

PRELIMINARY MOLECULAR AND MORPHOLOGICAL STUDY OF THE
CALAPPA LOPHOS SPECIES GROUP (DECAPODA:BRACHYURA:CALAPPIDAE)

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A B S T R A C T

The systematics of the *Calappa lophos* species group is clarified using morphological and molecular data. The phylogeny of some Indo-Pacific species of *Calappa* is discussed. Two species, *C. quadrimaculata* Takeda and Shikatani, 1990, and *C. guerini* (Brito-Capello, 1871), previously synonymised with *C. lophos* (Herbst, 1782), are shown to be valid species using morphological and molecular data. A new species in the group, *C. acutispina*, is described from Madagascar. The usefulness of Bayesian inference in elucidating the phylogenetic relationships of some of the species of *Calappa* based on partial cytochrome oxidase I (COI) sequences is examined.

INTRODUCTION

One of the more common species of box crabs in the Indo-West Pacific is *Calappa lophos* (Herbst, 1782). This species grows to large sizes (up to 100 mm carapace width) and is collected for food in some areas (Ng, 1998). In the most recent revision of the Indo-West Pacific *Calappa* species, Galil (1997) recognized two species as junior synonyms of *C. lophos*—*C. guerini* Brito-Capello, 1871, and *C. quadrimaculata* Takeda and Shikatani, 1990. Ng et al. (1999), however, argued that *C. quadrimaculata* was different morphologically and resurrected it as a valid species.

In recent years, the authors have examined a large number of specimens that have been referred to *C. lophos* from many parts of the Indo-West Pacific. In doing so, it became apparent that the taxonomy of these two species is not as simple as had been presumed. The present study revises the taxonomy of this group of species, and in doing so resolves the problems with the types and identities of the taxa.

A preliminary phylogenetic tree is presented for some Indo-West Pacific species of *Calappa* using the mitochondrial gene Cytochrome Oxidase I as a molecular marker and analysed with Bayesian inference. The Bayesian phylogenetic approach, although relatively new, has been shown to be extremely informative and comparable with methods such as maximum likelihood (see Huelsenbeck et al., 2002).

MATERIALS AND METHODS

Specimens examined in this study are deposited in the Zoological Reference Collection (ZRC) of the Raffles Museum of Biodiversity Research, National University of Singapore; Chiba Prefectural Museum (CBM), Chiba, Japan; National Science Museum of Tokyo (NSMT), Japan; Berlin Museum (ZMB), Germany; The Natural History Museum (NHM), London, England; Muséum national d'Histoire naturelle (MNHN), Paris, France; Zoological Museum of Berlin (ZMB); and Zoological Museum, Copenhagen University (ZMUC), Denmark. The lobes or teeth of the posterior carapace margin are counted from the postero-lateral corner inwards, with the first tooth being outermost. Measurements provided (in millimetres) are of the carapace width and length, respectively.

All voucher specimens from which mitochondrial COI data were obtained are deposited in the ZRC. Sequences have been deposited in Genbank (Accession numbers AY579998–AY580010). Genomic DNA of the various species of *Calappa* available to this study as well as *Murisia armata* (used as the out-group) was isolated from the muscle tissue of the

ambulatory legs. Taxa sampled and their locality data were presented in Table 1. All samples were preserved in 75–95% ethanol prior to DNA extraction using the phenol-chloroform method (Kocher and White, 1989). Polymerase chain reaction (PCR) amplification of the COI gene from total DNA was done with universal primers COI_f (5'-CCT GCA GGA GGA GGA GAY CC) and COI_a (5'-AGT ATA AGC GTC TGG GTA GTC) (Kessing et al., 1989). PCR products were purified with QIAquick PCR Purification Kit prior to sequencing with ABI PRISM Dye Terminator mix (Perkin-Elmer, NJ) in an ABI PRISM 377/3100 DNA Sequencer (Perkin-Elmer, NJ). Sequences obtained were analyzed using the program Sequencher (ver 4.1, Gene Codes Corporation, Ann Arbor, USA). The sequences were aligned with ClustalX Multiple Sequence Alignment Programme (ver. 1.7) and exported in NEXUS format for maximum likelihood (ML) analysis performed by (Phylogenetic Analysis Using Parsimony (PAUP) (ver. 4.08b) (Swofford, 2002) and Bayesian inference (BI) of phylogeny using MrBayes (ver. 3.0B4) (Huelsenbeck and Ronquist, 2001). For ML analyses, 1000 bootstrap replicates were sampled with an additional 100 replicates for random addition of sequence, and the General Time Reversible (GTR) model of nucleotide substitution was employed. Bayesian analysis was performed with the following settings. The maximum likelihood model employed six substitution types, with base frequencies estimated from the data. Rate variation across sites was modelled using a gamma distribution. Two independent Markov chain Monte Carlo (MCMC) search were run with four chains each for 6,000,000 generations until the log values for each chain had reached stability, with trees sampled every 1000 generations (the first 1000 trees were discarded as "burnin"). All trees saved from the MCMC search were then imported into PAUP and a consensus tree with posterior probabilities for each clade was computed.

The Bayesian inference of phylogeny is considered a relatively new method in reconstructing relationships between species, despite its long standing in the field of statistics. In recent years, it has been used to address phylogenetic questions. It is purported to be similar to the maximum likelihood model (Huelsenbeck et al., 2002) but has the advantage of being able to handle large amounts of data without compromising computational time, as well as producing trees with levels of support (in this case, posterior probabilities). In the present study, the two MCMC chains, run independently over six million generations, took six hours to reach stationarity, compared with the maximum likelihood method with 1000 bootstraps, which took 10 days.

SYSTEMATIC ACCOUNT

Family Calappidae H. Milne Edwards, 1837
Genus *Calappa* Weber, 1795
Calappa lophos (Herbst, 1782)
Fig. 1A, 3A

Cancer lophos Herbst, 1782: 201, pl. 13, fig. 77.

Calappa lophos Fabricius, 1798: 346; Bosc, 1802: 184, 1830: 214; Latreille, 1803: 393, 1829: 139; H. Milne Edwards, 1837: 104; White, 1847: 45; Gibbes, 1850: 183; Herklots, 1861: 25; Heller,

Table 1. Specimens examined, source, locality and genbank accession numbers.

Species	Catalogue number	Locality	Genbank accession numbers
<i>C. bicornis</i>	ZRC 1999.0812	Taiwan: I-Lan County	AY579998
<i>C. calappa</i> (mottled)	ZRC 2000.2392	Taiwan: He Ping Island, tangle nets	AY580008
<i>C. calappa</i> (plain)	ZRC 2000.0397	Taiwan: He Ping Island, tangle nets	AY580007
<i>C. capellonis</i>	ZRC 2000.0871	Thailand: Phuket, Pichai Fish Port	AY580006
<i>C. clypeata</i>	ZRC 1999.0215	Thailand: Phuket, Pichai Fish Port	AY580000
<i>C. gallus</i>	ZRC 2004.0459	The Philippines: Bohol, Panglao Beach	AY580001
<i>C. hepatica</i>	ZRC 2004.0458	Indonesia: Sulawesi, Manado	AY580003
<i>C. liaoi</i>	ZRC 2002.445	Philippines: Visayas, Bohol, Panglao	AY580002
<i>C. lophos</i>	ZRC 2000.1073	Thailand: Phuket, Pichai Fish Port	AY579999
<i>C. philargius</i>	ZRC 1998.067	Singapore: Changi Beach	AY580004
<i>C. quadrimaculata</i>	ZRC 1999.0677	Taiwan: I-Lan County, Geng Fang Fish Port	AY580009
<i>C. undulata</i>	ZRC 2000.0873	Thailand: Phuket, Pichai Fish Port	AY580005
<i>Mursia armata</i> *	ZRC 2003.0460	Japan: Kyushu, Amakusa Peninsula, Tomioka, Amakusa Marine Biology Laboratory, Kyushu University	AY580010

* Denotes outgroup used in present study.

