

CRUSTACEAN ISSUES 18



Decapod Crustacean Phylogenetics

edited by

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CRC Press
Taylor & Francis Group

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CRC Press

Taylor & Francis Group

Boca Raton London New York

CRC Press is an imprint of the
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CRC Press
Taylor & Francis Group
6000 Broken Sound Parkway NW, Suite 300
Boca Raton, FL 33487-2742

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Printed in the United States of America on acid-free paper
10 9 8 7 6 5 4 3 2 1

International Standard Book Number-13: 978-1-4200-9258-5 (Hardcover)

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Library of Congress Cataloging-in-Publication Data

Decapod crustacean phylogenetics / editors, Joel W. Martin, Keith A. Crandall, Darryl L. Felder.
p. cm. -- (Crustacean issues)

Includes bibliographical references and index.

ISBN 978-1-4200-9258-5 (hardcover : alk. paper)

1. Decapoda (Crustacea) 2. Phylogeny. I. Martin, Joel W. II. Crandall, Keith A. III. Felder, Darryl L.
IV. Title. V. Series.

QL444.M33D44 2009

595.3'8138--dc22

2009001091

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<http://www.crcpress.com>

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Phylogeny and Biogeography of Asian Freshwater Crabs of the Family Gecarcinucidae (Brachyura: Potamoidea)

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ABSTRACT

The phylogeny of the Asian freshwater crabs of the family Gecarcinucidae is investigated using the mitochondrial large subunit rRNA gene and the nuclear encoded histone 3 gene. The results confirm the monophyly of the Gecarcinucidae. A division into two families, Gecarcinucidae and Parathelphusidae, is not supported. Therefore, and in consideration of the unresolved family relationships, all Old World freshwater crabs are assigned to one superfamily, the Potamoidea. The evolution of structures of the second gonopod within the Gecarcinucidae is shown to involve convergent reduction of a complex-type groove to a simple-type groove or its complete absence. Gecarcinucids without a frontal triangle are shown to form a paraphyletic group. Thus, these morphological characters are of minor importance for clarifying phylogenetic relationships within the Gecarcinucidae. Genetically, the Gecarcinucidae can be differentiated and separated into seven monophyletic lineages and an assemblage of as yet unresolved Indian groups. We identify the Malay Peninsula and Borneo (particularly Sabah and Sarawak), where representatives of four of these lineages occur, as a hotspot of gecarcinucid diversity. In agreement with our phylogenetic results, an early radiation of the Gecarcinucidae on the Indian subcontinent is postulated along with several dispersal events from Sundaland into the Malesian (Malaysian) Archipelago.

1 INTRODUCTION

The Southeast Asian biota has been a constant focus of biogeography since the 19th century (e.g., Wallace 1869; Hall 2003). This interest is mainly because the region's biodiversity hotspots (Myers et al. 2000) coincide with a complex geography and geological history (Hall and Holloway 1998; Morley 2000). The phylogeny of the freshwater crab family Gecarcinucidae (*sensu* Klaus et al. 2006) appears to be well suited to reflect both the geography and history of Southeast Asia. In general, freshwater crabs are believed to have limited dispersal capabilities (Ng & Rodríguez 1995), and crabs within hydrographic drainage systems can be expected to be more closely related. This is of particular interest within Sundaland, consisting of the Malay Peninsula and the Greater Sunda Islands (Borneo, Sumatra, and Java), as these land masses, now separated by the sea, were connected by palaeoriver systems in times of lower sea level (Voris 2000).

The range of the Gecarcinucidae (*sensu* Klaus et al. 2006) covers both the Australian and Oriental zoogeographic regions, and it is the only freshwater crab family that crosses Wallace's Line.

With currently 345 described species in 57 genera, gecarcinucids make up about 35% of the total species diversity and 46% of the genus diversity of the Old World freshwater crabs (Ng et al. 2008). Important local species radiations, based on molecular markers, have been described for Sri Lanka (Bossuyt et al. 2004), Sulawesi (Schubart and Ng 2008), and Taiwan (Shih et al. 2007). Nevertheless, no phylogenetic analysis of the whole family has been conducted until now. Recent molecular phylogenies that included gecarcinucid species primarily addressed family and superfamily relationships with only a limited number of gecarcinucid representatives (Bossuyt et al. 2004: 40 specimens, 20 species, 10 genera; Daniels et al. 2006: 18 species, 10 genera; Klaus et al. 2006: 25 species, 19 genera). All previous systematic approaches to the Gecarcinucidae were based primarily on morphology, focusing on the mandibular palp (Alcock 1910), the frontal triangle (Bott 1970b), or second gonopod characters (Klaus et al. 2006).

Our aim is to identify major evolutionary lineages within the Gecarcinucidae. Our study includes 76 gecarcinucid species of 40 genera. These genera cover 70% of the gecarcinucid genus-level diversity and 85% of the known species. Several genera, especially among the Indian fauna (see Bahir and Yeo 2007), are not included. Nevertheless, the present data allow conclusions to be drawn on the historical biogeography of the Gecarcinucidae and provide a phylogenetic framework that sets the context for future locality or genus-based revisions. This study also contributes to a better understanding of the evolution of morphological characters previously used for taxonomic assignments.

2 HISTORICAL SYSTEMATIC APPROACHES TO THE GECARCINUCIDAE

Rathbun (1904) divided the Asian freshwater crabs (which were all included in the family Potamidae Ortmann, 1896) into two subfamilies: the Potaminae, containing most of the Asian freshwater crab fauna, and the monotypic Gecarcinucinae for the genus *Gecarcinucus*. This system was fundamentally altered by Alcock (1910). He assigned all Asian species with a bilobed terminal segment of the mandibular palp to the Gecarcinucinae, and retained species with a simple terminal segment within the Potaminae. Within this redefined Gecarcinucinae, Alcock (1910) recognized two genera: *Parathelphusa* and *Gecarcinucus*. Possibly because he doubted the validity of the genus *Gecarcinucus*, he introduced the name Parathelphusinae as a synonym for the Gecarcinucinae but kept the latter name throughout his work. Influenced by these ideas, Colosi (1920) established within the Gecarcinucinae the tribes Parathelphusini Alcock, 1910, and Hydrothelphusini Colosi, 1920, the latter to include the Madagascan genus *Hydrothelphusa* with a bilobed mandibular palp.

A major change to this taxonomy by Bott (1969, 1970a, 1970b) recognized a superfamily Parathelphusoidea Alcock, 1910 (later corrected to Gecarcinucoidea Rathbun, 1904, by Holthuis 1979), which included Alcock's Gecarcinucinae and several African genera with a bilobed mandibular palp. The Gecarcinucinae *sensu* Alcock (1910) was split into three families, applying diagnostic characters of the frontal triangle: the Gecarcinucidae Rathbun, 1904, with the subfamilies Gecarcinucinae Rathbun, 1904, and Liotelphusinae Bott, 1969; the Parathelphusidae Alcock, 1910, with the subfamilies Spiralothelphusinae Bott, 1968, the monogeneric Ceylonthelphusinae Bott, 1969, and the East- and Southeast Asian Somaniathelphusinae Bott, 1968; and as the third family the Sundathelphusidae Bott, 1969, from the Sunda islands, the Philippines, New Guinea, and Australia. The latter was not further divided into subfamilies. Bott recognized within the Gecarcinucoidea 31 genera with 98 species (115 including subspecies). Later, the Sundathelphusidae were synonymized with the Parathelphusidae (Ng and Sket 1996).

This system was adopted by Martin & Davis (2001) with the reservation that the African species should possibly be excluded from the Gecarcinucoidea. However, Bott's system of subfamilies was not generally adopted by other researchers, and there have been doubts about their validity (see Ng & Tay 2001; Ng 2004; Bahir & Yeo 2007). The distinction of the Gecarcinucidae and Parathelphusidae has been questioned by several workers (e.g., Holthuis 1979; Ng 1988, 2004; Yeo & Ng 1999; Daniels et al. 2006), but Klaus et al. (2006) formally recognized only one family of

gecarcinuoid freshwater crabs in Asia, the Gecarcinucidae, on the basis of gonopod morphology and mtDNA phylogeny. All African members of the Gecarcinucidae were assigned to the Deckeniidae (the Deckeniinae within the Potamonautidae according to Cumberlidge et al. 2008). The Gecarcinucidae was divided into two subfamilies based on the morphology of the second gonopod (Klaus et al. 2006): the Indian-Sri Lankan Gecarcinucinae and the Parathelphusinae with their main distribution in East- and Southeast Asia. Cumberlidge et al. (2008), Ng et al. (2008), and Yeo et al. (2008), however, provisionally recognized both Gecarcinucidae and Parathelphusidae as separate families, although, like Klaus et al. (2006), they excluded all African freshwater crabs from the Gecarcinucidae.

