CHAPTER 1

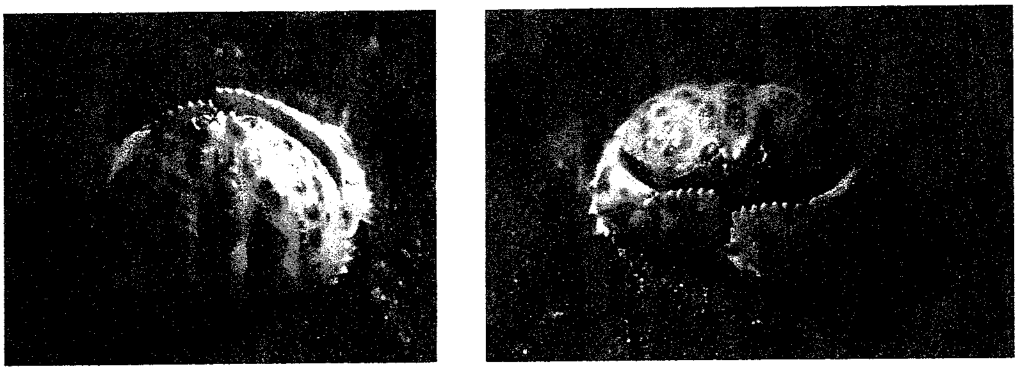
GENERAL INTRODUCTION

1.1. Introduction and Aims

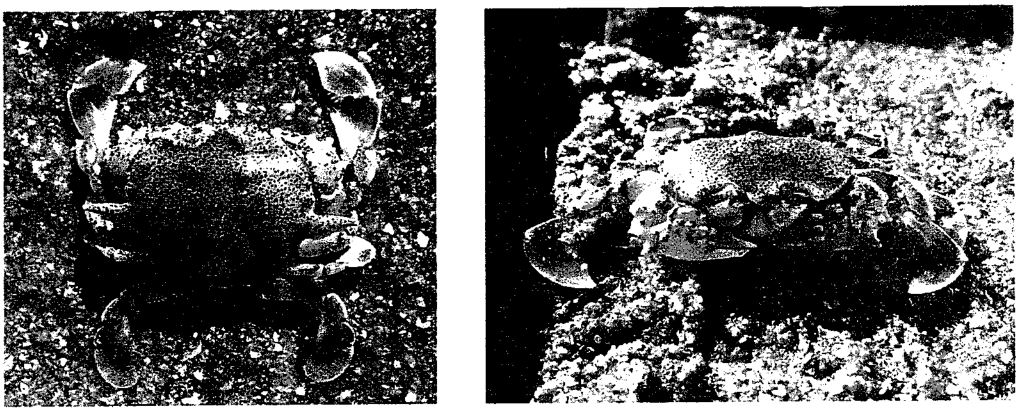
The box crabs (family Calappidae) are a distinctive group of marine crabs found in tropical and subtropical regions of the world. The family is best known for the shallow water genus *Calappa* with its unusual hooked chelae, but it contains many other, albeit less well-known, taxa. Calappids are found in the Atlantic, Indian and Pacific Oceans where they occur in waters from 0 to 1,000 meters deep (Alcock, 1896, Rathbun, 1937). They are amongst the most conspicuous and morphologically diverse brachyurans in soft substrata, with adult individuals ranging from approximately 20mm to 150mm in carapace width (Abele & Felgenhauer, 1982). Most members of the family are known for their burrowing habit and their ability to disappear rapidly into the sediment. They are one of the few brachyuran families capable of burying completely in soft substrata. A number of taxa within the family possess structural modifications which have been suggested to facilitate the burrowing process, e.g. accessory respiratory channels, flattened pereiopods and a posteriorly expanded carapace.

The family, as it is traditionally recognised, is composed of three or four subfamilies: the Calappinae, Matutinae and Orithyinae, with the occasional inclusion of the Hepatinae (Guinot, 1979, Stevcic, 1983) (Fig. 1). The group as a whole contains over 15 genera and about 65 species (Appendix III). Taxonomists have placed the various taxa together either as a family or as a superfamily, invariably incorporating all subfamilies, a reflection of their apparently close affinity. Placed under the section or tribe Oxystomata (= 'sharp mouthed'), the mouthparts of calappids taper narrowly towards the front, giving a triangular appearance. They share these characteristics with the other oxystomatoid crabs, the pebble crabs (f. Leucosiidae) and the shield crabs (f. Dorippidae).

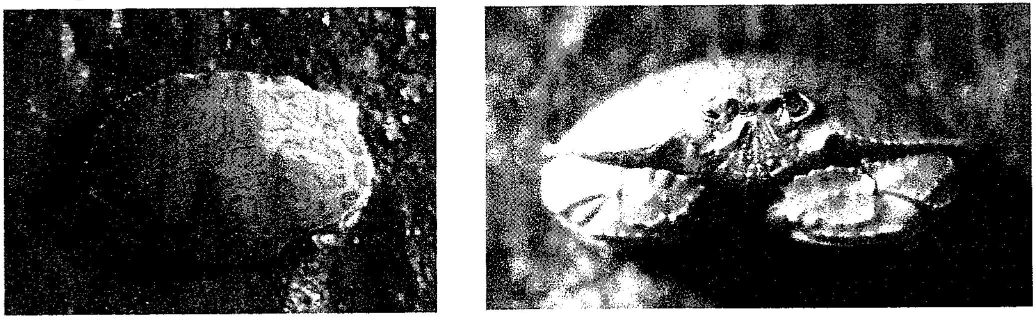
A. *Calappa granulosa* - subfamily Calappinae



B. *Matuta lunaris* - subfamily Matutinae



C. *Hepatus epilithicus* - subfamily Hepatinae



D. *Orithyia sinica* - subfamily Orithyinae

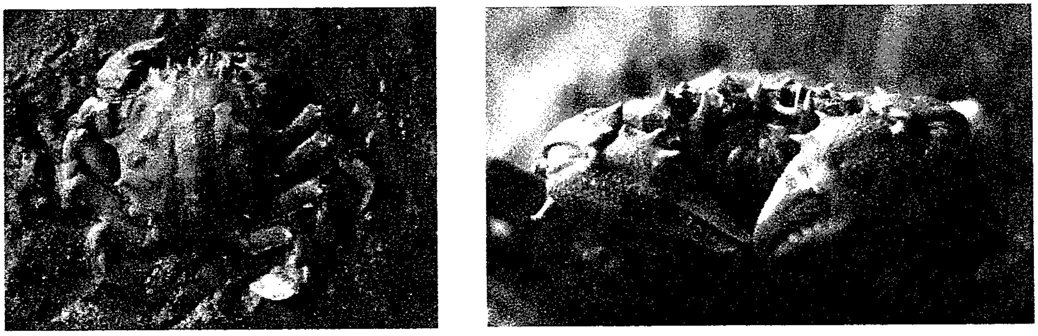


Figure 1. Dorsal and frontal view of representative species from each of the four subfamilies in the Calappidae showing their characteristic shape, colour and carapace patterns.

Box crabs do not represent a palatable, harvestable fishery resource, but they are a common food item in many coastal regions in the tropics (e.g. Guinot, 1966a, Schreiber & Cases, 1984). Biologically, however, they are efficient predators of molluscs and other crustaceans and it has been suggested that they have played a significant role in the evolution of modern molluscan forms (cf. Vermeij, 1977). To date, very little is known of the biology of the family as a whole. Much of the existing literature focuses on larval descriptions (e.g. Rajabai, 1959, Seridji, 1993, Taishaku & Konishi, 1995) or taxonomic descriptions of individual taxa (Galil, 1993, 1997, Galil & Clark, 1994, 1996). Basic aspects of their biology, such as feeding (e.g. Shoup, 1968, Ng & Tan, 1984, Perez, 1987, Haefner, 1981), growth (Bellwood & Perez, 1989) and reproduction (Perez & Bellwood, 1989, Perez, 1990) are largely restricted to two highly modified genera, *Calappa* and *Matuta*. The systematics of the group, in particular, is poorly understood. In the last 20 years, studies have identified a number of inconsistent features within the Calappidae and have highlighted the need for a detailed phylogenetic analysis and review of the status of the family (e.g. Guinot, 1979, Rice, 1980, Seridji, 1993).

The Calappidae is best known for the two highly modified taxa: *Calappa,* with its unique chelae (Ng & Tan, 1984) and *Matuta,* with its specialized 'swimming' legs (Perez, 1986) . Both genera are common in shallow tropical waters throughout the world and usually occur in sandy or sand-mud habitats. It is in these taxa that the full expression of the behaviour presumed to be associated with the oxystomatous condition is readily observed, i.e. the burying habit. This provides an excellent framework for investigating the evolution of burying and the function of the oxystomatous condition within the group and in a broader sense, within the Brachyura. This poses the basic question: What is the phylogenetic and functional basis of the oxystomatous condition?

The primary aims of this study therefore are:

- To reappraise the systematic status of the family Calappidae and the phylogenetic relationships of taxa within the family using morphological data and a cladistic methodology;
- To use the results of the phylogenetic analysis to evaluate the fossil record, biogeographic patterns and depth distributions of taxa within the family;
- To use the results of the phylogenetic analysis and recent findings from molecular and higher-level phylogenetic studies to investigate the evolution of the burying habit within the Brachyura;
- To review the occurrence and significance of the burying behaviour in Brachyura as a framework within which to investigate burying behaviour in two distinct forms within the Calappidae: *Calappa* and *Matuta*.
- To evaluate the functional basis of the oxystomatous condition, focussing on the burying behaviour, morphology and the functional attributes of the ventilatory systems in *Calappa* and *Matuta* in comparison with a non-oxystomatous, non-burying taxa.

1.2 Overview of the biology of the Calappidae

Currently, much of what is known of the biology of the Calappidae is based on the biology of two of its four component subfamilies, the Calappinae and the Matutinae. Relatively little is known of the Hepatinae and the Orithyiinae.

The Calappinae has 9 extant genera: *Calappa*, *Mursia*, *Acanthocarpus*, *Cycloes*, *Cryptosoma*, *Cyclozodion*, *Paracyclois*, *Platymera* and *Mursia*, with approximately 42 species in total. Commonly known as "box crabs" or "shame-faced crabs", the group is characterized by their greatly expanded chelae and the distinctive lobules at the base of the propodus and dactylus on one of the chelae which permits them to peel open gastropod shells. Much of the existing literature on calappine crabs deals with this unique feeding behaviour, particularly in *Calappa* (*e.g.* Shoup, 1968; Vermeij, 1982; Ng & Tan, 1984, 1985, Hughes & Elner, 1989). Based on their unique chelae morphology, *Calappa* species are considered to be among the most important predators of tropical molluscs, influencing both the distribution and characteristics of their prey (Vermeij, 1977). An inferred molluscivorous diet in other calappid genera (Stevcic, 1983), however, is not supported by gut content analysis. *Acanthocarpus alexandri* was found to consume a variety of benthic infauna, particularly polychaetes and microcrustaceans, with gastropods forming only a very small proportion of its diet (Haefner, 1981). Very little is known of the diet of other genera as well as the other aspects of their biology.

The Matutinae previously contained the single genus *Matuta* (*e.g.* Alcock, 1896, Dai & Yan, 1991). However in a recent revision, 3 other genera were established based on phenetic features: *Izanami*, *Ashtoret*, and *Mebeli* (Galil & Clark, 1994). Many aspects of the biology of the Matutinae are well known, particularly feeding and reproductive biology (Pillay & Nair, 1976, Seiler, 1976, Perez & Bellwood, 1988, 1989, Perez, 1990), absolute growth (Bellwood & Perez, 1989), larval morphology and development (Hashmi, 1969, Rajabai, 1959, Terada, 1983, Seridji, 1993) and the functional morphology of the stridulatory organs (Guinot-Dumortier & Dumortier, 1960, 1961) and anterolateral denticulations (Garstang, 1897a,b). From these studies, it appears that the Matutinae are facultative scavengers and opportunistic predators of benthic invertebrates, feeding primarily on small crustaceans and molluscs. *Matuta* shows a determinate growth pattern, marked by an anecdysic final instar with sexual maturity occuring only after the terminal moult. Characterized by precopulatory guarding behaviour, *Matuta* has been reported to breed continuously throughout the year with marked asynchrony in the reproductive activity of individuals within a population (Pillay & Nair, 1976, Perez, 1990). Matutines occur from the intertidal to the subtidal regions of tropical seas where they spend most of their time buried in soft sediment (Thomassin, 1974).

In comparison with the Calappinae and the Matutinae, very little is known about the Hepatinae and the Orithyiinae. Found mainly in the Atlantic and in the Eastern Pacific, the Hepatinae is composed of 3 genera (*Hepatus*, *Osachila* and *Hepatella*) and 14 species (Rathbun, 1937). Apart from one species, *Hepatus pudibundus*, the biology of hepatine crabs is largely unknown. Like *Matuta*, *H. pudibundus* was found to be facultative scavenger and predator of benthic invertebrates with its diet primarily composed of micro-crustaceans, fishes and molluscs (Mantellato & Petracco, 1997). Virtually nothing is known of the monotypic Orithyiinae. Found only in the China Seas from Korea to Hongkong (Stevcic, 1983), the genus *Orithyia* is typically collected from shallow soft sediment habitats (Sakai, 1976).

1.3 Thesis Structure

The thesis is divided into 5 chapters: the first and the last chapters being the Introduction and General Discussion.

Chapter 2 is a phylogenetic study of the Calappidae *sensu lato* based on a cladistic analysis of adult morphological characters. The focus of this chapter is: 1) to examine the evidence underpinning the monophyly of the family, 2) to re-evaluate the relationships among the component sub-families, and 3) to determine appropriate outgroups that can be used in further phylogenetic analysis of genera within the family. Although the inclusion of the three to four subfamilies within the Calappidae has rarely been disputed, recent studies have highlighted the value of and the need for a phylogenetic appraisal of their relationships. The Calappidae is ideal for morphology-based cladistic analysis as it is one of the few groups with distinctive morphological characters which promises a good, clear resolution of relationships between taxa.

Chapter 3 builds on the results of Chapter 2 and using cladistic methodologies, will examine the relationships between the genera in the Calappidae. The main aim of this chapter is to evaluate the fossil record, biogeographic patterns and depth distributions of genera within the Calappidae.

Chapter 4 examines burrowing behaviour in the Brachyura before focussing on a functional study of the burying behaviour and respiratory structures of *Calappa* and *Matuta*, representing two distinct forms within the Calappidae. Both genera share habitat and behavioural features despite seemingly disparate morphologies. The burying habit of these genera have long been associated with their oxystomatous condition (see Garstang, 1897), although these conclusions are usually only inferred from morphology. A comparative study of the functional morphology of their respiratory systems and burying behaviour was undertaken to examine the significance of the oxystomatous condition in these genera directly. A review of the occurrence and significance of the burying behaviour in other brachyuran taxa is included to evaluate the broader implications of the burying habit in the Brachyura.

Chapter 5 provides an overview of the evolutionary history of oxystomatous crabs and the unique features of this unusual condition.

This thesis is the first detailed study of an oxystomatoid group using a phylogenetic approach. While this approach has been used in other phyla, it is relatively underused in the Crustacea. The value of phylogenies in elucidating evolutionary and ecological hypotheses cannot be underestimated. This study links evolutionary, biogeographical, functional and ecological approaches to investigate the biology of the Calappidae.

CHAPTER 2

THE FAMILIAL STATUS OF CALAPPIDAE *SENSU LATO*: A PHYLOGENETIC APPRAISAL

2.1 INTRODUCTION

For the past 140 years, the systematic status of the Calappidae has remained stable, if unclear. Brachyuran taxonomists have traditionally placed the various genera together, either as a family or as a superfamily, thereby implying close relationships (e.g. Alcock, 1896, Rathbun, 1937, Glaessner, 1969, Bowman & Abele, 1982, Dai & Yang, 1991). In many taxonomic works, however, the dichotomy of forms is always recognized (the "calappine" and "matutine" form), yet a definition of the group and the relationships of the subfamilies remain elusive. A number of studies have cast doubt on the familial status of the Calappidae, pointing to a number of inconsistent features between taxa in terms of their adult and larval morphology and their biology, and have led to the suggestion that the family may not be a natural group (Guinot, 1979, Rice, 1980, Stevcic, 1983, Seridji, 1993). In addition, the broader group Oxystomata, in which the Calappidae has been traditionally placed, has increasingly been considered by many authors to be an unsupportable amalgam of disparate groups. As a first step to the understanding of the evolution of the Calappidae, it is therefore imperative that the phylogenetic status of the family should be clarified.

The aim of this chapter is to review the systematics of the Calappidae and to examine the phylogenetic relationships of the subfamilies within the Calappidae using a cladistic approach. The specific objectives are to identify appropriate outgroups which could be used in further phylogenetic analysis of genera and to establish the monophyly of the family. This chapter contains three major sections: i) historical review of the Calappidae and the Oxystomata, ii) comparative morphology and iii) phylogenetic analyses and discussion.

2.2 HISTORICAL REVIEW

2.2.1 The Calappidae

The Calappidae was established in 1837, apparently simultaneously and independently, by two workers: H. Milne Edwards and W. de Haan. H. Milne Edwards (1837) erected the tribe Calappiens to accommodate *Calappa*, *Platymera*, *Mursia*, *Orithyia*, *Matuta* and *Hepatus*, whilst de Haan (1837) erected the Calappidea as a family to accommodate *Cycloes*, *Calappa* and *Mursia*. The actual dates of publication of H. Milne Edwards' and de Haan's works has been further narrowed down by Holthuis (1979, 1993) and Yamaguchi (1993). The work of H. Milne Edwards precedes that of de Haan by one month, appearing in July 1837, whilst that of de Haan appeared in August 1837. H. Milne Edwards therefore has priority over de Haan as the authority of the Calappidae. De Haan (1841) later placed *Matuta* and *Hepatus* in a separate family, the Matutoidea.

The subsequent history of the family is reflected in the major crustacean publications arising from U.S. expeditions in the 1800's. Dana (1853) in his report on the Decapoda collected in the U.S. Exploring Expedition recognised two families: the Calappidae and the Matutidae. Within the Calappidae he established two subfamilies: the Calappinae and Orithyiinae; the Matutidae contained the genera *Hepatus* and *Matuta*. Stimpson (1871) in the U.S. coastal survey, subsequently divided the Matutidae into two subfamilies: the Matutinae and Hepatinae. Miers (1886) in his report on the *Challenger* collection accepted the classification of Dana and Stimpson.

Ortmann (1892) raised the Orithyiinae to full familial status and placed the three families Calappidae, Matutidae and Orithyiidae in the subdivision Calappinea. Alcock (1896) disagreed and united the three families into a single family: the Calappidae. Alcock's family Calappidae contained only two subfamilies: the Calappinae and Matutinae, each containing 2 alliances. The Calappinae contained the alliances

Calappoida and Orithyoida whilst the Matutinae contained the alliances Matutoida and Hepatoida.

Ortmann (1901) revised his earlier classification and relegated the three families Calappidae, Matutidae and Orithyiidae into subfamilies within the Calappidae. This classification was largely accepted by Borradaile (1907) and Ihle (1918) who, in his analysis of the brachyurans from the *Siboga* Expedition, provisionally accepted the three subfamilies but expressed doubts on the inclusion of Orithyiinae within the family.

For the succeeding 60 years this scheme featuring a single family, the Calappidae, containing three subfamilies: Calappinae, Matutinae and Orithyiinae, was widely accepted (*e.g.* Rathbun, 1937, Balss, 1957, Glaessner, 1969, Sakai, 1965, 1976).

Recently however, several authors have questioned this classification. Guinot (1966b, 1978a) removed *Hepatus*, *Hepatella* and *Osachila* from the Matutinae and erected the group Parthenoxystomata to contain these genera along with 2 other genera from the Leucosiidae and Parthenopidae. In a subsequent monograph on a new scheme of brachyuran classification, Guinot (1977, 1978b, 1979) rejected the group Oxystomata and assigned the Calappidae to the superfamily Calappoidea within the section Heterotremata. In addition, Guinot (1978b, 1979) re-erected the family Orithyiidae and also placed it under the Calappoidea. Guinot's family Calappidae now contained 2 subfamilies: the Calappinae and Matutinae (excluding *Hepatus*, *Hepatella* and *Osachila*). In a review of crab zoeal morphology and its bearing on brachyuran classification, Rice (1980) generally agreed with Guinot's classification scheme and found that the range of 'advanced' [sic] and 'primitive' [sic] features found in 'calappid' zoeae is much greater than that found within a single family, suggesting that the Calappidae is not a natural group. Rice, however, did not support Guinot's re-grouping of *Hepatus*, *Hepatella* and *Osachila* with parthenopids. His conclusions were supported by Seridji (1993) based on a detailed comparison of calappid zoeae and echoed by Stevcic (1983) in a review of the biology of the Calappidae.