1865: 69; Miers, 1880: 315; Nauck, 1880: 46, 1886: 286; Walker, 1887: 111; De Man, 1888a: 389; Walker, 1887: 111; Whitelegge, 1889: 231; Ortmann, 1892: 565 (key); Doflein, 1902: 654; 1904: 35; Rathbun, 1910: 15, 1923: 137; Parisi, 1914: 283; Ihle, 1918: 182; Balss, 1922: 123, 1935: 116; Sakai, T., 1934: 284, 1936: 44, text fig. 6a, 1937: 90, pl. 12 fig. 1, 1956: 8, 1965: 56, pl. 22 figs. 23, 1960: 33, pl. 16 fig. 5, 1965: 56, pl. 22 figs. 23, 1976: 129, pl. 37 fig. 1, pl. 38 fig. 2; Shen, 1936: 64; Serène, 1937: 78, 1968: 41 (list); Buitendijk, 1939: 231; Lin, 1949: 13; Dawydoff, 1952: 139; Utinomi, 1956: 70, pl. 35 fig. 5; Tyndale Biscoe and George, 1962: 70; Guinot, 1967: 245 (list); Kim, 1970: 11; Holthuis and Sakai, 1970: 117, pl. 9; Griffin, 1972: 64; Matsuzawa, 1977: pl. 91 fig. 2; Shirai, 1980: 415; Takeda, 1982: 105, fig. 309; Miyake, 1983: 19, pl. 7 fig. 3; Dai et al., 1986: 91, fig. 49, pl. 11 fig. 4; Dai and Yang, 1991: 103, fig. 49, pl. 11 fig. 4; Chen, 1993: 680, fig. 3; Yamaguchi and Holthuis, 1993: 664, figs. 81,82; Yamaguchi and Baba, 1993: 309, fig. 94 a,b; Huang, 1994: 580; Ho, 1996: 73; Galil, 1997: 302 (part); Ng, 1998: 571094 (part), 1999: 612,613 fig. 1c-f, 2b-c, 2001: 10, 2002: 57, Sakai, K. 1999: 19, 20, pl. 8a fig. Jeng et al., 2000: 136; Davie, 2002: 127.

Calappa (Lophos) lophos – de Haan, 1837: 72, pl. 20 fig. 1.

Type Locality.—“East Indies”.

Material Examined.—Lectotype – 1 ♂ 106.5 by 68.5 mm (ZMB 2168), East Indian Seas, Herbst Collection. Others – EAST INDIAN SEAS: 1 ♀ (43.0 by 34.0 mm) (ZMB13602), (photograph examined only). JAPAN: 2 ♀ (118.0 by 73.7 mm, 105.2 by 72.5 mm), 1 ♂ (53.3 by 38.1 mm) (ZRC 2004.0691), Kyushu Island, Amakusa, Tomioka Fish Port, coll. J.C.Y. Lai and S. Arakaki, 6 September 2002. PHILIPPINES: 1 ♂, (53.5 by 38.8 mm) (ZRC 2004.477), Bohol, Panglao, Balicasag Island, coll. local fishermen, 2 March 2004; 1 ♂, (120.9 by 77.7 mm) (ZRC 2002.466), Bohol, Panglao, Balicasag Island, coll. local fishermen, June 2002, 4 ♂ (largest 47.2 by 33.8 mm), 1 ♀ (87.9 by 61.8 mm), Bohol, Panglao, Balicasag Island, coll. local fishermen, June 2002. SOUTH AFRICA: 1 male (84.89 by 55.79 mm) (NHM 1928.12.1.175), Durban Bay, coll. Marley, J.D., 2 Oct 1921. TAIWAN: 2 ♂, 2 ♀, 1 ♀, parasitized with *Sacculina* (49.3 by 35.2 mm) (ZRC 1998.207), Kaohsiung, Tung Kang port, coll. P.K.L. Ng, 5 September 1996; 1 ♂ (96.9 by 63.4 mm) (ZRC 1995.587), 1 ♂ (100.4 by 64.8 mm), 1 ♀ (114.6 by 76.4 mm) (ZRC 1995.585), 1 ♂ (100.8 by 79.0 mm) (ZRC 1995.589), I-Lan county, northeastern Taiwan, 100-300 m depth, coll. P.K.L. Ng, June 1993; 1 ♂ (54.2 by 38.3 mm), 2 ♂ (54.2 by 38.3 mm, 40.9 by 29.9 mm) (ZRC

1995.614), I-Lan county, Hsing Kang, coll. T.C. Lin, 20 November 1987; 1 juv ♀ (30.6 by 23.3 mm) (ZRC 1999.757), I-Lan county, Tachi Fish Port, coll. P.K.L. Ng and K. Lim, May 1999. THAILAND: 5 ♂, 1 juvenile (ZRC 1999.126), Phuket, Pichai Fish Port, coll. P.K.L. Ng and H.H. Tan, April 1999; 1 ♂ (116.0 by 79.5 mm) (ZRC 1998.1141), loc. Phuket, Pichai Fish Port, coll. S. Chaitiamwong et al., December 1998; 6 ♂, 5 ♀ (ZRC), Phuket, Pichai Fish Port, coll. P.K.L. Ng et al., 22-25 August 1999.

Diagnosis.—Width to length ratio of carapace 1.46-1.61 (mean 1.52); dorsal surface smooth, strongly convex. Rostrum slightly projecting anteriorly, with deep sulcus separating two triangular frontal teeth. Orbit surrounded by eight notches. Antero-lateral margin carinate. Clypeiform expansions at posterolateral margins well developed, with four sharp teeth, gradually tapering to a sharp point. Posterior carapace margin beaded, with six rounded lobes, each tapering laterally to a blunt tip, length of second lobe approximately two-thirds of first lobe. Endostomial septum with anterior margin rounded, protruding outwards in adults, visible as a prominent rounded lobe even when third maxillipeds closed; distal margin of first maxillipeds straight. Crest of chela with seven teeth, first five triangular, similar in size; other two subtruncate; small tooth present at base of manus; exterior border of meral protrusion with two spiny teeth. G1 stout, curved distally, tapering apically to narrow tip.

Colour.—Live and freshly dead adults are pink-orange to orange-beige, with red to reddish-purple spots and markings. In some specimens, the posterior part of the carapace surface is transversely by short streaks of reddish-brown. The posterolateral teeth are separated by a prominent purple to red oblique streak. The external surface of the orbit has red spots and oblique markings, with the internal surface having red blotches and other markings (Ng et al., 1999). In juveniles, the dorsal surface of the carapace has two pairs of ocelli, with the posterior pair the first to be lost as the animal matures, followed by the anterior pair (Ng et al., 1999) and the anterior two-thirds of the carapace are also covered with numerous, very small and evenly spaced pale reddish spots which disappear as they become larger (Ng et al., 1999, 2002).

