

# THE RECLASSIFICATION OF BRACHYURAN CRABS (CRUSTACEA: DECAPODA: BRACHYURA)

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A reclassification of brachyuran crabs (Crustacea: Decapoda: Brachyura) including a re-appraisal of their whole systematics, re-assessment of the systematic status and position of all extant and extinct suprageneric taxa and their redescription, as well as a description of new taxa, has been undertaken. A great number of new higher taxa have been established and the majority of higher taxa have had their systematic status and position changed.

**Key words:** brachyuran crabs, Crustacea, Decapoda, Brachyura, systematics, revision, reclassification.

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Reklasifikacija kratkorepih rakova (Crustacea: Decapoda: Brachyura) odnosi se na preispitivanje cjelokupnog njihovog sustava, uključujući preispitivanje sistematskog statusa i položaja sviju recentnih i izumrlih svojiti iznad razine roda kao i njihove ponovne opise. Uspostavljeno je mnogo novih viših svojiti, a većini je izmijenjen sistematski status i položaj.

**Ključne riječi:** kratkorepi raci, Crustacea, Decapoda, Brachyura, sistematika, revizija, reklasifikacija

## INTRODUCTION

Brachyuran crabs (Crustacea: Decapoda: Brachyura) are one of the most diverse animal groups at the infra-order level. They exhibit an outstanding diversity in the numbers of extant and extinct taxa at all categorical levels. Recently, especially during the past several decades, judging from the number of publications and new taxa described, the knowledge of their systematics has increased rapidly. However, the data are very dispersed, written in various languages, and in publications that are often difficult to obtain. The rapid influx of knowledge concerning brachyuran

taxa may be attributed to the increasing interest of scientists in the group. New expeditions, improved methods of sampling, a better knowledge of systematic characters and systematic theories have also aided in this endeavour. The attention of specialists has been focused mostly on species and genera (alpha taxonomy). At the same time the higher-level systematics of the group, the suprageneric taxa (tribes, subfamilies, families and superfamilies) have been neglected by the majority of carcinologists, so much so that higher taxa have often remained vaguely delimited, imperfectly described and inappropriately arranged. The authors usually re-write the descriptions of higher taxa from ALCOCK (1895 – 1910), written more than a century ago, with little or no improvement, although theoretical and practical knowledge have advanced substantially. Rarely have new higher taxa been described. As such, new descriptions of higher taxa have often omitted their systematic status and position, with reclassification postponed to an indefinite future. One may see how some families have undergone complete revisions, while many others remain only partially revised or have never been revised at all. Thus, the historical development of brachyuran systematics has been very unbalanced, with prolific discoveries of new species and genera and incompletely described suprageneric taxa. The result of this unbalanced research program is an imperfect brachyuran classification. Systematic study of the crabs as a whole also remains incomplete and imperfect and therefore revision on all levels awaits a better time.

In the recent systematic literature the most frequent phrase is »a revision is badly needed«. All authors working on brachyuran systematics invariably agree that a general revision of the whole group is urgently needed, yet nothing has been done to accomplish it. Many carcinologists are conscious of the need for general revision, like, for example, Austin WILLIAMS, who in his letter to the author of Oct. 31, 1989 wrote: »The higher categories are ill defined. Many accepted definitions are nothing more than central tendencies around which are clustered conformers to those tendencies, but in many cases around which are appended the exceptions as well. Conservatism militates against creation of many small families or other higher subdivisions of the hierarchy to accommodate these problems in classification. The expert comes to know the labyrinthine structure, recognizes the dead ends, blind loops, deceptive paths, appended detours, i.e. the exceptions, and accepts these because redesign with aid of the tools available (morphology until now) is a daunting task«. To accomplish such a research project, it is necessary to perform three things: firstly to compile all up to date data on the suprageneric brachyuran, secondly, to critically re-examine the homogeneity, systematic status and position of all suprageneric taxa, and thirdly, to propose a new, updated system of classification. Unfortunately at this time no such comprehensive compilation exists. On the other hand every year produces many new lower taxa with only a temporary classification or often without attempts at any classification of the newly described taxa into a natural system. The result of such a practice is a chaotic state-of-the-art in brachyuran systematics. So many unresolved problems concerning brachyuran systematics have accumulated over the years that a project of complete revision will take an immense effort by experts. Due to the time-consuming nature of data compilation, their synthesis and critical reassessment, conspectus of

the brachyuran classification in the past has been extremely rare. BLACKWELDER (1967:98) is correct when he claims: »The studies which deal only with the grouping of animals and the arrangement of the groups into categories of the hierarchy are not very numerous«. The complete revision of the brachyuran higher taxa has been indeed »a daunting task«!

It is a matter of fact that research into the brachyuran system is confronted with subjective as well as objective circumstances. It is understandable that leading specialists working in the great museums, in spite of all the favourable facilities (collections, libraries and technical help), tend to avoid a general revision of the entire brachyuran systematics, which requires many years of painful study, and that they cannot find the time for such projects. It is also fact that they have large collections (usually sampled by expeditions) so that they have focused their attention on investigations of their own museum material, describing new species and genera, and seldom touching on the problems of higher classification. So much material has been accumulated that the specialists employed are hardly able to deal with this properly. Moreover, the number of scientists occupied with research into brachyuran crabs (specialists and technical staff) in museums has recently been reduced and collections are not arranged according to current brachyuran systematics. Numerous revisions have not been applied to the museum specimens. For example, although the genus *Pilumnoplax* Stimpson, 1858 (Goneplacidae *sensu* Balss, 1957) is invalid, in many museum collections all around the world, specimens are still labelled under this name. Furthermore, museum collections are often in bad condition because of reduced staff. There are often cases where the names of genera and species were changed but the labels were not changed for a long time so that any orientation in these museums became very difficult. For example I have found four different *Heterocrypta petrosa* Klunzinger, 1906 (Parthenopidae) in various museums, but the name was not correct for any of the four. Moreover, some genera are not at all classified, or only partially classified so that they are placed in a family without precise designation of subfamily or tribe, or some genera are classified into a subfamily, but the family is not denoted. On the other hand it is surprising (and nearly fashionable) that many modern authors in their revisions give neither diagnoses nor descriptions of the higher taxa under study, which makes further classification difficult. Discussions are frequently omitted or, if present, they are often confusing rather than clarifying. Furthermore, many proposed systematic changes are not supported by valuable data such as descriptions rather than by subjective opinions. For example it is clear that if a subfamily is excluded from one family and transferred into another so that both families changed their previous contents, then both should be re-described. All the problems mentioned above make it difficult to draw any further important generalisation from such studies. In the larger works (monographs) the authors usually reiterate more or less modified descriptions from the old authors that have been used for a century and therefore these descriptions are inappropriate (e.g. Oxyrhyncha, Oxystomata, Goneplacidae). The accumulated problems that I have outlined above have all contributed to the postponement of general revision. Consequently, the general critical re-examination of all brachyuran taxa is indeed urgently needed.

## HISTORICAL BACKGROUND

Contemporaneous brachyuran classification is the result of efforts by many generations of carcinologists, whose contribution is worthy of mention. At the onset of modern systematics all brachyuran crabs (as well as many other crustaceans) were placed by LINNAEUS (1758) into only one genus: *Cancer* or more precisely: subgenus *Brachyurus* (plural: Brachyuri). From this point on, progress was made by many authors who dismantled the taxon into many new taxa. LATREILLE (1802) made the first steps towards formal recognition of brachyuran crabs as a discrete higher group and first grouping. Later on, RAFINESQUE (1815), SAMOUELLE (1819), DE HAAN (1833 – 1850), H. MILNE EDWARDS (1834 – 1837) and MACLEAY (1838) made more progress when families were introduced into brachyuran classification. The meritorious work of H. MILNE EDWARDS was especially influential in brachyuran classification, and his groups such as Oxyrhyncha, Oxystomata, Cyclometopa and Catometopa have – »survived« – in the literature, even to the present day. Since he used the French nomenclature his taxa names were, regrettably, attributed to other authors, who used Latin nomenclature. Contributions to this general progress of brachyuran systematics were also made by the works of DANA (1852), STIMPSON (1858 a,b,c,d), BOAS (1880), MIERS (1886) and ORTMANN (1897 – 1901). Each of them described several higher taxa. ALCOCK (1895, 1896, 1898, 1900 a, b, and 1910) made many noteworthy innovations. He focused his attention not only on the description of new species and genera but also on suprageneric taxa. Besides the usual systematic categories (species, genera, subfamilies and families) ALCOCK introduced alliances (= tribes). His descriptions of families and subfamilies were so perfect that they are still used today. Most successive authors adopted ALCOCK's classification and descriptions of subfamilies and families. Regrettably, alliances, i.e. tribes, with some exceptions (e.g. of ORTMANN, 1901; SERÈNE, 1965, 1968; PRETZMANN, 1972; SAKAI, 1976; RODRÍGUEZ, 1982, 1992; ŠTEVČIĆ, 1994), have been ignored by the majority of carcinologists. At the beginning of the 20th century ORTMANN (1901) presented a completely modern review of brachyuran classification. Subsequently, BORRADAILE (1903, 1907) proposed a new classificatory system for the crabs, which was very influential and accepted by many generations of subsequent authors. Thereafter RATHBUN (1918–1937) worked out the brachyuran classification completely, although only for the American region. The contribution of BOUVIER (1940, 1942) was important for the illumination of some classification problems, especially of lower Heterotremata. As the number of newly described taxa increased and the situation became chaotic, the compilation made by BALSS (1957) of all data known at the time still constitutes the most comprehensive work on decapod systematics in general. BALSS assembled and synthesised all known data of extant and extinct taxa, presented descriptions for higher taxa from subfamilies to the Brachyura »Abteilung« (= section) and listed all known genera. His masterpiece remained the principal edifice in brachyuran systematics through the remainder of the 20th century. BALSS encompassed the complete brachyuran systematics with an unprecedented exhaustiveness, but he made no critical revision of suprageneric taxa and therefore did not make any substantial innovation in brachyuran classification. He merely assembled all taxa and placed them into the old classification scheme established mainly by BORRADAILE. Usually, with some rare ex-

ceptions, he did not »touch« any higher taxon that had been previously established. Since this basic work on brachyuran systematics is written in German, it has been neglected by many contemporary authors who unfortunately know only English. Later on, SERÈNE (1965, 1968) reclassified the crabs of East and Southeast Asia, reshuffled many genera and applied ALCOCK's category of the alliance. The last significant progress in a general revision of the brachyuran system was made by GUINOT (1977, 1978), who introduced many important innovations, and her contribution was a substantial advance for the modern brachyuran systematics. In her numerous publications (GUINOT, 1966–71, 1976, 1977, 1986, 1990/91, 1993a,b, 1995; GUINOT & BOUCHARD, 1998; GUINOT & RICHER DE FORGES, 1980/81, 1995, 1997; GUINOT & TAVARES, 2001, 2003) she provided some well-documented revisions of many higher taxa in her exhaustive studies of the brachyuran morphology. GUINOT (1979) was the first one to introduce a suite of new and important diagnostic characters, permitting a much better distinction and accurate description of the taxa than had been possible before (although, regrettably, modern workers apply these characters only rarely in their taxa descriptions). Instead of the unnatural groups of previous authors, Cyclometopa, Catometopa, Oxyrhyncha and Brachyrhyncha, she established a major new classification based on the position of sexual openings and she classified crabs into Podotremata, Heterotremata and Thoracotremata. Moreover, GUINOT revised a lot of enigmatic taxa and described many new genera and species as well as several new families and subfamilies. Furthermore, she partly dismantled the overloaded family Goneplacidae *sensu* BALSS (1957), which had a reputation as the most complex group. Regrettably, in her endeavours, many higher taxa remained only partly revised or even untouched (e.g. Potamidae) and many enigmatic genera that were difficult to place with any confidence in the existing systematic structure remained unnamed and unclassified. Finally, she introduced two informal categories: lineage and grade. At the same time DE SAINT LAURENT (1980) re-examined the major classification of Brachyura and introduced the section Eubrachyura (= Brachyura genuina of BOAS, 1880) for Heterotremata + Thoracotremata.

In parallel with the progress in classification of extant taxa, palaeontology made very considerable advances (FELDMANN, 2003). Many leading carcinologists have studied the fossil material and many new taxa have been recognised in the last several years. Among the palaeontological specialists of note are BEURLEN (1930) and especially GLAESSNER (1969) who applied superfamilies to the brachyuran classification. Considerable contributions to the knowledge of the extinct taxa were made by WRIGHT & COLLINS (1972), HU & TAO, 1996 and numerous contemporary authors.

Indeed, since BALSS' monograph several very important systematic works have been published. These works, were, however, either regional, and therefore incomplete, or complete but usually very short general overviews. However, a modern complete work similar to that of BALSS has not yet been published. Although DAVIE (2002) considerably updated descriptions of families and subfamilies, the families were arranged by alphabetical order and his monograph refers only to Australian crabs.

It should be noted that there are numerous well-founded monographs of regional faunas providing useful data for the study of brachyuran systematics e.g.: BOUVIER, 1940; MONOD, 1956; ZARIQUIEY ALVAREZ, 1968; CHRISTIANSEN, 1969; INGLE, 1980 and

MANNING & HOLTHUIS, 1981 for European and West African waters. RATHBUN, 1918 – 1937; HOLTHUIS, 1959; GARTH, 1946, 1957; RODRÍGUEZ, 1980; WILLIAMS, 1984; MELO, 1996; HENDRICKX, 1997, 1999 for American waters. Similarly, SAKAI, 1976 published a monograph on Japanese crabs, DAI & YANG, 1991 and CHEN & HAIBAO, 2002 on the crabs of Chinese waters, NG, 1988, 1998, NG *et al.* 2001 on the crabs of East Asian seas, BARNARD, 1950 on South African decapods, MCLAY 1988 for New Zealand, and DAVIE, 2002 on Australian crabs. At the same time many revisions of the families appeared e.g.: Prosopidae: MÜLLER *et al.*, 2000; Dromiacea: GORDON, 1950, 1963; HARTNOLL, 1975; GUINOT & TAVARES, 2001; Homolodromiidae: ŠTEVČIĆ, 1976; GUINOT, 1995; Poupinidae: GUINOT, 1990 (1991); Homolidae: SERÈNE & LOHAVANIJAYA, 1973; GUINOT & RICHER DE FORGES, 1995; Latreillidae: CASTRO *et al.* 2003; Dynomedinae: GUINOT, 1993a; MCLAY, 1999; Dromiidae: MCLAY, 1993; GUINOT & TAVARES, 2003; Cyclodorippidae and Cymonomidae: IHLE, 1913; ŠTEVČIĆ, 1969; TAVARES, 1993, 1996; Phyllostymolididae: TAVARES, 1998; Torynommidae: GLAESSNER, 1980; Raninidae: IHLE, 1918; SERÈNE & UMALI, 1972; ŠTEVČIĆ, 1973, 1995; GOEKE, 1981, 1985; TUCKER, 1990; GUINOT, 1993b; Dakoticantridae: BISHOP *et al.* 1998; Necrocarcinidae: FÖRSTER, 1968; Cancridae: NATIONS, 1975; SCHWEITZER & FELDMANN, 2000; Atelecyclidae: SALVA & FELDMANN, 2001; Cheiragonidae: ŠTEVČIĆ, 1988; SCHWEITZER & SALVA, 2000; Eriphiidae: CROSNIER (in SERÈNE, 1984); Pilumnoididae: GUINOT & MACPHERSON, 1987; Carpiiliidae: GUINOT, 1968c; CROSNIER (in SERÈNE), 1984; Trapeziidae: SERÈNE, 1984; GALIL 1986/87; Pseudoziidae: NG & WANG, 1994; Xanthidae: GUINOT, 1968a, 1976; GARTH & KIM, 1983; GARTH, 1986; SERÈNE, 1984; SCHWEITZER, 2003; Kraussinae: NG, 1993; Panopeidae: GUINOT, 1969a; SCHUBART *et al.* 2000; Pseudorhobilidae: HENDRICKX, 1998; Pilumnidae: NG, 1983, 1987; Eumedoninae: SERÈNE, & LUOM, 1958; ŠTEVČIĆ *et al.* 1988; CHIA & NG, 1998; NG & CLARK, 2000b; Tanaochelinae: NG & CLARK, 2000a; Portunidae: CROSNIER, 1962; APEL & SPIRIDONOV, 1998; Aethridae: GUINOT, 1966/67; Parthenopidae: FLIPSE, 1930; GORE & SCOTO, 1979; NG & RODRÍGUEZ, 1986; Mimilambridae: WILLIAMS, 1979; NG & RODRÍGUEZ, 1986; Trichodactylidae: RODRÍGUEZ, 1992; MAGALHÃES & TÜRKAY 1996 I – III; v. STERNBERG 1997; Bythograeidae: WILLIAMS, 1980; Calappidae: IHLE, 1918; ŠTEVČIĆ, 1983; CHEN, 1993, BELLWOOD, 1996; Matutidae: GALIL & CLARK, 1994; Majidae: NEUMANN, 1878; RATHBUN, 1925; GARTH, 1958; GRIFFIN & TRANTER, 1986; ŠTEVČIĆ, 1994; Lambrachaeidae: NG & MCLAY, 2003; Hymenosomatidae: TESCH, 1918a; LUCAS, 1980; MELROSE, 1985; NG & CHUANG, 1996; GUINOT & RICHER DE FORGES, 1997; Ex-Oxyrhyncha: ŠTEVČIĆ & GORE, 1981; Potamidae: BOTT, 1970; NG, 1988; CUMBERLIDGE, 1999; CUMBERLIDGE & v. STERNBERG, 1999; v. STERNBERG, CUMBERLIDGE & RODRÍGUEZ, 1999; BRANDIS *et al.* 1999; v. STERNBERG & CUMBERLIDGE, 2001b, v. STERNBERG *et al.*, 1999; YEO & NG, 2004; Pseudothelphusidae: RODRÍGUEZ 1982; Belliidae: GUINOT, 1976; Dorippidae: IHLE, 1916; CHEN, 1986; HOLTHUIS & MANNING, 1990; Palicidae: CASTRO, 2000; Goneplacidae s. l.: TESCH, 1918b; SERÈNE, 1964; GUINOT, 1969; KARASAWA & KATO, 2003a, b; Leucosiidae: IHLE, 1918; CHEN, 1989, CHEN & HAIBAO, 2002; Troglolplacidae: DAVIE & GUINOT, 1996; Hexapodidae: SCHWEITZER & FELDMANN, 2001; Hapalocarcinidae: FIZE & SERÈNE, 1957; Retroplumidae: DE SAINT LAURENT, 1989; Hexapodidae: SCHWEITZER & FELDMANN, 2001; Cryptochiridae: KROPP & MANNING, 1987; Pinnotheridae: TESCH, 1918b; MANNING, 1993; Grapsidae: TESCH, 1918a CROSNIER, 1965; v. STERNBERG & CUMBERLIDGE, 1998;

KARASAWA & KATO, 2001; Glyptograpsinae: SCHUBART *et al.* 2002; Gecarcininae: TESCH, 1918a; TÜRKAY, 1983; Ocypodidae: CROSNIER, 1965. The illustrated keys for identification of ABELE & KIM, 1986; MELO, 1996 and NG, 1998 are very useful in brachyuran studies. Many important items of information concerning various taxa can be found in works by SERÈNE, 1964; SERÈNE & LOHAVANIJAYA, 1973; SERÈNE & SOH, 1976; NG, 1983; GUINOT & RICHER DE FORGES, 1988/81; VEGA *et al.* 2001; SCHWEITZER *et al.* 2002, 2003. This list of authors and works is, however, not complete.

The systematics of the brachyuran crabs is usually based on the morphological diagnostic characters of classic methodology. However, there are many new approaches to brachyuran classification using various methods and novel data from sperm or molecular studies. So, for example, molecular methods were used by SPEARS *et al.*, 1992 and SCHUBART *et al.*, 2000, 2001. Cladistic analysis was used in several works, especially by v. STERNBERG 1997; v. STERNBERG & CUMBERLIDGE, 1998, 1999; v. STERNBERG *et al.* 1999; NG & CLARK, 2000b; KARASAWA & KATO, 2001. Numerical taxonomic analysis in brachyuran systematics was used by COELHO & COELHO FILHO, 1993. Unfortunately, no one has compiled and synthesised recent data and opinions. This has left the brachyuran system a chaotic mosaic composed of correctly revised, partly revised and unrevised taxa. Moreover, some authors offered their views in the form of various classifications of brachyuran crabs, such as SERÈNE, 1968; BOWMAN & ABELE, 1982; SCHRAM, 1986; ŠTEVČIĆ, 1998; MARTIN & DAVIS, 2001, NG *et al.* 2001. The classificatory schemes of families (without subfamilies and tribes) were proposed without any proper argumentation and additional explanation. Only in the papers of ABELE & FOLGENHAUER, 1982; NG, 1998 and DAVIE, 2002 are the descriptions of the families given, accompanied by the main references for the families, whereas in the work of MARTIN & DAVIS (2001) some aspects of brachyuran systematics were discussed. Some remarks on the latter work were given by ŠTEVČIĆ, 2001 (in MARTIN & DAVIS, 2001). However, what is needed is factual evidence i.e. a description of taxa rather than personal opinions. The appearance of numerous proposed schemes indicates that the higher systematics of the brachyuran crabs is very unstable. Finally, it should be added that some works deal with the general brachyuran organisation such as: GORDON, 1950, 1963, 1966; HARTNOLL, 1968a, 1975; GUINOT, 1979; SCHRAM, 1986; SCHOLTZ & RICHTER 1995; SECRETAN, 1998; GUINOT & BOUCHARD, 1998 while general evolutionary problems are considered by GLAESSNER, 1969, v. STERNBERG *et al.*, 1997, ŠTEVČIĆ 1971 a, b; v. STERNBERG & CUMBERLIDGE, 2001b, DIXON *et al.* 2003, SCHWEITZER, 2003; FELDMANN, 2003. Despite all the efforts of specialists in brachyuran classification, many studies have been incomplete and many questions remain unanswered.

The current situation, as mentioned above, is as follows – the majority of supra-generic taxa are not appropriately described and the great number of extant and extinct taxa are not at all properly classified.

How may the whole brachyuran system be reassessed? There are two ways: to revise step-by-step, piecemeal, or to revise the system as a whole. Step-by-step revision, i.e. family by family, supports a better knowledge of the pertinent families, but experience has shown that in such a way it is only possible substantially to revise a few families during a life span. The second way to revise the whole system is

to conduct a study (as e.g. BALSS, 1957) in »*grosso modo*« to a lesser degree of detail and in a more generalised form. A complete world-wide revision of the whole system, i.e. re-description of the main higher taxa, including further classification into families, subfamilies and tribes, is our objective, although, naturally, the work cannot be in such detail as in special studies of each family.

Not only is there the already mentioned resistance by experts in macrotaxonomic research, but such studies are connected with many objective difficulties caused by phyletic weighting of diagnostic characters. The first difficulty is homoplasy, where the similarity is not the consequence of common ancestry but of secondary acquisition (i.e. usually by convergence of characters, but also reversal), caused by a similar mode of life in similar habitats. This is, for example, well known in the Oxystomata. They indeed share many characters in common, but the organisation of the component families is quite different (e.g. Cyclodorippidae + Raninidae + Calappidae + Aethridae + Matutidae + Orithyiidae + Dorippidae + Leucosiidae) and they are at different evolutionary levels (Dromiacea – Heterotremata). It is noteworthy that the former Oxystomata families have been invariably placed at the beginning of the Heterotremata although it is evident that Dorippidae and Leucosiidae are highly derived in relation to the primitive Cancridae and Atelecyclidae. It has required more than a century to understand that Oxystomata are only an ecological group (*sensu* ŠTEVČIĆ, 2000) and not a natural group (taxon). Evolutionary reversal might be a second origin of misunderstandings among scientists. Although DOLLO's rule of the irreversibility of evolution is in principle correct, there are some exceptions. Some structures became secondarily simpler or similar to ancestral structures. For example Raninidae, Corystidae and some Belliidae share the elongated cephalothorax with the most primitive crabs Homolodromiidae or Poupinidae, although their body shape is a consequence of their back-burying mode of life, thus secondarily acquired, but their organisation is very much derived in relation to primitive ancestors. The most frequent cause of difficulties for systematic inferences is the so-called mosaic evolution. For not all organs are modified uniformly during phyletic evolution; instead, some organs change quickly and some slowly. Because of the unequal rate of evolution of various organs, all taxa invariably exhibit a combination of ancestral (primitive) and derived (advanced) character states. The most primitive heterotreme taxa have some advanced characters (e.g. fused abdominal segments in Cancridae and Atelecyclidae) whereas the most derived Grapsoidea have freely articulated abdominal segments, sternal sutures 1/2 – 2/3 usually distinct, and some of them have remnants of a cervical groove. The highly derived Hymenosomatidae possess longitudinally directed antennae and remnants of uropods. These three sets of difficulties were to cause disagreements among many successive generations of »crabologists«.

Finally, during the consideration of the brachyuran system the following basic facts must not be neglected: that the natural system is a result of adaptive radiation, in which all crabs originated from a single ancestor and that during invasion into new habitats they changed their body form, structures and mode of life (locomotion, feeding, breathing, protection, regulation, reproduction, orientation, inte-



gration, etc.) and became substantially different from their ancestors, finally resulting in the present state of organisation, adaptation, diversity and distribution. Adaptive radiation is also a key for understanding the brachyuran natural system. It is important to point out this fact here because only morphological diagnostic characters will be treated in the text below. In fact they are morpho-physio-ecological because the structures are connected with functions and adaptations e.g. respiratory currents in Leucosiidae are connected both with structures of mouth parts and mode of life, or in other words, form (and structure), function and adaptation are inextricably interconnected. The dactylo-propodal locking mechanism indicates a climbing mode of life whereas paddle-like ambulatory legs indicate the possibility of back-burying and swimming, while a prostomial chamber indicates the back-burying mode of life. Unfortunately, only few works have directly treated the problems of adaptive radiation (FRAAYE, 1996; ŠTEVČIĆ, 2000; FRAAIJE, 2003)

## OBJECTIVES

In reality, discrete (discontinuous) animal groups can be recognised. These groups are homogeneous and share a definite set of characters in common. They are related by descent from a single common ancestor and they are known as natural (monophyletic) groups or taxa. Such discrete groups with a common organisation are »separated from other taxa of the same rank by a gap greater than any found within the taxon« (MAYR & ASHLOCK, 1991: 418). Each of these discrete groups has its own name, systematic status (rank) and position in the brachyuran classification scheme. These groups can be classified into a hierarchical system of categories in which the taxa on the higher categorical level include all consecutively subordinated taxa at the lower categorical level, or in other words, the families include subfamilies, the subfamilies tribes and so on (e.g. Majoidea, Majidae, Majinae, Majini). In this system the taxa are grouped by common shared characters and ranked one above the other thus forming a (Linnean) hierarchical classification in an endeavour to indicate their evolutionary relationships. These statements raise the principal working goal of the present research: to identify the monophyletic groups of crabs, describe them, give them names and establish their rank and placement in the scheme of classification. To rephrase: the principal goal of this work is to establish the natural system of the brachyuran crabs and to illustrate the knowledge of their classification at the beginning of the 21st century. It encompasses all suprageneric brachyuran taxa ordered in the hierarchical system from infra-order (Brachyura) to tribes, indicating clearly their systematic status and position and presented here in an almost uniform manner. Such a procedure will tend to set up a system of classification reflecting the genealogical tree of the crabs as far possible. Moreover, the hierarchical subordination of taxa permits the economic usage of space as all diagnostic characters mentioned for a higher taxon refer to all subordinate subtaxa. Finally, it is desirable for the system to be well organised and to afford a good overview.

## MATERIAL AND METHODS

The first step in the research was the compilation of data concerning suprageneric taxa from the worldwide literature. The pertinent data were contained in the descriptions and illustrations of brachyuran crabs in old and recent literature. Since the majority of higher taxa were established many decades ago, the descriptions and illustrations were far from complete and therefore new data had to be added. With regard to this, for improvement of the descriptions, as well as for the inclusion of new literature data, the direct examination of specimens was often used. Since the present work does not start – »*ab ovo*« – but on foundations created by many generations of preceding authors, the current work is a revision of the old systems with the addition of new resolutions. A revision in systematics is defined as »the presentation of new material or new interpretations integrated with previous knowledge through summary and reevaluation« (MAYR & ASHLOCK, 1991: 427). The diagnostic characters used by former authors were also used in this revision although they have been augmented by some new ones, mostly as revealed by GUINOT, 1979 and some cladists as, for example, CUMBERLIDGE, 1999; VON STERNBERG *et al.* 1999; VON STERNBERG & CUMBERLIDGE 1998; 2001a,b; RODRÍGUEZ, 1992; KARASAWA & KATO, 2003. There are still more very useful characters for description e.g. larvae, ischium-merus articulation of chelipeds, cephalic structures, stomachal ossicles, 18S rDNA nucleotide sequences, ultrastructure of spermatozoa, etc. which are not known for the majority of crabs and therefore have not been used here for characterisation of the taxa. Despite all efforts, taxa descriptions often suffer from lack of accurate data of some important structures (gonopods, subfrontal and thoracic structures).

With all the available data assembled, each suprageneric taxon was critically re-examined, considering first of all matters of homogeneity. Special attention was focused on those taxa that indicated possible heterogeneity and which were dismantled into smaller but monophyletic groups. Taxa should be homogeneous, monophyletic groups, and as such should share a set of characters in common. For example, all Leucosiidae share several characters in common in which they differ from all other crabs and which are distinguished from all other families by distinct deep gaps (discontinuities). If a taxon is homogenous its description has been updated by the addition of new characters. However, many crabs seem to be very superficially similar (homoplasy), but phylogenetically unrelated. Such similarities are shown by closer inspection to be superficial and were achieved by different patterns of modification. Fortunately, at present, because of advanced knowledge of the diagnostic characters, heterogeneous groups can easily be identified. In this manner each suspect taxon was re-examined, and unrelated groups were excluded. When a group was recognised to be heterogeneous i.e. polyphyletic, it was dismantled and in turn two or more smaller but homogeneous groups were created. The procedure with the excluded groups was as follows; the genus or group of genera sufficiently different to merit separation into a suprageneric taxon were placed in the next taxon of a higher hierarchical level. For an excluded genus we look for a tribe which contains all diagnostic characters of the genus. If there is no such tribe then we look for the subfamily, family or even superfamily. For example the genus

*Pliosoma* Stimpson, 1860 was previously included into the Atelecyclidae (BALSS, 1957); however there is neither tribe nor subfamily in which it could be accommodated. On the other hand it shares all the main diagnostic characters of the family Majidae (GUINOT, 1979) and consequently belongs to the mentioned family, although as a subfamily (ŠTEVČIĆ, 1994). Its high hierarchical level is thus the expression of its isolated position in the majid system and therefore deserves subfamilial level. Thus the »depth« of gaps among newly observed taxa determined their categorical rank: the deeper the gap, the higher the level of systematic category. Therefore it is often the case that an isolated genus has a very high systematic category. In this way the brachyuran became a more complex but more natural system. In this case it is apparent that the next proximal higher taxon (Majidae for *Pliosoma*) also determines the hierarchical level of the taxon in question, and the categorical level of a taxon is at the next lower category, e.g. if it is impossible to include it in any majid subfamily, the taxon itself defines a new subfamily. Since some genera, despite all efforts, are not sufficiently described (especially the fossil forms) they remain temporarily in a critical state as *incertae sedis*. It is worth noting that the importance of diagnostic characters for the classification varies from one family to another's. For the majid classification, orbital structures are very important; for the Pinnotheridae and the Leucosiidae mouthparts, for the Potamidae the mandibular palps are characteristic, for the Panopeidae the first gonopods, etc. The fusion of abdominal segments 3–5 in male is very characteristic of some taxa (e.g. Xanthidae) while in some others this is very variable and cannot be a diagnostic character for higher taxa (Majidae, Leucosiidae, Pinnotheridae).

When the new higher taxa were established (i. e. delimited from others) they were described in the manner usual in contemporary systematic practice. It is very important to point out that the higher taxa cannot be separated as systematic units on the basis of only one character (»single-character classification« or »one character – one taxon«). Such a practice could lead to artificial groups as in the Oxyrhyncha with its separation being based on the form of the anterior portion of the cephalothorax only. Single-character classification dominated the earlier phases of brachyuran classification. On the other hand, very widely understood higher taxa lead to heterogeneous assemblages, in fact polyphyletic groups, as in the case of the family Goneplacidae *sensu* old authors as by both older and contemporary authors. A proper description should contain a sufficient set of carefully selected diagnostic characters i.e. weighted characters. Conservative, easily observed homologous diagnostic characters that can be used in higher taxa descriptions are from various parts of the body, including the anterior portion of the cephalothorax (eyes, orbits, antennulae folding), mouthparts (form, degree of covering, form of merus of third maxilliped), sternal sutures (entire – interrupted), sexual openings (coxal, coxo-sternal, sternal), form and lengths of gonopods, form of abdomen and fusion of the segments can be used in higher taxa descriptions. In this manner the animals, but not the characters are classified and the trap of »one character – one taxon« is avoided. An appropriate taxon description contains the relevant characters and therefore it is much more comprehensive and effective.

When a new taxon is established and described it is necessary to place it in the appropriate rank in the hierarchy of categories. In the present paper the following formal categories are used: tribe, subfamily, family, superfamily and infra-order. Informal or auxiliary ranks are also used: section, subsection, lineage, branch and grade. Since there is no universal rule for this gradation, the hierarchy of categories is determined by the relative amount (degree) of difference, or in other words, by the depth of the gap – the deeper the gap the higher the category. How may the categorical level be determined? The procedure has been explained before – a genus or group of genera excluded by previous revision, or newly described taxa is placed in the next higher taxon, its rank depending on the hierarchical level of that taxon within which it is placed. For example, if a genus is markedly different from all other crabs to such an extent that it cannot be accommodated in any other known tribe then one examines the subfamily, and if the subfamily cannot accommodate it then one tries for family or superfamily. If its next higher taxon is superfamily this means that the genus in question should be raised to familial status. In other words, if a genus does not exhibit a suite of characters that can be embraced by any currently recognised family then the elevation of the genus to familial level is justified. The ranking of higher taxa has very often been the subject of controversies among systematists (Gecarcinidae – Gecarcininae, Mictyridae – Mictyrinae, Lobocarcinidae – Lobocarcininae, Cyclograpsidae – Cyclograpsinae – Cyclograpsini and so on).

The next step in the reclassification is the arrangement of established taxa. The taxa are arranged here in ascending order. In other words, the most primitive, i.e. taxa with maximum ancestral and minimum derived characters, were placed at the beginning of the classification scheme and those with maximum derived (and minimum ancestral) characters have been placed at the end. For example, the most primitive Eubrachyura are the Cancroidea and the most derived higher taxa are Cryptochiroidea, Hexapodoidea, Hymenosomatoidea and Ocypodoidea. The same thing holds for the arrangement within higher taxa. The majid subfamily Majinae probably has orbits derived from primitive cancroid orbits, whereas the reduced orbits (e.g. in the Epialtinae) are in the derived character state. The taxa that have the most primitive subtaxa, with a greater number of primitive character states are placed in front of a taxon in which the most primitive members have fewer ancestral characters. Consequently the Xanthidae are in front of the Portunidae because the Kraussinae, the most primitive xanthid subfamily (narrow sternum, sternal sutures 1/2 – 7/8 entire), are more primitive than the most primitive Portunidae (with sternal sutures 4/5 – 5/6 interrupted) and therefore the Xanthidae should be placed in front of the Portunidae. The arrangement of the taxa is not without difficulties. It is worthy of note that in some rare works the arrangement is in descending order (e.g. BARNARD, 1950) or even in alphabetical order of the families (DAVIE, 2002).

In the Brachyura there are two major groups: Dromiacea (Podotremata) and Eubrachyura (= Brachyura genuina) including Heterotremata and Thoracotremata. Each of these three major groups consists of several lineages (lines of common descent) originating from a single hypothetical ancestor ending with the most derived

taxa. Because of the rocket-shaped clusters of branches due to adaptive radiation it is impossible to present the classification scheme in a linear arrangement, therefore some previously mentioned informal auxiliary terms such as »lineages« or »branches« were used. Sometimes »grades«, which designate a shared morphological level, were used for better illustration of the gradation in organisation within genealogical trees. A great number of the families and other higher taxa have had their systematic position changed, which is hardly surprising if we consider that no one after Alcock has tried to arrange the whole picture of brachyuran systematics.

The last step in the revision is the naming of newly established taxa. The naming is based on the INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE (1999). For references to authors and years regarding the majority of higher taxa I have generally followed the work of MANNING & HOLTHUIS (1981) but also some other works e.g. DAVIE, 2002. With regard to the names of new taxa I have chiefly used the names of (mostly dead) renowned decapodologists, some modifications of previous names and some old Slavic gods.

The current paper is relatively short and contains only valid names of taxa, abbreviated descriptions (or enlarged taxon diagnoses) of all higher taxa supported by type genera. The type genus, as claimed by MAYR & ASHLOCK (1999: 359), »reduces the amount of descriptive material that must be included«. The latter is given because of economy of space. In this way the taxon is minimally defined by the most specific diagnostic characters, usually taxon-specific (autapomorphies) or by a specific combination of some non-taxon-specific characters. It should be pointed out that this paper is based on arguments given as the diagnostic characters presented in the descriptions. In this way the work is open to verification and falsification, although on the basis of reasonable contra-arguments, not subjective impressions or *ipse dixit*. Moreover, the paper does not represent a review of opinions only but also presents arguments that may be appraised as correct or incorrect. A proper revision should be based not only on massive compilation of all known data but also on critical re-examination of the homogeneity, systematic status and position of all taxa, making the revision very complex and demanding. However, since the enterprise is endless and usually not completed during the life-span of an author (such as in the case of BALSS) I would like to present this abbreviated version reaching down to tribes. The entire text (if and when it is finished), upon completion (including genera and groups of genera), will be published elsewhere (at very least on an Internet website).

It is regrettable that the data on larvae were not included in this work, but it would have »consumed« much time. On the other hand I have included extinct taxa, but usually I did not alter their classification. I refer to them usually as – »*relata refero*« – from the palaeontological literature only.

Finally, here is some information on the manner in which the re-classification is written. The telegraphic style is for economy of space. The order of diagnostic characters used in taxa descriptions is more or less uniform. There are some differences with respect to prior works. For instance, I have used orientation terms e.g. »anterior« and »posterior«, »right« or »left« in relation to the observer. Therefore in the

majority of the crabs the posterolateral margins are »diverging«, rather than »converging«. The exorbital tooth (angle) is never considered as the first anterolateral tooth or lobe. In order to avoid much repetition, the word »thoracic« before sternum, sternite or suture is often omitted, but always understood. For the pereopods I have used the terms chelipeds and ambulatory (or walking) legs. In biology few things are absolute and there is no large taxon without exceptions and therefore I have used the words »almost«, »usually«, »mostly« to indicate that a structure is present in the majority of members but not all. For example the formulation »in the Portunidae the »portunid lobe« is usually present« means that the majority of portunid subtaxa have this structure, but not all. Moreover, since in many taxa a homologous organ exhibits numerous transitions between two extreme forms forming transformation series, this situation is expressed by the formulation »from.. to.« If the order of the numbers is reversed it means that the evolutionary changes constitute a reduction of elements. If »from 3 – 1« – is written, it means that the more primitive state had 3 elements and the most derived only one. Furthermore, the descriptions usually begin with »Cephalothorax...«, (e.g. cephalothorax subovate) but this is often omitted for reasons of economy of space and the description starts with »Subovate«. Since the length of cephalothorax and carapace are not equal (posterior sternite often projecting behind carapace margin), I preferred the term »cephalothorax« for general body form. In the greater number of higher taxa some abdominal segments are fused, but more frequently in males than females and if in the text only data for males are reported, that the females have freely articulated abdomen is omitted in the text. Finally, the names of higher taxa are written in plural and as a consequence it is: »the Majidae are« rather than »the Majidae is« (but »*Maja* is«). Finally, the word »crabs« refers here invariably to the »brachyuran crabs«

As a result of all the re-examination, the brachyuran classification is presented as follows:

## SYSTEMATIC ACCOUNT

### Infra-Order BRACHYURA Linnaeus, 1758

Cephalothorax progressively shortened and widened, developing lateral margins (side-edge, with lateral armature). Inhalant branchial opening at base of chelipeds, exhalant branchial opening mostly at anterior ridge of buccal cavern. Frontal margin usually spinose, lobate to entire, sometimes with antennular and/or antennal sinuses. Eyes more or less well developed, concealed in orbits. Orbits and antennular fossae almost always present. Interantennular septum (usually proepistome) mostly distinct. Antennulae three-segmented, and commonly retractile into their fossae beneath front, folding from longitudinally to transversely. Basal antennular segments swollen and enlarged, peduncles 2-segmented, their two flagella very short. Antennae five-segmented, usually longitudinally directed, first antennal segment fused with urinal pore. Antennal segments 2 + 3 fused into basal antennal segment. Antennal scale (scaphocerite) reduced or mostly absent. Next two anten-

nal segments (4 + 5) cylindrical forming antennal peduncle terminating in multi-segmented flagellum. Fifth segment together with flagellum often bent laterally. Proepistome anteriorly fused with front, posteriorly with epistome. Epistome fusing laterally with bent carapace margin. Mandibular palp usually three-segmented, sometimes bi-segmented. Palp of third maxilliped (three terminal segments) shorter than proximal segments. Endognath much larger than exognath. Flagella of exopods of maxillipeds 2 – 3 almost always bent inwardly nearly at a right angle. Epipodites of maxillipeds very large. Pereiopods articulating laterally, pleopods ventrally. Basis and ischium of pereiopods fused into basis-ischium. Only first pereiopod always chelate, fixed finger extending usually straight distally from palm sometimes bent. Ambulatory legs mostly of usual form, last one or two pairs often variously modified. Thoracic sternite 8 fused with anterior segments in compact thoracic sternum. Sternites often with episternites. Sterno-abdominal concavity (as depression or cavity) more or less developed. Posterior sternites usually upcurved, i.e. posterior segments in higher level than precedent ones, sometimes visible in dorsal view. Endophragmal system well developed. Gonopods originally three-segmented, composed by coxa, basis and endopod, exopodite mostly lacking. Abdomen 7-segmented (6 segments + telson) reduced in size, short, flattened and flexed under cephalothorax. Abdominal segments ranging from freely articulating to fused in various degrees. Usually segments 3 – 5 fused in male, freely articulating in female. Abdominal pleura in same plane and in same straight line with abdominal terga, fused, sutures generally indistinct. Abdomen in male narrow, in female wide. Retaining/locking mechanism of abdomen usually present.

### **Section DROMIACEA de Haan, 1833**

Cephalothorax varying from elongate to subquadrate. Front narrow, often with true rostrum (originating from larval rostrum), usually in lower position to two lateral pseudorostral spines or lobes. Posterior carapace margin usually narrow to moderately or very wide, mostly concave, rarely nearly straight. Dorsal surface mostly well sculptured. Cervical and branchiocardiac grooves usually well marked. Orbits and antennal fossae ranging from absent to more or less distinct. Antennal stalk with four movable articles, first (urinal) article mostly with conspicuous excretory pore on internal margin, largely exposed. Basal antennal segment (segments 2 + 3) well-developed, peduncle (segments 4 + 5) narrow, longer than basal segments, flagellum usually long. Scaphocerite (antennal scale) sometimes present, reduced in size. Third maxillipeds ranging from more or less pediform to operculiform. Chelipeds well developed, more or less symmetric. Last one or two pairs of legs reduced in size, usually subdorsal in position and subchelate. Epipodites on all pairs of maxillipeds and often on first pair of pereiopods. Gills number usually more than 9 on each side. Thoracic sternites variously fused, sutures variously long and variously directed, usually indicated laterally, exceptionally entire. Posterior part of thoracic sternum upturned, often almost perpendicularly to preceding ones, rounded posteriorly and projecting behind posterior carapace margin, so that coxae of posterior one or two ambulatory legs raised on back and visible in dorsal view, usually re-

duced in size, provided at tip with prehensile grip of chelate or subchelate mechanism (for camouflage). Last pair of legs often in front of third pairs. Coxae of last pair of legs often modified in male. Female genital opening on coxa of third pereopod (second pair of legs). Oviducts separated from spermathecae. Sternal grooves more or less deep over sutures 7/8 present in female. Paired spermathecal openings at end of suture 7/8. Male sexual opening on coxae of fifth pereopod (last pair of legs). First gonopod stout, uniramous and three-articulated: coxa (usually reduced in size to absent), basis and endopod. Endopod of first gonopod distally rolled up to form incompletely to completely closed tube, its single basal opening using for introduction of penis and second gonopod. Second gonopod typically as long as or longer than first one, ending in needle-like flagellum (*appendix masculina*), its exopodite sometimes present. Sterno-abdominal depression usually indistinct. Pleopods 3–5 usually vestigial or absent in adult male. Penis long, tubiform. Female first pleopod present, uniramous, remaining four pairs biramous. Abdomen relatively wide in both sexes, usually covering whole sternum, mostly 7-segmented (some segments sometimes fused), 2 – 3 proximal segments exposed dorsally. Vestigial uropods often present in form of dorsal plates or ventral lobes. Abdominal holding mechanism including coxae of thoracopods or press-button mechanism.

### **Superfamily HOMOLODROMIOIDEA Alcock, 1900**

Cephalothorax usually subcylindrical, elongate, rarely depressed and pentagonal or circular. Rostrum mostly wide, deflexed. Dorsal surface well sculptured. Lateral margins absent to incomplete. Cervical and branchiocardiac grooves distinct. True orbits absent, but commonly with elongate orbital groove. Vestigial antennal scale present. Last two pairs of legs, reduced in size, subchelate and dorsally posed. Vestigial pleopods 3 – 5 usually present in male, uropodal plates at least ventrally discernible. Male abdomen with distinct pleurae. Telson usually long. Type genus: *Homolodromia* A. Milne Edwards, 1880.

### **Family HOMOLODROMIIDAE Alcock, 1900**

Cephalothorax subcylindrical, elongate, longer than wide. Rostrum very small to absent, pseudorostral spines short. Lateral margins indistinct. Branchiostegite decalcified, membranous. Cervical and branchiocardiac grooves incomplete. Eyes, antennulae and antennae in common orbito-antennular pit. Gills trichobranchiae. Number of gills great (21 – 19 + 7 – 6 epipodits). Third maxillipeds pediform. Last two pair of legs reduced in size, subdorsal, subchelate to chelate. Propodi of two posterior pairs of legs with several spines, dactyli very curved with row of spines on ventral side. Coxa of last pair of legs of male modified, elongated, prolonging into long hard process including penis. Vestigial pleopods 3 – 5 in male uniramous. First pleopod in female uniramous. First gonopod uniramous, second gonopod lacking exopodite. Sternal suture 7/8 in female short, spermathecal aperture lying close to gonopore on second leg. Vestigial uropods present as ventral lobes. Male abdomen covering whole sternum, abdominal pleurae distinct. Telson very long, reaching third maxillipeds. Type genus: *Homolodromia* A. Milne Edwards, 1880.



### +Family PROSOPIDAE von Meyer, 1860

Cephalothorax subcylindrical, elongate, rarely subcircular or triangular. Dorsally convex transversely to flattened. Dorsal surface strongly sculptured to smooth, cervical and branchiocardiac grooves strong. Postcervical groove reduced to absent. Fronto-orbital margin wide. Rostrum simple to bilobed, more or less projecting. Lateral margins more or less incomplete to absent. Orbital grooves absent, if present elongate to circular. Abdominal pleura (seemingly) distinct, telson large, subtriangular with rounded apex. Posterior margin rather wide, more or less concave, rarely nearly straight. Third and especially fourth pair of legs reduced in size and upturned dorsally. Type genus: *Prosopon* von Meyer, 1835.

#### +Subfamily PROSOPINAE von Meyer, 1860.

Cephalothorax elongate, subcylindrical. Dorsal surface granulate, areolated and strongly sculptured. Rostrum of moderate size, blunt, gently projecting, usually deflexed, sometimes with median sulcus. Fronto-orbital margin wide, bilobed. Orbital grooves absent to rudimentary. Lateral margins incomplete. Type genus: *Prosopon* von Meyer, 1835.

#### +Subfamily PITHONOTINAE Glaessner, 1933

Cephalothorax suboval, elliptical to subquadrilateral, convex, thick. Dorsal surface generally smooth (exception for cervical and branchiocardiac grooves). Rostrum single, wide, turned down, usually with median sulcus, appearing bilobed from above. Fronto orbital margin wide. Orbital grooves very wide, directed anterolaterally. Lateral margin more or less distinct. Cervical and branchiocardiac grooves more or less transverse nearly subparallel, equally distinct or cervical groove more distinct. Posterior margin concave to nearly straight. Type genus: *Pithonoton* von Meyer, 1842.

#### +Subfamily GLAESSNEROPSINAE Patrulius, 1960

Cephalothorax ovoid to subrectangular, convex. Dorsal surface ornamented. Cervical and branchial grooves, distinct, subparallel. Branchial region slightly swollen, finely granulated. Rostrum extremely large, crown-shaped. Exorbital angle well-developed. Supraorbital margin with three large lobes. Posterior margin wide, uneven. Type genus: *Glaessneropsis* Patrulius, 1960.

### Superfamily DROMIOIDEA de Haan, 1833

Cephalothorax usually wider than long. Integument usually well calcified. Lateral margin well marked. Eyes, antennulae and antennae placed in common orbito-antennular pit, usually well protected. Antennal segments 1 and 2+3 movable. First antennal segment with lateral beak-like projection bearing urinal pore. Buccal cavern quadrangular. Third maxillipeds operculiform, covering completely buccal cavern. Sternum of female with longitudinal sternal grooves on suture 7/8. Sternites 1 – 3 fused into small shield, suture almost 3/4 entire. Gills 20 – 14 on

each side. Vestigial uropods in form of dorsal plates or ventral lobes usually present. Abdomen covering sternum, proximal segments exposed dorsally. Abdominal locking mechanism of various types almost present and usually functional. Last pair of legs usually subchelate. Sterno-abdominal cavity absent. First pleopod in female present, pleopods 3–5 in male often present, reduced in size. Type genus: *Dromia* Weber, 1795.

### Family DYNOMENIDAE Ortmann, 1892

Subcircular, subquadrilateral, ovoid to oblong, usually wider than long. Front widely subtriangular, short, bilobed with short longitudinal median groove. Cervical, cardiac and branchial grooves usually present. Orbits and lateral margins well defined. Buccal cavern completely covered by third maxillipeds. Ambulatory legs 1 – 3 similar, lacking distal propodal spines. Last pair of legs extremely reduced in size, oblique, directed anteriorly above proximal part of third pairs of legs, subchelate, but not prehensile. Dactylo-propodal locking mechanism usually distinct. 20 – 19 gills and 7 epipods on each side. Epipodites on cheliped, maxillipeds and ambulatory legs 1 – 2. Coxa in male modified, elongated, prolonging into hard process enclosing penis. Sternal plastron flat, not projecting behind posterior carapace margin. Suture 7/8 short, spermathecal aperture close to gonopore. 5 pairs of pleopods in both sexes. First gonopod stout, semi-rolled tube, with apical plate, setose, pleopods 3 – 5 in male biramous, vestigial. First pleopod rudimentary uniramous in female, three posterior pairs of pleopods in male vestigial. Second gonopod needle-like, bearing spinules, with exopod. Abdomen in male relatively large, segments 4 – 6 and base of telson nearly as same width, prominence on sternite 5. Uropods dorsally as distinct plates in both sexes. Type genus: *Dynomene* Latreille (in Desmarest) 1825.

### +Family DIAULACIDAE Wright and Collins, 1972

Cephalothorax wide, roughly widest anteriorly, flat transversely, steeply downward in front. Front wide. Rostrum short, bilobed, projecting or turned down. Orbits very large, directed forward. Lateral margins very sharp, anterolateral margin short, spinose, arched, posterolateral one long, straight. Cervical and branchio-cardiac grooves weak, nearly straight, transversely directed. Type genus: *Diaulax* Bell, 1863.

### Family DROMIIDAE de Haan, 1833

Almost subhexagonal, subpentagonal, ovoid to subcircular, usually convex in both directions, thick, tomentose, regions usually not well defined. Front narrow to wide, usually tridentate. Secondary frontal margin with distinct median incision. Rostrum, if present, in lower position, pseudorostral spines or lobes in upper position. Eyes, antennae and antennulae in common pit. Urinal and basal antennal segment movable. Eystalks short, stout. Orbits small, rather circular, directed horizontally. Lateral margins distinct, dentate, lobate to entire. Third maxillipeds operculiform covering completely buccal cavern. Chelipeds symmetrical, generally shorter than

walking legs. Two anterior pairs of walking legs often lobed or nodose, propodus short lacking distal spine, dactylus curved, armed with spines on inner margin prehensile. Grasping mechanism involving distal propodal spine and dactyl. Gills phylobranchiae 14 + 4 epipods. Epipods on maxillipeds and chelipeds, usually lacking on ambulatory legs. Thoracic sternum narrow posteriorly upturned. Sternal suture 3/4 entire, anteriorly convex, suture 7/8 (sternal groove, sternal furrow) in female furrowed, distinct. First gonopod stout, semi-rolled, setose, sharply tipped tube. Second gonopod simple, needle-like, subequal or longer than first one, sometimes with exopod. Pleopods 3 – 5 usually absent sometimes as vestiges in male present. Male abdomen narrow, segments 5 – 6 sometimes more or less fused, with pleurae sometimes distinct. Telson (when flexed) attaining coxae of third maxillipeds or diverse levels of coxae of chelipeds. Uropod plates usually always present. Type genus: *Dromia* Weber, 1795.