Almost all of these studies have relied on external characters and have assessed relationships in a largely phenetic sense although Guinot (1979) and Rice (1980) in particular have highlighted the value and need for a phylogenetic appraisal of relationships within the Calappidae. However, despite the prevalence of recent taxonomic revisions of its component genera, to date, there have been no phylogenetic analyses of the family.

2.2.2 The Oxystomata

The taxonomic history of the Oxystomata is not as problematical as that of its component families. Established by H. Milne Edwards in 1837, the group Oxystomata (="sharp-mouthed") contained those brachyurans in which the buccal frame or endostome is extended forward to form a triangle, namely the leucosiids, dorippids and calappids. This classification scheme was widely accepted (*e.g.* Dana, 1853; Miers, 1886; Ortmann, 1896) and remained unchallenged for many years. The only changes to this classification was the inclusion of the raninids by de Haan in 1841, a reclassification by Boas in 1880 and the removal of the raninids by Bourne in 1922. Since the beginning of the 19th century, the Oxystomata has remained one of the cornerstones of Brachyuran classification (*e.g.* Alcock, 1896; Borradaile, 1907; Rathbun, 1937; Barnard, 1950; Balss, 1957; Sakai, 1965; Glaessner, 1969; Bowman & Abele, 1982 and Dai & Yang, 1991).

Only in the last 20 years, with the advent of new techniques in systematics, have workers questioned the status of this group (e.g. Guinot, 1977; Rice, 1980; Spears, Abele & Kim, 1992). The present study represents the first detailed phylogenetic study of an oxystomatoid group using cladistic techniques and will address a broader question of the validity and composition of the Oxystomata.

2.3 MATERIALS AND METHODS

2.3.1 Selection of taxa and outgroups

Analyses were based on the four subfamilies within the Calappidae: the Calappinae Dana 1853 containing 8 genera (*Calappa*, *Acanthocarpus*, *Cycloes*, *Cyclozodion*, *Paracyclois*, *Mursia* and *Platymera*), the Matutinae Stimpson 1871 containing 4 genera (*Matuta*, *Ashtoret*, *Izanami* and *Mebeli*), the Hepatinae Stimpson 1871 containing 3 genera (*Hepatus*, *Hepatella* and *Osachila*) and the Orithyiinae Dana 1853 containing the single genus *Orithyia*. For each subfamily, all component genera were examined. For each genus, the material examined included the type species.

A total of 35 species were examined with representatives of all sixteen genera in the Calappidae (*sensu* Alcock, 1896; Williams & Child, 1988; Galil & Clark, 1994). The analyses were based on the examination and dissection of preserved material loaned from the Natural History Museum (London), National Museum of Natural History (Washington D.C.), Muséum National d'Histoire Naturelle (Paris) and the Queensland Museum (Brisbane). In addition, fresh specimens were collected from Cleveland Bay, Pallarenda Beach and Orpheus Island, Queensland, Australia. The material examined is listed in Appendix I. Morphological observations were made using a Nikon SMZ-1B dissecting microscope. Drawings were made with the aid of a *camera lucida* or were traced from photographs.

As the monophyly of the Calappidae is the issue in question, several outgroups were used in the analyses as a "test" for monophyly following Nixon and Carpenter (1993). The outgroup taxa were drawn from the Leucosiidae, Dorippidae, Xanthidae and Portunidae. The Leucosiidae and Dorippidae have long been associated with the Calappidae as traditional sister groups under the section Oxystomata as established by H. Milne-Edwards (1837). In the present study, the Leucosiidae was represented by *Leucosia* *ocellata*. The Dorippidae was represented by *Dorippe quadridens* and *D. sinica*.

Two non-oxystomatous families were also included in the analyses, the Xanthidae and Portunidae. The Xanthidae was represented by *Atergatis floridus*. Larval and rRNA evidence suggests that the Xanthidae may have a closer relationship with the Calappidae than previously thought (Rice, 1980; Spears et aL, 1992). The Portunidae, represented by *Portunus pelagicus*, was included in the analysis as a typical "generalised" crab which shares similar habitat and ecological requirements with the Calappidae. In terms of higher classification, all the outgroup families together with the Calappidae belong under the section Heterotremata (Guinot 1977).

2.3.2 Character selection and coding

The characters used in this study were obtained from as wide a range of structures and functional systems as possible. All character states were based on adult morphology. In all cases, both male and female specimens were examined. The characters chosen for inclusion in the analyses were those found to be of high taxonomic value at the subfamily level. That is, characters with clearly defined character states, which were consistent (invariant) within a group (*i.e.* subfamily). Care was taken to consider characters which may influence outgroup relationships.

A total of 78 characters were used. A list of characters and character states is given in Table 2.1. The characters and their respective states will be described in the Comparative Morphology section. A complete matrix of character states is given in Table 2.2. This matrix includes autapomorphic character states. These character states were not included in the analyses.

Table 2.1 List of characters used in the phylogenetic analysis of 4 subfamilies of the Calappidae *sensu lato* and 4 outgroup taxa. Each character is numbered and described, followed by the character state where 0=presumed plesiomorphy and 1,2,3,4 = presumed apomorphies.

1 Antennule: folded longitudinally (0); obliquely (1)
2 Antennae: basal segment 10-20% orbital width (0); <5% (1)
3 Antennae: basal segment fills inner orbital gap (0); does not fill inner orbital gap (1)
4 Antennae: 1st peduncle segment elongate and equal in length to basal segment (0); short and <50% of basal segment (1)
5 Antennae: flagellum ≥50% orbit diameter (0); reduced and <25% orbit diameter (1)
6 Orbital region: eyestalk long (0); short (1)
7 Orbital region: shape circular (1); ovoid (0)
8 Orbital region: lateral fusion complete (0); incomplete (1)
9 Orbital region: lateral carapace margin fuse laterally (0); extends suborbitally (1)
10 Orbital region: lateral supraorbital spine present (0); absent (1)
11 Anteroventral region: efferent channel absent (0); present & broad (1); present & narrow (2)
12 Anteroventral region: pterygostome flat or convex (0); concave (1)
13 Cheliped: coxal articulation to basi-ischium ball/socket (0) or ligamentous (1)
14 Cheliped: distal articulation simple and straight, posterior margin covered by ischium (0); with free posterior border, giving appearance of a rounded spine (1)
15 Cheliped: ischium distinct from merus (0); completely fused with merus (1)
16 Cheliped: merus perpendicular to body (0); oblique (1)
17 Cheliped: merus with distal lateral extension (1); no extension (0)
18 Cheliped: merus with dorsal flange (1); no dorsal flange (0)
19 Cheliped: merus ventral surface with 3-4 spines (1); no spines (0)
20 Cheliped: mero-carpal articulation with dorsal small spine (1); no spine (0)
21 Cheliped: propodus with expanded dorsal margin (1); no expanded dorsal margin (0)
22 Cheliped: propodus inner surface with setae (1); no setae (0)
23 Cheliped: pollex modified, dactylus with hooked lobule (1); not modified (0)
24 Pereiopods II-IV: dactylus narrow (0) broad (1)
25 Pereiopods II-IV: merus ventral surface smooth (0); adorned with either spines or granules (1)
26 Pereiopod V: segments similar to other periopods (0); paddle-shape (1); subchelate (2)
27 Pereiopod V: dactylus setose (0); not setose (1)
28 Abdomen: covers sterno-abdominal cavity completely (0); covers only 50% of sterno-abdominal cavity (1)
29 Abdomen: last abdominal suture (between segments 6 and 7) corresponds with s5/6 (0); s4/5 (1); none (2); s2/3 (3)
30 Abdomen: number of segments visible ventrally = 5 (0); 6 (1); 7 (2)
31 Abdomen: 1st segment width equal (1) or < 2nd segment (0)
32 Abdomen: 1st segment ornate (1); not ornate (0)
33 Abdomen: 3rd segment ornate (1); not ornate (0)

34 Abdomen: 3rd, 4th and 5th segments fused in males (0); all segments not fused (1); 2nd, 3rd and 4th segments & fifth and sixth segments fused (2)
35 Abdomen: telson (7th segment) length shorter than previous segment (0); ≥ previous segment (1)
36 Carapace: posterior edge with ventral process articulating with abdomen (1); no ventral process (0)
37 Sternum: number of continuous sutures = 4 (0); 2 (1); 1 (2)
38 Sternum: sternal cavity length up to s4 (0); s3 (1)
39 Sternum: median line up to s6(0); s5(1); s7(2)
40 Sternum: episternite distinct, 50% length of next somite (0); reduced, 20% length of next somite (1)
41 Sternum: episternite suture present (0); absent (1)
42 Sternum: episternites cover coxa of pII-pV (1); do not cover (0)
43 Sternum: ep7 elongate posteriorly (0); small and short (1)
44 Sternum: cohesive nodule location: below s4/5(1); above s5/6(0); central (2); absent (3)
45 3rd maxilliped: does not close completely (0); closes completely (1)
46 3rd maxilliped: merus broad and quadrate (0); elongate (1)
47 3rd maxilliped: merus anteromedial margin notched or lobed (1); no notch (0)
48 3rd maxilliped: merus lateral margin notched to fit exopod (1); lateral margin straight and confluent with ischium (0)
49 3rd maxilliped: merus inner surface excavate (1); not excavate (0)
50 3rd maxilliped: palp not concealed by merus (0); completely concealed by merus (1)
51 3rd maxilliped: palp segments equal in length (0); basal segment longer than other segments (1)
52 3rd maxilliped: exopod with flagellum present (0); flagellum absent (1)
53 3rd maxilliped: exopod width uniform throughout (0); tapering (1)
54 3rd maxilliped: exopod outer surface with row of thick setae (1); no setae (0)
55 3rd maxilliped: coxa small and narrow (0); enlarged and expanded dorsally (1)
56 3rd maxilliped: epipod with narrow lateral attachment (0); broad (1) narrow ventral (2)
57 2nd maxilliped: exopod length = endopod length (0); exopod length > endopod length (1)
58 2nd maxilliped: exopod robust (1); flimsy (0)
59 2nd maxilliped: flagellum long, >50% exopod length (0); short, <25% exopod length (1); absent (2)
60 1st maxilliped: endopod distal segment not elongate (0); elongate (1)
61 1st maxilliped: endopod distal tip not visible externally (0); visible externally (1)
62 1st maxilliped: exopod length = endopod length (0); exopod length < endopod length (1)
63 1st maxilliped: exopod flagellum long, >50% exopod length (0); <30% exopod length (1); absent (2)
64 Endostome: shape of buccal frame broad and short (0); elongate and narrow (1)
65 Endostome: anterior opening not modified (0); highly modified (1)
66 Penis: with swollen base (1); narrow and elongate (0)
67 Penis: naked (0); encased in sclerotized sheath (1)

68 1st pleopod: tapers along length (1); base and shaft of uniform in width (2); base enlarged (3); shaft conical (4); narrow and elongate (0); polymorphic (P)
69 1st pleopod: outer basal angle simple and small (0); expanded and flanged (1)
70 1st pleopod: ridge parallel to shaft (0); oblique (1)
71 1st pleopod: distal tip pointed (0); rounded (1)
72 1st pleopod: distal tip with no dorsal process (0); finger-like dorsal process present (1)
73 2nd pleopod: length < 1st pleopod (0); ≥ 1st pleopod (1)
74 2nd pleopod: basal half curved (0); straight (1)
75 2nd pleopod: flagella length < length of basal segment (0); ≥ basal length (1)
76 2nd pleopod: flagella straight (0); bent (1)
77 Vulvae: located inside sterno-abdominal cavity (0); outside sterno-abdominal cavity (1)
78 Vulvae: vaginal lining does not protrude out of lumen (0); protrudes out of lumen (1)

Table 2.2 Character matrix (8 taxa by 78 characters) used in the cladistic analysis of the Calappidae. The first four taxa are outgroups. Polymorphic character states coded as 'P'. Unknown character states are shown by ?

	0	**1**	**2**	**3**
Portunus	0000000000	0000000000	0000010000	0000000000
Leucosia	0000011011	?000110000	0000101032	0002?001?0
Dorippe	1000000100	0011010000	0000020000	10110000?1
Atergatis	0000011001	0000000000	0000000010	1000101000
Calappinae	1000011011	1100101001	1110001011	0000111100
Hepatinae	1001111011	1000100000	0000000010	0010111000
Matutinae	0111100100	2000010010	0001110000	0010012010
Orithyiinae	1000000100	0011010100	0000010120	1111000021

	4	**5**	**6**	**7**
Portunus	0000000000	0000000000	0000000000	000000??
Leucosia	1103110011	0100000021	0121000P01	P0010001
Dorippe	0000010000	0100020011	1111001400	10010000
Atergatis	1001000000	0000000100	0000010110	00000000
Calappinae	1111001010	1001111101	1101010110	00101100
Hepatinae	1012110111	0010000111	0111010110	00100000
Matutinae	0100110011	0110000011	0111010201	11111001
Orithyiinae	0003010000	0100001011	0011101300	10000000

2.3.3 Phylogenetic analyses

Character analyses were carried out using PAUP version 3.1 on a Macintosh LC475. A total of 8 taxa were used in the analyses, 4 outgroups (*Portunus*, *Leucosia*, *Dorippe* and *Atergatis*) and 4 ingroups (Calappinae, Hepatinae, Matutinae and Orithyiinae). All characters were unweighted and multi-state character states unordered. In the analyses, the branch-and-bound option (BANDB) was used to find the shortest and most parsimonious tree, otherwise, default options were used. The analyses were run without a specified outgroup to permit a simultaneous unconstrained resolution of ingroup and outgroup relationships (*cf.* Nixon & Carpenter, 1993). PAUP used the first taxon in the matrix as the default outgroup for rooting.

2.4 COMPARATIVE MORPHOLOGY

In the following section, character states are indicated in the text by numbers in parentheses, giving the character and character state where 0 = presumed plesiomorphy; n>0 = presumed apomorphy (*e.g.* 17.1 = character 17 state 1 which is derived). Where there is more than one apomorphic state these are indicated in a similar manner (*e.g.* 68.4). Numbering character states 1, 2, 3 etc. does not necessarily indicate a transformation series. N.B. The polarity of the character states was not determined *a priori* but during the construction of the cladogram.

2.4.1 Antennule and antennae

In the Calappidae, antennal characters primarily the size of the basal segment and the length of the flagella have been used both in generic and species level classifications. In this study, both antennular and antennal characters were found to be informative. The direction of the peduncular fold in the antennule as it fits inside the antennular fossettes is longitudinal (1.0) in the Matutinae, *Atergatis*, *Leucosia* and *Portunus*. In the Calappinae, Hepatinae, Orithyiinae and *Dorippe*, the antennules are folded obliquely (1.1).

Although previous studies have described the basal segment of the antennae of calappids as enlarged, the nature of this enlargement has not been well defined (Alcock, 1896; Stevcic, 1983). In the present study, the size of the basal segment relative to the orbit did not appear to vary amongst the ingroup or outgroup taxa (between 10 - 20% of the orbital width, 2.0), except in the Matutinae where it is less than 5% of the orbital width (2.1). In most brachyurans, the basal segment of the antennae is located at the inner angle of the orbit, filling the gap between the upper and lower orbital margins (3.0). This state was found in all taxa, except in the Matutinae where the basal segment does not reach the inner orbital gap (3.1). The 1st segment of the peduncle is typically elongate and approximately equal in length to that of the basal segment (4.0) in the Calappinae and Orithyiinae and in all the outgroup taxa. In the Matutinae and Hepatinae the first segment was found to be less than half of the basal segment length and smaller (4.1). The length of the antennal flagellum as a proportion of the orbit width was also found to vary amongst the taxa. In the Calappinae and Orithyiinae and all the outgroup taxa, the flagellum is equal or greater than half of the orbit width (5.0). In the Matutinae and Hepatinae, the flagellum is greatly reduced, measuring approximately 10% of the orbit width (5.1).

2.4.2 Orbital region

Traditional orbital characters such as eye size and relative orbital size which are often included in brachyuran taxonomic descriptions were found to be of limited use in this study. Although the eyes of the Calappidae are described to be relatively large (Alcock, 1896, Rathbun, 1937, Williams & Child, 1988), this appears to be an estimate of relative, rather than absolute, eye size. The Calappinae and Hepatinae, for example, have small circular orbits and short robust peduncles, the combination of which result in the eyes filling the whole orbital space, thus appearing large. Eye size *per se* was therefore not used in the analysis. Likewise, orbital size expressed as the ratio between orbital width and interorbital distance varies extensively both within and between taxa. It was also not used in the analysis.

Eyestalk length and orbit shape, however, were found to be useful. In the Matutinae, Orithyiinae, *Portunus* and *Dorippe*, the eyestalks are elongate with lengths greater than 60% of the orbit width (6.0). In the Calappinae, Hepatinae, *Atergatis* and *Leucosia*, the eyestalks are short with lengths less than 40% of orbit width (6.1). The orbit is circular (7.1) in the Calappinae, Hepatinae, *Atergatis* and *Leucosia*. In the Matutinae, Orithyiinae, *Dorippe* and *Portunus*, the orbit is ovoid (7.0) .

Incomplete orbits are widespread amongst the Brachyura. The most common type is the inner orbital hiatus, which results from the insertion of the basal segment of the antenna between the infraorbital lobe and the ventral projections of the front (Glaessner, 1969). All the taxa examined in this study were found to have incomplete orbits in terms of the presence of an inner orbital hiatus. Several taxa, however, also have a second orbital hiatus in the outer angle of the orbit. This is largely the result of an incomplete fusion of the upper and lower orbital margins, thus forming a deep gutter on the lower orbital floor (8.1). This state was found in the Matutinae, Orithyiinae and *Dorippe*. In the Calappinae and Hepatinae and in *Atergatis*, *Leucosia* and *Portunus*, the upper and lower outer orbital margins are completely fused (8.0).

The lateral carapace margin fuses with the outer angle of the orbit (9.0) in the Matutinae, Orithyiinae, *Portunus*, *Atergatis* and *Dorippe*. In the Calappinae, Hepatinae and *Leucosia*, however, the lateral carapace margin extends into the suborbital region, giving the orbits a raised appearance (9.1). An orbital spine on the outer angle of the orbit is present (10.0) in the Matutinae, Orithyiinae, *Portunus* and *Dorippe*. No supraorbital spines (10.1), were found in the Calappinae, Hepatinae, *Atergatis* and *Leucosia*.

2.4.3 Antero-ventral region

The antero-ventral region is defined as the region ventral to the lateral margin of the carapace consisting of the suborbital and subhepatic regions, as well as the pterygostomian region (Glaessner, 1969). This region is well developed in some subfamilies of the Calappidae. In this region, a number of characters unique to the Calappidae may be found, the most striking of which is a distinct efferent channel which opens into the bases of the chelae. Referred to as an 'exostegal channel' (i.e. formed by the chelae and pterygostome, Stevcic, 1983), this channel is absent in the Orithyiinae and all the outgroup taxa (11.0). In the Calappinae and Hepatinae, this channel occurs as a broad and shallow suborbital channel which connects anteriorly to the orbit via the antennal gap in the inner orbital angle (11.1). In the Matutinae, however, this channel occurs as a narrow and deep cleft which connects directly to the orbit via a lateral fissure of the orbital floor at the outer orbital angle (11.2)

In most brachyuran taxa, the pterygostomian region is flat or convex (12.0). This state was found in the Matutinae, Hepatinae, Orithyiinae and all the outgroup taxa. In the Calappinae, however, the pterygostomian region is concave and connects with the suborbital channel forming a continuous channel leading to the bases of the chelae (12.1).

2.4.4 Pereiopods

The pereiopods are frequently included in brachyuran taxonomic descriptions either in terms of their apparent function or their distinct appearances. Most taxonomic descriptions of the Calappidae, however, only include descriptions of the pereiopods primarily to emphasize the specialized function of the pereiopods in *Matuta* (*e.g.* Alcock, 1896; Rathbun, 1937, Sakai, 1965). Alcock (1896), for example, used the apparent functions of the pereiopods to separate the two subfamilies, with the Calappinae possessing "gressorial legs" and the Matutinae having "natatorial legs". Dai & Yang (1991) used pereiopod characters to describe *Cycloes*, whilst Galil (1993) provided detailed descriptions of the pereiopods in a revision of the genus *Mursia*. Pereiopod setation is the most common character used in taxonomic studies. However, this was not used in the present study as setation was found to be extremely variable between taxa with questionable homologies.

Pereiopods will be dealt with in the typical order used in general crustacean anatomical studies, starting with the chelipeds.