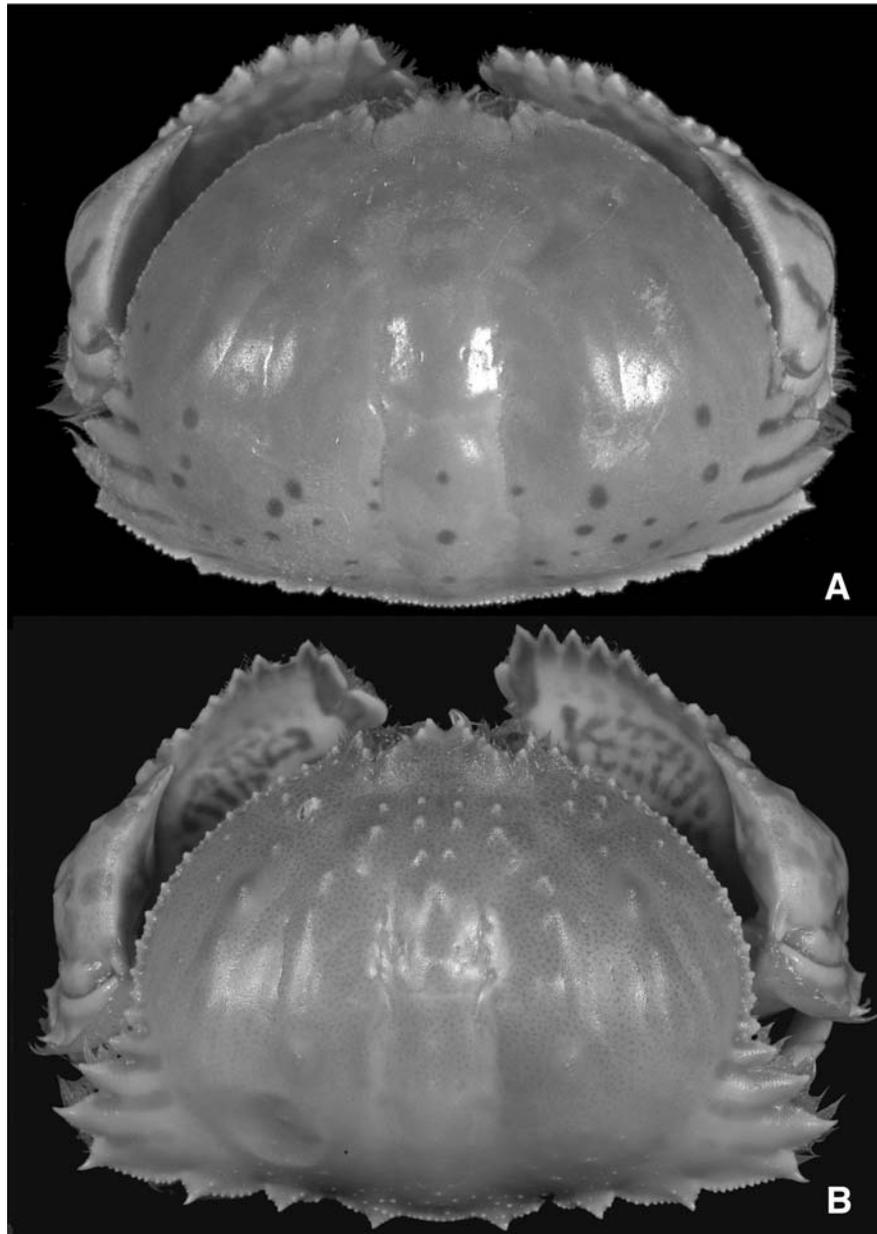


Fig. 1. Dorsal view a) *Calappa lophos*, male, (75.4 by 109.2mm) (ZRC 2002.0321); b) *Calappa guerini*, neotype male (30.4 by 48.9mm) (ZRC2005.0076).

Remarks.—The specimens referred to “*Calappa lophos*” by Galil (1997) belong to a complex of four species, viz., *C. lophos* (Herbst, 1782), *C. guerini* (Brito-Capello, 1870), *C. quadrimaculata* Takeda and Shikatani, 1990, and a new species (see below).

The taxonomic history of the species is confused. In describing *C. lophos*, Herbst (1782) had based his description and drawing on a specimen that fits well with what is here recognized as *C. guerini*. In his comments on the species, however, he indicated that he had other specimens that differed from what he described and figured in several carapace features, but he did not consider them significant. From Herbst’s remarks, it seems almost certain that these other specimens agree with what is here recognised as *C. lophos* sensu stricto. Since no type was selected by

Herbst, all his specimens are syntypes. Sakai K. (1999) found only one Herbst specimen in the Berlin Museum and identified it as the holotype of *C. lophos*. This is incorrect; it should be regarded as a lectotype instead. This lectotype of *C. lophos* conforms with the general concept of the species as defined by Ng et al. (1999) and most workers from the Pacific and eastern Indian Ocean. A check at the Berlin Zoological Museum confirmed that there are no other type specimens of *C. lophos*, and the specimen that was described and figured by Herbst (1782) is no longer extant (O. Coleman, personal communication). The Berlin Museum does have an old dried specimen of what is here defined as *C. guerini* (ZMB 730). Although it agrees with Herbst’s (1782) description and figure, it does not have any data associated with it and Coleman is confident it is not one

of Herbst's types. In any case, Sakai's (1999) type selection, which we accept, fixes the identity of *C. lophos* for the common and better-known Pacific and Indian Ocean species (see Ng et al., 1999).

Brito-Capello (1870) described *C. guerini* from India, and even though he was aware of Herbst's paper, he felt that his taxon differed from *C. lophos* in several aspects. His species has, however, generally not been recognised. Alcock (1896) first synonymised *C. guerini* with *C. lophos*, and all subsequent authors have followed suit. Takeda and Shikata (1990), however, commented that these two species may be different and the matter should be re-examined, but they did not elaborate.

Calappa lophos is known thus far for certain from the western Pacific and Indian Ocean while *C. guerini* is apparently restricted to the western Indian Ocean. All specimens from the western Indian Ocean which have been referred to *C. lophos* in the literature have been reidentified as *C. guerini*, although there is one specimen from South Africa that is clearly *C. lophos* (see discussion for *C. guerini*). As Herbst's specimens were from various parts of the Indian Ocean, it is not unexpected that Herbst obtained specimens of both species. *Calappa quadrimaculata* was recently shown to be a distinct species, contrary to Galil's (1997) conclusion that they are synonyms (see Ng et al., 1999). The present molecular data (table 2) supports this interpretation. In any case, the specimen of "*C. lophos*" figured in Galil's revision (1997: fig. 17a) is a new species.

Distribution.—Indian Ocean to western Pacific including the Andaman Sea, Japan, Taiwan and Australia (see also Ng, 1998).

Calappa guerini Brito-Capello, 1871
Fig. 1B, 3B

Calappa guerini Brito-Capello, 1871: 128-134, pl. 2, fig. 20.

Cancer lophos Herbst, 1782: 201, pl. 13, fig. 77.

Calappa lophos – Henderson, 1893: 395 (incerta sedis); Alcock and Anderson, 1895: 203; Alcock, 1896: 144; Laurie, 1906: 353; Monod, 1928: 124, fig. 13a; Chopra, 1933: 28; Stephensen, 1945: 65, figs. 5a-b; Barnard, 1947: 372, 1950: 351, fig. 66 j-m; Pillai, 1951: 8; Chhappargar, 1957: 404, fig. h; Serène, 1968: 41 (list); Kensley, 1969: 151 (list); Aravindakshan and Sundaram, 1983:169; Tirmizi and Kazmi, 1986: 54-56, fig. A-G, 1987: 313-314, fig. 1.

