AABBBAAAAAAABADHEBABAAAAAAAAAABAABBBBBABDBAAACAAAAAADABDDBCAJABAANAAAAAAABBBBAAABAAF
M.ferrierai	AABBBAAAAAAABADDEBABAAAAAAAAAABAABBBBBABDBAAACAAAAAADABDDBCAJABAANAAAAAAABBBBAAABAAF
M.cortezi	AABBBAAAAAAABADHEBABAAAAAAAAAABAABBBBBABDAAAACAAAAAADABDDBCAJABAANAAAAAAABBBBAAABAAF
M.quelchi	AABBBAAAAAAABADDEBABAAADAAAAABAABBBBBABDAAAACAAAAAADABDDBCAJABAANAAAAAAABBBBAAABAAF
M.dux	AABBBAAAAAAABADAABABAAADAAAAABAABBBBBABDAAAACAAAAAADABDDBCAJABAANAAAAAAABBBBAAABAAF
By.luscus	AABABAAAAAAABADDEAABAAADAAAAABAABBABBABDBAAACAAABAADABDDBCAJABAANAAAAAAABBBBAAABAAF
M.pectinatum	AABBBAACAAABBBAAAAABABAAAAAAAAAABBABBAAAABAACAAABAAAABKBBCALABAAOAAAAAAABBBBAAABAAF
M.jelskii	AABBBAACAAABBBAAAAABABAAAAAAAAAABBABBAABABAACAAABAAAABKBBCALABAAOAAAAAAABBBBAAABAAF
Ps.amazonensis	AABBBAACAAABBBAAAAABABAAAAAAAAAABBABBAAAABAAAAAAAAAAABKBBCALABAAOAAAAAAABBBBAAABAAF
M.depresimanum	AABBBAACAAABBBAAAAABABAAAAAAAAAABBABBAAAABAACAAABAAAABDBBCALABAAOAAAAAAABBBBAAABAAF
M.rodriguenzi	AABBBAAAAAAABAAAAAABABADAAAAAAAABBABBAAAABAACAAAAAAAABDBBCALABAAOAAAAAAABBBBAAABAAF
M.pumilum	AABBBADAAAAABAAAAAABABAAAAAAAAAABBABBAAAABAA?AAAAAAABDBBCALABAAOAAAAAAABBBBAAABAAF
Ps.gouldingi	AABBBADAAAAABAAAAAABABAAAAAAAAAABBABBAAAABAA??AAAAAAABDBBCALABAAOAAAAAAABBBBAAABAAF
Ps.chryseus	AABBBAAAAAAABAAAAAABABAAAAAAAAAABBABBAABABAAAAAAAAAAABDBBCALABAAOAAAAAAABBBBAAABAAF
Ps.nigramnis	AABBBAAAAAAABAAAAAABABAAAAAAAAAABBABBAAAABAAAAAAAAA?ABDBBCALABAAOAAAAAAABBBBAAABAAF
Ps.bouvieri	AABBBAAAAAAABAAAAAABABAAAAAAAAAABBABBAAAABAAAAAAAAAAABDBBCALABAAOAAAAAAABBBBAAABAAF
M.reyesi	AABBBAACAAAABBAAAAABAAAAAAAAAAAABBABBAABABAACAAABAAAABDBBCALABAAOAAAAAAABBBBAAABAAF
M.praecox	AABBBAAAAAAABAAAAAABAAAAAAAAAABAABBABBACDAAAACAAADAADABDBBCA9ABAANAABAAAABBBBAAABAA?
M.borelli	AABBBAAAAAAABAAAABABAAAAAAAAADAAABBABBACDAAAACAAABAADABDBBCA9ABAANAABAAAABBBBAAABAAF
M.villalobosi	AABBBAAAAAAABAAAAAABAAAAAAAAABAABBBBBAAAABABCAAABAAAABDABCA9ABAANA?AAAAABBBBAAABAAF
C.brasiliensis	AABBBAAAAAAABAADEBABAAAAAAAACABAABBBBBABDBAAACAAABAAAABDACCA9ABAANAAAAAAABBBBAAABAAF
Cr.morleyi	AADABAAAAAAABAAAAAABAAADADAAAAAABBBBDAHAAABBAAAAAADABDABCANABAANA?AAAAABBBBAAABAAF
Ne.nahuatlus	AABBBAAAAAAABAAAAAABAAAAAAAAAAAABBABBAAAABABBABABAADABDABCAKABAANA?AAAAABBBBAAABAAF
T.eingenmani	AABABAAAAAAAAAAAAAABCAAAAAAAAAAABBABCDABABAAAAAABAADAAEABAAAABAAAA?AAAAABBBBAAABAAF
T.inermis	AABABAAAAAA?AAAAAAABCAAAADAAAAAAAAABCDAAABACAAAABAAAABEABACOABAANA?AAAAABBBBAAABABF
T.calcis	AABABAAAAAA?AAAAAAABCAAAADAAAAAABBABCDAHABACAAAABAAAAAEABAAOABAANA?AAAAABBBBAAABABF
T.gibarensis	AABABAAAAAAAAAAAAAAABAAAAADAAAAAABBABCDAAABACAAAABAAAADEABAAAABAANA?AAAAABBBBAAABAAF
T.perezfarfantae	ABBABAEABAA?AFAAABCBCAAAADAAAAABDBABCDAHABABAAAAABDDABEABAAAABAANA?AAAAABBBBAAABAAF
T.jamaicensis	AABABAAAAAA?AAAAAAABCAADADAAAAAABBABCDAAABABAAAABADAADEABAAOABAANA?AAAAABBBBAAABAAF
Tr.phreaticus	AABABAADAAAAAFAA9AAAAAADADAAAAABBBABCAAGABABAAAACAAAABEABACDABAANA?AAAAABBBBAAABAAF
E.amazonensis	AABABAEDBAA?AFAA9ADEAACFCDAAAAABAAABCAABABADAEAAAAADADDAAACDABAAPABABAAABBBBAAABCAF
Ty.lethaea	ABBABAEDBAA?AFAA9AABAAAECDAAAAABBAABCAAGABAAAEAAAABDADDABC?AABAAQABAAAAABBBBAAABCAF
Ena.edingtonae	AABABAEDBAAAAFAA9ADEAACFCDAAAAABAAABCAABABADAEAAAAADADDAAACOABAAPCBABAAABBBBAAABCAF
Ec.holthuisi	AABABAEDBAAAAAAA9ADEAACFCDAAAAABAAABCAABABADAAAA????ADDA??CDABAAPABABAAABBBBAAABCAF
M.intermedius	AABBBAAAAAAABAAEACABAAABACAAAAAABBABBAABABAACABABAAEACADACBBABAAAAABAAAABBBBAAABAAM
B.biunguiculatus	AABBBAAAAAAABAAAABABAAABAAAAABAABBABBAABABAACABBBAAEACJDBCB7ABAAKBABBAAABBBBAAABAAM
Ln.tenuicornis	AAAABAAAAAAABBAAEACABAAAAACAAAAAABBABCAABABAABABBBAAAACABACF7ABAAKBABAAAABBBBAAABAAM
Lt.celebensis	AAAABAAAAAAABBAAEACABAAAAACAAAAAABBABBAABABAAAABBBAAAABABACF7ABAAKBABAAAABBBBAAABAAM
Pe.americanus	AABBBAAAAAAABAAEACABAAACAAAAAAAABBABBAA9ABAAAFBABAAAACJBBCF6ABAA6BABABAABBBBAAABAAM
Pe.longicaudatus	AABBBAAAAAAABAAEACABAAACAAAAAAAABBABBAA9ABAABFBBBAAAACJBBCFBABAA7BABBBAABBBBAAABAAM
Pn.holmesi	AABBBBAAAAAABAAEACABAAACAAAAAAAABBABBAA9ABAABFBABAAAACJBBCF6ABAA7BABABAABBBBAAABAAM
G.americanus	AABABAADAAFABAAEAAABCADCADDAAAACFEABBAABABAAAFBAAAAAABFEBCF7KBAA6BBBBBAABBBBAAABAAM
An.antiguensis	AABABCAAAAFABAAGKAFDAADCACAAAAECGFABBAABABAAAFBBAAAEAB9ABCF49AAAKBB?BABABBBBAAABAAM
Cm.rathbunae	ACCCBAAAACDCBGAFMAEEDADGAACDFAGDEDABBAAJABAADFAAAEAFABHFECK2JACA5DB?DDCABCBBBBABAAM
Ac.media	ABCABAGAADEADAAFNDEEAADGAECDFAGDEDACBAAAABAADGABAFAGABGGFCK2JAAA5DB?DEDABCAABBABAAM
Po.glabra	ABBABAFDAACDBFAALAEEAADGECCDFAGEEDADFGDLABCAAGBBAFAGABHGFCK0KAAA4DBBEHDBBDABBBBBAA9
V.chaceorum	ABBABAEEBACDAFAFAAABAADGDAADFAGDEDADEFAKABAEDGACAFAGABHGFCL1JAAA3DB?DFAAAAAABAAADAM

