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MORPHOLOGY BASED CLADISTIC ANALYSIS OF *METANEPHROPS*: THE MOST DIVERSE EXTANT GENUS OF CLAWED LOBSTER (NEPHROPIDAE)

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ABSTRACT

We performed the first cladistic analysis of *Metanephrops*, the most diverse extant genus of clawed lobster, using a morphology-based data matrix of all 20 species of *Metanephrops* and 35 cladistically informative characters, all external hard parts. Unweighted cladistic analysis corroborates previous studies that indicated that homoplasy is rampant in the evolution of clawed lobsters. Only 5 of the 68 synapomorphies identified by the analysis are unambiguous, unreversed synapomorphies. Recent species of *Metanephrops* have traditionally been divided (non-cladistically) into four morphology-based groups. Cladistic analyses support the traditional, *arafurensis*, Atlantic/*binghami*, and *japonicus* groupings; these groups are monophyletic. The *thomsoni* group is not supported by the cladogram. The (two) oldest known fossil *Metanephrops* species occur in Late Cretaceous, shallow marine rocks of the eastern/Atlantic side of the Antarctic Peninsula. The stratigraphic and geographic occurrences of these fossil species are the basis for the previously hypothesized, Late Cretaceous, southern high latitude origin of *Metanephrops*. Cladistic results corroborate that *Metanephrops* originated in the southern high latitudes. The cladistically most plesiomorphic single species, the recent *M. challengeri*, and the next most plesiomorphic species, the Late Cretaceous *M. rossensis*, are both known from the high southern latitudes. Likewise, the most plesiomorphic species group, the *binghami* group, is best known from the high southern latitudes.

INTRODUCTION

Metanephrops Jenkins, 1972, is an extant, clawed lobster genus (Family Nephropidae) with a very distinctive, carinate and spiny cephalothorax (Fig. 1). It is the most diverse extant lobster genus, known by 17 extant species and 3 fossil species. The recent species are mostly Indo-Pacific, deepwater (continental slope and deeper) dwellers.

The genus *Metanephrops* was erected to accomodate 13 recent species previously referred to *Nephrops* Leach, 1814, as well as a new, Pliocene fossil species, *Metanephrops motunauensis* Jenkins, 1972. Since that time, 4 recent and 2 Late Cretaceous fossil species have been discovered. Holthuis (1974, p. 824-826) provided a good definition of the genus, one that we follow herein.

Metanephrops is not distinguishable on the basis of any one morphologic feature. It is, however, unique in exhibiting the combination of: 1) prominent, spinose, supraorbital carinae that extend posteriorly to near the postcervical groove, 2) a prominent, narrow, antennal carina, 3) usually three pairs of thoracic carinae [except *M. neptunus* (Bruce, 1965) with two pairs] (Fig. 2), and 4) symmetrical chelipeds that are generally long, slender, and sometimes strongly carinated.

Metanephrops bears strong morphologic similarities to both the recent *Nephrops* [although a close relationship is disputed by DNA evidence of Tam and Kornfield (1998) and Tshudy et al. (2005)] and fossil *Paraclytia* Fritsch, 1887 (Fig. 3). *Metanephrops* is most easily distinguished from *Nephrops* by its possession of three features: 1) the branchial carina (absent on *Nephrops* and one species of *Metanephrops*, *M. neptunus*), 2) prominent supraorbital carina (much shorter and lower on *Nephrops*), and 3) prominent antennal carina (much shorter and lower on *Nephrops*). *Paraclytia* is distinguished from *Metanephrops* and *Nephrops* in exhibiting a unique sculpture of the pleon terga and pleura, and in possessing a telson with submedian carinae converging (instead of diverging) posteriorly.

Several authors (De Man, 1916; Yaldwyn, 1954; Jenkins, 1972; Chan and Yu, 1987, 1991; Holthuis, 1991; Chan, 1997) have maintained that recent species of *Metanephrops* can be divided into four morphologic groups, summarized below (Table 1).

Recent *Metanephrops* are dwellers of the outer continental shelf and, especially, continental slope. Species have been collected from depths between 50 and 994 meters, but most commonly greater than 150 m (list in Tshudy, 2003). Recent species occur at latitudes ranging from about 35°N (Japan) to almost 50°S (New Zealand), and are distributed mainly along the western edges of the ocean basins, especially the Indo-West-Pacific. Not a single occurrence is known from the central or eastern Pacific nor from the central or eastern Atlantic (Fig. 4).

Little is known about the evolutionary or biogeographic history of *Metanephrops*, despite its fossil record ranging back to the Late Cretaceous. Only 3 fossil species are known: *M. rossensis* Feldmann et al., 1993 [Late Cretaceous (Campanian)], 2) *M. jenkinsi* Feldmann, 1989 [Late Cretaceous (Maastrichtian — Paleocene)], and 3) *M. motunauensis* Jenkins, 1972 (Pliocene). Several workers (Jenkins, 1972; Feldmann and Tshudy, 1989; Feldmann et al., 1993; Chan, 1997) have presented hypotheses on the evolution and dispersal history of the genus.

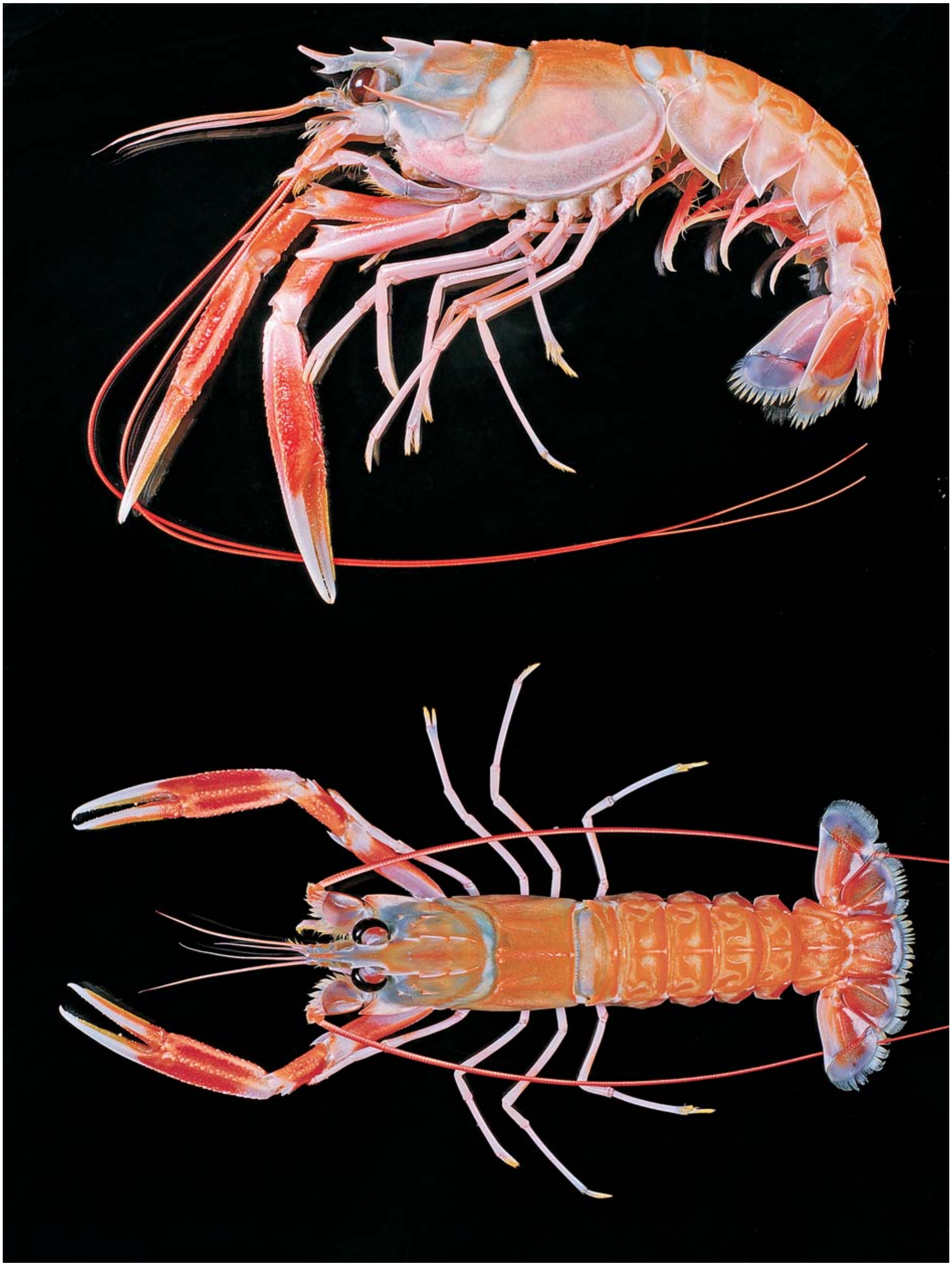

Fig. 1. Typical recent *Metanephrops*, *M. andamanicus* from Pratas, South China Sea.