#### Subfamily SPHAERODROMIINAE Guinot & Tavares, 2003

Cephalothorax subglobose, varying from longer than wide to wider than long. Dorsal surface tomentose. Regions not well defined. Front broadly triangular, grooved in midline, rostrum lacking. Orbits oblique. Lateral margins subparallel. 20 gills and 6 epipods on each side. Chelipeds with epipod and sometimes podobranch. First anterior pair of legs usually with epipods, often with podobranch. Propodi of two anterior pairs of legs long, neither lobed nor nodose, with long distal spine, dactyli with numerous spines on inner margin, not strongly curved. Last two pairs of legs similar and reduced in size, only last pair dorsal, three to five propodal spines opposing dactyli, numerous small spines on inner margin of dactyli, short propodi short, lacking spines on outer margin ventrally with 3 – 5 distal spines, dactyli with 2 – 4 small spines. Coxa of last pair of legs in male modified, elongated, prolonging into hard process enclosing penis. First gonopod with well developed apical plate. Second gonopod simple, long, with styliform flagellum, with exopod on basis. Vestigial pleopods 3 – 5 in male present. Female sternal sutures 7/8 short, spermathecal aperture minute, close to female gonopore. Male telson long. Uropods large, deeply inserted between segment 6 and telson, exposed dorsally. Type genus: *Sphaerodromia* Alcock, 1899.

#### Tribe Sphaerodromiini Guinot & Tavares, 2003

Front widely triangular, bilobed, rostrum absent. Pseudorostral lobes confluent with supraorbital margin. Exopod of basal antennal segment weakly or not at all produced. Coxae of third maxillipeds approximating. Sternites 1 – 3 not exposed, sternite 4 anteriorly exposed touching bases of third maxillipeds. Podobranchs usually present on pereopods. Two anterior pairs of legs long, not nodose, propodus very long, with distal propodal spine, dactyli with numerous spines. Two posterior pairs reduced, shorter than preceding pairs, subequal, only last pair dorsal. Propodi of last two pairs lacking outer spine, with multiple propodal spines opposing dactyli, dactyli with row of spinules. Aperture of spermathecae often concealed. Sternites 1 – 3 not exposed. Anterior part of sternite 4 not covered by abdomen when flexed. First gonopod with well developed apical plate, second gonopod with exopod. Ves-

tigial pleopods biramous. Suture 7/8 oblique. Abdominal segment 6 markedly laterally expanded. Uropods as intercalated platelets exposed dorsally. Type genus: *Sphaerodromia* Alcock, 1899.

Tribe *Frodromiini* trib. nov.

Cephalothorax longer than wide. Front trilobed (rostrum + pseudorostral spines). Lateral margins subparallel. Exopod of basal antennal segment with produced internal angle. Coxae of third maxillipeds not approximated. Podobranchs absent on pereopods. First two pairs of legs with long propodus, lacking distal propodial spine, dactylus strongly curved. Last two pairs of legs with 1 – 2 propodal spines. Sternites 1 – 3 exposed. Sternite 4 covered by abdomen when flexed. Apertures of spermathecae raised, each on tubercle, close to female gonopore. First gonopod sharply typed, second gonopod lacking exopod. Sutures 7/8 longitudinal. Coxa of last pair of leg very modified, without movable penial tube. Vestigial pleopods 3 – 5 uniramous. Abdominal segment 6 not expanded laterally. Telson in male long. Uropods visible dorsally, oblique. Abdominal holding apparatus efficient. Type genus: *Frodromia* McLay, 1993.

Subfamily *DROMIINAE* de Haan, 1833

Almost dorsally convex. Exoskeleton almost hard. Dorsal surface usually setose. Front narrow, trilobed to entire. Eyes visible in dorsal view. 14 gills + 4 – 3 epipods on each side. Chelipeds usually with epipod, lacking podobranch. First two pairs of legs usually without podobranchs. Propodi of two anterior pairs of legs short, usually lacking distal spine, inner margin of dactylus usually spinose. Two posterior pairs of legs more or less similar in size and shape, prehensile, third pair oriented subdorsally, last pair dorsally. 14 gills + 4 – 3 epipods on each side. Female sternal suture 7/8 usually long. Spermathecal aperture mostly far beyond gonopore on coxae of second pair of legs, ending either apart or together. Pleopods 3 – 5 variously developed in male. Coxa of last pair of legs unmodified, penis emerging as long, mobile, calcified tube. Male abdomen relatively narrow, rather long, not triangular. Type genus: *Dromia* Weber, 1795.

Tribe *Stebbingdromiini* trib. nov.

Cephalothorax distinctly wider than long. Dorsal surface smooth. Front projecting, rostrum small, acute, markedly deflexed, pseudorostral teeth distinct. Eystalks long, narrow, curved. Chelipeds with epipod. Posterior part of sternite 6 and sternites 7 – 8 abruptly upcurved. First two pair of legs neither lobed nor nodose, propodus long, with small distal propodal spine. Last two pairs reduced, very short, similar in size, last pair slightly longer, dactyli strongly curved, subcheliform, prehensile apparatus formed by multiple spines. Female sternal suture 7/8 short, spermathecal apertures besides gonopores. Penial tube on coxa of last pair of legs mobile. First gonopod without apical plate. Second gonopod very short, stout, lacking exopod, gradually tapering to pointed tip, lacking needle-like flagellum. Abdomen triangular, longer than wide, segments freely articulated reaching third maxillipeds, covering sternite 4. Telson bluntly triangular, longer than wide. In male uniramous, long, dissimilar vestiges of pleopods 3 – 5 present. Uropods deeply inserted between segment 6 and telson, visible dorsally. Type genus: *Stebbingdromia* Guinot & Tavares, 2003.

## Tribe Dromiini de Haan, 1833

Cephalothorax almost subcircular, convex in both directions. Dorsal surface usually covered by short pubescence. Front 3 – 2 dentate (rostrum + pseudorostrum). First two pair of legs lobed and nodose propodi short, lacking distal spine, inner margin of dactyli spinose. Posterior two pairs of legs subdorsal, reduced, almost subequal in size and shape or last pair of legs usually longer than third; dactylus curved and armed with spines on inner margin. Third pair of legs opposed or surrounded by one or more propodal spines. Coxa of last pair legs in male with long, movable, sclerotised tube with penis. Female sternal suture 7/8 long, spermathecal aperture usually far beyond gonopore on second pair of legs. Second gonopod longer than first gonopod with needle-like flagellum. Vestigial pleopods 3 – 5 variously developed. Uropods variously present to absent. Telson wider than long. Type genus: *Dromia* Weber, 1795.

## Tribe Conchoecetini trib. nov.

Subpentagonal, as long as wide or slightly wider than long, depressed, flattened. Dorsal surface partly membranous, with some regions well defined, cervical and branchial grooves distinct, pilose. Front narrow, tridentate, rostrum deflexed. Epipods on chelipeds only. Propodi of two anterior pairs of legs without distal spine. Propodi of two posterior pairs of legs very dissimilar in position, size and shape. Third pair of legs noticeably heavy ending in thick propodus and long, curved large talon-like dactylus, posterior margin of propodus bearing hollow, socket-like projection, with mobile process. Last pair very slender ending in simple, upturned, dactylus. Thoracic sternites 1 – 2 concealed, 4 wide, anteriorly truncate. Sternal suture 7/8 long, ending apart, each on conical tubercle between bases of first pair of walking legs. Vestigial pleopods lacking in male. Telson rounded at tip. Type genus: *Conchoecetes* Stimpson, 1858.

## Subfamily HYPOCONCHINAE Guinot &amp; Tavares, 2003

Hourglass-shaped, very depressed, flattened. Dorsal surface membranous, cervical, branchial and cardiac grooves well marked. Frontal and lateral margins greatly expanded, covering all parts of head, only antennal flagella exposed dorsally. Eyes small, not visible in dorsal view. Chelipeds with epipods. Buccal cavern widened anteriorly. Propodi of two anterior pair of legs short, unarmed, inner margin of dactylus smooth or nearly so. Two posterior pairs of legs dissimilar, not subchelate. Third pair not dorsal, robust, short. Dactyli of two posterior pairs peculiar: short, stout, lunate (crescent-shaped), upturned, movable in hollow at end of propodus, ending in corneous hook. Sternites 1 – 3 concealed, sternite 4 showing narrow elongated plate, in contact with third maxillipeds. Suture 3/4 concave anteriorly. Female sternal sutures 7/8 relatively short, located on bent posterior part of sternum. Spermathecal apertures apart, slightly beyond gonopore on coxa of second pair of legs. First gonopod not completely closed, apical plate lacking. Second gonopod long, styliform, lacking exopod. Abdomen in male wide, triangular, flexed at right angle in middle, uropods present ventrally. Vestigial pleopods 3 – 5 present, uniramous. Male coxa of last pair of legs unmodified, penial tube movable. Type genus: *Hypoconcha* Guérin – Méneville, 1854.

### Superfamily HOMOLOIDEA de Haan, 1839

Cephalothorax quadrangular, urn-shaped or longitudinally oval, longer than wide. Usually no distinct lateral margins. Rostrum present. Eyestalks and antennulae not retractile into their fossae. Eyestalks composed of two movable segments, basal segment (basiophthalmite) slender, terminal segment (podophthalmite) stout, bearing cornea. False orbits (»plage orbitaire«) distinct. Third maxillipeds pediform. Ambulatory legs long, slender, only last pair of legs directed upwards. Thoracic sternum wide. Suture 6/7 usually entire. No deep sternal groove on suture 7/8 in female. Coxa and basis of gonopods distinct. First gonopod completely tubulate, basal opening large. Abdomen enlarged, reaching coxae of third maxillipeds or coxae of three anterior pairs of pereopods (retaining system). Second retaining system of press-button type formed by prominence on sternite 4 and socket on segment 6. Abdomen in male wide, triangular, flexed at right angle in middle, uropods present ventrally. Two proximal abdominal segments exposed dorsally. Uropods and pleopods 3 – 5 in male absent. Type genus: *Homola* Leach, 1815.

#### Family POUPINIIDAE Guinot, 1991

Cephalothorax ovoid (longitudinally rectangular), broadest posteriorly. Rostrum bifid, thick. Pseudorostral spines short, pointed. Lateral margin indistinct. Cervical and branchiocardiac grooves distinct. Eyes reduced. Last pair of ambulatory legs subdorsal, with long setae, but neither substantially reduced in size nor prehensile. Epipods on first three pairs of pereopods. Coxae ambulatory legs visible from above, dactyli of last pair elongated, not subcheliform. Type genus: *Poupinia* Guinot, 1991.

#### Family HOMOLIDAE de Haan, 1839

Longitudinally quadrangular to ovoid, as long as wide to longer than wide, barrel-like. Sidewalls nearly vertical. Dorsal surface granulose to spinose, cervical and branchiocardiac grooves well marked, *linea homolica* present. Front narrow. Rostral and pseudorostral spines usually well developed. Eyes long, composed of two movable segments: slender basiophthalmite and stout podophthalmite. No true orbits. Basal antennular segment subglobular. Antennal flagella much longer than carapace. Interantennular septum distinct. Epistome distinct. Maxillipeds pediform to operculiform. Pereopods long and slender. Only last pair of legs reduced in size, subcheliform to cheliform. Epipodites on chelipeds and anterior two pairs of legs. Number of gills 14 – 10, epipods 6 – 4. Three anterior sternites fused into small sternal shield. Sutures 6/7 – 7/8 sometimes entire. Sterno-abdominal depression present. Penis short. First gonopod tubular, closed, second gonopod with vestigial exopod, apically truncated. Abdominal segments usually freely articulated, segments 5 – 6 sometimes fused in female, sutures distinct. Uropods transformed into fossets. Type genus: *Homola* Leach, 1815.

#### Family LATREILLIIDAE Stimpson, 1858

Cephalothorax subpyriform with long »neck« (*Macropodia*-like). Dorsal furrows usually indistinct. *Linea homolica* absent. Lateral margins indistinct. Rostrum small,

short, pointed, downturned. Supraorbital spines very long, diverging. Eyestalks very long, basiophthalmite much longer than podophthalmite. Antennulae long, antennae smaller. Epistome elongated. Third maxillipeds pediform. Ambulatory legs long, slender, coxae visible from above. Last pair of legs subdorsal in position with small subchela. 8 gills on either side. No epipods on pereiopods. Sternum wide, posteriorly upturned, not completely covered by abdomen, no sterno-abdominal depression. Abdominal segments 4 – 6 fused in female, sutures distinct. Press-button retaining system present. Type genus: *Latreillia* Stimpson, 1858.

#### **+Family MITHRACITIDAE fam. nov.**

Urn-shaped, as wide as or longer than wide, widest at posterior third. Dorsal surface strongly areolated. Cervical and branchiocardiac grooves well marked, short. Rostrum single, deflexed, connecting epistome through septum-like proepistome. Lateral margins distinct. Anterolateral margin short, posterolateral margin longer, partly bimarginated. Posterior margin wide, convex. False orbits large, in contact with cervical groove. Buccal cavern widened anteriorly. Third maxilliped operculiform. Chelipeds slightly unequal. Ambulatory legs elongate, last pair reduced, subdorsal. Abdomen in male large, entering between coxae of third maxillipeds, approaching coxae of pereiopods covering completely thoracic sternum. Two proximal segments narrow, exposed dorsally. Abdomen fixed anteriorly between coxae of three anterior pairs of pereiopods, telson entering between coxae of maxillipeds. Uropods transformed into sockets. Type genus: *Mithracites* Gould, 1859.

#### **Superfamily CYCLODORIPPOIDEA Ortmann, 1892**

Cephalothorax subsquare to subcircular, almost flatish. Front rounded, bilobed, rarely with rostrum. Posterior margin relatively wide, concave. Antennulae longer than antennae. Third maxillipeds elongated, completely covering buccal cavern, merus usually produced beyond palp insertion, forming floor for exhalent channels, their epipods reduced to absent. Chelipeds homiochelous. Last two pairs of legs reduced in size, subdorsal in position, subcheliform, propodus and dactylus very short, dactylus strongly curved. Thoracic sternum flat, wide, divided into two parts; two posterior sternites bending more or less upwards, projecting behind posterior carapace margin, largely exposed beyond and laterally to abdomen. Sternal groove on suture 7/8. First gonopod with foliaceous endopod enrolled up to form simple sheath. Second gonopod robust, basally thick, distally tapering, usually slightly longer than first one. Sterno-abdominal depression short. Abdomen short, not touching coxae of pereiopods, partly folded under thorax, true locking mechanism absent. Proximal abdominal segments largely exposed, often some distal segments fused, forming long pleotelson. No pleopods on abdominal segments 3 – 5 in male. Uropods absent. Type genus: *Cyclodorippe* A.Milne Edwards, 1880.

#### **Family CYMONOMIDAE Bouvier 1897**

Rectangular to squarish, slightly longer than wide. Rostrum short, triangular, sometimes absent. Eyestalks strong, calcified, immovable, completely fused at their

base, diverging. Eyes usually absent, directed anteriorly. Orbits absent. Antennulae large, unconcealed, antennular fossae absent. Antennae small, unconcealed. Buccal cavern elongate, quadrangular (not oxystomatous), completely covered by third maxillipeds. Endostome very short. Palp of third maxilliped exposed, exognath with flagellum. Pereiopods with fused basis + ischium. Pleurites at level of legs 1 – 2 uncovered by carapace. Sternal groove in female distinct. Posterior sternites and proximal abdominal segments projecting posteriorly, behind posterior margin of carapace. First gonopod simple sheath. Second gonopod styliform, as long as first one or slightly longer. Females with three pairs of pleopods. Pereiopods with fused basis + ischium. Abdomen very short, bent at right angle, segments usually freely articulated, only posterior segments applied against sternum, sometimes with pleotelson. Pleurites at level of legs 1 – 2 uncovered. Type genus: *Cymonomus* A. Milne Edwards, 1880.

### Family CYCLODORIPPIDAE Ortmann, 1892

Cephalothorax subpentagonal, subquadrate, subcircular to subovate. Orbits distinct. Eyestalk movable, transversely directed. Epistome reduced to absent. Buccal cavern elongate, triangular (oxystomatous). Endostome elongate, grooved, narrowed anteriorly, its apex touching and sometimes exceeding frontal margin. Third maxillipeds elongated, covering completely buccal cavern. Exognath of third maxilliped usually lacking flagellum. Pereiopods with movable basis-ischium articulation. First gonopod forming simple sheath. Second gonopod usually spatulate. Sternum wide. Pleurites covered by carapace at level of anterior pairs of pereiopods. Sternal grooves in females distinct. Sterno-abdominal cavity very short (on sternites 6 – 8). Abdomen short, wide, pleotelson long, segments 6 – 7 fused in female, 5 – 7 fused in male. Type genus: *Cyclodorippe* A. Milne Edwards, 1880.

#### Subfamily XEINOSTOMATINAE Tavares, 1992

Subcircular, obovate to rectangular, flatish. Front semicircular. Posterior margin concave. Palp of endognath of third maxilliped not concealed, exognath without flagellum. Propodi and dactyli of ambulatory legs 1 – 2 lined with rows of long setae on ventral and dorso-external sides. Abdomen in male 5 – 6 segmented. Abdomen in female relatively short, narrow, 6 – 7- segmented, pleotelson long, narrow, poorly calcified. First pleopod in female vestigial, uniramous, articulated ventrally. Pleomeres of segments 2 – 5 laterally narrowed bearing pleopods laterally near their apices. Pleopods 2 – 5 very long and calcified with long setae forming basket for eggs. Type genus: *Xeinostoma* Stebbing, 1920.

#### Subfamily CYCLODORIPPINAE Ortmann, 1892

Subcircular to subpentagonal. Rostrum absent. Antennulae very long, antennae slender. Anterior portion of endostome often projecting beyond frontal margin, visible dorsally. Maxillipeds very long, reaching frontal margin. Palp of third maxilliped articulating ventrally. Propodi and dactyli of ambulatory legs lacking rows of long hairs. Prostomial chamber present. Abdominal segments very calcified, convex



with borders curved down, pleotelson flared, posteriorly semicircular. Abdomen in male 5 – 7-segmented, in female wide, 6 – 7-segmented, pleopod 1 usually absent, pleopod 5 present to absent. Pleopods 2 – 5 articulating on ventral side of abdominal segments, lacking long setae. Type genus: *Cyclodorippe* A. Milne Edwards, 1880.

### **Family PHYLLOTYMOLINIDAE Tavares, 1998**

Subcircular, flattish. Integument well calcified. Slightly narrowing anteriorly and posteriorly. Front subtriangular, slightly projecting, rostrum very short. Eystalk short, movable, transversely directed. Exorbital angle distinct. Antennae robust, movable, urinal segment movable, basal segment enlarged, converging, segments 4 – 5 wide. Orbital and antennal cavities in communication. Buccal cavern subquadrangular, very elongated, anteriorly open, lateral margins very elongated, parallel, reaching basal antennal segment. Endostome short, shallow. Prostomial chamber present. Palp of third maxillipeds inserted near inner angle of merus, exposed. Two last pairs of legs reduced, subdorsal, dactyli prehensile. Abdomen 7-articulated in both sexes, short. First pleopod of female vestigial to usually absent, last pleopod reduced. Abdominal holding system absent. Type genus: *Phyllotymolinum* Tavares, 1993.

### **+Family TORYNOMMIDAE Glaessner, 1980**

Subsquare rectangular to pentagonal, slightly longer than wide, widest anteriorly, dorsally convex. Lateral margins not sharp. Sidewalls steep. Dorsal surface granular, furrows very distinct, regions well defined. Rostrum narrow, spatulate, more or less produced, gently deflexed. Fronto-orbital margin wide. Anterolateral margins short, posterolateral margins nearly parallel. Posterior margin concave. Eyes well developed. Orbits large, shallow, directed anteriorly. Two (or only one) last pairs of legs reduced in size, dorsal in position. Thoracic sternum posteriorly upturned, last sternites vertical and chevron-shaped. Proximal abdominal segments exposed dorsally. Type genus: *Torynomma* Woods, 1953.

### **+Family ETYIDAE Guinot & Tavares, 2001**

Cephalothorax transversely oblong, much wider than long, dorsally flattened, branchial region elongated. Dorsal surface markedly areolated. Fronto-orbital margin wide. Front not projecting, straight to bilobed. Lateral margin distinct. Anterolateral margin convex with teeth, longer than posterolateral, both well delimited. Posterior margin narrow, more or less concave. Orbits large, deep. Urinal tubercles well developed. Epistome triangular. Buccal cavern quadrangular. Third maxillipeds operculiform, palp well developed. Chelipeds elongated, merus long, stout fingers longer than palm. Anterior pair of legs long. Last two pairs subdorsal. Sternites 6 – 8 or 7 – 8, or only 8 subperpendicular to precedent sternites (upturned). Spermathecal openings at end of suture 7/8. Abdomen covering whole sternum in female. Sternite 4 large, visible beyond and laterally to telson in male. Abdomen fixed laterally by coxae of 1 – 2 anterior pairs of pereopods. Uropods absent. Type genus: *Etyus* Leach in Mantell, 1822.

## Superfamily RANINOIDEA de Haan, 1841

Characters as for the family.

### Family RANINIDAE de Haan, 1839

Cephalothorax odd-looking, subcylindrical, longitudinally ovate, greatest width usually in anterior third. Dorsal surface mostly lacking distinct furrows or lobes. Posterior margin slightly concave to nearly straight. Posterior thoracic pleura largely exposed in lateral view by reduction of branchiostegite (*Gymnopleura!*). Eystalks, antennulae and antennae well developed. Buccal cavity elongated, narrowing anteriorly, completely covered with third maxillipeds, palp of third maxilliped articulated subapically, concealed by merus, exognath short, usually lacking flagellum. Proximal articles of endopods and exopods of first maxilliped forming respiratory channel. Chelipeds robust, subequal, usually distally wide, more or less flattened. Fingers of chelipeds almost strongly bent, nearly at right angle. Ambulatory legs with flattened propodi and dactyli. At least one pair of legs paddle-like. Posterior pair of ambulatory legs subdorsal or dorsal in position, somewhat anterior to third pair of legs (inversion of sternum). Coxa of last pair of legs depressed, prolonged in long process terminating by semirigid penis. Supplementary paired inhalant opening between coxae of last pair of legs and terga of first abdominal segment. Number of gills usually 8 on each side. Thoracic sternum upturned posteriorly. Sternites 1 – 3 fused in shield, segment 4 widest, posterior sternites very narrow and keel-like, especially sternites 5 – 7, sternite 8 bending abruptly upwards, being perpendicular to preceding sternite, V-shaped. Sternal grooves absent in females. Distal segment of first gonopods more or less rolled up to form hollow, leaf-like tube, proximal aperture wider than distal one. Gonopods contiguous, usually longer than abdomen. Spermathecal openings usually very contiguous. Abdomen narrow, short, coiled to mostly uncoiled, 3 – 5 proximal abdominal segments largely exposed in dorsal view, segments freely articulated. Uropods and vestigial pleopods on segments 3 – 5 in male absent. Type genus: *Ranina* Lamarck, 1801.

+Subfamily PALAEOCRYSTINAE Lörenthey (in Lörenthey & Beurlen), 1929

Cephalothorax elongately ovate. Cervical and usually branchiocardiac grooves distinct. Longitudinal carina distinct, often centrally nodose. Rostrum narrow, bifid. Anterolateral margin with 2 or more spines. Buccal cavern wide, elongate. Fingers of cheliped slightly bent. Thoracic sternum moderately wide, not very narrowed posteriorly. Abdomen not markedly narrow, pressed against sternum between coxae of ambulatory legs, segments 1 – 2 or 3 exposed dorsally. Telson semioval, reaching sternite 4. Type genus: *Notopocorystes* M'Coy, 1849 (= *Palaecorystes*, Bell, 1863).

### Subfamily SYMETHINAE Goeke, 1981

Cephalothorax subovate, elongate. Front narrow, trilobed, projecting, rostrum rather long. Eyes very reduced. Orbits straight, directed forward. Antennulae small, completely concealed by antennal peduncle, latter massive, flagellum short. Chelipeds

rather long, palm swollen, fingers slender, slightly bent mesioventrally. Dactyls of ambulatory legs sickle-shaped. 7 pairs of gills on each side. Thoracic sternum very elongated, narrow. Sternite 4 relatively small, space between coxae of ambulatory legs rather very narrow. Spermathecal openings with overhanging hoods, distinctly separated. First gonopod close tube, stout, gradually tapering to pointed apex, setose. Second gonopod with elongated apically pointed distal segment. Type genus: *Symethis* Weber, 1795.

#### Subfamily CYRTHORINAE Guinot, 1993

Cephalothorax broadly subovate, wide. Fronto-orbital margin narrow, with 5 spines, rostrum triangular, short. Eystalks short, stout, cornea small. Orbits directed forward. Exorbital angle well developed closely associated with ventral and dorsal denticles. Chelipeds with very long spines on propodus and dactylus, fingers extremely slender, straight. Ambulatory legs subequal in length, dactyls of legs 3 – 4 sickle-shaped. Spermathecal orifices close together. Sternite 4 nearly linear between articulation of chelipeds. First gonopod short, stout, apically widened, truncate, second gonopod slightly shorter, with distal segment elongate, apically acuminate. Type genus: *Cyrtorhina* Monod, 1956.

#### Subfamily NOTOPODINAE Serène & Umali, 1972.

Subovate. Eystalks long, strongly folded downward and directed obliquely backward, completely hidden when retracted. Antennal peduncle very stout, hiding antennulae, flagellum long and stiff. Oblique crest on proximal part of ischium of third maxilliped. Chelipeds with short, wide, flattened propodi, fixed finger very short. Dactylus bent against anterior margin of palm and fixed finger. All ambulatory legs similar in form and size. Thoracic sternites 6 – 7 markedly narrow. First gonopod stout, with short, hollow, folded, foliaceous, terminal segment, not fitted into sulcus of shield. Second gonopod foliaceous, long, strong, apical process protruding slightly over tip of first gonopod. Spermathecal orifices near, but not confluent. Type genus: *Notopus* de Haan, 1841.

#### Tribe Notopodini Serène & Umali, 1972

Subovate, urn-shaped. Anteriorly wide, evenly transversely convex. Fronto-orbital margin long, with one or two fissures and 3 – 4 simple spines on each side of rostrum. Rostrum present as pointed triangular process. Exorbital spine usually indistinct. Hepatic spines distinct. Antennulae small, antennae long. Antennal peduncle stout, hiding antennulae. Orbits large. Palm of cheliped very wide. First gonopod with distal segment rolled up to form gutter, incompletely tubular with only distal aperture. Type genus: *Notopus* de Haan, 1841.

#### Tribe Cosmonotini trib. nov.

Urn-shaped, elongated, anteriorly narrowing, roof-like. Rostrum absent, replaced by V-shaped incision, continued by distinct medial dorsal carina. Eystalks very long, slender. Supraorbital margin very long, with two fissures. Exorbital angle distinct. Antennal peduncles very stout, reaching far beyond front, flagellum as long

as peduncle. Ischium of third maxilliped longer than merus. Fixed finger of cheliped very short. Last pair of legs not very reduced. Distal segment of first gonopod rolled up to form rather loosely folded sheath. Sternites 4 + 5 large, others sternites much narrower. Gonopods long, apices uncovered by abdomen. Type genus: *Cosmonotus* White, 1847.

#### Subfamily LYREIDINAE Guinot, 1993

Elongate-elliptical, fusiform. Dorsal surface smooth, regions indistinct. Fronto-orbital margin narrow. Rostral and exorbital teeth of equal size, hepatic spine usually present. Eystalks longitudinally directed. Supraorbital margin with one or two small fissures. Antennal peduncle slender, not hiding antennulae, flagellum short. Merus of third maxilliped longer than ischium. Claw of cheliped with fixed finger elongated, deflexed. Last pair of legs very reduced in size, filiform. Sternites 4 – 5 not very narrow, sternites 6 – 7 rather (but not extremely) narrow. Space between coxae of ambulatory legs not extremely narrow. Two well marked spermathecal orifices close together. Distal segment of first gonopod with wide posterior opening, apically truncate. Abdominal segments 4 – 6 + telson completely flexed against sternum. Press-button mechanism of abdomen present on sternite 5, functional. Abdominal segments 3 – 4 with spines or tubercles. Type genus: *Lyreidus* de Haan, 1841.

#### Subfamily RANININAE de Haan, 1841

Cephalothorax longitudinally ovate. Fronto-orbital margin relatively wide. Rostrum triangular. Eystalks longitudinally to transversely folded. Orbits directed forwards. Basal antennal segment well developed with distinct antennal scale. Antennal peduncle not completely hiding antennulae. Flagellum small. Ischium of third maxilliped lacking oblique crest. Palm of chelipeds compressed, fingers remarkably bent, nearly at right angle to palm. Spermathecal apertures very close together. First gonopod elongate, closed tube, apical margin laterally expanded. Second gonopod shorter than first one, regularly tapering to its tip, distally cutting slant and acuminate, ornamented at apex. Tips of pleopods fitted into sulcus of sternal shield. Sternites 1 – 6 in same plane. Type genus: *Ranina* Lamarck, 1801.

#### Tribe Raninoidini Lörenthey & Beurlen, 1929

Elongate-obovate, lateral margins nearly parallel. Dorsal surface smooth. Fronto-orbital width more than half width of carapace. Rostrum widely triangular, three simple spines on each side. Hepatic spine present. Eystalks folding longitudinally to transversely directed. Orbits of moderate size, supraorbital margin bifissured. Basal antennal segment well developed with prominent antennal scale (scaphocerite). Antennal peduncles slender, not hiding antennulae, flagellum small. Merus of third maxilliped shorter than ischium. Chelipeds with propodus flattened, elongate, fixed finger long. Last pair of legs short and slender, dactyli subovate, subdorsal. Sternite 4 large, sternite 5 narrowed, sternites 6 – 7 very narrow. Spermathecal orifices in two distinct apertures. First gonopod in sternal furrow. Type genus: *Raninoides* H. Milne Edwards, 1837.

**Tribe Raninini de Haan, 1839**

Urn-shaped, widest anteriorly. Frontal border very wide, multidentate, rostrum trifold. Antennulae slender. Basal antennular segment large, flagellum small. Eystalks completely hidden when retracted. Orbits directed forward. Antennal peduncle stout, hiding antennulae, flagellum long and stiff. Ischium of third maxilliped shorter than merus. All ambulatory legs similar in form and size, dactyli foliaceous. Spermathecal openings very close together, seeming to be single orifice. Sternite 4 very wide, sternite 5 laterally expanded. Thoracic sternum deflexed at level of sternite 7. Sternite 8 perpendicular to preceding sternites. Type genus: *Ranina* Lamarck, 1801.

**+Superfamily DAKOTICANCROIDEA Rathbun, 1917**

Characters as for the family.

**+Family DAKOTICANCRIDAE Rathbun, 1917**

Cephalothorax transversely ovate to rectangular, usually as long as wide to slightly longer than wide, convex. Carapace dorsally well sculptured, pleural sutures located on carapace sides. Median part of cardiac groove weak, branchiocardiac grooves strong. Front narrow, bilobed, downturned. Orbits well developed, rimmed. Eyes retractile in orbits. Last pair of legs subdorsal, reduced in size. Thoracic sternum very wide, largely exposed beyond and laterally to abdomen. Sternites 1 – 7 in same plane, sternite 8 small, slightly upturned. Sternites 4 – 8 regularly metamerized. Sutures 4/5 – 7/8 interrupted mesially. Sterno-abdominal cavity distinct. Spermathecal opening large situated at end of suture 7/8. Abdomen pressed against sternum in both sexes. No uropods (in dorsal view). Type genus: *Dakoticancer* Rathbun, 1917.

*Dromiacea* (?) *incertae sedis*

**+Family EOCARCINIDAE Withers, 1932**

Subcylindrical, elongated, widest posteriorly. Lateral margins weakly developed only anteriorly. Rostrum short, triangular slightly deflexed. Frontal margins with two sinuses. Posterior margin concave. No orbits. Cervical and branchiocardiac furrows distinct, latter touching posterior margin. Two posterior pairs of legs smaller, with slightly curved long dactyli, seemingly not subdorsal in position (uncertain). Abdomen well developed, in prolongation of cephalothorax, posteriorly curved. First abdominal segment narrowest, sixth largest, posterior segments downturned. Terga and pleura separated by deep groove, pleura elongated. Telson small. Uropods indistinct. Type genus: *Eocarcinus* Withers, 1932.

**+Family IMOCARIDIDAE fam. nov.**

Subcylindrical, elongated, box-like. Anterior margin nearly straight, posterior margin concave. Lateral margins seemingly subparallel. Dorsal surface tuberculate. Orbits absent. Cervical and branchiocardiac grooves deep. Type genus: *Imocaris* Schram & Mapes, 1984.

## Section EUBRACHYURA de Saint Laurent, 1980

Cephalothorax in variety of forms. Front usually mesially notched, sometimes entire or pointed and projecting. Beyond antennulae and antennae more or less distinct sinuses (antennular and antennal ones). Anterolateral and posterolateral margins usually well defined. Posterior margin of carapace usually as wide as fronto-orbital or frontal width, nearly straight to convex. Eyes well developed. Orbits almost present, secondarily absent. Ocular and antennular fossae well developed and more or less separated. Scaphocerite (antennal scale) absent. Antennulae longitudinally to mostly transversely folded in their fossae, antennular flagella usually short. Antennae almost well developed, usually longitudinally, sometimes obliquely, directed. First antennal (urinal) segment fixed, excretory pore usually inconspicuous, covered with operculum. Basal antennal segment usually well-developed, often touching ventral prolongation of frontal margin, segment 4 usually narrower, in prolongation of basal segment, both longitudinally to obliquely directed, segment 5 with flagellum often bent laterally. Inhalant openings in front of base of chelipeds. Exhalant openings in front of maxillipeds. Epipodites on pereopods absent. Number of gills reduced (9 and less). Proepistome and epistome ranging from distinctly separated by groove to completely fused. Epistome and endostome usually well marked, sometimes limits indistinct. Mandibular palp trisegmented, sometimes bisegmented. Merus of third maxilliped usually shorter than ischium. *Sella turcica* present. Thoracic sternum metamerized, posteriorly usually more or less upturned. Suture 1/2 rarely distinct, 2/3 usually distinct, 3/4 usually laterally indicated by incomplete suture or only lateral incision, sutures 4/5 – 7/8 entire or interrupted. Sternum of females without marked longitudinal sternal furrows on suture 7/8. Sterno-abdominal cavity almost present. Oviduct and *receptaculum seminis* (formed as dilatation of oviduct) connected. Female sexual opening (vulva) on sternite 6, in direct communication with *receptaculum seminis*. Gonopods three-segmented (coxa, basis, endopod), two proximal segments usually fused with sternum. First gonopod only with strong endopod, tightly rolling along its entire length completely closed, tubiform with two proximal apertures: for introduction of penis and for second gonopod. Form and size of first gonopod very varying. Second gonopod uniramous, ending with flagellum (= *appendix masculina*) of various length, inserted into first gonopod, exopod absent. Between endopod and flagellum often cup (spoon)-like structure. Abdominal segments ranging from freely articulated (7-segmented) to more or less fused, usually segments 3 – 5 in male, in female mostly freely articulated. Abdomen gradually tapering from segments 3 – 6, filling sterno-abdominal cavity. Two proximal segments and proximal part of third abdominal segment usually visible in dorsal view. Uropods transformed into sockets on sixth segment forming with prominence of fifth thoracic sternite press-button retaining mechanism of abdomen. Abdomen never covering whole sternum, large portion remaining uncovered at least beyond and laterally to telson. Telson triangular to rounded. Pleopods 3 – 5 in male absent. First pleopod in females absent.

### Subsection HETERO TREMATA Guinot, 1977

Cephalothorax of variety of forms. Anterolateral margin usually longer than posterolateral, posterior margin narrow to moderately wide, rarely very wide. Endostome with median gutter. Palp of third maxilliped usually articulating at inner distal or sometimes terminal margin of merus. Chelipeds usually pressed against anterolateral ventral side of carapace. Meri of ambulatory legs usually elliptical or rounded in cross-section. Coxae of posterior pair of legs usually exposed in dorsal view. Male sexual opening mostly coxal, on last pair of legs, sometimes coxo-sternal. Penis located in more or less distinct penial groove and rarely embedded under sternal plate forming penial tube. Vulva opening on thoracic sternite 6. Vagina usually of simple type. Sterno-abdominal cavity present. Third abdominal segment of male usually widest and covering sexual opening and penis (i.e. usually reaching coxae of last pair of legs). Proximal three abdominal segments in male usually cover whole space between coxae of last pair of legs, covering more or less sternite 8, sometimes portion of sternite 8 laterally to abdominal segments 1 – 2 remaining uncovered. Retaining mechanism of abdomen present and almost functional, mostly of push-button type: prominence on thoracic sternite 5, socket on abdominal segment 6.

### Superfamily CANCROIDEA Latreille, 1802

Cephalothorax much wider than long. Front narrow. Antennal sinus distinct. Antennulae and antennae longitudinally to gently obliquely posed. Supraorbital margin usually trilobed consisting of pre-supra- and post(ex)orbital lobes to bifissured. Basal antennal segment large, usually fixed, fused with preorbital lobe, separating orbital and antennular cavities, antennal flagella short. »Portunid lobe« present. Prostomial chamber usually present. Thoracic sternum narrow, sutures 4/5 – 7/8 entire, usually equidistant to 4/5 – 5/6 interrupted. Both gonopods long. Abdominal segments 3 – 5 fused in male. Type genus: *Cancer* Linnaeus, 1758.

### Family CANCRIDAE Latreille, 1802

Transversely ovate, widely hexagonal to subovate. Regions more or less defined. Front narrow, lobate to dentate. Antennal sinus present. Anterolateral margin strongly convex, dentate or lobate, posterolateral margin short, entire, diverging. Antennulae folding longitudinally. Basal antennal segment large, longer than wide, fixed, longitudinal, distally in contact with preorbital lobe, antennal flagella short, hairy. Orbits completely closed. Epistome narrow, often sunken, usually concealed by third maxillipeds. Chelipeds massive, subequal, palm and fingers usually with keels, spines or granules. Sternal sutures 4/5 – 7/8 entire, almost equidistant, subparallel. First gonopod stout, straight, long, distally tapering. Second gonopod of similar length. Type genus: *Cancer* Linnaeus, 1758.

### Subfamily CANCRINAE Latreille, 1802

Cephalothorax transversely subelliptical, wide. Front narrow, with odd (5) number of teeth or lobes. Antennal sinus distinct. Anterolateral margin distinctly dentate.

Basal antennal segment large, closing orbital hiatus. Antennal flagella short, more or less setose. Merus of third maxilliped auriculate. Third maxillipeds overlapping epistome. Prostomial chamber sometimes present. Palm of chelipeds with several keels, latter ranging from smooth, granular to spined. Type genus: *Cancer* Linnaeus, 1758.

+Subfamily LOBOCARCININAE Beurlen, 1930

Canceriform to subpentagonal, very wide. Regions distinct. Front moderately wide, slightly projecting beyond orbits, with even number of teeth (4 – 6), rarely with odd number (than central lobe small and in lower position). Supraorbital margin with 1 – 2 fissures. Antennulae plicated obliquely. Anterolateral margin usually 7-lobate, with bi- or trifurcate lobes. Posterolateral margin dentate. Posterior margin nearly straight. Chelipeds slender, homoiochelous. Type genus: *Lobocarcinus* Reuss, 1857.

**Family ATELECYCLIDAE Ortmann, 1893**

Pentagonal, subcircular to subovate, convex in both directions. Regions fairly well defined, dorsal furrows discernible. Dorsal surface with sparse setae, lateral margin, ventral part of cephalothorax and pereopods covered with long dense setae. Front 3 – 4 -dentate. Anterolateral margin dentate, longer than posterolateral. Eyestalks well developed. Orbits shallow, complete. Antennulae folding longitudinally. Antennae long, hairy, nearly parallel. Basal antennal segment strong, movable to fixed, basally in contact with preorbital lobe. Proepistome and epistome fused, sunken, overlapped by third maxillipeds. Endostomial ridge present. Maxillipeds anteriorly hairy, elongated, and extending to antennal base, covering incompletely buccal cavern. Pereopods short, coxae of last pair of legs behind posterior carapace margin. Thoracic sternum narrow, sutures 4/5 – 7/8 entire, nearly equidistant. First gonopod strong, second gonopod longer than first. Abdominal segments 1 – 2 exposed dorsally, segments 3 – 5 fused in male, telson triangular. Type genus: *Ateleyclus* Leach, 1814.

**Family CHEIRAGONIDAE Ortmann, 1893**

Subpentagonal to suboblong. Front 4-lobed. Supraorbital margin trilobed. Eyes not protected either dorsally or ventrally. Antennulae lengthwise. Basal antennal segment wide and flattened, its lateral wing-like projection filling orbital hiatus, separating from front, peduncle large, flagella setose. Prostomial chamber present. Sternal sutures 6/7 – 7/8 entire. Abdomen short segments 3 – 5 fused in male, female abdomen not covering vulvae. Gonopods long. Type genus: *Telmessus* White, 1846 (= *Cheiragonus* Brandt, 1851).

**Superfamily CORYSTOIDEA Samouelle 1819**

Characters as for the family.



### Family CORYSTIDAE Samouelle, 1819

Longitudinally ovate, transversely convex. Dorsal regions usually indistinct. Front 2 – 3 lobed, projecting. Lateral margins convex, not keeled, armed with teeth or spines along entire length, covered with dense setae, but not forming fringe. Posterior margin narrow, straight. Orbits usually incomplete, exorbital angle distinct. Antennulae folding longitudinally. Antennae very long, flagella feathered, setae interlocking to form respiratory tube, segment 4 flexed downward-inward, segment 5 in prolongation of cephalothorax. Basal antennal segment not fused with front. Third maxilliped subpediform, merus elongate, epistome very small to rudimentary, sunken, concealed by third maxilliped. Buccal cavity and mouth elongate extending almost to antennulae. Chelipeds long, not pressed against cephalothorax. Dactyli of legs usually styliform, dactyli of last pairs compressed and sometimes natatorial. Sternum narrow, elongated. First gonopod stout, distally slightly tapering, straight to curved. Second gonopod shorter. Abdomen very short in both sexes, uncoiled, not covering vulva in female. Segments 3 – 5 fused in male. Retaining mechanism of abdomen absent. Type genus: *Corystes* Bosc, 1802.

#### Subfamily CORYSTINAE Samouelle, 1819

Cephalothorax longitudinally elliptical. Front 2 – 4 spinose or bidentate. Antennulae small, longitudinal. Antennae extremely long, flagella forming tube. Buccal cavity and mouthparts very elongate, mandibular palp sometimes bisegmented. Ambulatory legs gressorial. Sternum narrow, elongate, sternal sutures 4/5 – 7/8 entire, nearly equidistant. Sterno-abdominal cavity absent to feebly developed. Some abdominal segments (2 – 4 or 3 – 5) fused in male. First gonopod short, stocky, apex sclerotized.

Second gonopod long to short. Type genus: *Corystes* Bosc, 1802.

#### Subfamily NAUtileCORYSTINAE Ortmann, 1893

Front tridentate to entire. Anterior part of lateral margin 4 dentate. Supraorbital margin bifissured. Inner infraorbital lobe projecting, visible dorsally. Antennae longer than carapace. Sternal sutures 4/5 – 5/6 interrupted near median line. Merus of third maxilliped narrower than ischium, bearing palp on summit. Exognath lacking flagellum. Dactyli of ambulatory legs 2 – 3 compressed, last pair compressed with blade-like dactylus (paddle-like). First gonopod long, slender, curving outwards laterally to telson. Second gonopod about half-length of first. Type genus: *Nautilocorystes* H. Milne Edwards, 1847.

### Superfamily THIOIDEA Dana, 1852

Characters as for the family.

#### Family THIIDAE Dana 1852

Cordiform, convex transversely. Dorsal surface smooth. Front gently arched, entire, lamellate. Lateral margins arcuated, lined with dense long setae forming fringe.

Posterior margin narrow. Antennulae folding obliquely. Antennae well developed, shorter than carapace, basal antennal segment fixed, touching front, segment 4 flexed mesially, segment 5 in prolongation of cephalothorax, peduncle and flagellum hairy. Epistome very short, partly covered with elongated third maxillipeds. Buccal cavity elongate, completely covered with third maxillipeds. Prostomial chamber present. Dactyli of legs T-shaped in cross section. Sternum very narrow, sternite 4 very long. Sternal sutures 4/5 – 7/8 entire. Second gonopod semi-long. Abdominal segments 3 – 5 in male fused, segments 1 – 3 dorsally exposed. Abdomen covering completely sternum between coxae of anterior pairs of legs Type genus: *Thia* Leach, 1815.

### Superfamily PIRIMELOIDEA Alcock, 1899

Characters as for the family.

#### Family PIRIMELIDAE Alcock, 1899

Subhexagonal, not transverse. Front produced, with odd number of teeth (3). Supraorbital margin trilobed. Inner infraorbital lobe distinct. Anterolateral margin dentate, antennulae slightly obliquely, nearly folded longitudinally. Antennae long, basal antennal segment fixed, peduncle stout, longitudinal, flagellum obliquely folded. Epistome sunken, overlapped by third maxilliped. Prostomial chamber present. Buccal cavern elongated. »Portunid lobe« present. Sternal sutures 4/5 and 5/6 interrupted near median line. First gonopod long, second one short. Abdominal segments 3 – 5 fused in male. Type genus: *Pirimela* Leach, 1816.

### Superfamily ERIPHIOIDEA MacLeay, 1838

Cephalothorax mostly xanthoid in shape, transversely hexagonal, subrectangular to transversely ovate. Dorsal surface with regions moderately distinct to indistinct. Front wide, notched medially, bi- or quadrilobed. Anterolateral margin short. Antennulae plicated transversely. Endostomial ridge present (Hyperomerista). Chelipeds more or less unequal. Male sexual opening coxal. Thoracic sternum almost narrow. First gonopod stout, straight to weakly curved, distally more or less tapering, second gonopod longer or subequal in length to first, rarely shorter, flagellum whip-like. Abdominal segments freely articulated in both sexes. Type genus: *Eriphia* Latreille, 1818.

#### Family ERIPHIIDAE MacLeay, 1838

Subhexagonal, transversely rectangular to transversely ovate. Front moderately wide, deflexed. Basal antennal segment cylindrical, not touching to touching front. Endostomial ridge complete. Sternum rather narrow to moderately wide. Sutures 4/5 – 5/6 interrupted, rarely entire. First gonopod stout long, almost straight to slightly curved, gradually tapering. Second gonopod elongate, subequal in length to usually longer than first one, with long filamentous (whip-like) flagellum. Type genus: *Eriphia* Latreille, 1818.

### Subfamily ERIPHIINAE MacLeay, 1838

Cephalothorax subquadrate to transversely oval. Front 2 – 4 – lobed. Antennular and antennal sinuses distinct. Orbits wide, open to usually closed by approaching lateral suborbital lobe and infraorbital margin, usually excluding antennae. Exhalent openings often large and circular. Sternum narrow, sutures entire to some interrupted. Sutures 1/2 – 3/4 often entire. Flagellum of second gonopod whip-like, curled. Type genus: *Eriphia* Latreille, 1818.

#### Tribe Menippini Alcock, 1898

Cephalothorax ovate to quadrangular. Fronto-orbital margin wide. Anterolateral margin usually from lobate to dentate. Orbital hiatus open, wide. Antennae not excluded from orbits, peduncle entering orbital hiatus. Basal antennal segment short, wide, far from front. Sternal sutures 4/5 – 7/8 entire, in some genera sutures 4/5 – 5/6 interrupted. Type genus: *Menippe* de Haan, 1833.

#### Tribe Eriphiini MacLeay 1838

Fronto-orbital margin moderately wide. Anterolateral margin spinose or lobate. Orbits circular, orbital hiatus completely closed. Basal antennal segment touching front. Antennae excluded from orbits. Eyes far from antennae. Sternal sutures 4/5 – 5/6 usually interrupted. Type genus: *Eriphia* Latreille, 1817.

### Subfamily PLATYXANTHINAE Guinot, 1977

Transversely elliptical. Dorsal regions indistinct. Front four-lobed, median notch, antennular and antennal sinuses distinct. Supraorbital margin bifissured. Posterior margin narrow. Antennulae folded obliquely. Basal antennal segment not in contact with front. »Portunid lobe« present, small. Thoracic sternum relatively narrow to large. Sternal sutures 4/5 – 5/6 interrupted. Vulva not covered with operculum. First gonopod strong, stout, distally gradually tapering, subdistally covered by spinules, slightly curved. Second gonopod long, with very long flagellum, not curled. Type genus: *Platyxanthus* A. Milne Edwards, 1863.

### Subfamily DACRYOPILUMNINAE Serène, 1984

Transversely subovate, dorsally convex, thick. Front truncate, markedly deflexed. Fronto-orbital margin widened, subequal to width of carapace. Orbits completely closed, located on dorsal surface far from frontal margin. Anterolateral margin very short, with few closed fissures to entire, deflexed. Posterior margin narrow. Sternum narrow, lateral margins subparallel. Sternal sutures 4/5 – 7/8 entire, subparallel. First gonopod stout, distally spinulose, second gonopod long, flagellum long, recurved. Type genus: *Dacryopilumnus* Nobili, 1906.

### Family LADOMEDAEIDAE fam. nov.

*Medaeus*-shaped. Dorsal surface markedly areolated. Front wide, bilobed, bimarinate, lobes subtruncate, antennal sinus distinct. Exorbital margin thick, obtuse. Anterolateral margin with 4 wide triangular teeth. Supraorbital margin bifissured. Endostomial ridge complete. Chelipeds massive, feebly heterochelous, inner carpal

spine distinct. Ambulatory legs compressed, crested at anterior margin, crest cut into teeth. Abdominal segments freely articulated in both sexes. First gonopod with flattened and spatulate tip. Second gonopod short, apically neither filamentous nor curled. Type genus: *Ladomedaeus* gen. nov. (Etymology: Lado = Old Slavic god. Type species: *Medaeus serratus* Sakai, 1965; gender: masculine).

### Family PILUMNOIDIDAE Guinot & Macpherson, 1987

*Pilumnus*-like, roundish. Regions well marked. Front bilobed. Antennular and antennal sinuses rather distinct. Antennulae oblique, nearly transversely folded. Basal antennal segment not touching front. Endostomial ridge present. Chelipeds tightly pressed against carapace, dactyli slanting. Sternum narrow, elongate, sternal sutures 4/5 – 7/8 entire. Abdomen in male narrow, segments freely articulated. First gonopod nearly straight, apex more or less ornamented. Second gonopod slightly shorter than first one, with distinct but rather short flagellum. Type genus: *Pilumnoides* Lucas (in H. Milne Edwards), 1844.

### Family CARPILIIDAE Ortmann, 1893

Cephalothorax heavily built, transversely ovate, dorsally strongly convex, dorsal surface smooth, compact looking, regions indistinct. Front sometimes deflexed, trilobed, median lobe bilobed (front appearing quadrilobed). Orbits circular, entire, rimmed or beaded, directed forward. Orbital hiatus narrow. Exorbital angle short, blunt. Anterolateral margin convex, thick, with small epibranchial knob, in fossil forms sometimes with blunt lobes or spines, much longer than posterolateral margin, posterolateral margin straight or weakly concave, short. Posterior margin nearly straight narrow. Antennulae nearly transverse. Antennae oblique, basal antennal segment in long contact with front, peduncle in orbital hiatus, flagellum minute. Endostomial ridge incomplete. »Portunid lobe« present. Buccal cavern anteriorly arched. Pereiopods smooth, naked, chelipeds massive, walking legs long, slender, cylindrical, smooth. Basis-ischium of chelipeds completely fused to merus, so merus and coxa articulating directly. Thoracic sternum narrow, with subparallel margins, sutures 4/5 – 7/8 entire, equidistant, parallel. No distinct sterno-abdominal cavity. First gonopod stout, conical, nearly straight to slightly curved, tip obliquely truncated, aperture distal. Second gonopod subequal to longer than first one, with curled long flagellum. Abdomen narrow, abdominal segments 3 – 5 in male immovable, suture 3/4 absent, suture 4/5 distinct. Abdominal segments in female freely articulating. Type genus: *Carpilius* Leach (in Desmarest), 1825.

### Superfamily ACIDOPOIDEA superfam. nov.

Characters as for the family.

### Family ACIDOPIDAE Števcíć, 2001 (*in* Martin & Davis, 2001)

Pilumnoid-shaped, wider than long, convex longitudinally, flat transversely. Carapace and pereiopods covered with short, dense pubescence. Dorsally areolated.

Front lamellate, bilobed, lobes hardly convex, not prominent, fringed by long setae. Anterolateral margin short, tridentate. Posterior margin wide. Orbits elongate, not concealing completely eyes, margins entire. Eyestalk long, movable, flattened, elongate with acute anterior edge, continuous with supraorbital margin. Basal antennal segment filling orbital hiatus, just reaching front. Merus of third maxilliped transversely oblong. Ischium-merus articulation constricted. Endostomial ridge distinct. Chelipeds short. Legs wide, compressed, dactyli narrow. Sternum narrow. Sternal sutures 4/5 to 7/8 entire. Sternite 8 upturned. First gonopod nearly straight, gradually tapering to pointed apex, second gonopod slightly shorter than first gonopod, with relatively long, filiform flagellum. Abdomen in male narrow, third segment produced laterally touching coxae of last pair of legs. Type genus: *Acidops* Stimpson, 1858.