Table 8. Character Diagnostics for the phylogenetic tree (Fig. 41) of the Family Palaemonidae

Character	Min. steps	Tree steps	Max. steps	CI	HI	RI	RC
1.CARAP	1	1	3	1.000	0.000	1.000	1.000
2.ANTSPINE	2	4	7	0.500	0.500	0.600	0.300
3.BRNSPINE	3	5	58	0.600	0.400	0.964	0.578
4.HEPSPINE	2	6	53	0.333	0.667	0.922	0.307
5.BRNGRV	1	1	54	1.000	0.000	1.000	1.000
6.SUORBSPN	2	3	3	0.667	0.333	0.000	0.000
7.ROSTRUM	6	11	25	0.545	0.455	0.737	0.402
8.RLENGTH	4	7	27	0.571	0.429	0.870	0.497
9.RLWKEEL	1	3	7	0.333	0.667	0.667	0.222
10.RLOWTH	3	7	20	0.429	0.571	0.765	0.328
11.CARTEETH	5	7	17	0.714	0.286	0.833	0.595
12.1stTEETH	3	10	48	0.300	0.700	0.844	0.253
13.RTOTTETH	3	7	30	0.429	0.571	0.852	0.365
14.DIST1/4	5	13	43	0.385	0.615	0.789	0.304
15.RTIP	3	6	32	0.500	0.500	0.897	0.448
16.TELSET	5	9	33	0.556	0.444	0.857	0.476
17.TELTIP	9	11	25	0.818	0.182	0.875	0.716
18.TINSPINE	3	11	50	0.273	0.727	0.830	0.226
19.DISTSPIN	4	5	9	0.800	0.200	0.800	0.640
20.D2nDSPINE	5	9	13	0.556	0.444	0.500	0.278
21.SPINLOC	3	7	10	0.429	0.571	0.429	0.184
22.SIX/FIFTH	1	4	13	0.250	0.750	0.750	0.188
23.ANT1FUSG	2	2	10	1.000	0.000	1.000	1.000
24.FREE/FUS	7	26	85	0.269	0.731	0.756	0.204
25.UROPSPIN	4	6	11	0.667	0.333	0.714	0.476
26.SCAPHO	3	14	26	0.214	0.786	0.522	0.112
27.MAXLAC	3	3	9	1.000	0.000	1.000	1.000
28.INNLAC	2	5	14	0.400	0.600	0.750	0.300
29.LACFRONT	5	9	18	0.556	0.444	0.692	0.385
30.UPLAC	2	11	48	0.182	0.818	0.804	0.146
31.UPLACSHP	7	8	13	0.875	0.125	0.833	0.729
32.IIMAXEND	4	6	15	0.667	0.333	0.818	0.545
33.MOLAR	6	9	17	0.667	0.333	0.727	0.485
34.INCISS	5	6	13	0.833	0.167	0.875	0.729
35.2ndLEG	2	7	26	0.286	0.714	0.792	0.226
36.1st/2nd	3	5	7	0.600	0.400	0.500	0.300
37.PALM	6	10	33	0.600	0.400	0.852	0.511
38.FINGSHP	6	8	20	0.750	0.250	0.857	0.643
39.FINGCOVER	4	5	37	0.800	0.200	0.970	0.776
40.FINGTEETH	11	29	84	0.379	0.621	0.753	0.286
41.FINGTUBRCL	1	3	10	0.333	0.667	0.778	0.259
42.LEG2	2	4	37	0.500	0.500	0.943	0.471
43.LEG3-5	3	3	3	1.000	0.000	0/0	0/0
44.EYSTLK	4	7	16	0.571	0.429	0.750	0.429
45.MANDPLP	3	12	61	0.250	0.750	0.845	0.211
46.MAXILLP3	7	12	27	0.583	0.417	0.750	0.438
47.LG5SDSET	1	4	11	0.250	0.750	0.700	0.175
48.APPINT	3	7	9	0.429	0.571	0.333	0.143
49.FSPINE	3	17	41	0.176	0.824	0.632	0.111
50.LTRIDGES	5	7	10	0.714	0.286	0.600	0.429

Table 8. Character Diagnostics for the phylogenetic tree (Fig. 41) of the Family Palaemonidae (cont.)

Character	Min. steps	Tree steps	Max. steps	CI	HI	RI	RC
51.LRDGSPIN	3	6	10	0.500	0.500	0.571	0.286
52.5STRGRVE	6	13	50	0.462	0.538	0.841	0.388
53.5STCOXA	1	1	10	1.000	0.000	1.000	1.000
54.5STSPIN	3	13	53	0.231	0.769	0.800	0.185
55.2STRLRIDG	9	12	74	0.750	0.250	0.954	0.715
56.4STERN	6	16	74	0.375	0.625	0.853	0.320
57.ANLPLTE	4	15	35	0.267	0.733	0.645	0.172
58.GILLAMELL	4	7	57	0.571	0.429	0.943	0.539
59.EPIPOD3	9	13	47	0.692	0.308	0.895	0.619
60.EXOP1	20	31	102	0.645	0.355	0.866	0.559
61.ENDT1MX	10	13	27	0.769	0.231	0.824	0.633
62.MX2ENDM.	1	2	8	0.500	0.500	0.857	0.429
63.5thPLR	2	2	7	1.000	0.000	1.000	1.000
64.3MASTIGOB	1	1	4	1.000	0.000	1.000	1.000
65.GONOP	20	24	81	0.833	0.167	0.934	0.779
66.STATOCYS	3	4	14	0.750	0.250	0.909	0.682
67.OCELLUS	1	4	13	0.250	0.750	0.750	0.188
*68.DEVELOP.	1	7	56	0.143	0.857	0.891	0.127
69.3-5DACT	3	6	12	0.500	0.500	0.667	0.333
70.TELDSPINE	7	9	11	0.778	0.222	0.500	0.389
71.#DRSLSPIN	4	4	5	1.000	0.000	1.000	1.000
72.SCAPHOG	1	2	2	0.500	0.500	0.000	0.000
73.P4-8PLBR	1	1	2	1.000	0.000	1.000	1.000
74.P4-8ARTRB	3	3	4	1.000	0.000	1.000	1.000
75.EPIPD4-8	1	2	4	0.500	0.500	0.667	0.333
76.EXOPD4-8	1	2	3	0.500	0.500	0.500	0.250
77.MSTGMX2	1	1	5	1.000	0.000	1.000	1.000
78.LWRMX1	1	1	3	1.000	0.000	1.000	1.000
79.MASTGMX1	1	1	1	1.000	0.000	0/0	0/0
80.SEG3MAX	1	1	2	1.000	0.000	1.000	1.000
81.EYEFACET	3	3	7	1.000	0.000	1.000	1.000
82.CARSHPE	1	1	2	1.000	0.000	1.000	1.000
*83.HABITAT	3	12	68	0.250	0.750	0.862	0.215