Material Examined.—Neotype (here designated): 1 ♂ (48.9 by 30.4 mm) (ZRC 2005.0076) from India, Chennai, Kasimedu Fish Landing. Others: EAST INDIAN OCEAN: 1 ♂ (75.0 by 49.0 mm) (ZMB 730) (photographs examined), 2 ♀ (71.0 by 44.9 mm and 74.1 by 47.4 mm) (ZMUC), 1 ♂ (46.0 mm carapace length, lateral spines broken), 1 female (damaged) (ZMUC), no other data; 2 ♀ (ZMUC), no other data. INDIA: 1 ♀ (82.1 mm carapace width, crushed anteriorly) (ZRC 2001.1133), 1 ♂ (43.2 by 70.9 mm), 1 ♀ (43.4 mm by 69.0 mm) (ZRC 2001.1134), Tamil Nadu, fish landing opposite vellar estuary, coll. A.S Fernando and N.K. Ng, 24 March 2001; 1 ♀ (85.1 by 55.5 mm) (ZRC 2001.1135), Tamil Nadu, Tranquebar, coll. A.S. Fernando and N.K. Ng, 16 March 2001; 1 ♀ (52.2 mm carapace length, laterally damaged) (ZRC 2000.2255), Bay of Bengal, south Chennai, Tamil Nadu Parangpitta (Porto Novo) landing point near Vellar estuary, coll. N. Sivasothi, 2000. 2 ♂ (larger 63.6 by 38.6 mm), 1 ♀ (62.6 by 40.3 mm) and

2 juveniles (ZRC2005.0077), Chennai, Kasimedu fish Landing, coll. Z. Jaafar, 23 Nov 2004. PAKISTAN: 1 ♀ (63.7 by 41.5 mm) (ZRC 2000.2398), Karachi fish harbour coll. 26 January 1983; 1 ♂ (67.3 by 40.1 mm) (ZRC 2000.2399), Karachi fish harbour, coll. 3 February 1983; 1 ♂ (66.8 by 39.2 mm) (ZRC 2000.2400), Karachi fish harbour, coll. 30 March 1983. PERSIAN GULF: 8 ♂ (ZMUC), Station 103. 3 Somil VNV. Chahbar, 10 m, sand, coll. Loppenthin, 31 March 1938.

Type Material.—Since the original female holotype specimen of Brito-Capello is lost, a male (48.9 by 30.4 mm) (ZRC2005.0076) is here designated as the neotype of *C. guerini*.

Type Locality.—Brito-Capello (1871) described the species from the "East Indies," but it has been documented that the type locality is Yanam along the northeast coast of India. The present neotype designation fixes the type locality as East Indian Ocean Bay of Bengal.

Diagnosis.—Width to length ratio of carapace 1.56-1.72 (mean 1.54); dorsal surface convex, smooth, some tubercles present near anterior margin; dorsal surface with numerous scattered red spots. Rostrum slightly projecting with deep sulcus separating two triangular frontal teeth. Orbit surrounded by eight notches. Anterolateral margin carinate. Posterolateral clypeiform extensions well developed, each side with four sharp teeth with tips slightly upturned. Posterior carapace margin with six rounded lobes, each lobe ends with a small but very acuminate tip medially; posterior carapace margin weakly granulated. Endostomial septum with deep cleft on anterior margin, appearing concave in adults, not strongly protruding outwards, appearing as a narrow triangular tooth when third maxillipeds closed. Crest of the cheliped with seven teeth, first five triangular, similar in size, the other two subtruncate; small tooth present at base of manus; exterior border of meral protrusion with two spiny teeth.

Colour.—Red streaks present between posterolateral teeth. External and internal surfaces of cheliped with numerous red spots and markings.

Remarks.—*Calappa guerini* was described by Brito-Capello (1871) on the basis of a female specimen from the collection of Guérin Méneville who obtained it from Yanaon (present day Yanam, northeast coast of India). The most diagnostic feature of *C. guerini* according to Brito-Capello (1871:129) is "... e finalmente a existencia de um par de dentes espiniformes a meio do bordo posterior da carapaca, constitue um caracter privativo da nossa especie" translated here to mean "presence of two spines on the posterior border of the carapace flanking the abdomen". Compared to *C. lophos*, these spines are much sharper (Brito-Capello, 1871: table 2, fig. 2). Brito-Capello did not mention any markings on the carapace, but noted that it was "Corpada, equal" (uniformly brown throughout) (Brito-Capello, 1871: 129).

The description and figure of *C. guerini* by Brito-Capello (1871) actually fits well that of *C. lophos* given by Herbst (1782: 201, pl. 13, fig. 77), with the perceived differences in

length of the spines between their two accounts relatively minor. However, compared with the lectotype of *C. lophos* the differences are more significant suggesting that two species are involved. As discussed earlier, it is clear that Herbst (1782) had specimens of two species but felt they were conspecific. It is likely that the specimen Herbst (1782: pl. 13, fig. 77) described and figured and regarded as typical *C. lophos* is conspecific with *C. guerini*. The only extant specimen of *C. lophos* (the present lectotype), which Herbst regarded as only a variant of typical *C. lophos*, however, just happened to be the more well known Pacific and eastern Indian Ocean species. This twist of events makes the name *Calappa guerini* Brito-Capello, 1871, again available for use.

Specimens of *C. lophos* examined by Henderson (1893), Alcock (1896), Ihle (1918), Barnard (1950), (Chhapgar (1957), Aravindakshan and Sundaram (1983) and Tirmizi and Kazmi (1988), Jayabaskaran et al., (1999) include (or are wholly) specimens of *C. guerini* based on their descriptions as well as the figures provided. We have on hand, however, one male specimen from Durban, South Africa (NHM 1928.12.1.175) that is clearly identifiable with *C. lophos* as presently defined. This individual was obtained from the Stebbing collection in NHM and we have no reason to doubt the authenticity of the stated provenance. Therefore, the range of *C. lophos* appears to extend to the western part of the Indian Ocean. More work will need to be done to ascertain if the two species are indeed sympatric and to what extent *C. lophos* occurs in the western Indian Ocean. On the other hand, we have no records of *C. guerini* east of India and Sri Lanka, and this species appears to be restricted to the western Indian Ocean.

Calappa guerini differs from *C. lophos* in the following aspects. The dorsal surface of the carapace of *C. guerini* is distinctly less convex than that of *C. lophos* (for specimens of equivalent sizes), and the carapace width to length ratio of *C. guerini* ranges from 1.56 to 1.72 (mean 1.54) while that of *C. lophos* is from 1.46 to 1.61 (mean 1.52). The carapace width is greater in *C. guerini* due to the more outwardly projecting clypeiform expansions. *Calappa lophos* on the other hand, appears more rounded. While both species have four teeth on the posterolateral border, the clypeiform expansions of *C. guerini* flare out more and the ends of the teeth have an upward tilt whereas the expansions of the posterolateral margin of *C. lophos* does not flare out at all and are directed downwards or laterally outwards, even when they are sharp. Six small but sharp spines also project from the lobes of the posterior carapace margin in *C. guerini*; these are absent in *C. lophos*. Perhaps the most outstanding difference is that the median septum of the endostome is deeply excised anteriorly forming a convex depression in *C. guerini* so much so that only a small part of this is visible (as an acute tooth), even when the third maxillipeds are closed (Fig. 3B). In contrast, the anterior margin of the endostomial septum is well produced, evenly rounded in *C. lophos* and is clearly visible as a prominent rounded lobe even with the third maxillipeds closed (Fig. 3A). *Calappa guerini* also appears to be a relatively smaller species. The largest female studied measured 74.1 by 47.4 mm (ZMUC).

The fresh colours of both species are superficially similar but there are notable differences. The dorsal surface of the

carapace of *C. guerini* has numerous small red spots, especially on the anterior part, even when adult. Young *C. lophos* also have these small red spots but they tend to be more or less uniformly arranged, and by the time they reach larger sizes (in excess of ca. 40 mm carapace width), these spots disappear, with the surface appearing plain. In *C. lophos*, the external surfaces of the chela, carpus and merus have spots and oblique streaks, with the spots gradually becoming fewer or merging to form short streaks in large specimens. In *C. guerini*, however, the external surface of the cheliped has only spots that never form long streaks. The reddish-purplish streak present between the posterolateral teeth are present in both species.

Brito-Capello's types in the old Lisbon Museum are no longer extant, having been lost in a fire many years ago. In view of the similarity of *C. guerini* and *C. lophos* and the complex taxonomy discussed above, a neotype of *C. guerini* is clearly necessary. We here select a male specimen collected from the Bay of Bengal as the neotype to stabilize its taxonomy.

Distribution.—*Calappa guerini* has so far only been reported from the Indian Ocean. It is the only species in the western Indian Ocean and Persian Gulf. In the eastern Indian Ocean, *C. lophos* is also present, but from the available records, it seems that *C. guerini* is absent from the Andaman Sea.