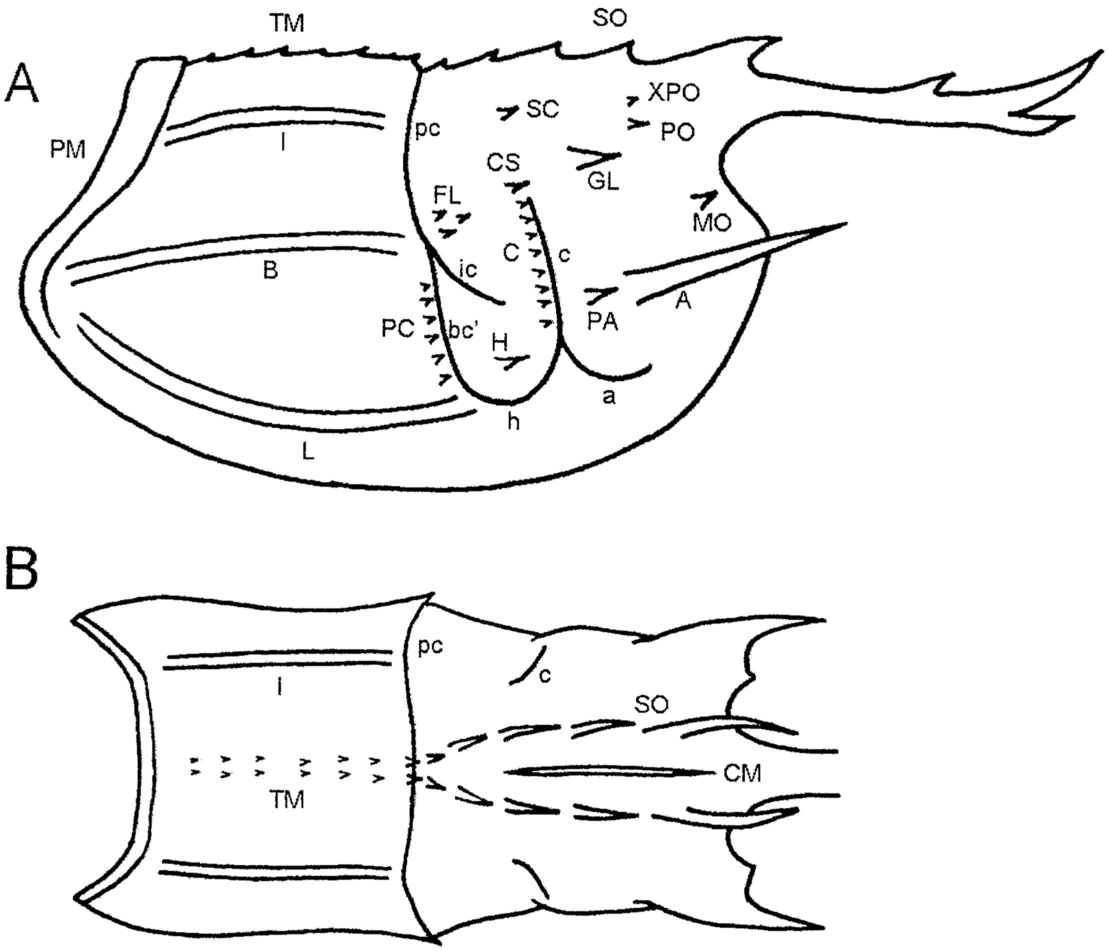

Fig. 2. Schematic line drawing of *Metanephrops* cephalothorax in A, right lateral and B, dorsal views, showing positions of grooves (lower case), carinae and spines (upper case). a = antennal groove; A = antennal spine; B = branchial carina; bc' = ventral extension of branchiocardiac groove (see Tshudy, 1993); c = cervical groove; C = cervical spinules; CM = cephalic median carina; CS = cervical spine; FL = flank spines; GL = glastro-lateral spine; h = hepatic groove; H = hepatic spine; I = intermediate carina; ic = intercervical groove; L = lateral carina; MO = metorbital spine; pc = postcervical groove; PA = postantennal spine; PC = postcervical spinules; PM = posteromarginal carina; PO = postorbital spine; SC = supracervical spine; SO = supraorbital carina/spines; TM = thoracic median carina/spines; XPO = extra postorbital spine(s).

Jenkins (1972) concluded that *Metanephrops* evolved in the Indo-West-Pacific, where it has diversified, adding that "*Metanephrops* possibly reached the Atlantic around southern Africa, but more probably migrated through the Tethys prior to or during the Lower Miocene. The sea connection between the Indian and Atlantic Oceans through Tethys was lost in the late Lower Miocene" (p. 175).

Feldmann (1989) named the then-oldest known fossil species of *Metanephrops*, *M. jenkinsi* (Maastrichtian—Paleocene of Antarctica), but he did not comment on the history of the genus. The discovery of *M. jenkinsi*, however, provided the first material basis for refining Jenkins' hypothesis that the genus originated in the Indo-West-Pacific. Feldmann and Tshudy (1989) suggested that *Metanephrops* evolved in the high southern latitudes, in shallow water, and then radiated into lower latitude, deeper settings. They also noted some underlying morphological similarities between *Metanephrops jenkinsi* and *Hoploparia stokesi* (Weller, 1903), which co-occur in the Antarctic Late Cretaceous-Paleocene, and suggested that *Hoploparia stokesi* may have been the root stock from which *Metanephrops* evolved.

Feldmann, Tshudy and Thomson (1993) described a still-older fossil *Metanephrops*, *M. rossensis*, from the Campanian of the Antarctic Peninsula. Noting the strong similarity between *M. rossensis* and the recent species of *Metanephrops*, they concluded that *M. rossensis* "seems certain to have been ancestral to most or all modern species" (p. 18). They further noted that *M. jenkinsi* is clearly less similar to recent *Metanephrops* than is *M. rossensis*, and added that *M. jenkinsi* "may be an offshoot off the *Metanephrops* main lineage" (p. 18-19). Having now two shallow-water, Cretaceous species, they reiterated the onshore-offshore, and high latitude to low latitude, dispersal theme (p. 19).