*Excluded character(s)

Table 9. Cladistic analysis of Palaemonids. Final tree length 606. Apomorphies List. Edited as in Final tree (Figure 41)

APOMORPHY LISTS:

Branch	**Character No.**	**Code**	**Steps CI**	**Change**
node_0 —> *Pr. ascensionis*	46.MAXILLP3	1	0.583	G ==>H
	48.APPINT	1	0.429	B —> D
node_0—> *V. chaceorum*	48.APPINT	1	0.429	B —> C
	70.TELDSPINE	1	0.778	A —> F
	74.P4-8ARTRB	1	1.000	B ==>A
	70.TELDSPINE	1	0.778	A —> G
node_0 —> node_1	7.ROSTRUM	1	0.545	E ==>A
	8.RLENGTH	1	0.571	E ==>A
	9.RLWKEEL	1	0.333	B ==>A
	12.1stTEETH	1	0.300	D —> A
	13.RTOTTETH	1	0.429	A ==>B
	14.DIST1/4	1	0.385	F —> A
	25.UROPSPIN	1	0.667	D ==>A
	36.1st/2nd	1	0.600	D —> B
	37.PALM	1	0.600	E ==>B
	38.FINGSHP	1	0.750	F ==>A
	40.FINGTEETH	1	0.379	K —> A
	44.EYSTLK	1	0.571	E ==>A
	45.MANDPLP	1	0.250	D —> A
	47.LG5SDSET	1	0.250	A —> B
	59.EPIPOD3	1	0.692	L —> F
	60.EXOP1	1	0.645	1 —> 0
	61.ENDT1MX	1	0.769	J —> K
	65.GONOP	1	0.833	3 —> K
	73.P4-8PLBR	1	1.000	A ==>B
	76.EXOPD4-8	1	0.500	A ==>B
	80.SEG3MAX	1	1.000	A ==>B
	81.EYEFACET	1	1.000	D ==>A
node_1—> node_10	17.TELTIP	1	0.818	A —> L
	19.DISTSPIN	1	0.800	A ==>E
	20.D2nDSPINE	1	0.556	B ==>E
	27.MAXLAC	1	1.000	A ==>C
	59.EPIPOD3	1	0.692	F —> K
	65.GONOP	1	0.833	K —> 4
	70.TELDSPINE	1	0.778	A —> D
	71.#DRSLSPIN	1	1.000	A ==>D
	74.P4-8ARTRB	1	1.000	B —> C
	78.LWRENDMX1	1	1.000	A ==>B
node_10—> *Po. glabra*	7.ROSTRUM	1	0.545	A ==>F
	8.RLENGTH	1	0.571	A ==>D
	12.1stTEETH	1	0.300	A —> D
	14.DIST1/4	1	0.385	A —> F
	16.TELSET	1	0.556	F ==>A
	25.UROPSPIN	1	0.667	A ==>E
	26.SCAPHO	1	0.214	A ==>C
	32.IIMAXEND	1	0.667	D ==>E
	36.1st/2nd	1	0.600	B —> D
	37.PALM	1	0.600	B ==>F
	38.FINGSHP	1	0.750	A ==>G
	39.FINGCOVER	1	0.800	A ==>D

Table 9. Cladistic analysis of Palaemonids. Final tree length 606. Apomorphies List. Edited as in Final tree (Figure 41)

APOMORPHY LISTS:

Branch	**Character No.**	**Code**	**Steps CI**	**Change**
	40.FINGTEETH	1	0.379	A —> L
	43.LEG3-5	1	1.000	A ==>C
	69.3-5DACT	1	0.500	D ==>E
	70.TELDSPINE	1	0.778	D —> H
	72.SCAPHOGNAT	1	0.500	A ==>B
	74.P4-8ARTRB	1	1.000	C —> D
	79.MASTGMX1	1	1.000	A ==>B
	*83.HABITAT	1	0.250	M ==>9
node_10—> node_11	3.BRNSPINE	1	0.600	B ==>C
	10.RLOWTH	1	0.429	A —> C
	11.CARTEETH	1	0.714	C —> D
	17.TELTIP	1	0.818	L —> M
	45.MANDPLP	1	0.250	A —> D
	47.LG5SDSET	1	0.250	B —> A
	60.EXOP1	1	0.645	0—> 2
	61.ENDT1MX	1	0.769	K —> J
	65.GONOP	1	0.833	4 —> 5
node_11—> *Cm. rathbunae*	2.ANTSPINE	1	0.500	B ==>C
	4.HEPSPINE	1	0.333	A ==>C
	12.1stTEETH	1	0.300	A —> C
	14.DIST1/4	1	0.385	A —> G
	21.SPINLOC	1	0.429	A ==>D
	40.FINGTEETH	1	0.379	A —> J
	46.MAXILLP3	1	0.583	G ==> F
	48.APPINT	1	0.429	B ==> A
	50.LTRIDGES	1	0.714	F ==> E
	52.5STRGRVE	1	0.462	G ==> F
	56.4STERN	1	0.375	G ==> F
	57.ANLPLTE	1	0.267	F ==> E
	63.5thPLR	1	1.000	A ==> C
	71.#DRSLSPIN	1	1.000	D ==> C
	75.EPIPD4-8	1	0.500	A ==> B
node_11—> *Ac. media*	7.ROSTRUM	1	0.545	A ==> G
	10.RLOWTH	1	0.429	C —> D
	11.CARTEETH	1	0.714	D —> E
	13.RTOTTETH	1	0.429	B ==> D
	17.TELTIP	1	0.818	M —> N
	18.TINSPINE	1	0.273	A ==> D
	26.SCAPHO	1	0.214	A ==> E
	36.1st/2nd	1	0.600	B —> C
	55.2STRLRIDG	1	0.750	H ==> G
	70.TELDSPINE	1	0.778	D —> E
	76.EXOPD4-8	1	0.500	B ==> A
node_1 —> node_2	2.ANTSPINE	1	0.500	B ==> A
	11.CARTEETH	1	0.714	C ==> F
	16.TELSET	1	0.556	A —> E
	24.FREE/FUS	1	0.269	G ==> C
	28.INNLAC	1	0.400	D ==> A
	29.LACFRONT	1	0.556	F ==> A
	31.UPLACSHP	1	0.875	G —> A
	32.IIMAXEND	1	0.667	D ==> C