Chelipeds (pI) (Fig. 2.1)

The nature of the articulation of the coxa to the basi-ischium varies between taxa (Fig. 2.1). In most ingroup and outgroup taxa, the proximal articulation of the basi-ischium to the coxa is a ball-and-socket type (13.0; Fig. 2.1A-C), where the basis articulates directly with the convex margin of the coxa. In the Orithyiinae and *Dorippe*, however, the basis is not directly articulated with the coxa, rather the two segments are connected by a broad ligamentous sheet (13.1; Fig. 2.1D). The distal part of the articulation also varies. In the Calappinae, Hepatinae, Matutinae, *Atergatis*, *Leucosia* and *Portunus*, the distal articulation of the coxa is simple and straight, with the posterior margin of the articulating condyle covered by a part of the ischium (14.0). In the Orithyiinae and *Dorippe*, however, this condyle is characterised by a free posterior border which protrudes, giving the appearance of a rounded spine (14.1; Fig. 2.1D).

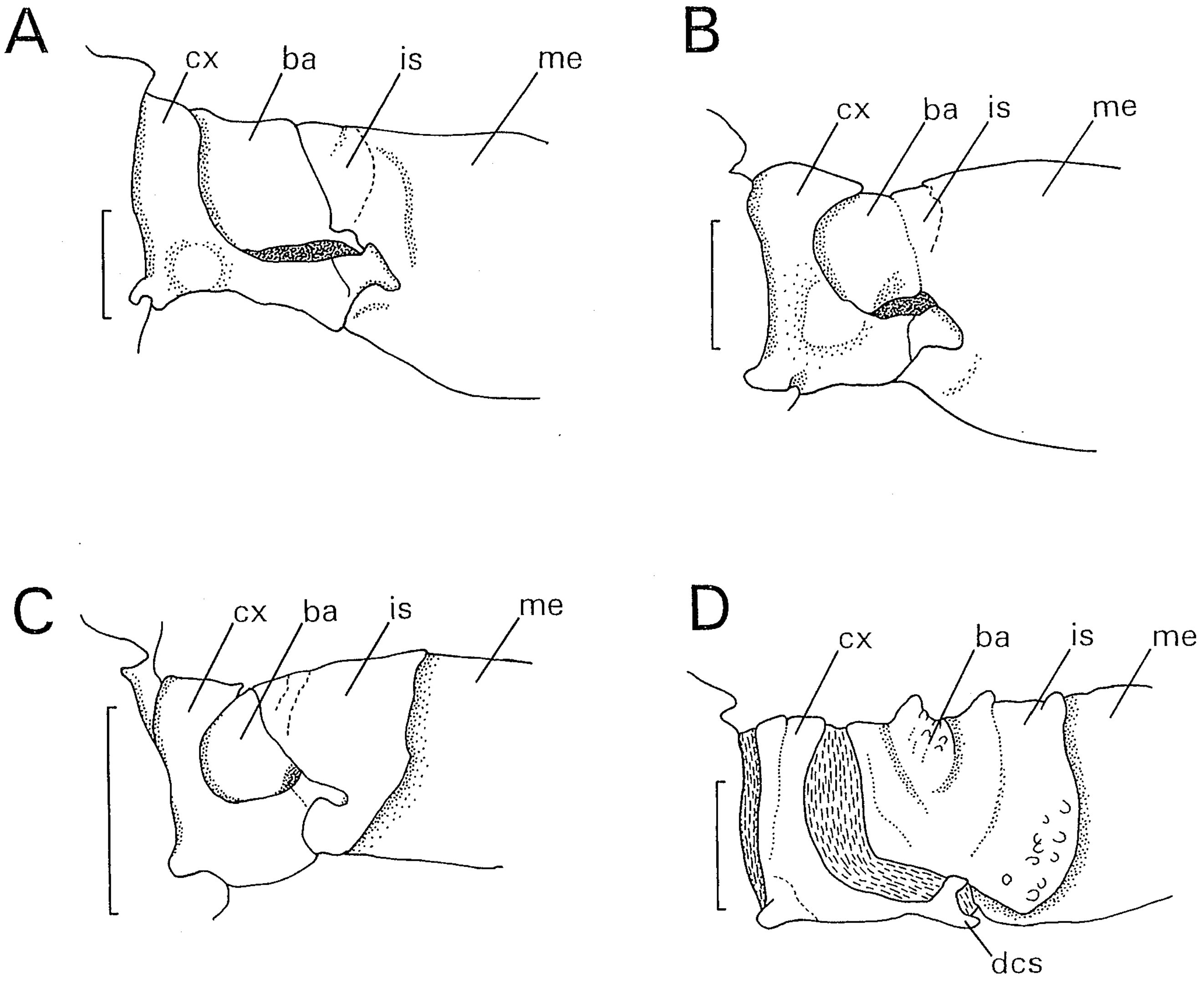


Figure 2.1 Proximal articulations of the cheliped A. Calappinae, B. Hepatinae, C. Matutinae and D. Orithyiinae. (cx, coxa; ba, basis; is, ischium; me, merus; dcs, dorsal coxal spine). Scale bar=5mm.

In the Matutinae, Orithyiinae, *Portunus*, *Atergatis* and *Dorippe* the ischium is a distinct and separate structure from the merus, the articulation between the two segments being clearly marked by a deep groove (15.0; Fig. 2.1C-D). In the Calappinae, Hepatinae and *Leucosia*, however, the ischium is completely fused to the merus, with the joint between the two segments being almost indistinguishable (15.1; Fig. 2.1A-B) (*cf.* Guinot, 1968).

The position of the merus when the chelae is flexed, relative to the vertical midline of the body was found to be informative. In the Calappinae, Hepatinae, *Portunus* and *Atergatis*, the merus is held perpendicular to the midline (16.0) whilst in the Matutinae, Orithyiinae, *Dorippe* and *Leucosia* the merus is held at an oblique angle (16.1). A number of merus character states are autapomorphies. The merus in the Calappinae is unusual in that it possesses a lateral extension (flange or spine) distally (17.1). On the dorsal margin of the merus, a flange is present only in the Orithyiinae (18.1), whilst the ventral surface of the merus in the Matutinae is characterised by a row of 3-4 spines (19.1).

The shape of the carpus is uniform throughout the taxa examined in this study. In the Calappinae, however, the mero-carpal articulation is characterised by a small spine on the dorsal aspect of the articulation (20.1). No such spine has been found in any of the other taxa (20.0).

The propodus in the Calappinae is distinctive in that it possesses a greatly expanded crest on the dorsal margin (21.1), doubling the overall depth of the propodus. It also possesses a distinctive setal patch on the proximal and ventral regions of the inner surface (22.1) Neither the crest (21.0) nor the setae (22.0) were found in the other taxa examined.

Distally, the propodus tapers into the pollex. This fingerlike structure in combination with the dactylus gives the pincerlike appearance of the chelae. The function of the chelae is mediated through the combination of the cutting/crushing surfaces on the pollex and dactylus which serve as opposable immovable and movable "fingers", respectively. In the Calappinae, a specialised structure is present at the base of these "fingers" (23.1). This structure consists of 2 parts: a hooked lobule on the proximal end of the dactylus and two blunt teeth at the proximal end of the cutting edge of the pollex. These teeth form a socket into which the lobule can fit. This structure is probably the most frequently cited attribute of the Calappidae and is used by many brachyuran taxonomists to distinguish calappids from other brachyurans (*e.g.* Alcock, 1896; Sakai, 1976, Dai & Yang, 1991). This structure is not found (23.0) in the Matutinae, Hepatinae, Orithyiinae or in any of the outgroup taxa examined.

pII, III, IV and V

The next three pairs of pereiopods (pII, pIII, pIV) in the taxa considered in this study are identical and will therefore be considered together. The last pair (pV) vary significantly in some taxa and will be considered separately. Pereiopods II, III and IV in the Calappinae, Hepatinae and Orithyiinae and all the outgroup taxa are typically long and slender with the propodus and dactylus being narrow and pointed (24.0). This dactylus form is often referred to as "styliform" and is associated with an ambulatory function (walking legs). In the Matutinae, however, both the propodus and dactylus are flattened and broad (24.1), a form termed "natatorial" by Alcock (1896), referring to its presumed swimming function (cf. Hartnoll, 1971). In the Calappinae, Hepatinae, Orithyiinae, *Dorippe*, *Portunus* and *Atergatis*, the ventral surface of the pII-pIV merus is unadorned (25.0) whilst in the Matutinae and *Leucosia* the ventral surface is adorned with a row of spines (*Leucosia*) or granules (Matutinae) (25.1).

The pV segments in the Calappinae, Hepatinae, *Atergatis* and *Leucosia* are identical to those of pII, pIII and pIV, *i.e.* slender and narrow (26.0). However, modified or specialised pVs were found in the Matutinae, Orithyiinae, *Portunus* and *Dorippe*. In the Matutinae, Orithyiinae and *Portunus* the segments are flattened to create a paddle-shaped appendage (26.1), with the dactylus being broad and flat and the propodus characterised by a lateral flange or keel. In *Dorippe*, pV is subchelate, with the propodus and dactylus being short and curved (26.2). In terms of setation, setae are found on the pV dactylus of all the taxa examined (27.0), except the Calappinae and *Leucosia* (27.1).

2.4.5 Abdomen

The abdomen in Brachyura consists of seven segments including the telson, typically infolded over the sternum. Abdominal characters are often used in taxonomic studies at a generic level. Some authors use the abdominal segment formula to describe a genus, whilst others use the shape of the segments and degree of fusion. The abdominal characters used in this study are based primarily on the male abdomen. Character state determination in females was more difficult as the female abdomen changes markedly during ontogeny. The male abdomen, however, often demonstrates isometric growth throughout (Hartnoll, 1982; Perez, 1986).

As with most brachyurans, the male abdomen in the Calappidae is long and narrow, the size and shape of the whole abdomen corresponding to that of the sterno-abdominal cavity which it covers. In most taxa, the abdomen completely covers the sterno-abdominal cavity (28.0). This state was found in the all the taxa examined in this study, with the exception of the Orithyiinae where the male abdomen is unusually short and covers only the lower half of the sterno-abdominal cavity (28.1).

The position of the last abdominal suture (between segment 6 and 7) relative to the corresponding sternal sutures varies amongst the taxa. In the Matutinae, *Portunus* and

Dorippe, the last abdominal suture corresponds with sternal suture s5/6 (29.0). In the Calappinae, Hepatinae and *Atergatis*, the last abdominal suture corresponds with sternal suture 4/5 (29.1). In the Orithyiinae, where the abdomen is unusually short (character 28), the last abdominal suture does not correspond with any sternal suture (29.2) whilst in *Leucosia*, where the abdomen is particularly long, the last abdominal suture corresponds with s2/3 (29.3)

The number of abdominal segments that are visible ventrally varies from 5 in the Matutinae, Hepatinae, Orithyiinae, *Portunus*, *Dorippe* and *Atergatis*, to 6 in the Calappinae (30.1), and 7 in *Leucosia* (30.2). In the Calappinae, Matutinae, Hepatinae, *Portunus* and *Leucosia*, the 1st abdominal segment is considerably smaller than the 2nd segment (31.0). However, in the Orithyiinae, *Atergatis* and *Dorippe*, the 1st and 2nd abdominal segments are of equal length (31.1). The 1st abdominal segment is devoid of any ornamentation in most of the taxa examined (32.0), with the exception of the Orithyiinae where the 1st segment is characterised by a narrow carina with a central spine (32.1). The 3rd segment also lacks ornamentation in the Calappinae, *Atergatis*, *Portunus* and *Leucosia* (33.0), but in the Matutinae, Hepatinae, Orithyiinae and *Dorippe*, it is characterised by a raised ridge (33.1).

Fusion of some abdominal segments is a common occurrence in brachyuran taxa (Glaessner, 1969). The 3rd, 4th and 5th segments are fused in the Calappinae, Hepatinae, Matutinae, *Atergatis* and *Portunus* (34.0). In *Leucosia*, segments 2-4 and 5-6 were fused (34.2). No fusion of the abdominal segments was found in the Orithyiinae and *Dorippe* where all 7 abdominal segments (6 + telson) are separate (34.1).

The length of the telson (7th segment) relative to the 6th segment varies. In the Matutinae and Orithyiinae and in *Portunus* and *Dorippe*, the telson is shorter than the 6th segment (telson:6th segment ratio <0.75; 35.0). In the Calappinae and Hepatinae and in

Atergatis, the telson is typically narrow and elongate, the length being equal or greater than the 6th segment (telson:6th segment ratio > 0.9; 35.1). This character could not be accurately assessed in *Leucosia* as the 6th segment is fused with the 5th.

2.4.6 Carapace

To date, descriptions of calappid taxa (both fossil and extant) rely heavily on carapace characters (e.g. Feldmann, 1993, Galil & Clark, 1994, Ng *et al*, 1999, Schweitzer & Feldmann, 2000). The utility of these characters, however, was found to be of limited value in the present study. Carapace characters are extremely variable both within and between the subfamilies and are therefore considered to be largely uninformative at the level of the present investigation. Only one character was found to be consistent. In the Calappinae, Hepatinae and Matutinae, a pair of ventral processes may be found on the medial posterior margin of the carapace where it articulates with the abdomen (36.1). No such processes were found in the Orithyiinae or any of the outgroup taxa (36.0).

2.4.7 Sternum (Fig. 2.2)

The use of sternal characters in brachyuran taxonomy has been limited. Guinot (1979), however, recognized the taxonomic and phylogenetic value of the sternal characters in her analysis of brachyuran relationships. Subsequent phylogenetic studies of individual brachyuran families have also found characters associated with the sternum to be of value in assessing intra-familial relationships (e.g. Tavares, 1993).

Fusion of the sternal plates in brachyurans is marked by distinct sutures between adjacent plates. These sutures are referred to by the sternite numbers they are associated with (e.g. s4/5 = suture between sternal plates 4 and 5). In this study, four sternal sutures traversing the sternal plastron have been found to be of phylogenetic significance: s4/5, s5/6, s6/7 and s7/8. These sutures may be either continuous (*i.e.* meeting in the midline) or discontinuous (*i.e.* separated medially). In the Orithyiinae, *Dorippe*, *Leucosia* and *Portunus*, all four sutures are discontinuous (37.0; Fig. 2.2D) whilst in the Calappinae, Hepatinae and *Atergatis*, two sutures are discontinuous (s4/5, s5/6) (37.1; Fig. 2.2A-B), the other two being continuous. In the Matutinae only one suture is discontinuous (s4/5) (37.2; Fig. 2.2C).

The region covered by the abdominal somites is marked by a depression in the plastron, referred to as the sterno-abdominal cavity. This cavity is unique, found only in the Brachyura (Guinot, 1979) and its functional significance is well-documented (Warner, 1977). The length of the sterno-abdominal cavity, as defined by the anteriormost sternal plate incorporated in the cavity, varies within the Calappidae. In the Matutinae, Hepatinae, Orithyiinae, *Dorippe*, *Atergatis* and *Portunus*, the anteriormost plate is S4 (38.0), whilst in the Calappinae and *Leucosia*, it is S3 (38.1). Within the sterno-abdominal cavity, a median line may be visible. This line runs along the length of the cavity, across the sternal plates, perpendicular to the sutures (Fig. 2.2A-D). The length of the median line may be defined by the sternal plate where the line terminates. In the Calappinae, Hepatinae, *Atergatis* and *Portunus*, the median line terminates on s6 (39.0) whereas in the Matutinae it terminates on s5 (39.1). In the Orithyiinae, it terminates on s7 (39.2). No median line was observed in *Dorippe* and *Leucosia*.

In most of the taxa considered in this study, the episternites (*sensu* McLaughlin, 1980) are distinct and extend halfway down the length of the next somite (40.0; Fig. 2.2A-C). This state was found in the Calappinae, Hepatinae, Matutinae, *Portunus*, *Leucosia* and *Atergatis*. The episternites in the Orithyiinae and *Dorippe*, however, are much smaller (< 20% of the next somite length) (40.1; Fig. 2.2D). A suture delimiting the episternite from its anterior somite may be found in Matutinae, Orithyiinae, *Portunus* and *Dorippe* (41.0;

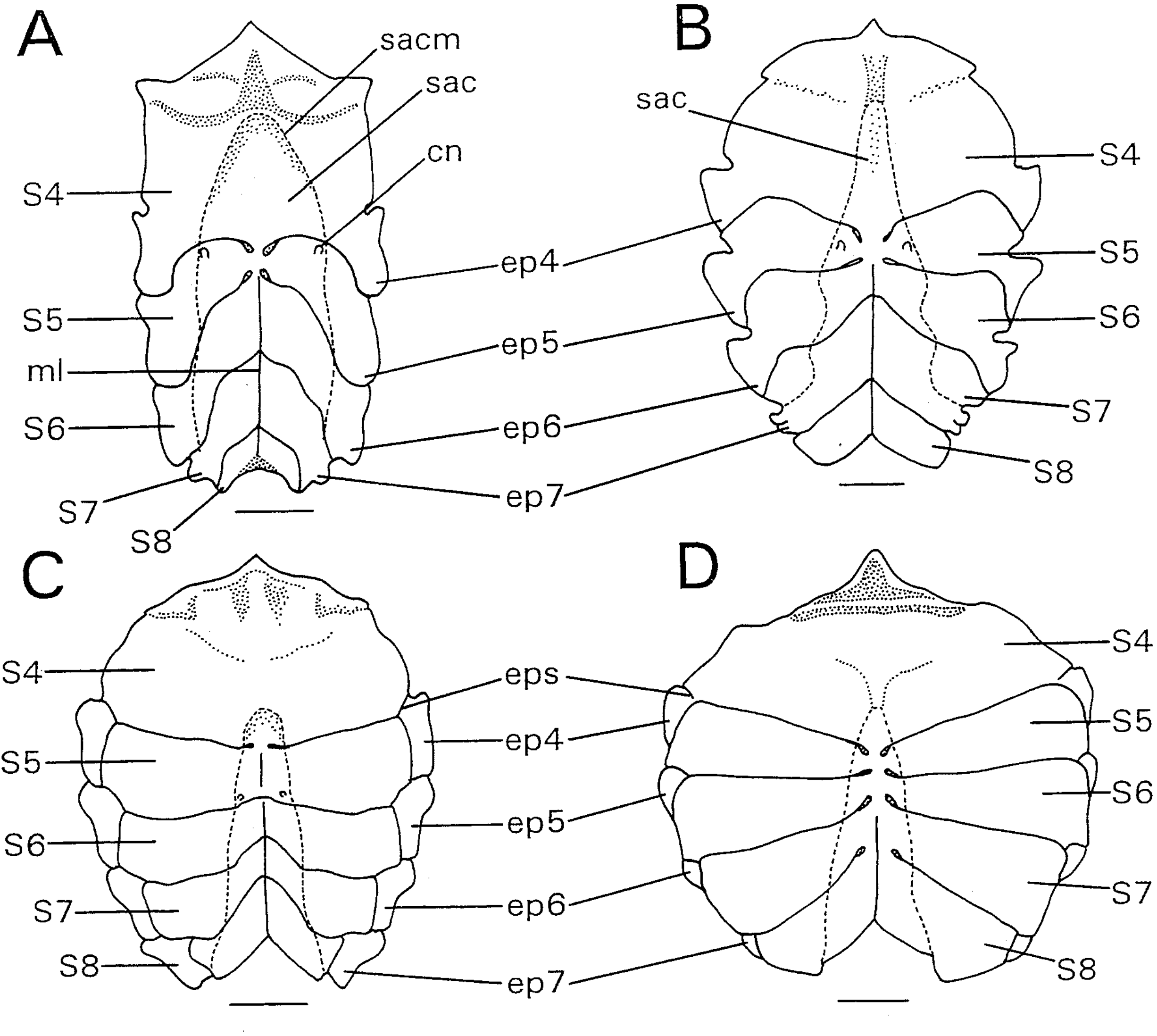


Figure 2.2 The sternum A. Calappinae, B. Hepatinae, C. Matutinae and D. Orithyiinae. (S4-8, sternite 4 to 8; ep4-7, episternite 4 to 7; sac, sterno-abdominal cavity; cn, cohesion nodule; ml, median line; eps, episternite suture; sacm, sterno-abdominal cavity margin). Scale bar=5mm.

Fig. 2.2C-D). No episternite sutures were found in the Calappinae, Hepatinae, *Atergatis* and *Leucosia* (41.1). In the Hepatinae, Orithyiinae, *Portunus*, *Dorippe* and *Atergatis*, the episternites do not cover the site where the coxa articulates with the sternum, leaving the condyles visible ventrally (42.0). In the Calappinae, Matutinae and *Leucosia*, the episternites completely cover the coxal condyles of all the pereiopods (42.1). The shape of the seventh episternite (ep7) varies between taxa. In the Matutinae, Orithyiinae and in all outgroup taxa, ep7 is elongated posteriorly (43.0); in the Calappinae and Hepatinae, ep7 is small and short (43.1).