They also reiterated the hypothesis that the closest known ancestor of *Metanephrops* is *Hoploparia* and further speculated that the ancestor of *Metanephrops* might be, or at least be close to, the Campanian-Maastrichtian *Hoploparia antarctica* Wilckens, 1907, of Antarctica and South America, as suggested by both the morphology and occurrence of *H. antarctica*. Unlike other, typical *Hoploparia*, but like *Metanephrops*, *H. antarctica* has thoracic carinae and keeled chelipeds. *Hoploparia antarctica* co-

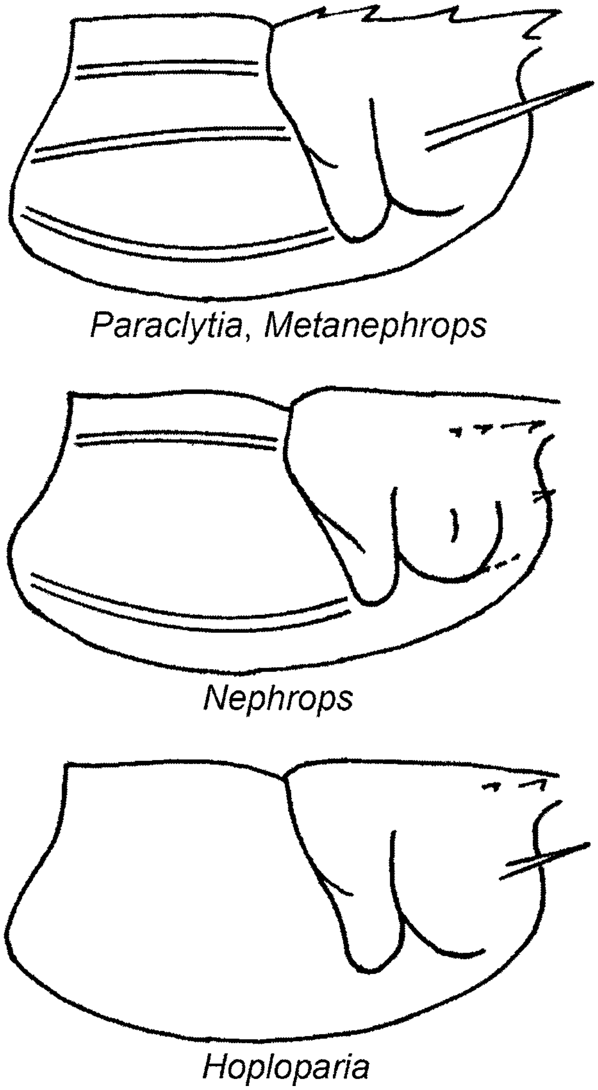

Fig. 3. Schematic drawings of cephalothoraxes of *Paraclytia*, *Metanephrops*, *Nephrops* and *Hoploparia*, emphasizing differences in supraorbital, antennal and thoracic ornamentation.

occurs with the oldest known *Metanephrops*, *M. rossensis*, in the Campanian portion of the Lachman Crags Member of the Santa Marta Formation on James Ross Island, Antarctic Peninsula (Feldmann et al., 1993).

Chan (1997) studied recent species extensively (and provided keys and geographic and bathymetric distribution maps for modern distributions) but, by an oversight, missed the two Cretaceous fossil species. Chan hypothesized that the genus probably originated in the Indo-Malay region, since most of the recent species (11 of 17) are present there. Chan said Jenkins (1972) was likely right in suggesting that the Atlantic group migrated to the Atlantic through the Tethys, instead of reaching the Atlantic via southern Africa.

Not since Jenkins' (1972) work has there been a taxonomically comprehensive examination of both the recent and fossil species of *Metanephrops*. Since 1972, six new species have been described, including the only two Cretaceous fossil species. Moreover, there has never been a cladistic analysis of the genus. Thus, the current study provides us a new opportunity to attempt reconstructing the history of the genus. We want to determine if the four, traditionally recognized, groups of *Metanephrops* species are supported by cladistic analysis. We also want to know what cladistic analysis indicates about the evolutionary and biogeographic history of the genus.

Four Traditional Groups

Recent species have traditionally been divided into four morphologic groups based on the ornamentation of the cephalothorax, pleon terga, and form and ornamentation of the chelipeds (Table 1). Neither of the two Cretaceous fossil species, *M. rossensis* and *M. jenkinsi*, fits neatly easily into any of the four groups.

The *binghami* or Atlantic group, *M. binghami* (Boone, 1925) and *M. rubellus* (Moreira, 1903), is characterized by a generally smooth (non-spiny) carapace, unsculptured pleon terga, uropods spineless dorsally, and by chelipeds that exhibit six spiny, longitudinal carinae and a flat outer margin. The Atlantic species are unique among congeners in possessing a postantennal spine, and in having a supracervical spine (named herein, character 9). Additionally, both species possess cervical and postcervical spinules that are absent in most Indo-Pacific species.

The *japonicus* group, consisting of *M. japonicus* (Tapparone-Canefri, 1873), *M. andamanicus* (Wood-Mason, 1892), *M. armatus* Chan and Yu, 1991, *M. formosanus* Chan and Yu, 1987, *M. mozambicus* Macpherson, 1990, *M. sagamiensis* (Parisi, 1917), and *M. velutinus* Chan and Yu, 1991, is characterized by a generally smooth (non-spiny) carapace, complexly sculptured pleon terga, uropods spine-

Table 1. Morphologic characteristics of the four traditionally (non-cladistically) recognized groups (modified from Chan, 1997), expanded here to include new characters (*) and the two Cretaceous fossil taxa, *M. jenkinsi* (J) and *M. rossensis* (R). Neither fossil species fits neatly into any of the four groups. **Chelipeds: *binghami* and *japonicus* groups with outer margin flat (squared off; not angular), but *japonicus* group also with longitudinal medial depression. Abbreviations: "ang.", angular; "sp.", spiny.

	BINGHAMI GROUP	*JAPON.* GROUP	*ARAFUR.* GROUP	*THOMPS.* GROUP
CARAPACE TEXTURE	smooth(JR)	smooth(JR)	spiny	smooth(JR)
CERVICAL SPINULES	yes(R)	no(J)	yes(R)	varies
POSTCERVICAL SPINULES	yes(JR)	no	varies	no
POSTANTENNAL* SPINES	yes(JR)	no	no	no
SUPRACERVICAL* SPINE	yes(J)	no(R)	no(R)	no(R)
TERGA SCULPTURED	no(JR)	highly	highly	none-little
SCALES* FACADE	no	yes (6 of 7)	no	no
CHELIPED OUTER MARGIN**	flat/sp.(J)	flat/sp.(J)	ang/less sp.(R)	ang./less sp.(R)
UROPODS SPINY	no	no	spiny	no