Table 9. Cladistic analysis of Palaemonids. Final tree length 606. Apomorphies List. Edited as in Final tree (Figure 41)

APOMORPHY LISTS:

Branch	**Character No.**	**Code**	**Steps CI**	**Change**
	33.MOLAR	1	0.667	E —> B
	34.INCISS	1	0.833	D —> B
Branch	40.FINGTEETH	1	0.379	A —> B
	46.MAXILLP3	1	0.583	G ==> F
	50.LTRIDGES	1	0.714	F ==> A
	52.5STRGRVE	1	0.462	G —> A
	55.2STRLRIDG	1	0.750	H —> A
	56.4STERN	1	0.375	G —> A
	57.ANLPLTE	1	0.267	F ==> B
	60.EXOP1	1	0.645	0—> 4
	66.STATOCYS	1	0.750	D ==> B
	69.3-5DACT	1	0.500	D ==> B
	75.EPIPD4-8	1	0.500	A ==> B
	77.MSTGMX2	1	1.000	B ==> A
node_2—> *An. antiguensis*	6.SUORBSPN	1	0.667	A ==> C
	16.TELSET	1	0.556	E —> G
	17.TELTIP	1	0.818	A ==> K
	19.DISTSPIN	1	0.800	A ==> F
	20.D2nDSPINE	1	0.556	B ==> D
	26.SCAPHO	1	0.214	A ==> C
	31.UPLACSHP	1	0.875	A —> E
	33.MOLAR	1	0.667	B —> G
	34.INCISS	1	0.833	B —> F
	52.5STRGRVE	1	0.462	A —> E
	55.2STRLRIDG	1	0.750	A —> 9
	61.ENDT1MX	1	0.769	K —> 9
	71.#DRSLSPIN	1	1.000	A ==> B
node_2—> node_3	48.APPINT	1	0.429	B ==> A
	56.4STERN	1	0.375	A —> B
	60.EXOP1	1	0.645	4—> 7
	62.MX2EDMSB	1	0.500	A ==> B
node_3—> *G. americanus*	8.RLENGTH	1	0.571	A ==> D
	21.SPINLOC	1	0.429	A ==> C
	26.SCAPHO	1	0.214	A ==> D
	27.MAXLAC	1	1.000	A ==> D
	33.MOLAR	1	0.667	B —> F
	34.INCISS	1	0.833	B —> E
	55.2STRLRIDG	1	0.750	A —> F
	56.4STERN	1	0.375	B —> E
	65.GONOP	1	0.833	K ==> 6
	70.TELDSPINE	1	0.778	A ==> B
node_3 —> node_4	11.CARTEETH	1	0.714	F ==> A
	23.ANT1FUSG	1	1.000	D ==> A

Table 9. Cladistic analysys of Palaemonids. Final tree length 606. Apomorphies List. Edited as in Final tree (Figure 41)

APOMORPHY LISTS:

Branch	**Character No.**	**Code**	**Steps CI**	**Change**
	24.FREE/FUS	1	0.269	C —> A
	32.IIMAXEND	1	0.667	C ==> A
	46.MAXILLP3	1	0.583	F ==> A
	49.FSPINE	1	0.176	A ==> B
	61.ENDT1MX	1	0.769	K —> A
	67.OCELLUS	1	0.250	B ==> A
	69.3-5DACT	1	0.500	B ==> A
node_4 —> node_12	18.TINSPINE	1	0.273	A ==> C
	54.5STSPIN	1	0.231	B —> C
node_12—> node_13	3.BRNSPINE	1	0.600	B ==> A
	12.1stTEETH	1	0.300	A ==> B
	26.SCAPHO	1	0.214	A ==> C
	48.APPINT	1	0.429	A ==> B
	57.ANLPLTE	1	0.267	B ==> A
node_13 —> *Ln. tenuicornis*	37.PALM	1	0.600	B ==> C
	45.MANDPLP	1	0.250	A ==> B
node_13 —> *Lt. celebensis*	54.5STSPIN	1	0.231	C —> B
node_12—> node_14	4.HEPSPINE	1	0.333	A ==> B
	24.FREE/FUS	1	0.269	A —> B
	55.2STRLRIDG	1	0.750	A —> J
node_14—> node_15	24.FREE/FUS	1	0.269	B —> C
	40.FINGTEETH	1	0.379	B ==> 9
	46.MAXILLP3	1	0.583	A ==> F
	60.EXOP1	1	0.645	7 ==> 6
	65.GONOP	1	0.833	K —> 6
	70.TELDSPINE	1	0.778	A ==> B
node_15—> node_16	45.MANDPLP	1	0.250	A ==> B
	65.GONOP	1	0.833	6 —> 7
node_16-> *Pe. longicaudatus*	48.APPINT	1	0.429	A ==> B
	60.EXOP1	1	0.645	6 ==> B
	69.3-5DACT	1	0.500	A ==> B
node_16—> *Pn. holmesi*	6.SUORBSPN	1	0.667	A ==> B
node_14—> node_17	45.MANDPLP	1	0.250	A ==> C
	52.5STRGRVE	1	0.462	A ==> E
	56.4STERN	1	0.375	B ==> D
	59.EPIPOD3	1	0.692	F ==> B
node_17 —> *M. intermedius*	26.SCAPHO	1	0.214	A ==> C
	55.2STRLRIDG	1	0.750	J —> A
	57.ANLPLTE	1	0.267	B ==> A
	60.EXOP1	1	0.645	7 ==> B
	65.GONOP	1	0.833	K ==> A
	66.STATOCYS	1	0.750	B ==> A

Table 9. Cladistic analysis of Palaemonids. Final tree length 606. Apomorphies List. Edited as in Final tree (Figure 41)

APOMORPHY LISTS:

Branch	**Character No.**	**Code**	**Steps CI**	**Change**
node_17 > *B. biunguiculatus*	16.TELSET	1	0.556	E ==> A
	18.TINSPINE	1	0.273	C ==> B
	30.UPLAC	1	0.182	A ==> B
	48.APPINT	1	0.429	A ==> B
	69.3-5DACT	1	0.500	A ==> B
node_4 —> node_5	16.TELSET	1	0.556	E ==> A
	40.FINGTEETH	1	0.379	B ==> A
	47.LG5SDSET	1	0.250	B ==> A
	59.EPIPOD3	1	0.692	F ==> A
	60.EXOP1	1	0.645	7 —> B
	65.GONOP	1	0.833	K —> A
	66.STATOCYS	1	0.750	B ==> A
	*68.DEVELOP.	1	0.143	B —> A
	*83.HABITAT	1	0.250	M ==> F
node_5 —> node_18	4.HEPSPINE	1	0.333	A ==> B
	45.MANDPLP	1	0.250	A ==> C
	55.2STRLRIDG	1	0.750	A ==> D
	60.EXOP1	1	0.645	B —> L
	65.GONOP	1	0.833	A —> N
node_18—> node_19	22.SIX/FIFTH	1	0.250	A —> B
	65.GONOP	1	0.833	N —> O
node_19—> node_20	49.FSPINE	1	0.176	B ==> A
node_20—> *M. rodriguezi*	24.FREE/FUS	1	0.269	A ==> D
node_20—> node_21	45.MANDPLP	1	0.250	C —> A
node_21—> node_23	7.ROSTRUM	1	0.545	A ==> D
node_22—> *Ps. chryseus*	40.FINGTEETH	1	0.379	A ==> B
node_22—> *Ps. nigrannis*	—			
node_22—> *Ps. buvieri*	—			
node_19—> node_24	8.RLENGTH	1	0.571	A ==> C
	14.DIST1/4	1	0.385	A ==> B
node_24 —> *M. reyesi*	22.SIX/FIFTH	1	0.250	B —> A
	40.FINGTEETH	1	0.379	A ==> B
node_24—> node_25	12.1stTEETH	1	0.300	A ==> B
node_25 —> node_26	55.2STRLRIDG	1	0.750	D ==> K
node_26 —> *M. jelskii*	40.FINGTEETH	1	0.379	A ==> B
node_26 —> *Ps. amazonensis*	45.MANDPLP	1	0.250	C ==> A
	49.FSPINE	1	0.176	B ==> A
node_18—> node_27	52.5STRGRVE	1	0.462	A —> D
	60.EXOP1	1	0.645	L —> 9
node_27 —> node_28	44.EYSTLK	1	0.571	A ==> B
	56.4STERN	1	0.375	B ==> A
	67.OCELLUS	1	0.250	A —> B
node_28—> *M. villalobosi*	30.UPLAC	1	0.182	A ==> B
	35.2ndLEG	1	0.286	A ==> B
	52.5STRGRVE	1	0.462	D —> A
node_28—> node_29	45.MANDPLP	1	0.250	C ==> B