Although the presence of a sternal structure which serves to attach the abdomen to the plastron in brachyurans has been noted for a long time (Pérez, 1928a,b), it is rarely used in taxonomy. Guinot (1979) included this character in her analysis of brachyuran phylogeny, where she noted its presence or absence in various genera. When present, this structure is represented by a pair of nodules located on S5 on the lateral margin of the sterno-abdominal cavity. Guinot (1979) referred to these nodules as "bouton-pression", alluding to their function in holding the abdomen in place like a press-stud. In this study, the nodules were found in most taxa, however, their location varied. In the Calappinae and *Atergatis*, these nodules are immediately below s4/5 (44.0; Fig. 2.2A), whilst in the Matutinae, *Dorippe* and *Portunus*, these nodules are immediately above s5/6 (44.1; Fig. 2.2C). In the Hepatinae, the nodules are halfway between these two sutures (44.2; Fig. 2.2B). No cohesion nodules were found in the Orithyiinae and *Leucosia* (44.3).

2.4.8 Mouthparts

3rd maxilliped

Previous taxonomic descriptions of the Calappidae have defined the subfamilies based on the degree of closure of the 3rd maxillipeds over the mouth (*e.g.* Alcock, 1896;

Rathbun, 1937). In the Calappinae, Orithyiinae, *Portunus*, *Dorippe* and *Atergatis*, the 3rd maxillipeds do not close completely thus exposing the underlying maxillipeds and the mandible (45.0). In the Matutinae, Hepatinae and *Leucosia*, the 3rd maxillipeds meet and completely cover the buccal cavity and all its underlying parts (45.1).

The form of the ischium varies extensively both within and between taxa and therefore was not used in the analysis. Characters associated with the merus, however, were useful. The merus in the Calappinae, *Portunus* and *Atergatis*, is broad and quadrate (46.0; Fig. 2.3A) whilst in the Matutinae, Hepatinae, Orithyiinae, *Leucosia* and *Dorippe*, it is elongate and rectangular (46.1; Fig. 2.3B-D).

In the Calappinae, the anteromedial margin of the merus is indented in the region where the palp articulates (47.1; Fig. 2.3A). This indentation creates a prominent medial lobe just above the articulation of the palp. No indentation nor lobe (47.0) was found in any of the other taxa. In the Hepatinae the lateral margin of the merus is notched proximally to fit the distal end of the exopod (48.1). In all other taxa, the lateral margin is straight and confluent with the lateral margin of the ischium (48.0). On the internal surface, the merus may be excavated to form a groove where the palp or part of the palp fits (49.1). This groove is present in the Calappinae, Hepatinae, Matutinae and *Leucosia*, but not in the Orithyiinae, *Portunus*, *Dorippe* nor *Atergatis* (49.0).

Previous taxonomic descriptions of the Calappidae have used the position of the palp in relation to the merus as a key character separating the subfamilies (*e.g.* Alcock, 1896, Glaessner, 1969). In the Calappinae, Orithyiinae, *Portunus*, *Atergatis* and *Dorippe*, the palp is exposed, *i.e.* not hidden behind the merus (50.0). In the Matutinae, Hepatinae and *Leucosia*, however, the palp is folded within the groove on the internal surface of the merus and is therefore not visible externally (50.1). In the Matutinae, Hepatinae, Orithyiinae and in all the outgroup taxa, the palp segments are of approximately equal

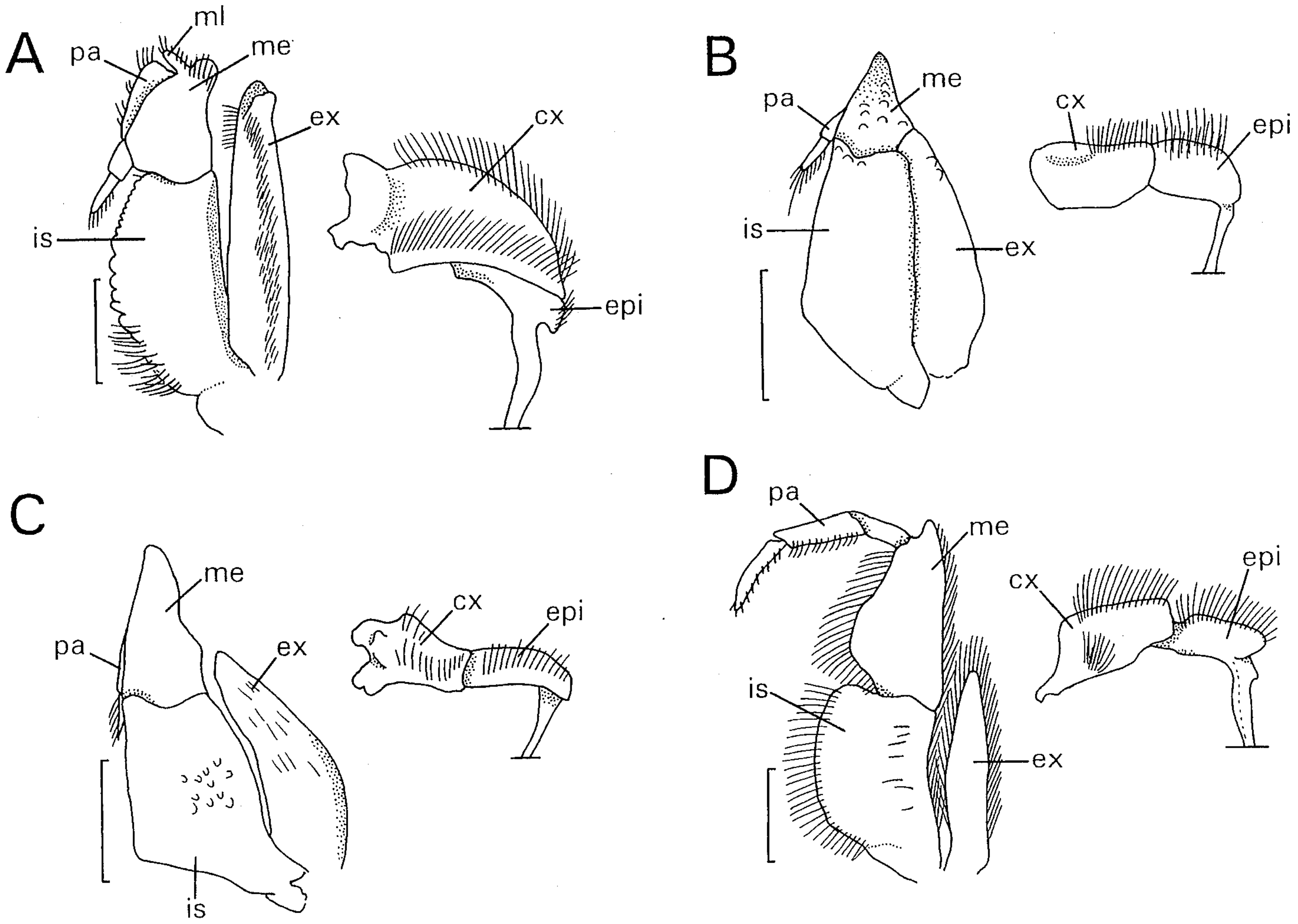


Figure 2.3 Ventral aspect of the third maxilliped A. Calappinae, B. Hepatinae, C. Matutinae and D. Orithyiinae. (pa, palp; ml, medial lobe; me, merus, ex, exopod; is, ischium, cx, coxa; epi, epipod). Scale bar=5mm.

length (51.0). In the Calappinae, however, the basal segment of the palp is longer than all the other segments (51.1).

Characters associated with the exopod are often neglected in descriptions of the 3rd maxilliped in the Calappidae. In this study, three characters associated with the exopod were found to be useful. The most striking of these is the presence or absence of a flagellum. In the Calappinae, Hepatinae, *Portunus* and *Atergatis*, the exopod possesses a flagellum (52.0). In the Matutinae, Orithyiinae, *Dorippe* and *Leucosia*, the flagellum is absent (52.1).

The exopod in the Calappinae may be described as "columnar" (cf. in *Mursia*; Galil, 1993). By definition, this refers to the width of the exopod which is uniform throughout its length (53.0). This state is also found in the Orithyiinae and in all the outgroup taxa. In the Matutinae and Hepatinae, however, the exopod width is not uniform, being widest proximally, tapering to a point distally (53.1).

In the Calappinae, the external surface of the exopod is characterised by a longitudinal row of thick brush-like setae (54.1; Fig. 2.3A). This has been associated with respiration, representing the internal boundary of the 'exostegal channel' (Garstang, 1898). These setae were not found in any of the other taxa examined (54.0).

In the Calappinae, Matutinae, Hepatinae and Orithyiinae, the coxa of the 3rd maxilliped is found at the entrance of the inhalant respiratory openings at the base of the chelae. Although this is listed as one of the key characters uniting the Calappidae by Stevcic (1983), the usefulness of this character is limited in phylogenetic analyses as this state is also found with few exceptions in most brachyuran taxa. The form of the coxa, however, varies. The coxa in the Matutinae, Hepatinae, Orithyiinae and in all the outgroup taxa is small and narrow (55.0). In the Calappinae, however, the coxa is distinct, as it is enlarged and expanded dorsally (anteriorly) (55.1; Fig. 2.3A).

The form of the epipod also varies between taxa. In the Matutinae, Hepatinae, Orithyiinae, *Portunus*, *Atergatis* and *Leucosia*, the proximal portion of the epipod has a narrow lateral attachment to the coxa (56.0; Fig. 2.3B-D). In the Calappinae, the proximal portion of the epipod possesses a broad attachment to the ventral (posterior) margin of the coxa (56.1; Fig. 2.3A). In *Dorippe*, the epipod articulates with a narrow protrusion on the ventral margin of the coxa (56.2).

2nd maxilliped

Compared with the 3rd maxilliped, the 2nd maxilliped is not often used in brachyuran taxonomic descriptions. The structure and function of the 2nd maxilliped appears to be conservative throughout the Brachyura. The general structure of the 2nd maxilliped consists of an elongate exopod, a 4-segmented endopod, the distal segment of which is characaterized by stiff setae, and an epipod. Functional morphology studies in brachyurans have shown that the endopod is used for tearing food material apart before it enters the mouth (e.g. Portunidae) (McLaughlin, 1980). The function of the exopod, however, remains unclear.

In this study, very few variations were found in the 2nd maxillipeds of both ingroup and outgroup taxa. Only 3 characters were found to be useful, all associated with the exopod. In the Matutinae, Hepatinae and in all the outgroup taxa, the exopod is as long as the endopod (57.0). In the Calappinae and Orithyiinae the exopod is over one and a half times longer than the endopod (57.1). In the Matutinae, Orithyiinae, *Portunus*, *Leucosia* and *Dorippe*, the exopod is flimsy (58.0) whilst in the Calappinae, Hepatinae and *Atergatis*, it is robust (58.1). The exopod flagellum is long (> half exopod length) in the Calappinae, *Portunus* and *Atergatis* (59.0) whilst in the Matutinae, Hepatinae, Orithyiinae and *Dorippe*, the flagellum is short (< 0.25 of the exopod length; 59.1). In the Orithyiinae, in particular, the flagellum is very short (rudimentary). No flagellum was found in *Leucosia* (59.2).

1st maxilliped

The structure of the 1st maxilliped in the Calappidae and other oxystomatous crabs is well documented and is used to define the section Oxystomata which includes the Calappidae (Alcock, 1896). The calappid 1st maxilliped follows the typical brachyuran arrangement being triramous, consisting of an endopod, an exopod and an epipod. The endopod consists of two segments with the distal segment often varying in size and shape. In this study, the elongate nature of the endopod attributed to oxystomatous crabs was found to be associated with the length of the distal segment of the endopod relative to the total endopod length. In the Calappinae, Hepatinae, Matutinae, Orithyiinae, *Dorippe* and *Leucosia*, the length of the distal segment is greater than 60% of the total endopod length (60.1). In *Atergatis* and *Portunus*, the distal segment contributes less than 40% of the total endopod length (60.0). In most taxa, the distal tip of the endopod is not visible externally and is completely covered by the 3rd maxilliped (61.0). In the Calappinae and in *Dorippe*, however, the distal tip of the endopod is visible externally as it protrudes beyond the extent of the 3rd maxillipeds (61.1).

In the Orithyiinae, *Portunus* and *Atergatis*, the length of the exopod is equal to that of the endopod lateral margin (62.0). In the Calappinae, Matutinae, Hepatinae, *Dorippe* and *Leucosia*, however, the exopod length is clearly less than that of the endopod lateral margin (62.1). The exopod flagellum is long (> half of the exopod length) in the Calappinae, *Portunus* and *Atergatis* (63.0). In the Matutinae, Hepatinae, Orithyiinae and *Dorippe*, however, the flagellum is short (< third of exopod length (63.1), being rudimentary in the Orithyiinae. In *Leucosia*, the flagellum is absent (63.2).

Maxillae, Paragnaths and Mandibles

Overall, the structure of the 1st and 2nd maxillae, the paragnaths and the mandibles show little variation. No character states could be identified which were of phylogenetic utility. The 2nd maxillae (maxilla) are biramous with bilobed endites and a broad scaphognathite. This structure was consistent amongst all the taxa considered in this study. The 1st maxillae (maxillule) is characterised by an endopodal palp which wraps around the mandibular arm. As in the 2nd maxillae, very little variation was found amongst the taxa.

The paragnaths are paired structures found behind the 1st maxillae and immediately in front of the mandibles. These are typically fleshy and their function is largely unknown. The paragnaths have never been used in brachyuran taxonomic studies.

All the mandibles examined in this study were strong and robust and possessed a mandibular palm, with very little variation in the size and shape amongst the taxa.

2.4.9 Endostome

The shape of the buccal frame and the endostome is well-documented in the Oxystomata where it is typically elongate and triangular (Alcock, 1896, Rice, 1980). In the Calappinae, Matutinae, Hepatinae, Orithyiinae, *Dorippe* and *Leucosia*, the endostome is typically elongate and narrow (64.1). In *Portunus* and *Atergatis*, however, the buccal frame and endostome is broad and short (64.0). The endostome in the Orithyiinae is unusual in that it is highly modified, forming two distinct tubes with separate openings (65.1). This state was not found in any of the other taxa, where the openings are not completely enclosed by the endostome (65.0). In some taxa, a septum which divides the endostome longitudinally may be apparent. However, the development of this septum varies extensively within and between taxa. As character designations were unclear, this character was not used in the analysis.

2.4.10 Male reproductive structures

The male gonadal opening of all the taxa considered in this study was found to be coxal, including *Leucosia* which was previously reported to have a coxo-sternal opening (*sensu* Guinot, 1979). In all taxa, the penis emerges from the coxa of pV near to the articulation between the coxa and the sternum. The penis of the Calappinae, Hepatinae, Matutinae and *Atergatis* is large and fleshy and characterised by a swollen (bulbous) base (66.1). In the Orithyiinae, *Portunus*, *Dorippe* and *Leucosia*, however, the penis is narrow and elongate (66.0). In most ingroup and outgroup taxa, the penis is "naked" and not encased in any structure as it emerges from the coxa of pV (67.0). In the Orithyiinae and in *Dorippe*, however, the penis is partly encased in a clear smooth sclerotized sheath (67.1).

The pleopods

After the carapace and chelae characters, the structure of the male pleopods is probably the most frequently used character in recent brachyuran taxonomic schemes. In the Calappidae, characters associated with the male pleopods have been often used to separate genera (*e.g.* Tyndale-Biscoe & George, 1962; Williams & Child, 1988; Dai & Yang, 1991, Galil & Clark, 1994) and species (*e.g.* Romimohtarto, 1972, Galil, 1993). Some are of phylogenetic utility.

In the Calappinae, Hepatinae and *Atergatis*, the 1st pleopod is conical in shape, being wide at the base with the shaft tapering sharply towards the tip (68.1). In the Matutinae, the 1st pleopod is elongate and columnar with the base and the shaft being of uniform width (68.2). In the Orithyiinae, the base is enlarged but the shaft does not taper sharply at the tip (68.3). In *Dorippe*, the shaft is conical with a modified spoon-shaped tip (68.4). The 1st pleopods in *Portunus* is elongate and narrow with a tapering shaft (68.0). Because of extreme species variation found within the genus *Leucosia*, the shape of the 1st pleopods in *Leucosia* is coded as "polymorphic" in the analyses.

The outer basal angle of the 1st pleopod is simple and small (69.0) in the Matutinae, Orithyiinae, *Portunus*, *Dorippe* and *Leucosia*. In the Calappinae, Hepatinae and *Atergatis*, however, the outer basal angle is expanded posterolaterally to form a flange (69.1). In all taxa, a ridge is visible running along the length of the shaft of the 1st pleopod. In the Calappinae, Hepatinae, Orithyiinae, *Portunus*, *Atergatis* and *Dorippe*, the ridge is parallel to the shaft (70.0). In the Matutinae and *Leucosia*, however, the ridge is oblique (70.1).

In the Calappinae, Hepatinae, *Portunus* and *Atergatis*, the distal tip is pointed (71.0) whereas in the Matutinae, Orithyiinae and *Dorippe*, it is rounded (71.1). The Matutinae, in particular, have an expanded tip which covers a finger-like dorsal process. *Leucosia* is extremely variable and is therefore coded as "polymorphic". In the Matutinae, the distal tip possesses a fingerlike dorsal process (72.1). This process is absent in all the other taxa (72.0).

In the Orithyiinae and all the outgroup taxa, the 2nd pleopod is shorter than the 1st pleopod (73.0). The 2nd pleopod in the Calappinae, Hepatinae and Matutinae, however, is typically long and narrow, and exceeds the length of the 1st pleopod (73.1). In the Calappinae, Hepatinae, Orithyiinae, *Portunus* and *Atergatis*, the basal section of the 2nd pleopod is curved outwards (74.0), whilst in the Matutinae, *Dorippe* and *Leucosia*, it is straight (74.1). The length of the flagellum relative to the basal segment varies between taxa. In the Hepatinae, Orithyiinae and all the outgroup taxa, the length of the flagellum is less than that of the basal segment (75.0). In the Calappinae and Matutinae, the flagellum length is equal to or greater than the length of the basal segment (75.1). In the Matutinae, Hepatinae, Orithyiinae and all outgroup taxa, the flagellum of the 2nd pleopod is straight (76.0). In the Calappinae, the long whiplike flagellum is bent (extends from cornute to looped; 76.1).

2.4.11 Female reproductive structures

In most brachyurans including all taxa examined in the present study, the vulvae are located in the sternum, on the 6th sternite (s6). However, the position of the vulvae relative to the sterno-abdominal cavity varies between taxa. In the Calappinae, Hepatinae, Matutinae, *Portunus*, *Atergatis* and *Leucosia*, the vulvae are inside the sterno-abdominal cavity (77.0). In the Orithyiinae and *Dorippe*, however, the vulvae are outside the cavity and are not covered by the abdomen (77.1).

The structure of the vulvae is extremely variable. In general, the vulvae are described as paired apertures on the 6th sternite, the margins of which consist of the rigid integument of the sternal plates. The lumen of the vulva is typically blocked by the flexible integument comprising the lining of the oviduct (or vagina, see Hartnoll, 1968). In most taxa examined, the vaginal lining does not protrude out of the lumen (78.0). Protrusion was only observed in the Matutinae and *Leucosia* (78.1).

2.5 RESULTS

The analyses of 78 characters with a total of 172 character states (with all terminal autapomorphies removed) yielded one tree, 104 steps long with a consistency index of 0.654 (rescaled CI = 0.403) (Fig. 2.4).

