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Phylogenetic analysis of the Brachyura (Crustacea, Decapoda) based on characters of the foregut with establishment of a new taxon

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Abstract

The Brachyura, within the decapod crustaceans, is one of the most species-rich taxa with up to 10 000 species. However, its phylogenetic history, evolution and fossil record remain subjects of controversy. In our study, we examined the phylogenetic relationships of the Brachyura based on morphological characters of the foregut. The cladistic analysis supports a monophyletic Brachyura including the Dromiidae and Raninidae. A clade comprising Dromiidae and Dynomenidae forms the most basal assemblage within the Brachyura, followed by the Homolidae and Latreilliidae. As a result, neither Podotremata nor Archaeobrachyura form a clade. In contrast, foregut data suggest that the classical taxon Oxystomata, comprising Calappidae, Parthenopidae, Dorippidae, Leucosiidae, Cymonomidae and Raninidae, is monophyletic. This makes the Heterotremata paraphyletic or polyphyletic. A newly established taxon, Neobrachyura, embraces some representatives of the Heterotremata and the monophyletic Thoracotremata.

Key words: Phylogeny – foregut ossicles – Podotremata – Heterotremata – Neobrachyura – Decapoda – Crustacea

Introduction

The taxon Brachyura, comprising up to 10 000 species (Martin and Davis 2001), is one of the most species-rich taxa within the Decapoda. Together with its sister group, the Anomala, the Brachyura form the monophyletic Meiura (Scholtz and Richter 1995).

The monophyly of the Brachyura and, in particular, the phylogenetic position of the 'Dromiacea', the so-called primitive crabs, has been contentious for more than a century (Tavares 2003). Based on adult morphological similarities, the taxon 'Dromiacea' was proposed to be within the Brachyura (Boas 1880; Borradaile 1907; Beurlen and Glaessner 1930; Bouvier 1940; Bals 1957; Glaessner 1969; Warner 1977; de Saint Laurent 1980a; Jamieson 1994; Jamieson et al. 1995; Scholtz and Richter 1995), a view which has been recently supported by molecular data (Ahyong and O'Meally 2004). However, the absence of some characteristic brachyuran characters led to question whether or not the representatives of the 'Dromiacea' are true crabs (Ortmann 1892, 1896; Gordon 1963; de Saint Laurent 1979). This idea was also discussed on the basis of larval morphological studies of several decapod crustaceans (Williamson 1974, 1988; Rice 1980, 1983; Martin 1991). Based on 18rDNA sequences, Spears et al. (1992) postulated that at least the Dromiidae should be excluded from the Brachyura and transferred into the Anomala. Investigations of the sperm ultrastructure show no clear evidence for an exclusion of the Dromiidae from the Brachyura (Jamieson 1990, 1991), and Scholtz and Richter (1995, p. 321) argued that 'the consequence of all these suggestions of either anomalan or thalassinid relationships would be that all brachyuran-like characters – some of them of high complexity – of dromiaceans, were the result of convergent evolution'. Based on apomorphic characters shared between dromiaceans and the true crabs, they support a monophyletic taxon Brachyura (Scholtz and Richter 1995).

An innovative idea was proposed by Guinot in her classification of the extant brachyuran taxa (1977, 1978, 1979). Based on the morphological characters of the gonopores and spermathecae, Guinot described three distinct sections of brachyuran crabs with a coxal position of the gonopores as a primitive condition (Podotremata) and a sternal position as derived (Heterotremata and Thoracotremata). Heterotremata and Thoracotremata share a female sexual opening on sternite six (Hartnoll 1968; Guinot 1977, 1979; Tavares and Secretan 1993) and the presence of a sella turcica (Audouin and Milne Edwards 1827; Milne Edwards 1851; Bourne 1922; Gordon 1963; Secretan 1998). Only in the Thoracotremata are the gonopores of both sexes found on the sternites. De Saint Laurent (1980a, b) united the Heterotremata and the Thoracotremata into the Eubrachyura.

This approach has been criticized on several occasions by claiming that Podotremata and Heterotremata are only defined by apparently plesiomorphic characters such as the coxal gonopores that cannot indicate monophyly (e.g. Scholtz and Richter 1995; von Sternberg and Cumberlidge 2001a, b; Dixon et al. 2003; Tavares 2003). However, a comprehensive cladistic analysis including representatives of all major brachyuran groups has not yet been undertaken.

To address the problem of brachyuran phylogenetic relationships, the character complex of the foregut ossicles have been chosen for use. The foreguts of malacostracans, in particular those of decapods, are highly complex structures exhibiting patterns of numerous distinct and definable elements such as characteristic ossicles, teeth and other elements with obvious phylogenetic information content. Accordingly, foregut characters have been used for several phylogenetic studies of Malacostraca and their subgroups (e.g. Wägele 1989; Kobusch 1999; Richter and Scholtz 2001; de Jong et al. 2004). The recent introduction of a new staining technique by us has led to an even higher resolution of foregut characters

and has created a promising basis for further comparative studies (Brösing et al. 2002).

Here, the first comprehensive morphological cladistic analysis of the Brachyura is provided. Our study of foregut characters in representatives of all major brachyuran taxa supports the monophyly of the Brachyura but disputes the validity of the Podotremata and Heterotremata concepts. In contrast, our data suggest the resurrection of the classical Oxystomata of Milne Edwards (1837).

Materials and Methods

Animals and characters

In this study, 66 brachyuran species arranged within 27 groups according to the classification of Martin and Davis (2001) were examined (Table 1). Additionally, two species from selected outgroup taxa were included for character polarization.

The analysis of such a species-rich taxon within the Decapoda required defining the criteria upon which terminal taxa should be selected. Depending on the practical consideration of obtaining specimens, several species of the same traditional taxon (i.e. family) according to Martin and Davis (2001) were examined as a starting point. This made it possible to test the monophyly of the taxon and the variability and stability of these foregut structures within the taxa. For the following cladistic analysis, the character polarization was carried out by rooting at the selected outgroup representatives of the Astacida and Anomala.