Table 9. Cladistic analysis of Palaemonids. Final tree length 606. Apomorphies List. Edited as in Final tree (Figure 41)

APOMORPHY LISTS:

Branch	**Character No.**	**Code**	**Steps CI**	**Change**
	60.EXOP1	1	0.645	9 —> A
node_29—> *Ne. nahuatlus*	47.LG5SDSET	1	0.250	A ==> B
	60.EXOP1	1	0.645	A —> K
node_29 —> node_30	4.HEPSPINE	1	0.333	B ==> A
	26.SCAPHO	1	0.214	A ==> D
	38.FINGSHP	1	0.750	A ==> D
	40.FINGTEETH	1	0.379	A —> H
node_30 —> *Cr. morleyi*	3.BRNSPINE	1	0.600	B ==> D
	24.FREE/FUS	1	0.269	A ==> D
	35.2ndLEG	1	0.286	A ==> B
	42.LEG2	1	0.500	B ==> A
	49.FSPINE	1	0.176	B ==> A
	60.EXOP1	1	0.645	A —> N
node_30 —> node_31	13.RTOTTETH	1	0.429	B ==> A
	21.SPINLOC	1	0.429	A ==> C
	37.PALM	1	0.600	B ==> C
	45.MANDPLP	1	0.250	B ==> A
	55.2STRLRIDG	1	0.750	D ==> E
	58.GILLAMELL	1	0.571	C ==> A
node_31—> node_32	40.FINGTEETH	1	0.379	H —> A
	52.5STRGRVE	1	0.462	D ==> A
	54.5STSPIN	1	0.231	B —> D
	60.EXOP1	1	0.645	A —> O
node_32—> *T. jamaicensis*	24.FREE/FUS	1	0.269	A ==> D
	51.LRDGSPIN	1	0.500	A ==> D
node_32—> node_33	44.EYSTLK	1	0.571	B ==> C
node_33—> *T. gibarensis*	21.SPINLOC	1	0.429	C ==> A
	60.EXOP1	1	0.645	O —> A
node_33—> node_34	54.5STSPIN	1	0.231	D —> A
	82.CARSHPE	1	1.000	A ==> B
node_34—> *T. inermis*	33.MOLAR	1	0.667	B ==> A
	34.INCISS	1	0.833	B ==> A
	54.5STSPIN	1	0.231	A —> B
	59.EPIPOD3	1	0.692	A ==> C
node_34—> *T. calcis*	40.FINGTEETH	1	0.379	A ==> H
node_35—> *T. eingenmani*	26.SCAPHO	1	0.214	D ==> A
	40.FINGTEETH	1	0.379	H —> B
	44.EYSTLK	1	0.571	B ==> A
	54.5STSPIN	1	0.231	B ==> A
	65.GONOP	1	0.833	N ==> A
node_35—> node_36	7.ROSTRUM	1	0.545	A —> E
	9.RLWKEEL	1	0.333	A —> B
	14.DIST1/4	1	0.385	A ==> F
	32.IIMAXEND	1	0.667	A ==> B
	49.FSPINE	1	0.176	B ==> A
node_36> *T. perezfarfantae*	2.ANTSPINE	1	0.500	A ==> B
	18.TINSPINE	1	0.273	A ==> B
	19.DISTSPIN	1	0.800	A ==> C
	33.MOLAR	1	0.667	B ==> D
	50.LTRIDGES	1	0.714	A ==> B
	51.LRDGSPIN	1	0.500	A ==> D

Table 9. Cladistic analysis of Palaemonids. Final tree length 606. Apomorphies List. Edited as in Final tree (Figure 41)

APOMORPHY LISTS:

Branch	**Character No.**	**Code**	**Steps CI**	**Change**
node_36—> node_37	8.RLENGTH	1	0.571	A ==> D
	17.TELTIP	1	0.818	A ==> 9
	21.SPINLOC	1	0.429	C ==> A
	24.FREE/FUS	1	0.269	A —> D
	38.FINGSHP	1	0.750	D ==> A
	40.FINGTEETH	1	0.379	H —> G
	59.EPIPOD3	1	0.692	A ==> C
	60.EXOP1	1	0.645	A —> D
node_37—> *Tr. phreaticus*	7.ROSTRUM	1	0.545	E —> A
	9.RLWKEEL	1	0.333	B —> A
	20.D2nDSPINE	1	0.556	B ==> A
	49.FSPINE	1	0.176	A ==> C
	52.5STRGRVE	1	0.462	D ==> A
node_37—> node_38	24.FREE/FUS	1	0.269	D —> E
	25.UROPSPIN	1	0.667	A ==> C
	34.INCISS	1	0.833	B ==> A
	44.EYSTLK	1	0.571	B —> A
	46.MAXILLP3	1	0.583	A ==> E
	54.5STSPIN	1	0.231	B ==> D
	55.2STRLRIDG	1	0.750	E ==> D
	65.GONOP	1	0.833	N —> P
	81.EYEFACET	1	1.000	A ==> C
node_38—> *Ty. lethaea*	2.ANTSPINE	1	0.500	A ==> B
	51.LRDGSPIN	1	0.500	A ==> B
	58.GILLAMELL	1	0.571	A ==> C
	60.EXOP1	1	0.645	D —> A
	65.GONOP	1	0.833	P —> Q
node_38—> node_39	19.DISTSPIN	1	0.800	A ==> D
	20.D2nDSPINE	1	0.556	B ==> E
	23.ANT1FUSG	1	1.000	A ==> C
	24.FREE/FUS	1	0.269	E —> F
	33.MOLAR	1	0.667	B ==> A
	40.FINGTEETH	1	0.379	G —> B
	44.EYSTLK	1	0.571	A —> D
	57.ANLPLTE	1	0.267	B ==> A
	69.3-5DACT	1	0.500	A ==> B
node_39—> *Ena. edingtonae*	60.EXOP1	1	0.645	D —> O
	66.STATOCYS	1	0.750	A ==> C
node_40—> *Ec. holthuisi*	14.DIST1/4	1	0.385	F ==> A
	46.MAXILLP3	1	0.583	E ==> A
node_27—> node_41	18.TINSPINE	1	0.273	A —> B
	39.FINGCOVER	1	0.800	A ==> C
	40.FINGTEETH	1	0.379	A ==> D
	42.LEG2	1	0.500	B ==> A
	*68.DEVELOP.	1	0.143	A —> B
node_41—> *M. borelli*	29.LACFRONT	1	0.556	A ==> D
node_41—> node_42	30.UPLAC	1	0.182	A ==> B
node_42—> *M. praecox*	18.TINSPINE	1	0.273	B —> A
	49.FSPINE	1	0.176	B ==> D
node_42—> node_43	24.FREE/FUS	1	0.269	A ==> D
	39.FINGCOVER	1	0.800	C ==> B