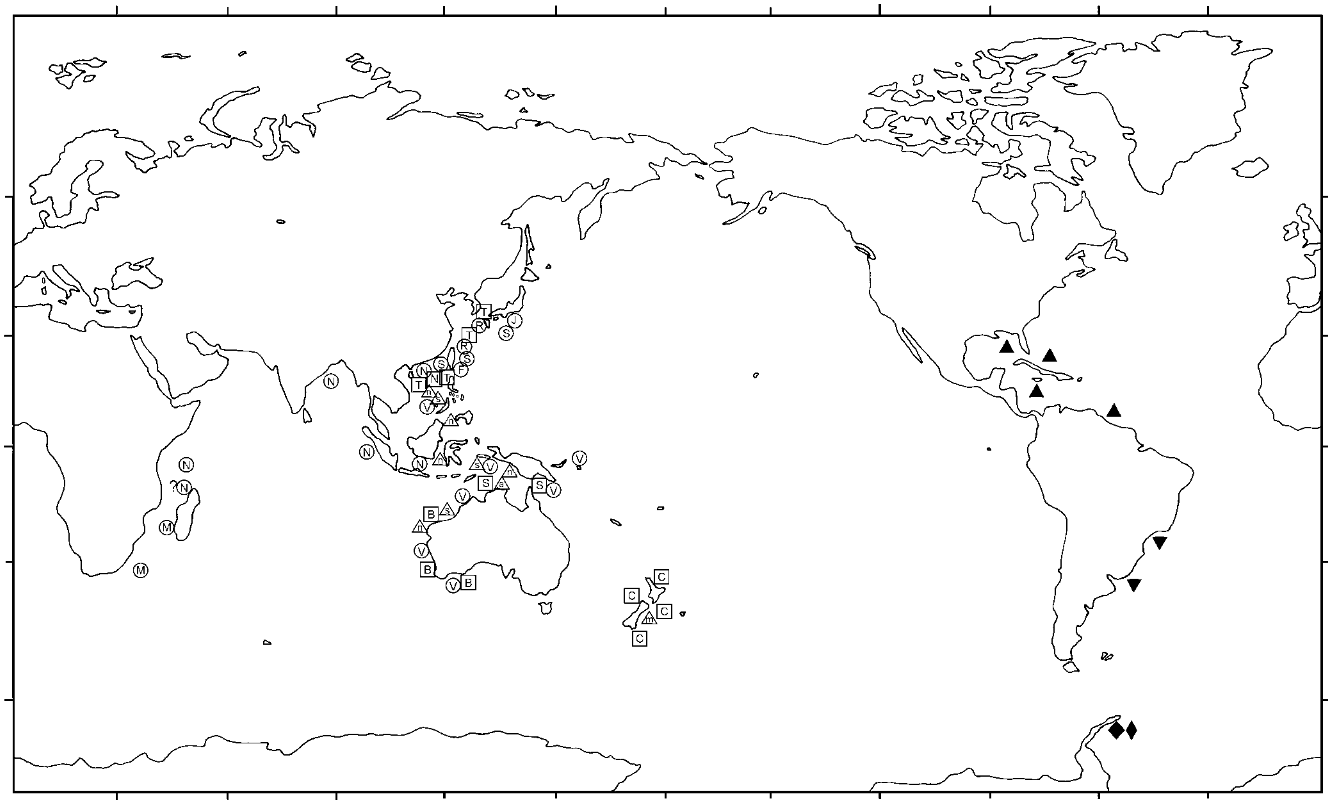

Fig. 4. Geographic distribution of all *Metanephrops* species, fossil (3) and recent (17), with symbols showing traditional groupings. The *arafurensis* group: △a = *M. arafurensis*, △m = *M. motunauensis*, △n = *M. neptunus*, △s = *M. australiensis*. The *binghami* group: ▲ = *M. binghami*, ▼= *M. rubellus*. The *japonicus* group: Ⓕ = *M. formosanus*, Ⓙ = *M. japonicus*, Ⓜ = *M. mozambicus*, Ⓝ = *M. andamanicus*, Ⓡ = *M. armatus*, Ⓢ = *M. sagamiensis*, Ⓥ = *M. velutinus*. The *thompsoni* group: $\boxed{B}$ = *M. boschmai*, $\boxed{C}$ = *M. challengeri*, $\boxed{N}$ = *M. sinensis*, $\boxed{S}$ = *M. sibogae*, $\boxed{T}$ = *M. thompsoni*. Cretaceous fossil species: ♦ = *M. jenkinsi*, ◆ = *M. rossensis*.

less dorsally, and spiny, carinate chelipeds with an outer border somewhat flat but with a longitudinal, medial depression. Terga have arched, lateral "eyebrow" furrows (character 15) that are absent in the *binghami* and *thomsoni* groups and in 2 of 4 of the *arafurensis* group. Terga also usually (6 of 7 recent species) have a "scales" shaped facade (character 16); "scales" are unique to this group. Chan and Yu (1987, 1988) initially said *M. formosanus* does not fit into any of the four groups, and was morphologically intermediate between the *japonicus* and *thomsoni* groups but, in 1997, Chan referred *M. formosanus* to the *japonicus* group (also see Chan and Yu, 1991).

The *thomsoni* group, consisting of *M. thomsoni* (Bate, 1888), *M. boschmai* (Holthuis, 1964), *M. challengeri* (Balss, 1914), *M. sibogae* (De Man, 1916) and *M. sinensis* (Bruce, 1966b), is characterized by a smooth (non-spiny) carapace, terga that are either completely unsculptured or (on *M. sinensis* and *M. thomsoni*) traversed by a transverse furrow interrupted medially, uropods spineless dorsally and also by weakly carinate, nearly smooth, e.g., *M. boschmai* and *M. sinensis*, to finely granulate chelipeds with outer margin always angular. This combination of features is unique to this group, although each of these features is exhibited independently in other *Metanephrops*.

The *arafurensis* group, consisting of *M. arafurensis* (De Man, 1905), *M. australiensis* (Bruce, 1966a), *M. neptunus* (Bruce, 1965), and the fossil *M. motunauensis* is characterized by a generally spiny carapace, pleon terga that are deeply marked by at least one or two transverse furrows, by uropods spinulose on the dorsal surface, and by weakly carinate, finely granulose to spiny (in *M. neptunus*) chelipeds with the outer margin always angular. These species are unique among congeners in having a generally spiny carapace, and in having spiny uropods.

The geographic ranges of the *arafurensis*, *japonicus*, and *thompsoni* groups largely overlap in the Indo-West Pacific. The *japonicus* group ranges (via two species) much farther across the Indian Ocean, all the away to Africa.

MATERIALS AND METHODS

Character Selection

We tried to make the matrix as big as possible, and used all known, cladistically informative characters (n = 35, App. I, II). Many other characters were considered but turned out to be invariant or autapomorphous, and therefore useless in determining phylogenetic relationships between *Metanephrops* species. Of the autapomorphous characters, several were those that made individual species distinctive and, thus, could be useful in species taxonomy, dichotomous keys, etc. All 35 characters describe external hardparts, including aspects of the cephalothorax (#1-13; Fig. 2), pleon and telson (#14-23, 35; Fig. 5), appendages (#24-34), and color pattern (#34-35). All but two characters (#3, #19) are coded as binary, with most character states being "absent" or "present".

Taxon Selection

All species of *Metanephrops* were used in the analysis. All 17 recent taxa were included in the matrix, and all of these were examined firsthand by

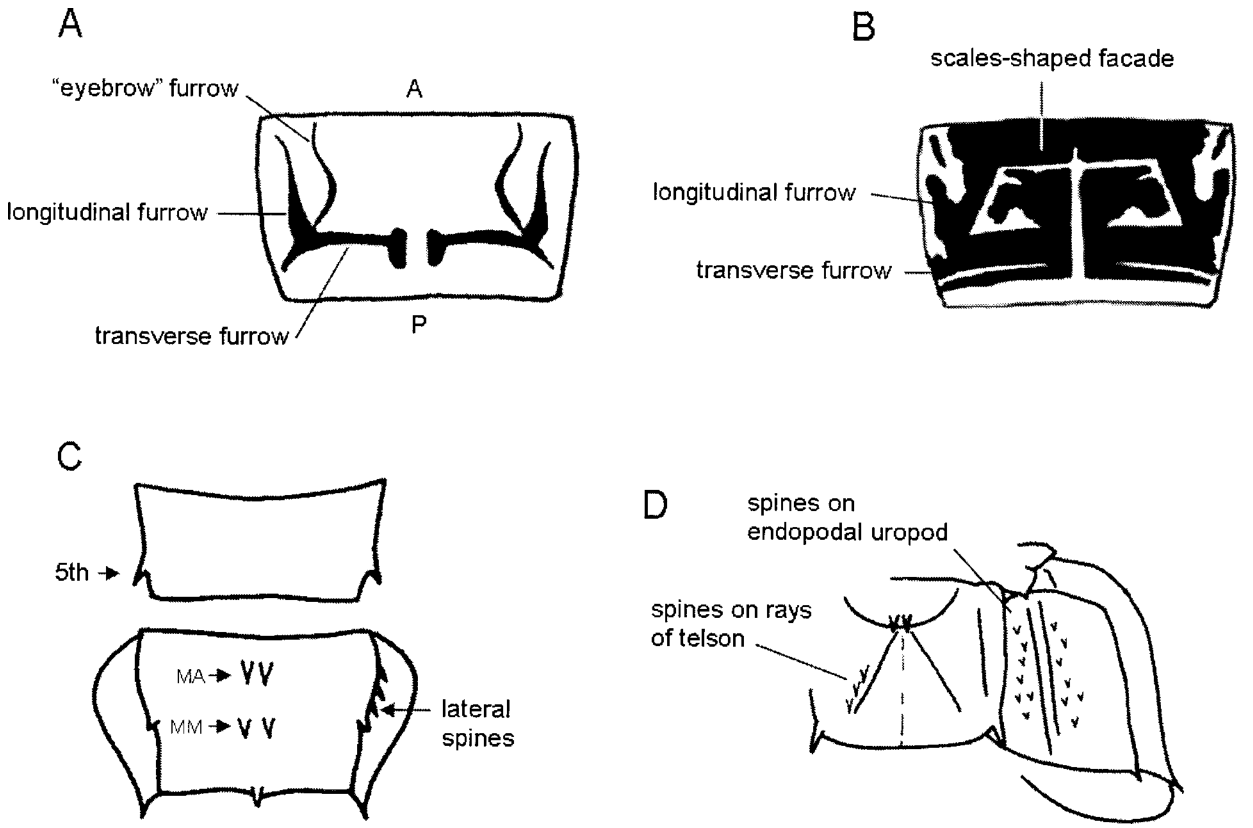

Fig. 5. Selected aspects of pleon morphology of *Metanephrops* used in the cladistic analysis. A, third tergum, *M. mozambicus*; B, third tergum, *M. japonicus*; C, fifth tergum, showing spine at posterior end of lateral ridge, as on *M. armatus*, and sixth tergum, showing positions of median anterior (MA) and median mid-length (MM) spine pairs and, also, lateral spines, as on *M. arafurensis*; D, telson and uropods, showing spines on rays of telson, as on *M. boschmai*, and spines on endopodal uropod, as in *arafurensis* group.