Methods

A numerical cladistic analysis was performed with the program NONA (Goloboff 1993) using Winclada (Nixon 1999–2000) as the shell program. Thirty-six binary and seven multistate characters of foregut morphology were analysed. All characters are described based on direct examination of specimens of 66 brachyuran and two outgroup species. The characters were treated as unordered and equally weighted. For the polarization of the characters, two species from selected outgroup taxa were involved. To test the results of the cladistic analysis, the bootstrap values (Felsenstein 1985) and the Bremer support (Bremer 1988) were calculated. The ossicles of the foregut were stained and treated for scanning electron microscopy according to the protocols published in Brösing et al. (2002).

Results

Ossicle nomenclature

According to the revised ossicle nomenclature (Brösing et al. 2002; Brösing 2002). We propose now 41 ossicles for the groundpattern of the Brachyura.

Characters

Characters used in the cladistic analysis are exclusively the aspects of the foregut morphology and as numbered here are independent from each other, with exception of the characters pairs [30, 31], [34, 35] and [39, 40].

- [1] Mesocardiac ossicle and pterocardiac ossicles clearly separated (0), partly/completely fused (1).
- [2] Prepterocardiac ossicle absent (0), present (1).
- [3] Postpterocardiac ossicles absent (0), present (1).
- [4] Lateral tip of pterocardiac ossicles as a single tip (0), ending in two processes (1).
- [5] Anterolateral process of pyloric ossicle as a straight, lateral boundary to the exopyloric ossicles (0), clearly surrounding the exopyloric ossicles (1), not touching the exopyloric ossicles (2).

- [6] Anterolateral process of pyloric ossicle straight and short (0), with a median directed hook (1).
- [7] Central notch of pyloric ossicle absent (0), present (1).
- [8] Anterolateral impression of the zygocardiac ossicles absent (0), present (1).
- [9] Crosswise lamella on lateral teeth of gastric mill absent (0), present (1).
- [10] Anteroventral hook on zygocardiac ossicles absent (0), present (1).
- [11] Dorsal margin of propyloric ossicle straight (in anterior–posterior direction) (0), bent (1).
- [12] Dorsal margin of propyloric ossicle rounded (in dorsal–ventral direction) (0), with a sharp middle piece (1), entire dorsal margin sharp (2).
- [13] Lateral process on ventrolateral margin of urocardiac ossicle absent (0), present (1).
- [14] Collar-like structure on dorsomedian gastric tooth present (0), absent (1).
- [15] Dorsomedian gastric tooth smooth and without crosswise ribs (0), with at least three crosswise ribs (1).
- [16] Ventral-lengthwise margin of urocardiac ossicle absent (0), present (1).
- [17] Pectinal ossicle irregularly formed (0), triangular (1), U-shaped (2), circular (3).
- [18] Accessory gastric teeth arranged irregularly (0), arranged in a row (1), arranged in a semicircle (2), as a single tooth (3).
- [19] Accessory gastric teeth short (0), clearly elongated (1).
- [20] More than one accessory gastric tooth (0), one single accessory tooth (1).
- [21] Ventromedian hook on prepectinal ossicle absent (0), present (1).
- [22] Crosswise middle piece on anteroventral part of prepectinal ossicle absent (0), present (1).
- [23] Quill of postpectinal ossicle absent (0), present (1).
- [24] Anteroventral part of the quill of postpectinal ossicle distal region not increased (0), areolarly increased (1).
- [25] Connection between inferior lateral cardiac ossicle and subdentate ossicle dorsal (0), dorsolateral (1), lateral (2).
- [26] Connecting piece between inferior lateral cardiac ossicle and subdentate ossicle absent (0), present (1).
- [27] Anteroventral overlapping at inferior lateral cardiac ossicle absent (0), present (1).
- [28] Anteromedian process at subdentate ossicle absent (0), present (1).
- [29] Anteroventral process at subdentate ossicle absent (0), present (1).
- [30] Posteroventral process at subdentate ossicle absent (0), present (1).
- [31] Posteroventral process at subdentate ossicle narrowed (0), areolarly increased (1).
- [32] Circular impression at the ventral part of subdentate ossicle absent (0), present (1).
- [33] Posterior part of the lateral ossicle of the cardiopyloric valve narrowed (0), distally enlarged (1).
- [34] Anterior mesopyloric ossicle present (0), absent (1).
- [35] Anterior mesopyloric ossicle unpaired (0), paired or tripartite (1).
- [36] Lateral mesopyloric ossicle present (0), absent (1).
- [37] Uropyloric ossicle areolar (0), wide crescentic area (1), narrow crescentic area (2), trapezoid (3).
- [38] Areolar, crescentic or trapezoid uropyloric ossicle without an additional area (0), with an additional area (1).