Calappa quadrimaculata Takeda and Shikatani, 1990

Fig. 2A

Calappa quadrimaculata Takeda and Shikatani, 1990:482; Jeng, 1998: 60, Ng et al., 1999: 609, Jeng et al., 1998:136, Huang and Lützen, 1998:1327, Ng et al., 2001: 11.

Calappa lophos – Galil, 1997: 302 (part) (not *Cancer lophos* Herbst, 1782).

Material Examined.—Holotype: 1 ♂ (76.6 by 47.4 mm) (NSMT-Cr 9626) Nakagusuku Bay, Okinawa, Ryukyus. Others: JAPAN: 1 ♂ (83.7 by 50.8 mm) (CBM 492), Ryukyus, Okinawa, Nakagusuku Bay, gill net, 10-20 m depth, coll. T. Komai, 22 June 1994; 1 ♀ (78.6 by 49.6 mm) (ZRC 2004.457), Okinawa, Naha Island, Ishikawa Fish Port, gill net, coll. J.C.Y. Lai et al., 26 November 2003. PHILIPPINES: 1 ♂ (NMCR 4254), Barangay Bacong Bacong, Gasan, Marinduque Province, coll. J. Cabrera and Velarde, 28 November 1976. TAIWAN: 1 ♂ (50.0 by 33.0 mm) (ZRC 1997.67), I-Lan county, Tachi Fish Port, coll. P.K.L. Ng, 3-4 August 1996; 1 ♂ (60.1 by 38.5 mm) (ZRC 1998.535), I-Lan county, Tachi Fish Port, coll. J. F. Huang, 11 April 1991; 1 ♀ (62.3 by 40.7 mm), I-Lan county, Tachi Fish Port, coll. T.Y. Chan, 9 September 1984; 1 ♀ (68.8 by 45.5 mm) (ZRC 1999.677), I-lan county, Geng-fang Fish Port, in shallow water tangle nets, coll. P.K.L. Ng, 28 May 1999.

Type Locality.—Ryukyu Islands, Japan.

Diagnosis.—Width to length ratio of carapace 1.55-1.73 (mean 1.61); dorsal surface smooth, convex; posteriormost areas with some tubercles. Rostrum slightly projecting, with a shallow sulcus separating two triangular frontal teeth. Orbit surrounded by six notches. Anterolateral margin carinate. Posterolateral clypeiform extensions well developed,

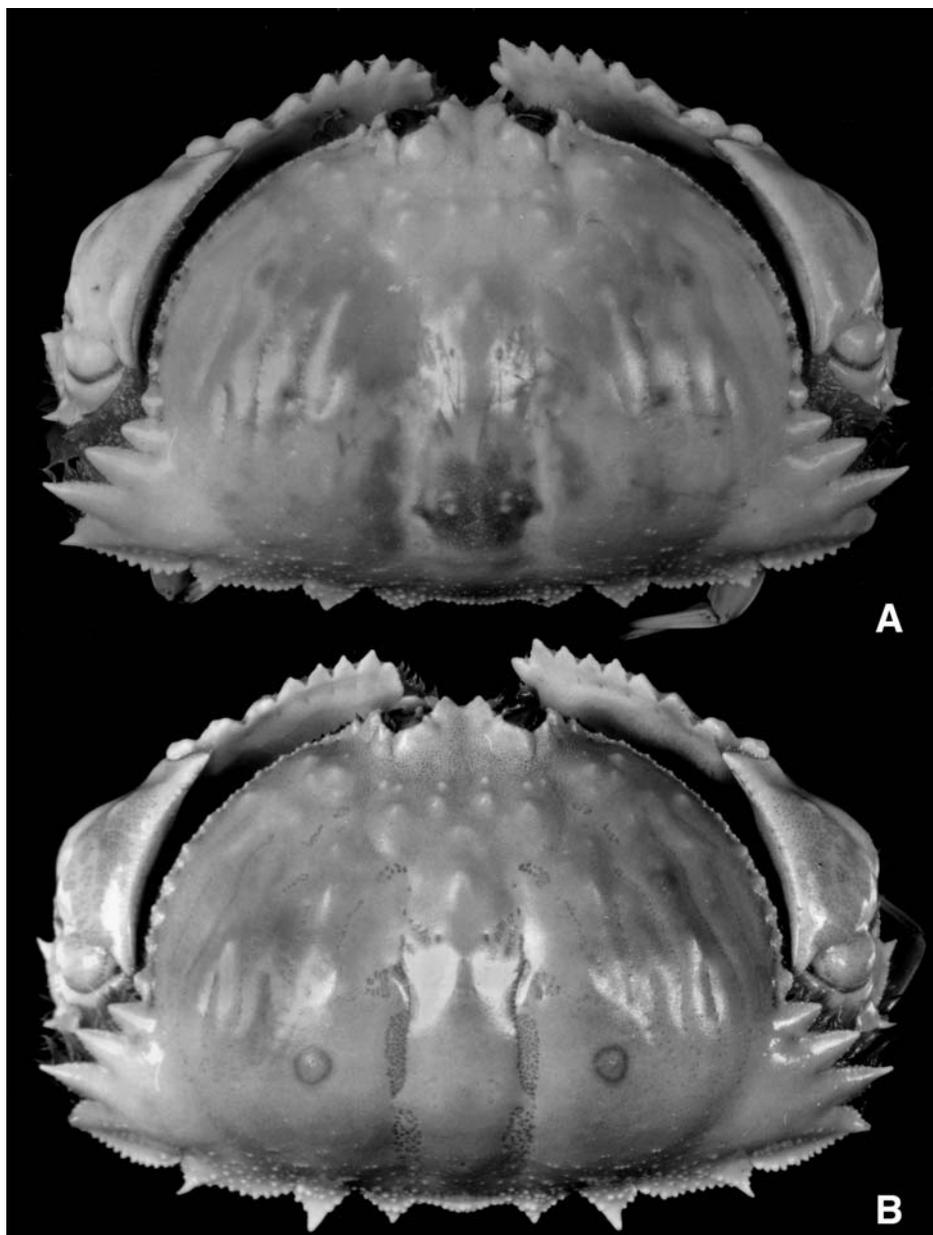


Fig. 2. Dorsal view a) *Calappa quadrimaculata*, female (45.5 by 68.8 mm) (ZRC 1999.0677); b) *Calappa acutispina* sp. nov., holotype male (46.7 by 78.8 mm) (MNHN B25701).

each side with four sharp teeth, with tips slightly upturned. Posterior carapace margin granulated, with six spines; first spine starting from second posterior lobe, second spine from third lobe, third tooth flanking convex area behind intestinal region. Endostomial septum with anterior margin rounded, visible as a rounded lobe in adults even when third maxillipeds closed. Crest of manus with five triangular teeth, followed by two teeth with broad base; small tooth present at base of manus, exterior border of meral protrusion with two spiny teeth. G1 stout with broad base, tapers apically to finely granulated narrow tip.

Colour.—Live specimens pale orange to cream. Four ocelli usually present on carapace, single spot on the carpus (see Ng et al., 1999: Fig. 1).

Remarks.—This species was synonymised with *C. lophos* by Galil (1997) in her revision of the Indo-West Pacific species of *Calappa*. She attributed the characters given by Takeda and Shikatani (1990) used to distinguish between the two as those seen in juvenile specimens of *C. lophos*. Ng et al. (1999) subsequently argued that the differentiating characters are valid for specimens larger than 30 to 40 mm in carapace length; and there were other differences. The carapace of *C. lophos* is distinctively more convex than that of *C. quadrimaculata*. The mean carapace length to width ratio for *C. quadrimaculata* is 1.61 whilst that of *C. lophos* is 1.52, suggesting that the carapace of *C. quadrimaculata* is longer than broad compared to *C. lophos*, which is broader than long.