3 MATERIALS AND METHODS

3.1 Molecular analysis

Samples for this study were obtained from different museum holdings, aquarists, and collections by the authors between 1999 and 2006 (Table 1). Some of the museum specimens, which include type material, were more than 100 years old and made amplification of longer DNA sequences impossible. Genomic DNA was extracted from the muscle tissue of walking legs using the Puregene kit (Gentra Systems). Selective amplification of an approximately 560 basepair (bp) fragment, excluding primers, from the mitochondrial large ribosomal subunit (16S rRNA) and of a 320-bp fragment of the nuclear histone 3 gene (H3) was carried out by polymerase chain reaction (PCR) under the following conditions: 40 cycles, with 45 sec denaturing at 94°C, 1 min annealing at 48°C, and 1 min extension at 72°C (with 4 min initial denaturation and 10 min final extension time). Especially for the H3 gene amplification, touchdown PCRs were performed to prevent unspecific binding of primers; denaturation and elongation times as well as the corresponding temperatures were identical to the previous PCR profile, but the annealing temperature in the first eight cycles was decreased from 52°C to 48°C (steps of 0.5°C), followed by 40 cycles with an annealing temperature of 48°C. Primers used were 16L29 (5'-YGCCTGTTT-ATCAAAAACAT-3', Schubart, this volume) and 16H37 (5'-CCGGTYTGAAC TCAAATCATGT-3', Klaus et al. 2006) or 16H12 (5'-CTGTTATCCCTAAAGTAACTT-3', Schubart, this volume) for the 16S and H3AF (5'-ATGGCTCGTACCAAGCAGACVGC-3') in combination with H3AR (5'-ATATCCTTRGGCATRATRG TGAC-3', both Colgan et al. 1998) or the H3H2 (5'-GGCATRATGGTGACRCGCTT-3') for the H3. PCR products were purified with the Sure Clean Kit (Bioline) and sequenced with the ABI BigDye terminator mix in an ABI Prism 310 Genetic Analyzer (Applied Biosystems, Foster City, USA). In addition to the sequences generated in this study, our phylogenetic analyses include previously published sequences corresponding to the same 16S and H3 gene regions from GenBank, originating from the studies of Bossuyt et al. (2004), Daniels et al. (2006), Klaus et al. (2006), and Shih et al. (2007).

Sequences were aligned manually with the software BioEdit 7.0.9.0 (Hall 1999) with alignment lengths of 557 bp for 16S RNA and 318 bp for H3. A partition homogeneity test as implemented in PAUP 4.0b was performed (100 replicates). As expected, this test showed significant differences between the genes, as the H3 sequences are much more conserved than the 16S rRNA gene. Thus within the phylogenetic analysis each gene supports different splits at different points in time. The data sets for both genes were combined in one alignment. *Epilobocera sinuatifrons* (Pseudothelphusidae) was designated as the outgroup taxon.

Bayesian analysis (MrBayes 3.1.2, Huelsenbeck and Ronquist 2001) was run with four MCMC chains for 20 million generations, until the average standard deviation of split frequencies decreased to 0.00248. A tree was saved every 1000 generations (with a corresponding output of 20,000 trees). Prior settings as suggested by MODELTEST 3.7 (Posada and Crandall 1998) following the Akaike information criterion were applied (the HKY+I+G model for the H3 and the TrN+I+G model for the 16S partition). The first 1,000,000 generations, i.e., 1000 trees ("burn-in phase"), were excluded

Table 1. Freshwater crab species used for DNA-sequencing and subsequent phylogeny reconstruction, including taxonomic authority, museum catalogue number, locality of collection, and genetic database (EMBL) accession numbers for the H3 and 16S sequences.

Species	Cat. No.	Provenience	H3	16S rRNA
<i>Epilobocera sinuatifrons</i> (A. Milne Edwards, 1866)	R 199	Puerto Rico, Guajataca	FM 178885	AJ 130810
<i>Johora singaporensis</i> Ng, 1986	SMF 32717	Singapore, Bukit Batok	FM 178886	FM 180114
<i>Malayopotamon aff. brevimarginatum</i> (De Man, 1892)	SMF 32718	S-Sumatra, Danau Ranau, Gng Raya	FM 178887	FM 180115
<i>Potamon persicum</i> Pretzmann, 1962	ZUTC	Zagros mountains, Iran	FM 178888	FM 180116
<i>Stoliczia bella</i> Ng & Ng, 1987	SMF 32719	Malaysia, Pulau Langkawi	FM 178889	FM 180117
<i>Deckenia mitis</i> Hilgendorf, 1898	SAEM	Tanzania, Mwangombe near Tanga, site 23	FM 178890	FM 180118
<i>Hydroithelphusa madagascariensis</i> (A. Milne Edwards, 1872)	SAEM	Madagascar, Ambolitsara; M. Vences coll.	FM 178891	FM 180119
<i>Madagapotamon humberti</i> Bott, 1965	MNH B 25562	Madagascar	FM 178892	AM 234641
<i>Platythelphusa armata</i> A. Milne Edwards, 1887	SAEM	Tanzania, Lake Tanganyika, Kigoma Bay	FM 178893	FM 180120
<i>Seychellium alluaudi</i> (A. Milne Edwards & Bouvier, 1893)	SMF 30157	Seychelles, La Digue	FM 178894	AM 234653
<i>Arachnoithelphusa rhadamanthysi</i> Ng & Goh, 1987	ZRC 1990.443; type	Malaysia, Borneo, Sabah	FM 178895	FM 180121
<i>Austrothelphusa transversa</i> (Roux, 1911)	RMNH 31622	Papua New Guinea	FM 178896	FM 180122
<i>Austroithelphusa</i> sp.	ZMB	Australia, 16°3'S, 129°11'E	FM 178897	FM 180123
<i>Bakoua sarawakensis</i> Ng, 1995	ZRC 1995.235	Malaysia, Borneo, Sarawak	FM 178899	FM 180124
<i>Balssiatelphusa cursor</i> Ng, 1986	ZRC 1989.3036; type	Indonesia, Borneo, E-Kalimantan, Wanariset	FM 178900	FM 180126
<i>Balssiatelphusa natunaensis</i> Bott, 1970	RMNH 29300; holotype	Indonesia, Natuna Island	-	FM 180125
<i>Ceylonithelphusa kandambyi</i> Bahir, 1999	uncatalogued	Sri Lanka	FM 178901	FM 180127
<i>Currothelphusa asserpes</i> Ng, 1990	ZRC 1989.2156	Indonesia, Moluccas, Halmahera	FM 178902	FM 180128
<i>Cylindrotelphusa</i> sp.	SMF 2754	India, Malabar	FM 178903	AM 234635
<i>Gecarcinus jacquemonti</i> H. Milne Edwards, 1844	NHML 1895.11.8	India, Bombay, Kaman River	FM 178904	AM 234637
<i>Geelvinkia holthuisi</i> Bott, 1974	RMNH 29371; paratype	New Guinea, Tanah Merah	FM 178908	FM 180129

Table 1. continued.

Species	Cat. No.	Provenience	H3	16S rRNA
<i>Geithusa pulchra</i> Ng, 1989	SMF 32720	Malaysia, Pulau Redang	-	FM 180130
<i>Heterothelphusa fatum</i> Ng, 1997	SMF 32721	Singapore, aquarist	FM 178905	FM 180131
<i>Holthuisana biroi</i> (Nobili, 1905)	SMF 7373	New Guinea, Borowei, Lake Senkani	FM 178906	FM 180132
<i>Holthuisana festiva</i> (Roux, 1911)	SMF 4280	Papua New Guinea	FM 178907	FM 180133
<i>Imengardia johnsoni</i> Ng & Yang, 1985	SMF 30158	Singapore, Nee Soon swamp forest	FM 178908	AM 234640
<i>Lepidothelphusa cognetti</i> (Nobili, 1903)	ZRC	Malaysia, Borneo, Sarawak	FM 178909	FM 180134
<i>Liotelephusa gageii</i> (Alcock, 1909)	NHMB 1027 a	Bhutan, Kaeme	FM 178910	FM 180135
<i>Maydellithelphusa edentula</i> (Alcock, 1909)	NHMB 1028 a	Bhutan, Samchi	FM 178911	FM 180136
<i>Maydellithelphusa lugubris</i> (Wood-Mason, 1871)	NHMB 1025	Bhutan	FM 178912	FM 180137
<i>Niasathelphusa wirzi</i> (Roux, 1930)	ZRC 1990.447-448	Indonesia, Nias	FM 178913	FM 180138
<i>Oziothelphusa ceylonensis</i> (Fernando, 1960)	uncatalogued	Sri Lanka, aquarist	FM 178914	FM 180139
<i>Oziothelphusa</i> sp.	uncatalogued	South India, aquarist	FM 178915	FM 180140
<i>Parathelphusa convexa</i> (De Man, 1879)	RMNH 348; syntype	Indonesia, East Java, Besuki	FM 178916	FM 180141
<i>Parathelphusa maculata</i> De Man, 1879	ZRC 1989.2472-75	Malaysia, Pahang, Sg. Kinchin	FM 178917	FM 180142
<i>Parathelphusa oxygona</i> (Nobili, 1901)	ZRC 1998.547	Malaysia, Sarawak, Sg. Sham	FM 178918	FM 180143
<i>Parathelphusa pantherina</i> (Schenkel, 1902)	ZRC 2000.1705	Tomcu	FM 178919	FM 180144
<i>Parathelphusa sarawakensis</i> (Ng, 1986)	ZRC 1998.545	Indonesia, Sulawesi	FM 178920	FM 180145
<i>Perithelphusa borneensis</i> (von Martens, 1868)	RMNH 33955	Malaysia, Borneo, Sarawak, Kuchas	FM 178921	FM 180146
<i>Perithelphusa lehi</i> Ng, 1986	ZRC 1989.2770	Malaysia, Borneo, Sarawak, Gunung Jambusan	FM 178922	FM 180147
<i>Phricotilephusa amnicola</i> Ng, 1994	ZRC 1997.315	Malaysia, Kedah, Gunung Jerai	FM 178923	FM 180148
<i>Phricotilephusa gracilipes</i> Ng & Ng, 1987	SMF 32722	Malaysia, Pulau Langkawi	FM 178924	FM 180149
<i>Phricotilephusa hockpingi</i> Ng, 1986	ZRC 7318-7346	Malaysia, Taiping, Bukit Larut	FM 178925	FM 180150
<i>Phricotilephusa limula</i> (Hilgendorf, 1882)	ZRC 2000.1917	Thailand, Phuket, Ton Sai Falls	FM 178926	FM 180151
<i>Phricotilephusa sirindhorn</i> Naiyanetr, 1989	SMF 32726; paratype	Thailand, Ranong Prov., Amphoe Muang	FM 178927	FM 180152
<i>Salangathelphusa brevicarinata</i> (Hilgendorf, 1882)	SMF 32723	Malaysia, Pulau Langkawi	FM 178928	FM 180153

Table 1. continued.