DT, T-YC, or both. All three recognized fossil taxa were included. The two Cretaceous species, *M. jenkinsi* and *M. rossensis*, were examined directly, but the Pliocene *M. motunaeunsis* could not be obtained for direct examination. Material used for the present analysis is listed in Appendix III. Topotypic material was examined for all species except *M. andamanicus*, *M. sibogae* and *M. sinensis* (though topotypic material of these three species had been examined by the second author in Chan and Yu, 1991; Chan, 1997; and at the Fisheries Research Station in Hong Kong). Specimens of each species of *Metanephrops* from different localities are generally similar. However, marked variations complicating the coding of one or two characters are found in three species: *M. australiensis* [#15 (see Chan, 1997), #34], *M. thomsoni* (#34), and *M. velutinus* (#34). In these cases, only topotypic material was used for coding the characters.

Metanephrops thomsoni from its type-locality in the Philippines differs from those found elsewhere in lacking the distinctive red bands on the large chelipeds (Chan, 1998). Although it seems that the topotypic material generally has the surface of the pleon less pitted, and the spines better developed on the thoracic median carina but less developed on the inner margin of palm, there is overlap in these characters which makes the separation rather difficult.

A very young (upper Miocene) fossil species, *Wongastacia taiwanica* Hu, 1983 had been described from Taiwan. A search of the holotype and paratypes of *W. taiwanica* deposited at the National Taiwan University, Taipei did not locate any specimens. Only one paratype, NMNS 007606 (also see Hu and Tao, 1996, Pl. 2-Fig. 6) deposited at the National Museum of Natural History, Taichung, was found, but it contains too little information to determine if it really belongs to the same species as the holotype (Hu and Tao, 1996 listed other paratypes NMNS 007618, 007618a-d at the National Museum of Natural History but they are fragments and were collected in 1994, long after the original description). Nevertheless, the general outline of the carapace and the sculpture of the pleon, particularly the characteristic pits on the surfaces of the pleon terga, in the photographs of the types show that *W. taiwanica* is almost identical with those recent *M. thomsoni* from Taiwan (see photos in Hu, 1983; Hu and Tao, 1996—fossil form; Chan and Yu, 1988; 1993—extant form). *W. taiwanica* is treated as a synonym of *M. thomsoni* in the present study.

We included two species of *Hoploparia*, one (*H. albertaensis*) as the out-group and the other (*H. antarctica*) because it has been hypothesized to be ancestral to *Metanephrops*. *Hoploparia*, the most diverse genus of fossil lobster, is well known from the Cretaceous (ranging from Valanginian—Lower Miocene), and pre-dates by over 50 million years the oldest known *Metanephrops* (Campanian — recent). *Hoploparia*, with its long-ranging and abundant fossil record, has been interpreted in both non-cladistic and cladistic studies as ancestral to modern lobster genera (Tshudy and Babcock, 1997), and seems a good, safe, reliable choice for determining character state polarity. Tshudy and Sorhanuus (2003) performed a cladistic analysis of *Hoploparia* species and concluded that *Hoploparia* is wastebasket genus. We stand by that conclusion but, nonetheless, believe it is possible to select a mainstream/typical-looking *Hoploparia* for out-group purposes. We selected the species *H. albertaensis* as out-group because it is an older species (Early Cretaceous: Coniacian) with a morphology typical of the genus. *Hoploparia antarctica* was also included in the matrix because, as discussed above, it has been hypothesized, on the basis of its morphology and co-occurrence with the oldest known fossil species of *Metanephrops*, to be ancestral or near to ancestral to *Metanephrops* (Feldmann et al., 1993).

Cladistic Analysis

The unweighted cladistic analysis discussed herein was performed with PAUP* 4.0 (written by David L. Swofford, 2002). The search was done using the branch-and-bound algorithm, which guarantees that the most parsimonious tree(s) is found. Character state optimization in this study was

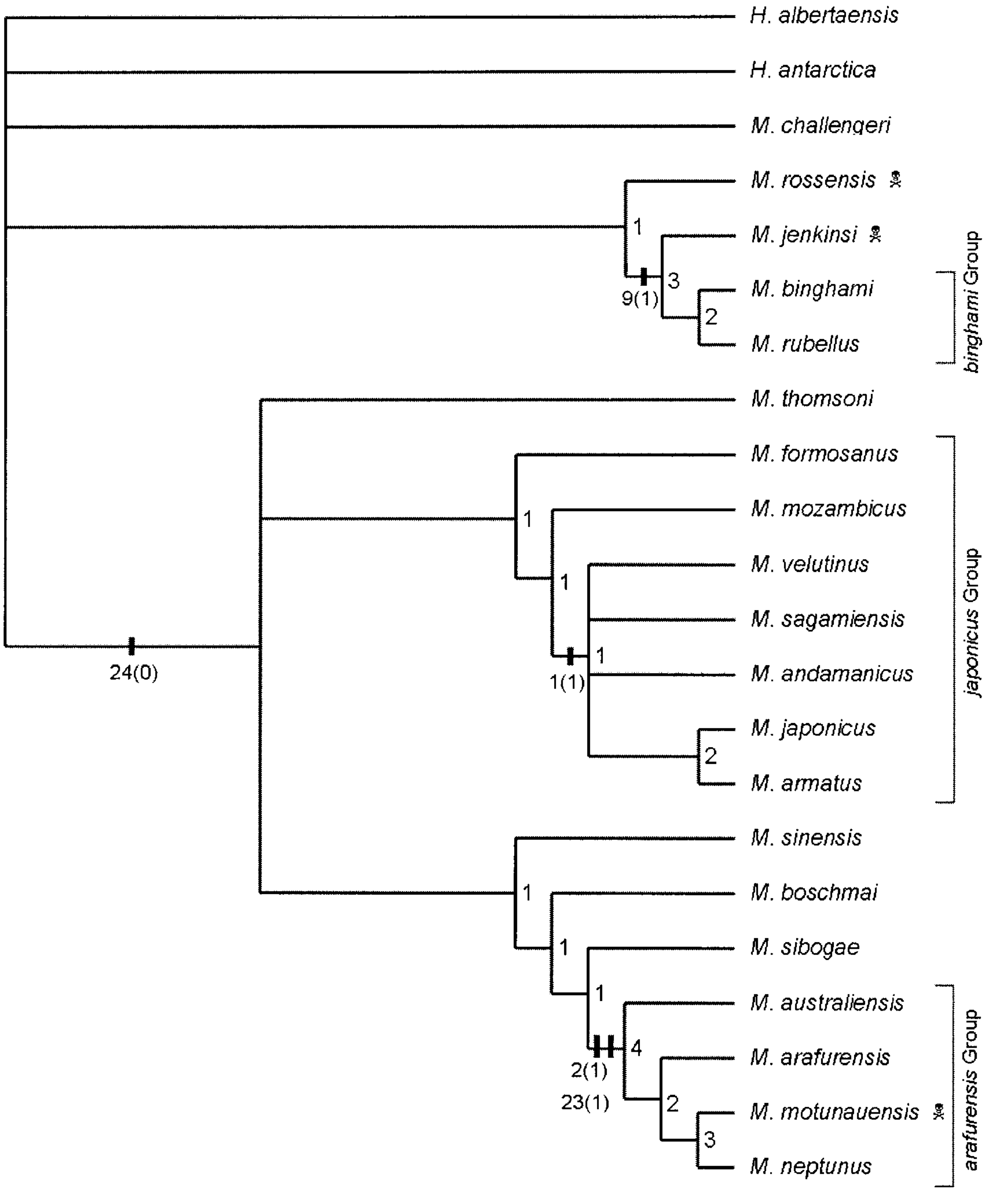

Fig. 6. Cladogram produced by unweighted analysis; represents strict consensus of 24 most parsimonious trees, and has a length = 97, retention index = 0.6907, consistency index = 0.3814, and rescaled consistency index = 0.2635. Character bars indicate unambiguous, unreversed synapomorphies. Unweighted Bremer support values are shown for resolved clades. ☠ referring to fossil species.

implemented using the accelerated transformation approach (ACCTRAN option in PAUP). This favors an early acquisition of a new character state with a subsequent homoplasy accounted for by a reversal.