The first and second lobes of the posterior margin in *C. quadrimaculata* are almost equal in length with a mean ratio of 0.95. However, in *C. lophos*, the second posterior lobe is very much shorter than the first (mean ratio 1.4). There is also a difference in the structure of the third posterior lobe. In *C. quadrimaculata*, it is a sharp tooth whereas in *C. lophos*, there is a ridge that tapers gently internally towards the median of the posterior margin. The teeth along the posterior margin of the carapace are also more distinct in *C. quadrimaculata* compared with *C. lophos* as the clefts separating them are distinctly deeper.

The patterns and markings of the two species are also different. When fresh, *C. lophos* has a series of streaks between the posterolateral teeth, scattered spots on the dorsal surface of the carapace with streaks of purple across it. The external surface of the manus always has oblique streaks and scattered spots of purple followed by two or three streaks of purple down the carpus. There is also a ring of purple in the anterior end of the merus where there is a flattened protrusion. In *C. quadrimaculata*, there are no streaks between the posterolateral teeth; four ocelli on the dorsal surface of the carapace without any streaks or markings and only a single median spot on the carpus of the cheliped and no other markings on the other segments of the cheliped. Small specimens of *C. lophos* (30–40 mm carapace width) also possess four ocelli on the dorsal surface of the carapace, but the posterior two are lost as the crab increases in size. Markings on the cheliped typical of *C. lophos* are also clearly visible as the crab becomes larger (> 40 mm).

Ng et al. (1999) noted that *C. quadrimaculata* is a smaller species compared to *C. lophos*. Specimens of *C. lophos* of up to 120.0 mm in carapace width have been collected whereas the largest *C. quadrimaculata* studied measured 84.0 mm. Specimens of *C. quadrimaculata* measuring 50.0 by 33.0 mm (ZRC 1997.617) are already mature, with the G1 well chitinised and setose. Specimens of *C. lophos* even larger than 50 mm in carapace width, however, are still immature, with the G1 relatively soft and setae sparse to absent (Ng et al., 1999). The carapace width to length ratio of *C. quadrimaculata* measured in this study also falls within the range noted by Takeda and Shikatani (1990) and Ng et al. (1999).

The discovery of a specimen (NMCR 4254) from Marinduque shows that the range of this species extends to the Philippines.

Distribution.—Known from Japan, Taiwan and the Philippines.

Calappa acutispina, new species

Fig. 2B

Calappa lophos – Galil 1997: 302, fig. 16, 17a, 20a, 32, 35c.

Material Examined.—Holotype: 1 ♂ (78.8 by 46.7 mm) (MNHN B25701), North West Coast, Nosy Bé, Madagascar, coll. R. Plante, 4 August 1965.

Type Locality.—Madagascar.

Diagnosis.—Width to length ratio of carapace 1.6; dorsal surface smooth; anterior surface covered with small tu-

bercles; convex, appearing as a flat dome when viewed posteriorly. Rostrum slightly projecting, with a shallow sulcus separating two triangular frontal teeth. Orbit surrounded by six notches. Anterolateral margin carinate. Posterolateral clypeiform extensions well developed, each side with four sharp teeth with tips slightly upturned. Posterior carapace margin granulated, with six sharp tips; first tip starting from side of second posterior lobe, second tip from third triangular protrusion, third tip flanking convex area behind intestinal region. Endostomial septum with anterior margin rounded in adults, distinctly visible as rounded lobe when third maxillipeds closed. Crest of manus with five triangular teeth, followed by two teeth with broad base; small tooth present at base of manus, exterior border of meral protrusion with two spiny teeth. G1 stout, with broad base, tapers apically to narrow tip, tip finely granulated.

Colour.—Two spots present on posterior surface of carapace. Single spot on the carpus of the cheliped.

Description.—Carapace broad, width to length 1.6; dorsal surface convex, highest part of dome relatively flat; anterior portion with numerous faint grooves and tubercles on hepatic, protogastric and epigastric regions, a pair of furrows flanking mesogastric, metagastric, cardiac and intestinal regions, grooves present along branchial regions; frontal region behind orbit and rostrum densely covered with tiny dense granules; posterior region of carapace along margin covered with scattered granules. Sulcus of rostrum U-shaped, not projecting beyond orbits, margins smooth. Orbital margin composed of four lobes, each lined with tiny fissures. Anterolateral margin convex, carinate, with five small notches increasing in size posteriorly.

Clypeiform expansion well developed margins slightly turned upwards; with four laciniate teeth, flared outwards; first two triangular in shape, conical, last two tapers sharply to a point, slightly upturned. Last tooth of posterolateral margin forming first lobe of posterior carapace margin, margin serrated; second lobe as wide as first, lateral end bears single sharp tooth; third lobe triangular in shape, length about a third of second lobe, with a tooth at apex; median lobe consists of a weak convex area flanked by two sharp triangular teeth behind intestinal region.

External surface of cheliped with seven faint tubercles; internal surface smooth save for fringe of dense setae basally. Crest of manus with seven teeth, five distal ones triangular in shape, with similar width of base, increasing in height distally, two proximal teeth wider at base, not as sharp as distal five. One tooth protrudes from proximal basal margin of manus, basal margin heavily beaded. Distal margin of merus flattened, lined with long setae, consisting of four lobes, median two lobes about half as wide as adjacent lobes, one tooth projects out of each of distal two sections, anteriorly directed.

Remarks.—This specimen was identified by Galil (1997) as *C. lophos*. While there are many similarities between these two species, it is easy to differentiate them with the following characters. *Calappa lophos* bears numerous red spots and markings on the external and internal surface of the cheliped, absent on *C. acutispina*. *Calappa acutispina* new species also has a single spot of the carpus which is

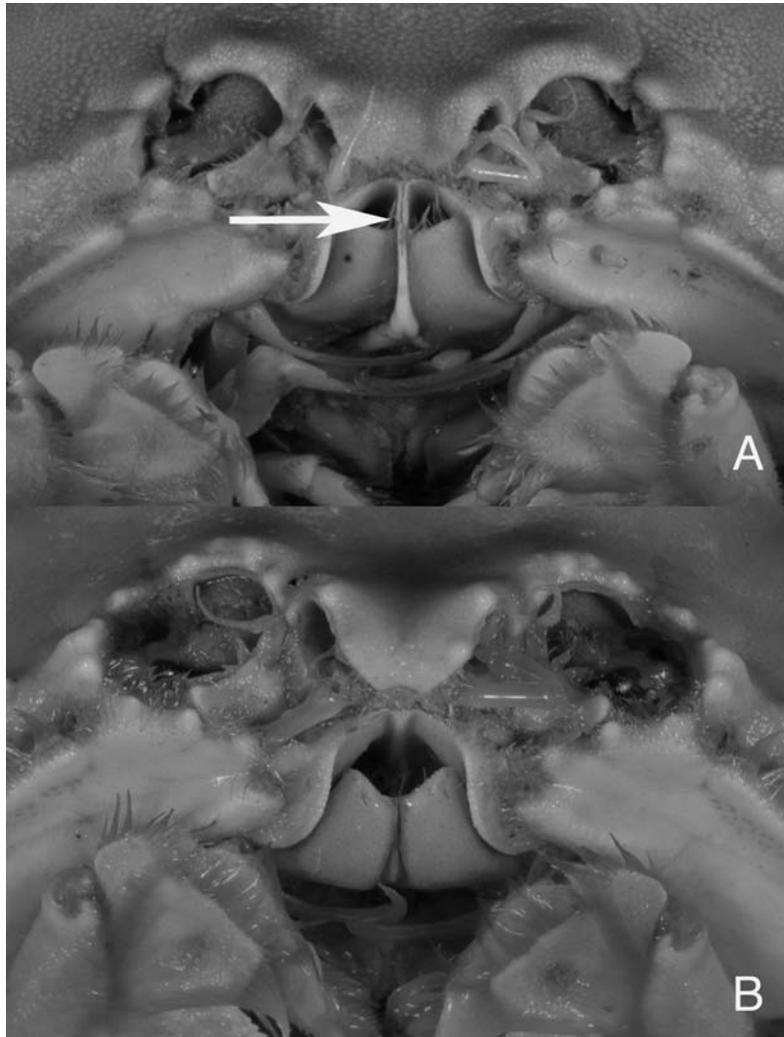


Fig. 3. Frontal view a) *Calappa lophos*; b) *Calappa guerini*. Arrow indicates prominent endostomial septum.

absent in *C. lophos*. In this respect, *C. acutispina* is more similar to *C. quadrimaculata* than *C. lophos*.