### Superfamily DAIROIDEA Serène, 1965

Cephalothorax reansversely oval or subhexagonal. Dorsal surface of carapace covered with confluent mushroom-like tubercles, forming secondary dorsal surface. Dorsal regions more or less distinct. Anterolateral margin arched, longer than posterolateral. Antennulae folding obliquely. Endostomial ridge present. Chelipeds heterochelous. First gonopod rather stout, gradually tapering distally, gently curved, terminal aperture large. Second gonopod long, with very long flagellum. Type genus: *Daira* de Haan, 1833.

### Family DAIRIDAE Serène, 1965

*Actaea*-like, convex in both directions. Dorsal surface areolated. Front gently projecting, bilobed, deflexed. Anterolateral margin ridged, arched, posterolateral margin shorter, slightly concave, posterior margin narrow. Antennular sinus wide, antennulae oblique. Antennal peduncle closing orbital hiatus. Interantennular septum wide. Endostomial ridge distinct posteriorly. Merus of third maxilliped deeply notched anteriorly (exhalent aperture). Chelipeds large, heterochelic, pressed against cephalothorax, fingers hollowed. Ambulatory legs, dorsally keeled, compressed, covered with long setae, with distinct dactylo-propodal locking mechanism, dactyli with acute apices. Branchiostegite not covering completely pleura above coxae of ambulatory legs. Sternum narrow. Sternal sutures 4/5 – 7/8 apparently entire in (young) male, 4/5 – 5/6 apparently interrupted in female. First gonopod straight, slightly tapering distally, second one longer than first, with long whip-like curled flagellum. Abdomen long and narrow in both sexes, segments 3 – 5 immovable in male, suture distinct. Type genus: *Daira* de Haan, 1833.

### Family DAIROIDIDAE Štević, 2001 (in Martin & Davis, 2001)

Cephalothorax subhexagonal, anteriorly narrowing, convex. Dorsal surface covered with fused mushroom-like perforate vesicular tubercles, with two deep grooves. Front narrow, tridentate, deflexed. Orbits small, deep, rounded. Antennular and orbital cavities in communication. Basal antennal segment mobile, short, not touching

front, peduncle slender lying loosely in orbital hiatus. Chelipeds strong, not pressed tightly against anterolateral margin, projecting far beyond carapace. Anterolateral margin with three teeth. Junction between anterolateral and posterolateral margins produced and armed with tooth. Endostomial ridge complete. Anterior margin of merus of third maxilliped straight. Sternal shield entering between third maxillipeds. Second gonopod very slender, longer than first, flagellum longer than basal segment, curved. Abdominal segments nearly freely articulated, segments 3 – 4 immovable, telson rounded in both sexes. Type genus: *Dairoides* Stebbing, 1920.

### Superfamily MATUTOIDEA de Haan, 1835

Characters as for the family.

#### Family MATUTIDAE de Haan, 1835

Subcircular to ovate, flatfish, with more or less distinct lateral spines at junction of antero- and posterolateral margins. Front narrow, trilobed (antennular sinus). Posterior margin narrow. Antennulae obliquely plicated. Antennae rudimentary, inconspicuous, inferior to antennal basal segment. Eyes and orbits elongate. Proepistome small, epistome reduced. Efferent channels together forming deep channel in endostome, latter covered with endopod of first maxillipeds. Afferent aperture between orbits and palm. Buccal cavern completely covered by third maxillipeds. Buccal cavern and mouth parts triangular, merus elongate, pointed apically, palp concealed under merus. Exognath widest proximally, lacking flagellum. Chelipeds subequal, robust, tightly pressed against ventral anterolateral portion of carapace, palm variously armed with spines, lobes or crests. All ambulatory legs paddle-like. Thoracic sternum flat, obovate, only suture 4/5 interrupted. First gonopod rather robust, setose, distally not tapering, apically rounded, sexual opening on lateral subapical palp.

Second gonopod as long as first or longer, flagellum nearly as long as basal portion, curved, curled or crotchet-shaped. Abdominal segments 3 – 5 fused in male. Minute portion of sternite 8 uncovered. Stridulating mechanism present. Type genus: *Matuta* Weber, 1795.

### Superfamily CALAPPOIDEA de Haan, 1833

Characters as for the family.

#### Family CALAPPIDAE de Haan, 1833

Subcircular subovate to transversely ovate, rounded anteriorly, widest posteriorly, strongly convex in both directions. Front narrow, bilobed, bidentate or tridentate, not very prominent. Posterolateral margin clypeiform in some genera, concealing entirely or partially ambulatory legs. Antennulae folding nearly longitudinally to obliquely. Antennae almost small, basal antennal segment distally lamellate to narrow, separating orbital from antennular fossae, peduncle and flagellum short.

Supraorbital margin trifissured (2 dorsal, 1 ventral). Exorbital angle indistinct. Epistome more or less reduced to absent, proepistome small. Buccal cavern triangular, elongate, approaching front, not anteriorly covered by third maxillipeds, leaving exposed anterior calcified prolongation of endopod of first maxillipeds. Merus of third maxilliped triangular, palp exposed. Endopod of first maxilliped lamellate, sclerotized, closing ventrally anterior portion of exhalent channel on endostome. Medium septum separating exhalent channels present. Chelipeds large, compressed, tightly coapted against anteriorly on ventral side of cephalothorax, subequal, heterodont. Ambulatory legs gressorial. Sternum narrow to moderately wide. Sternal sutures 4/5 – 5/6 interrupted. First gonopod conical, stout, distally gradually tapering to pointed tip. Second gonopod long, with long flagellum, often very long and curved, longer than first one, sometimes shorter than first gonopod. Abdomen narrow, segments 3 – 5 fused in male, 7 – segmented in female. Type genus: *Calappa* Weber, 1795.

### Superfamily TRAPEZIOIDEA Miers, 1886

Characters as for the family.

#### Family TRAPEZIIDAE Miers, 1886

Cephalothorax trapezoidal, subquadrilateral, polygonal to transversely oval, flattened to slightly convex, dorsally mostly smooth or finely granular. Front wide, almost straight, sometimes lobate or finely dentate. Orbits shallow, closed, placed on anterolateral angle. Eyes moderately large, not well protected by orbits. Supraorbital margin entire. Antennulae folding transversely. Basal antennal segment slender, oblique. Antennae usually excluded from orbits by meeting inner supraorbital and infraorbital teeth. Endostomial ridge complete. Dactylus of endopod of second maxilliped enlarged at apex, furnished with thick brushes of long setae. Merus of third maxilliped much shorter than ischium. Chelipeds long to very long far projecting beyond carapace, with pointed tips of fingers, cutting margins thin. Ambulatory legs with dactylo-propodal locking mechanism well developed. Dactyli of ambulatory legs setose, spinose, with corneous apices. Sternum moderately wide, margins subparallel. Sutures 1/2 indistinct, 2/3 entire, 3/4 indistinct, 4/5 and 5/6 interrupted near median line, 6/7 – 7/8 entire, directed forward. First gonopod moderately stout, almost straight to slightly sinuous, often in middle slightly constricted, distally covered with short setae or tubercles, second gonopod relatively short, longer than 1/4 of first one. Abdominal segments 3 – 5 usually fused in male, sutures sometimes distinct. Type genus: *Trapezia* Latreille, 1825.

#### Subfamily DOMECIINAE Ortmann, 1893

Xanthoid-shaped, dorsally feebly convex. Dorsal surface of carapace and pereopods hairy and tuberculate. Regions indistinct. Front wide, bilobed with granular or spinose margins. Anterolateral margins dentate. Orbits closed. Eyes well developed. Antennulae folded transversely. Basal antennal segment large, projecting lat-

erally, closing orbital hiatus, sometimes open, peduncle directed forward. Endopod of second maxilliped with propodus and dactylus fused into single large endite. Merus of third maxilliped extremely short, much wider than long. Chelipeds long, large, strongly unequal, spinose, fingers pointed. Ambulatory legs with dactylopropodal locking mechanism well developed, dactylus forming long, curved claw. Sternal sutures 1/2 – 3/4 indistinct, 4/5 – 5/6 interrupted, 6/7 – 7/8 entire. First gonopod strong, slightly tapering, twisted, second relatively long (half length of first). Abdomen 7-segmented in both sexes, sometimes segments 3 – 5 immovable in male, sutures distinct. Type genus: *Domecia* Eydoux & Souleyet, 1842.

#### Subfamily TETRALIINAE subfam. nov.

Trapezoid, lenticular, depressed. Dorsal surface naked, smooth. Front wide, straight to slightly convex, finely denticulate, median notch and antennal sinus indistinct. Basal antennal segment laterally produced, entering orbital hiatus. Chelipeds very dissimilar. Dactyli of ambulatory legs stocky, short, meri short, stout. First gonopod stout, gently curved, distally spinose. Abdominal segments 7-articulated in both sexes. Type genus: *Tetralia* Dana, 1851.

#### Subfamily TRAPEZIINAE Miers, 1886

Cephalothorax variable in shape: trapezoidal, subquadrangular, pentagonal almost depressed, dorsal surface smooth. Front much wider than posterior margin. Orbits shallow, eyes large, unprotected. Antennulae folding transversely. Basal antennal segment slender. Endognath of second maxilliped composed of 4 distinct segments. Pterygostomial ridge usually present. Chelipeds extremely long, mostly subequal, projecting far beyond carapace. First gonopod tubular, distally covered with hairs or tubercles, in middle of length slightly constricted. Second gonopod shorter than first. Abdominal segments 3 – 5 fused in male. Type genus: *Trapezia* Latreille, 1825.

#### Tribe Sphaenomeridini trib. nov.

Transversely ovate, strongly convex in both directions. Dorsal surface smooth. Fronto-orbital margin entire. Front bilobed, antennal sinus and exorbital angle lacking. Lateral margins convex with small epibranchial and intermediate teeth. Posterior margin narrow. Eyes inclined backwardly. Orbital hiatus shallow, hardly concealing eyes. Antennal peduncle filling large orbital hiatus. Ambulatory legs long and slender. First gonopod slender, slightly S-shaped, with very sparse spinules. Abdominal segments 3 – 5 fused in male, sutures between segments 3/4 – 4/5 distinct. Type genus: *Sphaenomerides* Rathbun, 1897.

#### Tribe Calocarcinini trib. nov.

Suboctagonal, wider than long, slightly convex. Lateral margins with two teeth forming summits of two angles separating anterolateral from lateral and posterolateral margins of subequal length. Posterior margin not considerably narrower than front. Orbits small, deep, hiding completely eye. Eyes of moderate size, orbital hiatus closed by fusion of inner infraorbital angle and frontal margin. Chelipeds



very long, unequal. First gonopod short, rather stout, gently sinused, gradually tapering, distally spinose, not constricted in the middle. Second gonopod relatively long, slender, flagellum of second gonopod moderately long, curved. Abdominal segments 3 – 5 fused in male, sutures distinct. Type genus: *Calocarcinus* Calman, 1909.

#### Tribe Trapeziini Miers, 1886

Lenticular. Frontal margin noticeably much wider than posterior one, sinuous, median notch, antennular and antennal sinuses almost feebly indicated. Frontal margin noticeably much wider than posterior one. Basal antennal segment cylindrical. Orbital hiatus closed by meeting of frontal and infraorbital margins, antennae excluded from orbits. Pterygostomial ridge present. Chelipeds disproportionately large, subequal to slightly asymmetric, anterior margin of manus dentate, carpal tooth small. Ambulatory legs long, slender, posterior margin of dactyls spinose. Dactyli armed with strong bristles and long setae. Abdominal segments 3 – 5 fused in male. Type genus: *Trapezia* Latreille, 1825.

#### Tribe Quadrellini trib. nov.

Hexagonal, slightly wider than long. Front wide, with 2 – 4 conspicuous, often triangular teeth-like lobes, antennal sinus distinct. Orbits large, shallow, not hiding most of the eye. Orbital hiatus closed, antennae excluded from orbit. Inner infra-orbital angle acute, visible in dorsal view. Epibranchial spines acute. Anterolateral margin with 1 – 2 acute spines. Posterior margin as wide as or slightly wider than frontal margin. Chelipeds slightly unequal and dissimilar. Ambulatory legs slender, dactyli serrated ventrally. Abdominal segments 3 – 5 fused in male. Type genus: *Quadrella* Dana, 1851.

#### **Trapeziidae (?) *incertae sedis***

#### Subfamily CORALLIOPINAE subfam. nov.

Xanthiform. Dorsal surface sparsely hairy. Front wide, distinctly bilobed, deflected. Anterolateral margin tridentate, exorbital and first hepatic lobes fused. Orbits large. Basal antennal segment far from front. Exorbital angle indistinct. Endostomial ridge present. Merus of third maxilliped short, auriculate. Dactylo-propodal locking mechanism not well developed. Sternal plastron relatively narrow, elongate. Sutures 4/5 – 5/6 interrupted. First gonopod nearly straight, subdistally with sparse straight setae, second gonopod short. Male abdomen narrow, segments 3 – 5 fused, third segment widest. Type genus: *Coralliope* Guinot, 1967.

### **Superfamily XANTHOIDEA McLeay, 1838**

Cephalothorax subhexagonal, transversely hexagonal, transversely oval, subelliptical to subcircular. Dorsal regions usually well defined, sometimes indistinct. Front moderately wide, usually bilobed. Anterolateral margins usually dentate or lobate to entire. Antennal flagellum short. Buccal cavern well delimited from epistome and completely covered with third maxillipeds. Endostomial ridge usually absent

(= *Hyperolissa* Alcock, 1898), if present confined to posterior part of endostome. Mandibular palp usually trisegmented, sometimes bisegmented. Chelipeds more or less heterochelous to homoiochelous. Ambulatory legs usually rounded in cross-section. Thoracic sternum relatively narrow, sternite 4 usually very wide. First gonopod long, relatively straight, slender, with simple apical part, subdistally or distally covered with tubercles and/or tuft of long setae. Second gonopod short, its apex short, rarely falciform. Abdominal segments 3 – 5 immovable in male, fused completely to almost completely, sutures rarely distinct at least laterally. Type genus: *Xantho* Leach, 1804.

### Family XANTHIDAE MacLeay, 1838

Cephalothorax almost subhexagonal to transversely oval, wider than long. Dorsal regions usually discernible. Front narrow to moderately wide usually with median notch, sometimes feebly square-cut. Anterolateral margin forming strongly convex arch, usually dentate or lobate. Posterolateral margins markedly diverging. Posterior margin usually narrow, sometimes wide. Antennular and antennal sinuses often discernible. Orbits not very deep. Exorbital angle and first anterolateral tooth usually distinctly separated by sinus or indentation. Basal antennal segment cylindrical, usually reaching front. Antennal flagellum short and slender, usually entering orbit. Anterior margin of endostome raised, sharply defined. Endostomial ridge almost absent, if present, located posteriorly. Merus of third maxilliped shorter than ischium. Sternal sutures 2/3 usually distinct, 3/4 – 5/6 interrupted, 6/7 – 7/8 entire. Male genital openings coxal. Penis not lying in sternal groove. First gonopod slender, sometimes slightly curved or sinuous, subdistally or distally covered with tubercles and/or tuft of long setae, tip relatively simple. Second gonopod very short, less than 1/4 of first one. Proximal abdominal segments covering entirely sternite 8. Type genus: *Xantho* Leach, 1804.

### Subfamily KRAUSSIINAE Ng, 1993

Cephalothorax almost subcircular, feebly convex in both directions, regions poorly defined. Front lamellar, projecting, 2 – 4-lobed, antennal sinus distinct. Anterolateral margin much longer than posterolateral, strongly arcuated, serrated, lined with granules or spines. Posterolateral margin diverging, straight to markedly concave. Supraorbital margins bifissured. Antennulae folding obliquely. Basal antennal segment closing orbital hiatus. Antennal peduncle long. Chelipeds strong. Legs short, stout, compressed, especially distal segments, dactyli of all legs strongly flattened, spade-like, sickle-shaped, curving upwards. Sternal suture 1/2 usually entire, sutures 2/3 – 7/8 entire (7/8 sometimes indistinct). Thoracic sternum and abdomen elongate, narrow, both projecting posteriorly, behind posterior carapace margin. First gonopod long, slender, with distal part with long setae. Second gonopod short, flagellum distinct. Abdominal segments 1 – 2 long with tufts of long, stiff setae. Type genus: *Kraussia* Dana, 1852.

## Subfamily XANTHINAE MacLeay, 1838

Cephalothorax subhexagonal to transversely oval, wider than long (typically xanthoid). Frontal margin with median notch and antennal sinuses more or less distinct. Anterolateral margin convex, confluent with exorbital angle, 4 – 5 – dentate or lobate, usually distinctly separated from posterolateral margin, latter diverging. Posterior margin rather narrow. Antennulae mostly transversely, rarely obliquely folded. Basal antennal segment broad, short, internal angle usually touching front, distal segments entering orbit. Exorbital lobe small to indistinct. Antennal flagellum short and slender. Sternite 4 very large. Sternal suture 2/3 usually distinct, 4/5 – 5/6 mostly interrupted. First gonopods various in shape, second gonopod short. Type genus: *Xantho* Leach, 1804.

## Tribe Paraxanthini trib. nov.

Transversely elliptical. Front lamellar, rather prominent, four-lobate. Median notch continued by long dorsal fissure. Dorsal surface nearly flat, regions well defined. Antennular and antennal sinuses distinct. Basal antennal segment touching front. Epistome small, deeply sunken. Buccal cavern much longer than wide, upturned anteriorly. Merus of third maxilliped oblique anterolaterally, prolonged noticeably beyond insertion of palp. Sternal plastron narrow in particular posteriorly, wider anteriorly. Sutures 3/4 interrupted medially, 4/5 – 7/8 entire. First gonopod distally curved, with some stronger hooked spinules. Abdomen short and narrow in both sexes. Type genus: *Paraxanthus* H. Milne Edwards & Lucas, 1834.

## Tribe Actaeini Alcock, 1898

Xanthoid in shape, wider than long. Dorsal surface of mulberry appearance, sometimes granular, tuberculate or spinose, noticeably areolated to nearly smooth, rarely with secondary dorsal surface formed by coalescent mushroom-like tubercles. Front bilobed, hardly to moderately projecting or spinose. Anterolateral margins 3 – 4 lobed. Posterolateral margin usually concave. Posterior margin narrow. Antennulae plicated obliquely to transversely. Basal antennal segment touching front, closing orbital hiatus. Antennal peduncle included within orbit. Chelipeds subequal, granulate or spinose. Thoracic sternum and abdomen relatively narrow. Sternite 4 usually with longitudinal furrow. Type genus: *Actaea* de Haan, 1833.

## Tribe Liomerini Sakai, 1976

Transversely oval, wide, convex to flattened. Dorsal surface convex, smooth, regions more or less defined. Front wide, deflexed, nearly straight to gently bilobed. Antennular sinus usually distinct. Anterolateral margin usually entire to gently divided into wide rounded lobes. Basal antennal segment directed obliquely, touching front, peduncle entering orbital hiatus, flagellum small. Orbital margins entire. Pereiopods coapted to carapace margins, tips of cheliped fingers elongate, occlusive ridges dentate, tips hollowed. Ambulatory legs subcylindrical in cross-section to moderately compressed, thin. Type genus: *Liomera* Dana, 1851.

## Tribe Zosimini Alcock, 1898

Transversely subelliptical, not very wide, convex, regions very distinct. Front feebly bilobed, antennal sinuses distinct. Anterolateral margin usually strongly crested. Posterolateral margin very diverging, sometimes slightly concave. Orbital margins entire. Antennae oblique, basal segment stout, flagella faint. Inner anterior lobes of basal antennal segment completely embracing subfrontal ventral prolongation, closing orbital hiatus. Chelipeds subequal, palm dorsally carinate, entire, rarely dentate, fingers slightly hollowed at tip. Ambulatory legs carinate dorsally, especially carpi and propodi. Type genus: *Zosimus* Leach, 1818.

## Tribe Euxanthini Alcock, 1898

Transversely ovate, not very wide. Dorsal surface convex, very distinctly areolated in high relief. Front slightly projecting, bilobed. Median notch and antennal sinuses distinct. Anterolateral margin often poorly indicated behind exorbital angle, distinctly separated from posterolateral one, former prolonged beneath orbit to anterolateral angle of buccal cavern (not to exorbital angle). Subhepatic cavities sometimes present. Posterolateral margins concave. Antennulae folded obliquely. Basal antennal segment slightly diverging. Lateral lobe of basal antennal segment filling orbital hiatus. Pereiopods usually tightly coapted against concavity of posterolateral margin. Chelipeds subequal. Sternum generally grooved. Sometimes very small portion of segment 8 uncovered. Type genus: *Euxanthus* Dana, 1851.

## Tribe Liagorini trib. nov.

*Carpilius*-shaped, thick, compact looking. Dorsal surface smooth, only H-shaped depression distinct, markedly convex in both directions. Front feebly bilobed, antennular sinus wide, shallow. Lateral margins nearly entire, posterior margin rather wide, gently concave. Orbits shallow, feebly rimmed. Basal antennal segment touching front, peduncle entering orbit. Chelipeds homiochelous. Ambulatory legs long, slender, unarmed, subcylindrical, dactyli sharp with short setae. First gonopod slender, elongate, subdistally with long, plumose setae. Small, but distinct, portion of sternite 8 laterally to abdominal segments 2 – 3 uncovered. Type genus: *Liagore* de Haan, 1835.

## Tribe Orphnoxanthini trib. nov.

Subquadrilateral, convex longitudinally, slightly concave transversely. Dorsal surface with short fur, regions well defined, branchial region slightly inflated. Front laminar, square-cut, bilobed, gently projecting. Supraorbital margin entire. Anterolateral margin thin, sharp, 4 – dentate. Branchial region slightly inflated throughout dorsal surface seeming concave. Pterygostomial region puffed out. Posterior margin wide. Endostomial ridge posteriorly distinct. Type genus: *Orphnoxanthus* Alcock, 1898.

## Tribe Xanthini MacLeay, 1838

Typically xanthoid-shaped more or less convex longitudinally, flat transversely. Dorsal surface usually well sculptured, regions distinct. Front more or less projecting, faintly square-cut. Median notch and antennal sinuses distinct. Anterolateral

margin cut into 4 – 10 sharp teeth, rarely obliterated, not carinate. Basal antennal segment simple, its internal angle touching front, peduncle entering orbital hiatus. Fingers of chelipeds with acute tips or cultrate, ambulatory legs rounded in cross section. Sternite 4 very large, telson covering only its posterior half. Type genus: *Xantho* Leach, 1804.

Tribe Etisini Ortmann, 1893

Xanthoid-shaped, transversely oval. Dorsal surface finely granular to smooth, regions of carapace variously distinct. Front straight, sublaminar, more or less projecting, median notch, antennular and antennal sinuses usually distinct. Anterolateral margin dentate, teeth sharp. Antennulae folding obliquely to transversely. Basal antennal segment in contact with front, anteroexternal lobe incompletely to completely closing orbital hiatus, when closed excluding peduncle from orbital hiatus. Merus of third maxilliped much shorter than ischium, auriculate. Dactyli of second maxillipeds with acute apex bearing some setae. Chelipeds subequal to slightly dissimilar in male. Fingers of chelipeds rounded, pronouncedly spooned. Locking mechanism of dactylo-propodal articulation usually very distinct, dactyli sometimes with subterminal spine. Type genus: *Etisus* H. Milne Edwards, 1834.

Subfamily LINNAEOXANTHINAE subfam. nov.

Subhexagonal, wider than long, slightly convex. Dorsal surface granular, regions partly indicated. Front deflexed. Median notch, antennular and antennal sinuses present. Eyes large, reniform. Supraorbital margin with distinct fissure. Exorbital angle distinct, dentiform. Basal antennal segment short, peduncle touching front, flagellum long. Anterolateral margin tridentate, much shorter than posterolateral one, latter slightly concave. Chelipeds long, unequal, merus, carpus and palm spinose, claw peculiar, finger of chelipeds thick, propod with large tooth near tip, dactyl with three prehensile teeth. Buccal cavity widened anteriorly, not completely covered with third maxillipeds. Legs of moderate length, merus, carpus and propodus spined anteriorly, dactyli spinose anteriorly and posteriorly. First gonopod stout, compressed, gently curved outward. Second gonopod much shorter than first one. Abdomen in male with segments 3 – 5 fused. Type genus: *Linnaeoxantho* gen. nov. (Etymology: according to Swedish scientist Carolus Linnaeus founder of the modern systematics and author of names *Cancer* and *Brachyuri* and *Xantho*, type genus of the family). Type species: *Pilumnoplax acanthomerus* Rathbun, 1911; gender: feminine.

Subfamily ANTROCARCININAE Ng & Chia, 1994

*Harrovia*-shaped i.e. distinctly hexagonal. Front wide, bilobed, lobes truncated. Anterolateral margin cut into three lobiform teeth. Cardiac region swollen. Cardio-intestinal groove very deep and joining postero-sub-branchial channel. Posterolateral margins interrupted posteriorly. Antennulae oblique. Basal antennal segment large, slightly oblique, usually not touching front, peduncle long, slender, entering orbits. Merus of third maxillipeds auriculate. Pereiopods cristate dorsally. Chelipeds with inner carpal spine. Only tips and cutting edges of chelae pigmented.

Endostomial ridge feebly developed. Legs markedly cristate. First gonopod slightly stout to slender, curved distally, distally lined with short, sharp spinules. Second gonopod short. Abdominal segments 3 – 5 immovable in male, sutures distinct. Type genus: *Antrocarcinus* Ng & Chia, 1994.

Subfamily EUCRATODINAE subfam. nov.

Cephalothorax suboval, thick, convex. Dorsal regions scarcely distinct. Frontal and posterior margins wide. Frontal margin wide, slightly bilobed, lobes entire, slightly convex, margins thin. Anterolateral margin arcuate, posterolateral margins diverging. Antennulae transversely folding. Anterolateral margin long, arcuate, feebly lobate, 3 posterior lobes distinct. Supraorbital margin entire. Exorbital angle indistinct. Basal antennal segment short, just touching front, peduncle entering orbital hiatus. No endostomial ridge. Ambulatory legs slender, smooth. Sternum very wide. Male sexual opening coxo-sternal, penial tube very short, penial groove over suture 7/8. First gonopod stout, nearly straight, medially slightly constricted, irregularly curved, distally twisted, gradually tapering to apex, with sparse subapical spinules, apical opening relatively large. Second gonopod short. Abdominal segments 3 – 5 fused in male, segments 1 and 2 short, 1 and 3 nearly equally wide, first touching, third nearly touching coxae of last pairs of legs, second segment narrow, leaving small portion of sternite 8 uncovered. Type genus: *Eucratodes* A. Milne Edwards, 1880.

Subfamily MEGAMETOPINAE subfam. nov.

Subpentagonal, nearly transversely elliptical, dorsally convex, regions distinct. Anterolateral margin convex, cristate, 4 – lobed. Dorsal surface smooth. Front wide, lamellate, horizontal to deflexed, convex, projecting, obtusely four-lobed. Frontal, supraorbital and anterolateral margins confluent. Posterolateral margin concave. Posterior margin very narrow. Orbits small, supraorbital margin bifissured. Basal antennal segments large, diverging, peduncles and flagella short. Pereiopods smooth, slightly compressed. Chelipeds short, coapted to carapace. Legs subequal in length, cristate. Sternal sutures 6/7 – 7/8 indistinct (apparently entire). First gonopod elongate, not tapering. Second gonopod very short. Abdominal segments 3 – 5 fused in male. Proximal abdominal segments covering completely sternite 8. Type genus: *Megametope* Filhol, 1886.

Subfamily CYMOINAE Alcock, 1898.

Subcircular, elongate pentagonal to subovate, slightly wider than long, slightly convex to flat. Dorsal surface of carapace and chelipeds covered by obtuse granules, regions indistinct. Front moderately wide, median notch U – shaped. Eyes and orbits large. Antennular and antennal sinuses present. Antennulae plicated obliquely. Basal antennal segment closing orbital hiatus. Anterolateral and posterolateral margins feebly dentate, arcuated, not clearly separated. Posterior carapace margin rather narrow. Merus of third maxilliped slightly auriculate. Chelipeds extremely heterochelous in both sexes, larger cheliped wide, rounded and hollowed

at extremities, smaller finger with pointed apex. Locking mechanism of ambulatory legs markedly strong. Sternite 4 remarkably large. Three proximal abdominal segments and last pair of legs dorsally exposed. Type genus: *Cymo* de Haan, 1833.

#### Subfamily POLYDECTINAE Dana, 1851

Cephalothorax subquadrate to rounded. Dorsal surface tuberculate to smooth, regions feebly indicated, sometimes setose. Front projecting, square-cut, truncate to bilobed. Antennal sinus distinct. Anterolateral margin bilobed to entire. Posterior margin relatively wide. Antennulae slightly obliquely to transversely folded. Basal antennal segment cylindrical, touching front, flagellum long. Maxillipeds slightly gaping. Endostomial ridge sometimes present. Chelipeds very slender, shorter and more slender than legs, similar and equal, cutting edges with sharp small teeth bearing sea anemone. Two proximal abdominal segments exposed dorsally. Thoracic sternum elongate, narrow. Telson covering only small portion of sternite 4. Type genus: *Polydectus* H. Milne Edwards, 1837.

#### Family ZALASIIDAE Serène, 1968

Xanthoid-shaped to ovoid, dorsally convex in both directions. Dorsal surface more or less pilose, well sculptured with common and additional furrows, regions well demarcated. Mesogastric triangle and branchiocardiac furrow usually distinct. Front narrow, bilobed. Anterolateral margin well arched, 4-lobed or dentate, posterolateral margin usually concave. Both margins distinctly separated. Eyestalks directed laterally backward. Antennulae more or less oblique. Basal antennal segment large, closing orbital hiatus, peduncle small, flagellum minute. Proepistome basally wide, anteriorly narrow, elongate (interantennular septum). Endostomial ridge present anteriorly. Buccal cavity elongated, slightly narrowing anteriorly. Third maxillipeds elongated to pediform. Pereiopods coapted to carapace. Chelipeds nearly subequal, pilose. Fingers of chelipeds thin, with acute occlusive margins, crossing apically. Thoracic sternum narrow, shield (composed by fused segments 1 – 2) large, triangular, far projecting between bases of maxillipeds. Sternal sutures 6/7 – 7/8 entire. Sterno-abdominal cavity deep. First gonopod stout, elongated, tapering distally, more or less curved distally, sabre-like, lying in special groove, with subdistal long setae and spinules, apices usually protruding beyond telson. Second gonopod short. Abdomen narrow, segments 3 – 5 fused in male. Type genus: *Zalasius* Rathbun, 1897.

#### Tribe Banareini trib. nov.

*Actaea*-shaped, convex. Numerous dorsal furrows distinct. Antennulae folding very obliquely. Buccal cavity subquadrangular, wide. Meri of third maxillipeds separated medially by space occupied by palps, meri wider than long, anterolateral angle rectangular, palps exposed, flagellum sometimes absent. Dactyli of walking legs apically with long claws. Type genus: *Banareia* A. Milne Edwards, 1869.

### Tribe Zalasiini Serène, 1968

Cephalothorax subcircular to slightly transverse, nearly as wide as long. Dorsal surface well sculptured, densely covered with thick coat of woolly setae. Front projecting. Antennulae folding slightly obliquely. Buccal cavity longitudinally oval, narrowed. Third maxillipeds subpediform, gaping, especially posteriorly, palp distally concealed under merus, exognath with flagellum. Type genus: *Zalasius* Rathbun, 1897 (= *Trichia* de Haan, 1839; nom. praeocc.)

### +Family ZANTHOPSIDAE Vía, 1959

Transversely oval, convex. Fronto-orbital width about half maximum carapace width. Dorsal surface ornamented with large nodes, sometimes arranged on raised ridges, sometimes punctate. Regions moderately to poorly defined. Branchiocardiac groove distinct, short, other grooves very shallow. Front moderately wide, distinctly four-lobed (including antennal sinuses). Antennulae folding obliquely. Orbits circular to rectangular, margins entire, rimmed, directed forward. Anterolateral margin convex with 3 – 5 blunt lobes or numerous small spines. Posterolateral margin sinuous or weakly convex. Posterior margin nearly straight. Chelipeds massive, subequal to weakly heterochelous, longer than ambulatory legs, merus and basis not fused completely. Sternum narrow, widest anteriorly at position of sternum 4, narrowing posteriorly. Abdominal segments at least 4 – 5 (probably 3 – 5) fused. Type genus: *Zantopsis* McCoy, 1849 (= *Xanthopsis* Bell, 1858).

### +Family PALAEOXANTHOPSIDAE. Schweitzer, 2003

Cephalothorax ovate-hexagonal, wider than long, widest between last anterolateral teeth, thick. Dorsal regions with well-developed, regions defined by grooves, often with large, spherical swellings. Cervical groove V-shaped separating gastric region from hepatic and branchial regions. Front quadrilobed, sometimes with median lobes, projecting well beyond orbits. Median notch V-shaped. Orbits rectangular. Supraorbital margin bifissured to nearly entire, fissures faint. Exorbital angle projecting as triangular spine. Anterolateral margin long, straight to weakly convex, with 3 – 4 triangular teeth separated by notches or fissures, last tooth very long, projecting laterally or posterolaterally. Posterolateral margin convex. Posterior margin narrow, straight to concave. Type genus: *Palaeoxanthopsis* Beurlen, 1958.

### Family PANOPEIDAE Ortmann, 1893

Cephalothorax subhexagonal, subquadrangular to subcircular, wider than long. Dorsal regions more or less defined. Front moderately wide, lamellate, medially notched (bilobed), not projecting. Orbits and eyes often elongate, orbits rimmed. Supraorbital margins usually bifissured. Anterolateral margin shorter than posterolateral one, dentate or lobed, exorbital angle usually fused with first hepatic tooth, next 2 – 3 teeth or lobes larger, last tooth more or less reduced. Antennal sinus indicated to distinct. Basal antennal segment not reaching or barely touching front, peduncle bent laterally. Endostomial ridge usually absent, if present confined to



posterior part of endostome. Inner carpal spine of chelipeds small to indistinct. Thoracic sternum relatively narrow to wide, usually wide behind sternum 4. Male sexual opening coxal to coxo-sternal. First gonopod moderately stout, straight to sometimes slightly curved, apex peculiar: tip with numerous complex lobes or folds, (having: spur, spine, hood, all of them variously developed). Second gonopod short. Lateral margins of abdomen concave. Male abdomen narrow, segments 3 – 5 fused, immovable, sutures sometimes discernible, second abdominal segment sometimes leaving laterally minute part of sternite 8 uncovered. Abdominal segments 3 – 5 in male fused, immovable, sutures sometimes discernible. Female abdomen freely articulated. Type genus: *Panopeus* H. Milne Edwards, 1834.

**a) Panopeidae** – »xanthid« grade.

Cephalothorax hexagonal (xanthoid-shaped), wider than long. Eyes and orbits short. Posterolateral margins diverging. Posterior margin usually narrow. Thoracic sternum relatively narrow, not very enlarged behind sternite 4. Male sexual opening coxal. Penial groove never closed. First gonopod typically panopeid. Proximal abdominal segments usually completely covering space between coxae of last pair of legs, sometimes small portion of sternite 8 uncovered.

Subfamily PANOPEINAE Ortmann, 1893

Cephalothorax xanthoid-shaped. Front moderately wide. Bilobed, antennal sinus usually distinct. Anterolateral and posterolateral margins well separated. Posterolateral margins diverging. Posterior margin moderately wide. Antennulae folded obliquely to transversely. Eyestalks moderately long. Thoracic sternum relatively narrow. Abdominal segments 3 – 5 fused, usually completely covering whole space between last pair of legs, sometimes small portion of sternite 8 remained uncovered. Male sexual opening coxal. Penial groove shallow, never making penial tube. Gonopods typically panopeid. Type genus: *Panopeus* H. Milne Edwards, 1834.

Tribe Panopeini Ortmann, 1893

Xanthoid-shaped. Dorsal surface areolate to smooth. Front bilobed, antennal sinus distinct. Orbits rimmed. Supraorbital margins usually bifissured. Posterior margin of carapace moderately wide. Anterolateral margin with 3 – 4 teeth or lobes. Exhalent opening usually large. First gonopods distinctly trilobed. Male sexual opening coxal. Third segment of male abdomen touching to not touching coxae, small portion of sternite 8 uncovered to completely covered. Type genus: *Panopeus* H. Milne Edwards, 1834.

Tribe Gonopanopeini trib. nov.

Xanthoid-shaped. Front very wide, bilobed, lobes gently arched. Orbits rather large, situated laterally. Intercalated apophyse absent. Anterolateral margin short. Eyes situated laterally. Endostomial ridge strong, incomplete. First gonopod, short, stout, distally widened, twisted, with long setae. Thoracic sternum relatively large. Abdomen in male short, wide, telson triangular. Type genus: *Gonopanope* Guinot, 1967.

## Tribe Micropanopeini trib. nov.

Xanthoid-shaped. Dorsal surface distinctly areolated. Front wide, bilobed, abruptly deflexed, antennal sinus present. Orbits and eyes very large, situated laterally. Anterolateral margin with 2 distinct teeth or lobes, posterior teeth absent. Posterior margin moderately wide. Chelipeds large. Small portion of sternite laterally to segment 2 uncovered by abdomen. First gonopod peculiar, straight, tip blunt, stout, distally strongly recurved. Type genus: *Micropanope* Stimpson, 1871 (Type species: *M. sculptipes* Stimpson, 1871).

## Tribe Lophoxanthini trib. nov.

Cephalothorax suboctogonal. Front narrow, thickened, and deflexed. Orbits small. Hepatic margin straight, unarmed, thick. Chelipeds heavy, asymmetric. Ambulatory legs compressed, laminiform, crested, eroded. First gonopod of panopeid type, peculiar: shaft distally twisted, apically with large hatchet-shaped expansion. Type genus: *Lophoxanthus* A. Milne Edwards, 1879.

**b) Panopeidae** – »goneplacid« grade.

Cephalothorax usually subquadrilateral. Front square-cut, of moderate width to rather narrow, bilobed. Eyestalks and orbits rather elongate. Basal antennal segment touching front, peduncle deflexed (bent). Buccal cavern not covered completely with third maxilliped. Pterygostomial ridge ahead articulation of chelipeds almost noticeable. Posterior margin wide. Thoracic sternum wide, especially behind sternite 4. Male genital opening either coxal, with genital ducts extending onto sternum in penial groove or coxo-sternal with ducts passing through involute sternal groove (penial tube) over suture 7/8. First gonopod derivable from panopeid type, sometimes gently curved. Third abdominal segment of male usually not reaching coxae of last pair of legs, lateral parts of sternite 8 variably covered with first and second abdominal segments.

## Subfamily EUCRATOPSINAE Stimpson 1871

Subquadrilateral to rounded, relatively wide, thick. Dorsal surface flattened. Regions more or less distinct, especially H-shaped depression and mesogastric triangle. Front rather narrow, bilobed. Antennal sinus indistinct. Eyestalks moderately to very long. Antennae entering orbit. Intercalated apophyse (occlusive tooth) between antero-internal margin of pterygostome and basal antennal segment present. Anterolateral margin with 2 – 4 teeth or lobes, rarely entire. Posterior margin wide. Buccal cavern widened anteriorly, not covered completely by third maxillipeds. Merus as wide as ischium, slightly auriculate. Ambulatory legs long. Pterygostomial ridge present. Thoracic sternum wide. Uncovered portion of sternum 8 large. Male sexual opening coxo-sternal, penial groove over suture 7/8 mostly closed, forming penial tube. First gonopod of panopeid type. Second gonopod short, curved. First and third segments subequally wide, not touching coxae. Type genus: *Eucratopsis* Smith, 1869.

## Tribe Malacoplacini trib. nov.

Cephalothorax quadrilateral. Anterolateral margin very short, arched. Posterolateral margins subparallel. Front narrow, nearly entire, slightly sinuous, fringed with long setae. Eyestalks and orbits very elongate. Antennulae with basal segment filling antennular fossae, distal segments slender, long, not folding into fossae. Basal antennal segment short, wide. Exorbital angle and anterolateral teeth rounded. Buccal cavern very widened anteriorly, third maxillipeds narrow, endognath looking pediform, diverging. Merus laterally widely rounded. Palp long, exognath well developed. Sternum narrow beyond articulation of chelipeds. Abdomen in male far from coxae of last pair of legs. Penis lying in incompletely closed penial groove. Type genus: *Malacoplax* Guinot, 1969.

## Tribe Eucratopsini Stimpson, 1871

Xanthoid-shaped. Front bilobed, not fringed with setae. Exorbital angle and anterolateral teeth acute. Antennulae folding almost transversely in their fossae. Eyestalks long, cornea well developed. Anterolateral margin dentate. Buccal cavern quadrangular to widened anteriorly, not covered by third maxillipeds small to distinct parts uncovered. Sternal plastron wide ahead articulation of chelipeds. Penial groove incompletely to completely closed. Type genus: *Eucratopsis* Smith, 1869.

## Subfamily CYCLOPLACINAE subfam. nov.

Subcircular. Dorsal surface smooth. Front entire, slightly sinused, confluent with supraorbital margin and lateral margins. Lateral margins entire, unarmed, arched. Antennulae oblique. Buccal cavern anteriorly widened. Merus of third maxilliped auriculate, palp long. Chelae very large, distally compressed, fingers very long. Penial groove open. First gonopod stocky, slightly curved, terminal portion peculiar but of panopeid type. Abdominal segments not touching coxae. Distinct portion of sternite 8 uncovered. Type genus: *Cyclopax* Guinot, 1969.

## Family PSEUDORHOMBILIDAE Alcock, 1900

Xanthoid – shaped, wider than long. Front moderately wide, square-cut, bilobed, lobes usually truncate, deflexed, antennal sinuses present. Anterolateral margin with 4 – 2 teeth. Posterior anterolateral tooth longest, acute. Anterolateral margins feebly diverging. Posterior margin relatively wide. Eyestalk short. Orbits elongate, oval, supraorbital margin bifissured. Intercalated apophyse (occlusive tooth) present. Basal antennal segment cylindrical, short, approaching to front. Pterygostomial ridge (cristate margin between infraorbital margin and coxae of chelipeds) usually present. Buccal cavern widened anteriorly. Proepistome and epistome distinct. Chelipeds heavy, long, with long more or less curved fingers. Sternum wide. Sternal sutures 6/7 – 7/8 entire. Variable portion of sternite 8 laterally to abdominal segments 1 – 2 uncovered. Male sexual opening coxal to coxo-sternal. Penis lying in open penial groove. First gonopod very variable, second gonopod short moderately or strongly sigmoid. Abdominal segments 3 – 5 fused in male, suture usually discernible. Type genus: *Pseudorhombila* A. Milne Edwards, 1837.

## Subfamily PSEUDORHOMBILIINAE Alcock, 1900

Carapace much wider than long, convex longitudinally. Regions moderately to weakly defined. Front straight, truncate, bilobed, square-cut. Supraorbital margin bifissured. Basal antennal segment short, peduncle standing in orbital hiatus. Intercalated apophyse present. Exorbital angle small, coalesced with first hepatic tooth. Anterolateral margin arched, dentate. Third maxillipeds gaping, not touching coxae of last pair of legs. Male sexual opening coxal to coxo-sternal. First gonopod with complex apex. Abdominal segments 3 – 5 and sometimes 6 fused, sutures usually distinct. Second abdominal segment in male short, third segment widest usually touching coxae of last pair of legs. Type genus: *Pseudorhombila* A. Milne Edwards, 1837.

## Tribe Thalassoplacini trib. nov.

Nearly subquadrilateral. Front wide, obscurely bilobed, truncate. Anterolateral margin short, tridentate. Front slightly bilobed. Antennulae slightly obliquely folded. Basal antennal segment cylindrical, just touching front. Eyes rather large. Intercalated apophyse minute. Posterior margin very wide. Posterolateral margins slightly diverging. Male sexual opening coxal. First gonopod rather stout, not tapering distally, apex simple, subapically twisted, with terminal lobe. Third abdominal segment reaching coxae of last pair of legs. Uncovered portion of sternite 8 small. Type genus: *Thalassoplax* Guinot, 1969.

## Tribe Euphrosynoplacini trib. nov.

Xanthoid-shaped. Carapace regions anteriorly distinct. Front narrow, bilobed, slightly convex. Antennulae folding transversely. Eyes small. Merus of third maxilliped strongly auriculate. First gonopod rather stout, slightly curved, with peculiar apical lateral lobe, opening large. First abdominal segment in male narrower than third one. Third abdominal segment widest, reaching coxae of last pair of legs, minute portion of sternite 8 laterally to segment 2 uncovered. First gonopod rather stout, slightly curved, its extremity with lateral flange, series of spines along shaft, opening large. Type genus: *Euphrosynoplax* Guinot, 1969.

## Tribe Robertsellini trib. nov.

Subsquarish. Dorsal surface convex, smooth, regions weakly defined. Front moderately wide, bilobed, deflexed. Orbits wide. Basal antennal segment touching front. Merus of third maxilliped auriculate. First gonopod with tongue-like apex. First abdominal segment nearly as wide as third, both touching coxa, small portion of sternite 8 uncovered. Type genus: *Robertsella* Guinot, 1969.

## Tribe Chacellini trib. nov.

Subhexagonal, transverse. Regions feebly defined. Front narrow, bilobed, antennal sinus distinct. Anterolateral margins relatively long, arcuate. Posterolateral margins diverging. Eyes small, supraorbital margin bifissured. Basal antennal segments slightly diverging, touching front. Third abdominal segment widest, reaching coxae of last pair of legs. Male sexual opening coxal. Minute portion of sternite 8 uncovered. First gonopod long slender, filiform, at least distally with only few spinules along shaft. Type genus: *Chacellus* Guinot, 1969.

## Tribe Bathyrhombilini trib. nov.

Subhexagonal. Regions of carapace rather distinct. Pterygostomial ridge very distinct. Third abdominal segment widest, second just touching coxae of last pair of legs. First gonopod long slender, twisted, with small spines along shaft, subterminally with two longitudinal series of many long spines, curved distally with hook-shaped short process. Type genus: *Bathyrhombila* Hendrickx, 1998.

## Tribe Pseudorhombilini Alcock, 1900

Xanthoid-shaped, thick. Dorsal regions partly distinct. Front rather truncated, square-cut, bilobed. Posterolateral margins slightly diverging. Posterior margin wide. Basal antennal segment short, touching front, peduncle standing in orbital hiatus. Antennal sinus minute. Intercalated apophyse present. Buccal cavern widened anteriorly. Endostomial ridge incomplete. Merus of third maxilliped auriculate. Carpal spine of chelipeds small. Male sexual opening coxal to mostly coxo-sternal. Sternum wide. Penial tube short. First gonopod stout, distally spinose, twisted with collar-shaped apical portion. First abdominal segment widest in both sexes, third segment in male not reaching coxae of last pair of legs. Type genus: *Pseudorhombila* A. Milne Edwards, 1837.

## Tribe Perunorhombilini trib. nov.

Subquadrate. Front deflexed. Anterolateral margin with three pointed teeth. Male sexual opening coxal. First gonopod peculiar, with subdistal long setae. Second gonopod short with falciform, short flagellum. Abdominal segments 1 – 2 short, first touching coxae, second narrow, leaving laterally small portion of sternite 8 uncovered, third segment widest, subequal in width, touching coxae. Type genus: *Perunorhombila* gen. nov. (Etymology: Perun = Supreme Old Slavic god). Type species: *Pilumnoplax nitida* Chace, 1940. Gender: feminine.

## Subfamily TRAPEZIOPACINAE subfam. nov.

Cephalothorax trapezoidal, transverse. Fronto-orbital and posterior margins very wide, lateral margins diverging. Antennal sinus lacking. Eyes very long. Orbits very wide, no supraorbital fissure, exorbital angle very distinct, pointed. Buccal cavern widened anteriorly. Merus of third maxilliped auriculate. Male opening coxo-sternal, penial tube short. Abdomen triangular, segments 3 – 5 fused. Moderate portion of sternite 8 laterally to second segment uncovered. First gonopod simple, feebly curved, apex simple, with short subapical spinnules. Second short. First abdominal segment wider than third one, touching coxae of last pair of legs. Type genus: *Trapezioplax* Guinot, 1969.

## Subfamily TETRAXANTHINAE subfam. nov.

Subhexagonal, convex longitudinally. Dorsal surface smooth, regions indistinct. Front lamellate, square-cut, truncate, nearly entire (median notch minute). Two lobes on anterolateral margin present. Orbits entire, exorbital angle indistinct. Basal antennal segment touching front, peduncle entering orbital hiatus. Intercalated apophyse absent. Endostomial ridge present. Merus of third maxilliped slightly auriculate.

Chelipeds elongate, unequal, fingers long compressed. Legs long, slender. Sternum very wide. Sternal sutures 1/2 – 2/3 indicated, 6/7 – 7/8 entire. Very small portion of sternite 8 laterally between segments 2 – 3 uncovered. First gonopod elongate, curved, triangular in cross section, with three longitudinal rows of spinules, apex bifid, inner branch thick, lateral lamellate distally, flexed outward. Second gonopod short, apical portion sickle-shaped. Abdominal segments 3 – 5 fused in male Type genus: *Tetraxanthus* Rathbun, 1898.

#### Subfamily CHASMOPHORINAE subfam. nov.

Subhexagonal, very wide, subcylindrical, very convex longitudinally. Dorsal regions well defined. Orbits and eyes elongate. Antennal sinus small. Eyes elongate, filling orbits. Intercalated apophyse present. Anterolateral margins short, 3 – dentate. Exorbital angle distinct. Basal antennal segment cylindrical approaching front, peduncle entering orbital hiatus. Buccal cavity widened anteriorly. Merus of third maxilliped wider than long, auriculate, wide. Sternum and abdomen of male wide. Abdominal segments not reaching coxae of last pair of legs, segments 4 – 5 fused. Uncovered portion of sternite 8 between segments 1 – 2 large. Male sexual opening coxo-sternal, penial tube long. First gonopod straight, not tapering distally, apically bilobed with perpendicular lateral projection, second short. Type genus: *Chasmophora* Rathbun, 1914.

#### Family SPEOCARCINIDAE fam. nov.

Subquadrate, rather thick, longitudinally convex, elliptical in sagittal cross section, widest at last anterolateral teeth. Dorsal regions partly defined. Front narrow, bilobed, nearly straight. Anterolateral margins arched, tridentate, teeth small. Posterolateral margins subparallel. Posterior margin wide, straight. Pterygostomial ridge present. Eyestalks stout, long, almost filling orbits, orbits elongate. Exorbital tooth indistinct. Antennulae transverse, long. Basal antennal segment short, reaching front, peduncle and flagellum in orbits below eyestalks. Intercalated apophyse present. Pterygostomial ridge distinct. Epistome with median prominence and lateral sinuses. Buccal cavity not completely covered with third maxillipeds, gap wide. Male genital opening coxo-sternal. Sternum very wide, posteriorly upturned, visible dorsally. Sternal sutures 6/7 – 7/8 entire. Penial tube long, completely closed. First gonopod more or less S-shaped, anteriorly faintly slender, apically recurved, spatulate, with wide aperture, second gonopod short. Abdominal segments 3 – 5 fused in male, first segment wide, second narrow, third widest, far from coxae, laterally angular, not covering great portion of sternite 8. Segments in female freely articulated, first segment widest. Type genus: *Speocarcinus* Stimpson, 1859.

### Superfamily PILUMNOIDEA Samouelle, 1819

Characters as for the family

### Family PILUMNIDAE Samouelle, 1819

Cephalothorax hexagonal (xanthoid-shaped), transversely rectangular to transversely ovate, moderately wide. Dorsal surface convex. Front feebly deflexed. Frontal margin usually bilobed or multidentate to entire. Anterolateral margin with 4 – 1 teeth, spines or lobes. Posterior margin ranging from narrow to wide. Antennulae plicated transversely, sometimes slightly obliquely. Basal antennal segment not touching or just touching front. Endostomial ridge entire, rarely absent. Third maxillipeds subquadrate. Chelipeds heterochelous, fingers when closed mostly without distinct gap or dense setae along cutting margins. Thoracic sternum elongate, narrow. First gonopod slender, elongate, S-shaped, (sinuous, distally usually hooked, sometimes straight), simple (without prominent folds or strong spines), second gonopod very short, sigmoid, flagellum very short, usually straight, basally forming distinct cup-like structure. Abdomen elongate, narrow, freely articulated in both sexes, minute portion of sternite 8 laterally to abdominal segment 2 usually more or less uncovered in male. Abdomen covering considerable portion of sternite 4. Type genus: *Pilumnus* Leach, 1815.

#### a. *Pilumnidae* – »xanthid« grade

Cephalothorax almost subhexagonal. Anterolateral margin not longer than, usually shorter, than posterolateral. Both margins well separated. Posterior margin ranging from narrow to moderately wide. Male sexual opening coxal.

### Subfamily PILUMNINAE Samouelle, 1819

Transversely rectangular to transversely ovate, dorsally convex, moderately wide. Dorsal surface granular, setose on most surface and near anterolateral margin, or pubescent to smooth, regions more or less distinct. Front moderately deflexed, median notch distinct, front rarely entire. Eyes well developed. Supraorbital margin with 2 shallow, hardly discernible fissures. Behind exorbital angle usually with three teeth, spines or lobes. Antennular and antennal sinuses usually distinct. Epistome posteriorly lamellar, perpendicular. Chelipeds heterochelous, usually granular or spinose or at least partly covered with setae. Carpal spine small. Endostomial ridge usually well developed along entire endostome. Thoracic sternum usually narrow. Male sexual opening coxal. First gonopod very slender, simple, sinuous (S-shaped) to straight, distally simple, sometimes distally blunted. Second gonopod very short, sigmoidal, distal segment short, straight, forming distinct, cup-like structure. Abdomen in male usually not covering completely sternite 8, small portion uncovered. Telson short. Type genus: *Pilumnus* Leach, 1815.