TreeView (Page, 1996) was used to draw the phylogenetic trees. Unweighted Bremer support values were calculated following the procedure outlined in Bremer (1994). Bremer support values indicate the number of extra evolutionary steps needed to collapse a node in the strict consensus tree; thus, the higher the value, the more stable the node. Bremer support values were computed, using the branch-and-bound algorithm, in the program PAUP (Version 4.0; Swofford, 2002) by successively including progressively longer trees in the strict consensus analysis; that is, until the tree was fully collapsed.

RESULTS AND DISCUSSION

General

Unweighted analysis produced a cladogram (Fig. 6) that represents the strict consensus of 24 most parsimonious trees, and has a length = 97, retention index = 0.6907, consistency index = 0.3814, and rescaled consistency index = 0.2635. Unweighted Bremer support values are shown for resolved clades. Bremer support values for the more basal clades are low, mostly "1"'s, indicating that the more basal nodes are not particularly stable. More derived clades are better supported, with Bremer support values of 2, 3, or 4.

This cladistic analysis corroborates a conclusion of previous cladistic analyses, that homoplasy is rampant in the evolution of clawed lobsters. Abundant homoplasy in the evolution of clawed lobsters was previously reported at the generic level (Tshudy and Babcock, 1997) and Tshudy and Sorhannus (2000) reported on convergence in cheliped form at high taxonomic levels within Crustacea. In the current, species-level analysis, only 5 of the 68 synapomorphies identified by the analysis were found to be unambiguous and unreversed synapomorphies (Fig. 6). These rare, unambiguous synaporphies include: character state 24(0), scaphocerite longest medially/sub-medially, instead of externally; 9(1), supracervical spine present; 1(1), velvet-like pubescence on carapace; 2(1), generally spiny cephalothorax; and 23(1), uropodal endopod dorsal surface with spines.

Testing the Four Traditional Groupings

The four traditional groupings of the species of *Metanephrops* were tested cladistically herein for the first time. Cladistic analyses support the traditional, non-cladistic, morphology-based *arafurensis*, *binghami* and *japonicus* groups made by Jenkins (1972) and maintained/emended by Chan (1997) and others (Fig. 6). Each of these three groups is monophyletic. Additionally, Chan's (1997) referral of *M. motunauensis* to the *arafurensis* group is supported by the current cladistic results. The *thomsoni* group is not well supported by the cladogram, although 3 of its 5 species plot out as part of a monophlyletic group.

Given the overall morphologic similarity between *M. sinensis* and *M. thomsoni* (two members of the traditional *thomsoni* group), it may be surprising that they would plot so far apart on the cladogram. As coded, the species differ by 7 character states (#4, #5, #10, #13, #28, #32, #33), although close inspection shows that there were some tough calls involved in coding (#28, #32), and that one or the other species is somewhat variable (character usually present, rarely absent) in 4 of the 7 characters (*M. sinensis* for #4, #5, #10; *M. thomsoni* for #33).

The two oldest fossil species, *M. rossensis* and *M. jenkinsi*, were previously concluded, by non-cladistic means, (Tshudy, 1993, p. 214-215) to be not accommodated by any of the four traditional groups. In Tshudy's (1993) judgement, *Metanephrops rossensis* and *M. jenkinsi* are most similar, but not identical, to the *binghami* group (Table 1). Cladistic analysis shows the fossil species forming a monophyletic group with the *binghami* group.

Phylogeny and Evolutionary History

Based on fossil occurrences, the evolutionary history of *Metanephrops* has been hypothesized to include origin from *Hoploparia* in the shallow-water, Late Cretaceous seas of the southern high latitudes and subsequent dispersal into deepwater settings worldwide (Feldmann and Tshudy, 1989). This is based on the fact that the oldest known fossil species, the Late Cretaceous *M. rossensis* (Campanian) and *M. jenkinsi* (Maastrichtian—Paleocene), are known from continental shelf deposits now exposed on the Antarctic Peninsula. We can further hypothesize here that *Metanephrops* originated specifically in the South Atlantic Ocean, this because the fossil species are from the eastern (Atlantic) side of the Antarctic Peninsula. In the Late Cretaceous, the Atlantic Ocean was narrower, and South America and Antarctica were contiguous [(until about the Eocene) (Scher and Martin, 2006)]. This would have made *M. rossensis* and *M. jenkinsi* Atlantic species living on the shallow shelf around the eastern (Atlantic) margin of the Antarctic Peninsula.

We wanted to test this hypothesized evolutionary history cladistically. That is, we wanted to determine which clades and which species are most plesiomorphic and most derived and, further, wanted to test the hypothesized origin of *Metanephrops*. The hypothesized history includes the following four testable components.

1. *Hoploparia* is morphologically/cladistically more plesiomorphic than *Metanephrops*.
2. The Late Cretaceous fossil species *M. rossensis* and *M. jenkinsi* are morphologically/cladistically the most plesiomorphic of all known *Metanephrops*.
3. *Metanephrops* originated in the southern high latitudes.
4. *Metanephrops* originated specifically the South Atlantic Ocean.

First Component.—The first component is not rigorously tested in this analysis, since a *Hoploparia* (*H. albertaensis*) is used as the out-group. For what it is worth, a second *Hoploparia* species, *H. antarctica*, is indeed shown to be as plesiomorphic as any *Metanephrops*, and more plesiomorphic than most. Given the heterogeneity of the genus *Hoploparia* (currently a "wastebasket genus" according to Tshudy and Sorhannus, 2003), this result was not as automatic as it might seem.

Second Component.—Cladistic results oppose that the oldest fossil species, the late Cretaceous *M. rossensis*, is morphologically most plesiomorphic. The recent species, *M. challengeri*, shows only 4 apomorphies, whereas *M. rossensis* has 10 apomorphies. The other *Metanephrops* species have more apomorphies than *M. rossensis* and *M. challengeri*. Neither *M. challengeri* nor *M. rossensis* possesses any unambiguous synamporphies (all of their apomorphies/synapomorphies are duplicated elsewhere on the cladogram).

The other Late Cretaceous fossil species, *M. jenkinsi*, was determined cladistically to be the next most derived member (after *M. rossensis*) of the Atlantic/*binghami* clade. *Metanephrops jenkinsi* shows 15 synapomorphies, 5 more than does *M. rossensis*.

The *binghami* group is most plesiomorphic, and the *arafurensis* group most derived, according to numbers of apomorphies. The stems of the *binghami*, *japonicus*, and *arafurensis* groups show 8, 12, and 26 apomorphies, respectively, with terminal taxa accumulating additional apomorphies. *Metanephrops neptunus*, the most derived species, has 38 apomorphies. The basal stem of the *arafurensis* and *japonicus* group clades is marked by an unambiguous, unreversed synapomorphy [24(0), scaphocerite longest medially/submedially (instead of exteriorly, as in the *binghami* Group)]. The *arafurensis* group is defined by two additional unambiguous synapomorphies [2(1), spiny cephalothorax, and 23(1), uropodal endopod with spines on dorsal surface]. The only other two unambiguous, unreversed synapomorphies on the cladogram occur within the *binghami* clade [9(1), supracervical spine present] and within the *japonicus* clade [1(1) velvet-like pubescence on cephalothorax].