The clypeiform expansion is less developed in *C. lophos* compared with *C. acutispina*, the teeth at the posterolateral carapace is directed downwards in *C. lophos* whereas it is flat with an upward tilt in *C. acutispina*. The carapace of *C. acutispina* is also distinctly much less convex than *C. lophos* and *C. quadrimaculata* due to it being broader at the width. *Calappa acutispina* also has a shallower sulcus in the epistome compared with equivalent sized specimens of *C. lophos* and *C. quadrimaculata*.

As with *C. quadrimaculata*, the width of the first and second protrusion on the posterior margin of the carapace is more or less equal in *C. acutispina* in contrast with *C. lophos* where the second lobe is two-thirds the length of the first lobe. The teeth on the posterior lobes are also sharper in *C. acutispina*, with deeper clefts and fissures separating them (see figures). In *C. acutispina* (and *C. quadrimaculata*), only the first and last posterior spine projects from a rounded lobe. The other four spines are triangular protrusions from the posterior margin. There is a distinct cleft that separates the first and second teeth from

the third in *C. acutispina* and *C. quadrimaculata*, but is absent in *C. lophos*.

Calappa acutispina, although superficially similar to *C. quadrimaculata*, cannot be considered as being conspecific with it on the basis of the different patternings on the carapace (two ocelli vs. four), the overall shape of the carapace (flat vs. more convex), and the shape of the spines on the posterior carapace (more defined in *C. acutispina*).

Etymology.—*Acutispina* means “sharp spines”. This is referred to the spines on the posterior margin which are distinct and sharp.

KEY TO MEMBERS OF *C. LOPHOS* SPECIES GROUP

- 1a. Endostomial septum excised deeply anteriorly, concave, anteriormost portion not visible with third maxillipeds closed *C. guerini*
- 1b. Endostomial septum rounded anteriorly, convex, anteriormost portion visible as a rounded lobe with third maxillipeds closed 2

Table 2. GTR corrected pair wise distance for COI between *Calappa* spp used in this study.

	1	2	3	4	5	6	7	8	9	10	11	12
1 <i>Mursia armata</i>	—	—	—	—	—	—	—	—	—	—	—	—
2 <i>C. bicornis</i>	0.195	—	—	—	—	—	—	—	—	—	—	—
3 <i>C. calappa</i>	0.218	0.200	—	—	—	—	—	—	—	—	—	—
4 <i>C. capellonis</i>	0.225	0.185	0.19	—	—	—	—	—	—	—	—	—
5 <i>C. clypeata</i>	0.250	0.225	0.222	0.220	—	—	—	—	—	—	—	—
6 <i>C. gallus</i>	0.265	0.196	0.209	0.136	0.226	—	—	—	—	—	—	—
7 <i>C. hepatica</i>	0.251	0.217	0.196	0.233	0.23	0.236	—	—	—	—	—	—
8 <i>C. liaoi</i>	0.201	0.210	0.196	0.139	0.222	0.195	0.221	—	—	—	—	—
9 <i>C. lophos</i>	0.207	0.194	0.188	0.214	0.227	0.228	0.245	0.211	—	—	—	—
10 <i>C. philargius</i>	0.230	0.180	0.186	0.217	0.250	0.215	0.22	0.192	0.170	—	—	—
11 <i>C. quadrimaculata</i>	0.244	0.182	0.191	0.211	0.212	0.240	0.223	0.229	0.176	0.185	—	—
12 <i>C. undulata</i>	0.213	0.176	0.209	0.119	0.207	0.148	0.216	0.127	0.198	0.202	0.220	—

- 2a. Length of second lobe of posterior carapace margin less than two-thirds length of first lobe *C. lophos*
 2b. Length of second lobe of posterior carapace margin more than two-thirds length of first lobe 3
 3a. Tips of spines on posterior carapace margin very sharp, elongated *C. acutispina*
 3b. Tips of spines on posterior carapace margin less developed *C. quadrimaculata*

species, the primer pair amplified a mitochondrial COI fragment of 690 basepairs of which 566 were used for phylogenetic analysis after excluding the PCR primer sequences. The percentage sequence divergence for all species examined based on the General Time Reversal (GTR) model is presented in Table 2. Percentage sequence divergence between the *C. lophos* and *C. quadrimaculata* was 18%. Intraspecific sequence divergence for *C. lophos* (based on three individuals sequenced) was 0.53%. Both *C. lophos* and *C. quadrimaculata* are in turn a sister group to *C. philargius* (from BI analysis). Interestingly, both morphs of *C. calappa* despite having low sequence divergence also split into two terminal nodes. Of the four plain and two mottled *C. calappa* specimens, sequence divergence between haplotypes obtained from plain specimens was 0.18% compared with

MOLECULAR PHYLOGENY

Of the 15 calappid species studied here, genomic DNA could not be obtained from *C. guerini* and *C. acutispina*, probably because either the specimens had not been well preserved, or were originally placed in formalin. For the remaining 13

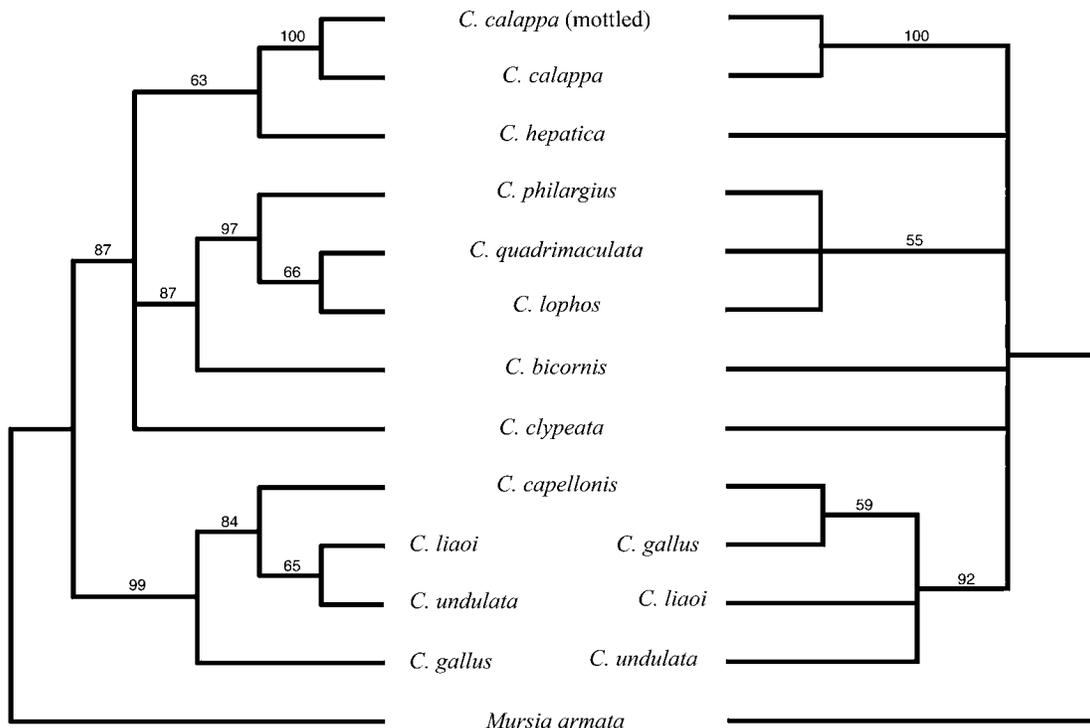


Fig. 4. Combined phylogenetic tree showing relationships between species of *Calappa* used in the study. Tree on the left is obtained via Bayesian Inference (BI) while the right is obtained via the Maximum Likelihood (ML) algorithm. Numbers on the branches denote posterior probability and bootstrap support for BI and ML methods respectively. Values less than 50 are not reflected.