Species	Cat. No.	Provenience	H3	16S rRNA
<i>Sartoriana blandfordi</i> (Alcock, 1909)	SMF 5524	Iran, Bam	FM 178929	FM 180154
<i>Sartoriana spinigera</i> (Wood-Mason, 1871)	SMF 9344	India, West Bengal	178930	FM 180155
<i>Sayamia sexpunctata</i> (Lanchester, 1906)	RMNH 38015	Malaysia, Pulau Langkawi	FM 178932	FM 180156
<i>Sandleria gloriosa</i> (Balss, 1923)	SMF 4350	New Britain, 35 km SE Cap Lambert	FM 178933	FM 180157
<i>Siamthelphusa improvvisa</i> (Lanchester, 1901)	SMF 32724	Malaysia, Pulau Langkawi	FM 178934	FM 180158
<i>Siamthelphusa</i> sp.	uncatalogued	Thailand, aquarist	FM 178935	FM 180159
<i>Snaha escheri</i> (Roux, 1931)	NHMB 803 a; paratype	India, Palnis, Vandaravu	-	FM 180160
<i>Sundathelphusa boe</i> Ng & Sket, 1996	ZRC 2000.2088	Philippines, Bohol, Anteguera	FM 178936	FM 180161
<i>Sundathelphusa cavernicola</i> Takeda, 1983	ZRC 2000.2080	Philippines, Bohol, Anteguera	FM 178937	FM 180162
<i>Sundathelphusa celer</i> (Ng, 1991)	RMNH 36577; type	Philippines, Luzon, Laguna de Bay	-	FM 180163
<i>Sundathelphusa hades</i> Takeda & Ng, 2001	ZRC 2001.1000; type	Philippines, Mindanao, Surigao del Sur	FM 178938	FM 180164
<i>Sundathelphusa halmaherensis</i> (von Martens, 1868)	SMF 4273; holotype	Indonesia, Moluccas, Halmahera	-	FM 180165
<i>Sundathelphusa minahassae</i> (Schenkel, 1902)	ZRC 2000.1681	Indonesia, Sulawesi, Tomohon	FM 178939	AM 234651
<i>Sundathelphusa picta</i> (von Martens, 1868)	RMNH 35242	Philippines, Luzon, Cabrazan River	FM 178940	FM 180166
<i>Sundathelphusa rubra</i> (Schenkel, 1902)	ZRC 2000.1695	Indonesia, Sulawesi, Kakassan	FM 178941	FM 180167
<i>Sundathelphusa sutteri</i> (Bott, 1970)	NHMB 35 a; holotype	Philippines, Luzon, Baguio	-	FM 180168
<i>Sundathelphusa tenebrosa</i> Holtuijs, 1979	RMNH 31972; type	Malaysia, Borneo, Sarawak, Gunung Mulu Nat. P.	FM 178942	FM 180169
<i>Sundathelphusa</i> sp.	ZRC 2000.1684	Indonesia, Sulawesi, Mayoa	-	AM 292919
<i>Stygothelphusa bidiensis</i> (Lanchester, 1900)	ZRC 1998.541	Malaysia, Borneo, Sarawak, Gua serih	FM 178943	FM 180170
<i>Stygothelphusa</i> sp.	ZRC 1999.8.0690	Malaysia, Borneo, Sarawak	FM 178944	FM 180171
<i>Terrathelphusa kuhli</i> (De Man, 1883)	SMF 32725	Indonesia, Java, Cibodas	FM 178945	FM 180172
<i>Thaksinithelphusa yongchindaratae</i> (Ng & Naiyanetr, 1993)	ZRC 1991.1882-1884; type	Thailand, Bang Phrik waterfall, Takua Pa Distr., Phangnga Prov.	FM 178946	FM 180173
<i>Thelphusula baramensis</i> (De Man, 1902)	ZRC 1997.804	Brunei, Laba, Bukit Teraja	FM 178947	FM 180174

Table 1. continued.

Species	Cat. No.	Provenience	H3	16S rRNA
<i>Thelphusula hulu</i> Tan & Ng, 1997	ZRC 1997.103	Malaysia, Borneo, Sabah	FM 178948	FM 180175
<i>Thelphusula sabana</i> Tan & Ng, 1998	ZRC 1997.808; type	Malaysia, Borneo, Sabah, Lahad Datu, Juraco	FM 178949	FM 180176
<i>Thelphusula tawauensis</i> Tan & Ng, 1998	ZRC 1997.810; paratype	Malaysia, Borneo, Sabah, Tawau Hills Park	FM 178950	FM 180177
<i>Travancoriana pollicaris</i> (Alcock, 1909)	NHMB 799 a	India, Tandikudi, Palnis	—	FM 180179
<i>Travancoriana schirmerae</i> Bott, 1969	SMF 5086; paratype	India, Nilgiris, Coonor	—	FM 180178
<i>Vanni malabarica</i> (Henderson, 1912)	NHMB 798 b	India, Naduar Riv., Anamalais	FM 178951	FM 180180
<i>Vanni nilgiriensis</i> (Roux, 1931)	NHMB 802 a; paratype	India, Ootacamund, Nilgiris	—	FM 180181

Abbreviations: MNHN: Muséum National d'Histoire Naturelle, Paris; NHML: Natural History Museum, London; NHMB: Naturhistorisches Museum Basel; R: Collection Rudolf Diesel; RMNH: Nationaal Natuurhistorisch Museum, Leiden; SAFM: Collection S.A.E. Marijmissen; SMF: Senckenberg Museum, Frankfurt am Main; ZRC: Zoological Reference Collection, Raffles Museum at the National University of Singapore; ZMB: Museum für Naturkunde, Berlin; ZUTC: Zoological Museum, University of Tehran.

Table 2. Freshwater crab species used for analysis of the second gonopod (G2), and the respective type of second gonopod groove. Histological data are new (in bold) or from Klaus et al. (2006).

Species	Catalogue No.	Provenance	Type of G2 groove
<i>Austrothelphusa angustifrons</i> (A. Milne Edwards 1869)	SMF 4272	Australia, Kimberley Res. Stat.	complex
<i>Ceylonthelphusa rugosa</i> (Kingsley 1880)	SMF 4378	Sri Lanka	simple
<i>Ceylonthelphusa soror</i> (Zehntner 1880)	SMF 4394	Sri Lanka	simple
<i>Deckenia imitatrix</i> Hilgendorf 1869	SMF 2877	East Africa	simple
<i>Gecarcinus jacquemontii</i> A. Milne Edwards 1844	SMF 1763	India, Bombay	simple
<i>Geithusa pulchra</i> Ng 1989	SMF 32720	Malaysia, Pulau Redang	simple
<i>Holthuisana biroi</i> (Nobili 1905)	SMF 7373	New Guinea, Borowai, Lake Sentani	complex
<i>Holthuisana subconvexa</i> (Roux 1927)	SMF 7373	New Guinea, Borowai, Lake Sentani	complex
<i>Irmengardia pilosimana</i> (Roux 1936)	ZRC 1984.7288-7302	Malaysia, Pahang, Bukit Chintamani	complex
<i>Oziothelphusa ceylonensis</i> (Fernando 1960)	uncatalogued	Sri Lanka	simple
<i>Oziothelphusa senex</i> (Fabricius 1798)	SMF 4368	Sri Lanka, Kanniyat, near Trincomalee	simple
<i>Oziothelphusa</i> sp.	SMF 24914	India, Kerala, Mavoor/Mapram	simple
<i>Oziothelphusa</i> sp.	uncatalogued	South India	simple
<i>Parathelphusa celebensis</i> Schenkel 1909	SMF 1790	Sulawesi, Mankoka	complex
<i>Parathelphusa bogorensis</i> Bott 1970	SMF 2753	Indonesia, Java, Bogor	complex
<i>Parathelphusa maculata</i> (De Man 1879)	SMF 2757	Singapore, Mardai Road	complex
<i>Perbrinckia enodis</i> (Kingsley 1880)	SMF 4391	Sri Lanka, Kandy	simple
<i>Potamonautes perlatus</i> (A. Milne Edwards 1837)	SMF 23255	South Africa	tube
<i>Phricotelphusa gracilipes</i> Ng & Ng 1987	SMF 32722	Malaysia, Pulau Langkawi	complex
<i>Phricotelphusa hockpingi</i> Ng 1986	uncatalogued	Malaysia, Bukit Larut	complex
<i>Playthelphusa armata</i> A. Milne Edwards 1887	SMF 6882	Tanzania, Lake Tanganyika, Gombe Nat. Park	tube
<i>Salangathelphusa brevicarinata</i> (Hilgendorf 1882)	SMF 12019	Thailand	simple
<i>Sartoriiana spinigera</i> (Wood-Mason 1871)	SMF 26 057	India, Nagaland, market in Dimapur	complex
<i>Snaha escheri</i> (Roux 1931)	SMF 5140	India, Shembaganur	complex
<i>Spiralothelphusa hydrodroma</i> (Herbst 1794)	SMF 2823	Sri Lanka, Lake Mundale	simple
<i>Spiralothelphusa wuellerstorffi</i> (Heller 1862)	SMF 4406	India, Nicobar islands	simple
<i>Stoliczia bella</i> Ng & Ng 1987	SMF 32719	Malaysia, Pulau Langkawi	tube

Table 2. continued.