#### Tribe Pilumnini Samouelle, 1819

Cephalothorax xanthoid, relatively narrow, thick. Dorsal surface almost granular, setose wholly or in parts. Anterolateral margin 3-spinose or lobate. Antennal sinus distinct. Inner infraorbital angle distinct. Chelipeds dissimilar, usually granular or spinose or even setose. Telson of usual size and shape, not reaching imaginary line connecting anterior edges of bases of chelipeds. Type genus: *Pilumnus* Leach, 1815.

## Tribe Tanaochelini Ng &amp; Clark, 2000

Cephalothorax transversely subovate. Dorsal surface smooth, glabrous, regions hardly indicated. Antennal sinus distinct. Anterolateral margin spinose or dentate. Chelipeds long, slender, fingers when closed with distinct gap, without setae on cutting margin, distally spoon-tipped. Dactylo-propodal locking mechanism of ambulatory legs present. First gonopod proximally stout, distally sinuous, second gonopod small, pilumnid. Type genus: *Tanaocheles* Kropp, 1984.

## Tribe Bathypilumnini trib. nov.

Pilumnoid-shaped, thick, wider than long. Anterolateral margin spiniform or dentiform. Anteroexternal lobe of basal antennal segment entering orbital hiatus. Male abdomen very slender, elongated, telson very long and narrow, longer than segment 6. First gonopod slender, straight, basal part bent at right angle, tip neither curved nor sharply tapered. Type genus: *Bathypilumnus* Ng & Tan, 1984.

## Tribe Heteropanopini Alcock, 1898

Cephalothorax widely ovate, dorsally moderately to slightly convex longitudinally. Dorsal surface weakly granular to almost smooth, regions almost weakly or not at all distinct. Front relatively wide, bilobed, lobes rounded to truncated. Supra-orbital margins nearly entire, vestiges of two fissures hardly discernible. Antennal sinus distinct to indistinct. Anterolateral margin shorter than posterolateral, arched, with 4 feeble teeth or wide lobes. Basal antennal segment wide, subquadrate, approaching but not touching front. Inner infraorbital angle very distinct. Exorbital angle confluent with first hepatic lobe. Posterolateral margins diverging, posterior margin moderately wide. Chelipeds very stout, heterochelous, smooth or very feebly granular. Sternite 8 not visible laterally to abdomen. Type genus: *Heteropanoppe* Stimpson, 1858.

## Tribe Calmaniini Števcíć, 1991

Cephalothorax elongate to wider than long. Dorsal surface with scattered tufts of long setae. Front bilobed, projecting horizontally. Anterolateral margin feebly lobulated. Antennulae folding obliquely. Third maxilliped not covering completely buccal cavern. Fingers of cheliped with distinct gap when closed, margins of gap densely lined with stiff setae. First gonopod relatively stout, sinuous, distally strongly recurved. Lateral margins of abdomen subparallel. Telson nearly subcircular, not elongate, wider than segment 6. Type genus: *Calmania* Laurie, 1906.

**Pilumninae (?) incertae sedis**

## Tribe Priapilumnini trib. nov.

*Pilumnus*-shaped. Antennal sinus and supraorbital fissures hardly discernible. Abdomen in male narrow, triangular, projecting posteriorly, covering completely sternite 8, segments 1 – 2 long, wide. First gonopod with bulbous basal part, nearly straight, not sinuous. Second gonopod with widened flared apical part. Type genus: *Priapilumnus* Davie 1989.



## Tribe Danielini trib. nov.

*Pilumnus* – shaped, subcircular. Dorsal surface of cephalothorax and pereopods very granular, setose. Front bilobed, deflexed. Antennal sinus present. Exorbital angle acute. Basal antennal segment not reaching front. Sternum moderately wide. Sternite 8 completely covered by abdomen. First gonopod slender, nearly straight, elongate, distally tapering, apex weakly lipped, not crooked. Second gonopod short, feebly sigmoid, terminal process curved, with small spinules, distally with pair of short flagella. Abdomen narrow, long. Type genus: *Danielum* Vázquez-Bader & García, 1995.

## Subfamily ITAMPOLINAE subfam. nov.

Cephalothorax hexagonal (*Globopilumnus*-shaped), much wider than long, dorsally slightly convex. Dorsal surface smooth. Front bilobed. Anterolateral margin with three teeth. Third maxillipeds wide. Abdomen narrow. First gonopod short, S-shaped, terminally bifurcated. Second gonopod very short, pilumnid. Type genus: *Itampolus* Serène & Peyrot Clausade, 1977.

## Subfamily EUMEDONINAE Dana, 1852

Cephalothorax varying in shape: polygonal, rhomboidal or pentagonal, anteriorly narrowing, dorsally nearly flat, regions usually indistinct. Dorsal surface smooth, sometimes with low pubescence. Front more or less projecting beyond orbits, bilobed or quadrilobed, rarely emarginate. Anterolateral margin dentate to entire. Posterolateral margins subparallel, posterior margin. Junction between anterolateral and posterolateral margins usually well marked, rarely rounded. Posterior margin usually moderately wide. Eyes well developed, not retractable, not protected. Eystalks stout. Orbits small, circular. Antennulae large, folded obliquely. Antennae small, flagellum short. Anterolateral angle of basal antennal segment closing orbital hiatus. Antennal peduncle and flagellum usually lying in antennal groove or sinus. Epistome short, wide. Chelipeds long, far projecting beyond anterolateral margin, carpal spine distinct. Dactylo-propodal locking mechanism of legs well developed. First gonopod slender, straight to sinuous, hooked apically, second very short, sigmoid. Telson not elongate. Type genus: *Eumedonus* H. Milne Edwards, 1834.

## Subfamily HALIMEDINAE Alcock, 1898

Subpentagonal, moderately wide. Dorsal surface smooth, regions partly defined. Front prominent, square-cut, bilobed, lamellate, with dorsal furrow, antennal sinus indicated. Anterolateral and posterolateral margins clearly demarcated. Anterolateral margin nodulated. Dorsal surface of carapace and chelipeds marked with isolated flat tubercles. Antennulae folding obliquely. Basal antennal segment not touching front. Endostomial ridge absent. Sternum elongate, lateral margins subparallel. Small part of sternite 8 uncovered. First gonopod basally stout, long, slender, almost straight, proximally not strongly bent, tip simple. Second gonopod short and hardly curved (not pilumnoid). Penial groove present. Minute portion of sternite 8 uncovered. Abdomen in male elongated, narrow. Telson narrow, very long. Type genus: *Halimede* de Haan, 1835.

## Subfamily DENTOXANTHINAE subfam. nov.

Cephalothorax almost hexagonal, wider than long, widest between spines at junction of anterolateral and posterolateral margins. Regions rather well defined. Front prominent, lamellar, bilobed, usually with median notch. Supraorbital margin bifissured. Exorbital angle present as small tooth fused with anterolateral margin. Anterolateral margin lamellar, crested, lobate or dentate. Antennulae folding obliquely. Endostomial ridge absent. Posterior margin wide. First gonopod slender, distally hooked. Second gonopod proximally bent, distally almost straight. Abdomen narrow, telson triangular, Type genus: *Dentoxanthus* Stephensen, 1945.

## Tribe Parapanopini trib. nov.

Hexagonal, wider than long, slightly convex. Dorsal surface covered with very short, dense, pubescence to smooth, regions clearly defined. Front bilobed, lamellar, prominent, antennal sinus distinct, lobes truncated or slightly concave. Exorbital tooth small. Anterolateral margin thin, sharp, nearly crest-like, dentate or lobate, teeth or lobes basally wide, incisions distinct. Posterior margin wide. Infraorbital margin with deep notch. Basal antennal segment touching front, closing orbital hiatus. Chelipeds well developed, heterochelous. Thoracic sternum narrow, lateral margins nearly parallel. First gonopod slender, more or less sinuous, tip hook-shaped, simple. Second gonopod short, basally wide, distally bent, straight to slightly curved, tapering distally to straight pointed apex (not typically pilumnid). Small portion of sternite 8 uncovered. Type genus: *Parapanope* de Man, 1895.

## Tribe Dentoxanthini trib. nov.

Subrhomboidal, thick. Regions rather distinct. Front wide, rounded to bilobed. Antennal sinus indistinct. Infraorbital margin bidentate. Anterolateral margin weakly four lobulate nearly entire, crest-like (sublamellar). Junction of anterolateral and posterolateral margins spiniform. Antennulae obliquely folded. Basal antennal segment touching front. Pereiopods compressed, keeled dorsally. Chelipeds strong, smooth, flat at inner side (like as in *Calappa*), fitted to anterolateral part of cephalothorax, homoiochelous. Legs slender, fingers acute. First gonopod slender, slightly curved in middle, hooked apically, lower inner margin provided with simple and plumose setae. Second gonopod minute, basal portion wide, with long plumose setae, distal end turned inward, lined with several minute spines. Type genus: *Dentoxanthus* Stephensen, 1945.

## Subfamily GALENINAE Alcock, 1898.

Subpentagonal, nearly subsquarish, slightly wider than long, thick, longitudinally convex. Anterolateral and posterolateral margins subequal in length, not distinctly separated. Dorsal surface nearly smooth, regions not well marked. Branchio-cardiac groove distinct. Front narrow, four-lobate, deflexed. Antennular sinus wide, shallow. Anterolateral margin with small blunt denticles. Posterior margin wide. Antennulae folding transversely. Basal antennal peduncle long, not touching front. Sternum wide, 2 small lateral portions on each side of sternite 8 exposed. Coxae of ambulatory legs with serrated prolongations. Male sexual opening coxal. Telson

narrow, elongate. First gonopod slender, basal part gently sinuous, nearly straight, tip fluted. Second gonopod almost pilumnid: stocky, short, distal segment lacking. Type genus: *Galene* de Haan, 1833.

Subfamily HAPALONOTINAE subfam. nov.

Cephalothorax subcircular, very bulbous, slightly wider than long, inflated, thick. Integument almost soft, covered with semitranslucent setae. Front short, lamellate, projecting downwards. Anterolateral margin arcuate, unarmed. Eystalks pyriform, cornea small. Orbital margins entire. Antennulae small, folding transversely. Basal antennal segment not touching front, flagellum short. Ambulatory legs cylindrical, with poorly developed dactylo-propodal articulation. Sternal sutures 6/7 – 7/8 entire. Gonopods pilumnid. Type genus: *Hapalonotus* Rathbun, 1897 (= *Malacosoma* de Man, 1879 nom. praeocc.).

Subfamily PELEIANINAE subfam. nov.

*Glabropilumnus*-shaped, transversely convex. Dorsal surface smooth. Front wide, nearly straight, bilobed, medial and antennal sinuses distinct. Anterolateral margin with two postorbital granules and two spine-like teeth, shorter than posterolateral, latter straight. Posterior margin wide, gently concave. Orbits wide, supraorbital margin entire. Basal antennal segment short, flagellum standing in orbital hiatus. Pereiopods long. Chelipeds large extending far beyond carapace margin, palm large. Third maxilliped narrow, abdomen wide. First gonopod straight, proximally stout, subapically bulbous, terminally narrow subterminally with tufts of hairs. Second gonopod almost pilumnid. Type genus: *Peleianus* Serène and Umali, 1971.

**b. Pilumnidae** – »goneplacid« grade.

Cephalothorax nearly subrectangular to semicircular, wider than long, posteriorly thick. Anterolateral and posterolateral margins confluent and arched. Posterior margin wide. Sternites 7 and 8 upcurved (perpendicular). Thoracic sternum wide. Sternal sutures 4/5 – 7/8 interrupted. Gonopods pilumnid. First abdominal segment wide to widest, usually touching coxae of last pair of legs. Male genital opening coxal to coxo-sternal. Male abdomen not covering wholly sternite 8.

Subfamily RHIZOPINAE Stimpson, 1858

Cephalothorax distinctly wider than long, subquadrate to subcircular. Front either narrow and more or less distinctly bilobed, deflexed or wide and square-cut. Frontal, supraorbital and anterolateral margins often appearing confluent. Anterolateral margin entire, lobulate to feebly dentate, very arched, not clearly separated from posterolateral margin. Posterolateral margins slightly diverging, nearly subparallel, posterior margin wide. Orbits shallow, small, transversely directed, usually filled by eyestalk, eyestalks fixed, cornea often depigmented and poorly developed. Supraorbital margin bifissured to entire, infraorbital margin entire, with two small sutures. Antennulae plicated slightly obliquely to almost transversely. Antennae small, flagellum short. Epistome well developed. Merus of third maxilliped often auriculate. Male sexual opening coxal to coxo-sternal. Dactyli of last

pair of legs upcurved. First gonopod slender, sinuous, apex simple, recurved, second one pilumnid (short, sigmoid). Abdomen not covering completely sternite 8, segments 1 and 3 widest, second segment narrow. Telson not elongate. Type genus: *Rhizopa* Stimpson, 1858.

Tribe Heteropilumnini Serène, 1984

*Pilumnus*-shaped, cephalothorax subquadrilateral, transverse, flattened. Dorsal surface covered with long setae, especially near frontal and anterolateral margins to smooth. Front bilobed. Frontal margin confluent with supraorbital margin. Antennal sinus absent. Anterolateral margins indistinctly lobulate to entire, not spinose. Posterolateral margin longer than anterolateral margin. Anterolateral and posterolateral margins not clearly demarcated. Posterior margin wide. Eyes well developed. Pereiopods fringed with long silky setae. Carpal spine of chelipeds short. Endostomial ridge distinct to absent. Penis lying in penial groove, latter not closed. Gonopods pilumnid: first gonopod sinuous slender, with pointed apex. Second one slender, sinuous. Portion of sternite 8 uncovered. Abdominal segment 1 slightly wider than segment 3 or subequal. Type genus: *Heteropilumnus* de Man, 1895.

Tribe Rhizopini Stimpson, 1858

Subglobular, transverse, widest posteriorly across posterior margin. Elliptical in sagittal cross section. Dorsal surface smooth. Lateral margins of carapace nearly parallel, unarmed. Margins of carapace and pereiopods sometimes fringed with long setae. Front narrow. Fronto-orbital width less than posterior one. Posterior margin wide, straight. Eyes reduced and immovable. Orbits shallow. Prostomial chamber sometimes present. Third maxillipeds gaping. Palm of chelipeds compressed. Carpal spine of chelipeds distinct. Dactyli of last pair of legs curving upward. Gonopods pilumnid, first gonopod sometimes with short tip blunt. Greater lateral portion of sternite 8 uncovered. Male sexual opening coxo-sternal, penial tube long. First gonopod sinuous, tip short, blunt, second gonopod short, sinuous. Proximal abdominal segments 1 and 3 not reaching coxae. Type genus: *Rhizopa* Stimpson, 1858.

Subfamily XENOPHTHALMODINAE subfam. nov.

Subsemicircular, widest posteriorly across posterior margin, elliptical in cross section. Dorsal surface smooth. Front relatively narrow, more or less bilobed. Anterolateral margin entire. Posterior margin wide, convex. Antennulae transverse. Eyestalks thick, immovable, cornea reduced to absent. Orbits small, oval, exposed dorsally. Merus of third maxilliped arched laterally, as wide as ischium. Chelipeds equal to subequal, palm compressed. Ambulatory legs fringed with setae, dactyli slightly curved, very acuminate. Sternites 3 – 4 deeply grooved for sterno abdominal cavity, not covered by abdomen. Sternum posteriorly upturned. Sternal sutures 2/3 and 6/7 – 7/8 entire, 3/4 indicated. Male genital opening coxo-sternal. First gonopod very long, slender, apically narrowed, extending beyond telson, approaching buccal cavern. Abdomen 7-segmented in both sexes (4 – 5 sometimes immovable, sutures distinct), segments 1 and 3 widest, far from coxae of last pair of legs. Type genus: *Xenopthalmodes* Richters, 1880. (Type species: *X. moebii* Richters, 1880).

## Superfamily LITOCHEIROIDEA superfam. nov.

Characters as for the family.

### Family LITOCHEIRIDAE fam. nov.

Cephalothorax nearly subquadrangular. Slightly longer than wide. Dorsal surface smooth and glabrous. Front wide, entire, lamellate, gently arched nearly straight, gently projecting. Frontal, supraorbital and anterolateral margins nearly confluent. Anterolateral margin very short, unarmed. Posterolateral margins feebly diverging, nearly parallel. Posterior margin wide. Antennulae transversely folded. Basal antennal segment approaching front. Chelipeds massive, carpal spine short. Ambulatory legs compressed, dactyli long, costate. Sternal sutures 6/7 – 7/8 entire. Posterior ventral portion of sternum upcurved. Male sexual opening coxal. Penial groove on suture 7/8 deep, long. First gonopod short, unusually stout, basally wide, twisted distally. Second gonopod much shorter than first. Male abdomen wide, completely covering sternite 8. Abdominal segments freely articulated in both sexes. Type genus: *Litocheira* Kinahan, 1856 (Type species *L. bispinosa* Kinahan, 1856).

## Superfamily PSEUDOZIOIDEA Alcock, 1898

Transversely ovate, flat. Regions poorly defined to indistinct, H-shaped depression and mesogastric triangle weakly developed to indistinct. Fronto-orbital width about half maximum carapace width. Front nearly straight, wide, deflexed, feebly bilobed with small antennal sinus, appearing quadrilobed. Orbits small, shallow, ovoid, with weakly rimmed orbital margins usually entire, exorbital angle lacking. Antennulae obliquely to nearly transversely folded. Basal antennal segment short, not touching front. Posterior margin of epistome with median cleft. Posterolateral margin feebly sinuous to nearly straight. Posterior margin moderately wide, nearly straight. Endostomial ridge present. Merus of third maxilliped wider than long. Chelipeds with carpal spine, basis-ischium and merus incompletely fused, suture visible. Sternum wide, oval, sternite 8 completely covered with abdomen. Thoracic sutures 2/3, 6/7 – 7/8 entire. First gonopod long, slender, relatively simple, gently sinuous, with numerous stiff spinules lining distal half, with apex simple to flared or spatulate. Second gonopod relatively long, shorter than first gonopod, straight to slightly curved, apically with short petaloid process, flagellum absent. Abdomen 7-segmented in both sexes, segments freely movable. Type genus: *Pseudozium* Dana, 1851.

### Family FLINDERSOPLACIDAE fam. nov.

Dorsal surface anteriorly granulate, with distinct mesogastric triangle. Front wide, bilobed. Anterolateral margin four-lobed, connecting orbits. Exorbital lobe indistinct. Basal antennal segment just touching front, antennae entering orbits. Merus and basis-ischium separated in male chelipeds. First gonopod long, moderately stout, nearly straight, stout, apically narrowed, bluntly pointed. Second gonopod

relatively long (about half-length of first one), tip short, recurved (falciform). Sternum ovate, very wide. Abdomen in male very wide, touching coxae of last pair of legs. Type genus: *Flindersoplax* Davie, 1989.

#### Family PSEUDOZIIDAE Alcock, 1898

Oval. Dorsal surface smooth. Front rather wide, gently bilobed, median notch hardly perceivable, antennal sinuses distinct. Orbital hiatus open. Supraorbital margins nearly entire. Anterolateral margin feebly lobate, sometimes not touching orbits, but running to buccal cavern. Antennulae nearly transversely folded. Basal antennal segment short, far from front, peduncle bent, entering to not entering orbital hiatus. Posterior margin wide. »Portunid lobe« present. Endostomial ridge present. Merus of third maxilliped gently auriculate, anterolaterally sinused. First gonopod long, slender, nearly straight, feebly sinuous, with stiff short spines lining distal half, apically more or less distinctly flared. Second gonopod short, curved, flagellum very reduced. Type genus: *Pseudozius* Dana, 1851.

#### Superfamily NOTONYCOIDEA superfam. nov.

Characters as for the family.

#### Family NOTONYCIDAE fam. nov.

Subquadrilateral, longitudinally convex, rather thick, wider than long, widest posteriorly across posterolateral margin. Dorsal surface smooth, regions indistinct. Front entire, straight, sublaminar. Frontal margin confluent with anterolateral margin. Fronto-orbital width nearly equal to greatest width of carapace. Lateral margins entire, subparallel, slightly concave. Posterior margin wide as greatest width of carapace. Antennulae transversely folded. Eyes small. Eyestalks obpyriform, elongate, movable. Basal antennal segment short, peduncle entering orbital hiatus. Anterolateral angle of merus of third maxilliped auriculate. Epistome well formed, nearly vertical. Buccal cavern narrowing posteriorly. Ambulatory legs elongate. Sternal sutures 6/7 – 7/8 entire. Both gonopods very long, first distally slightly curved, apically bifid, second much longer than first, distal parts exceeding telson. Abdomen widely triangular. Abdominal segments freely articulating in both sexes, segment 3 widest, not reaching coxae of last legs. Telson widely rounded. Type genus: *Notonyx* A. Milne Edwards, 1873.

#### Superfamily TYPHLOCARCINODOIDEA superfam. nov.

Characters as for the family.

#### Family TYPHLOCARCINODIDAE fam. nov.

Cephalothorax transversely elliptical, thick. Dorsal surface with distinct H-shaped depression. Anterolateral margin arcuated, lobate. Front narrow, prominent, deflexed, feebly bilobed, arched, lined with row of long setae. Eyestalks short, fixed,

cornea obsolete. Orbits wide, exposed dorsally. Antennae relatively well developed, directed longitudinally. Basal antennal segment wide, quadrate, touching front, peduncle covered with long setae, flagellum longer than peduncle, covered with short setae. Epistome very short, sunken, not distinctly separated from endostome. Buccal cavern anteriorly arched, nearly completely covered with third maxillipeds. Merus of third maxilliped short, nearly circular, wide, anterolaterally arched (not auriculated). Pereiopods hairy. Sutures 6/7 – 7/8 entire. Penis lying in penial groove. First gonopod stout, straight, basally thick, second one as long as or slightly longer than first, flagellum rather long. Abdominal segments distinct in male, third abdominal segment not covering completely space between coxae of last pairs of legs, telson subtriangular. Type genus: *Typhlocarcinodes* Alcock, 1900. (Type species: *T. integrifrons* Miers, 1881).

### Superfamily GONEPLACOIDEA MacLeay, 1838

Cephalothorax subhexagonal, subquarilateral to transversely ovate. Front relatively narrow. Posterolateral margin of carapace longer than anterolateral. Orbits often elongate. Interantennular septum thin. Basal antennal segment cylindrical. Palp of third maxilliped articulating on antero-internal angle of merus. Male sexual opening coxal to coxo-sternal. Penial groove, if present, not closed. First gonopod moderately stout, distally tapering, gently curved to sinuous. Second gonopod long, nearly as first, flagellum long. Thoracic sternum wide. Sternal sutures 3/4 – 5/6 always, others variously, interrupted. Abdominal segments freely articulated in both sexes, sometimes some segments immovable, sutures distinct. Type genus: *Goneplax* Leach, 1814.

### Family GERYONIDAE Colosi, 1923

Subhexagonal. Front moderately wide, sometimes square-cut, lobate to straight. Dorsal surface granular to smooth, regions more or less defined. Anterolateral margin 5 – 3, epibranchial tooth almost distinct. Basal antennal segment subcylindrical, movable, not touching front, peduncle bent. Pterygostomial ridge sometimes indicated. Endostomial ridge present at least posteriorly. Sternal suture 7/8 entire. Male sexual opening coxal. Penis usually not lying in penial groove. First pleopod basally stout, gradually tapering, straight to curved. Second gonopod nearly as long as first or longer, flagellum usually long. Abdomen in male widely triangular, touching coxae of last pair of legs. Segments 3 – 5 usually freely articulating, sometimes immovable, sutures usually distinct. Small portion of sternite 8 often uncovered. Type genus: *Geryon* Kröyer, 1837.

### Subfamily GERYONINAE Colosi, 1923

Subhexagonal to subtrapezoidal, slightly wider than long. Front usually 4-dentate, sometimes straight. Anterolateral and posterolateral margins distinctly separated. Orbits largely open. Antennae long, basal antennal segment and segment 4 slightly diverging, segment 5 with flagellum bent. Basal antennal segment well de-

veloped, movable, far from front, flagellum long. Antennulae folding gently obliquely to transversely. Basal antennular segment large. Endostomial ridge present at least posteriorly. Chelipeds subequal to unequal, inner carpal spine present. Ambulatory legs long. Thoracic sternum ovate, suture 2/3 entire, 6/7 interrupted usually near median line, 7/8 usually entire. Median groove on sternites 7 – 8. Male sexual opening coxal. Penial groove over suture 7/8. First gonopod conical, basally stout, distally tapering, nearly straight to curved, covered with short tubercles. Second gonopod elongate, more or less as long as first, flagellum shorter than basal part, curved. Abdomen in male 7-segmented, widely triangular, segments 3 – 5 movable to immovable, sutures distinct. Uncovered portion of sternite 8 small. Type genus: *Geryon* 1837.

Tribe Progerionini trib. nov.

Cephalothorax nearly trapezoidal. Dorsal surface covered with dense pubescence. Regions moderately defined. Front bilobed. Anterolateral margin arcuate, feebly lobate (undulate) much shorter than posterolateral margin, with distinct tooth on their junction. Posterolateral margins nearly straight to gently convex, feebly diverging. Posterior margin relatively wide. Antennulae plicated obliquely. Orbital hiatus rather wide. Exorbital angle indistinct. Endostomial ridge distinct anteriorly. Chelipeds heterochelous in male, less in female. Ambulatory legs long, unarmed. Sternal sutures 2/3, 4/5 – 6/7 interrupted 7/8 seemingly entire (check). First gonopod stout, almost straight, gradually tapering, distally covered with small sharp tubercles. Second gonopod longer than first gonopod, flagellum long, curved, shorter than basal part, tip rounded. Male abdomen triangular, sutures distinct, all segments freely articulated. Telson widely triangular. Abdomen covering whole space between coxae of last pair of legs. Type genus: *Progerion* Bouvier, 1922.

Tribe Paragalenini trib. nov.

Cephalothorax subhexagonal. Dorsal surface with two transverse ridges. Regions partly distinct. Front four-dentate, antennular and antennal sinuses distinct. Anterolateral margin dentate. Antennulae plicated obliquely. Two infraorbital teeth large, acute, projecting. Basal antennal segment short, cylindrical, peduncle entering orbital hiatus. Merus of third maxilliped auriculate. Ambulatory legs long, slender. Thoracic sternum narrowing anteriorly. Sternal suture 6/7 interrupted on median line, suture 7/8 entire. Median furrow on sternite 4. First gonopod feebly curved, distally straight, covered with small tubercles. Second gonopod nearly as long as first, with long laterally serrulated flagellum. Abdominal segments 3 – 4 fused in male, abdominal segments completely covering sternite 8. Type genus: *Paragalea* Nardo, 1868.

Tribe Mathildellini Karasawa & Kato 2003

Cephalothorax subhexagonal to subtrapezoidal, slightly wider than long, more or less flattened. Dorsal regions weakly defined. Front straight, truncate, deflexed, with shallow median notch, sometimes bimarginate, usually confluent with supraorbital margin. Antennal sinus hardly perceivable. Anterolateral margins short, widely rounded, dentate, exorbital and first hepatic teeth fused. Posterior margin



wide. Eyes and orbits well developed. Supraorbital margin with 1 – 2 fissures. Antennulae slightly obliquely, nearly transversely folded, antennular fossae large ovate. Antennae nearly obliquely directed (diverging), basal segment elongate, cylindrical, sometimes with lateral lobule, not touching front, sometimes movable, partly filling orbital hiatus, peduncle entering orbital hiatus. Endostomial ridge present, incomplete. Chelipeds heterochelous. Ambulatory legs long. Thoracic sternum ovate, narrowing anteriorly. Sternal sutures 2/3 entire, 6/7 usually interrupted near median line, 7/8 entire. First gonopod stout, strongly bent basally, not very narrow distally, apex simple. Second gonopod longer than first gonopod, flagellum long, apex simple (not spinose or lobate). Abdomen in male 7 – segmented, wide, abdominal segments 1 – 3 nearly completely covering sternite 8, minute portion of sternite 8 laterally to segment 2 uncovered, telson rounded. Type genus: *Mathildella* Guinot & Richer de Forges, 1981.

#### Tribe Geryonini Colosi, 1923

Subhexagonal to subquadrilateral. Regions weakly defined. Front four-lobate. Exorbital angle distinct. Lateral teeth spiniform, acute, isolated. Basal antennal segment short, slender, movable, far from front, flagellum long. Supraorbital margin entire, infraorbital margins with long acute inner infraorbital angle. Fingers of chelipeds not black. Endostomial ridge incomplete, distinct anteriorly. Inner carpal spine of chelipeds distinct. Dactyls of ambulatory legs depressed, dorsally flat, T-shaped in cross section. Sternal suture 7/8 entire. First gonopod, short, strong, distally tapering, curved out. Second gonopod nearly as long as first, flagellum shorter than basal part. Abdomen in female ovoid, in male triangular, in both sexes covering nearly entire sternum, third segment in male touching coxae of last pair of legs, segments 3 – 5 immovable, sutures distinct. Distinct portion of sternite 8 laterally to segments 1 – 2 uncovered. Abdomen in male ovoid. Type genus: *Geryon* Kröyer, 1837.

#### Tribe Intesiini trib. nov.

Subhexagonal, elongated, slightly wider than long. Dorsal surface lobulate, pilose. Front narrow, bilobed, bimarginate. Supraorbital margin bifissured. Anterolateral margin dentate with 4 serrated teeth. Antennae movable, pilose. Sternal sutures 7/8 entire. First gonopod relatively short, stout, proximally curved, gradually tapering. Second gonopod slightly shorter than first, flagellum of second gonopod much shorter than basal segment. Sternite 8 completely covered with abdomen. Abdominal segments 3 – 5 fused, sutures distinct to indistinct. Type genus: *Intesius* Guinot & Richer de Forges, 1981.

#### Tribe Platycheloniini trib. nov.

Cephalothorax very wide, transversely hexagonal, flattened. Dorsal surface with two transversal ridges, regions partly indicated. Front narrow, bilobed, lamellate, slightly projecting. Anterolateral margin with four V-shaped incisions, delimiting 4 lamellar teeth. Posterolateral margins nearly straight, slightly diverging. Posterior margin wide. Intercalated apophyse present. Sternal plastron rather wide, ovate. Distinct small portion of sternite 8 uncovered between segments 2 – 3. Mesogastric

triangle and H-shaped depression distinct. Antennal sinus distinct. Antennulae oblique. Basal antennal article slender, long, slightly movable, touching front. Eyes short, orbits small. Buccal cavern slightly widened anteriorly. Endostomial ridge distinct posteriorly. Thoracic sternum wide, ovate. Male sexual opening coxal. Penis lying in penial groove. First gonopod stout, curved with short spinules thorough whole length. Second gonopod shorter than first, flagellum rather thick, short, distally strongly tapering. Abdomen distally narrow. Abdominal segments in male freely articulated, lateral sides of segments 3 – 5 concave. Small portion of sternite 8 uncovered. Telson impressed into segment 6. Suture 7/8 not described. Type genus: *Platychelonion* Crosnier & Guinot, 1969.

#### Subfamily PLATYPILUMNINAE subfam. nov.

Subhexagonal, thin, dorsally flattened, slightly wider than long. Dorsal regions very faintly defined. Front wide, nearly straight, square-cut, bimaginate, prominent, bilobed, median notch U-shaped. Dorsal regions faintly defined. Supraorbital and anterolateral margins spinulose. Orbits positioned ventrally. Inner infraorbital margins distinct. Anterolateral margin spinose shorter than posterolateral margin. Posterior margin wide. Basal antennal segment not touching front, peduncle standing loosely in orbital hiatus. Pereiopods profusely spiny. Chelipeds heterochelous. Endostomial ridge present posteriorly, inconspicuous anteriorly. Third maxillipeds not completely closing buccal cavern. Legs long, slender, dactyli styliiform. First gonopod nearly straight, not tapering distally, subdistally spinose, opening large. Second gonopod longer than first, flagellum long, curved. Abdominal segments in male freely articulated, segments 1 – 2 usually reaching coxae of last pairs of legs, covering sternite 8, sometimes minute portion visible. Type genus: *Platypilumnus* Wood Mason, 1891.

#### Subfamily BATHYPLACINAE subfam. nov.

Cephalothorax subhexagonal. Front straight, rather wide. Anterolateral margin arcuate, with 2 pointed spines. Eyestalk short, immovable, cornea reduced. Ex-orbital spine absent. Antennae diverging, standing in orbital hiatus, flagellum long. Basal antennal segment touching downward prolongation of front. Buccal cavern broadened anteriorly. Endostomial ridge distinct. »Portunid lobe« present. Merus of third maxilliped auriculate. Chelipeds markedly asymmetric, basis-ischium and merus fused, subdistal dorsal spine on merus very distinct, palm compressed, paddle (spade)-like in adult. Sternum ovate. First gonopod stout, curved, tapering, distally covered with spinules. Second gonopod curved, half shorter than first gonopod, flagellum very short. Sexual opening in male coxal. Penial groove deep. Abdomen in male triangular, in female relatively narrow, borders nearly parallel. Abdominal segments freely-articulated, segment 3 in male touching to not touching coxae, uncovered portion of sternite 8 laterally to segments 1 – 2 notable. Stridulating apparatus present. Posterior margin with small projection between sternite 8 and coxa of last pairs of legs. Type genus: *Bathyplox* A. Milne Edwards, 1880.

### Family PLANOPILUMNINAE Serène, 1984

Subhexagonal, nearly squarish, wider than long, rather thick, dorsally depressed. Dorsal surface very sculptured with deep grooves or ridges of setae, well covered with short clavate setae arranged in irregularly reticulating lines. Cervical groove hardly indicated. Frontal margin wide, truncate, bilobed, slightly projecting, with small antennal sinuses. Eyes and orbits well developed, positioned ventrally. Supraorbital margin bifissured, in plane with anterolateral margin, infraorbital margin entire. Exorbital angle indistinct. Anterolateral margins much shorter than posterolateral, armed with 3 wide, triangular cristiform teeth, posterior teeth very small. Posterior margin relative wide, medially concave. Antennulae plicated slightly obliquely, nearly transversely. Basal antennal segment just touching subfrontal lobe, segment 4 entering orbital hiatus. Proepistome and epistome fused, deeply sunken. Endostomial ridge well developed. Buccal cavity widened anteriorly. Pereiopods coapted to carapace. Chelipeds unequal, deeply sculptured. Carpal spine of cheliped distinct, ischium and carpus eroded, palm and legs setose, setae in longitudinal rows. Ambulatory legs strong, sculptured, dorsal margin of merus and carpus bicefted, very shaggy. Thoracic sternum wide. Sternite 8 upturned. Sternal sutures 6/7 – 7/8 entire. First gonopod stout with spatulate apex. Second gonopod straight, relatively long, about half-length of first one. Abdominal segments freely articulated in both sexes. Type genus: *Planopilumnus* Balss, 1933.

### Family GONEPLACIDAE MacLeay, 1838

Subquadrilateral, hexagonal, transversely rectangular to subelliptical in shape, wider than long, more or less longitudinally convex. Dorsal surface smooth, regions poorly defined to indistinct, H-shaped depression often distinct. Front square-cut, moderately wide to rather narrow, deflexed, nearly straight, usually entire. Frontorbital margin wide to widest. Anterolateral margin spinose to unarmed. Posterior margin wide. Antennulae folding transversely. Basal antennal segment short, subcylindrical. Antennal peduncle standing loosely in orbital hiatus. Orbital margins entire, hiatus wide. Exorbital angle usually very distinct. Orbits and eyestalks very long, movable. Interantennular septum (proepistome) thin. Pterygostomial ridge distinct. Buccal cavern slightly widened anteriorly. Sternum wide. Sternal sutures 4/5 – 7/8 interrupted. Abdomen 7-articulated in both sexes, short penial groove over suture 7/8 imperfectly closed. First gonopod moderately long, basally stout, straight to gently curved, distally gradually tapering to blunt apex, apex distally often truncated obliquely (>cap-like«). Second gonopod long, slightly shorter, subequal to longer than first, with long flagellum, apex usually bifid to trifid. Abdomen in male largely triangular, 7 – segmented, third segment reaching coxae of last pair of legs variously covering sternite 8. Type genus: *Goneplax* Leach, 1814.

### Subfamily CARCINOPLACINAE H. Milne Edwards, 1852

Subhexagonal, transversely ovate, trapezoidal, more or less as wide as long, widest usually behind exorbital angle. Dorsal regions ill defined. Front relatively wide, truncate, nearly straight, only sometimes gently medially notched, slightly deflexed,

square-cut. Lateral margin convex, 3-spinose to unarmed. Eyes and orbits of usual size and form. Eystalks rather short. Orbits slightly elongated, more or less closed laterally. Supraorbital margin entire, rarely with minute fissure. Exorbital teeth, short, blunt to indistinct. Basal antennal segment short, subcylindrical, peduncle standing in orbital hiatus. Epistome well defined. Buccal cavity usually quadrangular, sometimes widened anteriorly, covered completely with third maxilliped. Pereiopods long, chelipeds far projecting. Sternal sutures 2/3 entire, 7/8 entire to interrupted. First gonopod long, slender, straight to curved, distally gradually tapering to simple or »cap-like« apex. Second gonopod long, flagellum long with pointed or lobular apex. Male abdomen widely triangular. Third abdominal segment reaching to not reaching coxae, uncovered portion of sternite 8 variously wide. Type genus: *Carcinoplax* H. Milne Edwards, 1852.

Tribe Carcinoplacini H. Milne Edwards, 1852

Subhexagonal, usually transversely ovate, wider than long. Frontoorbital width less than maximum width of carapace. Lateral margins arcuated, tridentate to entire. Exorbital angle distinct to indistinct. First gonopod often »cap-like«. Second gonopod reaching half-length of first gonopod, terminally bifid to trifid. Sutures 6/7 and 7/8 entire to interrupted. Considerable portion of sternite 8 remaining uncovered between abdominal segments 1 – 3 and coxae, abdomen rarely covering completely sternite 8. Type genus: *Carcinoplax* H. Milne Edwards, 1852.

Tribe Psopheticini trib. nov.

Cephalothorax varying from transversely elliptical to nearly subquadrate, widest between apices of lateral spines or exorbital spines. Front lamellate, projecting, straight. Orbits long. Supraorbital margin with small fissure. Exorbital angles well developed, projecting forward. Lateral margins with one tooth to unarmed. Posterior margin wide. Pereiopods long. Chelipeds usually with inner carpal spine. Meri of ambulatory legs usually dorsally dentate. Sternum wide, slightly ovate. First gonopod usually stout, gradually tapering to pointed apex. Second gonopod as long as first one, apically bifid. Penial tube short. Male abdomen widely triangular. Small portion of sternite 8 uncovered laterally to segments 2 – 3. Stridulating apparatus present. Type genus: *Psopheticus* Wood Mason, 1882.

Subfamily GONEPLACINAE MacLeay, 1838

Cephalothorax trapezoidal to subquadrate, wider than long, widest between exorbital angles. Dorsal surface with faintly indicated to indistinct regions. Front narrow to moderate in width, entire, straight, lamellate, square-cut. Front and orbits occupying entire anterior margin. Anterolateral margins with sparse spines to unarmed. Fronto-orbital width equal to greater than maximum carapace width. Median notch and antennal sinus absent. Orbits and eystalks very long. Orbits not concealing eystalks, laterally open. Exorbital angle acute. Basal antennal segment short, not reaching front, peduncle in orbital hiatus, flagellum long. Buccal cavity anteriorly widened, well separated from epistome. Pereiopods long, chelipeds far projecting beyond front. Thoracic sternum wide, suture 6/7 entire. Sutures of abdominal segments distinct, mobility variable. Penial groove on suture 7/8 very

short, open. First gonopod usually stout, distally covered with spinules, apically variable: pointed, slightly flared to »cap-like«, opening apically to laterally. Second gonopod longer than first, curled apically, apex entire to bifid. Abdomen widely triangular, lateral sides concave. Abdominal segments approaching but not reaching coxae of last pair of legs, uncovered portion of sternite 8 distinct. Type genus: *Goneplax* Leach, 1814.

**Goneplacidae (?) *incertae sedis***

**+Subfamily ICRIOCARCININAE subfam. nov.**

Cephalothorax pentagonal, transverse, widest between exorbital spines. Dorsal surface flattened, distinctly areolated, with deep grooves, areoles flat, epigastric region with transverse ridges. Pseudorostrum very narrow, downturned, not grooved, rounded at tip. Orbits wide. Eystalks long and slender, exorbital spine distinct, attenuated, directed laterally. Anterolateral margin short. Posterolateral margins straight, steep. Posterolateral margins diverging. Posterior margin wide, slightly concave. Pereiopods slender. Chelipeds long, slightly heterochelous, arched upward, keeled. Ambulatory legs long, first pair oval, pairs 2 – 4 flattened, last pair smallest, dactylus straight. Abdomen short. Type genus: *Icriocarcinus* Bishop, 1988.

**Goneplacoidea (?) *incertae sedis***

**+Family AMYDROCARCINIDAE fam. nov.**

Cephalothorax ovoid, wider than long, moderately convex longitudinally, weakly transversely. Dorsal surface finely granular, nearly smooth, regions very poorly defined. Front wide, appearing nearly entire, straight, granular, projecting hardly beyond orbits, with blunt, low protuberance axially, weakly sulcated of either side of protuberance. Eystalks short. Orbits square, fairly deep, supraorbital margin entire, directed weakly anterolaterally, rim weakly developed. Anterolateral margin short, convex, with thin closely spaced spines, merging smoothly with posterolateral margins. Posterolateral margin entire, smooth, long, weakly convex, diverging. Posterior margin short, nearly straight. Buccal cavern rectangular, wider than long, third maxillipeds longer than wide. Chelipeds massive. Ambulatory legs long, slender. Sternum wide in male, rectangular. Sternites 1 – 2 fused in shield. Sternites 3 – 4 fused. Sternite 8 covered by abdomen. Male abdomen narrow, lateral margins concave, segments freely articulated, segment 2 wide, segment 3 widest, touching coxae of last pair of legs, telson triangular. Type genus: *Amydrocarcinus* Schweitzer, Feldmann, Gonzáles-Barba & Vega, 2002.

**+Family MEGAXANTHIDAE fam. nov.**

Cephalothorax subhexagonal, wider than long, nearly subcircular, flattened. Dorsal surface apparently flat, pitted, with regions feebly defined. Cervical and branchiocardiac furrows feebly indicated. Front wide, entire, straight. Orbits large, semiquadrate, supraorbital margin bifissured. Anterolateral margin widely rounded with three semirectangular wide lobes and two triangular lobes. Posterolateral margin slightly

shorter than anterolateral, nearly straight. Posterior margin short, straight. Chelipeds massive, heterochelous. Thoracic sternum relatively small, elongate, subrectangular. Abdominal segments freely articulated. Telson distinctly triangular. Type genus: *Megaxantho* Vega, Feldmann, García-Barrera, Filkorn, Pimentel & Avendano, 2001.

### **Superfamily PARAPILUMNOIDEA superfam. nov.**

Characters as for the family

#### **Family PARAPILUMNIDAE fam. nov.**

Cephalothorax rounded to transversely ovate. Surface and carapace margins granulate. Frontal margin and pereopods covered with sparse long setae. Front bilobed, lobes truncatiform. Antennal sinus hardly discernible. Orbital margins lined with granules. Supraorbital margin concave. Exorbital angle indistinct. Eyestalks and orbits rather long, sloping posteriorly. Antennulae folding somewhat obliquely. Antennae well developed. Basal antennal segment large, filling orbital hiatus. Endostomial ridge low. Third maxillipeds relatively short and wide. Anteroexternal angle of merus subauriculate. Chelipeds homiochelous, cutting edges of chelae blade-like. Thoracic sternum anteriorly relatively narrow, elongate. Longitudinal grooves on sternites 4, 7 – 8. Sternal sutures 2/3, 6/7 – 7/8 entire. Male sexual opening coxal. Penis relatively long. First gonopod straight, relatively stout, distally tapering to sharp tip. Second gonopod subequal in length, distal segment about less than half-length of basal segment. Abdominal segments 3 – 5 in male completely fused. Type genus: *Parapilumnus* Kossmann, 1877.

### **Superfamily CONLEYODEA superfam. nov.**

Characters as for the family

#### **Family CONLEYIDAE fam. nov.**

Cephalothorax transversely quadrate, distinctly wider than long, dorsally feebly convex, regions weakly defined, anteriorly with epigastric and postorbital crests. Front wide, deflexed, hardly bilobed, lobes truncated, straight, bimarginate. Antennal sinus small, exorbital angle small. Anterolateral margin bidentate, feebly convex. Posterolateral margin feebly convex. Posterior margin wide, straight. Antennulae folding transversely. Basal antennal segment short, narrow, subquadrate, peduncle long, slender, flexed, entering orbital hiatus, flagellum rather short. Eyes well developed. Merus of third maxilliped auriculate. Chelipeds unequal. Inner carpal spine well developed. Ambulatory legs long, slender, dactyli of legs 1 – 3 long, slender, styliform, with corneous tip, dactyli of last pair, short, subspatuliform. Suture 1/2 ridged, sutures 1/2 – 3/4 entire, 4/5 – 7/8 interrupted. Sternites 4, 7 – 8 with median groove. Male sexual opening coxo-sternal, penial tube on sternite 8. Male abdomen relatively wide, laterally concave, segments freely articulating. First segment widest, second as wide as third, segments

4 – 5 laterally concave, segment 6 quadrilateral, telson semicircular. First gonopod sinuous, distal portion directed upward, tip slightly flared. Second gonopod as long as first, flagellum much shorter than basal part. Type genus: *Conleyus* P. K. L. Ng & N. K. Ng, 2003.

### **Superfamily EURYPLACOIDEA Stimpson, 1871**

Characters as for the family.

#### **Family EURYPLACIDAE Stimpson, 1871**

Subquadrilateral, subhexagonal to subtrapezoidal, transverse. Dorsal regions poorly defined to indistinct. Front moderately wide, almost square-cut, nearly straight, median notch shallow. Anterior margin mostly occupied by front and elongate orbits. Antennal sinus present. Inner infraorbital angle often distinct. Orbits and eyes usually elongated, supraorbital margin sometimes with 2 hardly discernible fissure. Orbital hiatus open to closed by basal antennal segment and intercalated apophyse, exorbital angle usually distinct. Antennulae transversely plicated. Antennae directed slightly obliquely. Anterolateral margin short, with 1 – 2 teeth. Posterolateral margins long, diverging to nearly parallel. Pterygostomial ridge in front of base of cheliped marked. Fingers of chelipeds not with dark coloured fingers. Thoracic sternum wide. Sternal sutures 4/5 – 5/6 interrupted, 6/7 – 7/8 appearing entire to interrupted just near median line. Sexual opening in male usually coxal to sometimes coxo-sternal. First gonopod elongate, slender, typically distally gradually tapering, apical portion sclerotized, armed with small tubercles over its length, second gonopod short with small flagellum. Male abdomen narrow, triangular. Abdominal segments freely articulated in both sexes, triangular in shape, segment 3 widest, segments 4 – 7 narrowing, telson long, triangular. Proximal abdominal segments 1 – 3 usually touching coxae of last pair of legs. Small portion of sternite 8 usually between segments 2 – 3 remaining uncovered. Type genus: *Euryplax* Stimpson, 1859.

### **Superfamily RAOULIOIDEA superfam. nov.**

Characters as for the family.

#### **Family RAOULIIDAE fam. nov.**

Cephalothorax widely elliptical, convex in longitudinal direction. Dorsal surface smooth, glabrous, regions scarcely indicated. H-shaped depression and mesogastric triangle indicated. Front straight, relatively wide, deflexed. Anterolateral margin arcuated, lateral margins subparallel, posterior margin straight, much wider than frontal margin. Margins of front, lateral margins and ambulatory legs fringed with feathered setae. Eyestalks pear-shaped, fixed, greatly bulging at base, dorsally exposed. Antennulae well developed. Antennae with lengthwise peduncles, peduncles fringed with long plumose setae. Epistome sunken. Merus of third maxilliped anterolaterally rounded, exognath slender, flagellum absent. First gonopod nearly

straight, proximally stout, distally slender. Second gonopod as long as first one, flagellum almost as long as basal portion. Apices of gonopods nearly reaching end of telson. Sternal plastron wide, sternite 8 upturned, uncovered laterally, visible dorsally. Sternal sutures 6/7 – 7/8 entire. First abdominal segment widest in both sexes, reaching coxae of last pair of legs, second segment in male very narrow, third very wide, not reaching coxae, segments 3 – 5 fused in male. Type genus: *Raoulia* Ng, 1987.

### Superfamily POTAMOIDEA Ortmann, 1896

Cephalothorax subhexagonal, wider than long. Front moderately wide, usually entire, sometimes abruptly deflexed and overhanging antennular fossae forming secondary frontal margin and subfrontal triangle. Epigastric and postorbital crests or lobes almost discernible, sometimes united into postfrontal crest. Cervical groove usually distinct dorsally and ventrally. Cervical groove and pterygostomial groove together with infraorbital margin often closing triangular infraorbital facet. Frontal and supraorbital margins usually entire and confluent. Antennulae plicated obliquely to almost transversely. Antennae short, basal antennal segment large, closing orbital hiatus, peduncle bent laterally. Posterior margin of epistome with sharp prominent posterior median triangle accompanied with distinct incision on each side. Mandibular palp remarkably well developed. Exhalent openings usually very large, rounded to oval. Endognath of first maxilliped strong, forming floor of exhalant channel. Endostomial ridges present. Buccal cavern completely closed by third maxillipeds. Meri of ambulatory legs compressed, triangular in cross section. Dactyli with 4 rows of corneous spines. Sternal suture 2/3 entire, sutures 4/5 – 5/6 interrupted, 6/7 – 7/8 variously interrupted (often indistinct, especially suture 6/7). Male genital openings coxal. Penial groove usually on sternite 8. First gonopod stout. Second gonopod long usually as long as first one or longer, with long flagellum, as sclerotized tube. Abdomen covering whole space between last pairs of legs, segments almost freely articulated. Type genus: *Potamon* Savigny, 1816.

### Family POTAMIDAE Ortmann, 1896

Cephalothorax subhexagonal, subsquarish, or transversely oval, wider than long. Dorsal surface smooth, rarely setose. Front deflexed. Frontal and supraorbital margins confluent. Branchial regions usually swollen, epigastric and postorbital crests usually present often medially fused into postfrontal crest. Supraorbital margins sometimes with traces of fissures. Basal antennal segment short, stout, touching front, segment 4 well developed touching front, segment 5 bent laterally. Pterygostomial suture anteriorly distinct and often grooved. Mandibular palp well developed, sickle-shaped, with either three or two segments, terminal segment either simple or bilobed. Third maxillipeds closing completely buccal cavern. Exognath of third maxilliped slender, with flagellum. Chelipeds strong, usually unequal, inner carpal spine present. Dactyli of ambulatory legs with 4 rows of spinules. Sternal sutures 4/5 and 5/6 always interrupted, 6/7 and 7/8 entire to interrupted (often indi-



stinct). First gonopod stout, consisting of three to four segments so that terminal segment being divided into subterminal segment and terminal joint. Second gonopod very long, usually as long as first one, sometimes shorter or longer. Type genus: *Potamon* Savigny, 1816.

#### Subfamily PARATHELPHUSINAE Alcock, 1910

Carcinoid- to potamoid-shaped, usually thick, convex longitudinally. Frontal region abruptly deflexed forming secondary frontal margin and subfrontal median triangle. Median triangle slanting backward. Dorsal margin of median triangle (secondary frontal margin) distinct to indistinct. Epigastric lobes and postorbital crests distinct sometimes fused into postfrontal crest, rarely indistinct. Anterolateral margin usually with one or more epibranchial teeth. Antennulae almost obliquely to nearly transversely plicated. Basal antennal segment closing orbital hiatus. Mandibular palp bisegmented, terminal segment bilobed. Exognath of third maxilliped with long flagellum. Penial groove on sternite 8. First gonopod relatively short, 3-segmented (endopod not divided into subterminal and terminal joints). Second gonopod shorter than first one, rarely longer. Abdomen in male laterally concave, usually (inverted) T-shaped (bottle-shaped). Type genus: *Parathelphusa* H. Milne Edwards, 1853.

#### Tribe Parathelphusini Alcock, 1910

*Carcinus*-shaped to subquadrilateral. Anterolateral margin of carapace arched with epibranchial and intermediate teeth. Subfrontal median triangle distinct, complete, secondary frontal margin cristate fused to anterolateral margin. Traces of supraorbital fissures discernible. Intercalated (occlusive) apophyse long. First gonopod almost simple (undivided), stout, short, straight. Second gonopod shorter than first. Abdominal segments freely articulated. Type genus: *Parathelphusa* H. Milne Edwards, 1853.

#### Tribe Somanniathelphusini Bott, 1968

*Carcinus*-shaped, subquadrilateral, thick, longitudinally convex. Dorsal surface nearly smooth. Epigastric and postorbital crests not fused. Subfrontal triangle distinct. No traces of supraorbital fissures. Exorbital angle distinct. Anterolateral margin with three distinct teeth. Cervical groove indistinct ventrally. Chelipeds very heterochelous. Penial groove over sternite 8. First gonopod undivided (three-segmented), basally very large, dilated, distal portion very slender, neck-shaped, curved outwards. Second gonopod long with very short flagellum. Abdomen in male very constricted subdistally. Type genus: *Somanniathelphusa* Bott, 1968.