Third Component.—Cladistic results corroborate the existing hypothesis that *Metanephrops* evolved in the southern high latitudes. The cladistically most plesiomorphic single species, the recent *M. challengeri*, and the next most plesiomorphic species, the Late Cretaceous *M. rossensis*, are both known from the high southern latitudes. Likewise, the most plesiomorphic species group, the *binghami* group, is best known from the high southern latitudes.

Fourth Component.—While origination of *Metanephrops* in the southern high latitudes seems likely, origination specifically in the South Atlantic is highly equivocal. The two Late Cretaceous fossil species reveal at least a long history in the south Atlantic. Moreover, these fossil species are arranged cladistically as forming a monophyletic group with the extant Atlantic/*binghami* group, the most plesiomorphic of the traditional species groups. Taken together, these findings at least suggest an origin in the South Atlantic. On the other hand, the recent *M. challengeri*, the most plesiomorphic species (not species group), is known today from around New Zealand in the South Pacific. Given preservational and sampling biases, it is obviously possible that *Metanephrops* may have evolved in the South Pacific or southern Indian Ocean, but that any fossil record has, thus far, gone unnoticed. If origination occurred in the south Atlantic, species of *Metanephrops* could have dispersed outward, in the Late Cretaceous, by way of the Tethys Sea and/or around southern Africa. Later, in the Eocene, *Metanephrops* could have also dispersed from the Atlantic and into the Indian Ocean via the Drake Passage, newly opened between Antarctica and South America in about the Eocene (Scher and Martin, 2006).

CONCLUSION

Cladistic analysis herein corroborates previous studies which indicated that homoplasy is rampant in the evolution of clawed lobsters. Only 5 of the 68 synapomorphies identified by the analysis are unambiguous, unreversed synapomorphies.

Cladistic analysis supports the traditional, non-cladistic, morphology-based *arafurensis*, *binghami* and *japonicus* groups made by Jenkins (1972) and maintained/emended by Chan (1997) and others. These three groups are monophyletic. The *thomsoni* group is not well supported by the cladogram, although 3 of its 5 species plot out as part of a monophyletic group. The two oldest fossil species, *M. rossensis* and *M. jenkinsi*, were previously concluded, by non-cladistic means, to be not accommodated by any of the four traditional groups, but most similar to the *binghami* group. Cladistic analysis shows the fossil species forming a monophyletic group with the *binghami* group.

Cladistic results oppose that the oldest fossil species, *M. rossensis*, is morphologically most plesiomorphic. *Metanephrops challengeri* shows the fewest number of apomorphies of all *Metanephrops* species, followed by *M. rossensis*. Of the three traditionally recognized species groups supported herein, the *binghami* group is most plesiomorphic, and the *arafurensis* is most derived, based on numbers of synapomorphies.

Based on geographic occurrences of fossil and recent species, and, now, corroborative cladistic results, it seems likely that *Metanephrops* originated in the southern high latitudes. A more precise location of origin remains highly equivocal. We look forward to new information, especially from new fossil occurrences and from molecular studies, for testing and refining hypotheses on the origin and evolution of *Metanephrops*.

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APPENDIX I

Morphologic Character-State Matrix Analyzed Cladistically

	00000	00001	11111	11112	22222	22223	33333
	12345	67890	12345	67890	12345	67890	12345
M. andamanicus	10010	00000	00011	11000	00000	11111	11011
M. arafurensis	01111	01001	11111	01111	11101	11100	11011
M. armatus	10110	00000	00011	11121	00000	11111	11101
M. australiensis	01111	01001	11110	00111	11101	10100	10001
M. binghami	00110	11111	10000	00121	00011	11111	1111?
M. boschmai	00111	01001	00100	00001	01001	00000	00000
M. challengeri	00010	00000	00?00	00100	00010	00000	00010
M. formosanus	00010	00000	00011	01000	00000	11111	11100
M. japonicus	10110	00000	00011	11121	00000	11111	11101
M. jenkinsi ☠	?0110	10110	11?10	00???	1?0?1	01011	111??
M. motunauensis ☠	?111?	011?1	1??11	11?21	111?0	1111?	110??
M. mozambicus	00010	00000	00011	11000	00000	11111	11000
M. neptunus	01011	01101	11111	01101	10100	01010	11000
M. rossensis ☠	?0100	11100	00?11	00???	0????	000?0	111??
M. rubellus	00110	11110	10000	00121	10011	11111	1111?
M. sagamiensis	10110	00000	00011	11000	00000	11111	11011
M. sibogae	00110	00000	00000	00011	11001	10100	11000
M. sinensis	00011	01001	00110	00000	00000	10100	10000
M. thomsoni	00000	01000	00010	00000	00000	10000	11100
M. velutinus	10010	00000	00011	11000	00000	11111	11011
H. albertaensis	?0210	00001	0??11	00???	?????	00000	011??
H. antarctica	?0210	10000	0??10	00?00	?0???	00000	111??

(☠) referring to fossil species.

APPENDIX II

Explanation of Characters Analyzed in Cladistic Analysis

All 35 characters describe external hardparts, including aspects of the cephalothorax (#1-13), pleon and telson (#14-23, 35), appendages (#24-34), and color pattern (#34-35). Details on the coding of any characters are available from the first author.

Cephalothorax

1. Velvet-like pubescence on cephalothorax (>80% coverage above branchial carina).
    0. Absent
    1. Present

2. Cephalothorax cuticle: general surface ornamentation
    0. Smooth/granulose
    1. Spiny

3. Supraorbital spines ("SO"): 3 or more than 3?
    0. (3 spines)
    1. (4 or more spines)
    2. (spinules dissimilar to the prominent spines of *Metanephrops*)

4. Postorbital spine ("PO"): positioned behind orbit (not more than half-way to cervical groove) and at about mid-orbital height (see *M. andamanicus* for example). In recent *Metanephrops*, this spine is situated above and anterior to the larger gastrolateral (GL) spine. It is often smaller than the metorbital spine ("MO"), which is located behind the base of the orbit.
    0. Absent
    1. Present

5. Extra, smaller postorbital spine(s) ("XPO") around PO (see *M. boschmai* for example).
    0. Absent
    1. Present

6. Postantennal spine(s) ("PA"), a spine posterior to the keel-like antennal spine (see *M. rubellus* for example).
    0. Absent
    1. Present

7. Cervical spinules ("C", along posterior edge of cervical groove and directed anteriorly; see *M. rubellus* for example).
    0. Absent
    1. Present

8. Postcervical spinules ("PC", along posterior edge of postcervical groove and directed anteriorly; see *M. rubellus* for example).
    0. Absent
    1. Present

9. Supracervical spine ("SC", named herein) above cervical groove (located midway to dorsal median and posterior to gastrolateral spine; see *M. rubellus* for example).
  0. Absent
  1. Present

10. Spinules above the gastrolateral spine ("GL").
  0. Absent
  1. Present

11. Flank spines ("FL", named herein) on cephalic region, just anterior to inflection of postcervical groove.
  0. Absent
  1. Present

12. Lateral carina ("L") with spines or subspiniform projections (coarser than common granulation; see *M. arafurensis* for example).
  0. No
  1. Yes

13. Relative spacing of the two rows of thoracic median dorsal spines (less than or equal to 0.1, or greater than 0.1) determined by dividing their spacing by the length of thoracic region (measured medially). Spacing measured at 2nd spine pair posterior to the much larger, anteriormost pair (unless few pairs, then roughly 1/3 to posterior margin).
  0. $</=$ 0.1 (close together)
  1. $>$0.1 (well spaced)

Pleon

14. Transverse furrow along posterior margin of pleon terga 2-4 (Fig. 5a, b). There is interspecific variation in the width of the furrow, the nature of its dorso-medial termination (simple or in combination with other furrows), and the degree to which the furrow parallels the posterior margin.
  0. Absent
  1. Present

15. "Eyebrow" furrows (Fig. 5a). These are crescentic, concave-down, longitudinal furrows that may or may not be contiguous with transverse furrow. Several species lacking this furrow do exhibit an apunctate (and often darker colored) crescentic region in the same position. Photos can be misleading here; need to examine specimens in oblique light. Furrow is usually of a width as seen on *M. mozambicus*, but is unusually wide in *M. japonicus*.
  0. Absent
  1. Present