Species	Catalogue No.	Provenance	Type of G2 groove
<i>Stygothelphusa bidiensis</i> (Lanchester 1900)	ZRC 1998.540	Malaysia, Sarawak, Guah Serih	complex
<i>Sundathelphusa boeii</i> Ng & Sket 1996	ZRC 2000.2088	Philippines, Bohol, Anteguera	simple
<i>Sundathelphusa cassiope</i> (De Man 1902)	SMF 1802	Moluccas, Bajjan	complex
<i>Sundathelphusa cavernicola</i> Takeda 1983	ZRC 2000.2080	Philippines, Bohol, Anteguera	simple
<i>Sundathelphusa rubra</i> (Schenkel 1902)	ZRC 2000.1695	Indonesia, Sulawesi, Kakaskasen	simple
<i>Sundathelphusa tenebrosa</i> Holthuis 1979	ZRC 2000.0064	Malaysia, Sarawak, Niah	simple
<i>Thehelphusula baramensis</i> (De Man 1902)	ZRC 1997.806	Brunei, Kuala Belait district, Seria	groove absent
<i>Terrathelphusa kuhlii</i> (De Man 1883)	SMF 5088	Indonesia, Java, Cibodas	complex
<i>Travancortiana schirmerae</i> Bott 1969	SMF 5086	South India, Nilgiris, Coono	complex

Abbreviations: SMF: Senckenberg Museum, Frankfurt am Main; ZRC: Zoological Reference Collection, Raffles Museum at the National University of Singapore.

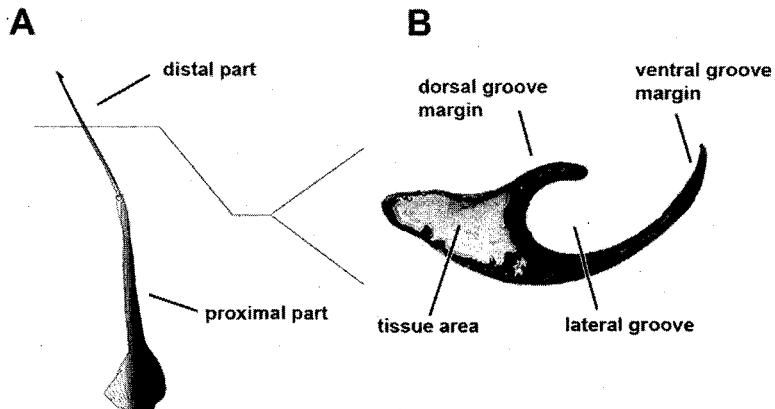


Figure 1. Terminology used for describing the second gonopod (G2) of freshwater crabs as proposed by Klaus et al. (2006). (A) Model of a G2. (B) Cross-section of the distal part of the G2 with a complex type of groove (*Parathelphusa bogorensis*). Scales are different.

from the analysis. Besides the combined analysis, the 16S partition was analyzed separately to show the contribution of each of the two genes to the final phylogenetic conclusions. The 87 sequences include additional sequences from GenBank (accession number indicated in the tree, see Fig. 2) and sequences of species for which we failed to amplify the orthologous H3 sequence (see Table 1). Bayesian analysis was run with four MCMC chains for 10 million generations (final average standard deviation of split frequencies = 0.00606) with the prior settings as suggested by MODELTEST 3.7 (HKY+I+G). The “burn-in” phase was of 1,000,000 generations and was excluded from the subsequent analysis.

3.2 Morphological analysis

Cross-sections of second gonopods (G2) available from the study of Klaus et al. (2006) and specimens additionally investigated for this study are listed in Table 2. Second gonopods were stored in 70% EtOH, decalcified in 5% trichloroacetic acid for 24 hours, dehydrated in a series of EtOH, and embedded in Spurr's resin or Durcupan® (Fluka AG, Buchs, Switzerland), respectively. Semi-thin sections of 2 μm thickness were cut using an ultramicrotome with a diamond-knife and stained with Richardson's blue. The terminology used for describing the different G2 morphologies is introduced in Figure 1.

4 RESULTS

The combined H3–16S phylogenetic analysis (Fig. 2) and the 16S-only analysis (Fig. 3) strongly support the monophyly of the Gecarcinucidae *sensu* Klaus et al. (2006) and confirm the separation of the Gecarcinucidae from the Potamidae by the morphology of the mandibular palp as proposed by Alcock (1910) and by sperm morphology (Klaus et al. 2008). Yet the division of the Gecarcinucidae into Gecarcinucinae and Parathelphusinae is not reflected by the molecular phylogenies. In contrast, several major clades are recognizable.

In the 16S-only analysis all deeper splits within the Gecarcinucidae remain polytomous or are weakly supported. Primarily congeneric groups have maximum posterior probabilities. This indicates a much faster evolution of this mitochondrial gene compared to the nuclear encoded histone H3. Nevertheless, the 16S rRNA sequence contains valuable phylogenetic information that increases

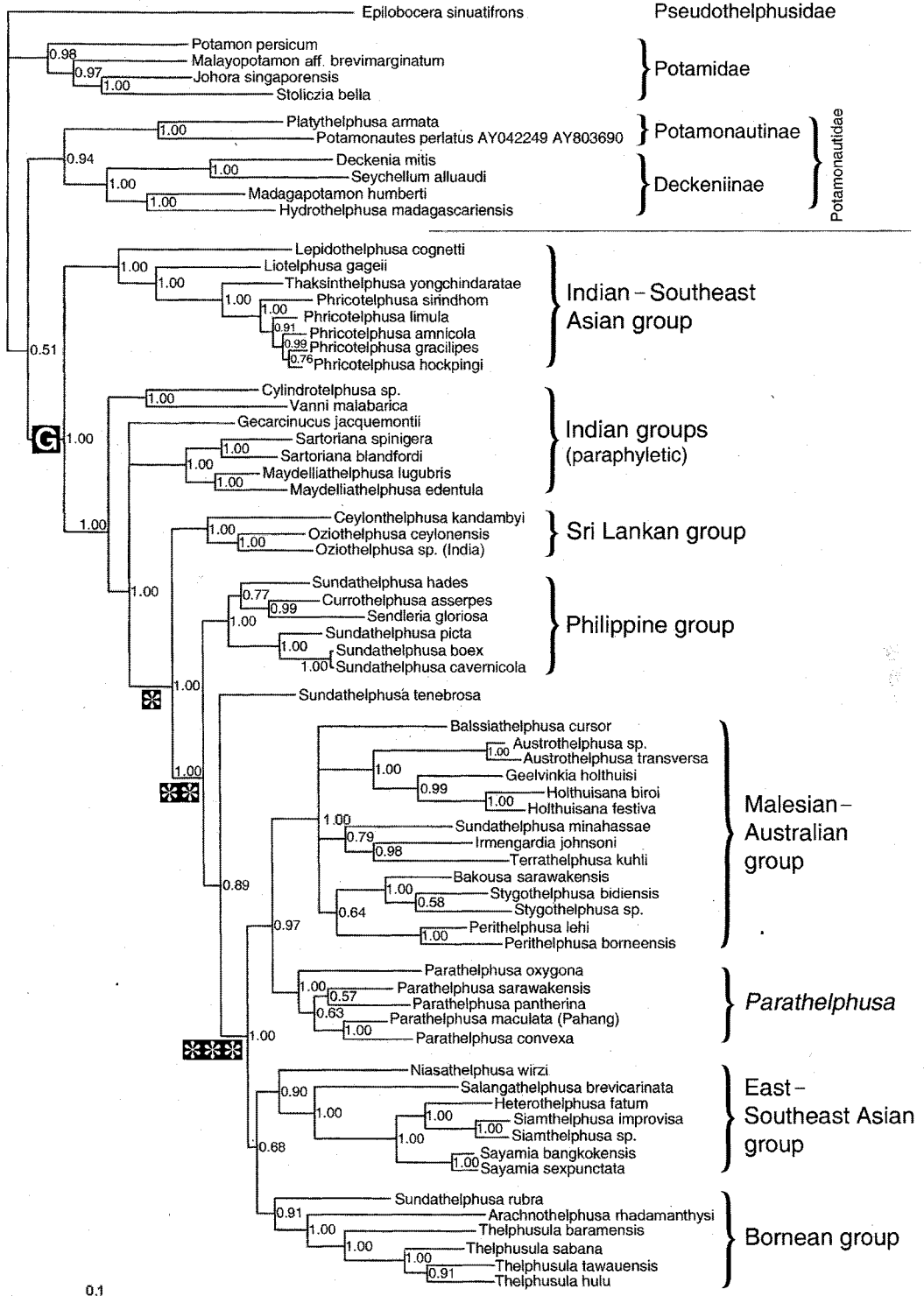


Figure 2. Bayesian analysis of the combined H3-16S rRNA data set, with the different lineages within the Gecarcinucidae (G). Indicated are: a clade similar to the “Parathelphusidae” of Bott (*); a monophyletic clade excluding all Indian species (**); and the sister clade to *Sundathelphusa tenebrosa* consisting of four gecarcinucid lineages (***)