The following is a compilation of synapomorphies which define the clades found

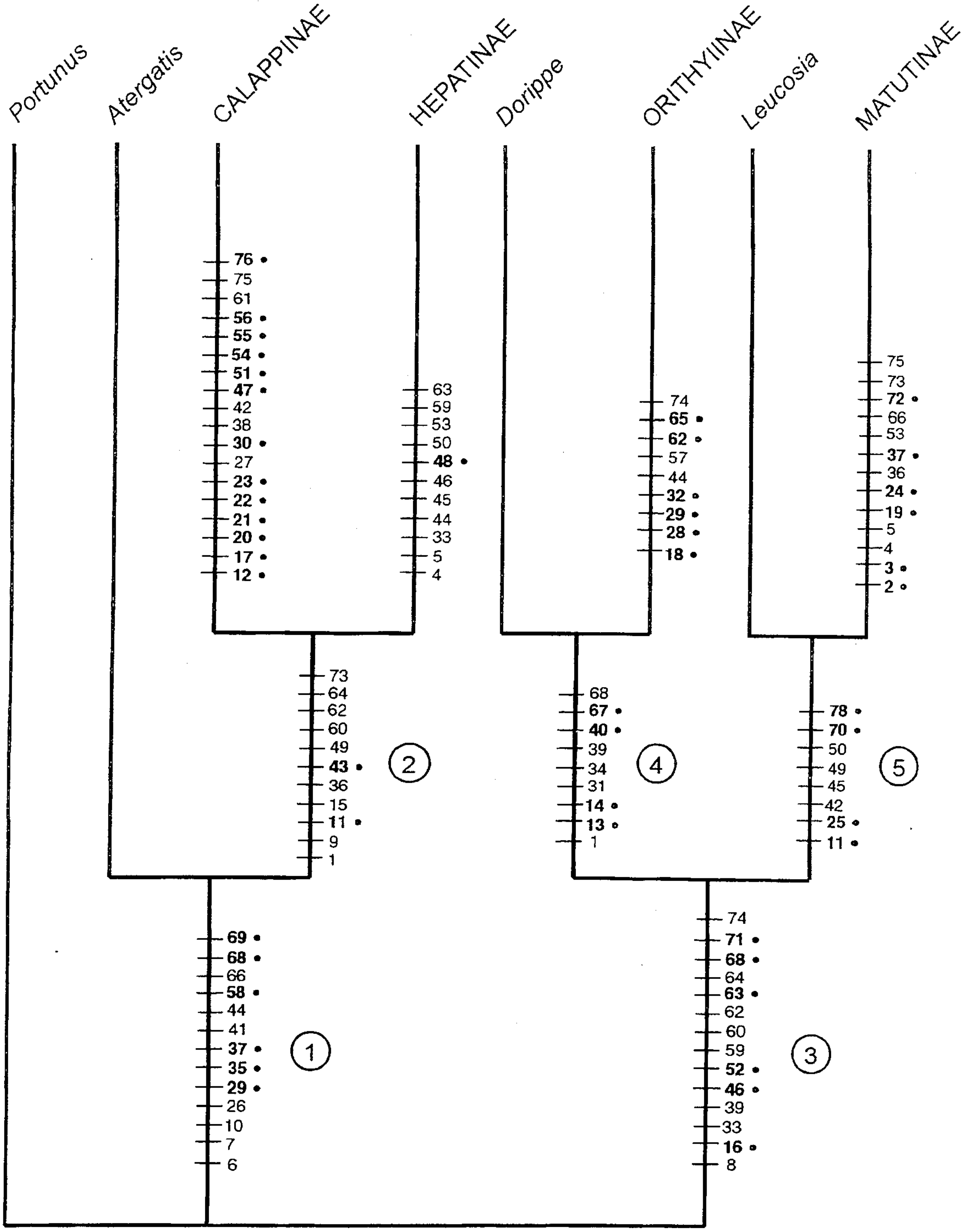


Figure 2.4 Cladogram of the relationships of the 4 subfamilies in the Calappidae and 4 outgroup taxa, generated from PAUP 3.1. Tree length = 104 steps, CI = 0.654, RCI = 0.403. Character numbers follow Appendix 2a; terminal autapomorphies and synapomorphies which are unique and unreversed are in bold and marked with a dot (•). Encircled numbers refer to clades as discussed in the text. A proposed classification based on this cladogram is provided in Appendix IV.

in the cladogram given in Fig. 2.4. Each clade is numbered, followed by its component taxa and by a list of synapomorphies, giving the character number (following Table 2.1) and the character state in parentheses. Synapomorphies (and terminal autapomorphies) which are unique and unreversed are given in bold. The proposed reclassification of the family Calappidae is addressed in the Discussion.

Clade 1: Atergatis + Calappinae + Hepatinae

6(1), 7(1), 10(1), 26(0), **29(1)**, **35(1)**, **37(1)**, 41(1), 44(1), **58(1)**, 66(1), **68(1) 69(1)**

The monophyly of this clade is supported by 12 synapomorphies of which 6 are unreversed: the correspondence of the last abdominal suture to sternal suture 5/6 (29), narrow and elongate telson which is equal to or longer than the 6th abdominal segment (35), the presence of only two discontinuous sternal sutures (37), a robust exopod on the 2nd maxilliped (58), a cone-shaped 1st pleopod (68) and a flange on the outer basal angle of the 1st pleopod (69). Other synapomorphies include orbital region (6,7,10), sternal (41,44) and reproductive (66) characters.

Clade 2: Calappinae + Hepatinae

1(1), 9(1), **11(1)**, 15(1), 36(1), **43(1)**, 49(1), 60(1), 62(1), 64(1), 73(1)

The monophyly of this clade is supported by 11 synapomorphies of which two are unreversed: the presence of a broad and shallow suborbital channel (11) and a reduction of the 7th episternite (43).

Calappinae: **12(1)**, **17(1)**, **20(1)**, **21(1)**, **22(1)**, **23(1)**, 27(1), **30(1)**, 38(1), 42(1), **47(1)**, **51(1)**, **54(1)**, **55(1)**, **56(1)**, 57(1), 61(1), 75(1), **76(1)** This is a very distinctive subfamily clearly defined by 13 autapomorphies. Of these, 5 were associated with the chelae: the lateral expansions on the merus (17), a small spine on the mero-carpal articulation (20), an expanded crest on the dorsal aspect of the propodus (21), a setal patch on the inner surface of the propodus (22) and the well-documented hooked lobule on the dactylus (23). Another 5 autapomorphies were associated with the 3rd maxilliped including the distinctive indentation on the anteromedial margin of the merus which creates a prominent medial lobe (47), a long basal segment on the palp (51), the presence of a longitudinal row of brush-like setae on the exopod (54), an enlarged and dorsally expanded coxa (55) and broad proximal section on the epipod (56). Other autapomorphies include the presence of a concave pterygostomian region which forms a continuous channel leading to the respiratory openings at the bases of the chelae (12), six abdominal segments being visible ventrally (30) and a bent flagellum on the 2nd pleopod (76).

Hepatinae: 4(1), 5(1), 33(1), 44(2), 45(1), 46(1), **48(1)**, 50(1), 53(1), 59(1), 63(1) This is a relatively weakly-defined subfamily supported by only one autapomorphy: the presence of a notch on the outer lateral margin of the merus of the 3rd maxilliped endopod (48).

Clade 3: *Dorippe* + Orithyiinae + *Leucosia* + Matutinae

8(1), **16(1)**, 33(1), 39(1), 46(1), **52(1)**, 59(1), 60(1), 62(1), 63(1), 64(1), 68(2), **71(1)**, 74(1)

This clade is united by 14 synapomorphies including 3 unreversed synapomorphies: the oblique position of the chelae merus at rest (16), the absence of a flagellum on the exopod of the 3rd maxilliped (52) and a rounded- or blunt-tipped 1st pleopod (71). Perhaps the most significant feature of this clade is the loss of the exopod flagellum on the 3rd maxilliped, this character state is found only in a few brachyuran taxa, *e.g.* the Raninidae, Gecarcinidae, Trichodactylidae and Cyclodorippidae (Guinot & Tavares, pers. comm.).

The remaining synapomorphies appear to be weak although this is probably a result of the highly derived nature of *Leucosia* and the Orithyiinae where 6 of the synapomorphies are subsequently reversed (8,33), lost (39,59,63) or coded "polymorphic" (68) in *Leucosia* whilst 2 are reversed in the Orithyiinae (62,74). There are also 2 synapomorphies which represent the traditional characters uniting the oxystomatous crabs (*sensu* Alcock, 1896): the elongation of the distal segment of the endopod of the 1st maxilliped (60) and the possession of an elongate and narrow endostome (64). These character states appear to have arisen independently in Clade 2. One other synapomorphy (the elongate and triangular merus of the 3rd maxilliped; 46) appears to have been independently derived in the Hepatinae.

Clade 4: Dorippe + Orithyiinae

1(1), **13(1)**, **14(1)**, 31(1), **34(1)**, 39(2), **40(1)**, **67(1)**, 68(3)

This clade is clearly defined by nine synapomorphies including five unique unreversed synapomorphies. Of these 5, the presence of a clear, smooth sclerotized sheath around the penis (67) is probably the most distinctive and has not been previously recorded in other brachyuran taxa (*cf.* Guinot, 1979). The only other taxa with sheaths around the penis are in the Podotremata and are invariably ornate (*cf.* Fig. 43 in Guinot, 1979). The other 4 unreversed synapomorphies are the ligamentous nature of the proximal articulation of the coxa to the basi-ischium (13), the protruding posterior border on the distal articulation of coxa to the basi-ischium (14), the lack of any fusion in the abdominal segments of adult individuals (34) and the reduction of the episternites (40).

Orithyiinae: **18(1)**, **28(1)**, **29(2)**, **32(1)**, 44(3), 57(1), 62(0), **65(1)**, 74(0). This distinctive monotypic subfamily is defined by 5 autapomorphies: the presence of a dorsal flange on the merus of the chelae (18), an unusually short abdomen (28), the lack of correspondence between the last abdominal suture and any sternal suture (29), the presence of ornamentation on the 1st abdominal segment (32) and a highly modified endostome (65).

Table 2.3 Traditional characters used for defining the family Calappidae

Based on Alcock, 1896	Based on Stevcic, 1983
1. carapace more or less oval or subcircular 2. carapace with either a single denticle, or a heavy spine at the junction of the antero-lateral and postero-lateral borders, or a posterolateral vault-like expansion over the ambulatory legs 3. front generally about as wide as the orbit 4. antennules generally fold obliquely 5. antennae generally small 6. efferent branchial channels form a deep channel in the endostome 7. deep efferent channel being covered below by long lamellar process of 1st maxillipeds 8. afferent branchial openings have normal position in front of the bases of chelipeds 9. chelipeds ponderous and greatly enlarged and practically symmetrical (except sometimes as to the fingers); hands especially are of great size - forming often the most conspicuous part of the chelipeds, are so curved as to shut closely against the pterygostomian regions of the carapace, acting as a sort of buckler 10. male abdomen composed of 5 segments (3-5 fused) 11. female abdomen composed of 7 segments (also young males) 12. male vasa deferentia perforate bases of the 5th legs	1. front narrow 2. orbits incomplete 3. antennulae obliquely plicated 4. antennal basal article large 5. antennal flagella reduced in size 6. endostome elongated 7. epistome very much reduced 8. exostegal channel (formed by pterygostome and chelipeds) exist 9. inhalant respiratory openings in front of the basis of chelipeds 10. coxae of Mxp3 enlarged on basis and placed on entrance of inhalant openings 11. exhalant respiratory opening near and beneath the front 12. endopodite of 1st maxilliped forms the ventral floor of exhalant channel 13. cheliped pressed tightly against anterolateral part of carapace 14. male abdomen composed of 5 segments (3-5 fused) 15. female abdomen composed of 7 segments 16. sterno-abdominal cavity well developed 17. male sexual opening coxal 18. 1st pair of male pleopods with simple top 19. 2nd pair of male pleopods long 20. female sexual opening sternal 21. 9 branchiae on each side

Calappidae continued to be accepted as single taxon (*e.g.* Bowman & Abele, 1982; Dai & Yang, 1991; Jones & Morgan, 1994). The inclusion of the four component subfamilies has rarely been disputed.

In the present study, the monophyly of each subfamily is supported. The Calappinae indeed is a very distinctive taxon clearly defined by 13 autapomorphies. The Matutinae and Orithyiinae are also well-defined, supported by 6 and 5 autapomorphies, respectively. Only the Hepatinae appears to be a relatively weakly-defined taxon supported by 1 autapomorphy.

The results of this study, however, clearly demonstrate that the family Calappidae as it currently stands is not monophyletic. The analyses leave little doubt that the Calappinae, Hepatinae, Matutinae and Orithyiinae do not form a natural group.

From the cladogram (Fig. 4), two main points can be made:

1. *The Calappinae and Hepatinae are sister groups and that as a lineage they are closer to some xanthids than they are to the Matutinae and Orithyiinae.*

From the phylogenetic analysis, there is evidence to support the monophyly of the Calappinae-Hepatinae lineage, with 11 synapomorphies, of which 2 are unreversed. While only one representative of the Xanthidae was used in this study, the close relationship between this species and the calappine-hepatine clade is unequivocal. The Calappinae-Hepatinae-*Atergatis* lineage (Clade 1) is clearly defined by 12 synapomorphies, 6 of which are unreversed.

These results are entirely consistent with the preliminary findings of Rice (1980) and Seridji (1993) based on larval evidence and Spears *et al.* (1992) using mRNA. Traditional characters linking the 4 subfamilies in the Calappidae, as listed by Stevcic (1983; see Table 2.3), are clearly of limited utility with several apparent examples of convergence and symplesiomorphy.

Rice (1980) noted that the larval stages of *Orithyia* were unusual and completely different from those of 'other' calappids and suggested that it should be recognised as a separate taxon. *Matuta* larvae also differed markedly from those of *Calappa* and *Hepatus*. Rice (1980) did not support the re-grouping of *Hepatus sensu* Guinot 1978 (*i.e.* not in the Calappidae but in a new group called Parthenoxystomata) nor the traditional grouping of *Hepatus sensu* Alcock 1896 (*i.e.* included in the Matutinae). He did, however, note the similarity between the larval characters of *Calappa* and *Hepatus*. These observations were echoed by Seridji (1993) who suggested that the genus *Hepatus* be placed under the Calappinae rather than in the Matutinae.

In the brachyuran phylogeny of Spears *et al.* (1992) based on mRNA studies, a close relationship between the 'Calappidae' (represented by *Hepatus*) and the Xanthidae was evident. Pairwise estimates of sequence divergence across taxa demonstrated the Calappidae and the Xanthidae to have the least sequence divergence among all the taxa examined. In the cladogram in Spears *et al.* (1992), the 'Calappidae' and the Xanthidae are figured as a distinct clade. However, as Spears *et al.* (1992) only used *Hepatus* to represent the 'Calappidae', it is quite possible that a different relationship would have been revealed had they used *Matuta* or *Orithyia*. Other studies supporting the close relationship between the Xanthidae, Calappinae and Hepatinae include Guinot (1979) and Rice (1980).

2. *There are clear links between some leucosiids and the Matutinae and between some dorippids and the Orithyiinae, with a strong suggestion that all four taxa are part of a single lineage.*

The distinctive nature of the Matutinae and Orithyiinae is well documented. In most taxonomic descriptions, the characteristics of the Matutinae and the Orithyiinae are specified as separate states within the Calappidae (*e.g.* Alcock, 1896; Guinot, 1979; Rice, 1980). The main problem, however, is in defining their relationships. These taxa often end up being shoehorned into the Calappidae for convenience. The analyses in the present study strongly support the independent status of the Matutinae and Orithyiinae and provide some indication of their relationships with other brachyurans.

Of the taxa examined, the Matutinae are most closely allied to the Leucosiidae, a relationship supported by 8 synapomorphies, of which 3 are unreversed. The need for further analysis of this clade, however, must be highlighted. The Leucosiidae as a taxon is in itself problematic. The family contains about 40 genera and 300 species with numerous highly modified forms. This family is commonly divided into subfamilies, the definition and composition of which vary markedly among authors (*cf.* Alcock, 1896; Rathbun, 1937; Balss, 1957). A reappraisal of the interrelationships within the Leucosiidae is urgently required.

Until the interrelationships of the Leucosiidae are fully resolved the status of the Matutinae must be treated with caution. *Matuta* may merely be a derived leucosiid, with the Leucosiidae as it presently stands being a paraphyletic (and possible polyphyletic) group. The only publication to place *Matuta* within the Leucosiidae is Jones & Morgan (1994). Unfortunately, this was merely the result of a printing error (D. Jones pers. comm.).

It is interesting to note, however, that Rice (1980) placed both the Leucosiidae and the Matutinae in amongst the Catometopa (*sensu* H. Milne Edwards) along with *Dorippe* and *Orithyia*, based on larval evidence. The Calappinae (*Calappa* and *Hepatus*) were placed in the Cyclometopa. This division was supported by a wide range of larval characters, with the larvae of *Leucosia* and *Matuta* having the more 'advanced' character states. The results of the present study are in agreement with the divisions proposed by

Rice (1980).

Rice (1980) also noted the overall similarity of the larvae of *Orithyia* and those of the Dorippidae, but stated that the Dorippidae could not have arisen from the Orithyiinae because of the advanced states in *Orithyia* larvae. However, this does not preclude a close relationship. The results of the present study are consistent with Rice's initial observation that the Dorippidae and Orithyiinae are closely related. The *Dorippe*-Orithyiinae lineage (Clade 4) is one of the most strongly supported clades in the cladogram with 9 synapomorphies, of which 5 are unique and unreversed.

The results of the present study are in sharp contrast to existing brachyuran classification schemes (*cf.* Alcock, 1896; Borradaile, 1907; Sakai, 1976; Dai & Yang, 1991). In the past, *Orithyia* has always been associated with the rest of the 'calappids' even though the morphological differences are overwhelming. The subfamily Orithyiinae is a very distinctive taxon containing only one genus and one species. Much of its biology, however, is unknown. This study points to the need to reconsider the status of the Orithyiinae as the possible sister group of the Dorippidae and may serve as a basis for further studies on the evolution, biology and ecology of the Orithyiinae.

In recent years, several evolutionary studies have suggested that the similarities between the constituent families of the Oxystomata may be a case of convergence arising from adaptation to a similar mode of life (*i.e.* burrowing), rather than proof of a common ancestry. Whilst most systematists have assumed the non-monophyly of the Oxystomata, the results of the present study provide support for this taxon in a modified sense. The *Dorippe*-Orithyiinae-*Leucosia*-Matutinae lineage (Clade 3) is supported by 14 synapomorphies, of which 3 are unreversed. The synapomorphies include two which are traditionally used to link the oxystomatous crabs (characters 60 and 64). These characters are now seen to have arisen independently in the Calappinae and Hepatinae (Clade 2). One of the unreversed synapomorphies: the loss of the exopod flagellum on the 3rd maxilliped has not been recorded in earlier definitions of the Oxystomata (*e.g.* Alcock, 1896, Borradaile, 1907, Bourne, 1922). In view of the results of this study, the Calappinae and Hepatinae can no longer be included in the Oxystomata. However, there is evidence to suggest that the Matutinae, the Orithyiinae, the Dorippidae and the Leucosidae are part of a single lineage, the Oxystomata *sensu stricto*.

Based on the above findings a revised classification of oxystomatoid crabs is proposed. Additional details are provided in Appendix IV.

Section	**Sub-section**	**Superfamily**	**Family**
Heterotremata	*Incertae sedis*	Calappoidea	Calappidae
			Hepatidae
	Oxystomata *emend.*	Leucosioidea	Leucosiidae
			Matutidae
		Dorippoidea	Dorippidae
			Orithyiidae

The suggestion that the Oxystomata may still be valid, in a revised sense, is in strong contrast to the conclusions of other studies (*e.g.* Guinot, 1979; Rice, 1980; Jamieson, 1991; Spears *et al.*, 1992), who question its validity as a natural group. Clearly, there is a need for a thorough reevaluation of the group. Indeed it may be preferable for clarity to rename the lineage currently retained as the Oxystomata *emend.* Further studies of the individual families are also urgently required.

CHAPTER 3
PHYLOGENY AND EVOLUTIONARY BIOGEOGRAPHY OF THE CALAPPIDAE *SENSU STRICTO*

3.1 INTRODUCTION

This chapter builds on the results of Chapter 2 and examines the relationships between the genera assigned to the Calappidae *sensu stricto*: *Calappa* Weber, 1795; *Paracyclois* Miers, 1886; *Cycloes* de Haan, 1837; *Cyclozodion* Williams & Child, 1988; *Cryptosoma* H. Milne Edwards, 1837; *Mursia* Desmarest, 1823; *Platymera* H. Milne Edwards, 1837 and *Acanthocarpus* Stimpson, 1871. The results of the phylogenetic analysis will be used to evaluate 1) the fossil record, 2) biogeographic patterns and 3) depth distributions of genera within the Calappidae *s.s.*.

3.2 MATERIALS AND METHODS

A total of 69 individuals from 20 species of calappids were examined with representatives from all 8 genera, including the type species for each genus. The analyses were based on the examination and dissection of preserved material loaned from the Natural History Museum, London (BMNH), National Museum of Natural History, Washington D.C. (USNM), Muséum national d'Histoire naturelle, Paris (MNHN), National University of Singapore Zoological Reference Collection, Singapore (ZRC) and the Queensland Museum, Brisbane (QM). In addition, fresh specimens collected from Orpheus Island, Queensland, Australia were also examined (PCNR - personal collection, not retained). The material examined is listed in Appendix I.

3.2.1 Phylogenetic analyses

Outgroup taxa were drawn from the Hepatidae (represented by *Hepatus princeps and H. epilithicus)* and the Xanthidae (represented by *Atergatis floridus*) as the two putative sister taxa of the Calappidae. This follows the results of Chapter 2 which found a close relationship between the Calappidae and the Hepatidae, suggesting a possible sister group association. An association between the Calappidae and the Xanthidae was also proposed by Rice (1980) based on larval evidence and by Spears, Abele & Kim (1992) based on RNA evidence.