#### Tribe Nautilothelphusini trib. nov.

Cephalothorax outline subquadrangular. Front narrow, medially concave. Exorbital angle formed into pointed tooth, two anterior teeth acute, distinct, directed forward. Exhalent tubes very remarkable. Posterior legs very compressed, paddle-like. First gonopod short, widely conical, 3-segmented. Abdomen in male (inverted) T-shaped, regularly concave. Type genus: *Nautilothelphusa* Balss, 1933.

## Tribe Ceylonthelphusini Bott, 1969

Potamoid-shaped. Anterolateral margin with single small epibranchial tooth. Epibranchial region striated. Supraorbital margins with incompletely fused fissures. Infraorbital facet distinct. Median tooth on epistome blunt. Dorsal (secondary) frontal margin cristate, laterally fused to lateral margin, First gonopod slender, 4-segmented, subterminal and terminal joints distinct, latter simple or bent outwards, two folds not overlapping. Abdomen in male (inverted) T-shaped. Type genus: *Ceylonthelphusa* Bott, 1969.

## Tribe Spiralothelphusini Bott, 1968

Potamoid-shaped. Dorsal surface lacking striae. Anterolateral margin with single, small low epibranchial tooth. Subfrontal median triangle very distinct. Epistomal median tooth acute. First gonopod either strongly twisted clockwise, or entirely bent laterally outwards, terminal joint distinctly separated. Lateral margins of abdomen regularly concave to almost bottle (or inverted T)-shaped. Type genus: *Spiralothelphusa* Bott, 1968.

## Tribe Sundathelphusini Bott, 1969

Potamoid-shaped, thick. Epigastric and postorbital lobes weakly defined. Front not projecting. Subfrontal triangle usually indistinct, secondary frontal margin simple bending downwards, not fused with lateral margins. Anterolateral margin unarmed. Epistome with very distinct posterior triangle. First gonopod with distinct subterminal and terminal joints (4-segmented). Abdomen in male (inverted) T-shaped. Type genus: *Sundathelphusa* Bott, 1969.

## Subfamily GECARCINUCINAE Rathbun, 1904

Almost subhexagonal to transversely oval, rather thick. Dorsal surface with distinct lobes and crests, cervical groove usually distinct. Frontal margin smooth. Subfrontal triangle indistinct. Anterolateral margin entire, no epibranchial tooth. Antennular fossae nearly completely covered by frontal margin. Mandibular palp 3-segmented to 2-segmented, usually consisting of bilobed terminal segment with large posterior lobe and anterior lobe about half size of posterior one. Endognath constricted at ischium-merus articulation. Exognath of third maxilliped with long flagellum. Sternal sutures 6/7 – 7/8 entire to mostly interrupted. First gonopod short, with terminal and subterminal joints not always distinctly separated, suture often incomplete. Abdomen narrow, elongated in both sexes. Abdomen in male subtriangular to inverted T-(bottle)-shaped. Telson narrow, elongated, distally rounded. Type genus: *Gecarcinucus* H. Milne Edwards, 1844.

## Tribe Gecarcinucini Rathbun, 1906

Transversely oval. Dorsal surface with distinct epigastric lobes and postorbital crests. Front deflexed covering antennular fossae, subfrontal triangle indistinctly demarcated. Mandibular palp bisegmented, terminal segment bilobed, anterior lobe larger than posterior one, basal segment with accessory lamellae. Exognath with long flagellum. Sternal suture 7/8 entire. First gonopod straight, slender, gradually tapering, 3 – 4-segmented (suture indistinct), terminal joint of first gonopod long,

straight, more than half-length of subterminal joint. Second gonopod with very short flagellum. Telson elongately triangular to tongue-shaped, never widely triangular. Type genus: *Gecarcinucus* H. Milne Edwards, 1844.

Tribe Liothelphusini Bott, 1969

Dorsal surface almost smooth, crests and lobes indistinct to absent, epibranchial tooth rudimentary to absent. Subfrontal triangle absent. Lobes of terminal segment of mandibular palp large, anterior lobe smaller than posterior one. First gonopod almost straight, 4 – segmented (suture between segments often indistinct), terminal joint tapering (cone-shaped), relatively short, about 1/3 length of subterminal. Type genus: *Liothelphusa* Alcock, 1909.

Subfamily GLOBONAUTINAE Bott, 1969

Cephalothorax ovoid, transversal, thick, inflated. Front wide, anterior margin straight. Subfrontal triangle lacking. Postfrontal crest usually distinct. Cervical groove ventrally distinct, touching epibranchial tooth. Mandibular palp large, bisegmented, bilobed, terminal segment consisting of single large posterior lobe with either subequal sized anterior lobe or small anterior process. Exognath of third maxilliped lacking flagellum. Chelipeds hetetrochelous. Carpus of cheliped bispinose. Sternal sutures 1/2 rarely distinct, 2/3 distinct 3/4 indicated only laterally, 4/5 – 5/6 interrupted, 6/7 not completely meeting in midline, 7/8 entire. Sternite 8 lacking distinct penial groove. First gonopod long, 4-segmented, slender, tapering, terminal joint short and tube-like with broad tip, almost straight, much narrower, obliquely inwardly deflexed or sometimes spirally twisted. Second gonopod flagellum very long to very short. Abdomen in male straight-sided triangular, segment 6 longest, apex of telson rounded. Abdomen usually completely covering sternum. Type genus: *Globonautes* Bott, 1959.

Subfamily SEYCHELLINAE subfam. nov.

Cephalothorax quadrangular. Regions well defined, cristae sharp, prominent. Antennulae and antennae obliquely positioned. Interantennular septum not compressed, triangular. Mandibular palp bisegmented, basal segment stout, terminal segment distinctly bilobed. Endopod of first maxilliped slender, lateral margins sinuous. Exhalent respiratory channel chimney-like. First gonopod with separated subterminal and terminal joints. Distal segment of second gonopod shorter than basal segment, tip rounded. Abdominal segments freely articulated, first segment hidden by carapace. Male abdomen triangular. Type genus: *Seychellum* Ng, Štević & Pretzmann, 1995.

Subfamily PLATYTHELPHUSINAE Colosi, 1920

Subhexagonal, subrounded to subsquare. Front projecting, straight to slightly deflexed, margins finely dentate or granulate. Postfrontal crest distinct, incomplete. Short triangular process of front descending into orbital hiatus. Infraorbital margin lined with small teeth or granules, inner tooth distinct. Exorbital angle acute to granular. Anterolateral margin of carapace with 2 – 4 forward-directed teeth. An-

tennulae plicated obliquely. Basal antennal segment large, in contact with front. Antennal peduncle longitudinally forward to slightly obliquely directed, visible dorsally. Mandibular palp 3 – segmented, terminal segment simple. Third maxillipeds completely covering buccal cavern, exognath with flagellum. Exhalant respiratory channel funnel-shaped, not projecting. Chelipeds asymmetric. Carpus of chelipeds with up to 5 spines. Sternal sutures 1/2, 2/3 entire, 6/7 – 7/8 almost entire. First gonopod long, very stout, gradually tapering, subterminal and terminal joints separated, terminal joint short, bent. Second gonopod slightly longer than first one with long flagellum, flagellum shorter than basal part. Abdomen in male relatively narrow, triangular. Type genus: *Platythelphusa* A. Milne Edwards, 1887.

#### Subfamily POTAMINAE Ortmann, 1896

Typically potamoid-shaped, transversely oval. Front entire, moderately deflexed. Subfrontal triangle absent. Infraorbital facet present. Infraorbital margin smooth. Basal antennal segment closing orbital hiatus. Mandibular palp trisegmented to bisegmented, terminal segment simple. Sternal sutures 6/7 and 7/8 usually interrupted. First gonopod with terminal and subterminal joints distinctly separated. Second gonopod with long sclerotized tube, equal to longer than first gonopod. Sternal sutures 6/7 and 7/8 usually interrupted. Male abdomen triangular, never constricted distally, segment 6 longest. Telson narrower than segment 6, widely triangular. Type genus: *Potamon* Savigny, 1816.

##### Tribe Potamiscini Bott, 1970

Longitudinal groove on sternite 7 – 8 entire. Transversal ridge on suture 7/8 absent. Sternal suture 7/8 usually interrupted, rarely entire. First gonopod twisted dorsally. Type genus: *Potamiscus* Alcock, 1909

##### Tribe Potamini Ortmann, 1896

Longitudinal groove on sternite 7 – 8 interrupted by narrow transversal ridge by suture 7/8. Suture 7/8 interrupted. First gonopod twisted ventrally. Type genus: *Potamon*: Savigni, 1816

#### Subfamily POTAMONAUTINAE Bott, 1970

Cephalothorax transversely oval, widest at anterior third. Front wide, lamellate, moderately deflexed. Frontal margin smooth. Antennulae folding transversely. Postfrontal crest complete to incomplete. Anterolateral margin cristate, serrate. Infraorbital facet usually present. Mandibular palp bisegmented, terminal article simple (not bilobed) with large simple posterior lobe. Third maxillipeds completely covering buccal cavity. Sternal sutures 4/5 – 6/7 interrupted, 2/3 and 7/8 entire, rarely suture 1/2 distinct, entire. First gonopod with terminal joint shorter than subterminal. Second gonopod longer to shorter than first one. Penial groove lacking on sternite 8. Male abdomen triangular, first segment not concealed under carapace. Type genus: *Potamonautes* MacLeay, 1838.

Tribe Potamonautini Bott, 1970

Frontal margin smooth, deflexed, covering antennular fossae. Postfrontal crest sharp, incomplete to complete, meeting lateral margin or not. Exorbital angle very distinct. Epibranchial tooth almost present, sometimes with intermediate tooth. Cervical groove ventrally distinct. Infraorbital facet usually distinct. Mandibular palp bisegmented, terminal palp simple consisting of large posterior lobe. Sternal sutures 1/2 usually indistinct, 2/3 distinct 3/4 – 7/8 interrupted, sometimes 7/8 apparently entire. First gonopod with terminal segment of medium length, shorter than subterminal one. Second gonopod as long as or shorter than first one. Type genus: *Potamonautes*. MacLeay, 1838

Tribe Hydrothelphusini Colosi, 1920

Front lamellate, projecting horizontally, gently deflected, slightly bilobed. Epigastric crest advanced anteriorly. Epibranchial tooth usually distinct. Exhalent opening very large. Mandibular palp bisegmented, terminal segment very variable, simple, basally thickened, undivided to deeply clefted (bilobed). First gonopod with terminal joint indistinctly to distinctly separated. Type genus: *Hydrothelphusa* A. Milne Edwards, 1872.

Subfamily DECKENIINAE Ortmann, 1897

Cephalothorax outline subovate. Postorbital crest absent. Antennulae folding nearly longitudinally. Antennae transversely posed. Interantennular septum (proepistome + subfrontal lobe) very compressed. Endopod of first maxilliped and lateral surface of endostome forming tubiform chimney-like efferent funnel. Mandibular palp bisegmented, terminal segment simple. Subterminal and terminal joints of first gonopod clearly separated. Distal segment of second gonopod longer than basal part. Abdominal segments in both sexes immovably fused, sutures distinct. First abdominal segment concealed by carapace in both sexes. Type genus: *Deckenia* Hilgendorf, 1868.

**Family PSEUDOTHELPHUSIDAE Rathbun 1893**

Transversely oval. Dorsal surface usually smooth, regions indistinct. Epigastric lobes distinct, not fused medially. Anterolateral margin often finely serrate, dentate to unarmed, lateral armature indistinct. Infraorbital facet indistinct. Cervical groove present. Frontal margin wide, gently arched, bimarginate, deflexed, no subfrontal triangle. Orbital margins entire, sometimes tuberculate. Antennulae oblique to transverse. Antennae transverse, flagellum short. Basal antennal segment and peduncle filling orbital hiatus. Median projection of epistome horizontal. Endostomial ridge present, low. Mandibular palp bisegmented, terminal segment bilobed. Merus of third maxilliped wider than long, shorter than ischium, lateral margin more or less arched. Exognath of third maxilliped highly reduced. Chelipeds more or less heterochelous. Dactyli of ambulatory legs with 5 rows of spinules. Exhalent opening large. Sternal sutures 4/5 – 7/8 interrupted. Penial groove rudimentary, located on posterior margin of episternite 7 and anterior margin of sternite 8. Penis emerging next to articular membrane adjacent to coxa of last pair of legs. First gonopod

trisegmented, stout, straight, distally thick, with typically very complex apex composed by lobes and projections. Second gonopod long. Pseudo-lungs present. Abdomen freely segmented, widely triangular, touching coxae of last pair of legs, telson rounded. Type genus: *Pseudothelphusa* de Saussure, 1857.

#### Tribe Epilobocerini Smalley, 1964

Exognath of third maxilliped usually exceeding ischium of endognath. Exognath with flagellum. Cervical groove on ventral side often distinct. Exorbital spine absent. Efferent branchial channel with tooth. Propodi of walking legs spinulose, dactyli with 8 – 9 spines in each row. First gonopod relatively long and slender, apical region with short stout spines (no spine field). Type genus: *Epilobocera* Stimpson, 1860.

#### Tribe Pseudothelphusini Rathbun, 1893

Front bimarginate. Exognath of third maxilliped highly reduced, not reaching length of ischium of endognath, palp usually absent. No tooth in efferent branchial channel. First gonopod thick and blunt, relatively short, apically with cup-shaped spine field. Type genus: *Pseudothelphusa* de Saussure, 1857.

### Superfamily BYTHOGRAEOIDEA Williams, 1980

Characters as for the family.

#### Family BYTHOGRAEIDAE Williams, 1980

Transversely elliptical, flattened. Front moderately deflexed, concealing antennular fossae. True orbits, antennular and antennal cavities and interantennular septum absent. Eyes, antennulae and antennae in common subfrontal cavity. Antennulae plicated transversely. Antennae inserted bellow eyestalks, slightly diverging nearly longitudinally or downward directed, segments 2 + 3 not completely fused into basal antennal segment. Epistome horizontal, medial tooth on posterior margin present. Buccal cavern quadrangular. Thoracic sternum wide, sutures 4/5 – 5/6 always, 6/7 – 7/8 sometimes interrupted. First gonopod long and slender, almost straight. Second gonopod relatively long, usually longer than first, flagellum whip-like. Abdominal segments freely articulated in both sexes, sometimes segments 4 – 5 fused in male. Type genus: *Bythograea* Williams, 1980.

### Superfamily PARTHENOPOIDEA MacLeay, 1838

Cephalothorax variously shaped, mostly »oxyrhynchous«-shaped i.e. narrowed anteriorly, widest posteriorly, usually at junction of anterolateral and posterolateral margins, sometimes subtriangular, subdeltoid, subpentagonal, ovate pentagonal, semicircular or transversely elliptical. Dorsal surface mostly uneven, tuberculate, granulate to eroded, sometimes smooth. Front narrow, more or less projecting. Anterolateral margins converging, longer than posterolateral ones. Antennulae and antennae nearly longitudinal to slightly oblique. Basal antennal segment long, partly or

completely closing orbital hiatus. Interantennular septum distinct. Eyes retractile in small circular orbits. Supraorbital margins usually entire or with one fissure. Chelipeds long. Ambulatory legs usually short and slender, often concealed under lateral projection of carapace. First gonopod, relatively simple, stout, gradually tapering, second gonopod long or of varying lengths, with long flagellum. Thoracic sternum wide, sternal sutures 6/7 – 7/8 entire to interrupted. Abdominal segments 3 – 5 usually fused in male, immovable, sutures sometimes distinct. Type genus: *Parthenope* Weber, 1795.

### Family AETHRIDAE Dana, 1851

Transversely subovate to subquadrate, laterally expanded, wider than long. Dorsal surface uneven. Front narrow, bilobed, more or less projecting. Lateral margin cristate, lamellate, with several deep fissures, forming vault, concealing pereopods. Anterolateral and posterolateral margins not clearly demarcated. Posterior margin narrow. Interantennular septum (proepistome) wide. Orbits usually small, visible to invisible from above. Eystalks directed latero-backwardly. Antennulae and antennae obliquely directed. Peduncle and flagellum of antennae rather reduced in size. Interantennular septum wide. Third maxillipeds elongate, quadrate to often triangular, completely covering buccal cavern. Palp of third maxilliped hidden by merus. Endostomial ridge well marked at least posteriorly. Chelipeds compressed, coapted tightly against anterior ventral part of cephalothorax, inner surface of chelipeds flattened, smooth. Ambulatory legs compressed, coapted to carapace. Thoracic sternum anteriorly wide, posteriorly narrowed. Suture 6/7 nearly entire, 7/8 entire. First gonopod stout, slightly curved, gradually tapering, tip pointed. Second gonopod longer to shorter than first gonopod, with long flagellum, at least half-length of first. Male abdomen covering completely sternite 8. Type genus: *Aethra* Leach, 1816.

### Subfamily HEPATINAE Stimpson, 1871

Cephalothorax pentagonal, octagonal, rounded to transversely elliptical, convex, narrowing anteriorly. Dorsal surface with inflated regions. Front narrow, ranging from straight to snout-like, bilobed. Orbits small, completely filled by eye, often ventrally placed, eyes sometimes visible in dorsal view. Anterolateral margin convex. Lateral expansion of carapace not concealing completely pereopods. Posterolateral margin short, often concave. Posterior margin narrow. Antennulae plicated obliquely. Basal antennular and basal antennal segments segment closing orbital hiatus, antennal peduncle reduced. Proepistome relatively wide, epistome reduced. Buccal cavity ranging from quadrangular to elongated and anteriorly triangular, anterior part usually upturned, nearly vertical. Merus of third maxilliped short, triangular. Flagellum of exognath reduced to absent. Sternal sutures 6/7 – 7/8 entire. First gonopod robust, slightly curved, distally tapering, apically pointed. Second gonopod as long as or longer than first gonopod, flagellum long. Abdominal segments 3 – 5 almost fused in male, sutures distinct. Telson narrow, elongate. Type genus: *Hepatus* Latreille, 1802.

### Subfamily AETHRINAE Dana, 1851

Cephalothorax transversely elliptical, much wider than long, very depressed. Lateral margins expanded (vaulted) laterally, but not posteriorly, crestiform, upturned, concealing pereopods laterally. Front hardly projecting, subtriangular. Primary frontal margin, deflexed, touching proepistome. Anterolateral margin indistinctly divided into 6 – 7 wide lobes with closed fissures. Orbits small, ventrally placed, eyestalk short. Antennulae and often antennae nearly longitudinally or slightly obliquely directed. Basal antennal segment closing orbital hiatus. Buccal cavern quadrangular Exognath of third maxilliped present. Chelipeds short, depressed. Ambulatory legs compressed. Sutures 4/5 – 7/8 interrupted. Second gonopod subequal in length to first, flagellum long. Abdomen 7-segmented in both sexes. Type genus: *Aethra* Leach, 1815.

### Family PARTHENOPIDAE MacLeay, 1838

Cephalothorax subtriangular, subpentagonal or subdeltoid to almost subcircular. Front simple to more or less trilobed, almost short. Branchial region usually swollen, distinctly separated from swollen gastric and cardiac regions. Eyes small, retractile. Orbits small, complete, subcircular. Antennulae plicated gently obliquely. Proepistome remarkable: basally wide, anteriorly abruptly narrowed forming elongate, triangular, apically acute interantennular septum. Buccal cavern subrectangular. Merus of third maxilliped subquadrate. Chelipeds very long, wing-like, not pressed against carapace, projecting laterally far from carapace margin, merus and palm usually prismatic in cross section, fingers in oblique angle to axis of palm. Ambulatory legs short and slender. Thoracic sternum wide. First gonopod stout, tapering to not tapering, relatively simple, mostly apically bluntly truncated, usually armed with dense spines, spinules or setae, with distinct lateral longitudinal furrow, distal segment usually with very wide posterior opening. Second gonopod of various length, usually shorter than first one, recurved distally, tip appearing semispatulate, flagellum long. Abdominal segments 3 – 5 immovable, often fused, sutures sometimes distinct. Type genus: *Parthenope* Weber, 1795.

### Subfamily DALDORFIINAE Ng & Rodríguez, 1986

Roughly subpentagonal. Dorsal surface heavily granulate and eroded with well-defined dorsal regions. Pseudorostrum short, if present downturned. Branchial region projecting laterally. Basal antennal segment large, usually touching inner infra-orbital angle filling orbital hiatus. Chelipeds very long and stout, rounded in cross section fingers slightly curved. Walking legs strongly tuberculate, not concealed by lateral carapace margins. Sternal sutures 6/7 – 7/8 entire. First gonopod stout, cylindrical, straight to slightly bent. Second gonopod varying in length. Abdominal segments 4 – 6 fused. Type genus: *Daldorfia* Rathbun, 1904.

### Subfamily PARTHENOPINAE MacLeay, 1838

Cephalothorax subpentagonal, ovate – pentagonal to subtriangular. Pseudorostrum single to three-lobed, directed forward to slightly downward. Branchial re-



gions usually separated from gastric and cardiac ones. Dorsal surface granular or eroded. Basal antennal segment short, not reaching inner apex of infraorbital angle, peduncle closing orbital hiatus. Chelipeds massive, triangular in cross section. Fingers of chelipeds very strongly bending inward and downward. Walking legs slender, visible in dorsal view. Sternal sutures 4/5 – 7/8 interrupted, sometimes sutures 6/7 – 7/8 entire. Abdomen appearing subtriangular, abdominal segments 3 – 5 usually fused in male, sutures distinct. First gonopod tubular, almost stout, straight to slightly sinuous, second gonopod usually shorter than first one, flagellum variable in length. Type genus: *Parthenope* Weber, 1795.

#### Subfamily CRYPTOPODIINAE Stimpson, 1871

Cephalothorax triangular to pentagonal in outline. Dorsal surface usually smooth, sometimes granular to eroded. Gastric region elevated. Front lamellate, sometimes slightly deflexed. Carapace laterally very expanded to form vault concealing proximal parts of walking legs. Basal antennal segment far from front, not filling orbital hiatus. Merus of third maxilliped auriculate. Merus of chelipeds flat. Thoracic sternum flat, neither last sternite nor first abdominal segments visible dorsally because carapace projecting more or less behind abdomen. Sternal sutures 4/5 – 7/8 interrupted, sometimes 6/7 – 7/8 entire. First gonopod relatively stout, straight to sinuous. Second gonopod shorter than first one, flagellum very short. Abdominal segments 3–5 fused in male. Type genus: *Cryptopodia* H. Milne Edwards, 1834.

**Parthenopoidea (?)** *incertae sedis*

#### Family MIMILAMBRIDAE Williams, 1979

Subcircular. Front narrow trilobed. Pseudorostrum triangular, short, antennular sinus distinct. Orbits large, inner and exorbital angles distinct, supraorbital margin with fissure. Antennulae plicated obliquely. Antennae small, basal antennal segment relatively small, not filling orbital hiatus. Segments 4 converging, segments 5 subparallel. Buccal cavern slightly narrowed anteriorly. Maxillipeds slightly gaping. Merus of third maxilliped subtriangular. Exognath of third maxilliped concealed beneath endognath. Chelipeds very long, spinose, fingers of chelipeds slender, not bending. Afferent branchial channel laterally to buccal cavern, opening anterior to bases of maxillipeds. Efferent channels fused, located at anteromedial part of endostome. Sternal sutures 4/5 – 7/8 interrupted. First gonopod with subterminal crown of spines, second much shorter. Abdomen subtriangular, abdominal segments freely articulated in both sexes, segments 3 – 5 in male not completely movable. Telson triangular in both sexes. Type genus: *Mimilambrus* Williams, 1979.

### Superfamily PORTUNOIDEA Rafinesque, 1815

Subhexagonal, sometimes subovate or subquadrilateral, usually wider than long, mostly depressed, flat. Exoskeleton usually thin. Front wide, horizontal, not deflexed. Lobe on endite of first maxilliped («portunid lobe») usually present. Chelipeds well developed, often with longitudinal carinae. Legs compressed, propodi and

dactyli with upper and lower margins with rows of setae (not spinules), last pair usually natatorial. Endostomial ridge usually present. Sternum wide, sutures 4/5 – 7/8 interrupted (6/7 often indistinct). Male sexual opening coxal. Penial groove usually on sternite 8. First gonopod usually C-shaped, proximally stout, distally tapering, long, second gonopod short. Abdominal segments 3 – 5 generally fused in male, sutures sometimes discernible. Type genus: *Portunus* Weber, 1795.

### Family PORTUNIDAE Rafinesque, 1815

Cephalothorax subhexagonal, transversely oval, subovate or subquadrangular, usually wider than long, mostly depressed, flat, widest at posterior anterolateral teeth, almost depressed to slightly convex. Integument usually thin. Dorsal surface with transversal ridges, epibranchial ridge often present, regions not well defined. Front horizontal, usually wide, cut into even number of lobules or teeth, antennular and antennal sinuses usually distinct. Inner infraorbital spine often distinct. Epistome often sunken. Endostomial ridge often distinct. Prostomial chamber often present. Chelipeds well developed, usually variously spinose, internal carpal spine present, palm and fingers often longitudinally sulcate or crested with longitudinal carinae, fingers usually sharply pointed, rarely spoon-like. Propodi and dactyli of last pair of legs mostly flatly expanded, margins strongly fringed with setae, natatorial, dactyli rarely styliform. Thoracic sternum wide, sutures 4/5 – 7/8 interrupted (6/7 often indistinct). Sometimes small portion of sternite 8 uncovered. Penis lying in wide penial groove usually on sternite 8 in several forms penial groove supplemented by rudimentary sternal lobe. First gonopod long, basally stout, distally tapering to point tip, second usually short. Abdominal segments 3 – 5 fused in male, sutures rarely distinct. Type genus: *Portunus* Weber, 1795.

#### Subfamily CARCININAE MacLeay, 1838

Cephalothorax subhexagonal, relatively narrow, gently convex in both directions. Dorsal surface without transversal ridges. Anterolateral margin with 4 – 3 teeth. Supraorbital margin with 1 – 0 supraorbital fissures. Fissures on infraorbital margin reduced to absent. Antennulae plicated obliquely, basal antennal segment narrow, cylindrical, free to fixed, longer than wide, longitudinal, flagellum standing in orbit. Prostomial chamber present. Endostomial ridge indistinct. »Portunid lobe« inconspicuous. Epistome gently sunken, partly covered with maxillipeds. Inner carpal spines present, other spines usually absent. One pair of legs usually longer than chelipeds, longitudinal crest on palm lacking. Dactyli of last pair of legs lanceolate or styliform. First gonopod robust, without subterminal spines. Type genus: *Carcinus* Leach, 1814.

#### Tribe Portumnini Ortmann, 1899.

Cephalothorax about as long as wide. Front trilobed (antennular sinus). Anterolateral margin with 4 teeth. Posterior margin narrow. Supraorbital margin with 2 – 1 fissures. Antennal peduncles converging anteriorly. Antennulae oblique. Basal antennal segment movable to fixed, not filling orbital hiatus. Endostomial ridge absent. »Portunid lobe« indistinct. Prostomial chamber present. Third maxillipeds elon-

gated. Merus of third maxilliped, ahead articulation with palp, projecting near to basal antennular segment. Palm of chelipeds smooth. Legs natatorial, dactyli of 1 – 3 pairs of legs distally lanceolate and flattened, apically acute, last pair natatorial. Sternum narrow. Sutures 2/3 – 3/4 distinct. First gonopod nearly straight, distally outcurved. Abdomen narrow. Type genus: *Portumnus* Leach, 1814.

#### Tribe Carcinini MacLeay, 1838

Cephalothorax typically carcinoid, slightly wider than long. Front widely trilobed. Anterolateral margin 4-dentate, single supraorbital and infraorbital fissures present. Antennulae plicated obliquely. Basal antennal segment fixed, narrow. Endostomial ridge interrupted or lacking. No prostomial chamber. Sternal sutures 1/2 – 3/4 distinct, suture 7/8 seemingly entire. Dactyli of 1 – 3 pairs of legs apically acute, propodi and dactyli of last pair lanceolate. First gonopod curved. Abdomen in male subtriangular. Type genus: *Carcinus* Leach, 1814.

#### Tribe Brusinini Števčić, 1991

Cephalothorax elongate-elliptical. Front trilobed, slightly projecting. Anterolateral margin tridentate. No supraorbital fissure. Voluminous chelipeds with short fingers. Dactyls of three anterior ambulatory legs compressed, last lanceolate. Abdominal segments 3 – 5 immovable, but sutures distinct. Second gonopod much longer than first. Type genus: *Brusinia* Števčić, 1991.

#### Subfamily POLYBIINAE Paul'son, 1875

Cephalothorax relatively narrow, slightly wider than long, depressed. Transversal ridges usually absent. Anterolateral margin 2 – 4 – dentate. Supraorbital margin with 2 – 1 fissures. Antennulae plicated obliquely. Basal antennal segment fixed, longitudinally to obliquely directed, entering orbits. Prostomial chamber sometimes distinct. Endostomial ridge present to absent. »Portunid lobe« distinct. Pereiopods long, one pair of legs as long as chelipeds, palm of chelipeds cristate, inner carpal spine present. Last pair paddle-like. Type genus: *Polybius* Leach, 1820.

#### Tribe Platyonichini Dana 1851

Front tridentate to four-dentate. Front not projecting. Posterior margin narrow. Orbital hiatus not completely closed by basal antennal segment, latter movable, with lateral lobule, entering orbit. Antennular sinus distinct, peduncle large, visible dorsally. Supraorbital margin with 2 – 1 fissures. Posterior margin narrow. Epistome reduced. Prostomial chamber present. Sternal sutures 4/5 – 7/8 interrupted (6/7 indistinct). Dactyls of last pair of legs broadly oval, abdomen in male oblong. First gonopod curved, tapering distally, with relatively long setae on both inner and outer sides. Abdominal segments 3 – 5 incompletely to completely fused, sutures distinct. Type genus: *Ovalipes* Rathbun, 1898 (= *Platyonichus* Latreille, 1825, nec 1818).

#### Tribe Polybiini Paul'son, 1875

Cephalothorax hexagonal to subcircular. Front trilobed. Antennular and antennal sinuses distinct. Anterolateral margin four-dentate. Antennae cylindrical. Supra-

orbital margin with 2 – 1 fissures. Basal antennal segment cylindrical, far from front, loosely standing in orbital hiatus. Prostomial chamber sometimes more or less well developed. Merus of third maxilliped longer than wide. Palm of cheliped ridged, inner carpal spine long, acute. All pairs of legs paddle-like. Dactyli of legs 1 – 3 enlarged, propodi and dactyli of last pair very enlarged. First gonopod with subterminal spines. Male abdomen triangular. Type genus: *Polybius* Leach, 1820.

#### Tribe Coenophthalmini Alcock, 1899

Cephalothorax subquadrilateral. Front nearly entire, obscurely four-lobed. Anterolateral margin bidentate. Posterior margin wide. Orbits completely closed, antennae excluded from orbits. Merus and carpus of chelipeds dentate, meri of ambulatory legs dentate. Last pair of legs not natatorial. Type genus: *Coenophthalmus* A. Milne Edwards, 1879.

#### Subfamily CARUPINAE Paul'son, 1875

Cephalothorax subrectangular to transversely oval, wide, slightly convex in both directions, dorsally smooth. Front narrower than posterior margin. Anterolateral margin convex. Posterior margin of carapace very wide. Epibranchial ridge sometimes present, regions indistinct. Supraorbital margin bifissured to entire, infraorbital margin with 4 nearly equal lobes. Basal antennal segment narrow, short, not lobulate, antennal peduncle oblique, entering orbital hiatus. »Portunid lobe« present. Chelipeds longer than legs, palm inflated, sparsely dentate to unarmed, nearly smooth. Last pair of length not natatorial, dactyli styliform or lanceolate. First gonopod distally slender, covered with sparse spinules. Type genus: *Carupa* Dana, 1851.

#### Tribe Carupini Paul'son, 1875

Cephalothorax transversely oval. Front wide, lamellate, four-lobate. Epibranchial ridge sometimes present. Two supraorbital fissures usually hardly perceivable. Anterolateral margin with six teeth. Infraorbital margin with 4 nearly equal lobes. Basal antennal segment narrow, directed obliquely, peduncle entering orbital hiatus. Merus of third maxilliped auriculate. Chelipeds longer and more massive than ambulatory legs, merus and carpus spinose. Fingers longitudinally grooved. First gonopod straight, slender, not tapering, bent near tip. Abdominal segments 2 – 5 fused. Type genus: *Carupa* Dana, 1851.

#### Tribe Catoptrini Borradaile, 1907

Cephalothorax transversely ovate, feebly convex in both directions, smooth. Front divided into two subtruncate lobes. Anterolateral margin arched, 5-dentate, last tooth acute, projecting forward. Eystalks short. Supraorbital margin entire confluent with frontal margin. Infraorbital margin with two small lobes. Inner infraorbital angle blunt. Exorbital tooth small. Basal antennal segment rather long, touching front, peduncle and flagellum entering orbital hiatus. Merus of third maxilliped longer than wide, gently auriculate. Chelipeds longer than ambulatory legs, merus with two spines, finger long, slender, finely dentate. Merus of chelipeds dentate with small 1 – 2 teeth, carpus unarmed. Ambulatory legs slender, dactyls of last

pair narrow straight, feebly, applanated. Sternum enlarged. First gonopod stout, curved, distally tapering to apex, distal portion finely spinulose. Type genus: *Catoptrus* A. Milne Edwards 1870.

#### Subfamily CAPHYRINAE Paul'son, 1875

Cephalothorax relatively not much wider than long, subhexagonal to subcircular, rather thick. Epibranchial ridge usually present. Antennal sinus often feebly indicated. Anterolateral margin with 4 – 3 teeth or lobes. Supraorbital margin (2 – 1) bifissured. Basal antennal article lying obliquely, with anterolateral lobe entering orbital hiatus, peduncle excluded from orbit. Pereiopods relatively short. Merus, carpus and palm of chelipeds bearing reduced set of spines, carpal spine present, fingers not at all or very feebly grooved. Last pair of legs compressed, dactyli variously modified. First gonopod with subterminal spines. Abdomen in male very wide. Type genus: *Caphyra* Guérin – Méneville, 1835.

#### Tribe Caphyrini Paul'son, 1875

Cephalothorax nearly as wide as long. Dorsal surface smooth with feeble epibranchial ridge. Front lamellate, wide, entire, bilobed to 4-8-lobate, inner supraorbital angle (lobe) distinct. Buccal cavern anteriorly widened. Merus of third maxilliped auriculate. Palm of chelipeds rugose, fingers of chelipeds weakly grooved. Last pair of ambulatory legs dorsal in position, dactyli claw-shaped. First gonopod with subterminal spines. Type genus: *Caphyra* Guérin – Méneville, 1835.

#### Tribe Lissocarcinini Paul'son, 1875

Cephalothorax as wide as long to slightly wider than long, dorsal surface almost smooth. Front prominent, lamellate, 2 – 4 lobate to entire. Exorbital angle small. Basal antennal segment touching front. Merus of chelipeds unarmed. Last pair of legs paddle-like, not dorsal in position. Fused part of male abdomen concave, segment 6 laterally convex. First gonopod nearly straight, subapically bordered by long plumose setae, tip flared, or claw-like curved with wide opening, bordered by strong spinules. Abdomen in male triangular. Type genus: *Lissocarcinus* Adams and White, 1848.

#### Tribe Coelocarcinini trib. nov.

Cephalothorax rounded. Front produced into blunt feebly projecting lobe. Dorsal surface smooth, glabrous. Regions rather distinct, transversal ridges absent. Anterolateral margin strongly convex, margin sublamelliform, divided into 3 – 4 lobes. Posterolateral margin concave. Posterior margin narrow, prominent. Antennulae folding obliquely. Basal antennal segment short, narrow, rectangular, gently obliquely directed, not reaching front, peduncle entering orbital hiatus, flagellum minute. Eyestalks short, prominent. Supraorbital margin concave, lacking fissures. Third maxilliped elongate, ischium much longer than merus, exognath wide, tapering distally, with strongly convex outer margin. Chelipeds unarmed, short, stout, fingers short. Ambulatory legs short with bases of last pair more or less at same level with anterior pairs. Dactyli of anterior three pairs of legs subspatuliform. Last pair of legs well developed, short, with very wide subcircular foliaceous propodus and

dactylus. Dactylus hidden when folded back under propodus. Thoracic sternum elongate, narrow. Sternal suture 2/3 entire, suture 6/7 appearing entire, other interrupted. Medial sternal groove on sternites 7 – 8. First gonopod very slender, sinuous, distally curved outwards, sickle-shaped, second very short, tip spatuliform. Abdomen in male long, narrow, triangular. Type genus: *Coelocarcinus* Edmondson, 1930.

#### Subfamily PORTUNINAE Rafinesque, 1815

Cephalothorax usually subhexagonal, wide to very wide. Dorsal surface with transversal ridges or granular areas in front of epibranchial ridges. Anterolateral margin with greater number of teeth (8 – 4). Supraorbital margin bifissured. »Portunid lobe« distinct. Prostomial chamber sometimes present. Chelipeds longer than walking legs bearing set of spines on merus, carpus and palm, fingers of cheliped deeply grooved. Last pair paddle-like, dactyli with pointed tips. First gonopod without subterminal spines. Third abdominal segments often projecting laterally. Type genus: *Portunus* Weber, 1795.

##### Tribe Atoportunini trib. nov

Cephalothorax hexagonal, dorsally feebly convex. Dorsal regions feebly defined. Front not projecting beyond orbits, bilobed, lobes medially concave, with double rimmed margins. Orbits relatively small, eyes reduced. Orbital hiatus wide. Exorbital lobe wide, rounded. Anterolateral margins very long, with 6 lobes (anteriorly) and teeth (posteriorly). Epibranchial ridge lined with granule, joining tip of last lateral tooth. Antennulae oblique. Basal antennal segment short, longitudinal. Chelipeds symmetrical, very slender, elongate, inner margin of merus with spines, palm compressed, fingers styliform, tip strongly hooked, cutting edge with long spines. Ambulatory legs very long, slender, unarmed, last pair paddle-like. First gonopod C-shaped, distally tapering, with short spinules and setae. Second gonopod rather long, terminally furca-like. Abdomen in male triangular, telson triangular. Type genus: *Atoportunus* Ng & Takeda, 2003.

##### Tribe Lupocyclusini Paul'son, 1875

Cephalothorax nearly subcircular, convex in both directions, slightly wider than long. Dorsal regions faintly indicated, surface tomentose. Front projecting beyond level of orbits, with even (4 – 6) number of teeth or lobes, antennal sinus minute. Epibranchial ridge not always discernible. Antennulae and antennae very long. Antennulae directed obliquely. Basal antennal segment short, narrow, cylindrical, not lobulate, movable, peduncle entering orbit, flagellum long. Anterolateral margin with 4 – 8 teeth. Anterolateral margin subequal in length to posterolateral margin. Third maxillipeds covering epistome. Chelipeds long, spinose, fingers very long and slender. Three anterior pairs of legs slender, last pair natatorial. Type genus: *Lupocyclus* Adams & White, 1848.

##### Tribe Portunini Rafinesque, 1815

Cephalothorax subhexagonal, much wider than long. Front divided usually into odd number of lobes. Anterolateral margin with 8 – 4 teeth. Anterolateral and

posterolateral margins subequal in length and curvature. Basal antennal segment narrow, immovable, lying obliquely, standing loosely in orbit, not feeling orbital hiatus. Prostomial chamber almost absent. Merus, carpus and palm of chelipeds with set of spines, carpus with one or two spines on outer margin. First gonopod without subterminal spines. Third abdominal segment markedly wide, segments 4 – 5 narrowing, segment 6 narrow, telson elongate. Type genus: *Portunus* Weber, 1795.

Tribe Thalamitini Paul'son, 1875

Cephalothorax subhexagonal to subtrapezoid, markedly wider than long. Front cut into even number of teeth. Anterolateral margin with 6 – 3 teeth, longer than posterolateral one. Basal antennal segment transversely directed, broadened, usually filing orbital hiatus. Antennal peduncle usually excluded from orbit. Chelipeds longer than ambulatory legs. Merus, carpus and palm of chelipeds spinose, carpus with three spines on outer face. First gonopod with subterminal spines. Type genus: *Thalamita* A. Milne Edwards, 1869.

+Subfamily PSAMMOCARCININAE Beurlen, 1930

Cephalothorax subhexagonal, usually wider than long, sometimes nearly equidimensional. Dorsal surface with granular or tubercular ornamentation. Orbits circular, shallow. Anterolateral margin dentate, last teeth on anterolateral margin extremely produced, mostly ornamented with smaller spines, rarely unarmed. Last pair of legs paddle-like. Type genus: *Psammocarcinus* A. Milne Edwards, 1860.

Subfamily PODOPHTHALMINAE Dana, 1851

Cephalothorax subtrapezoidal to transversely oval. Transverse epibranchial ridge present. Front extremely narrow, T-shaped. Anterolateral margin with sparse teeth. Orbits and eyestalks strikingly long, supraorbital fissures lacking. Antennulae not retractile into their fossae. Basal antennal segment short, flagellum standing in orbital hiatus. Epistome short. Prostomial chamber present. Chelipeds much longer than legs, merus, carpus and palm spinose. Last pair of legs natatorial. Sternite 8 laterally uncovered. First gonopod with subterminal spines. Penis long, lying in shallow sternal groove. Type genus: *Podophthalmus* Lamarck, 1801.

Subfamily LIBYSTINAE Serène, 1966

Cephalothorax transversely subquadrangular or subelliptical, convex in both directions. Dorsal surface smooth, regions indistinct. Front entire, wide, straight. Anterolateral margin with three small granules, nearly entire, arched, not distinctly separated from posterolateral one. Antennulae long. Antennal sinus and supra-orbital fissure lacking. Posterior margin of carapace very wide, straight. Antennal peduncle short, narrow, loosely standing in orbital hiatus. Merus of third maxilliped wider than long, distinctly auriculate. Chelipeds unarmed, smooth. Legs slender, unarmed. »Portunid lobe« present. Thoracic sternum wide. Last pair of legs with propodus elongate, slightly flattened, dactylus sinuous, upturned, subspatuli-form. Both segments with fringes of bristles. First gonopod short, very stout, apically widened, truncated, with row of long spines along distal half of lateral face

seeming not completely closed longitudinally. Second gonopod half as long as first one. Male abdomen subtriangular, segments 1 – 2 very small, 3 – 5 completely fused. Type genus: *Libystes* H. Milne Edwards, 1867. (Type species: *L. nitidus* H. Milne Edwards, 1867, cf. Stephensen, 1945)

#### +Family CARCINERETIDAE Beurlen, 1930

Cephalothorax subsquare, nearly roughly urn-shaped, flat to convex longitudinally. Fronto-orbital margin nearly equal to maximum carapace width. Dorsal surface with one or more prominent transverse ridges, regions distinct, well marked by grooves and ridges. Front narrow, bilobed, deflexed. Supraorbital margin wide, with distinct fissure. Lateral margins unarmed, straight, posteriorly arched. Antero-lateral and posterolateral margins not distinctly separated. Posterior margin narrow, straight. Eyestalks and orbits long, exorbital angle distinct, pointing in acute angle. Propodi and dactyli of third or fourth pair of legs flattened, paddle-like. Type genus: *Carcineretes* Withers, 1922.

*Portunoidea* (?) *incertae sedis*

#### Family MELYBIIDAE Števčić (in Martin & Davis), 2001

Cephalothorax roughly portunid-shaped. Front wide, bilobed, median notch wide. Antennal sinus distinct. Supraorbital margin bifissured. Exorbital angle small. Anterolateral margin tridentate. Eyes and orbits very large. Antennae not excluded from orbit. Endostomial ridge and »portunid lobe« present. Maxillipeds not covering completely buccal cavern. Chelipeds unequal, long, strong, merus and carpus dentate. Ambulatory legs long, meri dorsally spinose. Sternal sutures 6/7 – 7/8 entire. First gonopod with bifid apex. Abdominal segments 3 – 5 fused. Type genus: *Melybia* Stimpson, 1871.

### Superfamily TRICHODACTYLOIDEA H. Milne Edwards, 1853

Characters as for the family.

#### Family TRICHODACTYLIDAE H. Milne Edwards, 1853

Cephalothorax subhexagonal to subcircular, wider than long. Cervical groove absent. Postgastric pits usually present. Frontal margin straight to gently bilobed, entire. Orbital margins entire. Antennulae folding obliquely to transversely. Basal antennal segment relatively short, basally stout, with expansion in outer lobe, which together with intercalated apophyse (occlusive tooth) closing orbital hiatus, segment 5 together with flagellum bent, entering orbits. Mandibular palp trisegmented, terminal segment simple. Maxillipeds not covering completely buccal cavity. Endognath of third maxilliped relatively narrow ischium-merus articulation obliquely posed, merus longer than wide, often antero-laterally produced into distal external spine, giving impression of triangular shape, palp articulating at antero-mesial angle of merus. Exognath well developed, flagellum present. Endostomial ridge usually in-



conspicuous. »Portunid lobe« present. Efferent branchial opening large, restricted on corners of endostome by structure of endopod of first maxilliped, very varying in structure. Walking legs compressed, propodi and dactyli with rows of setae (not denticles) on upper and lower margins, propodi of last pair widened. Sternal sutures 2/3 – 3/4 indicated laterally, 4/5 – 7/8 interrupted. Penial groove across middle of sternite 8, supplemented by rudimentary sternal lobe of sternite 8 and sometimes with episternite of segment 7. Small portion of sternite 8 sometimes uncovered. First gonopod trisegmented, conical to flask-shaped, basal portion stout, distal portion armed with conical spines, apical opening (gonopore) V-shaped. Second gonopod long, as long as or longer than first, rarely short, flagellum long. Abdominal segments in both sexes almost fused, sometimes freely articulated. Male abdomen widely triangular. Type genus: *Trichodactylus* Latreille, 1828.

#### Subfamily TRICHODACTYLINAE H. Milne Edwards, 1853

Cephalothorax suborbicular. Postgastric pits absent. Anterolateral margin with 5–0 teeth, postgastric pits absent. Front lamellar, feebly bilobed. Meri of third maxillipeds trapezoidal, not very narrow. Sutures of abdominal segments usually distinct. Sternum widely ovate. Median furrow on sternites 7 – 8. Penial groove overlapped by sternal lobe and tergite 8. First gonopod single tube, flash-shaped, without marked torsion of spermal channel, distal spermal opening V-shaped, open caudally, subdistal spine fields on both sides of stem. Second gonopod of equal length to shorter than first. Sutures between abdominal segments completely or partly visible. Type genus: *Trichodactylus* Latreille, 1828.

#### Subfamily DILOCARCININAE Pretzmann, 1978

Cephalothorax subhexagonal to suborbicular. Postgastric pits present. Sternal plastron relatively narrow. Penial groove open. First gonopod conical, elongate, apical setae long, with marked torsion of spermal channel. Second gonopod more or less longer than first, usually sinuous. Some abdominal segments fused (exception for segment 6 and telson), sutures between segments 3 – 5 usually obsolete. Type genus: *Dilocarcinus* H. Milne Edwards, 1853.

##### Tribe Valdiviini Pretzmann, 1978

Cephalothorax subhexagonal. Upper surface moderately convex. Regions well marked. Anterolateral margin with 6 – 2 teeth. Median furrow on sternite 7 – 8. First gonopod stout, strong lateral lobe on proximal half. Gonopore terminal, slit-like. Some abdominal segments always fused. Type genus: *Valdivia* White, 1847.

##### Tribe Dilocarcinini Pretzmann, 1978

Cephalothorax suborbicular, wider anteriorly, upper surface strongly arched, smooth. Front bilobed, more or less retracted, exposing epistome. Anterolateral margin with 11–3 teeth. Median furrow on sternites 5 – 6 and 7 – 8. First gonopod expanded laterally at base, with long plumose setae on lateral margin, apex bulbiform, distal spermal opening apical. Second gonopod moderately longer than first. Some abdominal segments usually fused. Type genus: *Dilocarcinus* H. Milne Edwards, 1853.

## Superfamily MAJOIDEA Samouelle, 1819

Cephalothorax oxyrhynchous-shaped (anteriorly narrowing, widest posteriorly), subpyriform (pear-like) to subovate, dorsally more or less convex. Dorsal regions variously defined. Frontal region narrow, usually two, rarely one, pseudorostral spines. Pseudorostral spines almost well developed, interantennular spine (true rostrum) often present. Lateral margins usually spinose. Carapace and pereopods covered with hooked hairs. Orbits composed by basal antennal segment, supraorbital eave with anterior preorbital and posterior antorbital spines, intercalated and postorbital spines, some of these spines often reduced to absent. Antennulae plicated longitudinally or nearly longitudinally. Antennular fossae squarish to longer than broad, longitudinal. Basal antennal segment well developed, generally fused with epistome and often with front. Epistome large. Buccal cavity quadrate. Palp of third maxilliped articulated either on summit or at antero-internal angle of merus. Chelipeds very mobile, usually far projecting beyond anterolateral margin of cephalothorax. Dactylo-propodal locking mechanism sometimes present. Sternal sutures 4/5 – 7/8 interrupted. Thoracic sternites usually 4 – 8 radially directed. First gonopod long, varying in form, second gonopod short. Abdomen very variously fused, telson sometimes fused with segment 6 to form pleotelson. Type genus: *Maja* Lamarck, 1801.

### Family MAJIDAE Samouelle, 1819

Cephalothorax mostly subpyriform, longer than wide. Pseudorostrum usually bifid, mostly long. Orbits present to absent. Branchiostegite well developed, pleural plates covered. Male sexual opening coxal. Abdomen rarely with pleotelson. First abdominal segment not fused to carapace. Endoskeleton of usual structure. Type genus: *Maja* Lamarck, 1801.

#### Subfamily MAJINAE Samouelle, 1819

Subpyriform to subcircular. Pseudorostrum bispined. Eystalks usually long, retractile in orbits. Orbits nearly complete (but not closed) formed by supraorbital eave and postorbital spine. Intercalated spine often present. Basal antennal segment well developed, not forming floor to orbit, often armed with strong spine at antero-lateral angle. Merus of third maxilliped at least as wide as ischium. First gonopod slender, feebly curved, aperture usually subterminal and protected by lobes or flaps, apex slender, simple. Abdomen usually 7-segmented. Male abdomen elongate, sixth segment as wide as third. Type genus: *Maja* Lamarck, 1801.

#### Tribe Majini Samouelle, 1819

Subpyriform, pseudorostral spines long. Antennal flagellum arising from within orbits. Intercalated spine well separated from eave and postorbital spine. Supraorbital eave and intercalated spine very prominent. No preorbital spine. Branchial margin usually spinose. Type genus: *Maja* Lamarck, 1801.

## Tribe Cyclacini Dana, 1851

Suborbicular-quadrate to pyriform. Pseudorostral spines very short, separated by V-shaped notch. Eystalks short, cornea rounded, terminal. Supraorbital eave not very prominent, antorbital and intercalated spines present, postorbital lobe. Preorbital angle armed with blunt tubercle. Postorbital lobe with prominent accessory spine on upper anterior edge near base, excavated or cupped anteriorly. Basal antennal segment wide, tridentate. Orbit open ventrally. Antennal peduncle excluded from orbit. Lateral margin with 5 – 6 teeth. Type genus: *Cyclax* Dana, 1851.

## Tribe Schizophrysini Miers, 1879

Pyriform to suboval. Supraorbital eave not very expanded, smooth, laterally concave. Pseudorostral spines with accessory spines. Preorbital angle rounded, not produced in spine or tubercle. Postorbital lobe cupped anteriorly, close to eye. Eystalks short. Orbit open ventrally, antennal peduncle excluded from orbit. Type genus: *Schizophrys* White, 1848.

## Tribe Naxiini Stimpson, 1871

Subpyriform. Orbit open ventrally. Cornea not protected either dorsally or ventrally. Preorbital and antorbital spines distinct, intercalated spine present. Postorbital lobe as conical to acuminate spine, not cupped. Eystalks slender. Antennal peduncle excluded from orbits. Basal antennal segment rather narrow with anterior spine, widely separated from postorbital spine. Propodi of ambulatory legs usually expanded ventrally near distal margin. Type genus: *Naxia* Latreille, 1825.

## Tribe Prionorhynchini Dana, 1851

Widely subpyriform. Pseudorostral lobes very short, lamellar, wide, fused, apically rounded, deflexed. Orbits consisting of supraorbital eave, intercalated spine, and postorbital lobe, all three closely approximated, closed ventrally. Postorbital lobe excavated anteriorly. Basal antennal segment greatly expanded laterally, in broad contact with postorbital lobe. Antennal flagellum short, excluded from orbit by process of basal antennal segment. Abdomen 7-segmented in both sexes. Type genus: *Jaquinotia* Rathbun, 1915 (= *Prionorhynchus* Jaquinot, 1853, nom. praeocc).

## Tribe Eurynomini Neumann, 1878

Subpyriform to subovate. Dorsal surface strongly tuberculate. Tubercles of carapace surface often boletate and more or less fused. Antennulae slightly oblique. Supraorbital eave lacking spines, intercalated spine small. Postocular lobe close to eye. Type genus: *Eurynome* Leach, 1814.

## Tribe Paramicippini Dana, 1851

Subpyriform. Pseudorostrum very short, flattened, deflexed, spines fused basally. Eystalk almost long, slender, projecting, not retractile, basally bulbous. Orbits very short, open below, eave reduced, barely covering base of eystalk, preorbital spine absent. Postorbital lobe lamellate, not excavate. Antennal peduncle long, not protected, flattened and dilated, last segment of antennal peduncle bent at right angle to fourth, directed laterally. Merus of third maxilliped wider than ischium, auriculate. Abdomen 7-segmented in both sexes. Type genus: *Pippacirama* Griffin & Tranter, 1986. (Type species: *Paramicippe tuberculosa* H. Milne Edwards, 1834).