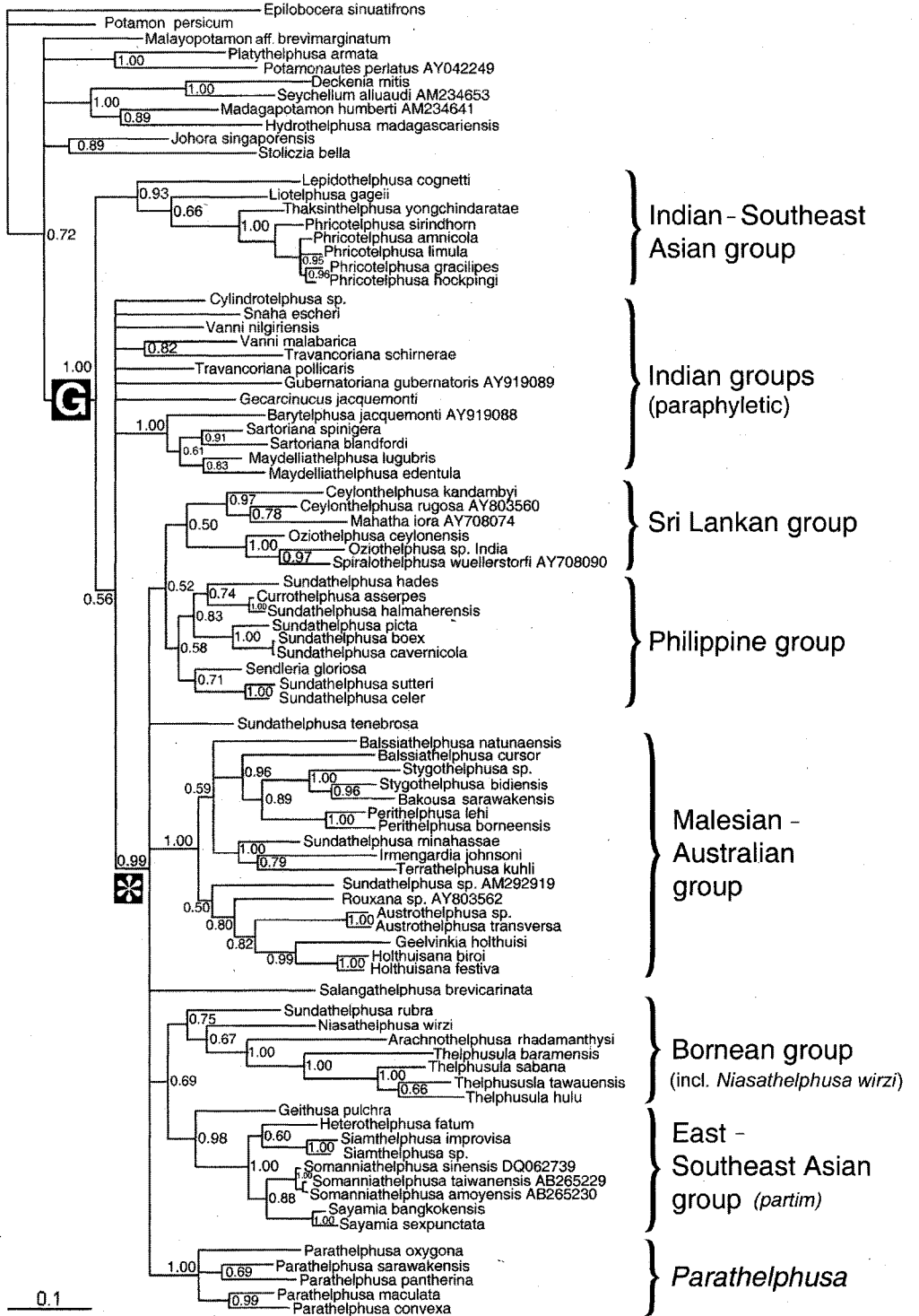


Figure 3. Bayesian analysis of the 16S rRNA data only, including sequences of species for which the amplification of the H3 fragment failed and sequences of further species from GenBank. Indicated are the Gecarcinidae (G), the clade similar to Bott's "Parathelphusidae" (*), and the different gecarcinucid lineages.

the accuracy of the combined analysis. The following groups can be identified within the Gecarcinucidae (referring to the combined H3–16S rRNA analysis, if not indicated otherwise).

4.1 Indian–Southeast Asian group

This monophyletic clade branches off first in the Gecarcinucidae and is the basal sister group to all other gecarcinucids. It consists of the genera *Lepidothelphusa* (Borneo), *Liotelphusa* (India and the Himalayas), *Thaksinthelphusa* (Thailand), and *Phricotelphusa* (northern Burma to the Malay Peninsula).

The groove of the second gonopod of *Phricotelphusa gracilipes* and *P. hockpingi* is intermediate in morphology between the complex (where both ventral and dorsal groove margins are broadened, e.g., in *Travancoriana schirmerae*) and simple (where only the ventral groove margin is broadened, e.g., in *Gecarcinucus jacquemonti*) types of the G2 grooves. In *P. hockpingi* the groove is formed by a much thicker cuticle compared to the cuticle surrounding the tissue area, typical of the complex type of G2. However, a true dorsally broadened groove margin is absent. The dorsal margin is more prominent in *P. gracilipes* but is not solid and contains soft tissue.

4.2 A paraphyletic group of continental Indian species

Several Indian species included in this analysis dissociate in the combined analysis into several clades. In the first assemblage, the genera *Vanni* and *Cylindrotelphusa* cluster together and form the earliest split with respect to all other gecarcinucids listed below. Well supported is a clade that includes the genera *Sartoriana* and *Maydelliathelphusa* (and *Barytelphusa*, 16S-only). This clade occurs on the Indian subcontinent excluding Sri Lanka, and its range extends north into the Himalayas with *Maydelliathelphusa* and into Afghanistan and Iran in the west with *Sartoriana blandfordi*. The relationship of *Gecarcinucus jacquemonti*, representing the type genus of the Gecarcinucidae, to this clade and to all other gecarcinucids is unresolved. In the 16S-only analysis, all continental Indian species, even congeners, remain polytomous, except the clade that contains *Sartoriana*, *Maydelliathelphusa*, and *Barytelphusa*.

Different character states of the second gonopod occur within these Indian species. *Cylindrotelphusa* and *Maydelliathelphusa* have the distal part of the G2 completely reduced, while the continental Indian species of *Travancoriana*, *Sartoriana*, and *Snaha escheri* (*Gubernatoriana* in Klaus et al. 2006) possess the complex type of second gonopod groove. The specimen identified as *Travancoriana* sp. (see Klaus et al. 2006, SMF 24914), and showing the simple type of second gonopod, turned out to belong to *Oziothelphusa* after reexamination. *Gecarcinucus jacquemonti* is so far the only species of this set of Indian gecarcinucids with the ventral groove margin of the G2 broadened (simple type of G2).

4.3 Sri Lankan group

This clade from the Indian subcontinent is represented in the combined analysis by *Oziothelphusa* and *Ceylonthelphusa*. In the 16S-only analysis, *Oziothelphusa* and *Spiralothelphusa* cluster together but connect to the Sri Lankan genera *Ceylonthelphusa* and *Mahatha* with only weak support. The study of Bossuyt et al. (2004), based on mitochondrial sequence data, shows that two more genera of Sri Lanka that are not included here, *Pastilla* and *Perbrinckia*, also belong to this clade. The sister group relationship of the Sri Lankan group to the following lineages of East and Southeast Asian gecarcinucids is well supported (not in the 16S-only analysis). In all investigated species of this group, the simple type of G2 occurs (Klaus et al. 2006). Within the genus *Ceylonthelphusa*, the groove of the G2 is reduced and the distal part of the G2 forms a leaf-like structure.

All non-Indian gecarcinucids, excluding the genera *Lepidothelphusa*, *Thaksinthelphusa*, and *Phricotelphusa* from the Indian–Southeast Asian group, form a monophyletic clade (Fig. 2).