Table 1. Species list

Species/author	Family or Superfamily	Museum/Catalogue number
<i>Orconectes limosus</i> (Rafinesque, 1817)	Cambaridae Hobbs, 1942	Teaching collection, HU
<i>Lithodes maja</i> (Linnaeus, 1758)	Lithodidae Samouelle, 1819	ZMUC CRU-4417
<i>Paradynomene tuberculata</i> Sakai, 1963	Dynomenidae Ortmann, 1892	MP-B. 26608
<i>Dynomene praedator</i> A. Milne-Edwards, 1879	Dynomenidae Ortmann, 1892	MNHN-B. 6903
<i>Dynomene filholi</i> Bouvier, 1894	Dynomenidae Ortmann, 1892	p.c.
<i>Dromia wilsoni</i> Fulton and Grant, 1902	Dromiidae de Haan, 1833	MNHN-B. 26255
<i>Dromia spirostris</i> Miers, 1881	Dromiidae de Haan, 1833	p.c.
<i>Dromia personata</i> (Linnaeus, 1758)	Dromiidae de Haan, 1833	SMF 9685
<i>Lauridromia intermedia</i> Laurie, 1906	Dromiidae de Haan, 1833	MP-B. 26370
<i>Hypoconcha spinosissima</i> Rathbun, 1933	Dromiidae de Haan, 1833	FSBC I 48297 EJ67063
<i>Homola ranunculus</i> Guinot and Richter de Forges, 1995	Homolidae de Haan, 1839	MNHN-B. 19869
<i>Homola barbata</i> (Fabricius, 1793)	Homolidae de Haan, 1839	SMF 14939
<i>Paramola cuvieri</i> (Risso, 1816)	Homolidae de Haan, 1839	p.c.
<i>Dagnaudus petterdi</i> (Grant, 1905)	Homolidae de Haan, 1839	AMS P 53426
<i>Latreillia valida</i> de Haan, 1839	Latreilliidae de Haan, 1840	ZMB 27446
<i>Latreillia metanesa</i> Williams, 1982	Latreilliidae de Haan, 1840	ZMB 27447
<i>Hyas araneus</i> Linnaeus, 1758	Majoidea Samouelle, 1819	ZMUC CRU-4411
<i>Hyas coarctatus</i> Leach, 1815	Majoidea Samouelle, 1819	ZMUC CRU-4412
<i>Inachus dorsettensis</i> (Pennant, 1777)	Inachidae MacLeay, 1838	ZMUC CRU-4413
<i>Libinia dubia</i> H. Milne Edwards, 1834	Majoidea Samouelle, 1819	p.c. (Tarpon Bay, Florida)
<i>Calappa granulata</i> (Linnaeus, 1758)	Calappidae de Haan, 1833	SMF 6025
<i>Parthenope notialis</i> Manning and Holthuis, 1981	Parthenopidae MacLeay, 1838	ZMUC CRU-4409
<i>Dorippe sinica</i> Chen, 1980	Dorippidae MacLeay, 1838	SMF 15134
<i>Medorippe lanata</i> (Linnaeus, 1767)	Dorippidae MacLeay, 1838	ZMUC CRU-4405
<i>Cymonomus granulatus</i> (Thomson, 1873)	Cymonomidae Bouvier, 1898	p.c.
<i>Raninoides hendersoni</i> Chopra, 1933	Raninidae de Haan, 1839	MNHN-B. 13401
<i>Raninoides bouvieri</i> Capart, 1951	Raninidae de Haan, 1839	MNHN-B. 16176
<i>Raninoides personatus</i> Henderson, 1888	Raninidae de Haan, 1839	MP-B. 11558
<i>Lyreidus tridentatus</i> de Haan, 1841	Raninidae de Haan, 1839	MNHN-B. 13368
<i>Lyreidus brevifrons</i> Sakai, 1937	Raninidae de Haan, 1839	MP-B. 18959
<i>Lyreidus channeri</i> Wood-Mason, 1887	Raninidae de Haan, 1839	MP-B. 11562
<i>Notopoides latus</i> Henderson, 1888	Raninidae de Haan, 1839	MP-B. 18964
<i>Ranina ranina</i> (Linnaeus, 1758)	Raninidae de Haan, 1839	MNHN-B. 16183
<i>Ilia spinosa</i> Miers, 1881	Leucosiidae Samouelle, 1819	ZMUC CRU-4407
<i>Philyra variegata</i> (Fabricius, 1798)	Leucosiidae Samouelle, 1819	ZMUC CRU-4408
<i>Philyra laevis</i> (Bell, 1855)	Leucosiidae Samouelle, 1819	p.c. (Phillip Island, Australia)
<i>Leucosia anatum</i> Herbst, 1783	Leucosiidae Samouelle, 1819	p.c. (Phillip Island, Australia)
<i>Portunus pelagicus</i> (Linnaeus, 1758)	Portunidae Rafinesque, 1815	p.c.
<i>Portunus depurator</i> (Linnaeus, 1758)	Portunidae Rafinesque, 1815	ZMB 16417
<i>Carcinus maenas</i> Linnaeus, 1758	Portunidae Rafinesque, 1815	Teaching collection, HU
<i>Callinectes sapidus</i> Rathbun, 1896	Portunidae Rafinesque, 1815	p.c. (Tarpon Bay, FL, USA)
<i>Cancer pagurus</i> Linnaeus, 1758	Cancridae Latreille, 1802	p.c. (Roscoff, France)
<i>Carpilius convexus</i> (Forskål, 1775)	Carpiliidae Ortmann, 1893	MP-B. 7669
<i>Austinograea alayseae</i> Guinot, 1989	Bythograeidae Williams, 1980	MNHN-B.
<i>Segonzacia mesatlantica</i> (Williams, 1988)	Bythograeidae Williams, 1980	MNHN-B.
<i>Hexaplax</i> sp.	Hexapodidae Miers, 1886	p.c.
<i>Trapezia cymodoce</i> (Herbst, 1799)	Trapeziidae Miers, 1886	ZMUC CRU-4410
<i>Trapezia lutea</i> Castro, 1997	Trapeziidae Miers, 1886	ZMB 27450
<i>Tetralia fulva</i> Serene, 1984	Trapeziidae Miers, 1886	p.c.
<i>Leptodius sanguineus</i> H. Milne Edwards, 1834	Xanthidae Dana, 1851a	ZMB 15618
<i>Rhithropanopeus harrisi</i> Gould, 1841	Panopeidae Ortmann, 1893	p.c. (Tarpon Bay, Florida)
<i>Potamonautes lirrangensis</i> (Rathbun, 1904)	Potamonautidae Bott, 1970	ZMUC CRU-4406
<i>Pinnotheres villosulus</i> Guerin-Méneville, 1830	Pinnotheridae de Haan, 1833	AMS G 4226
<i>Retropluma quadrata</i> de Saint Laurent, 1989	Retroplumidae Gill, 1894	p.c.
<i>Pseudopalicus declivis</i> Castro, 2001	Palicideae Bouvier, 1898	p.c.
<i>Parapalicus clinodentatus</i> Castro, 2001	Palicideae Bouvier, 1898	ZMB 27449
<i>Micropalicus vietnamensis</i> (Zarenkov, 1968)	Palicideae Bouvier, 1898	ZMB 27448
<i>Crossotonotus compressipes</i> A. Milne Edwards, 1873	Palicideae Bouvier, 1898	p.c.
<i>Ocypode cursor</i> (Linnaeus, 1758)	Ocypodidae Rafinesque, 1815	MNHN-B.
<i>Ocypode gaudichaudi</i> Milne Edwards and Lucas, 1843	Ocypodidae Rafinesque, 1815	p.c.
<i>Uca tetragonum</i> (Herbst, 1790)	Ocypodidae Rafinesque, 1815	p.c.
<i>Minuca rapax</i> (Smith, 1870)	Ocypodidae Rafinesque, 1815	p.c.
<i>Mictyris longicarpus</i> Latreille, 1806	Mictyridae Dana, 1851b	ZMUC CRU-4415
<i>Mictyris platycheles</i> H. Milne Edwards, 1852	Mictyridae Dana, 1851b	ZMUC CRU-4416
<i>Cardisoma armatum</i> Herklots, 1851	Gecarcinidae MacLeay, 1838	p.c.