The characters used in this study were obtained from a wide range of structures and functional systems. All character states were based on adult morphology with examination of both male and female specimens. The characters chosen for inclusion in the analyses were those found to be of high taxonomic value at the generic level. That is, characters with clearly defined character states, which were consistent (invariant) within a group (*i.e.* genus). A total of 55 characters were used. A list of characters and character states is given in Table 3.1. The characters and their respective states will be described in the Comparative Morphology section. A complete matrix of character states is given in Table 3.2. This matrix includes autapomorphic character states. These character states were not included in the analyses.

Analyses were carried out using PAUP version 3.1 on a Macintosh LC475. A total of ten taxa were used in the analysis, eight ingroups and two outgroups. All characters were unweighted and multi-state character states unordered. In the analyses, two outgroups (*Hepatus* and *Atergatis*) were specified and the branch-and-bound option (BANDB) was used to find the shortest and most parsimonious tree. The DELTRAN option was used for character-state optimization.

Table 3.1 List of characters used in the phylogenetic analysis of the 8 calappid genera and 2 outgroup taxa Each character is numbered and described, followed by the character state where 0 = presumed plesiomorphy and 1,2,3,4 = presumed apomorphies.

---

1 Carapace: posterolateral projection absent (0), flanged (1), series of irregular spines (2), pair of spines (3)
2 Carapace: pair of lateral branchial spines present (1)
3 Front: interorbital dist.:orbit diam ratio = 1(0), >2(1)
4 Orbital region: cleft in lower orbital margin absent (0), present (1)
5 Orbital region: number of supraorbital sutures = 2 (0), 1(1)
6 Orbital region: suborbital stridulatory surface absent (0), present (1)
7 Endostome: well developed septum absent (0), small and incomplete (1), well developed (2)
8 Anteroventral region: exostegal channel absent (0), present (1)
9 Antennae: setae on peduncle absent (0), present (1)
10 1st maxilliped: endopod distal segment triangular (0), diamond (1)
11 1st maxilliped: endopod length </= (0), > (1) length of 3rd maxilliped
12 1st maxilliped: endopod medial edges do not meet at midline (0), meet (1)
13 1st maxilliped: endopod with channel on inner medial face absent (0), present (1)
14 2nd maxilliped: exopod length = endopod length (0), > (1)
15 2nd maxilliped: lateral flange narrow (0), broad (1)
16 2nd maxilliped: endopod ischium margin smooth (0), finely granular (1)
17 3rd maxilliped: coxa small and narrow (0), enlarged and expanded dorsally (1)
18 3rd maxilliped: exopod outer surface naked (0), with row of thick setae (1)
19 3rd maxilliped: epipod articulation with coxa lateral & narrow (0), broad & dorsal (1)
20 3rd maxilliped: epipod not flanged (0), flanged (1)
21 3rd maxilliped: exopod distal tip entire (0), notched (1)
22 3rd maxilliped: distal tooth on exopod inner margin absent (0), present (1)
23 3rd maxilliped: exopod inner surface naked (0), with row of fine setae (1)
24 3rd maxilliped: granular row on ischium anterior margin absent (0), present (1)
25 3rd maxilliped: ischium medial margin straight (0), crenate (1)
26 3rd maxilliped: merus anterodorsal margin simple (0), notched or lobed (1)
27 3rd maxilliped: palp basal segment = next segment (0), > (1)
28 Cheliped: chelae do not overlap (interdigitate) when flexed (0), interdigitate when flexed (1)
29 Cheliped: suture on coxal condyle incomplete (0), complete (1)
30 Cheliped: granules on coxa absent (0), present (1)
31 Cheliped: mero-carpal articulation without spine (0), with dorsal small spine (1)
32 Cheliped: merus ventral surface smooth (0), granular (1)
33 Cheliped: merus with distal lateral extension absent (0), spinous (1), flanged (2)
34 Cheliped: propodus inner surface naked (0), with setae (1)
35 Cheliped: propodus dorsal margin not raised or expanded (0), with expanded and raised dorsal margin (1)

36 Cheliped: propodus length:depth ratio <0.7 (0), >0.8 (1)
37 Cheliped: propodus ventral margin with no double row of granules (0), with double row of granules (1)
38 Cheliped: hooked lobule at base of dactylus absent (0), present (1)
39 Pereiopods: merus dorsal margin smooth (0), granulated (1)
40 Pereiopods: posterior margin of pereiopod V merus w/ longitudinal row of spines (1), none (0)
41 Sternum: sternal plates visible = 7(0), 6(1)
42 Sternum: episternites visible=4(0), 3(1)
43 Sternum: episternites do not cover coxa of cheliped and pereiopods (0), covers coxa of cheliped and pereiopods (1)
44 Sternum: stridulatory surface (granular row) on s2 absent (0), present (1)
45 Sternum: pair of raised projections (spines) on s4 absent (0), present (1)
46 Sternum: ep7 distinct (0), absent (1)
47 Abdomen: number of segments visible ventrally = 5(0), 6(1)
48 Abdomen: 1st segment distinct (0), barely visible (1)
49 Abdomen: sternum:abdomen length ratio <0.75(0), >0.8 (1)
50 1st pleopod: seminal opening terminal (0), subterminal (1)
51 1st pleopod: shaft setose proximally (0), naked (1)
52 2nd pleopod: distal tip straight (0), curved (1)
53 2nd pleopod: flagella length >/= basal length
54 2nd pleopod: median junction naked (0), with stiff setae (1)
55 2nd pleopod: distal tip smooth (0), with spinules (1)

Table 3.2 Character matrix (10 taxa by 55 characters) used in the cladistic analysis of the Calappidae *sensu stricto*. The first two taxa are outgroups; includes autapomorphies not used in tree construction.

	0	**1**	**2**
Atergatis	0000000000	0000010000	0000000000
Hepatus	0000000000	0000000000	0000000000
Calappa	1010002111	1111001111	1110111110
Paracyclois	2010101111	1111001111	1110111110
Cyclozodion	2010101111	1111001111	1110111110
Cryptosoma	0111100111	1111001111	1110111110
Cycloes	0011100111	1111001111	1110111110
Acanthocarpus	3010111111	1111001111	1010111111
Mursia	0111100111	1111111111	0111111011
Platymera	0111100111	1111111111	0110111011

	3	**4**	**5**
Atergatis	0000000000	0100000000	00000
Hepatus	0000000000	0000000000	00000
Calappa	1121111100	1110001011	01100
Paracyclois	1121110101	1110001011	01100
Cyclozodion	1121110100	1110001011	01100
Cryptosoma	1121111100	1111011011	01111
Cycloes	1121111100	1110011011	01111
Acanthocarpus	1111100100	0010101011	11100
Mursia	1111100110	0010101111	11110
Platymera	1111100110	0010101110	11110

3.2.2 Analyses of biogeographic and depth distributions

Biogeographic data were based on published area records (Rathbun, 1937; Barnard, 1950; Sakai, 1976; Tyndale-Biscoe & George, 1963; Williams & Child, 1988; Davie & Short, 1989; Dai & Yang, 1991; Galil, 1993; Galil & Clark, 1996) and museum collection records in the Muséum national d'Histoire naturelle and the Australian Museum. Depth data were extracted from published collection records (Rathbun, 1937; Sakai, 1976; Tyndale-Biscoe & George, 1963; Williams & Child, 1988; Davie & Short, 1989; Dai & Yang, 1991; Galil, 1993; Galil & Clark, 1996). Data in fathoms presented by these authors were converted to meters. However, the nature of their depth data varied. For example, in some studies the absolute depth at which samples were collected was given but, in most instances, only the minimum and maximum depths of the area where sampling took place were indicated. From the latter, the minimum depth was taken as a conservative estimate of the collection depth. For each genus, all absolute and minimum depth data of all available specimens in all species were combined and the mean and standard error calculated. Depth data were mapped onto the cladogram (i.e. replacing terminal taxa) then optimized to reveal historical patterns of habitat use (cf. Brooks & McLennan, 1990).

3.3 COMPARATIVE MORPHOLOGY

In the following section, character states are indicated in the text by numbers in parentheses, giving the character and character state where 0 = presumed plesiomorphy; n > 0 = presumed apomorphy (*e.g.* 17.1 = character 17 state 1 which is derived). Where there is more than one apomorphic state these are indicated in a similar manner (*e.g.* 68.4). Numbering character states 1, 2, 3 etc. does not indicate a transformation series. The polarity of the character states was not determined *a priori* but during the construction of the cladogram.

The Calappidae is defined by a number of unique and unreversed autapomorphies (described in Chapter 2; designated character numbers 8, 17, 18, 19, 26, 27, 31, 34, 35, 38, 47 and 52 in the present study). These characters will not be redescribed in this section.

3.3.1 Carapace and anterior regions

The calappid carapace is distinctive and much of the taxonomy of various genera is based on its appearance (Alcock, 1896; Rathbun, 1937; Dai & Yang, 1991; Galil & Clark, 1996). In the present study, however, only two characters were found to be phylogenetically informative. Projections on the posterolateral margin of the carapace are only present in *Calappa*, *Paracyclois*, *Cyclozodion* and *Acanthocarpus*. These projections are either: (a) flanged and extend over the top half of the walking legs, the maximum width of the posterolateral margin being equal or greater than the maximum width of anterior margin as in *Calappa* (1.1); (b) a series of irregularly sized broad spines which do not extend over the walking legs, the maximum width of the posterolateral margin being less than the maximum width of the anterior margin as in *Paracyclois* and *Cyclozodion* (1.2) or (c) a pair of well developed spines as in *Acanthocarpus* (1.3). No posterolateral projections are found in *Cryptosoma*, *Cycloes*, *Mursia*, *Platymera*, *Hepatus* and *Atergatis* (1.0).

The carapace of *Cryptosoma*, *Mursia* and *Platymera* is characterized by a pair of lateral branchial spines (2.1). No lateral spines are found in *Calappa*, *Paracyclois*, *Cyclozodion* and *Acanthocarpus* and in the outgroup taxa (2.0).

A number of characters associated with the anterior region of the carapace were also found to be useful. In all calappid taxa, the interorbital distance:orbital diameter ratio is approximately 1 (3.1). In *Hepatus* and *Atergatis*, however, the ratio is greater than 2 (3.0). A narrow V-shaped cleft was found in the lower orbital margin (4.1) of *Cycloes*, *Cryptosoma*, *Mursia* and *Platymera*. In *Calappa*, *Paracyclois*, *Acanthocarpus*, *Cyclozodion* and *Hepatus*, the lower orbital margin is entire (4.0). The upper orbital margin contains a number of sutures, ranging from 1 in *Paracyclois*, *Cyclozodion*, *Cryptosoma*, *Cycloes*, *Acanthocarpus*, *Mursia* and *Platymera* (5.1) to 2 in *Calappa*, *Hepatus* and *Atergatis* (5.0). A suborbital stridulatory surface consisting of a row of regularly spaced tubercules is found only in *Acanthocarpus* (6.1).

The endostome of some calappid taxa possesses a septum which varies in the degree of development. In *Acanthocarpus*, *Paracyclois* and *Cyclozodion*, this septum is small and incomplete (7.1). *Calappa*, however, has a well developed septum dividing the endostome longitudinally (7.2). No septum in present in *Cryptosoma*, *Cycloes*, *Mursia* and *Platymera* and the outgroup taxa (7.0).

3.3.2 Antennule and antennae

The antennule in all taxa examined was invariant with no characters of phylogenetic use. Only one antennal character was found to vary: setae are present on the peduncle of all taxa in the Calappidae (9.1), whilst in *Hepatus* and *Atergatis*, the peduncle is naked (9.0).

3.3.3 First maxilliped

In all calappid genera, the total length of the endopod of the 1st maxilliped is greater than that of the 3rd maxilliped such that the distal portion of the 1st maxillipeds are still visible even when the 3rd maxilliped are closed (11.1). In *Hepatus* and *Atergatis*, the endopods are completely covered by the 3rd maxillipeds (11.0). The medial margins of the endopods meet in the midline in *Calappa*, *Paracyclois*, *Cycloes*, *Acanthocarpus*, *Mursia* and *Platymera* (12.1). In *Hepatus* and *Atergatis*, there is no contact between the endopods of each maxilliped (12.0). A shallow channel on the inner surface of the endopod in *Calappa*, *Paracyclois*, *Cycloes*, *Acanthocarpus*, *Mursia* and *Platymera* is formed by the raised margins of the distal segment (13.1). No such channel is found in *Hepatus* and *Atergatis* (13.0).

3.3.4 2nd maxilliped

Three characters of the 2nd maxillipeds were found to be informative. The length of the exopod (excluding the flagellum) in all calappid genera is over 1.5 times the length of the endopod (14.1); in *Hepatus* and *Atergatis*, the exopod is as long as the endopod (14.0). The lateral margin of the exopod is flanged in all the taxa examined. The size of the flange, however, was found to vary. In *Calappa*, *Paracyclois*, *Cycloes*, *Acanthocarpus* and in *Hepatus* and *Atergatis*, the flange is thin and narrow (15.0); in *Mursia* and *Platymera,* the flange is broad (15.1). The medial margin of the ischium of the endopod is finely granular in *Mursia* and *Platymera* (16.1); in all other taxa, the medial margin is smooth (16.0).

3.3.5 3rd maxilliped

The Calappidae possess a number of unique and unreversed synapomorphies associated with the 3rd maxilliped (characters 17-19, 26, 27 *cf.* Bellwood, 1996). In this study, additional characters were found to be of phylogenetic utility at the generic level. The epipod of all calappids is flanged at the point of attachment to the coxa (20.1). The epipod is not flanged (20.0) in either outgroup taxa. In *Calappa*, *Paracyclois*, *Cycloes*, *Cyclozodion* and *Acanthocarpus*, the distal tip of the exopod is notched resulting in two small lobes (21.1), whilst in *Mursia*, *Platymera* and in *Hepatus* and *Atergatis*, the distal tip is entire (21.0). The medial margin of the exopod also possesses a small tooth (sharp protuberance) distally (22.1) in *Calappa*, *Paracyclois*, *Cycloes*, *Cyclozodion*, *Mursia* and *Platymera*. No such tooth is found (22.0) in *Acanthocarpus*, *Hepatus* or *Atergatis*. A row of fine setae can be found on the inner margin of the exopod (23.1) in all calappid taxa but not in the outgroups (23.0). The anterior margin of the ischium of the endopod is characterized by a row of granules in *Mursia* (24.1). The granular row is not found (24.0) in any of the other taxa. The medial margin is crenate (25.1) in all calappid taxa; in the outgroup taxa, it is straight (25.0).

3.3.6 Chelipeds

The form of the calappid cheliped is well documented. The possession of a specialized structure at the base of the pollex and the dactylus has been used by many taxonomists to distinguish calappid genera from other brachyurans (*e.g.* Sakai, 1976, Williams & Child, 1989; Dai & Yang, 1991). In Chapter 2, a number of synapomorphies of the Calappidae associated with the cheliped (characters 31, 34, 35, 38; Table 3.1) were identified. In this chapter, seven other characters were found to be informative both at the family and the generic level.

When completely flexed, the chelipeds in some calappid taxa meet and interdigitate near the propodal-dactylar junction to form a single unit which is held close to the body (28.1). In this position they form the "exostegal channel" (Garstang, 1898) which appears to have a respiratory function. This condition is found only in *Calappa*, *Paracyclois*, *Cycloes*, *Cyclozodion* and *Acanthocarpus*. In *Mursia*, *Platymera* and in both outgroup taxa, the chelae do not interdigitate (28.0).

In all taxa a faint suture may be found above the coxal condyle near the point of articulation with the sternum. This suture may either be complete (29.1) as in the

Calappidae or incomplete (29.0) as in *Hepatus* and *Atergatis*. Granulation on the coxa is apparent (30.1) in *Acanthocarpus*, *Mursia* and *Platymera*; in *Calappa*, *Paracyclois*, *Cycloes*, *Cyclozodion Hepatus* and *Atergatis*, the coxa is smooth (30.0).

The ventral surface of the merus is also granulated in all calappid taxa (32.1); in *Hepatus* and *Atergatis*, the ventral surface of the merus is smooth (32.0). The merus in the Calappidae is unusual in that it possesses a lateral extension distally (Bellwood, 1996). The nature of the extension, however, varies between taxa. In *Calappa*, *Paracyclois*, *Cycloes* and *Cyclozodion* the distal end of the merus bears a lateral flange (the margins in some species is highly serrate, *e.g. Paracyclois*) (33.2). In *Acanthocarpus*, *Mursia* and *Platymera*, the distal end of the merus bears one or two well-developed spines (33.1). No lateral extension is found in *Hepatus* and *Atergatis* (33.0).

The propodus length:depth ratio also varied between taxa. In *Acanthocarpus*, *Mursia*, *Platymera*, *Hepatus* and *Atergatis*, the length:depth ratio was <0.7 (36.0) whilst in *Calappa*, *Paracyclois*, *Cycloes* and *Cyclozodion* the ratio was >0.8 (36.1). The ventral margin of the propodus in *Calappa*, *Cryptosoma* and *Cycloes* is characterized by a distinctive double row of granules (37.1) extending from the proximal angle of articulation with the carpus to the distal tip of the pollex. This condition is not found in any of the other taxa (37.0).

Stridulatory surfaces are found on the cheliped of a number of calappid taxa. These surfaces when rubbed against a corresponding surface on the body produce a distinctive "rasping" sound. Whilst stridulatory organs have been found to be useful in calappid taxonomy (*e.g.* Galil, 1993, Galil & Clark, 1996), the phylogenetic value of these characters at the generic level is limited. The structure and location of stridulatory surfaces varies considerably and homology is often difficult to establish. In many cases, the structures are autapomorphic. Stridulatory characters were not used in the analysis due to unclear character designations.

3.3.7 Other pereiopods

In this study, two pereiopod characters were found to be informative, both were associated with the merus. The external (dorsal) surface of the merus is granulous (39.1) in *Acanthocarpus*, *Mursia* and *Platymera*, whilst in *Calappa*, *Paracyclois*, *Cryptosoma*, *Cycloes*, *Cyclozodion*, *Hepatus* and *Atergatis* the external surface is smooth (39.0). The posterior margin of the merus of the last pair of pereiopods (pV) in *Paracyclois* bears a row of spines (40.1). These spines were not found in any of the other taxa examined (40.0).

3.3.8 Sternum

When the abdomen is in place, only the lateral portions of the sternal plates are visible ventrally in male and juvenile individuals. The number of sternal plates visible when the abdomen is in place ranged from 6 (41.1) in *Calappa*, *Paracyclois*, *Cryptosoma*, *Cycloes* and *Cyclozodion* to 7 (41.0) in *Acanthocarpus*, *Mursia*, *Platymera*, *Hepatus* and *Atergatis*. The number of episternites visible also varied, ranging from 3 (42.1) in *Calappa*, *Paracyclois*, *Cycloes*, *Cyclozodion* and *Atergatis* to 4 (42.0) in *Acanthocarpus*, *Mursia*, *Platymera* and *Hepatus*. In all calappids, the episternites cover the site where the coxa articulates with the sternum (43.1). In *Hepatus* and *Atergatis*, however, the episternites do not cover the articulation joint and the coxal condyles are visible ventrally (43.0).

A distinct row of granules is found on the anteriormost sternal plate (44.1) (S1 and S2 being fused) of *Cryptosoma* but not in the other taxa examined (44.0). This row appears to be the corresponding stridulatory surface of the dactylar striae in *Cryptosoma* (*cf.* Guinot-Dumortier & Dumortier, 1960).

A pair of raised projections are found on the 4th sternal plate (S4) near the base of the chelipeds (45.1) in *Acanthocarpus*, *Mursia* and *Platymera* but not in *Calappa*, *Paracyclois*, *Cryptosoma*, *Cycloes* and *Hepatus* (45.0). These projections are most distinct in *Platymera* where they resemble a pair of spines on the sternum. In some species of *Acanthocarpus* and *Mursia* these projections may appear as clusters of raised granules. The seventh episternite (ep7), although relatively small compared to the other episternites, is distinct in all taxa examined (46.0), except in *Cryptosoma* and *Cycloes* where it is absent (46.1).

3.3.9 Abdomen

The 1st abdominal segment is considerably smaller than the 2nd segment in all taxa examined. In *Calappa*, *Paracyclois*, *Acanthocarpus*, *Cryptosoma*, *Cycloes*, *Cyclozodion*, *Hepatus* and *Atergatis*, the 1st segment is distinctly visible (48.0), in *Mursia* and *Platymera*, however, the 1st segment is largely covered by the posterior carapace margin (48.1). The male abdomen in calappids is long and narrow, with the sternum:abdomen length ratio $\geq$0.8(49.1). In *Hepatus* and *Atergatis*, however, the sternum:abdomen ratio is <0.75 (49.0)

3.3.10 Reproductive structures

The distal aperture of the 1st pleopods is large, ovoid and subterminal (50.1) in *Calappa*, *Paracyclois*, *Acanthocarpus*, *Cycloes* and *Mursia*. In *Platymera*, *Hepatus* and *Atergatis*, however, the distal aperture is small, rounded and terminal (50.0). The proximal half of the shaft of the 1st pleopod is setose (51.0) in *Calappa*, *Paracyclois*, *Cryptosoma*, *Cycloes*, *Cyclozodion*, *Hepatus* and *Atergatis*; in *Acanthocarpus*, *Mursia* and *Platymera*, the shaft is naked (51.1). The length of the flagellum relative to the basal segment varies between taxa. The flagellum is longer than the basal segment (53.1) in the Calappidae; in *Hepatus* and *Atergatis* it is shorter than the basal segment (53.0).