4.4 Philippine group

Branching off first within this clade is a group containing species from the Philippines and the Moluccas and reaching with the genus *Sendleria* to New Guinea and the Solomon Islands. *Sundathelphusa picta*, *S. boex*, and *S. cavernicola* from the Philippines cluster together in both the combined H3–16S and 16S-only analyses. *Currothelphusa asserpes* from Halmahera and *Sendleria gloriosa* from the Solomon Islands group together, while in the 16S-only analysis *Sundathelphusa halmaherensis* is sister species to *C. asserpes*, and *Sundathelphusa sutteri* and *S. celer* from Luzon form the sister group to *Sendleria gloriosa*. The G2 of *Sundathelphusa picta* and *S. boex* is of the simple type. Interestingly, *Sundathelphusa tenebrosa* from Borneo does not cluster with the previous clade but is the sister group to all remaining freshwater crabs from East and Southeast Asia. These in turn form a strongly supported monophyletic assemblage (Fig. 2). This set can be subdivided as outlined below.

4.5 East–Southeast Asian group

Within this group, *Siamthelphusa*, *Heterothelphusa*, and *Sayamia* cluster together with high support. *Salangathelphusa* separates at a more basal level, and *Niasathelphusa wirzi* appears as the sister group to all other species of this group.

In the 16S-only analysis *Salangathelphusa brevicarinata* and *Niasathelphusa wirzi* do not connect to this clade. The East Asian genus *Somaniathelphusa* appears as the sister group to the Southeast Asian species, while *Geithusa pulchra* (Redang Island, Malay Peninsula) appears as the sister taxon to all other species of the East–Southeast Asian group. Although having a very weak posterior probability, *Niasathelphusa wirzi* clusters in the 16S-only analysis within the Bornean assemblage. However, in the combined H3–16S analysis, its relationship to the East–Southeast Asian group is well supported.

The range of this group covers East Asia (China, Taiwan) and Southeast Asia down to the Malay Peninsula with the isolated occurrence of *Niasathelphusa wirzi* on Nias island west of Sumatra. In the species *Salangathelphusa brevicarinata* and *Geithusa pulchra* the simple type of G2 occurs, whereas all other species in this clade show a completely reduced distal part of the G2. This argues for the simple type of G2 being the plesiomorphic character state within this group, with complete reduction being an apomorphy.

4.6 Bornean group

In both analyses, this clade clusters with the East–Southeast Asian group, although this interrelationship is not supported by the very low posterior probabilities. The topology of the deeper splits is similar in both analyses, with *Sundathelphusa rubra* of Sulawesi diverging first, followed by *Arachnothelphusa rhadamanthysi* and then the species of the genus *Thelphusula*. As mentioned above, however, in the 16S-only analysis *Niasathelphusa wirzi* arises between *S. rubra* and *A. rhadamanthysi*. This is not supported by the posterior probabilities, but again this indicates the close relationship of the East–Southeast Asian group and the Bornean group. The G2 of *Sundathelphusa rubra* is of the simple type with a broad ventral groove margin. Although *Thelphusula baramensis* has a G2 with elongated distal part, it lacks any groove structures.

The Malesian–Australian group and the genus *Parathelphusa* cluster together in the combined H3–16S analysis as a monophyletic clade.

4.7 Malesian–Australian group

With *Austrothelphusa*, *Balssiathelphusa*, *Geelvinkia*, *Holthuisana*, *Irmengardia*, *Perithelphusa*, members of the genus *Sundathelphusa*, *Stygothelphusa*, *Rouxana*, and *Terrathelphusa*, this group

contains a diverse set of genera. Its range covers most of the phylogeographic region of Malesia (ranging from the Isthmus of Kra on the Malay Peninsula to the Solomon Islands in the East) including northern Australia.

Within the Malesian–Australian freshwater crabs, there are two well-supported clades. One clade contains the New Guinean–Australian genera *Austrohelphusa*, *Geelvinkia*, *Holthuisana*, and *Rouxana* (16S-only), and the other clade contains the three species *Irmengardia johnsoni* (Malay Peninsula), *Terrathelphusa kuhli* (Java), and *Sundathelphusa minahassae* (Sulawesi). Of the Bornean genera belonging to the Malesian–Australian group, the genera *Bakousa* and *Stygothelphusa* cluster together. The phylogenetic relationships of these clades along with the Bornean genera *Balssiathelphusa* and *Perithelphusa* are not sufficiently resolved. In the Malesian–Australian group, a G2 with both groove margins broadened is present, although weaker developed in *Terrathelphusa kuhli* and *Irmengardia pilosimana*. *Sundathelphusa cassiope* from Halmahera (Moluccas), which has a complex type of G2 groove, probably also belongs to this lineage, and not, like *S. halmaherensis*, to the Philippine group.

4.8 The genus *Parathelphusa*

The five representatives of the speciose genus *Parathelphusa* form a monophyletic group with identical topologies in both analyses. In the combined H3–16S analysis, *Parathelphusa* is the sister group to the Malesian–Australian clade. Compared to the other Southeast Asian groups, rather short branches occur within *Parathelphusa*, even between species from the western (*P. maculata*, Malay Peninsula) and the eastern (*P. pantherina*, Sulawesi) margin of the range. *Parathelphusa oxygona* from Borneo is in a sister group relationship to the other species. All examined second gonopods of this genus have a complex type of groove.

5 DISCUSSION

5.1 Monophyly of the Gecarcinucidae

This study supports the monophyly of the Gecarcinucidae as previously defined by Klaus et al. (2006), corresponding to the Gecarcinucinae *sensu* Alcock (1910) and the Gecarcinucoidea *sensu* Cumberlidge et al. (2008) and Ng et al. (2008). The family relationships among the Gecarcinucidae, Potamidae, and Potamonautidae are not resolved. This is also the case in the molecular analyses of Daniels et al. (2006) and Klaus et al. (2006). Sperm morphology also provides no evidence on the familial relationships (Klaus et al. 2008). The only morphological character shared between Potamidae and Potamonautidae (Potamonautinae) is the distal part of the G2 forming a closed tube (Klaus et al. 2006). However, the Deckeniinae within the Potamonautidae have a G2 with a lateral open groove. If this simple character state is the plesiomorphic condition in the Potamonautidae, then the conformation of the G2 tube in the Potamidae and Potamonautinae are convergent developments. In fact, the potamid tube is formed by groove margins that are involuted, while in the Potamonautinae these margins broadly overlap (see Klaus et al. 2006).

There is therefore no phylogenetic evidence to unite Potamidae and Potamonautidae in a superfamily Potamoidea and on the other hand maintain a separate superfamily Gecarcinucoidea with the single family Gecarcinucidae. As already proposed by several authors (von Sternberg et al. 1999; von Sternberg & Cumberlidge 2001; Klaus et al. 2006; Klaus et al. 2008), we favor the recognition of only one superfamily of Old World freshwater crabs, the Potamoidea, that includes the Gecarcinucidae, Potamidae, and Potamonautidae.

5.2 Gecarcinucid lineages and the morphology of the frontal triangle and the second gonopod

The present analysis does not support the differentiation of the Gecarcinucidae into two or three families based on character states of the frontal triangle as introduced by Bott (1970a) and adopted

by Martin & Davis (2001) and Cumberlidge et al. (2008). The use of the absence or presence of the frontal triangle as a diagnostic character for the two sister groups (Gecarcinucidae and Parathelphusidae) implies that one of the two groups might be paraphyletic, as one of the two character states must represent the plesiomorphic condition. This is confirmed by the present molecular phylogeny. Moreover, there are several genera (e.g., *Ceylonthelphusa* and *Perbrinckia*) for which it is difficult to separate the different character states, as they show intermediate morphologies. It appears that the plesiomorphic character state within the Gecarcinucidae is the complete absence of the frontal triangle, as indicated by its absence in the Indian and Indian–Southeast Asian groups, not to mention its absence in the Potamidae and Potamonautidae as comparative outgroups. The same criticism for the use of the frontal triangle can be applied for the two character states of the second gonopod (simple groove versus complex groove) that were used by Klaus et al. (2006) as diagnostic characters for the gecarcinucid sister groups Gecarcinucinae and Parathelphusinae. However, it is more difficult to identify the plesiomorphic state of the second gonopod. If the complex type of G2 groove of the genus *Phricotelphusa* and several Indian species is homologous, it would probably represent the plesiomorphic character state in the Gecarcinucidae. In the paraphyletic Indian group, both types of G2 groove occur. In the common ancestors of the Malesian–Australian group and the genus *Parathelphusa*, the complex type of G2 groove evolved, while the East–Southeast Asian and the Bornean groups retained a simple type of G2 groove, as it occurs in the Philippine group (Fig. 4).

The complete reduction of the distal part of the second gonopod occurs independently in several Indian genera and in the East–Southeast Asian group. Probably this correlates with a dramatic change in the mechanisms involved in sperm transfer. This is also evident from the absence of a flexible terminal joint in the first gonopod, the generally reduced length of the first gonopod, and in modifications of the female genital apparatus in species lacking the distal part of the second gonopod (unpublished data).

5.3 Similarities with the system of Bott

Superficially, the splitting of the Gecarcinucidae into several subclades resembles the taxonomic grouping of Bott (1970a), although his use of the frontal triangle as a diagnostic character and the resulting system of three different families (Gecarcinucidae, Parathelphusidae, and Sundathelphusidae) is strongly contradicted by this study. Most of Bott's subfamilies appear as para- or polyphyletic assemblages. In detail, groups with certain congruence to Bott's taxa are:

(1) The Indian–Southeast Asian group. This clade corresponds to Bott's Liotelphusinae with exclusion of *Sartoriana*, *Thelphusula*, and *Travancoriana*, while the position of *Adeleana* with representatives on Borneo and Sumatra still remains unknown. *Lepidothelphusa cognetti* of Borneo was previously suggested to be closely related to *Phricotelphusa* based on morphological characters (Bott 1970a).