Table 9. Cladistic analysis of Palaemonids. Final tree length 606. Apomorphies List. Edited as in Final tree (Figure 41)

APOMORPHY LISTS:

Branch	**Character No.**	**Code**	**Steps CI**	**Change**
	56.4STERN	1	0.375	B ==> D
node_43—> node_44	37.PALM	1	0.600	B ==> C
node_44—> node_45	12.1stTEETH	1	0.300	A ==> B
node_45—> node_46	41.FINGTUBRCL	1	0.333	A ==> B
	49.FSPINE	1	0.176	B ==> A
node_46—> *M. lujae*	35.2ndLEG	1	0.286	A ==> B
node_46—> *M. raridens*	14.DIST1/4	1	0.385	E —> A
	14.DIST1/4	1	0.385	A —> E
	*83.HABITAT	1	0.250	F ==> 9
node_45—> node_47	30.UPLAC	1	0.182	B —> H
	39.FINGCOVER	1	0.800	B ==> C
node_47—> node_48	52.5STRGRVE	1	0.462	D ==> A
node_48—> *M. weberi*	30.UPLAC	1	0.182	H —> B
node_48—> *M. equidens*	14.DIST1/4	1	0.385	E —> A
node_47—> node_49	8.RLENGTH	1	0.571	A ==> F
	13.RTOTTETH	1	0.429	B ==> C
node_49—> node_50	17.TELTIP	1	0.818	A ==> D
node_50—> *M. amazonicum*	49.FSPINE	1	0.176	B ==> A
	55.2STRLRIDG	1	0.750	D ==> A
node_50—> node_51	52.5STRGRVE	1	0.462	D ==> A
node_51—> *M. rosembergi*	28.INNLAC	1	0.400	A ==> C
	54.5STSPIN	1	0.231	B ==> A
	57.ANLPLTE	1	0.267	B ==> A
node_43—> node_52	15.RTIP	1	0.500	A ==> D
	35.2ndLEG	1	0.286	A ==> B
node_52—> node_53	60.EXOP1	1	0.645	9 ==> J
	*68.DEVELOP.	1	0.143	B ==> A
node_53—> *M. dux*	49.FSPINE	1	0.176	B ==> A
node_53—> node_54	16.TELSET	1	0.556	A ==> D
node_54—> *M. nepalense*	39.FINGCOVER	1	0.800	B ==> E
node_54—> node_55	17.TELTIP	1	0.818	A ==> E
node_55—> *M. quelchi*	49.FSPINE	1	0.176	B ==> A
node_55—> node_56	41.FINGTUBRCL	1	0.333	A ==> B
node_56—> *M. potiuna*	29.LACFRONT	1	0.556	A ==> E
	37.PALM	1	0.600	B ==> G
	38.FINGSHP	1	0.750	A ==> E
node_56—> *By. luscus*	4.HEPSPINE	1	0.333	B ==> A
	18.TINSPINE	1	0.273	B ==> A
	35.2ndLEG	1	0.286	B ==> A
node_56—> node_57	24.FREE/FUS	1	0.269	D ==> A
node_57—> node_58	49.FSPINE	1	0.176	B ==> A
node_58—> node_59	16.TELSET	1	0.556	D ==> H
node_59—> *M. cortezi*	41.FINGTUBRCL	1	0.333	B ==> A
node_57—> node_60	28.INNLAC	1	0.400	A —> C
node_60—> *C. brasiliensis*	15.RTIP	1	0.500	D ==> A
	52.5STRGRVE	1	0.462	D ==> A
	56.4STERN	1	0.375	D ==> A
	57.ANLPLTE	1	0.267	B ==> C
	60.EXOP1	1	0.645	J ==> 9
node_60—> node_61	1.CARAP	1	1.000	A ==> B
node_61—> *M. nattereri*	28.INNLAC	1	0.400	C —> A

Table 9. Cladistic analysis of Palaemonids. Final tree length 606. Apomorphies List. Edited as in Final tree (Figure 41)

APOMORPHY LISTS:

Branch	**Character No.**	**Code**	**Steps CI**	**Change**
	17.TELTIP	1	0.818	E ==> A
node_61—> node_62	30.UPLAC	1	0.182	B ==> H
node_62—> *M. brasiliense*	29.LACFRONT	1	0.556	A ==> E
node_62—> *M. iheringi*	24.FREE/FUS	1	0.269	A ==> D
	37.PALM	1	0.600	B ==> G
	57.ANLPLTE	1	0.267	B ==> C
node_52—> node_63	30.UPLAC	1	0.182	B ==> H
	57.ANLPLTE	1	0.267	B ==> C
	*83.HABITAT	1	0.250	F ==> 9
node_63—> *M. ohione*	7.ROSTRUM	1	0.545	A ==> C
node_63—> node_64	16.TELSET	1	0.556	A ==> D
	35.2ndLEG	1	0.286	B —> C
node_64—> node_65	11.CARTEETH	1	0.714	A ==> B
	49.FSPINE	1	0.176	B ==> A
	53.5STCOXA	1	1.000	A ==> B
node_65—> node_66	42.LEG2	1	0.500	A ==> C
node_66—> node_67	37.PALM	1	0.600	B ==> D
	38.FINGSHP	1	0.750	A ==> B
	40.FINGTEETH	1	0.379	D ==> F
	64.3MASTIGOB	1	1.000	A ==> B
node_67 —> *M. felicinum*	49.FSPINE	1	0.176	A ==> B
node_67—> node_68	51.LRDGSPIN	1	0.500	A ==> B
	56.4STERN	1	0.375	D ==> C
node_68 —> *C. caementerius*	4.HEPSPINE	1	0.333	B ==> A
node_65—> node_69	28.INNLAC	1	0.400	A ==> C
	35.2ndLEG	1	0.286	C —> B
node_69—> node_70	40.FINGTEETH	1	0.379	D ==> E
node_70 —> *M. horstii*	42.LEG2	1	0.500	A ==> C
node_69—> node_71	7.ROSTRUM	1	0.545	A ==> C
	51.LRDGSPIN	1	0.500	A ==> B
node_71—> node_72	15.RTIP	1	0.500	D ==> B
	56.4STERN	1	0.375	D ==> C
node_72 —> *M. lar*	11.CARTEETH	1	0.714	B ==> A
	12.1stTEETH	1	0.300	A ==> B
	16.TELSET	1	0.556	D ==> A
	50.LTRIDGES	1	0.714	A ==> D
	37.PALM	1	0.600	B ==> D
	40.FINGTEETH	1	0.379	D ==> E
	50.LTRIDGES	1	0.714	A ==> C
node_5 —> node_6	3.BRNSPINE	1	0.600	B ==> A
	5.BRNGRV	1	1.000	B ==> A
node_6 —> node_73	29.LACFRONT	1	0.556	A ==> B
	33.MOLAR	1	0.667	B ==> C
	52.5STRGRVE	1	0.462	A ==> B
	55.2STRLRIDG	1	0.750	A ==> B
	56.4STERN	1	0.375	B ==> A
	59.EPIPOD3	1	0.692	A ==> E
	60.EXOP1	1	0.645	B —> H
	61.ENDT1MX	1	0.769	A ==> G
	65.GONOP	1	0.833	A —> L
node_73 —> *P. mercedes*	18.TINSPINE	1	0.273	A ==> B