Table 3. List of *Calappa* species worldwide.

<i>Calappa acutispina</i> , new species
<i>Calappa bicornis</i> Miers, 1884
<i>Calappa bilineata</i> Ng, Lai and Aungtonya, 2002
<i>Calappa calappa</i> (Linnaeus, 1758)
<i>Calappa capellonis</i> Laurie, 1906
<i>Calappa cinerea</i> Holthuis, 1958
<i>Calappa clypeata</i> Borradaile, 1903
<i>Calappa conifera</i> Galil, 1997
<i>Calappa convexa</i> De Saussure, 1853
<i>Calappa depressa</i> Miers, 1886
<i>Calappa dumortieri</i> Guinot, 1962
<i>Calappa flammea</i> (Herbst, 1794)
<i>Calappa galloides</i> Stimpson, 1859
<i>Calappa gallus</i> (Herbst, 1803)
<i>Calappa granulata</i> (Linnaeus, 1758)
<i>Calappa guerini</i> Brito-Capello, 1871
<i>Calappa hepatica</i> (Linnaeus, 1758)
<i>Calappa japonica</i> Ortmann, 1892
<i>Calappa liaoi</i> Ng, 2002
<i>Calappa lophos</i> (Herbst, 1782)
<i>Calappa monilicanthus</i> Galil, 1997
<i>Calappa nitida</i> Holthuis, 1958
<i>Calappa ocellata</i> Holthuis, 1958
<i>Calappa ocellaria</i> Ng, 2002
<i>Calappa pelii</i> Herklots, 1851
<i>Calappa philargius</i> (Linnaeus, 1758)
<i>Calappa pokipoki</i> Ng, 2000
<i>Calappa pustulosa</i> Alcock, 1896
<i>Calappa quadrimaculata</i> Takeda and Shikatani, 1990
<i>Calappa rosea</i> Jarocki, 1825
<i>Calappa rubroguttata</i> Herklots, 1851
<i>Calappa sebastieni</i> Galil, 1997
<i>Calappa springeri</i> Rathbun, 1931
<i>Calappa sulcata</i> Rathbun, 1898
<i>Calappa tortugae</i> Rathbun, 1933
<i>Calappa torulosa</i> Galil, 1997
<i>Calappa tuerkayana</i> Pastore, 1995
<i>Calappa undulata</i> Dai and Yang, 1991
<i>Calappa yamasitae</i> Sakai, 1980

0.7% for haplotypes obtained from mottled specimens. All *C. calappa* specimens used in this study were obtained from the same locality.

The combined COI gene tree of the 13 species of *Calappa* used in the study using Bayesian phylogenetic as well as maximum likelihood approach is shown in Fig. 4. The BI tree was generally well resolved with high posterior probability support although the relationships at the more basal nodes could not be inferred. The *C. gallus* group of species is basal to the other *Calappas*, and relationships between species in this group are well resolved with high posterior probabilities. *C. quadrimaculata* and *C. lophos* are placed as sister taxa, *C. philargius* is basal to them. The position of *C. clypeata* was unresolved while *C. hepatica* and the two colour forms of *C. calappa* were placed in the same group. The ML bootstrap tree, while not in conflict with the BI tree, offered less resolution; four clades were supported with bootstrap values over 50%.

GENERAL DISCUSSION

Calappa quadrimaculata was synonymized with *C. lophos* by Galil (1997) on the premise that *C. quadrimaculata* was no more than a juvenile *C. lophos*. Molecular data from the

partial COI fragment shows that the morphological characters used in the present study as well as that of those used by Ng et al. (1999) are concordant. The molecular data supports the recognition of *C. lophos* and *C. quadrimaculata* as distinct species (Takeda and Shikatani, 1990; Ng et al., 1999; current study). From the taxonomic study, it is clear that within the sister species of the *C. lophos* group, *C. lophos* is more closely allied with *C. guerini*, and *C. quadrimaculata* with *C. acutispina*. Unfortunately, attempts to extract genomic material from these *C. guerini* and *C. acutispina* were unsuccessful. However, when the COI gene sequence of *C. guerini* and *C. acutispina* become available, it will probably further support the present hypothesis of relationships based on adult morphological characters.

Results on the *C. gallus* group of species also agree with the *a priori* inference based on morphological data (Ng, 2002). *Calappa gallus*, *C. capellonis*, *C. liaoi* and *C. undulata* consistently form a single monophyletic clade with high branch support for both analyses. The “*C. gallus*” group of species are typically defined by the shape of their carapace, extent of clypeiform expansions, and outline of their posterior margins. Other species which have been included in this group but whose DNA are not available for this study are *C. matsuzawa*, *C. torulosa* and *C. pokipoki*.

Though the internal tips of the tree are generally well resolved (BI analysis tree), the trichotomy between *C. clypeata*, *C. lophos* group and *C. calappa* group indicate that the relationships between these clades are unresolved in the present study. This is probably due to the lack of other *Calappa* species. The only well-resolved clade in this study is the “*C. gallus*” group of species. The strong support shown for this clade from both analyses indicate that the morphological characters used for this group are valid. The inclusion of four out of seven species in this group also defined the relationships between members of this grouping. However, the same cannot be said for the rest of the groups. The placement of *C. clypeata* is unclear and the low posterior probability support for the *C. calappa* and *C. hepatica* clade indicates that the inclusion of *C. hepatica* makes the clade unstable. The relatively high support for the clade which includes *C. bicornis*, *C. philargius*, *C. quadrimaculata* and *C. lophos* indicates that this grouping is stable, however, the support for *C. quadrimaculata* and *C. lophos* as sister taxa, can probably be improved with the addition of genomic data from *C. guerini* and *C. acutispina*. Other taxa which would be useful to elucidate the relationships within this clade could be *C. dumortieri* and *C. bilineata*, both allied with *C. philargius*; with *C. ocellaria* a likely sister taxon to *C. bicornis*.

Bayesian posterior support values have been likened to be the equivalent of non-parametric bootstrap support values, but this is being debated by many (see Huelsenback et al., 2002; Erixon et al., 2003; Alfaro et al., 2003; Douady et al., 2003). There is currently no consensus of how posterior probabilities should be interpreted relative to more traditional measures such as the bootstrap value. Generally Bayesian posterior probabilities are higher compared with bootstrap support. Wilcox et al. (2003) concluded that BI values provide much closer estimates of phylogenetic accuracy and bootstrap supports carry a conservative bias and

thus are usually lower. It has also been suggested that Bayesian support values and bootstrap values may form the upper and lower bounds of node reliability (Douady et al., 2003). The present study has found the above observations to be largely true. The two trees produced by both BI and ML are not in conflict with each other even though relationships could not be resolved clearly in the ML tree. Node support values are also higher in the BI tree. The suggestion of Douady et al. in regard to value interpretation using both methods is accepted.

With 39 species of *Calappa* spread across the Indo-Pacific and Atlantic (Table 3), the number of species used in this study are too few and insufficient to establish a 'complete' picture of the phylogeny of *Calappa*. Nevertheless, the datasets presented here will be a useful start to a better understanding of phylogeny and relationships within the Calappidae.

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