(2) The Sri Lankan group. This group comprises, with *Oziothelphusa* and *Spiralothelphusa*, part of Bott's Spiralothelphusinae (excluding *Balssiathelphusa* and *Irmengardia*) and, with *Ceylonthelphusa*, his Ceylonthelphusinae.

(3) The East–Southeast Asian group. This monophyletic clade includes all the genera of Bott's subfamily Somanniathelphusinae (*Salangathelphusa*, *Somanniathelphusa*, and *Siamthelphusa*).

(4) The genus *Parathelphusa*. Bott's Parathelphusinae included the genera *Parathelphusa*, *Nautilothelphusa*, and *Palawanthelphusa*. The latter was synonymized with *Parathelphusa* (Ng & Goh 1987), while *Nautilothelphusa* seems to nest deeply within the genus *Parathelphusa* of Sulawesi (Schubart & Ng 2008), making the latter paraphyletic.

As this study includes only selected gecarcinucid representatives, it is likely that the phylogeny may change with a larger sample size. This might affect the placements of the Indian gecarcinucid taxa and relationships within the described groups. However, we are reasonably confident that many of the present ideas will be reinforced. Certainly, a clade of *Lepidothelphusa* and *Phricotelphusa*

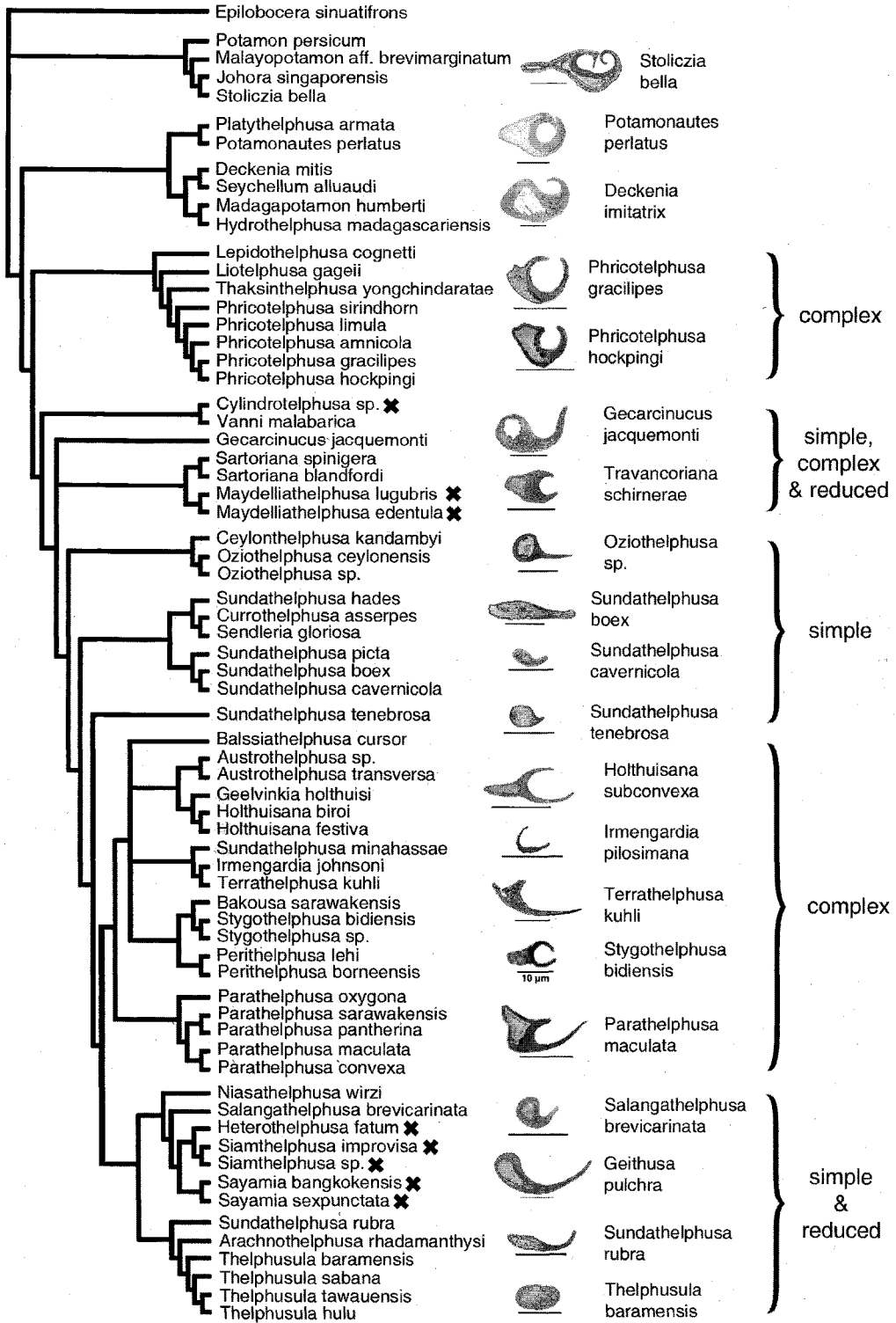


Figure 4. Different morphologies of the second gonopod (cross-sections of its distal part) correlated with the topology of the combined gecarcinucid H3-16S rRNA data (Fig. 2). Crosses (x) indicate complete reduction of the distal part of the G2. Scale bars = 50 µm if not indicated otherwise.

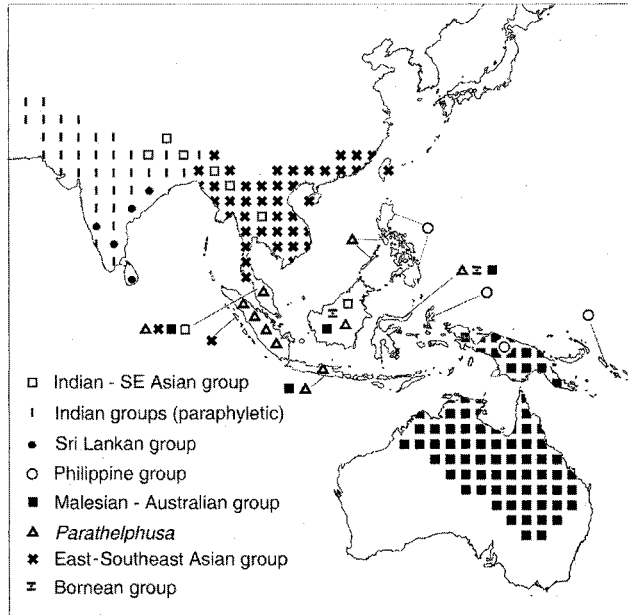


Figure 5. Approximate distribution of the different lineages of the Gecarcinidae.

can also be justified through a suite of morphological characters (unpublished data). We refrain from recognizing formal taxonomic ranks here.

5.4 *The genus Sundathelphusa* Bott, 1969

The genus *Sundathelphusa* contains 27 species, of which 18 are described from the Philippines with several dozen more that need to be described (unpublished data). Together with *Parathelphusa* and *Somanniathelphusa*, it is one of the most speciose genera within the Gecarcinidae.

It is evident that the current taxonomic definition of *Sundathelphusa* is flawed, as the species included here are distributed among at least three different lineages. *Sundathelphusa rubra* (Sulawesi) is sister to the other species of the Bornean lineage (Fig. 2). Within *Sundathelphusa* from the Philippines and Halmahera, *Currothelphusa* and *Sandleria* are nested, and *Sundathelphusa* sp. from Sulawesi clusters within the Malesian–Australian assemblage (Fig. 3). The same applies for *S. minahassae* from Sulawesi, described as a subspecies of *S. cassiope* by Bott (1970b). *Sundathelphusa cassiope* itself is the type species of *Sundathelphusa* and originates from Sulawesi. Therefore, the genus name will stay with the species from Sulawesi (excluding *S. rubra*). The genus *Sundathelphusa* needs to be revised (Chia and Ng 2006), and only more detailed morphological and molecular investigations will clarify relationships and taxonomy of this polyphyletic assemblage.