16. Scales-shaped facade (Fig. 5b), a region of positive relief in a scales-like configuration; i.e., two posterior elements "suspended" from a transverse anterior element ["main facade" of Chan and Yu (1991, p. 22)]. Best displayed by *M. japonicus* (note: significant variation in details of the scales, e.g.,USNM 104182, n = 4). *Metanephrops sagamiensis* and *M. andamanicus* also good examples but scales shape is less detailed.
  0. Absent
  1. Present

17. Longitudinal furrow above (and parallel to) tergum-pleuron boundary (Fig. 5a, b). Well developed on *M. andamanicus*. Minimum standard is *M. formosanus*.
  0. Absent
  1. Present

18. 5th somite: spine(s) near posterior end of (longitudinal) lateral ridge at tergum-pleuron boundary (Fig. 5c) (see *M. armatus* for example); i.e., on about posterolateral corner of tergum.
  0. Absent
  1. Present

19. 6th tergum: median anterior spine or spine pair (Fig. 5c). See *M. japonicus* for example of spine pair.
  0. Absent
  1. Single spine
  2. Pair of spines

20. 6th tergum: median, mid-length (approximately) spine pair (Fig. 5c) See *M. japonicus* for example.
  0. Absent
  1. Present

21. 6th pleomere tergum-pleuron boundary w/lateral spines (other than large one at posterior termination) (Fig. 5c). See *M. arafurensis* for example.
  0. Absent
  1. Present

22. Telson: spines on rays of V-shaped carina (Fig. 5d). See *M. boschmai* for example.
  0. Absent
  1. Present

23. Uropodal endopod—dorsal surface spinules (Fig. 5d). See *M. arafurensis* for example.
  0. Absent
  1. Present

Appendages

24. Scaphocerite—longest medially/sub-medially, e.g., *M. japonicus*, or exteriorly, e.g., *M. binghami*?
  0. Medially/submedially
  1. Exteriorly

25. Merus of cheliped: ventral (sharp) edge with many sharp spinules, i.e. serrated, e.g., *M. japonicus*, or large spines, e.g., *M. binghami*?
  0. Many sharp spinules/serrations
  1. Large spines

26. Cheliped upper surface: median/submedian keel (well developed on *M. japonicus*).
  0. Absent
  1. Present

27. Cheliped upper surface: spines on (longitudinal) median/submedian (spines well developed on *M. japonicus*).
  0. Absent
  1. Present

28. Cheliped lower surface: median/submedian keel (for reference, it is well developed on *M. japonicus*; *present but least developed on M. sinensis*).
    0. Absent
    1. Present

29. Cheliped lower surface: spines on (longitudinal) median/submedian (spines well developed on *M. japonicus*).
    0. Absent
    1. Present

30. Cheliped outer margin: double-ridged/squared-off keel (for reference, *M. andamanicus*).
    0. Absent
    1. Present

31. Cheliped inner margin: pronounced keel (for reference, *M. andamanicus*).
    0. Absent
    1. Present

32. Cheliped inner margin: spines? (for reference, *M. andamanicus*).
    0. Absent
    1. Present

33. Cheliped inner margin with some large spines? [reference for "large" is *M. japonicus*; surprisingly, there are no "gray areas" (intermediate conditions); coding is easy].
    0. No
    1. Yes

Color Patterns

34. Large chelipeds distinctly banded (reddish brown or deep orange markings).
    0. No
    1. Yes

35. Lateral surfaces of pleon with distinctive white spots (at hinges between somites).
    0. No
    1. Yes

APPENDIX III

Material Examined

"TYC"—National Taiwan Ocean University collection except otherwise stated, examined by Chan, "DT"—examined by Tshudy.

For TYC, "(F)" indicates direct observation on coloration of fresh material, "(P)" of color photograph on fresh material. For DT, all recent specimens preserved in alcohol unless otherwise indicated.

M. andamanicus—TYC: 16 specimens (F) from Pratas, South China Sea. DT: one male, one female on loan from Chan (collected 1989 by Taiwan Fisheries Research Institute; Pratas, S. China Sea, identified by Chan).

M. arafurensis—TYC: 2 specimens (P) from Indonesia (Zoologisch Museum, University of Amsterdam and Muséum national d'Histoire naturelle, Paris, examined by T-Y Chan in 1997 and with many photographs taken for the present analysis). DT: used photos in Chan, 1997 (figs. 1, 2, 5).

M. armatus—TYC: 47 specimens (F) from Taiwan; 2 specimens (P) from East China Sea. DT: one male, two females from Chan (collected 1998 by commercial trawler, Dasi, NE Taiwan).

M. australiensis—TYC: 9 specimens (P) from Australia; 21 specimens (F) from the Philippines; 1 specimen from Indonesia (on loan by Chan from the Muséum national d"Histoire naturelle, Paris) . DT: one male from Chan (collected 1985 by CSIRO, NW Australia, 18°19′S, 117°49′E, 414 m).

M. binghami—TYC: photo in Sea Frontiers 21(3): cover page. DT: many specimens (9 jars) from Caribbean (United States National Museum numbers USNM 11429, 98656, 136712, 136720, 136724, 136716, 170695, 170697, 170698).

M. boschmai—TYC: 16 specimens (P) from Australia. DT: two ovigerous females on loan from Chan (collected CSIRO, W. Australia, 31°29′S, 114°54′E).

M. challengeri—TYC: 6 specimens (P) from markets in Paris and Sydney, supposedly imported from New Zealand. DT: one male on loan from Chan (supermarket, Paris).

M. formosanus—TYC: 44 specimens (F) from Taiwan DT: two males, one female on loan from Chan (collected 1998 by commercial trawler, Dasi, NE Taiwan, 5/7/98).

M. japonicus—TYC : 10 specimens (P) from Japan. DT: one male, one ovigerous female from Chan (collected in lobster pot in Tokyo Submarine Canyon, 180-210 m, mud and fine sand).

M. jenkinsi—DT: borrowed several specimens from Smithsonian (holotype USNM 424598; paratypes USNM 424599-424603, 424605, 424613-424614).

M. motunauensis—None; examined only from the original description and figures in Jenkins (1972).

M. mozambicus—TYC: 1 specimen (P) from Madagascar, 2 specimens from fish markets in Japan with places of origin unknown. DT: Paris Museum paratype (one ovigerous female) from Chan (collected Madagascar, 1972, 12°38′S, 48°15.5′E, identified by Macpherson, 1987).

M. neptunus—TYC: 1 specimen (P) from Pratas, South China Sea; 4 specimens (F) from the Philippines; 4 specimens (P) from Australia. DT: two females (one large and ovig., one small) on loan from Chan (collected 1986 by CSIRO, NW Australia, 18°19′S, 117°49′E, 414 m, identified by Chan, 1986).

M. rossensis—DT: borrowed from British Antarctic Survey, BAS IN. 2161, 2181, and two unnumbered specimens.

M. rubellus—TYC: 6 specimens specimens from Brazil. DT: one male on loan from Chan (collected 1961 by Calypso, South America, 35°5′S, 52°33′W, 11fm.)

M. sagamiensis—TYC: 26 specimens (F) from Taiwan; 1 specimen (P) from Japan.

M. sibogae—TYC: 8 specimens (P) from Australia. DT: two females from Chan (collected 1990 by CSIRO, N. Australia, 7°45′S, 130°10′E; identified by Chan).

M. sinensis—TYC: 44 specimens (F) from the Philippines. DT: one male on loan from Chan (collected Musorstom III, Philippines, identified by Chan).

M. thomsoni—TYC: 36 specimens (F) from the Philippines; 61 specimens (F) from Taiwan; 2 specimens (P) from Viet Nam. DT: one male, one ovigerous female on loan from Chan (collected 1985 by Musorstom III; Philippines, 12°6′N, 121°15′E, identified by Chan).

M. velutinus—TYC: 3 specimens (F) from the Philippines; 7 specimens (P) from Australia; 1 specimen from Salomon Island. DT: two females on loan from Chan (collected 1989 by CSIRO, W Australia. 28°9′S, 113°10′E, approx. 600 m).

RECEIVED: 20 June 2006.
ACCEPTED: 23 November 2006.