The junction between the basal segment and the flagellum of the 2nd pleopod is marked by a small raised node in all taxa examined. In *Cryptosoma*, *Cycloes*, *Mursia* and *Platymera*, the node is characterized by the presence of short stiff setae (54.1). No setae are found in any of the other taxa (54.0). The distal tip of the flagella of the 2nd pleopod is smooth (55.0) in all taxa examined, except in *Cryptosoma* and *Cycloes* where the tip bears numerous spinules (55.1).

3.4 RESULTS

The analysis of 55 characters with a total of 113 character states (excluding terminal autapomorphies) yielded one tree, 66 steps long with a consistency index of 0.833 (rescaled CI = 0.717) (Fig. 3.1). Six distinct clades are apparent. In the following section, each clade is numbered (as in Fig. 3.1), followed by its component taxa and a list of synapomorphies giving the character number and in parentheses, the character state. Synapomorphies which are unique in the taxa examined and unreversed, are listed in bold.

Clade 1: *Calappa*, *Cycloes*, *Cryptosoma*, *Paracyclois*, *Cyclozodion* - 21(1), 22(1), 28(1), **33(2)**, **36(1)**, **41(1)**, 42(1)

This monophyly of this clade is supported by seven synapomorphies, three of which are unique and unreversed: the possession of a lateral flange at the distal end of the cheliped merus (33), a high propodus length:depth ratio of the chelipeds (36), and

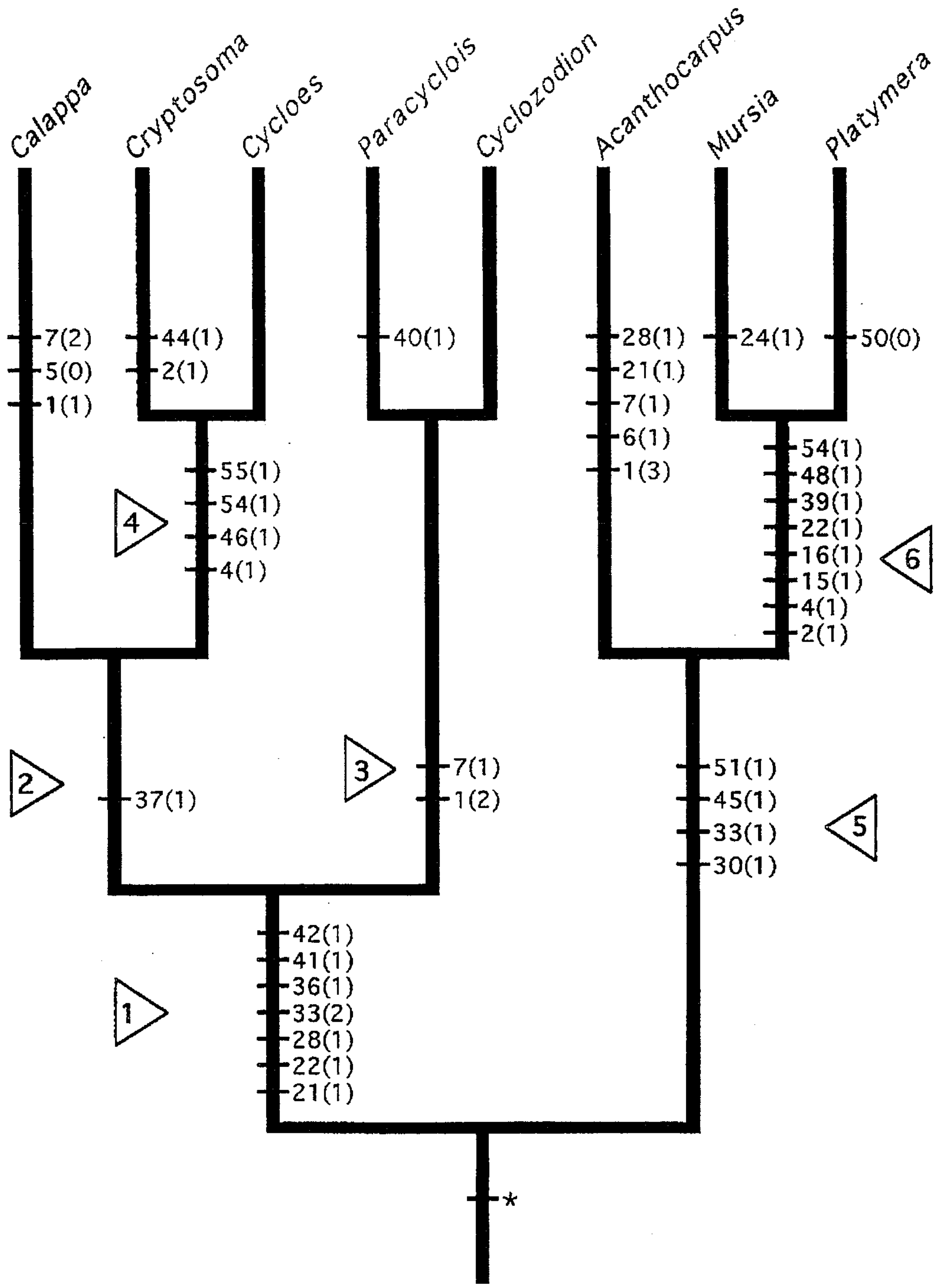


Figure 3.1 Cladogram of the relationships of the eight genera within the Calappidae *sensu stricto*. Tree length = 66 steps, CI = 0.83, RCI = 0.72. Character numbers follow Appendix II, character states are given in parentheses. Numbers in triangles refer to clades discussed in the text. * = synapomorphies of the Calappidae: 3, 8-14, 17-20, 23, 25-27, 29, 31, 32, 34, 35, 38, 43, 47, 49, 52, 53.

six sternal plates visible ventrally (41). Other synapomorphies include the presence of a notch at the distal tip (19) and a small tooth on the medial margin (20) of the exopod of the 3rd maxilliped and interdigitating chelae when the chelipeds are flexed completely (28).

Clade 2: *Calappa*, *Cryptosoma* and *Cycloes* - **37(1)**

This is a poorly defined clade which is united by only one unique and unreversed synapomorphy: a double row of granules on the ventral aspect of the cheliped propodus.

Calappa: **1(1)**, 5(0), **7(2)**. This genus is defined by the possession of a flanged posterolateral expansion of the carapace (1) and the possession of a well developed septum in the endostome (7). The reacquisition of the ancestral double suborbital sutures (5) is a reversal of a state synapomorphic in the Calappidae.

Clade 3: *Paracyclois* and *Cyclozodion* - **1(2)**, 7(1)

This is a relatively weakly defined clade supported by two synapomorphies, of which only one is unreversed: the possession of posterolateral projections on the carapace consisting of a series of irregularly sized broad spines which do not extend over the walking legs (1). The other synapomorphy: presence of an incomplete septum in the endostome (7) appears to have arisen independently in *Acanthocarpus*.

Paracyclois: **40(1)**. This genus is defined by a single autapomorphy, the presence of a row of spines on merus of the last pair of pereiopods (40)

Cyclozodion: There are no autapomorphies defining this genus.

Clade 4: *Cryptosoma* and *Cycloes* - 4(1), **46(1)**, 54(1), **55(1)**

This clade is defined by four synapomorphies, two of which are unique and unreversed: the marked reduction of the 7th episternite (46) and the presence of spinules on the distal tip of the 2nd pleopod (55). Other synapomorphies are the presence of a cleft in the lower orbital margin (4) and the presence of stiff setae at the median junction of the 2nd pleopod (54).

Cryptosoma: 2(1), **44(1).** This genus is defined by a single autapomorphy: the presence of a row of granules on the 2nd sternite (44). The possession of lateral branchial spines on the carapace (2) appears to have arisen independently in Clade 6.

Cycloes: There are no autapomorphies defining this genus.

Clade 5: *Acanthocarpus*, *Mursia* and *Platymera* - **30(1), 33(1), 45(1), 51(1)**

This clade is clearly defined by four unique unreversed synapomorphies: presence of granules on the coxa of the chelipeds (30), possession of spinous projections at the distal end of the cheliped merus (33), presence of raised projections on the 4th sternal plate (45) and presence of setae on the proximal half of the 1st pleopod (51).

Acanthocarpus: **1(3)**, **6(1)**, 7(1), 21(1), 28(1). This genus is clearly supported by two autapomorphies: the possession of a pair of posterolateral spines on the carapace (1) and a row of regularly spaced tubercules on the suborbital region (6). The other three synapomorphies appear to have been independently derived in Clades 1 (21, 28) and 3 (7).

Clade 6: *Platymera* and *Mursia* - 2(1), 4(1), **15(1)**, 16(1) 22(1), **39(1)**, **48(1)**, 54(1)

This is a well-defined clade united by eight synapomorphies. Of the eight, three are unique and unreversed: possession of a broad lateral flange on the exopod of the 2nd maxilliped (15), granulation on the dorsal margin of the merus of the pereiopods (39) and the 1st abdominal segment being covered by the posterior margin of the carapace (48).

Mursia: **24(1).** This genus is supported by a single autapomorphy: the presence of a row of granules on the 4th sternal plate (24).

Platymera: 50(0). The character state which distinguishes this genus is the reacquisition of a terminal seminal opening on the 1st pleopod (50), a reversal of the state identified as a synapomorphy of the Calappidae.

3.5 DISCUSSION

3.5.1 Phylogeny and classification

The monophyly of the family Calappidae *s.s.* is unequivocal. This study reaffirms the findings of Chapter 2 and provides additional characters supporting the monophyly of the family. The status of the component taxa and clades within the family, however, are less clear. The data reveal two distinct lineages within the Calappidae: the *Calappa-Cryptosoma-Cycloes-Paracyclois-Cyclozodion* clade (the 'calappine' clade) and the *Acanthocarpus-Mursia-Platymera* clade (the 'mursiine' clade), supported by seven and four synapomorphies, respectively.

In the calappine clade, the relationships of the terminal taxa requires further consideration. Two clades are apparent: the *Calappa-Cryptosoma-Cycloes* clade and the *Paracyclois-Cyclozodion* clade. Within the *Calappa-Cryptosoma-Cycloes* clade, the close relationship between *Cryptosoma* and *Cycloes* is clearly supported by four synapomorphies, two of which are unique. Historically linked since the 1800's, a recent taxonomic revision (Clark & Galil, 1996) designated the genus name *Cryptosoma* for all the Atlantic species of the *Cycloes-Cryptosoma* complex, and *Cycloes* for all Indo-

Pacific species. However, the characters used to define *Cycloes* [*sensu stricto*] were either symplesiomorphic or too variable to be of phylogenetic use. In the present study, only *Cryptosoma* can be defined by one autapomorphy whilst *Cycloes* had none.

A similar situation is apparent in the *Paracyclois-Cyclozodion* clade. Their close association is supported by two synapomorphies. However *Paracyclois* is defined by only one autapomorphy whilst *Cyclozodion* has none. Established only in 1988, the genus *Cyclozodion* was originally based on specimens previously assigned under *Calappa* (Williams & Child, 1988). Noting their similarity in general carapace shape and orbital characteristics with *Paracyclois*, the authors chose to erect a new genus instead of broadening the definition of *Paracyclois* to accommodate them. This decision was based on the absence of spination on the pereiopods (a symplesiomorphy) and the presence of a small low ridge on the proximal end of the propodus, near the meral junction (a highly variable structure found in a wide range of calappid taxa).

For now, these four genera are tentatively retained. However, their close association as two distinct clades within the 'calappine' lineage and the lack of autapomorphies highlight the need for a reevaluation of these genera. The recognition of *Cycloes* and *Cyclozodion* as junior synonyms of *Cryptosoma* and *Paracyclois*, respectively, may be warranted.

The second major lineage, the *Acanthocarpus-Mursia-Platymera* clade, is strongly supported by 4 unreversed synapomorphies. However, whilst *Acanthocarpus* is clearly defined by two autapomorphies, the status of *Mursia* and *Platymera* is uncertain. Although the *Mursia-Platymera* clade is united by 3 unreversed synapomorphies, *Mursia* and *Platymera* have only one defining character state each: an autapomorphy in *Mursia* and a reversal in *Platymera*. *Platymera* is a monotypic taxon with a restricted distribution. Established by H. Milne Edwards (1837), it was synonimized with *Mursia* by Alcock (1896). In a recent revision of the genus *Mursia*, however, Galil (1993) reinstated *Platymera* as a separate genus. This decision, however, was based on characters which were either symplesiomorphies or highly variable within the family.

In the present study, *Platymera* is distinguished from other calappids by the reacquisition of the ancestral state of a terminal seminal opening on the 1st pleopod. *Mursia* is defined by the possession of a row of granules on the anterior margin of the ischium of the 3rd maxilliped. Given these autapomorphies, *Platymera* and *Mursia* are tentatively retained as separate genera.

This is the first phylogenetic study of the group and although it has offered support for some genera, others are in urgent need of re-evaluation. Furthermore, this study found that carapace characters, which previously formed the basis of taxonomic descriptions, were of limited utility in resolving phylogenetic relationships at the generic level.

3.5.2 Fossil record and historical biogeography

The data from the present study on Recent calappids provides a basis for re-evaluating the status of fossils previously placed in the Calappidae. There are currently 18 calappid genera described from the fossil record (*cf.* Förster, 1968; Glaessner, 1969; Karasawa, 1993). Of these, four are extant. However, the identification of most specimens remains uncertain as published descriptions reveal few, if any, features which are phylogenetically informative. Most calappid fossils are identified based on carapace characters alone. Unfortunately very few carapace characters were found to be informative in the present study. In addition, these fossils were placed in the Calappidae *sensu lato* which may have included members of the Orithyiidae, Hepatidae, and Matutidae (*cf.*Chapter 2).

Based on the synapomorphies listed in Chapter 2 and additional ones listed in this chapter, the oldest published record of the Calappidae *sensu stricto* appears to be from the Oligocene. Both *Calappa* and *Mursia/Platymera* have been described from the Oligocene of North America (Rathbun, 1926). The identification of the *Calappa* specimen is well supported. The material includes both carapace and minor cheliped fragments. The cheliped possesses: 1) a distal crest on the merus and 2) an expanded crest on the dorsal margin of the propodus - both being synapomorphies of the family (*cf.* Chapter 2). Furthermore, the carapace possesses a posterolateral flange - a synapomorphy of the genus *Calappa*. The *Mursia/Platymera* material includes carapace, sternal, pereiopod and cheliped fragments. The possession of an expanded dorsal crest on the propodus of the cheliped clearly places the material in the Calappidae, whilst the possession of sternal spines strongly points to its inclusion in the 'mursiine' clade. The possession of granules on the merus points to a *Mursia/Platymera* association rather than *Acanthocarpus*. The nature of the material, however, precludes any further generic distinction.

An extinct genus *Calappilia* (type species: *C. verrucosa*) was described from the Mid-Oligocene of France (A. Milne-Edwards, 1873 in: Williams & Child, 1988) based on material consisting of chela and carapace fragments. From the description of the chelae ("dactyl armed at base with large tubercule recalling that developed in *Calappa*"), inclusion in the Calappidae appears to be valid. Unfortunately, the status of several other specimens identified as *Calappilia* species, including those of an earlier age, could not be confirmed as these were based solely on carapace characters (*e.g.* Ross & Scolaro, 1964; Quayle & Collins, 1981; Feldmann, 1993; Blow & Manning, 1996). While the appearance of the carapace in some *Calappilia* species is broadly comparable with some calappid taxa, there are no synapomorphies associated with the carapace which clearly define the genus or place it within the Calappidae (*cf.* Chapter 2). The status of published species within the genus *Calappilia* therefore, is uncertain. It appears to be a "catch-all" genus containing many disparate taxa. Some taxa possess features reminiscent of the *Paracyclois-Cyclozodion* lineage, *i.e.* the possession of a series of irregularly shaped posterolateral spines the maximum span of which are less than the maximum width of the carapace, *e.g. Calappilia maxwelli*, *C. dacica* and *C. scopuli.* Given the lack of definitive characters such as those of the chelae, there remains no firm basis for inclusion of these taxa within the genus *Calappilia* or in the Calappidae. They are effectively referred to as *indet.* (*i.e.* unable to be assigned to genus or family). However, an undescribed collection of calappid material consisting of chelae remnants has recently been located at the Natural History Museum (UK), dating back to the Upper Eocene (pers.obs.). The collection of up to 15 intact dactyli show distinct hooked lobules characteristic of the Calappidae. Preliminary identification of carapaces found along with the chelae remnants suggest that these may be *Calappilia* species (*cf.* A. Milne-Edwards, 1873). Whilst awaiting formal description, these specimens strongly suggest that the Calappidae may have existed as far back as the Eocene.

The fossil described by Feldmann & Wilson (1988) as a *Calappa* from Antarctica cannot be placed with confidence in the genus *Calappa* nor in the Calappidae *sensu stricto.* As a dextral chela (right hand) this chela would be the major claw (Ng & Tan, 1985). In all calappid genera one of the most characteristic features (and a synapomorphy of the clade) is the possession of a hooked lobule on the proximal end of the dactylus and two blunt teeth at the proximal end of the pollex of the major chela. Given the level of preservation of the specimen it is striking that these features are not present. Although the overall shape does indeed resemble that of a calappid, the lack of these structures precludes inclusion in the family. This species may represent the sister taxon to the Calappidae (prior to the appearance of the hooked lobule) although it could easily be related to other taxa. The chela bears a superficial resemblance to those of *Hepatus* and *Osachila*. Whilst a calappid association is possible, inclusion in the family at this stage appears unwarranted.