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APOMORPHY LISTS:

Branch	**Character No.**	**Code**	**Steps CI**	**Change**
	20.D2nDSPINE	1	0.556	B ==> F
	40.FINGTEETH	1	0.379	A ==> B
	49.FSPINE	1	0.176	B ==> A
	15.RTIP	1	0.500	D ==> B
node_73 —> node_74	31.UPLACSHP	1	0.875	A ==> D
node_74 —> *P. carteri*	14.DIST1/4	1	0.385	A ==> B
	24.FREE/FUS	1	0.269	A ==> B
node_74 —> *P. ivonicus*	50.LTRIDGES	1	0.714	A ==> C
node_6—> node_7	24.FREE/FUS	1	0.269	A ==> B
	*68.DEVELOP	1	0.143	A —> B
	*83.HABITAT	1	0.250	F —> E
node_7 —> *P. octaviae*	50.LTRIDGES	1	0.714	A ==> C
node_7 —> node_8	58.GILLAMELL	1	0.571	C ==> A
node_8 —> node_75	10.RLOWTH	1	0.429	A ==> B
	40.FINGTEETH	1	0.379	A ==> B
node_75 —> node_76	12.1stTEETH	1	0.300	A ==> B
node_76 —> node_77	54.5STSPIN	1	0.231	B ==> A
node_77 —> node_78	45.MANDPLP	1	0.250	A ==> C
node_78 —> *Pl. peruanius*	24.FREE/FUS	1	0.269	B ==> A
node_78 —> node_79	59.EPIPOD3	1	0.692	A ==> B
	*83.HABITAT	1	0.250	E —> M
node_79 —> node_80	40.FINGTEETH	1	0.379	B ==> A
node_80 —> *Pl. longirostris*	60.EXOP1	1	0.645	B ==> C
	*83.HABITAT	1	0.250	M —> E
node_80 —> *Pl. gladiator*	24.FREE/FUS	1	0.269	B ==> A
node_79 —> node_81	57.ANLPLTE	1	0.267	B ==> A
node_81 —> node_82	30.UPLAC	1	0.182	A ==> B
node_82 —> *Pl. serrifer*	31.UPLACSHP	1	0.875	A ==> C
	65.GONOP	1	0.833	A ==> F
node_82 —> node_83	24.FREE/FUS	1	0.269	B ==> D
node_83—> Pl.ritteri	56.4STERN	1	0.375	B ==> A
	57.ANLPLTE	1	0.267	A ==> B
	56.4STERN	1	0.375	B ==> A
node_83 —> node_84	14.DIST1/4	1	0.385	A ==> B
node_84—> *Pl. xiphias*	15.RTIP	1	0.500	A ==> C
	26.SCAPHO	1	0.214	A ==> C
node_84 —> node_85	24.FREE/FUS	1	0.269	D ==> A
node_85—> *Pl. pacificus*	7.ROSTRUM	1	0.545	A ==> B
	49.FSPINE	1	0.176	B ==> A
node_85 —> node_86	60.EXOP1	1	0.645	B ==> C
node_86 —> node_87	65.GONOP	1	0.833	A —> F
node_87—> *Pl. macrodactylus*	56.4STERN	1	0.375	B ==> A
node_87 —> node_88	10.RLOWTH	1	0.429	B ==> A
	57.ANLPLTE	1	0.267	A ==> B
	*83.HABITAT	1	0.250	M ==> E
node_88—> *Pl. concinus*	31.UPLACSHP	1	0.875	A ==> C
node_88—> *Pl. paucidens*	22.SIX/FIFTH	1	0.250	A ==> B
	40.FINGTEETH	1	0.379	B ==> A
	65.GONOP	1	0.833	F —> G
node_81 —> node_89	14.DIST1/4	1	0.385	A ==> B

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APOMORPHY LISTS:

Branch	**Character No.**	**Code**	**Steps CI**	**Change**
node_89 —> node_90	45.MANDPLP	1	0.250	C ==> B
node_90 —> *Pl. elegans*	72.SCAPHOG	1	0.500	A ==> B
node_90 —> node_91	56.4STERN	1	0.375	B ==> A
node_91 —> *Pl. squilla*	24.FREE/FUS	1	0.269	B ==> A
node_91 —> node_92	57.ANLPLTE	1	0.267	A —> B
node_93 —> *Pl. floridanus*	7.ROSTRUM	1	0.545	A ==> B
	26.SCAPHO	1	0.214	A ==> C
node_93 —> *Pl. northropi*	—			
node_92 —> node_94	10.RLOWTH	1	0.429	B ==> A
	40.FINGTEETH	1	0.379	B —> A
	59.EPIPOD3	1	0.692	B ==> A
	*83.HABITAT	1	0.250	M —> E
node_94 —> *P. atrinubes*	57.ANLPLTE	1	0.267	B —> A
	*68.DEVELOP.	1	0.143	B ==> A
node_94 —> node_95	60.EXOP1	1	0.645	B ==> C
node_95—> *Pl. semmelinkii*	40.FINGTEETH	1	0.379	A —> B
	65.GONOP	1	0.833	A ==> J
	*83.HABITAT	1	0.250	E —> M
node_95 —> *Pl. maculatus*	13.RTOTTETH	1	0.429	B ==> C
node_89 —> node_96	7.ROSTRUM	1	0.545	A ==> B
	8.RLENGTH	1	0.571	A ==> C
	13.RTOTTETH	1	0.429	B ==> C
	15.RTIP	1	0.500	A ==> C
node_96 —> *Pl. ortmani*	26.SCAPHO	1	0.214	A ==> C
node_96 —> node_97	10.RLOWTH	1	0.429	B ==> A
	14.DIST1/4	1	0.385	B ==> D
	40.FINGTEETH	1	0.379	B ==> A
	57.ANLPLTE	1	0.267	A ==> B
node_97 —> *Pl. debilis*	59.EPIPOD3	1	0.692	B ==> A
node_97 —> node_98	17.TELTIP	1	0.818	A —> B
node_98 —> node_99	26.SCAPHO	1	0.214	A ==> C
node_99 —> *E. orientis*	43.LEG3-5	1	1.000	A ==> B
node_99 —> node_100	12.1stTEETH	1	0.300	B ==> A
	60.EXOP1	1	0.645	B —> F
	18.TINSPINE	1	0.273	A ==> B
	24.FREE/FUS	1	0.269	B —> A
	63.5thPLR	1	1.000	A ==> B
	65.GONOP	1	0.833	A ==> 9
	*83.HABITAT	1	0.250	M ==> E
node_100 —> *N. schmitti*	30.UPLAC	1	0.182	A ==> B
	43.LEG3-5	1	1.000	A ==> D
	58.GILLAMELL	1	0.571	A ==> D
	61.ENDT1MX	1	0.769	A ==> F
	67.OCELLUS	1	0.250	A ==> B
	81.EYEFACET	1	1.000	A ==> B
node_100 —> *L. potamiscus*	3.BRNSPINE	1	0.600	A ==> B
	18.TINSPINE	1	0.273	B ==> A
	60.EXOP1	1	0.645	F —> G
	65.GONOP	1	0.833	9 ==> 8
node_98 —> node_101	24.FREE/FUS	1	0.269	A —> D