+Subfamily ACTINOTOCARCININAE Jenkins, 1974

Suboval. Pseudorostrum odd, truncate. Orbits incomplete, intercalated spine present, postorbital spines large, biramous. Anterolateral margin with two large spines. Type genus: *Actinotocarcinus* Jenkins, 1974.

Subfamily MITHRACINAE MacLeay, 1838

Subpyriform, ovate to oblong-ovate, considerably widened anteriorly by orbits. Pseudorostrum more or less deflexed. Orbits mostly complete, tubular, often large, formed above by expanded basal antennal segment, supraorbital eave and postocular lobe. Eyes well protected by orbits. Anterolateral spine of basal antennal segment visible in dorsal view. Intercalated spine sometimes present. Antennal peduncle projecting rather far from front. First gonopod usually slender, straight to weakly curved, aperture terminal, apex simple to complex, sometimes expanded into 2 – 3 processes. Type genus: *Mithrax* Desmarest, 1823.

Tribe Mithracini MacLeay, 1838

Carapace widely subovate, usually longer than wide to slightly wider than long. Pseudorostrum very small. Orbits slightly projecting laterally, but not completely tubular. Intercalated spine sometimes present. Pereiopods robust, legs spinose. Abdomen in male 7-segmented. Type genus: *Mithrax* Desmarest, 1823.

Tribe Micippini Dana, 1851

Oblong to nearly subquadrilateral. Pseudorostral spines wide, flattened, proximally fused, deflexed strongly downwards. Orbits incomplete below, consisting by tube-like supraorbital eave, preorbital, postorbital and intercalated spines, fissure between postocular spine and basal antennal segment. Type genus: *Micippa* Leach, 1817.

Tribe Thoini Števcíć, 1994

Subtriangular to triangulo-subovate, not very thick. Tubular orbits not projecting laterally beyond general outline of carapace. Preorbital spine absent. Intercalated spines present. Meri of ambulatory legs with thin, lamellate, posterior expansion. Abdomen 7-segmented in both sexes. Type genus: *Thoe* Bell, 1835.

Tribe Pericerini Dana, 1851

Subdeltoid, subpyriform, to suboblong, thick, widened anteriorly by projecting orbits. Pseudorostral spines long, slender, cylindrical. Orbits usually tubular, neither completely closed nor very projecting. Intercalated spine absent. Abdomen 7 – segmented in both sexes. Type genus: *Macrocoeloma* Miers, 1879 (= *Pericera* H. Milne Edwards, 1834 partim).

Tribe Coelocerini trib. nov.

Widely subovate, swollen, spinose. Pseudorostrum long, hollowed out ventrally in form of gutter, flanked by antennae, apically bifid. Eyestalks stout. Orbits not completely tubular, with narrow dorsal and ventral buttonhole fissures dorsally and ventrally. Preorbital angle spiniform. Postorbital cup large, squarish, armed by

two spines, projecting laterally. Basal antennal segment thick, quadridentate. First gonopod apically expanded with prominent median lobe. Type genus: *Coelocerus* A. Milne Edwards, 1875.

#### Subfamily PLANOTERGINAE Števcíć, 1991

Irregularly subrectangular. Dorsally flat, smooth, ventrally convex. Lateral and posterior margins slightly cristiform. Front projecting beyond orbits, lamellar, wide, anteriorly truncated. Eystalks short, eyes unprotected. Antennulae oblique. Forth antennal segment lamellar, quadrangular, exposed dorsally, fifth segment lamellar, small, flagellum minute. Epistome reduced. Prostomial chamber present. Third maxillipeds not covering buccal cavity completely. Chelipeds minute, not visible in dorsal view. Ambulatory legs short, crestiform, distal segments in same plane as carapace. Telson very small in both sexes. Type genus: *Planotergum* Balss, 1935.

#### Subfamily TYCHINAE Dana, 1851

Oblong-subovate, convex in both directions, truncate in front. Eystalks long, retractile. Orbits incomplete, supraorbital eave very expanded, preorbital spine horn-like, intercalated spine lacking, postorbital spine small to absent, if present remote from eye. Merus of third maxilliped as wide as ischium, often auriculate. First gonopod slender, slightly curved, apices lyrate, aperture terminal to subterminal. Abdominal segments 7-segmented in both sexes. Type genus: *Tyche* Bell, 1835.

##### Tribe Tychini Dana, 1851

Oblong-subovate, truncate anteriorly. Eyes partially protected above by lamellar projection consisting of expanded supraorbital eave and outgrowth of hepatic region. Eystalks long, retractile. Orbit unprotected ventrally. Merus of third maxilliped as wide as ischium, ischium-merus articulation S-shaped, exognath with basal falciform prolongation lodged in groove of ischium of endognath, merus extending backward into ischium. First gonopod slender, weakly curved, apices outcurved, aperture terminal or subterminal. Type genus: *Tyche* Bell, 1835.

##### Tribe Othonini Dana, 1851

Oblong, elongate. Fronto-orbital margin broadly truncate, wide. Pseudorostrum minute. Orbits small, deep, completely closed, often outstanding tubular, projecting beyond general outline of carapace. Postocular lobe present. Antennae short, with stiff hairs on margins, basal segment lamellate, forming floor of orbit, segment 4 flat, short, wide, lamellate, with leaf-like outer expansion, segment 5 small, flattened. Abdomen 7-segmented in both sexes. Type genus: *Pitho* Bell, 1835 (= *Othonia* Bell, 1836)..

##### Tribe Thersandrini trib. nov.

Oblong-ovate, depressed. Dorsal surface setose. Pseudorostrum bifid, long, narrow, flattened, slightly deflexed. Eystalks slender. Orbits tubular, deep, not projecting beyond general outline of carapace, preorbital spine lacking. Basal antennal segment very wide closing orbit bellow, segment 4 large, slightly flat, flagellum small. Antennal peduncles depressed, long, projecting, fringed with long setae on

each side, flagellum small. Merus of third maxilliped auriculate, palp short. Ambulatory legs folded forward, feather-like, bordered by thick fringes of long setae, dactyli very slender, hooked, sharp, strongly folded under propodus, subprehensile. Abdomen 7 – segmented in both sexes. Type genus: *Thersandrus* Rathbun, 1897.

#### Subfamily PISINAE Dana, 1851

Subpyriform to subdeltoid. Pseudorostrum almost bifid. Eystalks short. Orbits incomplete. Supraorbital eave prominent, usually with distinct preorbital spine. Postorbital tooth or lobe large, blunt, cupped, usually isolated. Basal antennal segment wide, anterior angle produced to form tooth or spine. Intercalated spine sometimes present. Merus of third maxilliped usually distinctly auriculate, wider than ischium. Legs often long. First gonopod usually slender, gently curved, apical portion sometimes slender, apex simple, aperture usually terminal. Type genus: *Pisa* Leach, 1814.

##### Tribe Pisini Dana, 1851

Subpyriform to subdeltoid. Pseudorostral spines small, cylindrical, basally fused, distally diverging. Preorbital spine long. Intercalated spine present. Abdomen almost 7-segmented in male, 7 – 5 segmented in female Type genus: *Pisa* Leach, 1814.

##### Tribe Amathini Dana, 1851

Subdeltoid to subpyriform, rather wide, thick. Pseudorostral spines slender, diverging. Supraorbital eave and postorbital lobe not closely approximate, orbits open above by distinct hiatus. Intercalated spine almost absent. Ambulatory legs long. Abdomen 7-segmented in both sexes, sometimes 5-segmented in female. Type genus: *Rochinia* A. Milne Edwards, 1880 (= *Amathia* Roux, 1828).

##### Tribe Libinini Dana 1851

Suboblong to subpyriform. Pseudorostral spines basally coalesced. Supraorbital eave and postorbital lobe closely approximated. Basal antennal segment enlarged. First gonopod apically expanded with prominent median lobe. Abdomen usually 7 – segmented in both sexes, sometimes 5-segmented in female. Type genus: *Libinia* Leach, 1815.

#### Subfamily PLIOSOMINAE Števčić, 1994

Subovate. Dorsal regions defined, with sparse blunt spines. Front very narrow. Pseudorostrum medially fissured. Orbit longitudinally extended composed by eave and postorbital lobe. Exorbital spine distinct. Epistome very short, nearly obsolete, covered by third maxillipeds. Basal antennal segment filling orbital hiatus. Chelipeds long. Third maxilliped elongated, approaching to base of antennulae. Two anterior pairs of legs cylindrical. Two posterior pair of legs strong. Dactyls of legs 3 – 4 compressed, fringed with setae, dactyli natatorial. Thoracic sternum wide, posteriorly narrowed. First gonopod nearly straight, apically bilobed. Abdominal segments in male freely articulating. Type genus: *Pliosoma* Stimpson, 1860.

## Subfamily EPIALTINAE MacLeay, 1838

Subdeltoïd. Lateral margin often lamellate. Pseudorostrum double to single. Orbits very sunken, reduced, never entirely concealing cornea, postorbital spine sometimes present, intercalated spine absent. Eyestalks short, feebly movable to immovable, either concealed by preorbital and/or postorbital spine or sunken in sides of large beak-like pseudorostrum. Basal antennal segment trapezoidal. Merus of third maxilliped as wide as ischium sometimes auriculate. First pair of ambulatory legs longer than other three pairs. Dactyli of ambulatory legs prehensile or subchelate. First gonopod usually slender, weakly curved, aperture usually terminal, apex simple or expanded into lobes. Abdominal segments from freely articulating to variously fused. Type genus: *Epialtus* H. Milne Edwards, 1834.

## Subfamily EURYNOLAMBRINAE Števc̃ić, 1994

Transversely subelliptical, much wider than long, depressed. Carapace vaulted, concealing ambulatory legs. Pseudorostrum short, bilobed. Orbits composed by eave, postorbital lobe and intercalated spine. Basal antennal segment large, projecting, visible in dorsal view. Ambulatory legs crested. First gonopod slender, proximally straight, distally curved, apex complex. Type genus: *Eurynolambrus* H. Milne Edwards & Lucas, 1841.

## Subfamily INACHINAE MacLeay, 1838

Subtriangular, subpyriform to subcircular. Orbits absent. Eyestalks generally long, non-retractile or retractile against sides of carapace or acute postorbital spine, not concealed. Basal antennal article usually slender, subcylindrical throughout its extent, usually long, flattened or channelled ventrally, usually free distally. Urinal opening usually distant from base of antennae. Merus of third maxilliped usually narrower than ischium. Pereiopods long, slender. First gonopod distally rather slender, simple, straight to slightly curved, opening terminal or subterminal, sometimes protected by flap. Type genus: *Inachus* Weber, 1795.

## Tribe Eurypodini MacLeay, 1838

Elongate subtriangular. Dorsal surface of carapace lacking long spines. Pseudorostral spines narrow, partly contiguous. Supraorbital eave unarmed, smooth. Intercalated, postorbital and interantennular spines distinct. Merus of third maxillipeds as wide as ischium. Ambulatory legs long, prehensile, propodi more or less dilated, compressed. Abdomen 7-segmented in both sexes. Type genus *Eurypodius* Guérin 1825.

## Tribe Pleistacanthini trib. nov.

Subtriangular to subpyriform. Carapace hairy and very spinose. Pseudorostrum formed by two slender spines, sometimes with accessory spinules. Supraorbital eave weakly produced, margins nearly straight, sometimes spinose. Interantennular spine well developed (often bifid). Urinal pores close behind of base of antennae. Basal antennal segment very slender more or less movable, often spinose. Postorbital cup present, preorbital and intercalated spines usually present. Carpus of chelipeds spinose or tuberculate. Abdominal segments freely articulated in both sexes, sometimes female with pleotelson. Type genus: *Pleistacantha* Miers, 1879.

## Tribe Macrocheirini Dana, 1851

Subcircular. Pseudorostral spines short, curved outwards. Preorbital, intercalated and postocular spines distinct, posterior angle of supraorbital eave produced into spine. Interantennular septum well developed, with spine. Chelipeds cylindrical, extremely long. Abdominal segments freely articulated in both sexes. Type genus: *Macrocheira* de Haan, 1839.

## Tribe Macroregoniini trib. nov.

Oblong-ovate. Dorsal surface of carapace alike to human mask. Pseudorostral spines short, slender. Orbits composed by supraorbital eave and basal antennal segment. Interantennular spine projecting downward, perpendicular, sulcate. Telson impressed into segment 6. Type genus: *Macroregonia* Sakai, 1978.

## Tribe Camposcini Dana, 1851

Elongate subpyriform. Carapace and pereopods densely covered with long hooked setae and bristles. Pseudorostral spines highly obsolete, not concealing antennular basal segments. Frontal margin with shallow median sinus. Eystalks long, strongly curved. Preorbital spine absent, postorbital spine or lobe small. Intercalated spine reduced to absent. Antennal peduncle long, flattened, densely hairy. Antennular fossae coalesced into single cavity. Basal antennal segment immovable. Abdominal segments freely articulating in both sexes. Type genus: *Camposcia* Latreille, 1829.

## Tribe Ehippiini trib. nov.

Elongate-subdeltoid. Pseudorostral spines long, separated from base. Supraorbital eave narrow, unarmed, lacking pre- and antorbital spines, nuchal spine small, far from orbit. Basal antennal segment slender, with distinct anterior spine. Antenna excluded from orbit. Pereiopods very long. Abdominal segments freely articulated in both sexes. Type genus: *Ehippias* Rathbun, 1918.

## Tribe Anomalopini Stimpson, 1871

Cephalothorax very elongated, subdeltoid, almost subcylindrical. Pseudorostrum very long, distally bifurcated. Eystalks short, thick. Orbits absent, preorbital and postorbital spines small, acute. First two pair of legs long, two last pair of legs shorter, prehensile. Abdominal segments freely articulated in both sexes. Type genus: *Anomalothir* Miers, 1879 (= *Anomalopus* Stimpson, 1871).

## Tribe Oregoniini Garth, 1958

Subtriangular to subpyriform. Pseudorostral spine long, slender. Preorbital spine absent. Postorbital spine large, remote from eye. Basal antennal segment narrow. Ambulatory legs of moderate size. First gonopod with bulbous base, distally lanceolate, longitudinally grooved with rows of filamentous setae on either side of groove. Abdominal segments free-articulated in both sexes. Male abdomen terminally widened, telson deeply inserted into segment 6. Type genus: *Oregonia* Dana, 1851.



## Tribe Trichoplatini trib. nov.

Subpyriform. Pseudorostrum strongly deflexed. Supraorbital eave moderately produced, margin convex, smooth, postorbital spine distant, intercalated spine absent. Basal antennal segment narrow, straight-sided, with antero-external spine. Third maxillipeds subpediform, merus crested. All ambulatory legs flattened, prehensile, propodi greatly expanded, truncate distally, dactyli slender, feebly curved, apically acute. Abdomen 6 – segmented (pleotelson present) in both sexes. Type genus: *Trichoplatus* A. Milne Edwards, 1876.

## Tribe Grypachaeini trib. nov.

Narrowly pyriform. Neck long. Dorsal surface very hairy and spiny. Pseudorostrum spiny, short spines diverging. Interantennular spine strong, deflexed. Eyes-talks retractile backwards, bot concealed. Supra- and postorbital spine small. Basal antennal segment proximally fused to epistome, distally free, similar to peduncle. Merus of maxilliped narrow, elongate. Last pair of legs subchelate, prehensile, propodus and dactylus armed ventrally with numerous spinules. Abdomen with pleotelson, in male 6-segmented, in female 5-segmented. Type genus: *Grypachaeus* Alcock, 1894.

## Tribe Chorinachini trib. nov.

Elongate, narrowly pyriform. Pseudorostrum long, spines fused most of their length, accessory spines present, apically bifid. Orbital eave weakly expanded, pre-orbital spine small, antorbital spine lacking, postorbital spine small, remote from eye. Interantennular spine lacking. Antennae excluded from orbit. Basal antennal segment narrow, with strong anterolateral spine. Merus of third maxilliped strongly auriculate. Abdomen in male 7-segmented, 5-segmented in female (4 – 6 fused). Type genus: *Chorinachus* Griffin and Tranter, 1986.

## Tribe Sunipeini trib. nov.

Pyriform, slender. Dorsal surface with few spines or tubercles, intestinal spine very distinct, hepatic margin with slender spine. Pseudorostral spines fused basally, diverging distally, margins with spinules. Preorbital spine slender, antorbital lobe small, postorbital lobe lacking. Interantennular spine lacking. Merus of third maxilliped strongly auriculated. Abdomen in male 7 – segmented. Abdomen in female with junction between segments 4 – 6 indistinct. Type genus: *Sunipea* Griffin and Tranter, 1986

## Tribe Inachini MacLeay, 1838

Subpyriform, slender. Pseudorostral spines short. Carapace with two dorsal spine in midline interantennular spines well developed. Postocular lobe cupped, basally wide. Eyestalk short, nearly straight. Basal antennal segment extremely slender and usually long. Abdomen with pleotelson. Type genus: *Inachus* Weber, 1795.

## Tribe Leptopodiini Bell, 1844

Elongate-subtriangular. Dorsal surface smooth. Pseudorostrum single, extremely long, armed with numerous spinules on lateral margin. Orbits not defined, post-orbital spine small. Antennae long, slender. Basal antennal segment convex ven-

trally. Merus of third maxilliped usually narrower than ischium, palp large, coarse. Chelipeds slender, ambulatory legs extremely long, spinose. Last pair of legs dorsal in position. Abdomen 6-segmented in male, 5-segmented in female. Type genus: *Stenorhynchus* Lamarck, 1818 (= *Leptopodia* Leach, 1818).

Tribe Alcockiini trib. nov.

Ovate-triangular. Pseudorostral spines short, emarginate, bifid, spines basally fused. Preorbital and postorbital spines large, prominent. Hepatic region lacking spine. Epibranchial spines very distinct. Eyes slender, retractile against strong postorbital spine, not completely concealed. Basal antennal segment narrow, anteriorly bidentate. Ambulatory legs short, prehensile. Abdomen of female 5-segmented. Type genus: *Alcockia* gen. nov. (Etymology: according to the British carcinologist Alfred W. Alcock). Gender: feminine. (Type species: *Collodes malabaricus* Alcock, 1895).

Tribe Eucinetopini trib. nov.

Suboblong, wide. Front depressed, bilobed. Pseudorostrum short, bifid, slightly deflexed, pseudorostral lobes tipped with small sharp upturned spines. Anterolateral margins converging, nearly straight. Eystalks very long, slender, exposed from bulbous base. Orbits reduced, filled by eyes, intercalated spine lacking, postorbital spine well developed cupped, upturned. Basal antennal segment small, slightly longer than wide, segment 4 foliaceous, wide, segment 5 much narrower, both exposed laterally to pseudorostrum. Merus of third maxilliped as wide as ischium, very auriculate, palp short, thick. Abdomen 7 – segmented in both sexes. Type genus: *Eucinetops* Stimpson, 1860.

Tribe Encephaloidini trib. nov.

Heart-shaped, as wide as long. Branchial region extremely inflated, approximated in midline. Pseudorostrum simple, beak-like, wide. Orbits incomplete. Supraorbital eave feebly expanded. Preorbital lobe small. Postorbital lobe small, like conical tubercle, removed far from eye. Basal antennal segment slender, fixed. Antennae excluded from orbits. Merus of third maxilliped as wide as ischium, produced antero-externally forming foliaceous lobe covering enlarged respiratory efferent opening. Abdominal segments in male freely articulated, segments 4 – 6 immovable in female. Type genus: *Encephaloides* Wood Mason, 1891.

+Subfamily MICROMAJINAE Beurlen, 1930

Pyriform. Carapace regions well developed. Orbits absent. Basal antennal segment freely articulated. Type genus: *Micromaja* Bittner, 1875.

Subfamily ONCINOPINAE Dana, 1852

Elongate, rounded triangular, depressed. Exoskeleton imperfectly calcified. Dorsal surface lacking spines. Pseudorostrum obtusely bilobed. Posterior margin wide, nearly straight. No orbits. Eyes not retractile in orbits, no teeth or spines around eyes. Antennulae obliquely folded, interantennular septum reduced, antennulae in contact with each other. Basal antennal segment short, cylindrical, very slender, distally free, movable, segment 4 bent, flagellum long. Urinal pore not in contact with

basal antennal segment. Merus of third maxilliped elongate, palp articulated at summit. Two anterior pairs of legs compressed and dilated, with two rows of very long hairs, two posterior pairs of legs subchelate, last pair subdorsal in position. First gonopod twisted about 3 times. Abdomen 7-segmented in both sexes. Type genus: *Oncinopus* de Haan, 1839.

### Family INACHOIDIDAE Dana, 1851

Cephalothorax almost subpyriform or widely triangular. Regions well defined. Pseudorostrum short. Front not very narrow. Orbits absent. Eyestalks stout, far projecting, usually not retractile, or retractile against strong postorbital lobe, or carapace sides. Postorbital lobe usually very distinct, projecting laterally. Basal antennal segment flattened or concave ventrally, fused with neighbouring parts, peduncle sometimes visible from above. Buccal cavern elongate. Merus of third maxilliped usually cordiform, usually as wide as ischium, palpus short. Legs long, slender, coxae visible dorsally. Sternum flat, wide, nearly subcircular. Sterno-abdominal cavity long. Coxae of pereopods separated by pleuro-sternal trabecula. Pleurites almost horizontal. Lateral edges of carapace inserted into setting gutter of pleural walls. Lateroexternal parts of pleurites extending beyond each side of carapace. Pleural plates between carapace and sternites visible dorsally. True branchiostegite absent. Endophragmal skeleton with both dorso-ventral partition and lateral compartment, with formation of vertical pilars in anterior region. Male sexual opening coxo-sternal, far from suture 7/8. First gonopod nearly straight, distally tapering, apically pointed, sometimes with lateral prolongation, aperture subapically, laterally. Abdomen with pleotelson in both sexes, male abdomen 6-segmented (6 + 7 fused), female 5-segmented (5 – 7 fused). First abdominal segment fused to carapace. Type genus: *Inachoides* H. Milne Edwards & Lucas, 1843.

#### Tribe Collodini Stimpson, 1871

Cephalothorax subovate-subpyriform to triangular, depressed. Pseudorostrum bifid, shorter, or not longer, than its basal width. Branchial region usually flattened. Postorbital lobe usually well developed. Antennal peduncle usually not slender, rarely slender. Interantennular septum narrow, spine rarely present. Merus of third maxilliped obcordate, as wide as or wider than long. Type genus: *Collodes* Stimpson, 1860.

#### Tribe Inachoidini Dana, 1851

Subpyriform, subtriangular to subovate. Pseudorostrum single, subtriangular, shorter, or not longer than its basal width, spiniform. Postorbital spine distinct to indistinct. Antennal peduncle slender. Merus of third maxilliped as wide as ischium, basally narrow, palp of moderate size. Type genus: *Inachoides* H. Milne Edwards & Lucas, 1843.

#### Tribe Salacini Dana, 1851

Broadly suborbicular, depressed, regions defined. Postorbital cup large, close to orbit. Pseudorostrum single, very short, subtriangular, narrow. Eyestalks short, retractile. Orbits large, open dorsally and ventrally, directed forward. Basal antennal segment wide, reaching tip of pseudorostrum, with lateroexternal lobe. Peduncles

well developed, depressed, far projecting. Epistome reduced. Merus of third maxilliped cordiform. Sternal sutures 2/3 – 3/4 marked. Type genus: *Leurocyclus* Rathbun, 1897 (= *Salacia* H. Milne Edwards & Lucas, 1844).

**Majoidea (?) *incertae sedis***

### Family LAMBRACHAEIDAE Števčić, 1994

*Stenorhynchus*-like, extremely elongate. Pseudorostrum single, markedly longer than carapace proper, spinose laterally with strong ventral spine. Anterior part of cephalothorax prominently elongate to form very long »neck« at least as long as remainder carapace, posterior part posteriorly rectangular. Dorsal regions hardly discernible. Antennulae with long flagellum, nearly longitudinally folded. Antennae short, cylindrical, slender, basal antennal segment short, cylindrical near to urinal opening, segment 5 and flagellum with toothed spines. Eyes large, mobile, not retractile. Orbits poorly defined, very shallow, reduced dorsally, with three supra-orbital spines, open ventrally. Postorbital spine long, infraorbital spine small. Epistome extremely long. Proepistome (interantennular septum) compressed, with strong ventrally directed spine. Buccal frame with strong, dorsally visible curved spine. Third maxillipeds narrow, spinose, merus much shorter than ischium, palp well developed. Pereiopods extremely elongate, longer than carapace, slender, chelipeds spinose, triangular in cross section, slightly heterochelous, fingers short, dentate. Ambulatory legs unarmed. First gonopod stout, tip spinose, second gonopod longer than first gonopod, flagellum much shorter than basal peduncle, cup distinct. Abdominal segments 3 – 5 fused in male, freely segmented in female. Type genus: *Lambrachaeus* Alcock, 1895.

### Family PARATYMOLIDAE Haswell, 1882

Elongate, ovoid to subpentagonal, slightly convex, regions indistinct. Anterolateral margin dentate, shorter than posterolateral. Exoskeleton imperfectly calcified. Lateral carapace margins, pereiopods and third maxillipeds usually covered with scale-like pubescence, sometimes smooth. Front very short, obtusely bilobed. Eyes well developed, not retractile. Orbits composed by feebly developed unarmed supraorbital eave and feebly developed postorbital spine. Antorbital angle sometimes present. Antennulae and antennae well developed. Antennular cavities in contact with each other. Interantennular septum reduced, lacking spine. Basal antennal segment short, wide, cylindrical, movable, anteriorly not fused to carapace. Urinal pores close to basal antennal segments. Posterior margin wide, straight. Epistome very narrow, sunken. Third maxillipeds partly covering epistome, ischium wider than merus. Carpal spine of chelipeds distinct, palm compressed. Ambulatory legs short, compressed, in usual position, dactyli claw-shaped. Sternites 5 – 8 subparallel, sutures 4/5 – 7/8 entire (check in all genera). First gonopod variously shaped, usually stout and C-shaped, or long, slender, apically tapering, basal segments fused forming transverse plate (check in all genera). Abdomen in male 5-segmented (segments 3 – 5 fused), 7 – segmented in female, telson triangular in both sexes. Type genus: *Paratymolus* Miers, 1879.

## **Superfamily HYMENOSOMATOIDEA MacLeay, 1838**

Characters as for the family.

### **Family HYMENOSOMATIDAE MacLeay, 1838**

Cephalothorax oxyrhynchous-shaped (anteriorly narrowed), remarkably thin. Dorsal surface almost flat, smooth, with special hymenosomidean grooves encircling dorsal surface of carapace. Cuticle poorly calcified. Antennular fossae poorly developed. No orbits. Antennulae long, slender, longitudinally directed. Antennae short, cylindrical, segments not fused, fused only with epistome. Standing loosely in large orbital hiatus. Epistome reduced to absent. Palp of third maxilliped articulated near antero-lateral angle of merus. Sternal sutures 1 – 3 forming shield prolonged between third maxillipeds, sutures 4/5 – 7/8 interrupted, confined laterally, radially directed. Incubation pocket within cephalothorax sometimes present. First gonopod various in form, second shorter. Inhalant opening on pterygostome ahead bases of chelipeds. Transformed intercalated plates into sockets on abdominal segment 6. Press-button apparatus modified, intercalated plates distinct, from movable to fused with pleotelson. Male sexual opening coxo-sternal. First gonopod ranging from stout to slender, straight to very curved, second gonopod small. Broad cavity within abdomen and posterior portion of carapace often present. Abdomen not covering completely sternite 8. Abdominal segments 6 – 7 always fused in both sexes (forming pleotelson) and often other segments. Type genus: *Hymenosoma* Desmarest, 1825.

## **Superfamily TROGLOPLACOIDEA Guinot, 1986**

Characters as for the family.

### **Family TROGLOPLACIDAE Guinot, 1986**

Subrounded, wider than long. Dorsal surface smooth. Exoskeleton thin. Front nearly straight, deflexed. Median notch minute to absent. Anterolateral margin entire to dentate, arched, cristate, angle indistinct. Eyes small. Supraorbital margin entire, confluent with frontal and anterolateral margins. Antennular flagella folding transversely into their fossae. Antennal peduncle entering orbit. Interantennular septum thin. Buccal cavity quadrangular, large, covered almost completely by third maxillipeds. Third maxillipeds short, wide, merus subquadrangular, about as long as wide, slightly shorter than ischium, exognath moderately wide, with flagellum. Chelipeds slightly unequal, fingers uncoloured. Sternum wide, sterno-abdominal cavity deep. Sternal sutures 4/5 – 7/8 interrupted. Abdomen far from coxae of last pair of legs. Lateral portion of sternite 8 uncovered. Male sexual opening coxo-sternal. Penial tube on sternite 8, supplementary plate present. First gonopod stout, nearly straight, gently sinuous, gradually tapering, apex simple, aperture apical. Second gonopod subequal in length or longer than first gonopod, with flagellum about same length as peduncle. Abdominal segments 3–5 fused in male, far from coxae, large part of sternite 8 uncovered. Type genus: *Trogloplax* Guinot, 1986.

## Superfamily ORITHYIOIDEA Dana, 1852.

Characters as for the family.

### Family ORITHYIIDAE Dana, 1852

Cephalothorax elliptically-globose, slightly longer than wide. Dorsal surface with large tubercles symmetrically distributed in centre of each region. Front tridentate (antennular sinuses). Lateral margins with strong spines. Posterior margin very rounded, narrow. Orbits not separated from antennular fossae. Inner infraorbital angle long, projecting. Exorbital angle distinct. Antennulae long, plicated obliquely. Antennae smaller than antennulae, basal antennal segment movable, standing loosely in orbital hiatus, with antero-external lobus entering orbit. Merus of third maxilliped subtriangular, elongate, pointed anteriorly, covering short, deep endostomial paired tubes formed by anterior portion of endostome. Exognath of third maxilliped short, lacking flagellum. Chelipeds compressed, fitted to carapace. Last pair of legs paddle-like. Thoracic sternum subcircular, flat, wide. Sternal sutures 4/5 – 7/8 interrupted near median line. Sterno-abdominal cavity short. Penis partly encased in smooth, sclerotized sheath. First gonopod short, finger-like (basally thick, distally straight) subdistally spinulose. Second gonopod relatively long, flagellum long. Abdomen very short, triangular. Abdominal segments 3 – 6 immovable in male, sutures distinct, locking mechanism lacking. In male considerable portion of sternite 8 visible laterally. Female abdomen 7-segmented. Vulva not covered by abdomen. Type genus: *Orithyia* Fabricius, 1798.

### Superfamily BELLIOIDEA Dana, 1852

Cephalothorax varying from transversely elliptical to elongated. Frontal and posterior margins rather narrow. Antennulae well developed, plicated obliquely. Antennal peduncle markedly reduced to microscopical. First gonopod stout, distally tapering, curved, short. Second gonopod shorter than first, flagellum short. Male sexual opening coxal. Abdominal segments 3 – 5 fused in male. Type genus: *Bellia* H. Milne Edwards, 1848.

### Family HETEROZIIDAE fam. nov.

Subhexagonal, transversely elliptical (*Ozius*-shaped). Frontal margin arched, feebly bilobed. Anterolateral margin much longer than posterolateral, posterior margin narrow, slightly concave. Eyes well developed, not protected. Orbito-antennular cavity containing eyes, antennulae and antennae. Antennulae well developed, plicated obliquely, nearly transversely. Antennae reduced in size, movable. Basal antennal segment stocky, narrowing distally. Peduncle reduced in size, flagellum minute. Third maxilliped short, merus auriculate. Sternal sutures 4/5 – 7/8 interrupted. First gonopod stout, curved, bifid terminally. Second gonopod shorter than first, slightly curved. Abdomen covering nearly complete width of sternum with exception of minute portion between segments 1 – 2. Type genus: *Heterozius* A. Milne Edwards, 1867.

### Family BELLIIDAE Dana, 1852

Subcircular to suboblong. Antennular fossae and orbital cavities absent. Antennulae well developed, not retractile, subparallel, directed forward. Antennal peduncle extremely reduced, microscopical. Proepistome and epistome short, sunken, covered with third maxillipeds. Male sexual opening coxal. First gonopod basally wide, distally tapering, curved, with long hairs, apex sclerotized. Second gonopod shorter than first. Small portion of sternite 8 uncovered by abdomen. Type genus: *Bellia* H. Milne Edwards, 1848.

#### Subfamily ACANTHOCYCLINAE Dana, 1852

Cephalothorax subcircular. Orbits complete. Basal antennal segment voluminous and closing orbital hiatus, segment 4 small, fifth microscopical. Buccal cavern quadrangular. Merus of third maxilliped short, wide. Sternal suture 6/7 interrupted near median line, 7/8 entire. Two small portions of sternite 8 uncovered by abdomen. Type genus: *Acanthocyclus* Lucas 1844.

#### Subfamily BELLIINAE Dana, 1852

Elongated. Front trilobed or tridentate. Eyes long, not retractile into their fossae. Antennulae long, directed forward, subparallel, apically hairy, forming tube. Vestige of peduncle minute. Buccal cavern narrowing anteriorly. Third maxillipeds elongate, pediform. Prostomial chamber present. Type genus: *Bellia* H. Milne Edwards, 1848.

#### Tribe Corystoidini trib. nov.

Urn-shaped. Front three-lobed (antennular sinuses). Eyestalks long. Orbits completely closed. Antennulae very long, longitudinal. Ambulatory legs compressed, dactyli long, slender. Sternum ovate, relatively narrow. Vulvae covered with abdomen. Sternal sutures 6/7 – 7/8 entire. Type genus: *Corystoides* Lucas 1844.

#### Tribe Belliini Dana 1852

Elongate. Eyestalks short. Orbits nearly complete. Pterygostomial projection large, projecting laterally, visible in dorsal view. Vulvae not covered with abdomen. Sternum wide. Sternal sutures 4/5 – 7/8 interrupted. Type genus: *Bellia* H. Milne Edwards, 1848.

### Superfamily DORIPPOIDEA MacLeay, 1838

Characters as for the family.

### Family DORIPPIDAE MacLeay, 1838

Subtrapezoidal, elongate-hexagonal, subquadrangular to subcircular, as long as wide or slightly wider than long, widest posteriorly, usually flat. Dorsal surface typically strongly sculptured (sometimes giving impression of human mask). Front of moderate width, frontal lobes separated with deep V- (or U) – shaped median

notch. Supraorbital margin deeply fissured. Inner supraorbital angle sometimes present separating antennular and antennulo-ocular sinuses. Frontal and exorbital angles often strong and projecting. Antennulae and antennae large, directed obliquely. Buccal cavern and mouthparts elongated and anteriorly narrowed, not covered completely with third maxillipeds anteriorly. Endostome produced forward to form gutter. Floor of exhalent channel formed by calcified endopod of first maxilliped. Merus of third maxilliped much narrower than ischium, so gaping especially between meri, exognath lacking flagellum. Chelipeds stout, short. Two anterior pairs of legs strong, long, two posterior pairs of legs reduced in size, turned upwards, forming small subchela. Sternum very wide, projecting behind posterior margin, Posterior part of thoracic sternum inverted, sternite 8 facing dorsally. Sternal sutures 4/5 – 7/8 interrupted. First gonopod very variable second gonopod more or less as long as first one. Around penis smooth sclerotized sheath. Abdominal segments 1–3 dorsally exposed, not reaching coxae of last pair of legs, portion of sternite 8 uncovered. Type genus: *Dorippe* Weber, 1795.

#### Subfamily DORIPPINAE MacLeay, 1838

Cephalothorax cordiform, subtrapezoidal. Dorsal surface strongly sculptured. Front bilobed. Anterior extremity of buccal cavern and endostomial groove reaching frontal margin, anterior part sometimes visible in dorsal view. Inhalant opening separated from base of chelipeds by narrow process of carapace reaching sternum. Chelipeds unequal. Exognath of third maxilliped lacking flagellum. Two posterior pairs of legs subdorsal, reduced, chelate, prehensile, dactylus closing against tubercle on propodus. Thoracic sternum very wide anteriorly, narrow posteriorly. Vulva placed near to locking prominence. Sternal suture 5/6 curved medially around sternal button and in front of vulva. Male sexual opening coxal. First gonopod long, apex complex with lobes and projections, second gonopod sometimes shorter than first. Abdominal segments freely articulated in both sexes. Type genus: *Dorippe* Weber, 1795.

#### Subfamily ETHUSINAE Guinot, 1977

Cephalothorax subquadrangular, ovate to cordiform. Dorsal surface flat, smooth. Front four-lobate. Antennular and antenno-orbital sinuses well defined. Eyes sometimes placed ventrally. Anterior extremity of buccal cavern not reaching frontal margin. Merus of third maxilliped very narrow, lacking flagellum. Inhalant opening contiguous to base of cheliped. Last two pairs of legs not subchelate, dactyli short and claw-shaped. Portion of sternite 8 exposed dorsally. Thoracic sternum moderately wide. Suture 5/6 normally directed. Male sexual opening coxo-sternal. Penial tube between sternites 7/8 First gonopod slightly curved, rather short, second gonopod long, sometimes longer than first, flagellum longer than basal peduncle. Abdominal segments 3 – 5 fused in male, in female freely articulated. Type genus: *Ethusa* Roux, 1830.

### Superfamily PALICOIDEA Bouvier, 1898

Characters as for the family.



### Family PALICIDAE Bouvier, 1898

Subquadrilateral, roundish, widely transverse, almost depressed. Dorsal surface granular, often with tubercles of varying size. Front of moderate width, bilobed to four-lobed, median notch distinct. Anterolateral margin 4 – 1 spinose or lobate. Posterior margin wide. Eyes long, orbits deep, wide. Supraorbital margin with two distinct incisions, separating two lobes. Exorbital and inner infraorbital angles well developed. Antennulae long, transverse. Basal antennal segment cylindrical, directed longitudinally, freely movable. Interantennular septum narrow. Pterygostomial lobe well developed, often projecting, visible dorsally. Buccal cavern square. Third maxilliped not covering completely buccal cavern. Prostomial chamber present. Ischium of third maxilliped with strong antero-internal projection, merus very small, subtriangular, with notch on inner distal side for articulation of carpus. Chelipeds smaller than ambulatory legs. Ambulatory legs elongated. Meri of legs strong, compressed, distal segments slender. First pair slender, last pair of legs very reduced in size. Sternum large, suture 3/4 entire, sutures 4/5 – 7/8 interrupted. Sternite 8 reduced, laterally not completely covered by abdomen. Male sexual opening coxosternal. Penial tube over suture 7/8. First gonopod very variable, usually relatively short, basally helicoidal or sinuous, distally uniramous or biramous with complex apices, second gonopod short. Vulva large, apparently on sternite 5, actually on sternite 6. Distal abdominal segments often with more or less developed transversal ridges, third segment widest in male. Type genus: *Palicus* Philippi, 1838.

#### Subfamily CROSSOTONOTINAE Moosa and Serène, 1981

Dorsal surface of carapace relatively relatively flat. All margins dentate to tuberculate. Last pair of legs reduced in size, but of usual shape and position, with articulation to carapace at same level as walking legs. Epistome very narrow, not expanded dorsoventrally. Sternite 8 at same level as anterior ones. Episternal processes lacking. Abdominal segments freely articulated in both sexes, segments 1 – 2 wide in both sexes, not very depressed. Type genus: *Crossotonotus* A. Milne Edwards, 1873.

#### Subfamily PALICINAE Bouvier, 1898

Dorsal surface of cephalothorax slightly convex. Anterolateral margin dentate to tuberculate. Epistome dorsoventrally widened. Last pair of legs very reduced in size, filiform, almost subdorsal in position, articulation to carapace dorsal to walking legs. Sternite 8 reduced in size and upturned in relation to remaining sternal plastron. Often with distinct episternal process of sternite 7 posterior to last pair of legs visible dorsally. Abdominal segments 1 – 2 depressed and narrower than remaining segments, some segments may be fused in male. Type genus: *Palicus* Philippi, 1838.

### Superfamily RETROPLUMOIDEA Gill, 1894

Characters as for the family.

### Family RETROPLUMIDAE Gill, 1894

Transversely subquadrangular to oval, depressed. Dorsal surface with two distinct transversal ridges. Front very narrow, triangular to spatulate. Orbits incomplete, dorsally exposed. Eyes unprotected. Eyestalks slender, basiophthalmite very reduced. Inner infraorbital angle acutely lobiform, sometimes visible dorsally. Posterior margin wide, crested. Antennular fossae incomplete. Antennulae transversely folding. Basal antennular segment swollen, large, together with flagellum visible in dorsal view. Antennae slender, basal segment cylindrical, peduncle and flagellum long. Interantennular septum thin. Epistome reduced. Exognath of third maxilliped subpediform, palp in prolongation of merus. Exognath longer than endognath. Third maxilliped not covering completely buccal cavern. 6 – 7 gills on each side. Sternite 8 reduced in size, covered nearly completely by abdomen. Last pair of legs reduced in size and plumose (feather-like), dorsally exposed, dactyli straight, tip blunt. Sternum wide behind articulation of chelipeds. Sternal shield entering between coxae of third maxillipeds, posteriorly excavated as prolongation of sterno-abdominal cavity. Sternal sutures 3/4 – 7/8 interrupted. Male sexual opening coxal. First gonopod gradually tapering distally, curved medially. Second gonopod short, flagellum reduced. Second pleopod in female uniramous. Abdomen triangular in both sexes, in male narrow, covering almost completely space over sternite 8, (but not sternite 7), segments 1 – 2 exposed dorsally, segments 3 – 5 fused in male. First abdominal segment in male touching coxae of last pairs of legs, minute portion of sternite 8 between segments 1 – 2 uncovered. Telson reaching middle of sternal shield. Type genus: *Retropluma* Gill, 1894.

### Superfamily CHASMOCARCINOIDEA Serène, 1964

Subquadrate to subcircular, wider than long, widest posteriorly, sidewalls high, thick. Regions poorly defined to indistinct. Front moderately narrow not projecting, gently bilobed, slightly deflexed, overhanging antennular fossae. Frontal, supraorbital and anterolateral margins confluent. Anterolateral margin usually entire, arched, posterolateral margins subparallel, converging to rounded, posterior margin wide. Orbit circular, filled by eye. Eyestalks small, fixed, transverse, cornea reduced. Supraorbital margin entire, confluent with frontal margin. Posterior margin wide. Basal antennular segment usually well developed to globose, completely filling fossae, flagellum long, not folding into their fossae. Interantennular septum thin. Exorbital angle usually indistinct. Epistome sunken, posteriorly not sharply delimited from endostome. Third maxillipeds gaping. Merus of third maxilliped subovate, palp articulated distally. Chelipeds slightly asymmetric. Walking legs long, slender. Antennular fossae incomplete. Dactyli of ambulatory legs compressed, with rows of setae. Thoracic sternum wide, great portion laterally and beyond abdomen uncovered. Sutures 4/5 – 7/8 interrupted. Sternite 8 upturned, laterally to abdomen visible from above. Coxae of walking legs visible dorsally. Male sexual opening coxosternal. Penial tube on sternite 8. First gonopod stout, nearly straight, distal portion gradually tapering to simple apex. Second gonopod elongate, shorter than first one, flagellum falciform. Abdominal segments 3 – 5 fused in male, third segment widest. Female abdomen 7-segmented. Type genus: *Chasmocarcinus* Rathbun, 1898.

### Family SCALOPIDIIDAE fam. nov.

Semicircular, flattened, slightly wider than long, widest posteriorly. Dorsal regions smooth, regions hardly discernible. Front short, lamellate, slightly obliquely deflexed, gently bilobed, antennal sinus distinct. Anterolateral margin arched, crestiform. Posterolateral margins gently converging, nearly subparallel. Posterior margin wide, gently concave. Eyes short, fixed, directed transversely. Orbits small, ventral in position, invisible dorsally. Antennular flagella folding transversely in shallow rather inadequate fossae. Basal antennal segment short, movable. Flagellum long. Epistome short, sunken, not well delimited from endostome. Endostome forming short median tube. Third maxillipeds gaping, anteroexternal angle of merus of third maxilliped broadly auriculate, palp articulating in antero-mesial angle of merus. Chelipeds asymmetric especially in male, very flattened, ventrally thin, enlarged, fingers long, acute, curved downward. Meri of ambulatory legs slender, elongate, dorsally and ventrally spinose, dactyli styliiform, depressed. Sternum very wide. Sternite 7 with semicircular episternite, covering lateral portion of sternite 8. Sternal sutures 4/5 – 5/6 interrupted, 6/7 apparently entire, 7/8 apparently interrupted near median line. Penis lying in penial tube on sternite 8, quite near to suture 7/8, laterally covered by episternite 7. Supplementary plate on sternite 8 extremely narrow. Posterior part of sternite 8 laterally to abdomen exposed dorsally. Abdominal segments 3 – 5 fused, far from coxae of last pair of legs, not covering wholly sternite 8. First gonopod rather stout, nearly straight, compressed, distal portion tapering, spinulose. Second gonopod relatively long, shorter than first, flagellum distinct, nearly falciform. Abdominal segments 1 and 3 widest, second narrow, 3 – 5 fused. Abdomen in female relatively narrow, first segment widest. Type genus: *Scalopidia* Stimpson, 1858.

### Family CHASMOCARCINIDAE Serène, 1964

Subtrapezoidal, wider than long, usually widest posteriorly, thick, sidewall high. Front moderately narrow, slightly projecting, gently bilobed. Frontal, supraorbital and anterolateral margins confluent. Ridge on anterolateral margin indistinct. Eyes small. Basal antennular segment short, globose, completely filling antennular fossae, flagellum excluded, unprotected. Basal antennal segment, short not touching front, segment 4 approaching front, flagellum long. Orbital hiatus transverse, long, inner infraorbital margin indistinct. Exorbital angle not produced. Epistome reduced. Buccal cavern narrowing anteriorly. Merus of third maxilliped subovate (not auriculate), palp articulated at summit of merus. Buccal cavern not covered completely. Chelipeds shorter than legs, dactyli of last pair of legs compressed, weakly falciform. Carpal angle of cheliped distinct. Ambulatory legs long, slender. Dactyli of last pair of legs compressed, recurved, feebly falciform. Coxae of ambulatory legs visible in dorsal view. Thoracic sternum upcurved posteriorly. Considerable part of sternite 8 laterally to abdomen exposed dorsally. Penis lying in groove of sternite 8. Supplementary plate on sternite 8 distinct. First gonopod stout, nearly straight, distal portion tapering, apex truncate. Second gonopod long, shorter than first one, feebly curved flagellum short, falciform. Third abdominal segment widest, none segment reaching coxae. Type genus: *Chasmocarcinus* Rathbun, 1898.

### Subfamily CHASMOCARCININAE Serène, 1964

Subtrapezoidal to subquadrate, thick, widest posteriorly. Dorsal regions partly feebly defined. Front entire, nearly straight, no antennal sinus. Eystalk thick, distally tapering, exposed dorsally, sometimes cornea reduced. Orbital margins entire, no inner infraorbital angle. Orbital hiatus wide, imperfectly closed by cylindrical basal antennal segment and peduncle. Antennulae long. Basal segment filling antennular fossae, flagella not retractile. Epistome short, wide, posteriorly trilobate, perpendicular. Third maxillipeds gaping. Ambulatory legs long. Chelipeds without dark-coloured fingers. Dactyli of walking legs sickle-shaped, lacking corneous tip. Genital openings far from coxae and suture 7/8 forming supplementary plate. Penis lying in open or usually enclosed groove on sternite 8. First gonopod stout, sinuous to straight, distally tapering, subdistally spinose, apex simple, truncate. Second gonopod long, usually shorter than first gonopod, flagellum shorter than peduncle. Distal process curved and distally tapering (sickle-shaped). Abdominal segments 1 – 2 narrow, 3 – 5 fused in male, third segment widest. Type genus: *Chasmocarcinus* Rathbun, 1898.

### Subfamily MEGAESTHESIINAE subfam. nov.

Quadrangular, slightly wider than long, thick. Front very narrow, deflexed. Anterolateral margin short, forming distinct angle with posterolateral margins, latter long, subparallel. Eystalks extremely long, reaching lateral margin, transversely directed, swollen proximally, narrowed distally, embedded into orbits. Orbits occupying entire anterior margin of carapace, dilated proximally, narrowing distally. Antennulae very long, basal segment thick, filling antennular fossae, last two segments of peduncle movable. Antennae short. Buccal cavern narrowing anteriorly. Third maxilliped gaping, merus longitudinally ovate, exognath minute. Ambulatory legs with long movable spinules. Gonopods peculiar, apically bidentate (not described in detail). Abdominal segments 3 – 5 fused. Type genus: *Megaesthesius* Rathbun, 1909.

**Chasmocarcinoidea (?) *incertae sedis***

### +Family CARINOCARCINOIDIDAE Karasawa & Kato, 2003

Cephalothorax transversely hexagonal to nearly quadrate, widest at anterolateral angle. Dorsal surface almost smooth, regions more or less defined, cervical and branchiocardiac grooves distinct. Front straight, square-cut, entire. Supraorbital margin entire. Frontoorbital margin wide. Inner infraorbital and exorbital angles distinct. Anterolateral margin strongly convex, bearing 2 small spines. Merus of third maxilliped subquadrate, much longer than ischium. Chelipeds elongate. Thoracic sternum narrowing anteriorly and posteriorly. Abdominal segments 3 – 5 fused in male. Fingers of chelipeds long, elongate, not dark in colour. Sternite 8 overlying posterolaterally sternite 7, visible ventrally. Type genus: *Carinocarcinoides* Karasawa & Fudouji, 2000.

## Superfamily LEUCOSIOIDEA Samouelle, 1819

Characters as for the family.

### Family LEUCOSIIDAE Samouelle, 1819.

Almost polygonal, subcircular to suboval. Dorsal regions sometimes defined. Front more or less narrow, wider than orbits, usually bilobed (median notch dividing supraantennular lobes), not projecting to projecting beyond orbits often snout-like. Eyes small. Orbits small, subcircular, supraorbital margin usually trifissured (two fissures dorsally, one laterally). Infraorbital margin distinct to fused with pterygostome. Antennulae small, sometimes obsolete, plicated more or less obliquely. Antennae small to rudimentary, more or less obliquely directed. Antennulo-orbital septum present. Epistome reduced to absent, usually posed vertically. Distinct afferent channel on pterygostome along sides of buccal cavern, adjacent to endostome, covered by exognath of third maxilliped (»oreopterygostomian field«) present. Afferent water current starting on anterior boundary of pterygostome below orbits, later entering inhalant opening in front of base of third maxilliped. Odd efferent branchial channels covered by pair of lamellar processes from first maxilliped. Exhalant opening below front. Buccal cavern elongated, subtriangular, completely covered with third maxillipeds, anterior part of third maxillipeds often more or less upturned. Basis of third maxilliped well developed. Palp of third maxilliped concealed. Exognath wide. Chelipeds homoichelous, usually long, far projecting, fingers opening from vertical to horizontal plane. Sternum wide, sternal sutures mostly 4/5 – 7/8 interrupted. Sterno-abdominal cavity deep. Male sexual opening coxal to coxo-sternal on sternite 8. First gonopod usually slender with various apices, second gonopod usually short. Gill number less than 9 on each side. Abdomen long, approaching buccal cavity. Abdominal segments variously fused in both sexes (usually 1–2 freely articulated, 3–6 fused, telson freely articulated), proximal segment completely covered by carapace, usually invisible in dorsal view. Typical press-button mechanism absent, but abdomen firmly fixed. Type genus: *Leucosia* Weber, 1795.

#### Subfamily EBALIINAE Stimpson, 1871

Cephalothorax wider than long. Dorsal regions often well defined. Front usually not very narrow, bilobed. Anterior margin of pterygostome well separated from infraorbital margin by distinct space. Epistome distinct. Buccal cavern anteriorly arched. Anterior extremity of buccal cavern projecting beyond level of anterior boundary of pterygostomian region and more or less upturned. Exognath distinctly shorter than endognath. Palm usual, fingers closing obliquely. Abdominal segments 4 – 6 or 3 – 6 fused in male. Type genus: *Ebalia* Leach, 1817.

#### Tribe Ebalii Stimpson, 1871

Cephalothorax pentagonal to hexagonal, little or not at all wider than long. Dorsal surface tumid, nodose, granular with defined regions. Front not very narrow. Orbital hiatus open, communicating with antennular fossae. Antennae minute, basal antennal article movable, entering orbital hiatus, not fused with suborbital lobe. Chelipeds moderately stout, fingers gradually tapering from base to tip. Fingers usually stout, opening in horizontal plane. Second gonopod shorter, sometimes longer than first one. Abdominal segments 3 – 5 fused in male, 3 – 6 in female. Type genus: *Ebalia* Leach, 1817.

## Tribe Praebebaliini trib. nov.

Cephalothorax subglobose, dorsally even. Front broadly bilobed. Regions distinct to ill-defined, posteriorly intestinal prominence and 2 – 3 spines. Orbital hiatus open, communicating with antennular fossae. Exognath slightly shorter than endognath. Anterior margin of pterygostomian groove laminate, projecting, one-fissured, apparent in dorsal view. Pereiopods long. Palm of chelipeds slender, prismatic, fingers long. First gonopod with stout basal stalk, flanged on anterior margin, tapering distally, setose. Second gonopod longer to shorter than first one. Abdominal segments 3 – 5 (6) fused in male 3 – 6 in female. Type genus: *Praebebalia* Rathbun, 1911.