Table 1. (Continued.)

Species/author	Family or Superfamily	Museum/Catalogue number
<i>Cardisoma hirtipes</i> Dana, 1851b	Gecarcinidae MacLeay, 1838	ZMUC CRU-4414
<i>Eriocheir sinensis</i> H. Milne Edwards, 1854	Grapsidae MacLeay, 1838	Teaching collection, HU
<i>Pseudosarma moeschi</i> de Man, 1892	Grapsidae MacLeay, 1838	QM W 25869

MNHN, Muséum national d'Histoire naturelle, Paris; MP-B, Museum Paris – Brachyura; SMF, Senckenberg Museum, Frankfurt; FSBC, Florida Marine Research Institute, St. Petersburg, Florida; AMS, Australian Museum, Sydney; ZMUC, Zoological Museum, Copenhagen; ZMB, Zoologisches Museum, Berlin; QM, Queensland Museum, Brisbane; HU, Humboldt University, Berlin; p.c., private collection, A. Brösing.

[39] Anterior process of ampullary-roof-ossicles (upper portion) absent (0), present (1).

[40] Anterior process of ampullary-roof-ossicles (upper portion) vertically arranged (0), posteriorly disposed (1), anteriorly disposed (2).

[41] Anterior pleuropyloric ossicle extending to the subdentate ossicle (0), not extending to the subdentate ossicle (1).

[42] Lateral area of the anterior pleuropyloric ossicle absent (0), present (1).

[43] Anterodorsal area of the cardiopyloric valve absent (0), present (1).

The data matrix is presented in Appendix.

Cladistic analysis

In the analysis, 66 species of the Brachyura as well as two outgroup representatives were included. This analysis resulted in 207 most parsimonious trees with 121 steps. The consistency index was 0.43 and the retention index was 0.89. The strict consensus tree is given in Fig. 1.

One of the most parsimonious trees (Fig. 2) is shown with character state changes at the nodes.

A summary of the cladistic analysis is given in Fig. 3.

The Brachyura, including the Dromiidae and Raninidae, is supported by seven unique foregut characters as monophyletic 2(1), 17(1), 23(1), 29(1), 35(1), 37(1) and 39(1).

The Dromiidae and Dynomenidae together form the sister clade to all other brachyuran taxa. Furthermore, a closer relationship of the Homolidae and the Latreilliidae to the 'higher' brachyuran taxa is supported by the characters 14(1), 17(2), 24(1), 25(1).

The Majoidea represented by four species in our analysis is paraphyletic. A clade comprising *Hyas araneus*, *Hyas coarctatus* and *Libinia dubia* is monophyletic [supported by the single foregut character 10(1)]; but this clade is the sister clade to the remaining brachyuran crabs including *Inachus dorsettensis*, which is generally considered as belonging to the majoids.

Based on the occurrence of two unique apomorphic characters 12(2) and 25(2), we suggest a monophyletic taxon Oxystomata *sensu lato*, including the Parthenopidae and Cyonomidae. Within the Oxystomata, foregut characters support two monophyletic sister clades. First, for the Calappidae and Parthenopidae, a shared derived character in the subdentate ossicle 32(1) exists. Secondly, the clade, comprising Leucosidae, Dorippidae, Cyonomidae and Raninidae, possesses a single accessory tooth.

The sister clade to the Oxystomata includes taxa from the Heterotremata and Thoracotremata *sensu* Guinot (taxon E, Fig. 3). The whole of the included representatives of the 'Xanthoidea' and species of the Portunidae and Cancridae occur within this clade. *Rhithropanopeus harrisi* and *Leptodius*

sanguineus share a derived character in the cardiopyloric valve 43(1), an indication for a possible closer relationship of these two taxa. Furthermore, the Portunidae are supported as monophyletic based on a trapezoidal *uropyloric ossicle* 37(3).

A new taxon Neobrachyura is proposed for the entire Thoracotremata and some taxa of the Heterotremata (Potamonautidae, Retroplumidae, Pinnotheridae and Palicidae). These species are characterized by a medially directed hook on the *pyloric ossicle* 6(1). Within the Neobrachyura, taxa of the genera *Uca* and *Minuca* and the taxon Mictyridae (genus *Mictyris*) share two apomorphic characters 9(1) and 16(1).

Interestingly enough, the unresolved branches with identical character states correspond very well with the traditional brachyuran families, indicating for many of them that they are indeed monophyletic.