Table 9. Cladistic analysis of Palaemonids. Final tree length 606. Apomorphies List. Edited as in Final tree (Figure 41)

APOMORPHY LISTS:

Branch	**Character No.**	**Code**	**Steps CI**	**Change**
	54.5STSPIN	1	0.231	A ==> B
	60.EXOP	1	0.645	B ==> E
node_101 > *Pl. pandaliformis*	17.TELTIP	1	0.818	B —> A
node_101 —> node_102	12.1stTEETH	1	0.300	B ==> A
	59.EPIPOD3	1	0.692	B ==> D
	61.ENDT1MX	1	0.769	A ==> F
node_102 —> Pl. gracilis	31.UPLACSHP	1	0.875	A ==> H
node_77 —> *P. argentinus*	40.FINGTEETH	1	0.379	B ==> A
node_77 —> node_103	10.RLOWTH	1	0.429	B ==> A
node_104 —> *P. intermedius*	—			
node_103 —> node_104	58.GILLAMELL	1	0.571	A ==> C
node_104 —> *P. pugio*	31.UPLACSHP	1	0.875	A ==> B
node_104 —> *P. vulgaris*	—			
node_8 —> node_9	24.FREE/FUS	1	0.269	B ==> C
	60.EXOP1	1	0.645	B ==> A
	61.ENDT1MX	1	0.769	A ==> B
	*68.DEVELOP.	1	0.143	B —> A
	*83.HABITAT	1	0.250	E —> F
node_9 —> node_105	46.MAXILLP3	1	0.583	A ==> B
node_105 —> node_107	29.LACFRONT	1	0.556	A ==> D
	65.GONOP	1	0.833	A ==> C
node_107 —> *P. mesogenitor*	30.UPLAC	1	0.182	A ==> B
node_107-> *P. mesopotamicus*	—			
node_105 —> node_106	22.SIX/FIFTH	1	0.250	A ==> B
node_106 —> *P. antenarius*	30.UPLAC	1	0.182	A ==> B
node_106 —> *P. africanus*	24.FREE/FUS	1	0.269	C ==> B
	26.SCAPHO	1	0.214	A ==> C
	32.IIMAXEND	1	0.667	A ==> B
	38.FINGSHP	1	0.750	A ==> C
node_9 —> node_108	29.LACFRONT	1	0.556	A ==> C
node_108 —> *P. varians*	46.MAXILLP3	1	0.583	A ==> C
	*68.DEVELOP.	1	0.143	A —> B
node_108 —> node_109	54.5STSPIN	1	0.231	B ==> A
node_109 —> *P. cummingi*	20.D2nDSPINE	1	0.556	B ==> A
	60.EXOP1	1	0.645	A ==> D
node_109 —> node_110	65.GONOP	1	0.833	A ==> B
node_110 —> node_111	29.LACFRONT	1	0.556	C ==> A
node_111—>*P. texanus*	—			
node_111—>*P. paludosus*	—			
node_110 —> node_112	46.MAXILLP3	1	0.583	A ==> B
node_112 —> node_113	58.GILLAMELL	1	0.571	A ==> B
node_113 —> *P. lindsayi*	25.UROPSPIN	1	0.667	A ==> B
node_113 —> *P. kadiakensis*	60.EXOP1	1	0.645	A ==> D
node_112 —> node_114	61.ENDT1MX	1	0.769	B ==> A
node_114 —> *P. sutkusi*	25.UROPSPIN	1	0.667	A ==> B
node_114 —> node_115	29.LACFRONT	1	0.556	C ==> A
node_115 —> *P. mexicanus*	20.D2nDSPINE	1	0.556	B ==> A
node_115 —> node_116	24.FREE/FUS	1	0.269	C ==> A
	27.MAXLAC	1	1.000	A ==> B
	56.4STERN	1	0.375	B ==> A

Table 9. Cladistic analysis of Palaemonids. Final tree length 606. Apomorphies List. Edited as in Final tree (Figure 41)

APOMORPHY LISTS:

Branch	**Character No.**	**Code**	**Steps CI**	**Change**
node_116 —> *P. sinensis*	46.MAXILLP3	1	0.583	B ==> C
	61.ENDT1MX	1	0.769	A ==> C
	70.TELDSPINE	1	0.778	A ==> C
node_116 —> node_117	36.1st/2nd	1	0.600	B —> A
	38.FINGSHP	1	0.750	A ==> C
node_117 —> node_118	61.ENDT1MX	1	0.769	A —> D
	62.MX2ENDSBR	1	0.500	B ==> A
node_118—> *P. tonkinensis*	36.1st/2nd	1	0.600	A —> B
node_118 —> *D. trispinosus*	6.SUORBSPN	1	0.667	A ==> B
	18.TINSPINE	1	0.273	A ==> B
	19.DISTSPIN	1	0.800	A ==> F
	20.D2nDSPINE	1	0.556	B ==> C
	21.SPINLOC	1	0.429	A ==> B
	24.FREE/FUS	1	0.269	A ==> H
	26.SCAPHO	1	0.214	A ==> C
	31.UPLACSHP	1	0.875	A ==> 9
	32.IIMAXEND	1	0.667	A ==> B
	33.MOLAR	1	0.667	B ==> C
	40.FINGTEETH	1	0.379	A ==> C
	46.MAXILLP3	1	0.583	B ==> D
	52.5STRGRVE	1	0.462	A ==> C
	54.5STSPIN	1	0.231	A ==> B
	58.GILLAMELL	1	0.571	A ==> E
	59.EPIPOD3	1	0.692	A ==> 9
	60.EXOP1	1	0.645	A ==> M
	61.ENDT1MX	1	0.769	D —> H
	65.GONOP	1	0.833	B ==> M
	67.OCELLUS	1	0.250	A ==> B
	71.#DRSLSPIN	1	1.000	A ==> E
node_117 —> node_119	13.RTOTTETH	1	0.429	B ==> A
	21.SPINLOC	1	0.429	A ==> C
	25.UROPSPIN	1	0.667	A ==> B
	33.MOLAR	1	0.667	B —> D
	44.EYSTLK	1	0.571	A ==> B
	54.5STSPIN	1	0.231	A ==> D
	59.EPIPOD3	1	0.692	A ==> G
	65.GONOP	1	0.833	B ==> D
node_119 —> *A. antrorum*	11.CARTEETH	1	0.714	A ==> B
	20.D2nDSPINE	1	0.556	B ==> A
	37.PALM	1	0.600	B ==> A
	40.FINGTEETH	1	0.379	A ==> C
	49.FSPINE	1	0.176	B ==> A
	51.LRDGSPIN	1	0.500	A ==> C
node_119 —> *A. holthuisi*	17.TELTIP	1	0.818	A ==> G
	34.INCISS	1	0.833	B ==> C
	61.ENDT1MX	1	0.769	A ==> E
	70.TELDSPINE	1	0.778	A ==> C

*** Excluded character(s) not included in length calculations**

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