3.5.3 Biogeography

The distribution patterns of the calappid genera present an interesting biogeographic pattern. Based on distributions, there appears to have been a major vicariance event in the Middle-East dividing *Cryptosoma* and *Cycloes* in the 'calappine' clade and *Acanthocarpus* and *Mursia* in the 'mursiine' clade (Figs 3.2 and 3.3). The usual vicariance event identified in this location is the Terminal Tethyian Event with the closure of the Red Sea land bridge between 12 and 18 Ma (Rosen & Smith, 1988). Whilst the Terminal Tethyan Event may have divided *Cycloes* and *Cryptosoma*, the presence of *Mursia/Platymera* and *Calappa* from Oligocene deposits (*i.e.* 23 to 37 Ma) suggest that the major lineages were already well established prior to the Terminal Tethyan Event. Given the probable age of the lineages, it is difficult to identify the geological events associated with major divisions between taxa. Land bridges in the region of the Isthmus of Panama may have been present as far back as the Cretaceous (Smith *et al.* 1981) whilst several divisions in the Middle East prior to the Terminal Tethyan Event have been postulated (Adams, 1981). Furthermore, following faunal loss in the Mediterranean during the Messinian Salinity Crisis, Atlantic - Indian Ocean divisions can not be clearly separated from Tethyian regionalization of the Caribbean and Indian Ocean, which dates back to the mid Cretaceous (Coates, 1973)

In this respect the distribution patterns of *Acanthocarpus* and *Platymera* are interesting, with the striking absence of *Platymera* in the Atlantic (Fig. 3.2). Three

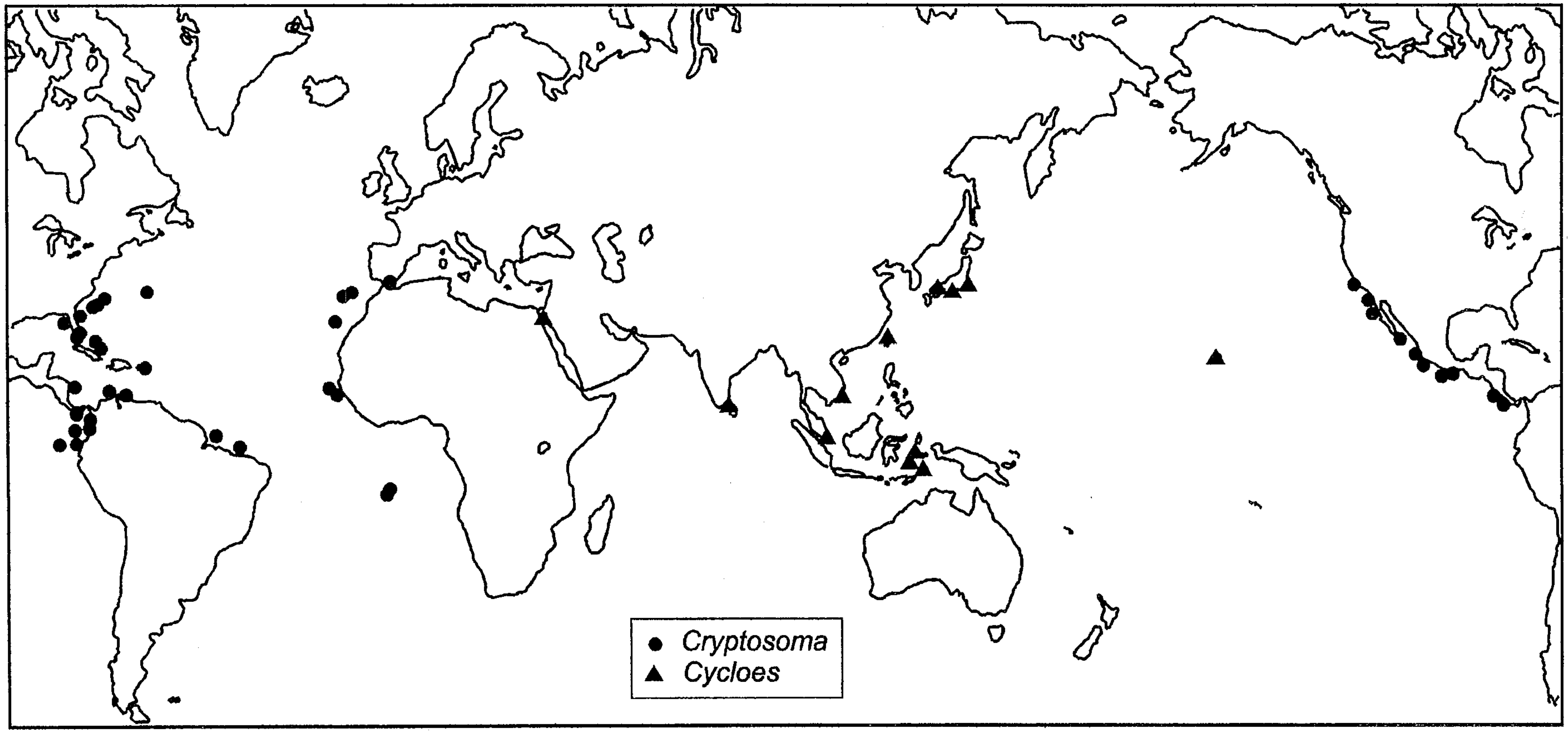


Fig. 3.2 Distribution records of *Cryptosoma* and *Cycloes*.

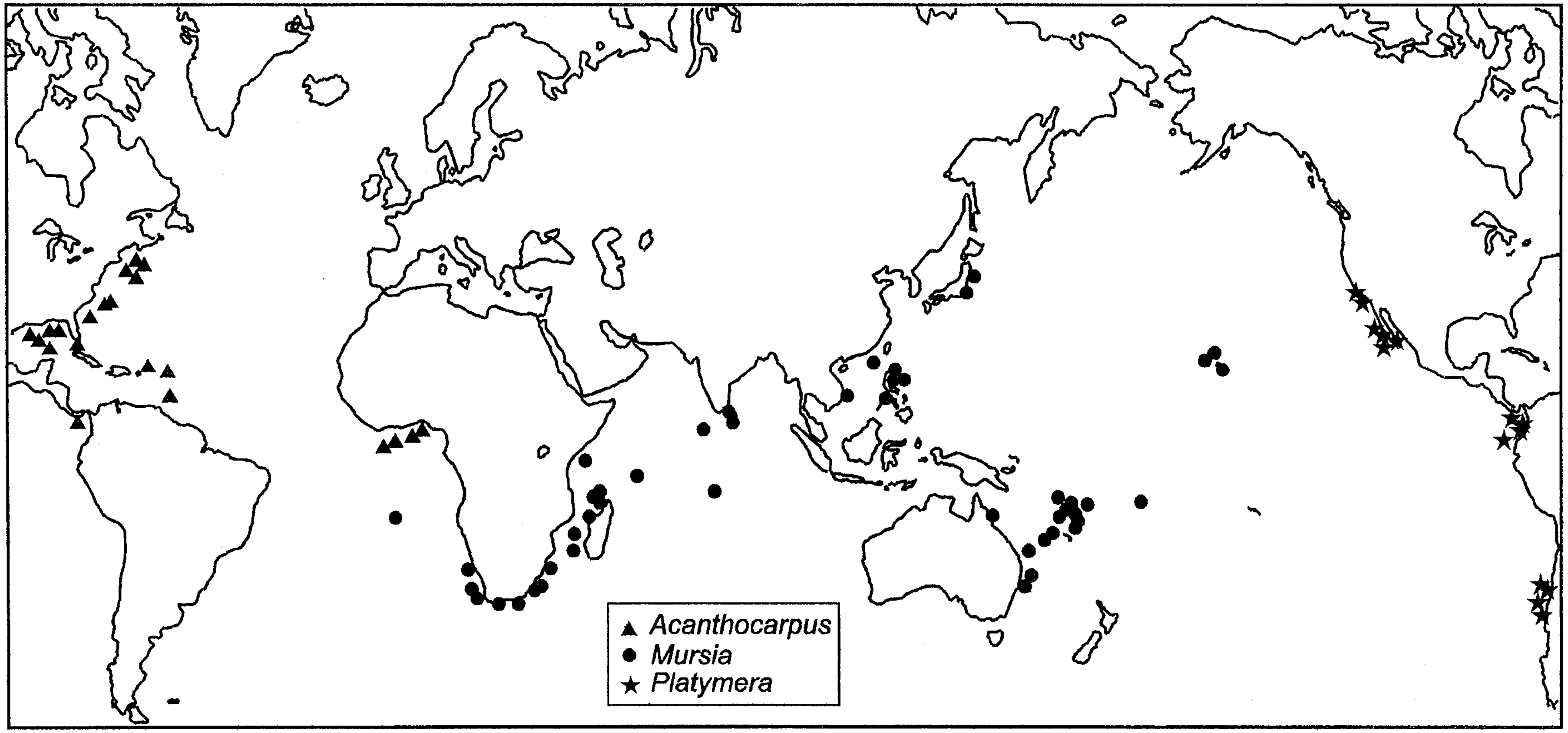


Fig. 3.3 Distribution records of *Acanthocarpus*, *Mursia* and *Platymera*.

possibilities arise, either: (1) *Platymera* has recently colonized the Eastern Pacific after the closure of the Isthmus of Panama (a peripheral fragment of the *Mursia* lineage) as in some corals and fish (Rosenblatt & Waples, 1986; Veron, 1995); (2) *Mursia/ Platymera* was widespread but has been lost from the Caribbean, or (3) the *Mursia/Platymera* - *Acanthocarpus* division is much older than the currently viewed division of the Isthmus of Panama at 3 Ma. The first scenario seems unlikely as the *Platymera/Mursia* lineage has been present in Panama since the Oligocene (Rathbun, 1926). At present, the remaining two alternatives can not be resolved. However, there is evidence which may support the third scenario. Shallow tropical marine waters between North and South America with a prevailing east-west flowing current may have provided an effective barrier to movement of deep-water taxa from the Eastern Pacific into the Caribbean. Thus as deep water taxa (see below) the *Mursia/Platymera* lineage may have been restricted to the Eastern Pacific since the Oligocene. Furthermore, several authors have suggested that marine connections between the two regions were disrupted prior to the Pliocene formation of the Isthmus of Panama, with possible isolation of marine taxa as far back as the late Cretaceous (Klassen, 1995).

The remaining genera appear to be represented by relic populations (*Paracyclois* and *Cyclozodion*; Fig. 3.4) or are widespread (*Calappa*). An Oligocene fossil of *Calappa*, suggests that these genera were all present prior to the Terminal Tethyan Event, the distributions of the genera today being indicative of a range reduction in *Paracyclois* and *Cyclozodion*

Overall, whilst existing barriers (Isthmus of Panama, Terminal Tethyan Event, Eastern Pacific Barrier) may maintain distribution patterns, the original vicariance events associated with the major calappid divisions between lineages remain unclear. The only clear pattern is of western and eastern Tethyian components (*Cryptosoma*-

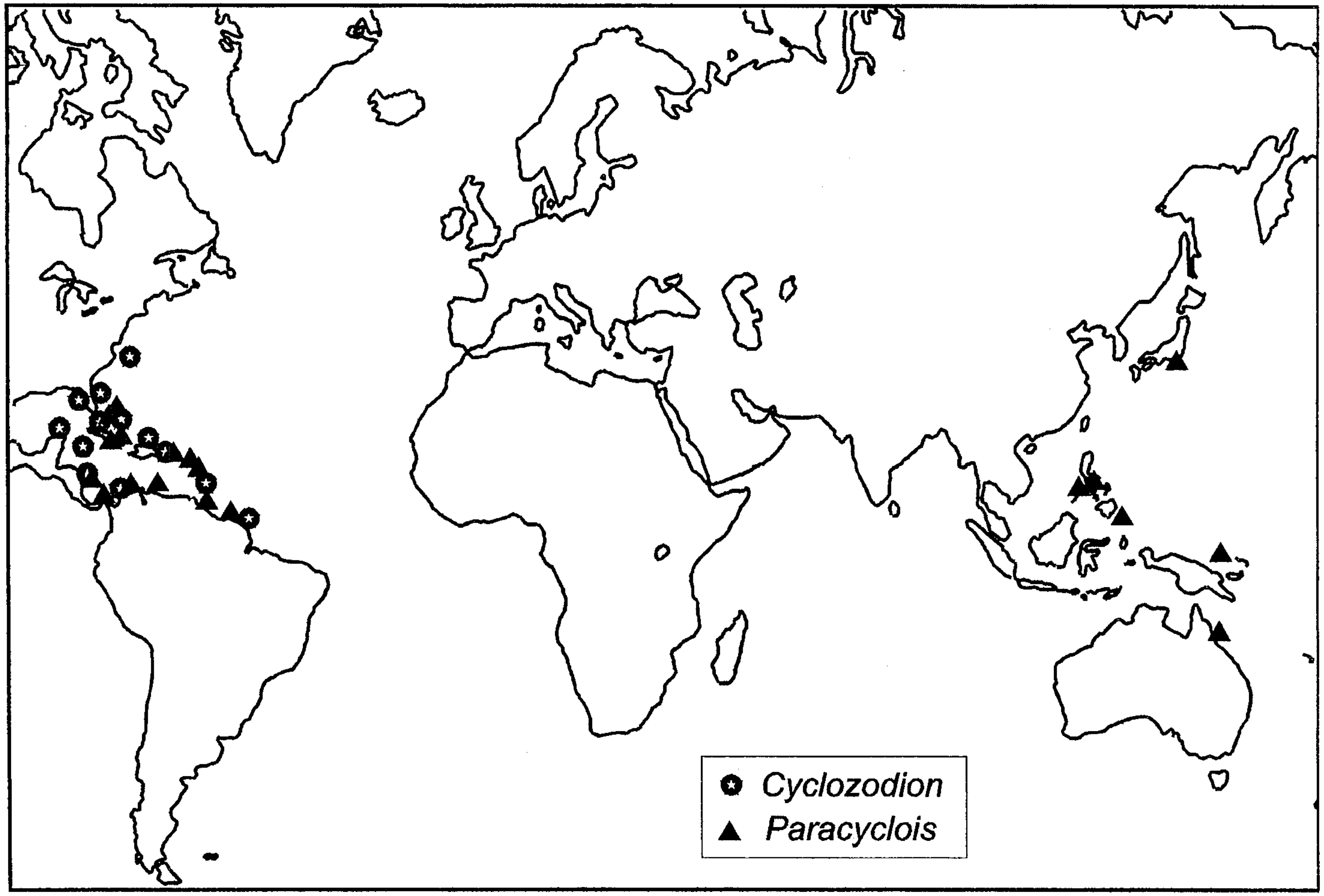


Fig. 3.4 Distribution records of *Paracyclois* and *Cyclozodion*.

Cycloes and *Acanthocarpus-Mursia/Platymera* respectively). Given the age of the lineages it appears that the most parsimonious explanation for observed patterns is related to the breakup of Gondwana, with the isolation of *Acanthocarpus* in the North Atlantic, possibly associated with the opening of the Atlantic 120-60 Ma ago.

3.5.4 Depth distributions

Although the Calappidae is often regarded as a shallow-water family a reappraisal of the depth distribution patterns of the Calappidae *sensu stricto* reveals an interesting pattern (Fig. 3.5). The Calappidae is basically a deep-water group. Of the 10 genera, only three had a significant proportion of specimens recorded in waters less than 50 m: *Calappa*, *Cycloes* and *Cryptosoma* (Fig. 3.5). The remaining genera were largely restricted to water between 100 and 300m deep. At these depths these taxa would be located on the continental shelf break (mean depth 130 m) and upper reaches of the continental slope (Gross, 1993). If depth is mapped onto the cladogram and then optimized (shallow = with 95% CI less than 70m; deep = with 95% CI greater than 100m), a distinctive pattern emerges (Fig. 3.6). It appears that the origin of the family was in deep water, probably on the upper continental slope. A shallow water distribution is restricted to a single albeit poorly defined clade (*Calappa*, *Cryptosoma* and *Cycloes*).

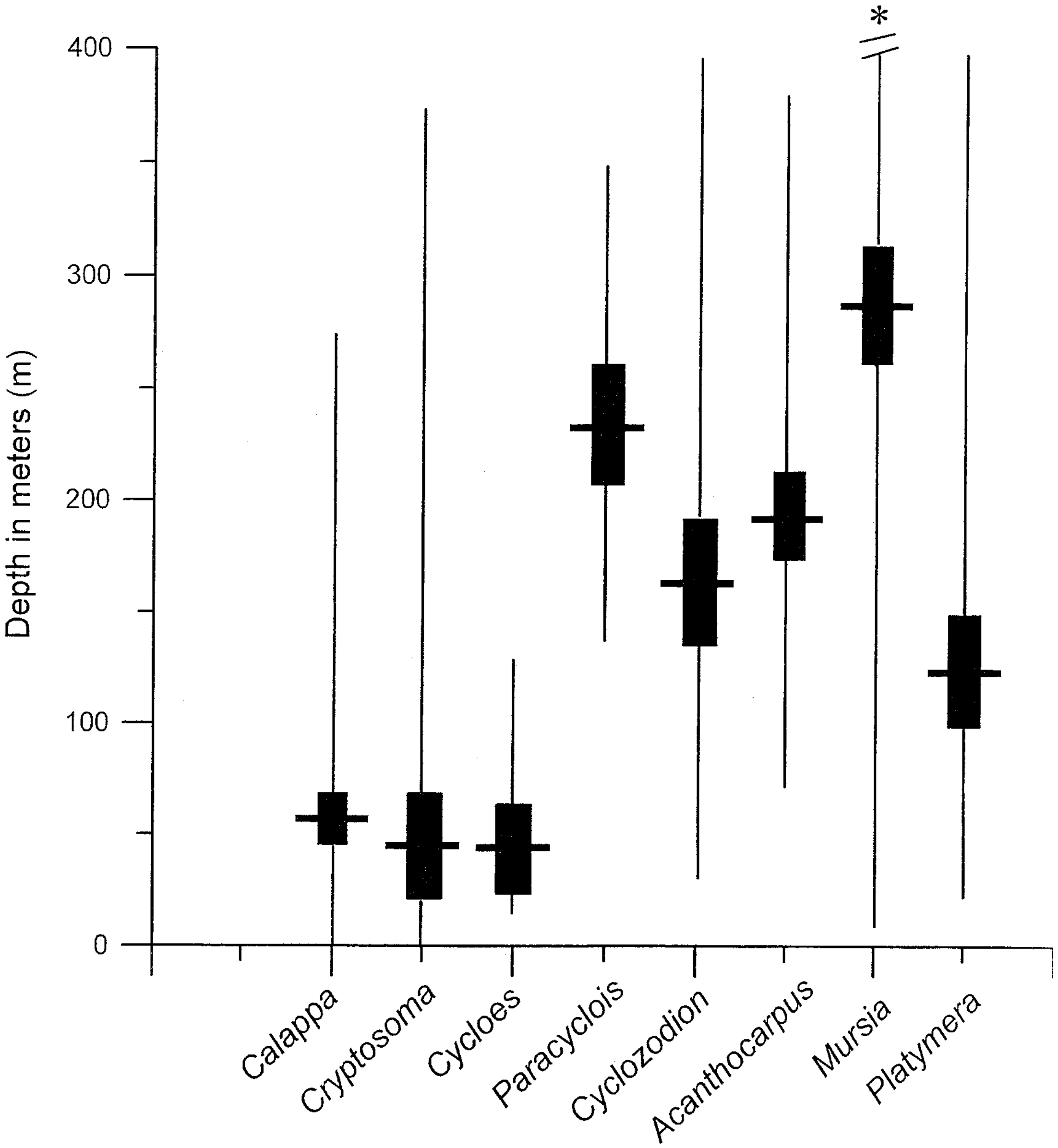


Figure 3.5 Depth distribution of calappid genera. Expressed as mean ± S.E. (black boxes). Thin lines connect minimum and maximum depths recorded. * = *Mursia*, maximum depth 1,252 m.

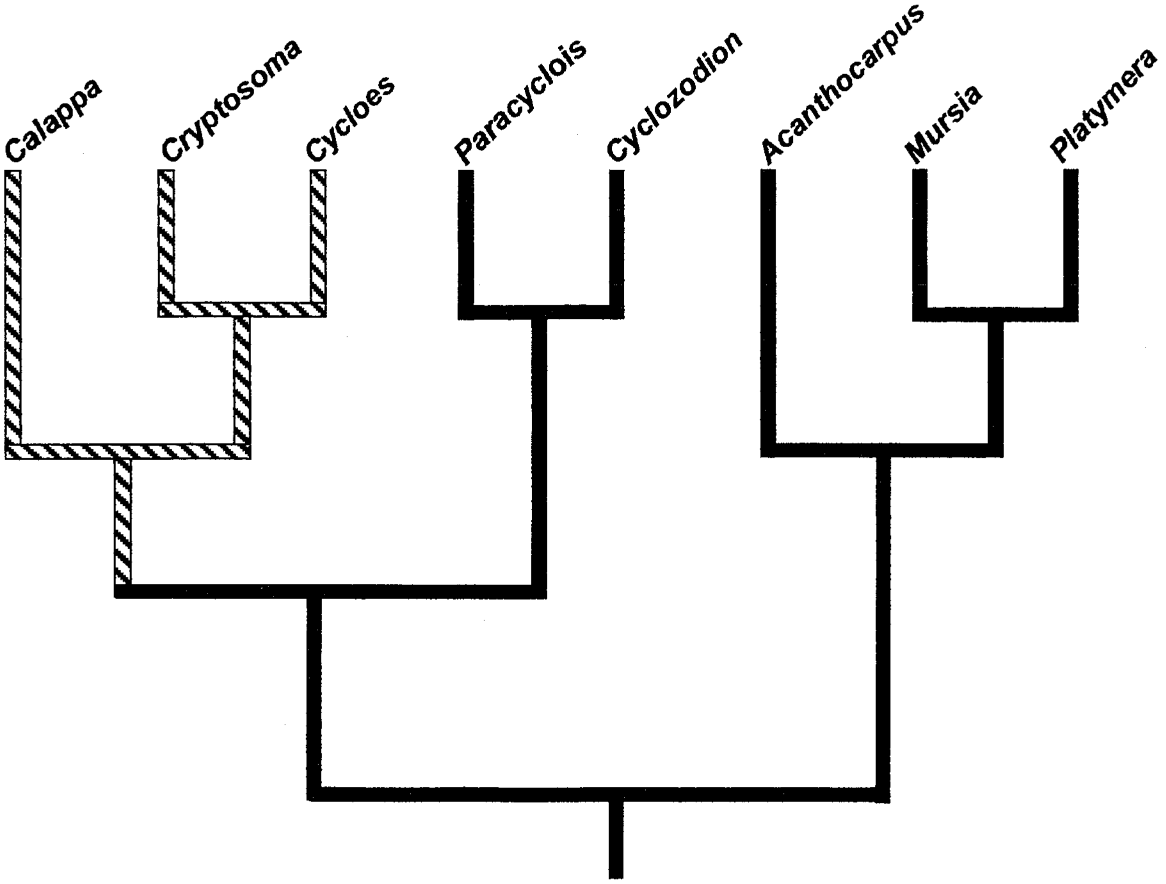


Figure 3.6 Cladogram of depth distribution within the Calappidae. Solid black = deep, 95% CI >100m; hatched = shallow, 95% CI, <70m.