Discussion

Phylogenetic analysis

Monophyly of the Brachyura

The results of the presented study reaffirm the utility of the foregut characters for phylogenetic reconstructions (see also Wägele 1989; Kobusch 1999; Richter and Scholtz 2001). The analysed foregut characters strongly suggest a monophyletic origin of the Brachyura (Figs 1–3) including the Dromiidae and Raninidae (e.g. Borradaile 1907; Guinot 1977, 1978; Bowman and Abele 1982; Scholtz and Richter 1995; Martin and Davis 2001). In contrast to our results, Spears et al. (1992) postulated, in a molecular study, that the Dromiidae, represented by *Hypoconcha arcuata* and *Dromia antillensis*, should be excluded from the Brachyura and that *H. arcuata* appeared to be more related to the anomuran hermit crab *Clibanarius vittatus* than to the few included Brachyura. The herein examined species of *Dromia* and *Hypoconcha* show, to a large extent, a similar pattern in their foregut morphology, therefore rejecting the exclusion of *Hypoconcha* from the Brachyura. Furthermore, a recent molecular and total evidence analysis of reptant phylogeny by Ah Yong and O'Meally (2004) clearly supports brachyuran monophyly including dromiceans.

Neither the Podotremata nor the Archaeobrachyura are monophyletic

Based on the identical foregut character states, the families Dromiidae and Dynomenidae form a clade with unresolved internal relationships (Figs 1 and 2). Several hypotheses exist regarding the question of monophyly of these two taxa. Resulting from the investigations of the sperm ultrastructure and their combination with non-sperm morphological characters, neither the Dromiidae nor the Dynomenidae is supported as monophyletic (Jamieson 1994; Jamieson et al. 1995; Guinot et al. 1998). On the contrary, morphological (non-sperm)

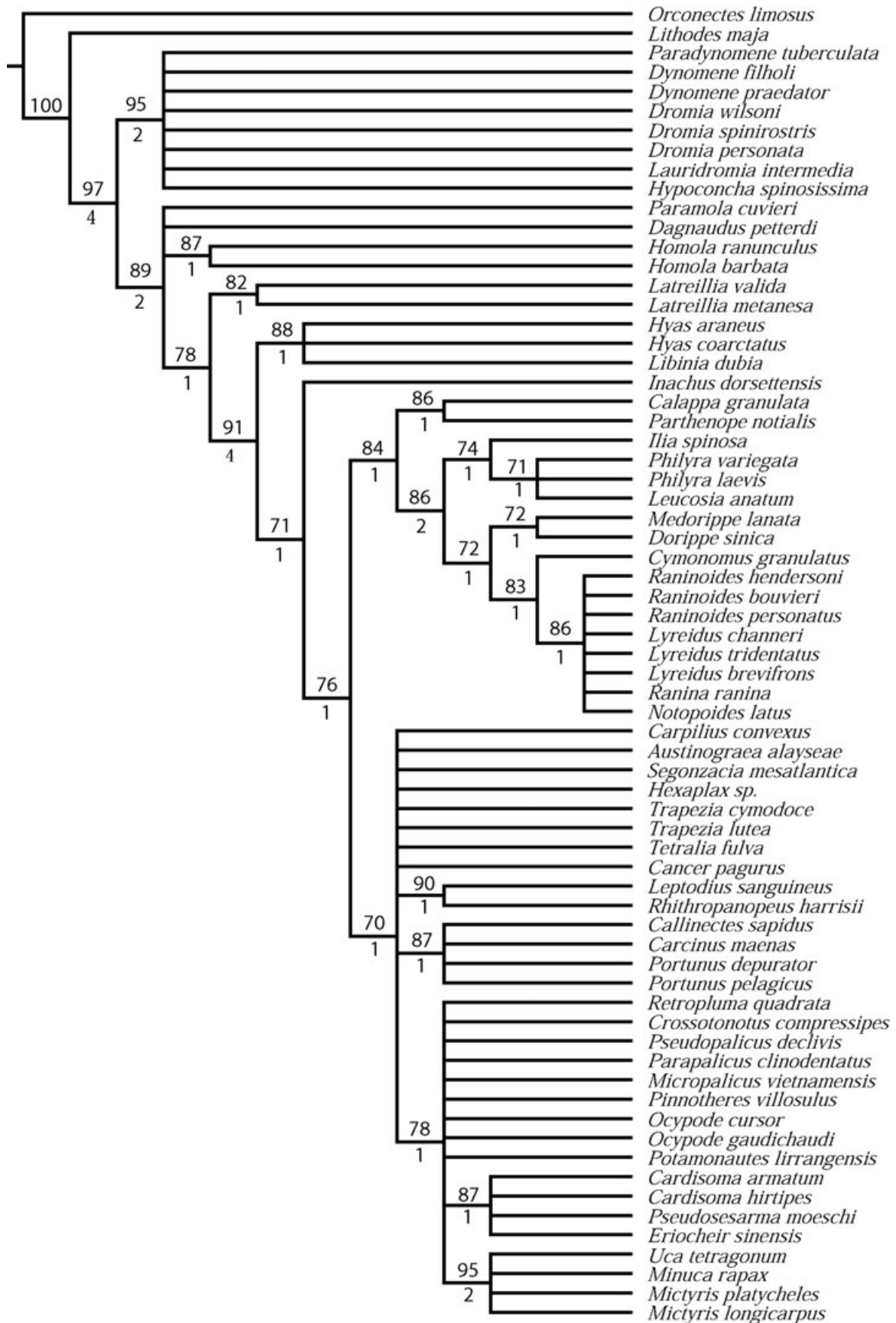


Fig. 1. Phylogenetic analysis of the Brachyura (66 taxa) and two outgroup representatives based on 43 foregut characters. Strict consensus tree of 207 calculated trees with 121 steps. Upper number = bootstrap values, lower number = Bremer support, CI = 0.43; RI = 0.89; used program: NONA (Goloboff 1993)