## Tribe Oreophorini Miers, 1886

Cephalothorax markedly wider than long, not narrowed distinctly anteriorly, anteriorly and posteriorly more or less upturned. Dorsal surface tuberculate, uneven. Branchial regions usually more or less expanded laterally, concealing ambulatory legs in flexion. Orbits completely closed. Antennular fossae oblique. Basal antennal segment immovable, fused with inner infraorbital antantennulo-orbital septum, closing completely orbits. Antennal peduncle minute to obsolete. Chelipeds massive, immovable finger more massive than dactylus. First gonopod straight. Abdominal segments 3 – 5 fused in male, freely articulated to segments 3 – 6 fused in female. Type genus: *Oreophorus* Rüppel, 1830.

## Tribe Nuciini Alcock, 1896

Transversely oval, strongly convex. Dorsal surface covered with mulberry-like vesiculose granules. Front widely bilobed, not projecting to slightly projecting. Eyes large. Orbits usually complete. Supraorbital margin deeply emarginate, eye hardly concealed. Branchial region not expanded laterally. Orbits closed by meeting of infraorbital and subfrontal lobes. Antennae small, distinct, very directed obliquely, flagellum reduced to absent. Pereiopods very short and stout, fingers of chelipeds thin, shorter than palm. Posterior margin straight. Abdominal segments 3 – 5 fused in male, 3 – 6 in female. Type genus: *Nucia* Dana, 1852.

## Tribe Leuciscini trib. nov.

Cephalothorax subcircular, depressed. Dorsal surface smooth, flattened. Lateral margin entire, raised, beaded. Front wide, projecting, square-cut, truncate. Eyes invisible in dorsal view. Orbits separated from antennular fossae. Antennae minute, epistome absent. Apex of buccal cavity approaching antennular fossae. Anterior margin of pterygostomian groove far from orbit, medially notched. Endognath of third maxilliped much longer than exognath. Abdominal segment 3 – 6 fused in both sexes. Type genus: *Leucisca* MacLeay, 1838

## Tribe Nursiini Alcock, 1896

Irregularly pentagonal, wider than long, depressed. Dorsal surface usually with ridges radiating from center. Front moderately wide, feebly projecting, bluntly rounded to nearly concave. Lateral margins thin, expanded. Posterior margin widely bilobed. Anterior extremity of endognath slightly projecting beyond exognath. Chelipeds stout, chela usual, fingers short, tapering. Abdominal segments 2 – 4, 3 – 5 to 3 – 6 fused both sexes. Type genus: *Nursia* Leach, 1817.

## Tribe Cryptocnemini Stimpson, 1907

Cephalothorax pentagonal to transversely oval, flattened to even concave, smooth, laterally expanded and lamelliform, concealing more or less legs in flexion, unarmed. Obtuse tooth at junction of anterolateral and posterolateral margins. Front produced, obtusely triangular or with U-shaped median notch, upturned. Posterior margin straight. Orbits small, deep. Eyes visible in dorsal view. Antennae almost obsolete. Anterior extremity of endognath sharply triangular, projecting beyond extremity of exognath, dividing epistome into two halves. Exognath dilated, laterally arched. Infraorbital lobe large. Chelipeds stout, compressed, carinate, fingers slender, much shorter than palm. Legs short. Abdominal segments (2), 3 – 6 usually fused in both sexes. Type genus: *Cryptocnemus* Stimpson, 1858.

## Tribe Onychomorphini trib. nov.

Shape unguliform (human nail-shaped), longer than wide, anteriorly narrowed, medially constricted, posteriorly expanded, depressed, flat, dorsally smooth. Front wide, not projecting, gently upturned. Regions indistinct. All margins behind front forming continuous, laminar. Antennulae oblique. Antennae obsolete. Orbit minute. Epistome small. Merus of third maxilliped much longer than ischium. Exognath wider than endognath, with arcuated lateral margin. Anterior margin of pterygostome entire. Chelipeds massive, depressed, laminar, palm large, fingers very short. Legs slender, compressed, merus carpus and propodus carinate, dactylus filiform, fingers slanting, short, almost concealed beneath cephalothorax. Abdominal segments 1 – 6 fused in both sexes, only two proximal segments indicated. Type genus: *Onychomorpha* Stimpson, 1858.

## Subfamily IPHICULINAE Alcock, 1896

Cephalothorax subglobular, nearly as long as wide. Body covered with close spongy pubescence, lateral margins spinose. Intestinal region circumferenced by groove. Front narrow, bilobed, projecting. Eystalks relatively long, obliquely directed. Orbital hiatus wide, supraorbital margin bifissured, inner infraorbital tooth well developed. Antennulae and antennae long. Epistome, infraorbital margin and anterior margin of pterygostome well separated. Two lobes on two anterior boundaries of pterygostomial region rounded, entire. Merus of third maxilliped short, upturned. Chelipeds slender, palm short, proximally very swollen, fingers filiform, much longer than palm. Sternal sutures 6/7 – 7/8 nearly entire (or interrupted close to median line). Second gonopod usually shorter than first gonopod. Abdominal segments in female freely articulated, in male segments 3 – 4, 3 – 6 or 3 – 5 fused, sutures often distinct. Type genus: *Iphiculus* Adams and White, 1848.

## Subfamily ILIINAE Stimpson, 1871

Almost hemispherical, strongly convex, compact looking. Intestinal spines sometimes distinct. Anterior edge of pterygostomial groove close to or coalesced with infraorbital margin, usually two-notched (trilobed) extremity of pterygostomial groove. Supraorbital margin trifissured. Infraorbital lobe rarely distinct. Orbital hiatus closed. Epistome very reduced to absent. Anterior extremity of buccal cavity at

level of anterior margin of pterygostomian region. Exognath of third maxilliped not, or not much shorter than endognath, laterally not expanded. Merus of third maxilliped about half-length of ischium. Cheliped subcylindrical, elongate, slender. Palm subcylindrical to inflated, fingers long, slender, not tapering, apically slightly curved. First abdominal segment not always concealed by carapace. Type genus: *Illia* Leach, 1815.

Tribe Pariliini trib. nov.

Subcurcular, strongly convex, wider than long, hepatic region inflated, intestinal region distinct. Front bilobed, not projecting. Supraorbital angle with deep incision. Posterolateral margin with one spine. Posterior margin with three projections. Anterior margin of pterygostomian groove far from infraorbital margin. Epistome sometimes projecting beyond front. Exognath of third maxilliped extremely laterally expanded, foliaceous. Chelipeds very long, palm subcylindrical, elongated, longer than fingers, fingers slender. First gonopod with bifurcated tip. Some abdominal segments usually fused in both sexes, sutures usually distinct. Type genus: *Parilia* Wood Mason, 1891.

Tribe Randalliini trib. nov.

Subglobular to widely rhomboidal, as long as wide, thick. Front slightly or not at all projecting, widely bilobed. Posterolateral and posterior margin dentate or lobed. Posterior margin three-dentate (lobate) Infraorbital margin far from anterior pterygostomian margin. Anterior margin of pterygostomian groove cut into two obtuse lobes, mesially concave, with cleft. Lateral margin of exognath nearly straight. Chelipeds very long, palm not markedly swollen, fingers stout, nearly as long as palm. Some abdominal segments (3 – 5 – 6) fused in both sexes, sutures distinct. Type genus: *Randallia* Stimpson, 1857.

Tribe Myrini Alcock, 1896

Strongly ovate, longer than wide, convex. Dorsal regions scarcely marked to indistinct. Front wide, feebly projecting, gently bilobed. Posterior margin trispinose, anterior extremity of pterygostomian groove trilobed (tridentate), each separated by two shallow sinuses. Infraorbital lobe and epistome almost rudimentary to absent. Chelipeds long, slender, cylindrical, fingers as long as or shorter than palm, not very slender, subequal width throughout. Abdominal segments 3 – 6 fused in male, (3) – 4 – 6 in female. Type genus: *Myra* Leach, 1817.

Tribe Persephonini trib. nov.

Subglobular. Front slightly snout-like, widely bidentate, slightly upturned. Posterior margin with three spines, median on higher level than two lateral spines on posterior margin. Antennulae long, plicated obliquely to nearly transversely. Antennae loosely lodged in orbital hiatus. Supraorbital margin trifissured. Anterior margin of pterygostomian groove fused with infraorbital margin. Dentiform prolongation of branchial channels projecting beyond front. Anterior pterygostomian margin bilobed. Epistome reduced. Chelipeds relatively strong, not inflated, fingers shorter than palm. Dactyli of ambulatory legs depressed. Abdominal segments 3 – 5 fused in male, 4 – 6 in female. Type genus: *Persephona* Leach, 1817.



## Tribe Iliini Stimpson, 1871

Elongately suboval to subglobular. Front feebly produced. Supraorbital margin bifissured. Anterolateral margin unarmed, posterolateral margins four-spinose (posterior margin bilobed, two spines on higher level). Anterior margin of pterygostomian groove trilobate (tridentate). Intestinal region distinct. Infraorbital lobus weakly developed. Merus of endognath of third maxilliped shorter than half length of ischium. Chelipeds long, slender and cylindrical, fingers usually longer than palm. Ambulatory legs short. Abdominal segments 3 – 5 fused in male, 4 – 6 in female. Type genus: *Ilia* Leach, 1817.

## Tribe Arcaniini trib. nov.

Form very variable: pyriform, oval, rhomboidal, subglobular, sometimes longer than wide. Front not very projecting, bilobed (bidentate). Lateral margins tuberculate, granulose to often spinose. Front gently prominent, upturned. Distinct spine usually at junction of anterolateral and posterolateral margins. Posterior margin with 3 – 5 spines. Infraorbital spine prominent and acuminate. In adult infraorbital margin and anterior pterygostomian margin distinct to fused. Anterior margin of pterygostomian groove with two acuminate teeth (mesial spine visible in ventral view corresponding to infraorbital spine). Epistome small, vertical. Exognath narrow. Chelipeds slender, elongate. Palm subcylindrical tapering from base. Fingers slender, filiform, nearly as long as palm, or slightly shorter, occlusive margins spinose. First gonopod strong, usually straight. Abdominal segments 3 – 5 fused in male, 4 – 6 fused in female. Type genus: *Arcania* Leach, 1817.

## Tribe Ixini trib. nov.

Cephalothorax transversely elliptical to subrhomboidal, usually with long stout cylindrical lateral processes. Front very short, widely bilobed. Posterior margin usually with distinct processes on each side. Intestinal spine obtuse. Pterygostomian anterior margin bilobed, wide, separated from infraorbital margin by short deep groove. Buccal frame quadrate, oreopterygostomian field wide. Chelipeds hardly stouter than legs. Pereiopods very slender, fingers of chelipeds much shorter than palm. Abdominal segments 3 – 5 in male 3 – 6 in female fused. First abdominal segments concealed under carapace. Type genus: *Ixa* Leach, 1815.

## Tribe Nursiliini Alcock, 1896

Broadly polygonal, wider than long, depressed. Dorsal surface usually transversely by ridges radiating from centre. Margins of carapace thin, laminar, expanded. Front wide, bilobed. Posterior margin bispinose. Infraorbital lobe fused with anterior margin of pterygostome. Anterior margin of pterygostomian groove straight, posed obliquely. Oreopterygostomian field wide (giving impression of quadrate buccal frame). Exognath shorter than endognath. Palm short, inflated, fingers very long, slender curved at tip, cutting edges finely dentate, much longer than palm. First gonopod apically bifid. Abdominal segments 2 – 6 fused in male, 3 – 6 in female. Type genus: *Nursilia* Bell, 1855.

## Subfamily LEUCOSIINAE Samouelle, 1819

Cephalothorax generally rounded to urn-shaped, dorsally convex, compact looking. Dorsal surface smooth, laterally, posteriorly and dorsally unarmed. Front very variable: usually relatively wide to narrowed often snout-like, anteriorly tridentate (trilobed), bilobed to bluntly rounded. Anterior margins of buccal cavity and pterygostomial groove in nearly same transverse plane. Anterior pterygostomial margin entire. Infraorbital lobus almost rudimentary to absent. Epistome very reduced. Merus of third maxilliped slender, as long as or shorter than ischium, basis well developed. Exognath relatively wide, elongate. Chelipeds massive, fingers slender, shorter than palm. Male sexual opening coxo-sternal. Type genus: *Leucosia* Weber, 1795.

## Tribe Lissomorphini trib. nov.

Subpentagonal, wider than long, strongly convex in both directions. Front wide, square-cut, truncate. Orbits entire. Antennulae transverse. Buccal cavern subsquare. Part of exognath of third maxilliped adjacent to merus of endognath wide, anteriorly globular. Chelipeds short, thick, carinate. Type genus: *Lissomorpha* Ward, 1928.

## Tribe Leucosiini Samouelle, 1819

Cephalothorax porcelaneous, unarmed. Fronto-orbital region very narrow, snout-like, sometimes anteriorly truncate or arcuate. Posteriorly regularly arched. Cavity or sinus above base of chelipeds (thoracic sinus) often present. Antennulae well developed. Anterior margin of pterygostomial region nearly entire, sometimes with three hardly discernible lobes. Exognath relatively wide, outer margin nearly straight. Third thoracic segment and basis of third maxilliped well developed. First gonopod usually spirally twisted, distal end with styliform process. Abdominal segments variously fused in both sexes (usually 3 – 5 in male, 3 – 5, 3 – 6, 4 – 6 in female). Type genus: *Leucosia* Weber, 1795.

## Subfamily PHILYRINAE Rathbun, 1937

Shape subcircular, discoidal, more or less globose. Carapace surrounded by beaded margin. Regions scarcely defined. Front relatively wide, subtruncate to lobate, not produced. Hepatic facets behind orbits present. Margins of carapace granulate. Supraorbital margins bifissured to one-fissured. Anterior margins of pterygostomial groove scarcely separated from infraorbital margin. Apex of buccal cavity and pterygostomial edge projecting beyond front, visible dorsally. Epistome usually reduced. Anterior margin of pterygostomial margin wide, lobate to entire. Buccal cavern wide. Merus of third maxilliped shorter than half of inner margin of ischium. Exognath of third maxilliped widely expanded, its outer margin semicircular. Chelipeds well developed, palm inflated, fingers long. Second gonopod as long as or even longer than first one. Abdominal segments 2 – 5, 2 – 6 or 3 – 6 fused in both sexes, first segment in female hidden beneath carapace. Type genus: *Philyra* Leach, 1817.

## Superfamily HEXAPODOIDEA Miers, 1886

Characters as for the family.

### Family HEXAPODIDAE Miers, 1886

Transversely rectangular, trapezoidal to subelliptical, much wider than long, almost widest posteriorly. Regions usually poorly defined, H-shaped depression usually distinct. Front narrow, usually straight, sometimes axially sulcate. Lateral margin steep. Anterolateral and posterolateral margins indistinguishable. Posterior margin very wide. Eyes small, movable to fixed. Orbits small, rimmed. Antennulae obliquely to transversally directed, antennae small, diverging to converging. Basal antennal segment short, small. Epistome distinct. Buccal cavern narrowing anteriorly, not completely covered by third maxillipeds. Endognath of third maxilliped ranging from wide to narrow. Palp of third maxilliped markedly well developed, long, inserted at summit of merus, propodus slender to dilated distally. Exognath much shorter than endognath, sometimes lacking flagellum. Meri of ambulatory legs triangular in cross-section. Last pair of legs lacking (Hexapodidae!). Sternite 8 highly reduced, concealed beneath carapace. Sternum very wide. Sutures 4/5 – 6/7 interrupted. Sterno-abdominal cavity elongated, usually reaching suture 2/3, cavity usually anteriorly with two lateral furrows for apices of first gonopods. First gonopod slender, nearly straight to slightly curved, apices often bent at right angle, lying in transversal grooves, apices not covered by abdomen. Male sexual opening coxo-sternal. Abdominal segments variously fused (3–5, 3–4, 2–6, 5–6) in male, in female almost freely articulated. Abdomen in male narrow, two proximal segments usually short, far from coxae of ambulatory legs. Type genus: *Hexapus* de Haan, 1833.

## Superfamily CRYPTOCHIROIDEA Paul'son, 1875

Characters as for the family.

### Family CRYPTOCHIRIDAE Paul'son, 1875

Longitudinally oblong to longitudinally rectangular, semicylindrical. Integument decalcified. Front narrow, subtruncate or emarginate. No orbits. Infraorbital margin feebly developed. Antennulae well developed, plicated longitudinally, basal segments markedly strong, prominent, exposed dorsally, not retractile in their fossae. Antennae small, basal segment short, peduncles directed lengthwise. Epistome feebly developed. Buccal cavern large, anteriorly arched, not covered completely by third maxilliped. Mandibular palp absent. Third maxillipeds separated at base by sternal shield. Ischium of third maxillipeds with large inner lobe, merus much smaller than ischium, seating well back, palp strong, articulating in notch of inner angle, exognath reduced to absent, flagellum absent. Chelipeds small. Ambulatory legs short, slender, dactyli short, with hooked claws. Thoracic sternites 1 – 4 fused into thoracic shield, anteriorly subovate, posteriorly narrowed, between bases of chelipeds concave. Sternal sutures 4/5 – 5/6 always interrupted, 6/7 – 7/8 sometimes entire. Male sexual opening coxo-sternal. First gonopod usually columnar. Abdominal segments freely

articulated in male, remarkably large in female, fused, forming basket for eggs. Proximal abdominal segments not exposed in dorsal view in male, segments 1 – 3 exposed in females. Retaining system of abdomen lacking. Last pleopod in female uniramous. Males smaller than females. Type genus: *Cryptochirus* Heller, 1861.

### Superfamily PINNOTHEROIDEA de Haan, 1833

Characters as for the family.

#### Family PINNOTHERIDAE de Haan, 1833

Almost subcircular to transversely ovate. Integument usually poorly calcified membranous, dorsal regions generally indistinct. Front and posterior margin narrow. Lateral margins entire, unrimed, almost indistinct. Sidewalls steep to vertical. Antennulae well developed, obliquely folded. Antennae very small, basal segment not touching front, peduncles entering orbital hiatus. Eyes small, imbedded in orbits, often reduced, visible to invisible in dorsal view. Orbital margins entire. Interantennular septum very thin to absent. Endostomial ridge sometimes present. Buccal cavern usually very wide, usually semicircular. Ischium of third maxillipeds small and usually fused with merus (forming ischio-merus), palp articulated with dactylus subterminally. Exognath small more or less concealed, flagellum often reduced to absent. Chelipeds symmetric, carpal spine absent. Walking legs of variable length. Meri of ambulatory legs triangular in cross-section, dorsal surface rugose to carinate. Male sexual opening coxo-sternal, usually far from coxae of last pair of legs, rather near to suture 7/8. First gonopod either long, slender and distally tapering or usually columnar, second gonopod short. Number of gills reduced (up to 3). Abdomen in male narrow, elongate, sides nearly subparallel, in female extremely wide, sometimes covering third maxillipeds. Abdominal segments sometimes fused. Type genus: *Pinnotheres* Latreille, 1802.

#### Subfamily PINNOTHERELIINAE Alcock, 1900

Transversely elongate to subquadrangular, subcylindrical. No posterolateral facets. Eyestalks short. Orbits wide, transverse. Antennulae plicated obliquely to transversely. Maxillipeds directed longitudinally to slightly obliquely. Ischium and merus not completely fused, ischium small. Palp almost very large, sometimes as large as ischium and merus together. Dactyli often fringed with long setae. Last pair of legs smallest. First gonopod long, slender, straight to more or less curved, gradually tapering to simple apex, usually with short or long hairs. Telson subtriangular. Type genus: *Pinnotherelia* A. Milne Edwards & Lucas, 1843.

#### Tribe Pinnothereliini Alcock, 1900

Subquadrangular to transversely oblong. Front wide, deflected. Eyes pyriform, short. Orbits transverse. Antennal peduncle deflected. Third maxillipeds longitudinal, merus wide, palp large, dactylus articulated at distal end of inner side of propodus, distally fringed with long setae, exognath lacking flagellum. Chelipeds stout. Ambulatory legs subequal to unequal in size, usually second pair longest. Type genus: *Pinnotherelia* A. Milne Edwards & Lucas, 1843.

## Tribe Tritodynamiini trib. nov.

Cephalothorax almost transversely hexagonal to trapezoidal. Dorsal regions ill-defined, posterolaterally with facet on each side. Front narrow, not projecting beyond orbits. Eyestalks long, well developed, orbits wide. Infraorbital ridge distinct. Third maxillipeds not covering completely buccal cavern, directed lengthwise. Ischium shorter than merus. Dactylus of third maxilliped large, flattened, articulated at inner basal part of propodus. Propodus, dactylus of third maxillipeds and ambulatory legs fringed with long, often plumose, setae. Ambulatory legs long, stout, last pair shortest. First gonopod stout, nearly columnar, apically blunt, with or without depression, sometimes slightly widened distally, nearly straight, rarely gently curved. Type genus: *Tritodynamia* Ortmann, 1894.

## Tribe Pinnixini trib. nov.

Cephalothorax transversely elliptical, much wider than long, often with distinct sharp transverse crest across posterior part of carapace. Integument hard. Antennular fossae in communication to each other beneath front. Third maxillipeds directed longitudinally to obliquely, palp usually large, dactylus articulating near proximal end of inner side of propodus, flattened distally. Third pair of legs longest, last pair smallest. First gonopod distally bent, hooked. Abdomen narrow, far from coxae, long in both sexes, telson widely rounded in male, wide, subcircular to subovate in female. Type genus: *Pinnixa* White, 1846.

## Tribe Glasselini trib. nov.

Transversely oblong. Integument firm. Regions indistinct. Antennulae oblique. Third maxillipeds oblique ischio-merus pyriform, completely fused, palp as long as ischio-merus, dactylus shorter than propodus, inserted subdistally on inner face of conical propodus, carpus larger than propodus and dactylus together. Telson in female widely subtriangular, apically blunt. Type genus: *Glassela* Campos & Wicksten, 1997.

## Tribe Alarconiini trib. nov.

Transversely oval, widest posteriorly. Dorsal regions well defined. Antennal flagellum long. Buccal cavity with parallel sides. Third maxilliped narrow, ischium and merus not fused, subequal in length, dactylus as long as or longer than propodus, inserted proximally on ventral margin of propodus. Sternal suture 4/5 and suture between abdominal segments 5/6 lined with row of long setae. Third pair of legs longest. First gonopod (number) 3-shaped, exceeding telson, entering sternal semicircular excavation on sternum. Abdomen in male widest at junction of segments 2 – 3, segments 4 – 5 coalesced. Type genus: *Alarconia* Glassel, 1938.

## Subfamily PINNOTHERINAE de Haan, 1833

Cephalothorax not markedly transverse, variable in form: suborbicular, subquadrate to transverse, usually thick. Integument mostly not well calcified. Antennulae plicated obliquely to transversely. Ischium and merus of third maxilliped fused into ischio-merus, typically very obliquely to almost transversely directed, palpus smaller than ischio-merus, dactylus much smaller than propodus, styliform, inserted at

inner side of propodus. Last pair of legs smallest. First gonopod long, slender, straight to more or less curved, gradually tapering to simple apex, usually with short to long setae subdistally. Abdomen in male very slender. Abdomen in female very wide. Type genus: *Pinnotheres* Latreille, 1802.

#### Tribe Pinnotherini de Haan, 1833

Suborbicular to subquadrate, almost pea-like, not distinctly wider than long. Lateral margins indistinct. Integument poorly calcified. Lateral margins of sternite 4 more or less converging. Epistome well developed. Endostomial ridge present. Exognath of third maxilliped with flagellum. Legs slender, dactyli of three anterior pairs of legs simple and acute, third pair usually longest. First gonopod long, slender, curved medially, distally tapering. Abdomen in male narrow, widest proximally, tapering gradually to relatively short, telson arched, segments freely articulated, rarely segments 5 – 6 fused. Type species: *Pinnotheres* Latreille, 1802.

#### Tribe Dissodactylini Smith, 1870

Cephalothorax distinctly wider than long, subpentagonal, feebly convex longitudinally. Integument well calcified. Transverse groove on carapace distinct. Lateral margin of carapace distinct, sometimes sharp, sidewalls vertical. Anterolateral margins arched, posterolateral straight to concave, slightly diverging. Endostomial ridge absent. Exognath reduced, lacking flagellum. Epistome well developed. Ambulatory legs short, relatively robust. Dactyli of three anterior pairs of legs bifurcate in both sexes. Lateral margins of sternite 4 subparallel. Abdomen in male widest proximally, sometimes segments 1 – 2 and segments 3 – 6 fused, sides nearly straight, subparallel, telson subtriangular. Female abdomen usually freely segmented, sometimes segments 2 – 4 fused. Type genus: *Dissodactylus* Smith, 1870.

#### Tribe Parapinixini trib. nov.

Cephalothorax transversely ovate, convex longitudinally. Integument well calcified. Anterior margin nearly straight. Front depressed, widely triangular, short, deflexed. Anterolateral margins with distinct ridge. Orbits circular, filled by large eyes. Antennulae folding obliquely to transversely. Antennular fossae communicating with each other. Epistome well developed. Buccal cavity small, widely subtriangular. Endostomial ridge well developed. Ischiomerus of third maxilliped well developed, dactylus joined to distal end and in prolongation of propodus. Exognath reduced to absent, lacking flagellum. Fingers of chelae stout. First pair of legs largest, last pair very reduced in size. Abdominal segments freely articulating in both sexes. Third abdominal segments largest in both sexes, telson in male narrow, elongate, in female telson widely triangular, tip blunt. Type genus: *Parapinixa* Holmes, 1894.

### Family XENOPHTHALMIDAE Stimpson, 1858

Cephalothorax subtrapezoid, pinnotherid-like, very thickened, elliptical in sagittal cross section. Pterygostomial suture distinct (pseudolateral margin). True lateral margin reduced. Front narrow, deflected. Eyes situated in narrow slits on dorsal side. Orbits longitudinal. Pterygostomial region markedly swollen so that orbits and antennae being exposed dorsally. Ischium and merus of third maxilliped longi-

tudinally directed, distinctly separated, both well-developed, dactylus not enlarged distally. Epistome lacking. Abdominal segments freely articulated and narrow in both sexes. Type genus: *Xenophthalmus* White, 1846.

#### Subfamily XENOPHTHALMINAE Stimpson, 1858

Subtrapezoidal, transverse, thickened. Dorsal surface of carapace very hairy especially anteriorly and laterally, margins densely setose, especially anteriorly. Eyes in narrow slits situated dorsally, directed longitudinally. Epistome absent. Anterior portion of buccal cavity in communication with antennular fossae. Meri of walking legs armed with row of spinules along posterior margin. First gonopod nearly straight, equally thick, proximally with row of plumose setae, terminally with very short and very long setae or without setae. Abdomen narrow, 7-segmented in both sexes. Type genus: *Xenophthalmus* White, 1846.

#### Subfamily ANOMALIFRONTINAE Rathbun, 1929

Pterygostomian region very swollen. Orbital slices directed obliquely backward and outward. Antennulae minute, fossets shallow or none. Antennae robust. Eyes minute, movable plicated longitudinally in deep slits. Buccal cavity closed and separated from antennular fossae. Epistome indistinct, separated from buccal cavern by median piece of buccal cavern. Palp of third maxilliped small, usually articulated. First gonopod gently curved, slightly tapering distally, proximally with simple setae, subterminally lacking setae. Type genus: *Anomalifrons* Rathbun, 1929.

**Heterotremata (?) *incertae sedis***

#### +Family NECROCARCINIDAE Förster, 1968

Cephalothorax subcircular, subovate to subquadrate, as long as wide to slightly wider than long, widest between last anterolateral spines. Cephalothorax dorsally convex in both directions, sidewalls steep. Dorsal regions moderately to poorly defined, usually surface with strong tubercles concentrated in transverse rows across hepatic and gastric regions and three longitudinal ones, sometimes forming serrated keels. Cervical and gastrocardiac grooves well developed on axial and branchial regions, usually parallel to one another. Fronto-orbital margin moderately wide. (Pseudo)rostrum narrow, moderately produced, sometimes downturned, simple to bifid, sulcate at tip, sometimes with lateral spines. Orbits usually small, circular, close together, turned obliquely upward. Supraorbital margin with two fissures, 2 – 4 elongate postrostral slits often present. Exorbital angle sometimes distinct. Cervical and partially branchiocardiac grooves distinct. Anterolateral margin long, arched, with several spines or blunt protuberances, last anterolateral spine sometimes very long. Posterolateral margin entire or with spines or blunt tubercles. Posterior margin moderately wide, concave. Buccal cavern elongated. Endognath of third maxilliped slightly wider than exognath, ischium much shorter than merus. Sternum narrow. Sternite 8 and coxa of last pair of legs reduced in size. Sternal depression wide, reaching coxae of thoracopods. Last pair of legs reduced in size, (probably) subdorsal in position, possibly third pair too. Abdominal segments freely articulated in both sexes. Type genus: *Necrocarcinus* Bell, 1863.

**+Family ORITHOPSIDAE Schweitzer, Feldmann, Fam, Hessin,  
Hetrick, Nyborg & Ross, 2003**

Cephalothorax hexagonal, angular, wider than long or about as wide as long, widest between last anterolateral spines. Dorsal surface flattened longitudinally and transversely. Regions moderately to weakly defined, with little or no tuberculate ornamentation. (Pseudo)rostrum well developed, projecting beyond orbits, with 2 – 4 long spines. Fronto-orbital width relatively wide. Orbits wide. Supraorbital spines (and 2 deep fissures) long, exorbital angle long, sometimes bifid. Anterolateral margin short, with several spines. Cervical and branchiocardiac grooves shallow, not well defined. Branchial regions sometimes with longitudinal ridges and small nodes anteriorly, axial regions sometimes with longitudinal ridge. Posterior margin concave. Female gonopore sternal. Type genus: *Orithopsis* Carter, 1872.

**+Family SECRETANELLIDAE fam. nov.**

Cephalothorax transversely elliptical, much wider than long, widest between last anterolateral spines. Lateral margins distinct. Dorsal surface almost smooth, with distinct cervical, branchial and especially cardiac furrows, some regions distinct. Fronto orbital width about half of maximum width. Front moderately wide, not projecting, gently deflexed, apically rounded laterally feebly sinused. Supraorbital margin entire. Exorbital angle absent. Inner infraorbital angle distinct. Anterolateral margin with several spines. Posterior margin moderately wide, gently concave. Last pair of legs in dorsal position. Sterno-abdominal cavity deep. First abdominal segment exposed dorsally. Abdominal segments freely articulated (in female), telson large, rounded. Considerably portion of sternite 4 beyond and laterally to telson uncovered. Uropods indistinct. Type genus *Secretanella* Guinot & Tavares, 2001.

**Subsection THORACOTREMATA Guinot, 1977**

Cephalothorax broad, subsquarish, usually broader than long, truncated or arcuated anteriorly. Epigastric and postorbital lobes often present. Front almost entire, never far projecting. Supraorbital margin almost always entire. Lateral margins nearly straight and subparallel to arched, often sharp and keeled along their length, at least anteriorly. Posterior margin usually very wide (usually as frontal or fronto-orbital one). Cervical (vertical, grapsoid) groove sometimes distinct dorsally and ventrally. Pterygostomial suture distinct, often anteriorly grooved. Supraorbital margin almost always entire. Infraorbital margin, cervical groove and anterior part of pterygostomial suture often closing triangular field – infraorbital facet. Eyes and orbital cavities well developed. In orbital cavity often located subocular thin ridge starting from supraorbital margin ending in inner infraorbital tooth. True infra-orbital margin sometimes replaced by infraorbital crest. Antennulae transverse. Antennae sometimes reduced in size, variously directed. Epistome with posterior medial projection. Endostome medially undivided. Palp of third maxilliped articulated usually at or near anteroexternal angle of merus, or at summit, carpus widest distally. Median margins of meri third maxillipeds smooth. Chelipeds flexed ahead of



cephalothorax, not pressed against ventral side of anterior part of carapace, usually homiochelic. Meri of ambulatory legs flattened, triangular in cross-section, dorsally carinate to rugose, dactyli usually with corneous spines. Thoracic sternum very wide, sutures 1/2 – 2/3 usually distinct, sutures 4/5 – 7/8 always interrupted. Sterno-abdominal cavity deep, often anteriorly delimited by crestiform margin. Male and female sexual openings sternal, male sexual opening on sternite 8, female on sternite 6. Vagina of concave type. First gonopod usually columnar (rod- or baton-like), rather stout, straight to slightly curved, with terminal dense tuft of long setae, apex with corneous tip, often with subterminal (lateral) palp, almost triangular in cross section. Second gonopod short, flagellum highly reduced to absent. Abdomen usually 7-segmented, rarely some segments fused, forming thin plate, that of male usually narrow, sometimes narrower than segment 6 (tongue-shaped), chiefly rounded distally. Two proximal segments usually very short. Abdominal holding apparatus of press-button type present to absent.

### **Superfamily GRAPSOIDEA MacLeay, 1838**

Cephalothorax subquadrilateral to subcircular, slightly wider than long, with lateral margins straight to slightly arched, spinose, lobate to entire, flattened to thick and swollen. Anterolateral and posterolateral margins usually not clearly demarcated, forming lateral margin. Dorsal surface setose, granular to smooth, regions poorly to moderately defined, H-shaped depression usually distinct. Front usually, entire, more or less deflexed. Eyes and orbits well developed, eyes at or near anterolateral angle. Interantennular septum wide. Exorbital margin usually distinct. Antennulae folding gently obliquely to usually transversely. Basal antennal segment well developed, peduncles parallel to slightly diverging, segment 5 with flagellum usually bent. Buccal cavern square. Third maxillipeds not covering completely buccal cavern, gap rhomboidal, exognath present, with flagellum. Chelipeds stout, usually symmetric. Ambulatory legs well developed. Thoracic sternum wide, not narrowing posteriorly. Sternal sutures 1/2 – 2/3 usually distinct, 3/4 indistinct, 4/5 – 7/8 interrupted. First gonopod stout, very stiff, usually with corneous tip or process more or less developed usually covered by dense brush of long setae, usually with subterminal lateral palp. Telson usually narrower than segment 6, longer than wide, distally rounded. Type genus: *Grapsus* Lamarck, 1801.

### **Family GRAPSIDAE MacLeay, 1838**

Cephalothorax squarish, transversely rectangular, trapezoid to subcircular. Usually dorsally flat, to feebly convex, granular to smooth. Dorsal regions poorly to moderately defined. Anterior part of frontal region deflexed giving impression of sublaminar front. Secondary frontal margin usually entire to nearly notched or lobate. Epigastric lobe (crest) usually distinct. Lateral margin well defined, either dentate anteriorly or carinate, rarely smooth. Cervical groove more or less distinct dorsally and ventrally. Front wide, wider than orbits. Eyes at or near anterolateral angle. Orbits very wide, short, not protecting eyes dorsally. Antennae small, peduncles and flagella minute. Interantennular septum (proepistome) markedly wide. Buccal cav-

ity subquadrangular. Exognath slender, palp present. Meri of ambulatory legs with dorsal distal spine, dactyli spinose. Sternal sutures 1/2 and 2/3 more or less distinct, other sutures interrupted. First gonopod columnar with corneous tip obscured by brush of setae, second gonopod short. Abdominal segments freely articulating, two proximal abdominal segments short, segments 4 – 6 sometimes immovable (coalesced). Telson in male usually subequilateral to tongue-shaped. Proximal abdominal segments filling whole space between last pair of legs. Typical press-button apparatus present to absent. Type genus: *Grapsus* Lamarck, 1801.

#### Subfamily GECARCININAE MacLeay, 1838

Cordiform, subcircular to transversely ovate, thick, branchial region inflated. Dorsal surface smooth. H-shaped depression present. Anterolateral borders strongly arched. Sidewalls steep. Front entire, moderately wide, strongly deflexed. Lateral margin entire, keeled only behind anterolateral tooth, posteriorly indistinct. Secondary frontal margin almost straight, primary frontal margin touching proepistome. Infraorbital margin often present sometimes reduced and eclipsed by infraorbital ridge. Inner infraorbital angle well developed. Antennulae folded obliquely to nearly transversely. Antennae very small, nearly longitudinal, peduncle bent. Proepistome short, basally wide. Eyes relatively small. Epistome wide, long, not clearly delimited from endostome. Buccal cavern very wide, widest in middle, laterally arched. Ischium and merus of third maxillipeds typically very wide, constricted at point of their articulation, leaving remarkable rhomboidal gap, mandibles exposed. Palp more or less concealed under endognath, articulating either at anteroexternal or at middle of anterior margin of merus, usually reduced in size. Exognath reduced in size, concealed behind endognath, flagellum sometimes lacking. Ambulatory legs stout, dactyli long, with longitudinal ridges, often with spine-like stiff setae. Male sexual opening on or near suture 7/8 and more or less coxae of last pair of legs. Abdomen freely articulated, completely covering space between last pairs of legs, segment 6 longest. Type genus: *Gecarcinus* Leach, 1814.

#### Subfamily GRAPSINAE MacLeay, 1838

Cephalothorax quadrangular to subcircular, almost depressed. Dorsal surface rough, rugose or setose. Postfrontal lobes distinct. Front wide, strongly deflexed, lamellate, overhanging antennulae and antennae. Secondary frontal margin usually straight. Lateral striae present. Infraorbital margin running downwards toward buccal cavity. Scattered setae on pterygostome present. Lateral carapace margin very sharply defined, overhanging sidewalls. Hepatic tooth sometimes present. Pterygostomial suture anteriorly grooved. Submarginal row of setae lacking. Proepistome anteriorly wide. Infraorbital margin entire, extending to anterolateral angle of buccal cavity. Infraorbital facet present. Antennulae and antennae lying obliquely nearly transversely. Antennal peduncle bent, flagellum very short. Third maxillipeds slender, ischium and merus constricted at point of their articulation, leaving rhomboidal gap, mandibles often exposed throughout, palp articulated at anterior margin of merus. Exognath narrow, exposed, with flagellum. Dorso-interior margin of merus of cheliped with prominent shelf-like expansion. Meri of legs wide, distally with

spine, dactyli spinose. Sternal sutures  $1/2 - 2/3$  distinct. Male sexual opening located on lateral margin of sternite 8 near coxa of last pair of leg and almost far from suture  $7/8$ . Abdomen in male covering whole space between last pair of legs, press-button apparatus present. Type genus: *Grapsus* Lamarck, 1801.

#### Subfamily VARUNINAE H. Milne Edwards, 1853

Subquadrate to nearly subcircular, slightly wider than long, depressed. Dorsal surface moderately convex to nearly flat, anteriorly feebly sloping, usually smooth, no lateral striae. Secondary frontal margin mostly entire, slightly to moderately deflexed, sometimes sublaminar, subfrontal triangle distinct. Anterolateral margin with two or more epibranchial lobes more or less crested, sometimes with submarginal row of setae. Cervical groove ventrally rarely distinct. Infraorbital facet rarely perceivable. Pterygostomian ridge smooth. Supraorbital fissures absent, rarely one small fissure present. Infraorbital margin eclipsed by infraorbital ridge. Epistome triangular. Inter-antennular septum wide. Antennulae folding obliquely. Antennae well developed, diverging. Antennal flagellum relatively long. Infraorbital crest, often paralleled posteriorly by groove. Buccal cavern square-shaped. Third maxillipeds covering nearly completely buccal cavern, slightly gaping, mandible invisible, merus auriculate, palp articulating with middle of anterior margin or near antero-external angle of merus. Ischium and merus with longitudinal sulci, exognath narrow to very wide, with long flagellum. Dactyli of ambulatory legs lacking spines. Male sexual opening on inner part of sternite 8 far as from coxae as suture  $7/8$  Transversal groove between male sexual opening and lateral margin of sternum on sternite 8 present. Locking mechanism of abdomen often lost. Type genus: *Varuna* H. Milne Edwards 1830.

#### Tribe Euchirograpsini trib. nov.

Subquadrate slightly wider than long. Dorsal surface setose. Regions and ridges indistinct. Front relatively wide, slightly produced, lamellate, overhanging antennular fossae and epistome. Primary frontal margin notched for proepistome, subfrontal triangle distinct, secondary frontal margin medially notched, bilobed, lobes straight, antennal sinus minute. Antennulae large, folding nearly transversely. Antennae straight. Basal antennal segment stout, movable peduncle, flagellum longitudinally directed to slightly diverging. Eyes large. Supraorbital margin with small fissure. Exorbital angle distinct, pointed. Lateral margin neither lamellate nor keeled, with  $3 - 1$  teeth. Buccal cavern widened anteriorly, wider than long. Third maxillipeds not completely covering buccal cavern, exognath long, relatively narrow, with flagellum. Palp of third maxilliped articulated at inner median angle of merus. Chelipeds subequal, shorter than ambulatory legs. Dorso-interior margins of chelipeds with prominent shelf-like expansion, lined with sharp irregular teeth. Legs very long, compressed. Posterior margin of dactyli of walking legs with corneous spines. Male sexual opening near coxa, transversal sternal groove on sternite 8 very short. First gonopod rather thick, apical process pointed. Sutures  $2/3 - 3/4$  distinct. Male abdomen triangular, segments  $3 - 6$  fused, sutures distinct. Abdominal segments  $1 - 3$  covering whole space between coxae of last pair of legs, telson widely subtriangular. Type genus: *Euchirograpsus* A. Milne Edwards, 1853.

## Tribe Varunini H. Milne Edwards, 1853

Subquadrangular, with thin, sharp edges. Front wide, lobate to entire, nearly straight, anteriorly hardly to moderately deflexed to secondary frontal margin, where very deflexed, giving impression of sublaminar front. Anterolateral margin with two teeth. Supraorbital margin notched. Antennulae very oblique. Interantennular septum wide. Antennae slightly oblique. Third maxillipeds leaving moderate gap, ischium with one sulcus, merus with two wide shallow sulci, meri auriculate. Chelipeds almost symmetrical. Fingers of chelipeds slender. Articulation carpus – propodus usual. Second pair of legs longest. First gonopod with short distal chitinous palp. Male abdomen rarely or not at all covering whole space between last pairs of legs, segments 1 – 2 reduced, segments 5 – 6 immovable, freely articulating in female. Type genus: *Varuna* H. Milne Edwards 1830.

## Tribe Glyptograpsini Schubart, Cuesta &amp; Felder, 2002

Subgloboid. Front relatively narrow, four-lobed, with distinct median notch, anterolateral margins trispinose. Buccal cavity almost completely covered. Ischium with two, merus with three longitudinal sulci. Chelipeds in male extremely heterochelous, carpus of major cheliped articulated subproximally to palm (not proximally as usually). Chelipeds in female homiochelous. Fingers of chelae spoon-tipped. Third pair of legs longest. First gonopod lacking distal flange, with uncinata distal portion, apex elongate, narrowed. Male abdomen completely covering sternum between last pair of legs, segments 1 – 2 hardly movable, 3 – 5 immovable, sutures distinct. Type genus: *Glyptograpsus* Smith, 1870.

## Subfamily SESARMINAE Dana, 1851

Subquadrate, subquadrangular to trapezoidal, widest between exorbital angles, thick, sidewalls nearly vertical, greatest width usually anteriorly, rarely posteriorly. Regions often discernible. Pterygostomian, subbranchial and subhepatic regions covered with reticulated network of short, hooked setae and granules or setae usually having small granulae at its base. Epigastric lobe usually reduced to absent. Secondary frontal margin wide, strongly deflexed, but not forming eave over propistome. Four postfrontal lobes slightly ridged anteriorly. Anterolateral margin entire or with one to several epibranchial teeth. Lateral margin nearly straight, keeled, with submarginal row of setae, setae arranged in wave-like pattern. Infraorbital margin usually eclipsed by infraorbital ridge. Behind infraorbital margin deep groove. Cervical groove ventrally feebly marked, adjacent to orbital cavity just below exorbital tooth, infraorbital facet usually discernible. Antennulae folding slightly obliquely to nearly transversely. Antennae small, entering orbital hiatus, sometimes excluded. Basal antennal segment large, laterally expanded, obliquely to transversely directed, peduncle and flagellum slender, short. Proepistome wide, epistome usually with obliquely positioned groove on posterolateral region. Rhomboid space between third maxillipeds wide, mandibles exposed. Merus subovate, ischium and merus with distinct oblique setose ridge, exognath narrow, more or less concealed, with flagellum. Palp of third maxilliped articulated at summit or at antero-external angle of merus. Exognath slender, flagellum present, rarely absent. Chelipeds massive

usually subequal. Dorso-anterior margin of chelipeds often with shelf-like expansion. Male sexual opening near coxae of last pair of legs, far from suture 7/8. Transversal groove on sternite 8 very short to absent. Abdomen in male touching coxae of last pair of legs covering more or less completely sternite 8. Press button apparatus present to absent. Stridulating apparatus often present. Type genus: *Sesarma* Say, 1817.

Tribe Sesarmini Dana, 1851

Cephalothorax subsquarish to trapezoidal. Dorsal surface flat. Front wide, strongly deflexed. Four postfrontal lobes sharply ridged anteriorly. Infraorbital margin finely denticulate, running towards buccal cavern below urinal segment. Proepistome anteriorly wide. Antennae very obliquely to nearly transversely directed, mostly entering orbital hiatus, rarely excluded. Basal antennal segment large, laterally expanded, transversal, filling orbital hiatus, peduncle obliquely to transversely directed, flagellum short. Pterygostomian region typically well reticulated. Postero-lateral region of epistome with oblique groove. Rhomboidal gap between third maxilliped wide. Ambulatory legs very compressed. Exognath of third maxilliped narrow, more or less concealed, with flagellum. Male sexual opening near coxae of last pair of legs far from suture 7/8. Transversal groove on sternite 8 absent. Abdomen in male touching coxae of last pair of walking legs, covering more or less complete space between last pair of legs. Type genus: *Sesarma* Say, 1817.

Tribe Paragrapsini trib. nov.

Cephalothorax subsquarish, feebly vaulted. Dorsal surface uneven, not completely smooth, regions sometimes defined. Epigastric lobes positioned at region of frontal deflexion. Front square-cut, deflexed, bilobed, lobes projecting, rather shelf-like. Lateral margins subparallel to convex posteriorly, with 1 – 2 teeth. Supra-orbital margin entire. Subfrontal triangle present. Third maxillipeds slightly constricted at articulation ischium – merus. Dactyli of ambulatory legs lacking spines. Abdomen in male slightly converging anteriorly, not covering whole space between coxae of last pair of legs. Type genus: *Paragrapsus* H. Milne Edwards, 1853.

Tribe Aratini trib. nov.

Trapezoidal, appearing longer than wide. Frontal margin much wider than posterior one, overhanging antennular and antennal fossae. Lateral carapace margins diverging, submarginal groove present. Front strongly deflexed, with 4 distinct lobes, subfrontal triangle absent. Frontal margin lamellate hiding proepistome, antennulae and partly antennae. Infraorbital facet discernible. Exorbital teeth distinct. Eystalks long. Antennulae folding transversely. Antennae directed transversely, excluded from orbit by subcircular lamellate tooth at inner infraorbital margin. Proepistome moderately wide. Epistome posteriorly triangular, oblique groove distinct. Outer surface of chelae covered with tufts of black bristles and blunt tubercles. Dactyls of ambulatory legs short. Exognath slender, hidden under endognath, flagellum present. Ambulatory legs very compressed. Male sexual opening near coxae. Transversal groove on sternite 8 in male very short. Abdomen in male very widening from segments 3 – 6, subcircular, covering completely sternum between 3

– 5 pairs of pereopods touching their coxae. Stridulating mechanism present. Type genus: *Aratus* H. Milne Edwards, 1853.

#### Subfamily CYCLOGRAPSIINAE H. Milne Edwards, 1853

Cephalothorax subquadrangular to roundish, depressed, greatest width across middle of carapace. Anterior half of carapace arcuated. Dorsal surface usually smooth (no tufts of setae), regions often discernible, H-shaped depression present. Front entire, moderately wide, deflexed, not bordered by postfrontal ridges. Orbits open laterally. Infraorbital margin supplemented by infraorbital ridge. Secondary frontal margin indistinct. Lateral margins convex to subparallel, entire or with one or two epibranchial teeth or notches, keeled, submarginal row of setae usually distinct. Pterygostome with longitudinal more or less deep groove running subparallelly to buccal cavity. Pterygostomial reticulation of hooked setae not fully developed. Cervical groove ventrally usually indistinct and infraorbital facet rarely discernible. Proepistome wide, triangular. Epistome lacking distinct obliquely oriented groove. Infraorbital ridge, often with strong (stridulating apparatus), composed by large tubercles. Antennulae more or less transversal. Antennae very short, not excluded from orbits. Basal antennal segment thick directed longitudinally, peduncle oblique. Ischium and merus of third maxilliped with oblique (sesarmid) ridge. Exognath narrow, flagellum present. Rhomboidal space between third maxillipeds very wide. Chelipeds unequal, massive. Ambulatory legs strong, oval or circular in cross – section, propodi and dactyli unarmed. Male sexual opening on inner part of sternite 8, far from coxa and suture 7/8. Transversal groove of sternite 8 present. Abdomen in male neither covering whole space between last pair of legs, nor touching coxae. Type genus: *Cyclograpsus* H. Milne Edwards, 1837.

#### Family PLAGUSIIDAE Dana, 1851

Cephalothorax subquadrate to discoidal. Front wide, dentate, divided into three lobes by deep clefts. Anterolateral margin with several teeth. Cervical groove ventrally indistinct. Pterygostomial ridge fringed by row of setae. True orbits present. Infraorbital margin complete, entire. Antennulae stout, longitudinally to slightly obliquely folded in very deep antennular clefts, visible dorsally. Basal antennal segment well developed, distally sinused. Flagellum short. Interantennular septum more or less wide. Posterior margin of epistome projecting forward to form shelf-like region. Third maxillipeds incompletely covering buccal cavity, no distinct rhomboidal gap, mandibles invisible. Palp of third maxilliped articulating near anteroexternal angle of merus. Exognath slender, with or without flagellum. Sternal suture 2/3 indistinct. Male sexual opening on lateral part of sternite 8, near coxae of last pair of legs, usually in contact with episternite 7, far from suture 7/8. Abdomen touching coxae of last pair of legs. Two proximal abdominal segments reduced, segments 3–5 or 3–6 more or less coalesced in both sexes. Telson not narrower basally than segment 6, distally rounded. Press-button holding mechanism present, projection on posterior part of sternite 6. Type genus: *Plagusia* Latreille, 1804.

**Tribe Plagusiini Dana, 1851**

Thick, subcircular. Surface uneven, squamose. Front deflexed. Anterolateral margin tridentate. Antennulae oblique, diverging, basal segment very wide. Proepistome anteriorly triangular, posteriorly wide. Posterior margin of epistome lobate, projecting anteriorly, visible dorsally. Merus of third maxilliped as wide as ischium, exognath reduced in size. Behind infraorbital margin deep groove. Pereiopods rugose-granulose sometimes tuberculate or spinose. Palm of cheliped not swollen, longitudinally grooved, rugose or granulose. Meri of ambulatory legs with one distal dorsal spine. First gonopod stout. Abdominal segments almost freely articulated in both sexes, segments 3 – 5 or 3 – 6 often more or less coalesced, immovable. Type genus. *Plagusia* Latreille, 1804.

**Tribe Percnini trib. nov.**

Depressed, flatfish. Longer than wide, much narrower posteriorly. Front wide, spinose. Frontal margin overhanging epistome. Anterolateral margin of carapace spinose. Posterior margin of epistome spinose, directed forward, not visible in dorsal view. No infraorbital ridge. Interantennular septum narrow. Antennulae longitudinally folded. Merus of third maxilliped much smaller and narrower than ischium. Meri of pereiopods noticeably spinose. Palm of cheliped swollen, in male smooth. Sternal plastron flat, smooth. First gonopod ending in hook. Abdominal segments 3 – 5 completely fused in both sexes. Type genus: *Percnon* Gistel, 1848.

**Family ASTENOGNATHIDAE Stimpson, 1858**

Subtrapezoidal, transverse, widest posteriorly. Sidewalls steep. Integument hard, lateral ridge indistinct. Regions not well defined. H-shaped depression sometimes distinct. Posterolateral facets distinct. Epigastric lobe reduced to absent. Branchial groove distinct. Front downturned, narrowed anteriorly, touching proepistome. Lateral margin well defined anteriorly. Posterior margin wide, straight. Eyes well developed. Orbits shallow, wide. Orbital hiatus wide, open. Infraorbital ridge present. Inner infraorbital angle short, blunt. Interantennular septum (subfrontal lobus + proepistome) thin to indistinct. Basal antennal segment stout, peduncle standing loosely in orbital hiatus. Epistome very short. Buccal cavern anteriorly nearly subcircular, lateral margins convex. Third maxillipeds well developed, widely distant. Merus of third maxilliped shorter than ischium, palp of moderate size. Exognath moderately wide, with flagellum. Ischium-merus articulation constricted. Palp articulated at summit of merus. First and last pair of legs small. Sternum posteriorly upturned. Abdomen in male widely triangular, segments usually freely articulated, sometimes segments 4 – 6 fused. Type genus: *Astenognathus* Stimpson, 1858.

**Superfamily CAMPTANDRIOIDEA Stimpson, 1858**

Characters as for the family.