5.5 *Biogeography*

Remarkably, species distribution among the lineages is more or less equal (treating the poorly resolved Indian groups as one paraphyletic assemblage, see Figs. 5, 6). Only the Bornean group and the Indian–Southeast Asian group show comparably lower species numbers (Fig. 6). As expected, most of the gecarcinucid species occur in continental Asia. Nevertheless, there are remarkable radiations of gecarcinucid crabs on Sri Lanka and Borneo. New Guinea and Sulawesi also display

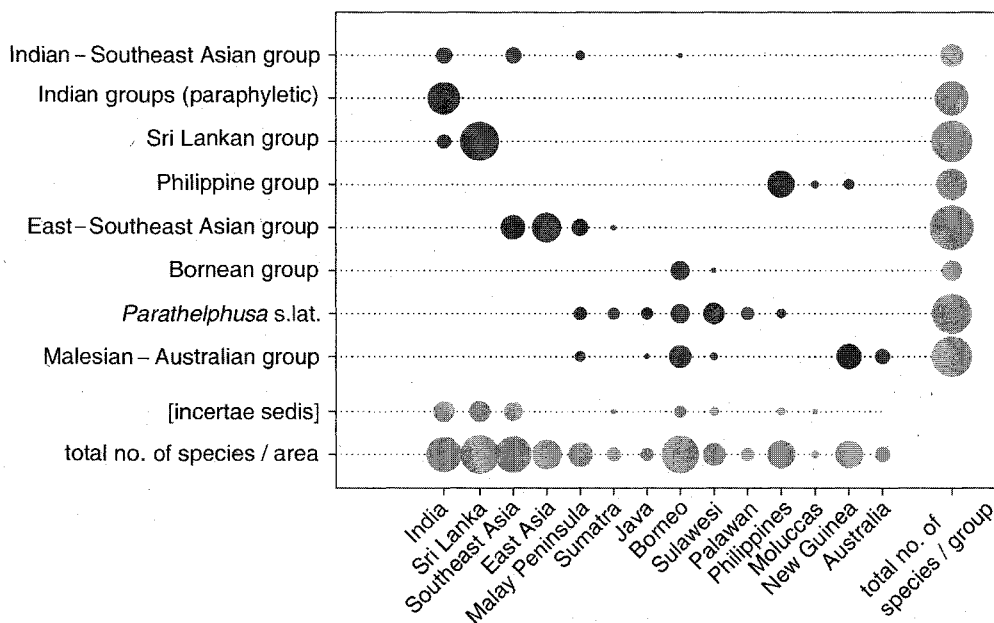


Figure 6. Diversity patterns of the Gecarcinucidae. The diameter of the circles is proportional to the species number within the respective gecarcinucid lineage (ordinate) and geographic area (abscissa). Species *incertae sedis* belong to genera not included in the phylogenetic analyses.

relatively high species diversity. In contrast, well-explored Sumatra and Java are depauperate in species number, even when considering cryptic speciation (unpublished data). Australia also shows a minor species and lineage diversity (Fig. 6), most likely due to a more recent dispersal of freshwater crabs from New Guinea across the Torres Strait, although there are still several species that need to be described (P.J.F. Davie, pers. comm.). The present analyses and the previous molecular phylogenies of the Old World freshwater crabs (Daniels et al. 2006; Klaus et al. 2006), as well as the fossil record (Klaus et al. 2006), argue against an origin of the Potamoidea predating the fragmentation of the former Gondwana continent. The fact that the Australian and New Guinean species nest deeply within the Gecarcinucidae, given the diversity pattern of the Australian region, excludes an Australian origin for the Gecarcinucidae.

Klaus et al. (2006) hypothesized that the Gecarcinucidae initially evolved on the Indian subcontinent, with subsequent dispersal to East and Southeast Asia. Based on the present data, this is difficult to resolve. The fact that the Indian groups (including the Sri Lankan group) branch off early within the gecarcinucid phylogeny could indicate an early radiation on the Indian subcontinent. But within the earliest separated Indian–Southeast Asian clade, taxa of both groups cluster together, with the species branching off first being *Lepidotherphusa cognetti* from Borneo.

For the sister group of the Sri Lankan clade (Fig. 2), an Indian origin seems to be most parsimonious with this phylogenetic split having already occurred on the Indian subcontinent (see also Bossuyt et al. 2004). As these non-Indian gecarcinucids are monophyletic, they are most likely the result of a single dispersal event eastward out of India. It was proposed by Klaus et al. (2006) that this dispersal event out of India could have occurred during the Miocene, when the climate became more humid again in northern India (Morley 2000), allowing the gecarcinucid crabs to expand their range.

Because only derived members of the East–Southeast Asian lineage occur in East Asia, the direction of gecarcinucid dispersal was probably first via the Malay Peninsula to the islands of the

Sunda Shelf. As regression events of variable magnitude were frequent during the glaciation periods of the Pliocene and Pleistocene, the resulting terrestrial connections could have allowed freshwater crabs to access the Greater Sunda Islands, although it is difficult to assign this initial and later dispersal events to defined periods of low sea level. The spreading of the Gecarcinucidae beyond the Sunda Shelf to the Philippines, Sulawesi, Halmahera, and further to New Guinea and Australia can be explained only by hypothetical dispersal via rafting, as there is no geological evidence to suggest terrestrial connections between these regions. The Philippine group contains the earliest separated descendants of such a gecarcinucid dispersal event with subsequent radiation on the Philippine islands. The distribution of this lineage covers a dispersal pathway following the Sangihe Island chain from the Philippine Islands to the Moluccas and with *Sendleria* onwards to New Guinea. This dispersal pathway was proposed as a track of general faunal exchange with New Guinea/Australia (Moss and Wilson 1998).

All of the four younger lineages (the Malesian–Australian group, the East–Southeast Asian group, the Bornean group, and *Parathelphusa*) probably evolved on the Sunda Shelf. *Sundathelphusa tenebrosa* from Borneo, sister group to these lineages, could represent an early clade within this radiation. A probable hypothesis is that the initial splits occurred on Borneo itself. Borneo certainly represents a biodiversity hotspot with respect to gecarcinucid diversity. Approximately 14% of the known gecarcinucid species occur on this island, as do representatives of four of the five lineages with Malesian representatives (Fig. 6). In addition, several new genera and species remain undescribed (unpublished data). The distribution pattern of the diverse Malesian–Australian group is congruent with this hypothesis, with an early differentiation of the Bornean genera *Balssiathelphusa*, *Bakousa*, *Perithelphusa*, and *Stygothelphusa*. Based on the present data, this lineage reached Sulawesi and New Guinea/Australia independently.

The East–Southeast Asian group successfully dispersed back into continental Asia. The species branching off first, *Niasathelphusa wirzi* (Nias island), *Salangathelphusa brevicarinata* (Phuket, Pulau Langkawi), and *Geithusa pulchra* (Pulau Redang Island, Malay Peninsula; 16S rRNA only), occur as relics on small islands off the coast of Sumatra and the Malay Peninsula. Therefore, it is probable that the East–Southeast Asian clade evolved in the area of Sumatra and the Malay Peninsula and spread to East Asia secondarily. During times of low sea level this could have occurred via the Siam palaeo-river system that drained the rivers of the Gulf of Thailand to the South China Sea (Voris 2000).

The genus *Parathelphusa* appears as sister group to the Malesian–Australian lineage. The relatively short branch lengths within *Parathelphusa* could indicate a more recent spreading of this genus, with high diversity on Borneo, and remarkable species radiations on Palawan (Ng & Takeda 1993; Freitag & Yeo 2004) and Sulawesi (Chia & Ng 2006; Schubart & Ng 2008). The genus reaches Mindoro and Balabac via Palawan (Ng & Takeda 1993) but is not reported from other Philippine islands. To the east, *Parathelphusa* has crossed Wallace's Line onto Sulawesi and Lombok and occurs in the west in the Malay Peninsula (Bott 1970b; Ng 1988, 1997).

6 CONCLUSIONS

Besides validation of gecarcinucid monophyly, this phylogenetic analysis increases profoundly our knowledge of the relationships within the Gecarcinucidae. In contrast to most previous approaches based on morphology alone, we can draw a much more detailed picture, identifying several lineages within the Gecarcinucidae.

Biogeographically, our phylogeny appears to support an early radiation of the Gecarcinucidae on the Indian subcontinent with subsequent dispersal to Southeast Asia. It allows the identification of diversity hotspots (Borneo and the Malay Peninsula) based on genetic diversity. It also provides insights to the historical freshwater crab biogeography of the Malesian (Malaysian) archipelago. Most conspicuously, the complex geography and palaeogeographical history of this region lead to reticulate area-lineage relationships, indicating: (1) independent colonization events at different

time points, e.g., the Philippine group and *Parathelphusa* in the Philippines; the Philippine group and the Malesian–Australian group in New Guinea; or the Malesian–Australian group, the Bornean group, and *Parathelphusa* in Sulawesi; (2) recolonization events, e.g., the dispersal of the East–Southeast Asian group back to continental Asia; and (3) species radiations of related lineages on the same island, e.g., the Malesian–Australian group, the Bornean group, and *Parathelphusa* in Borneo. Although most of the gecarcinucid distribution patterns can be explained only by dispersal, vicariant events also contributed to the present distribution of gecarcinucid lineages, as sea level fluctuations both enabled isolation and faunal exchange on the Sunda Shelf.

ACKNOWLEDGEMENTS

We thank Daisy Wowor (Bogor) and Peter Koller (Regensburg) for their companionship on various field trips; Agnes Lautenschlager (Warrnambool), Maria Schiwiek, and Birgit Lautenschläger (Regensburg) for support with the histological work; Saskia Marijnissen (Amsterdam) for providing potamonautid tissue samples; and Aquarium Glaser (Offenbach) and Chris Lukhaup (Stuttgart) for supplying various specimens. We are deeply grateful to the following persons for access to material under their care and permission to take tissue and/or gonopod samples: Danièle Guinot and Regis Clever (MNHN), Ambros Hängi and Urs Wüest (NHMB), Paul Clark (NHML), Charles Fransen (RMNH), Michael Türkay and Kristin Pietratus (SMF), and Alireza Sari (ZUTEC). Richard von Sternberg, Joel Martin, and an anonymous reviewer kindly streamlined our English and gave valuable comments on the manuscript. We also thank the Deutsche Forschungsgemeinschaft for their financial support of this project (Br 2264/2-1, 2-2 and Schu 1460/6-1).

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