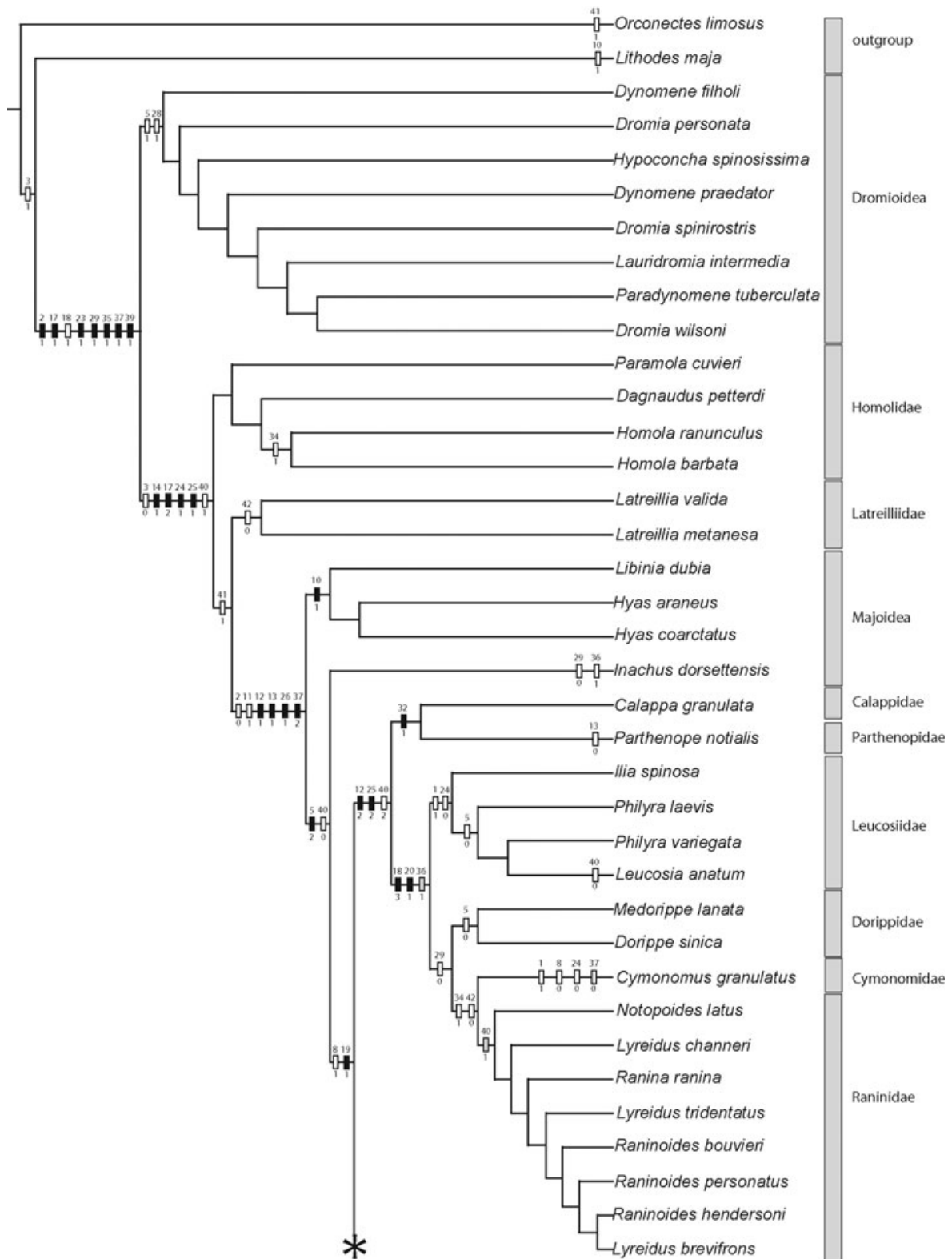


Fig. 2 Phylogenetic analysis of the Brachyura (66 taxa) and two outgroups based on 43 foregut characters, one selected tree of 207 calculated trees with characters, black boxes = unique apomorphies, open boxes = homoplastic apomorphies, upper number = number of character, lower number = character state

characters indicate a possible monophyly of both taxa (cf. McLay 1993,1999; Jamieson et al. 1995; McLay et al. 2001). The position of the clade (Dromiidae + Dynomenidae) as the sister taxon to the remaining brachyuran crabs (taxon A, Fig. 3) contradicts a monophyletic Podotremata (Guinot 1977).

According to Guinot (1977, 1978, 1979) "Podotremata" comprise two large groups, the Dromiacea (including the Dynomenidae, Dromiidae and Homolodromiidae) and the Archaeobrachyura (comprising the Homolidae, Latreilliidae, Raninidae and Cyclodorippoidea) (Guinot 1977,1978,1979).