**Family CAMPTANDRIIDAE Stimpson, 1858**

Broadly hexagonal, quadrilateral to oval, generally dorsally flattened, rather thick. Dorsal regions usually distinct. Epigastric lobes sometimes distinct. H-shaped de-

pression present. Gastro-cardiac groove often distinct. Cervical groove usually ventrally indistinct. Front relatively narrow, deflexed, touching proepistome. Anterolateral margin variable: dentate, lobate to entire. Orbits and eyestalks relatively long, orbital hiatus wide. Antennulae plicated very obliquely to transversely, not at all hidden beneath frontal margin. Basal antennal segment short, stocky, approaching to nearly touching front. Segment 4 longitudinal, touching front, closing orbital hiatus, segment 5 bent, flagellum rather long. Proepistome and epistome well developed. Buccal cavern wide. Third maxillipeds wide more or less completely covering buccal cavern, merus subequal to longer than ischium. Palp of third maxilliped articulated at inner-medial angle of merus, carpus large, two distal segments of palp slender, exognath narrow, with flagellum partly concealed under endognath. Longitudinal groove parallel to buccal cavern often distinct. Chelipeds usually symmetric. Tips of fingers of chelipeds often hoof-shaped. Ambulatory legs strong, usually stronger than chelipeds. Second and third pairs of ambulatory legs strongest. Male sexual opening contiguous to suture 7/8, far from coxae. First gonopod typically very strongly recurved. First abdominal segment in male short, very wide to widest, variable number of abdominal segments fused, not covering space between last pair of legs. Some abdominal segments in male sometimes constricted (usually fifth segment), not completely covering first gonopods. Typical press-button apparatus present, functional. Type genus: *Camptandrium* Stimpson, 1858.

### Superfamily OCYPODOIDEA Rafinesque, 1815

Cephalothorax subsquarish pentagonal to transversely rectangular, usually thick. Front narrow, deflexed, lying between bases of eyestalks. Cervical groove often ventrally present. Eyestalks and orbits usually very long, occupying whole anterior margin of carapace, laterally to front. Infraorbital margin almost eclipsed by infraorbital margin. Antennulae with inflated basal segment more or less concealed by front, flagella usually obliquely to nearly longitudinally folded. Antennae small. Basal antennal segments more or less converging (not subparallel or diverging as in the majority of crabs), segment 4 converging or subparallel, segment 5 with flagellum bent. Buccal cavern large, posteriorly widened. Palp of endognath of third maxilliped articulating at or near antero-external angle of merus. Exognath of third maxilliped slender, more or less concealed, inconspicuous. Dactyli of ambulatory legs lacking spines. Sternum wide, sternites 1 – 2 very reduced, forming shield, mostly widest posteriorly. Male sexual opening far from coxae, near to suture 7/8. First gonopod usually columnar, nearly straight, rarely slightly curved. Second gonopod short. Male abdomen narrow, segments rarely fused, approaching to base of third maxillipeds. Telson subtriangular, usually narrower than segment 6. Retaining abdominal system almost absent, sometimes vestigial. Type genus: *Ocypode* Fabricius, 1798.

### Family MACROPHTALMIDAE Dana, 1851

Cephalothorax subquadrilateral, moderately wide to markedly wider than long, depressed, more or less flattened. Widest usually between apices of exorbital an-



gles. Dorsal regions usually well defined with cervical and branchiocardiac grooves. Front variable, relatively wide to almost narrow, deflexed, anteriorly nearly straight to slightly concave, overhanging (but not concealing from anterior side) both antennular fossae and antennae. Cervical groove ventrally usually indistinct. Lateral margins distinct, sharp, with fringe of setae. Exorbital angle very distinct. Deep incision behind exorbital angle followed by one or more teeth or lobes. Eyes-talks and orbits usually remarkably long, transversely directed, infraorbital margin entire, no infraorbital ridge. Antennulae well developed, folded slightly obliquely to transversely, concealed under front, flagellum well developed. Antennae of usual form, exposed, basal antennal segment and segment 4 longitudinal to slightly converging, segment 5 bent. Interantennular septum very narrow, at least anteriorly. Third maxillipeds more or less gaping. Merus of third maxilliped shorter than ischium, but of equal width, two distal segments of palp long, relatively thick. Palp inserted in middle of anterior margin of merus, depressed, widened, ventrally flattened. Exognath of third maxilliped not or not completely concealed under endognath. No supplementary breathing opening formed as hairy-ridged pouch between legs. Chelipeds nearly homiochelous, shorter than ambulatory legs, fingers slanting, gaping proximally. Thoracic sternum wide posteriorly. Male sexual opening far from coxae, near suture 7/8. First gonopod nearly straight to curved, distally with numerous fine setae. Abdomen in male narrow, 7-segmented, not covering whole space between last pair of legs, first abdominal segment wide, not touching coxa of last pair of legs, second very short, third one usually widest. Telson short, semicircular, not narrower basally than segment 6. Type genus: *Macrophthalmus* Latreille, 1809.

#### Tribe Ilyograpsini trib. nov.

Subquadrangular, flattened. Dorsal regions indistinct, epigastric lobes distinct. Front of medium size, slightly deflexed. Lateral margin 3 – 2 dentate with sparse short setae or lacking setae. Postfrontal ridge distinct. Orbits large. Eyestalks long, unprotected. Infraorbital margin entire. Exorbital angles distinct. Antennulae plicated very obliquely, nearly transversely. Interantennular septum thin. Basal antennal segment and segment 4 longitudinally directed, nearly parallel to slightly diverging, entering orbital hiatus, segment 5 bent. Endognath wide, merus shorter than ischium, rounded anterolaterally, not closing completely buccal cavern. Chelipeds shorter than ambulatory legs, with pointed fingers. First gonopod slender, outer margin setose, apex of lateral palp not reaching apex of shaft. Telson narrower than segment 6, distally semi-circular. Type genus: *Ilyograpsus* Barnard, 1955.

#### Tribe Macrophthalmini Dana, 1851

Transverse. Front usually very narrow, sometimes nearly T-shaped, slightly deflexed, widest between exorbital angles. Regions often distinct. Lateral margins with marked incisions behind exorbital angle, first lateral tooth large. Postfrontal ridge absent. Eyestalks slender, moderately long to very long. Orbital hiatus very wide. Antennal peduncle converging to parallel, segment 5 bent, entering orbital hiatus. Proepistome (interantennular septum) thin, concealed under front. Merus of third maxilliped as wide as ischium, shorter than ischium. Gap between third

maxillipeds relatively narrow. Chelipeds very long, longer than ambulatory legs, fingers obliquely folded, gaps between fingers large, tips of fingers spooned. Telson short, narrower than segment 6. Type genus: *Macrophthalmus* Latreille, 1809.

### Family OCYPODIDAE Rafinesque, 1815

Subsquarish, transversely rectangular, pentagonal, trapezoidal to transversely ovate, thick, dorsally more or less convex. Dorsal surface rather smooth, regions indistinct, epigastric lobes reduced to absent. Front narrow, in form of deflexed lobe lying between bases of eyestalks lobate or subspatulate, strongly deflexed, partly covering antennulae. Lateral margins lacking teeth, exorbital angle usually small to indistinct. No lateral striae. Cervical groove ventrally usually indistinct, sometimes partly distinct. Eyestalks slender, elongate, usually longer than width of orbit. Orbits wide, occupying nearly entire anterior margin (except front), laterally open. Exorbital angle distinct. Antennulae plicated obliquely to nearly longitudinally. Antennular basal segment well developed, long, inflated, globose to ovate, nearly longitudinally posed, largely exposed laterally to front, flagellum minute, articulated posterointernally. Basal antennal segment, segments 4 longitudinal (subparallel) to converging. Proepistome (interantennular septum) and epistome wide, both triangular. Buccal cavern large, anteriorly slightly narrower, usually completely covered with third maxillipeds, sometimes leaving gap, but never rhomboidal. Palp of third maxilliped coarse, articulated at antero-external angle of merus. Exognath generally narrow, more or less concealed under endognath, flagellum present to absent. Between bases of second and third pair of legs hairy-edged pouch (supplementary breathing opening) leading to branchial cavity present. Sternum wide, posteriorly upturned. Male sexual opening far from coxae and near suture 7/8. First gonopod columnar with corneous tip, second gonopod short. Abdomen in male narrow. Type genus: *Ocypode* Fabricius, 1798.

#### Subfamily HELOECIINAE H. Milne Edwards, 1852

Subtrapezoidal, thick, narrowing posteriorly. Dorsal regions not well defined. Epibranchial region swollen. Front spatulate, deflected. Antennular basis large, ovate, flagella exposed, obliquely folded, not covered completely by front. Antennal segments 4 converging. Infraorbital ridge well developed. Interantennular septum (proepistome) triangular, narrow, touching front. Inner infraorbital angle minute. Infraorbital facet small. Antennae small, basal antennal segment and segment 4 converging. Exorbital angle small. Eyestalk very long. Third maxillipeds almost closing buccal cavern, exognath exposed, with long flagellum. Chelipeds asymmetric, fingers slender, slightly down flexed. Dactyli of legs depressed, long. Ischium and merus of third maxilliped with longitudinal groove. Supplementary breathing opening between coxae of 2 – 3 pairs of ambulatory legs, with tufts of setae. Thoracic sternum narrowed posteriorly. Male sexual opening coxo-sternal. Distal part of first gonopod twisted, endpiece directed fronto-laterally. Abdominal segments in male freely articulated, covering nearly completely space between last pair of legs. Type genus: *Heloeccius* Dana, 1851.

## Subfamily UCIDINAE subfam. nov.

Cordiform, very thick. Front narrow, deflexed, convex, not spatulate. Dorsal regions partly distinct. Antennal sinus minute. Lateral margin anteriorly feebly keeled. Posterior margin narrow, slightly wider than frontal one. Eyestalks not very elongate. Infraorbital margin tuberculated. Infraorbital facet distinct. Antennulae oblique, basal segment hidden under front. Basal antennal segment and segment 4 converging. Interantennular septum (proepistome), wide, triangular, touching front. Epistome large, posterior triangle with deep lateral sinuses, projecting downward-forward, visible from above. Buccal cavern elongate anteriorly not completely covered. Ischium and merus of third maxilliped long, fringed internally with long setae. Exognath of third maxilliped with flagellum mostly concealed under endognath, palp long. Ambulatory legs bearing long silky setae on ventral side. No distinct brush of hairs between coxae of 2 – 3 pair of legs. Sternum narrowed behind. Sternite 8 nearly completely covered by abdomen, small portion of sternite 8 laterally to segment 1 uncovered. Sexual opening of male on suture 7/8, far from coxae. Abdominal segments 5 – 6 fused, other more or less immovable in male. Type genus: *Ucides* Rathbun, 1897.

## Subfamily OCYPODINAE Rafinesque, 1815

Cephalothorax almost subquadrilateral to subpentagonal, widest between ex-orbital angles. thick. Dorsal regions indistinct. Front spatulate, narrow, deflexed apically touching proepistome, covering antennular flagella. Lateral margin unarmed. Eyestalks long. Orbits deep, laterally open. Exorbital angle distinct. Basal antennular segment large, globose, exposed laterally to front. Antennular flagellum small to rudimentary, folding obliquely to almost longitudinally, concealed partly beneath lateral frontal margin. Interantennular septum wide. Antennae small, basal antennal segment and segment 4 subparallel to converging, segment 5 bent. Supplementary breathing aperture between coxae of legs 2 – 3 present. Sternum wide, especially posteriorly. Abdomen in male narrow, far from coxae of pereopods. Abdominal segments freely articulated in both sexes. First gonopod long, nearly straight, sometimes distally curved, with numerous setae and chitinous endpiece. Type genus: *Ocypode* Fabricius, 1798.

## Tribe Ocypodini Rafinesque, 1815

Subquadrangular, widest behind exorbital angles. Proepistome wide, touching front. Eyestalk long, stout, large cornea on ventral side. Orbits large. Inner infra-orbital angle distinct. Infraorbital facet distinct. Basal antennular segment globose, exposed laterally to front. Antennular flagella reduced in size, nearly completely hidden beneath front. Basal antennal segments converging, segments 4 parallel. Maxillipeds covering nearly complete buccal cavern. Exognath slender, more or less concealed beneath endognath. Chelipeds unequal in both sexes. Telson much smaller than segment 6, slightly impressed into segment 6. Floating system absent. Type genus: *Ocypode* Fabricius, 1798.

## Tribe Ucaini Dana, 1851

Transverse, trapezoidal, widest between exorbital angles. Eystalks slender, remarkably long, cornea terminal. Inner infraorbital angle indistinct. Antennular flagella small, not completely concealed beneath front. Basal antennal segment and segment 4 converging. Proepistome relatively wide, apically triangular, touching frontal margin. Maxillipeds covering completely buccal cavern. Exognath not concealed. Some abdominal segments sometimes coalesced. Noticeable heterochelity in male. Floating system present. Type genus: *Uca* Leach, 1814.

## Subfamily DOTILLINAE Stimpson, 1858

Subquadrilateral to subglobose, widest posteriorly, very thick. Dorsal surface usually sculptured with convoluted grooved. Anterior and posterior ventral parts upcurved, visible dorsally. Lateral margin usually toothed or indented behind exorbital angle. Front narrow, deflexed. Frontal margin touching proepistome or epistome. Eystalks elongate. Orbits shallow. Proepistome (interantennular septum) triangular, relatively wide, covered by deflexed front, epistome triangular. Basal antennular segment globose, large, antennular flagella rudimentary, folding longitudinally to obliquely, hidden beneath front. Antennal segment 4 nearly longitudinal, segment 5 bent. Buccal cavity very large, covered completely with third maxillipeds. Third maxilliped longitudinally grooved. Chelipeds homiochelous, to weakly heterochelous, fingers elongate, slender, pointed. Supplementary breathing aperture between coxae of legs 1 and 2 present to absent. Tympanic apparatus on meri of some or all pereopods usually present. Thoracic sternum wide posteriorly. First gonopod straight to sinuous, distally setose. Abdomen in male narrow, 7 – segmented in both sexes sometimes constricted, telson reaching buccal cavern. Floating system present. Type genus: *Dotilla* Stimpson, 1858.

## Subfamily MICTYRINAE Dana, 1852

Cephalothorax globular, slightly longer than wide, very thick. Dorsal surface with cervical and branchiocardiac grooves well defined. Branchial region swollen. Posterior margin straight, relatively wide, fringed with dense setae. Eystalks relatively short, exposed. Orbits absent. Postorbital spine small. Basal antennular segment globose, exposed. Antennular flagellum rudimentary, nearly longitudinally folded, covered with front. Antennae small. Interantennular septum very thin. Proepistome and epistome triangular. Buccal cavity and third maxillipeds very large, oval. Third maxilliped foliaceous, convex covering completely buccal cavern, palp well developed. Exognath slender, lacking flagellum, partly concealed by endognath. Laterally to buccal cavern situated deep groove. Chelipeds slender, elongate, homiochelous. Ambulatory legs long, slender, compressed. Large circular inhalant opening laterally to coxae of chelipeds. Sternum very wide, sterno-abdominal cavity shallow, margins not well delimited laterally. First gonopod strong, nearly straight. Abdomen 7-segmented, very large, broadly truncate, completely covering sternum in both sexes. Telson small, semicircular. Type genus: *Mictyris* Latreille, 1806.

NEW GENERA *INCERTAE SEDIS*

Brachyuran taxa with incomplete descriptions, previously inappropriately classified, their status and position therefore remaining uncertain.

*Aldrovandia* gen. nov.

Etymology: according to Ulisses Aldrovandi, Italian naturalist. Type species: *Micropanope taylori* Garth, 1986. Gender: feminine.

*Aristotelopanope* gen. nov.

Etymology: according to Aristotle, Greek scientist, founder of systematics in general. Type species: *Micropanope ashcrafti* Garth 1986. Gender: feminine.

*Balssomedaesus* gen. nov.

Etymology: according to Heinrich Balss, German carcinologist. Type species: *Medaeus rouxi* Balss, 1935. Gender: masculine.

*Garthopilumnus* gen. nov.

Type specimen very damaged. Etymology: according to John S. Garth, American carcinologist. Type species: *Pilumnus palmeri* Garth 1986. Gender: masculine. Probably new family (Garthopilumnidae).

+*Glaessneroplax* gen. nov.

Etymology: according to Martin F. Glaessner, Australian palaeontologist. Type species: *Pilumnoplax petrificus* Hu & Tao, 1996. Gender: feminine.

*Henryalphonsia* gen. nov.

Etymology: according to Henry and Alphonse Milne Edwards, French carcinologists. Type species: *Pilumnoplax elata* Boone, 1925. Gender: feminine.

*Helleria* gen. nov.

Etymology: according to Camilo Heller, Austrian carcinologist. Type species: *Micropanope manteri* Garth, 1986. Gender: feminine.

*Ihleorandallia* gen. nov.

Etymology: according to Johan E.W. Ihle, Dutch carcinologist. Type species: *Randallia pila* Tan, 1998. Gender: feminine.

*Lazaropilumnus* gen. nov.

Etymology: according to Lazar Car, Croatian carcinologist. Type genus: *Planopilumnus minabensis* Sakai, 1969. Gender: masculine.

*Lipkeplax* gen. nov.

Etymology: according to Lipke B. Holthuis, Dutch carcinologist. Type species: *Euryplax bevisi* Stebbing, 1921. Gender: feminine.

+*Marydromilites* gen. nov.

Etymology: according to Mary J. Rathbun, American carcinologist. Type species: +*Dromilites americana* Rathbun, 1935. Gender: feminine.

*Olivioxantho* gen. nov.

Etymology: according to Giuseppe Olivi, Italian carcinologist. Type species: *Xantho denticulatus* White, 1848. Gender: masculine.

*Otmaroplax* gen. nov.

Etymology: according to Otmar Karlovac, Croatian carcinologist. Type species: *Goneplax maldivensis* Rathbun, 1902 (nec Tesch 1918). Gender: feminine.

*Pestoxanthias* gen. nov.

Etymology: according to Otto Pesta, Austrian carcinologist. Type species: *Xanthias incornutus* (Rathbun, 1898). Gender: masculine.

*Pseudoxanthodes* gen. nov.

Etymology: pseudo = false + *Xanthodes*. Type species: *Xanthodes sulcatus* Faxon, 1893. Gender: masculine.

*Stimpsonia* gen. nov.

Etymology: according to William Stimpson, American zoologist. Type species: *Medaeus spinulifer* Rathbun, 1898. Gender: feminine.

*Teschia* gen. nov.

Etymology: According to Johan H. Tesch, Dutch carcinologist.: Type species: *Goneplax sinuatifrons* Miers, 1886. Gender: feminine.

## DISCUSSION

Having critically re-examined and re-worked the whole brachyuran system and presented its new system of classification it is advisable to comment briefly on the results in their totality.

Firstly, I should explain some of the main changes in this revision. The revision concerns the whole brachyuran system from the tribe to infra-order categorical levels. The brachyuran crabs are divided here into two main sections – Dromiacea and Eubrachiura (=Brachiura genuina), which are not only the two main grades of the

Brachyura but two sister groups probably separated from the Ur-Dromiacea (or Pre-Dromiacea) i.e. the brachyuran stem (ancestral) group. However, this requires further investigation of brachyuran evolutionary history (phylogenesis), which is outside the scope of the present paper.

The smallest change in the current brachyuran re-classification happened within the Dromiacea. The Homolodromioidea are usually placed at the beginning of the classification scheme because they show the most primitive organisation. The Homolodromioidea and Dromioidea (both forming subsection Dromiacea *sensu* Guinot & Tavares, 2003) are also the most primitive lineages, more primitive than those of the Homoloidea and Cymonomoidea. The origin and phylogenetic relationships of Raninoidea, as well as of some extinct dromiacean families such as Diaulacidae, Torynommidae and Dakoticancridae remain obscure at present. Two new extinct families are added: Etyidae and Mithracitidae. The former family is described by GUINOT and TAVARES (2003) while genus *Mithracites* Gould, 1859, is so distinctly different from any known family that the elevation of this genus to family status is well justified. Since it lacks the diagnostic characters of the families, the genus is recognised here as the type of a new monotypic family Mithracitidae. The systematic status and position of the family Dakoticancridae deserves special attention because their regularly metamerised sternum although with interrupted sutures, is unknown for other Dromiacea where the sutures are irregularly directed and almost indistinct. Especially interesting is the new genus *Marydromilites* gen. nov. with complete sternal sutures, which is probably the most primitive sternal structure in lower crabs and very near the brachyuran ancestors. The main alteration in the dromiacean classification is the enigmatic position of the Eocarcinidae and Imocarididae. There is no proven evidence to assimilate them into the Brachyura, and therefore they are temporarily designated here as groups of the Dromiacea *incertae sedis*. It is worthwhile noting that the Dromiacea, because of their organisation (aberrant sternal structures, dorsal position of posterior pair of legs), remain a true "cul-de-sac" of evolution.

The greatest changes in classification, especially concerning the arrangement of their superfamilies, happened within the Eubrachyura particularly within the Heterotremata. The first question is: what is the most primitive eubrachyuran taxon? Previous authors usually placed the Oxystomata (Leucosiidae, Dorippidae, Calappidae) as the supposedly most primitive true crabs at the beginning of the eubrachyuran system. The majority of modern authors have abandoned the old names, but not the old practice: they have not abandoned the traditional arrangement of higher taxa and they continue to place the former oxystomatian families at the beginning of the heterotrematan scheme of classification (GUINOT, 1977; WILLIAMS, 1984; MARTIN & DAVIS, 2001; NG *et al.* 2001 and others). These »oxystomatian« families share some secondarily acquired ancestral structures (elongated and narrowed buccal cavern and mouthparts) as adaptation to the back-burying mode of life and this is not evidence of phyletic relationships. These groups seem to be somewhat highly derived and therefore should be placed in the middle or at the end of the heterotrematan classification scheme. It is noteworthy that only ŠTEVČIĆ (2001) proposed an ascending (from the most primitive to the most derived) arrangement of the

families, while DAVIE (2002) arranged the brachyuran families in alphabetical order. The most primitive true crabs (Eubrachyura) are characterised by coxal male sexual opening, very narrow and elongated regularly metamerised thoracic sternum, all sternal sutures entire (continuous), sterno-abdominal cavity absent or very feebly indicated and abdominal segments freely articulated in both sexes. Furthermore they have antennulae longitudinally folded, first gonopod stout and second gonopod usually as long as or longer than the first. Thus, the most primitive Heterotremata are the Cancroidea. It is from their (extinct) ancestor (with freely articulated abdominal segments and antennulae folded longitudinally) that all the higher crabs (Eubrachyura) have probably descended. At the same morphological grade as the Cancroidea are the Thioidea and Corystoidea, which remained blind ends of evolution i.e. without descendants. The Corystidae were sometimes considered the most primitive higher crabs which was not correct because their elongated body, long, hairy antennae and elongated mouth parts are an adaptation for the back-burying mode of life, not ancestral character states. It is noteworthy that Cancroidea *sensu* elder authors (e.g. GLAESSNER, 1969) or Corystoidea *sensu* BOUVIER (1942) are polyphyletic groups, not natural taxa; – thus they are grade not clade.

Behind the ex-Oxystomata, previous authors often placed the ex-Oxyrhyncha (Majidae, Parthenopidae and Hymenosomatidae) in which carapaces are anteriorly narrowed, but these features were acquired independently and the families are not closely related. The Ocypodidae, and sometimes the Cryptochiridae and Hymenosomatidae as the most derived crabs, are usually placed at the end of the brachyuran scheme. Sometimes, quite groundlessly, either the Majidae or the Potamidae were placed at the final position.

The Heterotremata re-classification has involved considerable transformation in ranking as well as in arrangement. The central heterotrematan stem taxon, as mentioned, is the Cancroidea, with maximum ancestral characters (trilobed supraorbital margin, antennulae folding longitudinally, narrow thoracic sternum, thoracic sutures entire and nearly equidistant, first gonopod simple, stout, second gonopod as long as the first gonopod or even longer, male abdomen covering completely sternite 8, touching coxae of last pair of legs). From Ur- (Pre-)Cancroidea all other brachyuran lines of descent probably arose.

The most complex and largest heterotrematan group was the Xanthidae *sensu* BALSS (1957). They share a subhexagonal (xanthoid) carapace shape and have similar pereopods. The weight of existing evidence however suggests that this group is a heterogeneous assemblage comprising three main lineages or clades: Eriphioidea, Xanthoidea and Pilumnoidea and some small taxa of uncertain affinities (e.g. Notonycidae, Acidopidae).

The Eriphioidea are a very primitive heterotrematan group (abdominal segments freely articulated, first gonopod stout, usually nearly straight, more or less gradually tapering, with simple apex, second gonopod very long with usually long flagellum, endostomial ridge present). In the most primitive eriphiids (Menippini) the sternal sutures 4/5 – 7/8 are entire, all others have the sutures 4/5 – 5/6 interrupted. The Pilumnoididae share the main eriphioid characters, while the Acidopidae,



remain rather isolated. It seems highly probably that the great number of eubrachyuran families descended from the eriphioids.

The Dairidae have uncertain relationships with the Dairoididae and have been placed together tentatively in the superfamily Dairoidea. That is, the »cyclometopous« Dairidae differ from the »oxyrhynchous« Dairoididae in many important diagnostic characters so that the unity of these two groups is not quite clear and awaits further re-examination.

In the classification of the Trapezioidea there are some problems. This involves the relationships among Coralliopinae, Domeciinae and Trapeziinae. The first two groups are xanthiform, and third is typically trapezoidal. Moreover the Domeciinae and Trapeziinae have similarities in mouthparts and pereopods, but these similarities can be the result of adaptations to living in corals not of any common ancestry. Coralliopinae are insufficiently known, the result being that the unity of the superfamily remains rather obscure.

The next very large taxon, with very complex composition of subtaxa, is the Xanthoidea. They were previously considered as a group having a central position, but now they are divided into several separate families belonging to various clades. The Xanthoidea s. s. are more derived than the Eriphioidea because the xanthoids possess more advanced diagnostic characters (sternal structures, gonopods, abdominal fusion in male). The Xanthoidea are characterised by a long and slender first gonopod usually with relatively simple apex and very short second gonopod, abdominal segments 3 – 5 fused and sternal sutures 4/5 – 5/6 interrupted. Their classification is indeed very complex. It is noteworthy that Xanthidae and Panopaeidae are very closely related and the gap between them (different first gonopods) is not very deep, although they are considered here as families for the sake of easier classification. Two new fossil families Zathopsidae and Palaeoxanthopsidae are added to this superfamily, although their position remains open to re-examination.

The Pilumnoidea with slender, elongated, simple, usually sinuous first and short sigmoidal second gonopods, freely articulated abdominal segments in both sexes and endostomial ridges are recognised as a separate clade, that is not a part of the Xanthoidea, to which they are only superficially similar (carapace, pereopods). The pilumnoids are derived seemingly from the primitive eriphiid ancestors. Their the most derived taxon is the Rhizopinae. Their classification is very complex and the composition of the Pilumnoidea remains an unsettled question.

The Majidae are the largest brachyuran family, with a very complex subdivision. The taxon can be derived from some cancrioid or pirimeloid taxa with trispinose supraorbital margin and even pseudorostral spines or lobes. Their derived condition is characterised by complication of the orbits (Mithracinae) as well as their reduction (Epialtinae). The systematic position of the Inachinae because their slender usually freely movable antennae deserve re-examination. The Inachoididae have some very distinct specific derived characters but their organisation is basically majid. The latter taxon shares some similarities with the Hymenosomatidae (GUINOT & RICHER DE FORGES, 1999) as a very derived and highly aberrant group. These authors affiliated and tentatively classified the hymenosomatids together with the

majids. It is noteworthy that the majid classification is almost entirely based on the frontal and orbital structures and the Oregoniinae *sensu* GARTH (1958) seem to be an artificial group in which the similar structures of their abdomen and first gonopods were probably independently acquired.

Two very aberrant groups previously accommodated with the Majidae, Paratymolidae and Lambrachaeidae, are classified here as the Majoidea *incertae sedis* because their affinity with the Majidae is very questionable and need further examination. The Lambrachaeinae here raised to the familial status are a highly aberrant group, whose systematic status and position remains highly uncertain. They share majority characters in common with the Inachinae as, for example, long »neck« and pseudorostrum, long pereopods, orbits poorly defined and some characters-in-common with the Parthenopidae (NG & MCLAY, 2003): fusion of abdominal segments 3 – 5 in the male, chelipeds triangular in cross section, chelipeds slightly heterochelous, fingers with molariform teeth, relatively long »neck« in some species of *Rhinolambrus* A. Milne Edwards, 1878 yet with all the efforts of the previously mentioned authors Lambrachaeidae cannot be considered a proper parthenopid (sub)family. They exhibit a suite of specific characters (orbits, antennulae, antennae, propistome triangular anteriorly, but with ventral spine) that cannot be embraced by any currently recognised family and therefore it is necessary to view their systematic status and position as an unsettled problem. Finally, the status and position of Paratymolidae are very enigmatic. They are not appropriately described in, for example, the sternal structures. It is observed that sternal sutures in *Dumea latipes* (Haswell, 1880) are entire and regularly metamerised, although this requires further confirmation and re-examination, and they are temporarily referred to as the family Paratymolidae of the Majoidea *incertae sedis*. As with all highly aberrant groups it is very difficult to ascertain their true status and position, but it is probable that they both do not belong to the Majoidea.

The classification of the Goneplacoidea, especially of the family Goneplacidae, has been a stumbling block for many generations of carcinologists. GUINOT was among the first to start dismembering this overloaded group. In fact the problem is rather simple. The Goneplacidae s.s. are a very small family distinctly separated from the Xanthoidea. Only those taxa which share all diagnostic characters of the Goneplacidae (sternal sutures 4/5 – 7/8 interrupted, second gonopod long, abdominal segments freely articulated in both sexes) can be placed in this family. All other »goneplacid« higher taxa (*sensu* BALSS, 1957) were placed, based on their diagnostic characters, in their appropriate positions. The »goneplacid« Pseudorhombilidae are placed with the Xanthoidea, the Eucratopsinae and Cycloplacinae into the Panopeidae, the »goneplacid« Rhizopinae s.l. are divided into the pilumnid Rhizopinae s.s., and many families are accommodated into various superfamilies within the classificatory scheme: Acidopidae, Notonycidae, Raouliidae, Chasmocarcinidae, Scalopidiidae, Litocheiridae, Euryplacidae Typhlocarcinodidae, Speocarcinidae and Hexapodidae. Some newly named »goneplacid« taxa should after re-examination be reclassified. The newly described extant family Planopilumnidae and the extinct Amydrocarcinidae and Megaxanthidae, because of a specific combination of characters, are temporarily and questionably placed within Goneplacoidea, although be-

cause of the sternal male sexual opening of the latter family its position remains uncertain. The systematic status and position of the fossil *Amydrocarcinus* Schweitzer, Feldmann, Ganzález-Barba & Vega, 2002 is still rather obscure. SCHWEITZER *et al.* 2002 classified it into the Xanthidae *sensu lato* so indicating their isolated position. It is markedly different from all other known xanthoids so that no xanthoid family can accommodate it and hence the elevation of this genus to familial level is well justified. The same could be mentioned for the fossil Megaxanthidae, which are here temporarily placed into the Goneplacoidea.

The heterotrematan genera *Parapilumnus* Kossmann, 1877 and *Conleyus* Ng & Ng, 2003 because of their very peculiar combinations of diagnostic characters cannot be incorporated into any currently recognised superfamily and therefore they are raised to familial and superfamilial levels.

Some groups are relatively poorly studied and therefore their classification proves troublesome. For example, the Chasmocarinoidea. The family Chasmocarcinidae is relatively well worked out and rather clear. The problem is that the genus *Scalopidia* Stimpson, 1878 is always placed in the Chasmocarcinidae although it is rather different from this family. The Megaestesidae are very aberrant and hence it is difficult to understand their proper status and position. In the absence of sufficient data the fossil family Carinocarcinoididae is questionably and temporarily added to this superfamily.

The classification of the Potamoidea, as always, is very difficult and currently in a state of intensive revision by many specialists, so the classification of them is not yet stable. The cause of the difficulty is their expressed »mosaic evolution«, where ancestral and derived characters are mixed causing many difficulties in the delimitation and arrangement of the subtaxa. The nature of their classification has been the subject of many controversies. For some workers the fresh-water potamid-shaped crabs are composed of only one family (BALSS, 1957) whereas other carcinologists place them in several superfamilies (BOTT, 1970). The principal difference with respect to the previous classifications is that it was based on the hypothesis that the four-segmented first gonopod is a more primitive character state than a three-segmented gonopod. In fact during evolution the endopod was divided into subterminal segment and terminal joint (not fused, as considered by precedent authors) and the more primitive state is the three-segmented gonopod (BRANDIS *et al.* 1999). Quite to the opposite, the three-segmented mandibular palp is primitive whereas the bi-segmented palp is consequently derived. Because of various interpretations of these polarity states misunderstandings among the numerous workers were very frequent. Here the freshwater crabs are divided into two main groups: Potamoidea s. s. (Potamidae and Pseudothelphusidae) whereas the Trichodactylidae are placed as the superfamily Trichodactyloidea near to the Portunoidea

The Aethridae are provisionally classified into the Parthenopoidea. While they possess some characters in common with the Partenopidae they nevertheless possess many particular characters such that their placement awaits re-examination. It should be noted that the name Aethridae is older than Hepatidae.

The parthenopid classification was subject to some minor changes. The main problem pending was the systematic status of the genus *Mimilambrus* Williams, 1979 because of its somewhat aberrant organisation. The understanding of their rank has varied from superfamily (WILLIAMS, 1979) to genus (NG and RODRÍGUEZ, 1986). This taxon differs from the typical parthenopids in the form of buccal cavern, mouthparts, orbits, gonopods and ways of respiratory current water and therefore deserves family status.

The Portunidae have a rather complex classification structure. The majority of them share typical portunid organisation and only some small groups are aberrant. For example, Catoptrinae have an uncertain position because of their atypical last pair of legs and frontal structure. It is noteworthy that *Libystes* A. Milne Edwards, 1867 has many specific features and therefore it is viewed here as a separate subfamily. While the Podophthalminae are also very aberrant because of their frontal structure, their organisation is nevertheless basically portunid.

The Leucosiidae are a large and well-defined family yet with extreme diversity, causing difficulty in their division (as already remarked by ALCOCK, 1896) into subfamilies and tribes, and whose classification awaits radical revision. The expressed »mosaic evolution« causes difficulty in their revision, and therefore it was avoided by many generations of carcinologists.

The set of families mentioned below remain very enigmatic in their origin and systematic position.

The Orithyiidae are a well-defined and well-isolated family.

The Heteroziidae and Belliidae are possibly related, but are more likely represent two different and separate families. It is noteworthy that more canceriform taxa are less specialised and more primitive than elongated forms (back-burrowers).

The Matutidae are well-defined but have a »mosaic« organisation (primitive sternal structure and complex respiratory structures) and therefore their systematic position remains uncertain. They are only superficially similar to the Calappidae.

The next group of families often classified together: Dorippidae, Palicidae and Retroplumidae are well defined by pronounced gaps. They are not closely related, but at a similar morphological grade

The unity of the Pseudozoidea, despite some similarities to the Flindersoplacidae and Pseudoziidae (NG & WANG, 1994), remains an open question.

The families Troglolacidae and Typhlocarcinodidae are separated by very distinct gaps and they have no clear relation to other families. The affiliations of these groups are difficult to ascertain. The same may be said for many other small families.

The Cryptochiridae are one of the most derived crabs. They are very dissimilar to all other crabs because they inhabit the galls of corals. Their relationships with other groups remain obscure.

The systematic position and any affinities of the Pinnotheridae are rather obscure. They have a coxo-sternal position for the male sexual opening but they share some thoracotrematan features (mouth parts, gonopods) and therefore are consid-

ered as either heterotrematan (GUINOT & RICHER DE FORGES, 1997) or thoracotrematan crabs (v. STERNBERG & CUMBERLIDGE, 1998).

At the end of the Heterotremata the families Secretanellidae, Necrocarcinidae and Orithopsidae are placed as heterotrematan (?) families *incertae sedis*. There are also three fossil families, whose classification, as always, is very difficult. The mentioned families share some dromiacean characters. They are very old with concave posterior margin and rather strong carapace sculpturation. The systematic position of the Necrocarcinidae remains obscure, the Secretanellidae exhibit some heterotrematan characters and therefore were included into the Heterotremata by GUINOT & TAVARES (2001) whereas only Orithopsidae have a sternal female gonopore, and they also belong to the Heterotremata. Their systematic position must await better times when more preserved specimens will be found.

The unity of the former Catometopa, now Thoracotremata, was the subject of controversy among recent brachyurologists (GUINOT, 1978, 1979; GUINOT & RICHER DE FORGES, 1997 and v. STERNBERG & CUMBERLIDGE, 1998) and problem remains unsettled. The systematic status and position of some thoracotrematan families requires further re-examination. It is noteworthy that the Thoracotremata are a special clade, probably originating from the Potamoidea (v. STERNBERG *et al.* 1999).

The Grapsoidea occupy a central position within the Thoracotremata, but familial classification remains unsettled. The main family is the Grapsidae in whose classification two main changes occurred. Firstly the Gecarcinidae of older authors are included in Grapsidae as their subfamily. However, as they share the main grapsoid diagnostic characters yet express a »mosaic evolution«, their systematic position remains rather obscure. Another alteration is the separation of the Plagusiidae from the Grapsidae, as separate family. The Plagusiidae have atypical frontal structures, antennulae longitudinally (secondary) plicated and visible in dorsal view. Moreover some of them have completely fused abdominal segments in which they differ from other grapsoids.

The Astenognathidae are considered here as a family of the Grapsoidea. All previous authors included them in the Pinnotheridae. I do not see the reason for such a classification, because the Astenognathidae are small (and very rare) symbiotic grapsoid crabs, but the whole organisation indicates an aberrant nature. Revision is, of course, desired.

The Camptandriidae, previously considered as the Ocypodidae, are characterised by the usual brachyuran subfrontal structures (the front is short and never covering the subfrontal structures: antennulae, antennae, interantennular septum) whereas their strongly recurved first gonopods are quite peculiar, indicating their isolated position.

The reclassification of the Ocypodoidea reveals some new puzzles. The consideration of frontal and subfrontal structures (mostly overlooked by previous authors) led to the conclusion that the Macrophthalminae of older authors, because of primitive frontal and subfrontal structures (usual antennae, antennulae, lack of accessory breathing aperture between the bases of walking legs) should be raised to the familial level, as should Macrophthalmidae. The Ocypodinae are characterised by a

more derived frontal complex (tongue-shaped and recurved front covering bases of antennulae and accessory breathing aperture). The opposite is the case with the Mictyrinae, which are very derived ocypodids (like the Dotillinae) because their organisation is basically ocypodid. Therefore they should be placed in the Ocypodidae. In the literature the Ocypodidae were sometimes placed in front of the Grapsidae, which is not justified because the Ocypodidae are more derived than the Grapsidae.

Let me now return to the explanation of the brachyuran system as a whole. The proposed classification system contains many novelties. What at first may seem strange is the great number of new taxa. Are these warranted? There are indeed many new families, with most described quite recently, and yet nearly all previously described families (with the exception for the Mictyridae and Gecarcinidae) »survived« all revisions and maintained their identity in the current system. Moreover, many families have been divided into old and newly described subfamilies and the latter into tribes, a practice avoided by my predecessors. By splitting these families their existence is neither questioned nor is their importance diminished, only the classification scheme has become more complex. The taxa descriptions given and accompanied with the type genus confirm the justification for the establishment of new higher taxa. The same can be said for the numerous new subfamilies and especially for the tribes. The great number of tribes is a consequence of their being ignored formerly. The new diagnostic characters used permitted an accurate description of the taxa and showed that some groups cannot be classified into already described subtaxa, for which reason the new higher taxa have been established. The case of the Majidae is the best example. Many subgroups of the Majidae were known previously (NEUMANN, 1878) yet authors such as BALSS ignored them and mentioned only the sparse subfamilies, recognised by BORRADAILE (1903, 1907). The same may be said for the Leucosiidae for which ALCOCK established many alliances (i.e. tribes), that were omitted by subsequent authors (exception for ORTMANN, 1901). After reappraising of his system, I would concur with ALCOCK.

At first glance it seems that the proposed classification is overly complex. Is it so? The answer is that brachyuran evolutionary history has been very complex and consequently its presentation in the form of a classification scheme is also inevitably bound to be complex. There are in fact many new families, subfamilies and especially tribes. It should be pointed out that the number of higher taxa, especially extinct ones, rapidly increased in the past several (2 – 3) years (GUINOT & TAVARES, 2001; SCHWEITZER *et al.* 2002; SCHWEITZER, 2003; KARASAWA and KATO, 2003 a, b and others). In the previous (20th) century, despite rapid development of knowledge of the brachyuran crabs, only four extant and six extinct families were described. Now, in the present paper the superfamily number is 49 with 92 families, 119 subfamilies and 169 tribes recognized; – for comparison: BALSS (1957) recognised 4 tribes (*sensu*: sections), 31 families and 52 subfamilies). Most of the higher taxa are the result of elevating previously recognised suprageneric taxa obtained as a result of the present revision.

During the revision of the brachyuran system I have encountered many small, often monotypic, genera which cannot be included in any of the previously recognised higher taxa and therefore it was necessary to raise them to a higher categorical level and establish new higher taxa. Previous authors avoided elevating taxa with a small number of species, often only one, to a higher categorical level. It is worth mentioning that small higher taxa are very often found in zoology. MAYR and ASHLOCK (1991: 271) claims that, »Most higher taxa of organisms contain some 20 to 30 percent monotypic genera«. There are, for crabs, indeed many families comprising only one genus (Acidopidae, Raouliidae, Notonycidae, Parapilumnidae, Typhlocarcinodidae, etc.) yet there are certainly very good grounds for recognising them as separate families because they possess sufficiently distinctive and exclusive features to merit them family status, apart from their size. The small taxa often cause many difficulties in ranking and ordering, yet they should not be overlooked, ignored or craftily avoided. The (non)justification of these changes could be easily verified as valid or invalid as from the descriptions of the taxa the justification for the current revision is easily accessible.

It is a fact that there are many new taxa and consequently new names. Is this indeed an inflation of names? The principal working goal of the present research, as mentioned before, is to recognise monophyletic groups and not the creation by any means new taxa and new names. The new taxa names are only the result of re-assessment and where some inconsistencies in the old system were observed I undertook to make the appropriate changes. Future investigations, as always, will confirm or reject the justification for these changes. In a case where I found a supra-generic group which is sufficiently distinct to warrant its recognition as a separate higher taxon I have described it, proposed a new name, defined its rank and placed it in the appropriate position within the system. (What is the alternative?) In this way many groups were split into several taxa or lumped into one. I can not see another resolution. For previous authors, although conscious of the necessity for the changes, did not attempt the revision. Therefore it is only at first glance that there seems to be a huge inflation of new taxa and their accompanying names. It is worthwhile pointing out that the practice of listing higher taxa without descriptions or diagnoses is worse; this is avoided here by giving appropriate short descriptions (or enlarged diagnoses). The pure taxon name is merely a label deprived of content and therefore it is in itself valueless for systematics, e.g. when a higher taxon is not properly described and the type genus not mentioned

As apparent from the text above, the results of revision and remaining open questions have been gathered here in the same place. This current attempt, I believe, resolves some previous problems while many new problems have been revealed and, regrettably, remain unresolved. It is a matter of fact that any systematic research reveals not only what is certain and clear, but also many *lacunae* and open questions remain for further investigation as well. Every complete classification also reveals two sides – what is known and what is not known. This work is not only a massive compilation, but has also indicated a new classification structure for the brachyuran crabs and their new inter- and intrarelations of suprageneric taxa. At the same time many *lacunae* remain in the knowledge of the phylogenetic rela-

tionships of the crabs. Finally, the present paper is intended to act as a catalyst to stimulate further revisions.

It goes without saying that behind the »authoritative« style (as is usual in works of similar type) there are many reservations, dilemmas and hesitations. The open questions should not be hidden or carefully avoided, but on the contrary should be stressed because it is in the interest of the progress of knowledge of brachyuran systematics that these difficult questions should be »attacked« and resolved. The questions include, for example, are the extinct Lobocarcininae members of Cancridae, and the Priapipilumnini and Danielini indeed members of the Pilumnidae (because of different gonopods)? And what about the Melybiidae, Bythograeidae and Speocarcinidae? Despite all efforts some groups remain inadequately described (usually because of insufficient information on their morphology, in particular by fossil forms, and when structures such as subfrontal structures, sternal sutures or gonopods are not at all described) and therefore a new general revision is needed for some families (especially: Leucosiidae, Potamidae, Xanthidae, Portunidae etc.). The systematic status and position of many taxa remains enigmatic because they were not re-examined by previous authors. For example the relationship *Daira* de Haan, 1833 – *Dairoides* Stebbing, 1920 is not clear and no new knowledge has been added. Sometimes systematic positions were very difficult to establish for many taxa (Acidopidae, Matutidae, Orithyiidae, Dorippidae, Retroplumidae, Hexapodiidae, Raouliidae, Palicidae, and Typhlocarcinodidae). Sometimes this happened due to confusion and inadequate description of genera e.g. *Micropanope* Stimpson, 1871, *Xenophthalmodes* Richters, 1880 and the establishment of a higher category remained rather questionable. On the other hand some families exhibit such great diversity that any sound subdivision was impossible (Hymenosomatidae, Hexapodidae, Bythograeidae, Campandriidae). Finally, some genera remained very difficult and await revision e.g. *Micropanope*, Stimpson, 1871 *Heteropilumnus* de Man, 1895, *Pilumnus* Leach, 1815, *Carcinoplax* H. Milne Edwards 1852, *Uca* Leach, 1814, *Trapezia* Latreille, 1825, *Potamon* Savigny, 1816, *Cancer* Linnaeus, 1758 and *Pinnotheres* Latreille, 1802 too). These are the weak points of this piece of work.

The proposed classification of crabs reveals quite different views of the major taxa size. The largest family is no longer the Xanthidae, as was believed (CHACE, 1951), but the Majidae. The Goneplacidae are no longer the most complex family and have a distinct gap with respect to the Xanthidae. However they are not quite distinct from the Geryonidae. The inner subdivisions of the Xanthidae, Panopeidae, Leucosiidae, Portunidae, Potamidae etc. became more complex. As seen from the aforementioned, this revision of the brachyuran system resulted not only in some new solutions, but also new open questions – many resolutions contained hesitations and dilemmas. This is the destiny of scientific work: resolutions of some problems reveal many new ones. The task is endless!

There are indeed many changes from the previous classification of the crabs. Since the supreme rule of systematic study is to start from one's own specimens the novelties of the proposed system could be, after critical re-assessment of one's own material, accepted or rejected (I believe in the first option). The final judgement of the solutions is left to the test of time. The proposed updated classification, as with



all previous ones, is provisional and therefore could be subject to later revision. In fact, revision is nearly a synonym for systematics.

The majority of earlier systematists faced with the difficulty of distinctly defining and ranking the taxa under study raised them to the higher categorical level. So for example BOTT (1970) inflated the potamoid classification by elevation of some families to superfamily rank and subfamilies to the family rank. He established the superfamily level for the freshwater crabs Potamoidea, Parathelphusoidea and Pseudothelphusoidea. In systematics there is a tendency permanently to increase the levels of the systematic categories. However the Crustacea are a class and the Decapoda are their order (for some systematists the Crustacea are superclass or even subphylum and so on). However, I accept that the Brachyura are an infra-order and consequently all lower taxa should inevitably have lower levels than infra-order in the hierarchy of categories. The problem of potamoids has been resolved by having them remain at the familial level whereas the numerous main subtaxa are on the lower categorical levels.

Classification is a human work and as such it is subject to errors and omissions. Some small errors (erroneous observation or interpretation) are inevitable (*errare humanum est*) in particular in such an immense field of research such as classification of the brachyuran crabs. These errors can be easily corrected by re-examination of specimens. It is not difficult to go wrong e.g. in the observation of sternal suture 6/7 in some potamoid taxa, fusion proepistome-epistome, etc. More »dangerous« are those conceptual mistakes or inadequate methods that are impossible to correct. Furthermore there are several schools (cladism, phenetism, classic) and various approaches (such as morphological, ecological, functional, constructivistic etc.) which exclude one another. Each of these schools and approaches has some strengths and weaknesses, and it is necessary to choose only that school with the minimum number of errors. The present approach, as seen, is classic and it is based on the need and possibility that all crabs should be classified in the natural (Linnean) hierarchical system. My standpoint is that if in nature discrete groups that can be delimited, named, arranged and ranked do not exist, then the effort presented herein will be invalid. Consequently all observed groups of crabs were described so that it will be evident what they comprise and in which characters they differ from the other groups. All previous classifications were a product of their times, or more precisely, the state of knowledge at that time, and the same is true for the present work. It is a result of the present state of knowledge and will quite naturally be changed by progress in knowledge of the crabs. Concerning the other approaches to brachyuran systematics, it is to be expected that they will encompass all crabs, and new and completely different classifications will be proposed. However, incomplete and one-sided classifications may be interesting but never decisive for true progress. I believe and hope that the majority of innovations introduced here will survive on-going revisions.

The long history of the study of higher taxa shows that improvement of the classification brings it nearer and nearer to the natural system, i.e. mirroring the evolutionary history of the brachyuran crabs. Therefore I believe that this attempt represents a step forward in approaching this final aim, (although the goal is very

distant) and it will be only one link in the historical sequence of brachyuran investigations. »Mosaic evolution«, homoplasies and reversals will cause controversies among workers in the near and far future. This is inevitable! Finally, there exists a »reciprocal illumination« with the particular revision of various brachyuran taxa. These studies, which deal with the study of the whole system of higher taxa on the other hand enable better classification of lower taxa.

Since complete revision has been neglected for about a century, this work is not as perfect as one might wish. This study can be understood as a suggestion for new attempts for the revision of the brachyuran system as a whole and as for certain parts. The current work is not the last word in the brachyuran systematics, but only a link in an endless chain in the history of brachyuran systematics.

I hope everybody who is familiar with the brachyuran classification will understand the difficulties I have encountered in this study. It is indeed very difficult to include all crabs at one time. Moreover, I am conscious that my proposed solutions are not always perfect and that such a system is »scientifically expendable«. However, I believe that it will nevertheless be useful or at least a challenge or stimulation for suggestions for further systematic research. It goes without saying that the brachyuran system is a result of collective efforts of generations of students and this attempt is only a modest contribution to their collective result.

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## SAŽETAK

### Revizija viših svojti kratkorepih rakova (Crustacea: Decapoda: Brachyura)

Z. Števcić

Sistematska istraživanja deterenožnih kratkorepih rakova (Crustacea: Decapoda: Brachyura) vrlo su intenzivna i imaju dugu povijest. Dok se broj novoopisanih rodova i vrsta kako recentnih tako i izumrlih brzo povećava, istraživanja svojti iznad razine roda znatno zaostaju. Dok su neke više svojte više ili manje temeljito revidirane većina ostaje desetljećima netaknutima. Zadnji potpuni opis svih do tada poznatih viših svojti i njihova klasifikacija potječu od BALSSA (1957), a od tada ima mnogo novosti kako u otkrivanju novih oblika tako i u poznavanju sistematskih obilježja (karakteristika). Istovremeno i teorija sistematike bilježi brzi razvoj. Zbog nagomilanih neriješenih problema svako snalaženje u sistematici ove skupine poslalo je vrlo otežanim pa je stoga temeljita revizija neophodna. Budući da jedna takva revizija na svjetskoj razini zahtijeva veliki napor i mnogo vremena, a vodeći sistematičari pretrpani vlastitim materijalom nemaju vremena za jedan takav poduhvat, tako da se revizija viših svojti stalno odgađala za neka bolja vremena. Prihvativši se revizije bilo je potrebno najprije prikupiti iz literature sve relevantne podatke o višim svojtima te kritički preispitati svaku svojtu ponaosob, njenu homogenost, kategorijalni rang i položaj u sustavu. Tamo gdje se je pokazalo da su skupine heterogene (tj. polifiletičke) trebalo ih je razdijeliti na manje ali homogene (dakle, monofiletičke) skupine – svojte. Svaku od tih svojti valjalo je ponovno opisati, a ako su nove, imenovati te odrediti im sistematsku kategoriju kao i položaj u filogenetskom sustavu. Dosljedno tome u ovom radu su dati sažeti opisi svih viših svojti od plemena (tribi) pa na više, koje su raspoređene u hijerarhijski sustav, a za svaku svojtu naveden je i tipski rod (lat.: *genus typicum*) čime je svojta nedvosmišleno određene. Na taj način predloženi sustav kratkorepih rakova potpunije odražava suvremeno stanje poznavanja sistematike ove skupine početka 21. stoljeća.

## ADDENDUM

**Superfamily ERIPHODEA MacLeay, 1938****+Family TUMIDOCARCINIDAE Schweitzer, 2005**

Cephalothorax mostly subhexagonal to nearly roundish, slightly wider than long, dorsally convex longitudinally, especially in anterior third. Carapace regions more or less well defined. Epibranchial regions usually arcuate. Front with distinct median notch, four-lobed to bilobed. Anterolateral margins with 3 – 4 small blunt spines or almost entire and granular. Orbits directed weakly anterolaterally to anteriorly, margins with completely fused fissures to almost entire, rimmed. Inner and exorbital angles small and not produced. Antennulae folding obliquely. Chelipeds massive, subequal to very unequal, smooth, fingers with black tips. Ambulatory legs slender. Sternal sutures 1 / 2 indistinct, 2 / 3 entire, clearly deep, 3 / 4 interrupted mesially, groove over suture well marked, oriented at very high angle. Sternite 4 with longitudinal grooves near lateral margins. Sterno-abdominal cavity prolonged over sternite 4 forming with groove over suture 3 / 4 Y-shaped well marked formation. Abdominal segments in male freely articulated, apex of telson almost reaching or not quite reaching imaginary line connecting posterior edges of coxae of chelipeds. Abdomen completely covering sternite 8. Type genus: *Tumidocarcinus* Glaessner, 1960.

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