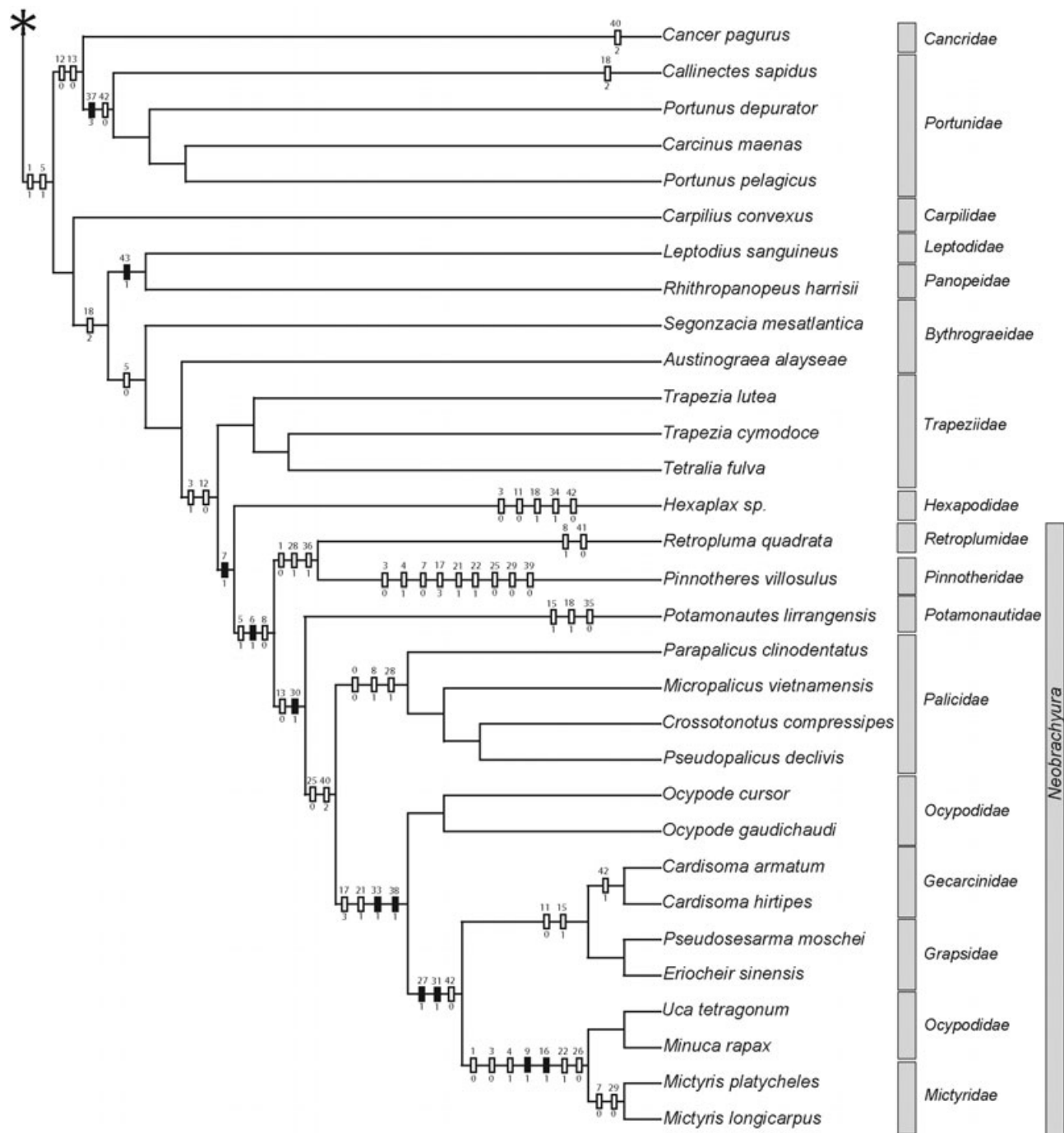


Fig. 2. (Continued.)

As a result of the lack of specimens of the Homolodromiidae, the question of a monophyletic origin of the Dromioidea (Guinot 1977, 1978, 1979), based on foregut characters, remains unresolved.

In order to put the Homolidae in a systematic context, the coxal position of the gonopores in both sexes, morphological characters of the thoracic sternum and the absence of uropods suggest placement of the Homolidae within the Archaeobrachyura (Guinot and Bouchard 1998; Guinot and Tavares 2001, 2003). Based on the foregut morphology, however, the Homolidae is proposed to be the sister clade to the remaining brachyuran crabs (taxon B, Fig. 3) whereas the Latrillidae are

the sister group of taxon C in Fig. 3. Based upon this result, and the divergent placement of the Raninidae, a monophyletic Archaeobrachyura is not supported.

The analysed foregut structures of the majoid crabs *H. araneus*, *H. coarctatus*, *I. dorsettensis* and *L. dubia* reveal a most basal position of these taxa within the 'higher' crabs. This is also suggested by sperm data (Jamieson et al. 1995). In our study, a monophyletic origin of the Majoidea is not supported. Further investigations of the foregut morphology including a broader taxon sampling of the more than 800 extant species of Majoidea (Manning and Holthuis 1981) might alter this result and might support monophyly of this group. Investigations of

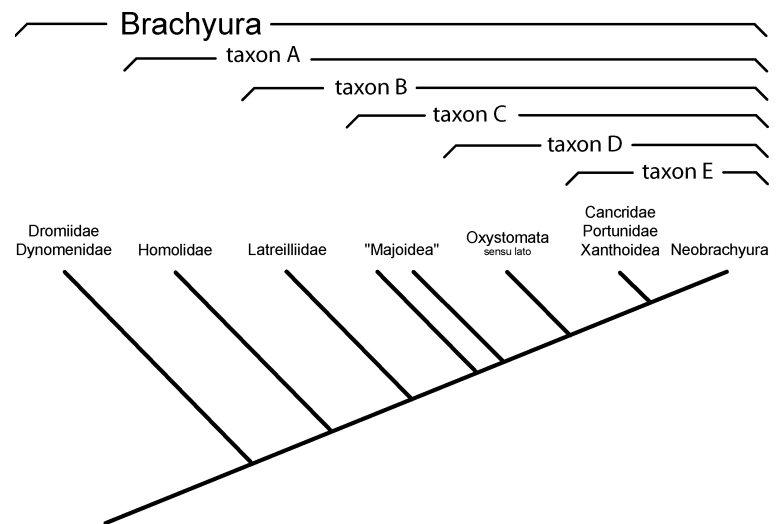


Fig. 3. Summary hypothesis of the phylogeny of the Brachyura based on foregut characters

larval characters do indeed suggest the monophyly of this taxon (Rice 1980).

Heterotremata and the Eubrachyura are not monophyletic and the resurrection of the Oxystomata

Based on the morphology of the endostome and the first maxillipeds, Milne Edwards (1837) proposed the taxon Oxystomata for the Calappidae, Leucosiidae and Dorippidae. In 1841, de Haan added the Raninidae to the Oxystomata. This concept of classification was accepted by many authors for a long time (Dana 1852; Miers 1886; Ortmann 1896). Our results resurrecting the Oxystomata, including the Parthenopidae and Cymonomidae, raise some questions concerning character evolution and contradict some other classifications.

A consequence of our results would be the reverse evolution of the gonopores towards a coxal position in raninids and cymonomids or a convergence of the sternal position of the female gonopores between Calappidae, Leucosiidae, Parthenopidae and Dorippidae within the Oxystomata and the other heterotrematan and thoracotrematan crabs. The Cymonomidae, deep-sea forms of small body size, is arranged after Ortmann (1892) together with the Cyclodorippidae and the Phyllostomolidae in the superfamily Cyclodorippoidea. According to Guinot (1978), they are a part of the Archaeobrachyura together with the Homoloidea and the Raninoidea. Morphological studies of the abdominal retaining structures of representatives of the Cymonomidae (Guinot and Bouchard 1998) show, however, clear differences in the structure of the sternum compared with all other podotrematan crabs. A phylogenetic analysis of sperm and other morphological characters also suggest a closer relationship of the Cymonomidae to the Raninidae (Jamieson 1994), a result which is supported by our studies.

The discussion regarding the phylogenetic position of the Raninidae dates back to the nineteenth century. In 1801, de Lamarck described a new genus *Ranina* and assigned it to the Macrura. A few years later, this genus was placed by Latreille (1806) in the Oxyrhyncha. After that, Milne Edwards (1837) favoured a position of the Raninidae within the Anomura, whereas de Haan (1833–1850) put this taxon in the Oxystomata. After a revision of the Decapoda, Ortmann (1892) suggested a closer relationship of the Raninidae to the Leucosiidae within the Oxystomata, which was confirmed by

Alcock (1896). Apart from further regroupings (see Gordon 1963; Stevcic 1973), this classification was accepted up to the revision of the Brachyura by Guinot (1977, 1978). On the contrary, Williamson (1974) and Rice (1980) described a number of shared derived larval characters of the Raninidae and the 'higher' crabs. In their molecular study of the phylogeny of the Brachyura, Spears et al. (1992) confirmed a closer relationship of the Raninidae to the 'higher' crabs; however, no further representatives of the 'Archeobrachyura' (Guinot 1977, 1978) were included in their study.

The position of the Raninidae and of the Cymonomidae within the Oxystomata argues against a monophyletic Heterotremata and accordingly the taxon Eubrachyura (=Heterotremata + Thoracotremata) (de Saint Laurent 1980) finds no support either.

Neobrachyura and the putative sister group of the monophyletic Thoracotremata

All Thoracotremata and some representatives of the Heterotremata are herein combined within a newly established taxon Neobrachyura. This, again, contradicts the concept of monophyletic heterotreme crabs (see above). In contrast, the Thoracotremata are unambiguously shown as monophyletic in our study (Fig. 2).

One question is the relatedness of the Retroplumidae, Palicidae and Potamonautidae to the Thoracotremata. The Retroplumidae is one of the smallest taxa within the Brachyura. It contains two extant genera with altogether nine described species and three fossil genera (de Saint Laurent 1989). In 1899, Alcock assigned this family to the Catometopa. Based on morphological similarities, Balss (1957) postulated a closer relationship to the Palicidae. A later classification of this family into the taxon Dorippoidea (Guinot 1978) was rejected by de Saint Laurent (1989) and she placed the Retroplumidae into the superfamily Retroplumoidea within the Heterotremata, but without any close connection to another brachyuran taxon. The above-proposed classification of the Retroplumidae in a monophyletic taxon Neobrachyura, together with the Palicidae and the Pinnotheridae, is supported by a further non-foregut character. In these taxa, a remarkably smaller fifth pair of pereopod is to be found. The structure of these reduced pereopod is unlike the often smaller pereopod within some species of the Xanthoidea or the Dromiidae.

The phylogeny of the Palicidae has been discussed just as controversially. Guinot (1978) described in detail the strange characters of this family, including the sternal position of the gonopores of the males and later came to the opinion that it was a representative of the advanced heterotreme crabs (Guinot and Bouchard 1998). In an extensive revision of the Palicidae, the sternal position of the male genital pores was confirmed (Castro 2001). Two molecular studies of 16S mtDNA sequences (Schubart et al. 2000a,b) supported a closer relationship of the Palicidae to the Thoracotremata, which in that study consisted of Mictyridae, Ocypodidae, Pinnotheridae, Grapsidae and Gecarcinidae.

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Zusammenfassung

Phylogenetische Analyse der Brachyura auf der Grundlage von Vorderdarmstrukturen mit der Etablierung eines neuen Taxons

Das Taxon Brachyura stellt innerhalb der decapoden Krebse eines der artenreichsten Taxa mit bis zu 10000 Arten dar. Seine Stammesgeschichte, Evolution und Fossilbericht ist Thema vieler Diskussionen. In unserer Studie wurden die phylogenetischen Verwandtschaftsbeziehungen der Brachyura auf der Grundlage morphologischer Merkmale des Vorderdarmes untersucht. Die kladistische Analyse unterstützt ein monophyletisches Taxon Brachyura, einschließlich der Taxa Dromiidae und Raninidae. Ein Taxon, welches die Taxa Dromiidae und Dynomenidae enthält, stellt die basalste Gruppierung innerhalb der Brachyura dar, gefolgt von den Taxa Homolidae und Latreillidae. Weder das Taxon 'Podotremata' noch ein Taxon 'Archaeobrachyura' stellen eine natürliche Einheit im Sinne eines Monophylums dar. Die Merkmale der Vorderdarmstrukturen deuten weiterhin darauf hin, dass das klassische Taxon Oxystomata mit den Taxa Calappidae, Parthenopidae, Dorippidae, Leucosiidae, Cymonomidae und Raninidae ein Monophylum darstellt. Dies hat ein para- oder polyphyletisches Taxon Heterotremata zur Folge. Ein in dieser Studie neu etabliertes Taxon Neobrachyura vereint sowohl Vertreter der ursprünglichen Heterotremata als auch der Thoracotremata.

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