

HOPLOPARIA, THE BEST-KNOWN FOSSIL CLAWED LOBSTER (FAMILY NEPHROPIDAE), IS A “WASTEBASKET” GENUS

Dale Tshudy and Ulf Sorhannus

(DT, correspondence) Department of Geosciences, Edinboro University of Pennsylvania, Edinboro, Pennsylvania 16444, U.S.A. (dtshudy@edinboro.edu); (US) Department of Biology, Edinboro University of Pennsylvania, Edinboro, Pennsylvania 16444

A B S T R A C T

Hoploparia McCoy, 1849 (Lower Cretaceous (Valanginian)–Miocene) is, by far, the most diverse clawed lobster genus (fossil or Recent); 49 species are known. The genus has been interpreted intuitively to be morphologically primitive and ancestral to some or many modern nephropid genera. Prior to the present study, two separate issues raised the suspicion that *Hoploparia* is a “wastebasket” genus—a default genus for any fossil lobster with a mainstream nephropid morphology. One issue is the difficulty in characterizing (i.e., coding) the morphology of *Hoploparia*, as a genus, for cladistic analysis. For *Hoploparia*, and far more than for other lobster genera, many characters show variable character states. A second issue is that the morphologies of some Recent genera (e.g., *Eunephrops* and *Nephropides*) seem easily accommodated within the fossil genus *Hoploparia*. Both issues stem from an originally ambiguous diagnosis of *Hoploparia* that has been variously expanded in *de facto* fashion to the point that, today, nobody really knows what *Hoploparia* means. Cladistic analyses herein indicate that *Hoploparia* is paraphyletic and, therefore, support the intuitive judgement that *Hoploparia* is a wastebasket genus. This paper, the first species-level cladistic analysis of *Hoploparia*, is not intended to be the sole basis for taxonomic revision but is, instead, intended to generate discussion among lobster specialists. Hopefully, this discussion will bring forth additional characters for cladistic analysis and other new insights that may lead to better supported cladograms addressing lobster taxonomy.

Hoploparia McCoy, 1849, is a well-known, clawed lobster genus with a record extending from the Lower Cretaceous (Valanginian) to the Miocene. *Hoploparia* is, by far, the best known genus of fossil clawed lobster, and the most diverse lobster genus, fossil or Recent. Fifty-one species are known: 17 Lower Cretaceous, 27 Upper Cretaceous, and 9 Tertiary (two species span these time ranges; Appendix I). The next most diverse nephropid lobster genus is the extant *Metanephrops* Jenkins, 1972, known by 17 species (14 Recent, 3 fossil). *Hoploparia* was cosmopolitan in geographic range, extending from Canada and Greenland to the Antarctic Peninsula. *Hoploparia* has been interpreted intuitively to possess a morphology that is primitive for the Nephropidae. This, plus its diversity in the Lower Cretaceous, strongly suggests that *Hoploparia* was ancestral to some or many modern nephropid genera (Mertin, 1941; Secretan, 1964; Glaessner, 1969; Tshudy, 1993).

McCoy (1849) created the genus *Hoploparia* to accommodate the existing species *Astacus longimanus* Sowerby, 1826, from the Lower Cretaceous (Aptian-Albian) of England. Essen-

tially, *Hoploparia* was proposed as a genus of fossil lobsters generally resembling the Recent American lobster *Homarus* Weber, 1795 but having a more sculptured (grooved, locally inflated, etc.) and ornamented carapace. In fact, the name *Hoploparia* refers to the lobster’s “spiny cheeks,” the locally inflated and ornamented regions on anteroventral sides of the cephalothorax (Figs. 1, 2). *Homarus* lacks these locally inflated “cheeks,” and is less spiny. The diagnosis of *Hoploparia* was brief but, in McCoy’s opinion, sufficient to distinguish the new species *Hoploparia longimanus* (Sowerby, 1826) from *Homarus*.

Since 1849, many other fossil lobster species have been discovered. Most of these fossil species exhibit “cheeks,” if not “spiny cheeks,” and most (50 species) have been referred to *Hoploparia*. Only a few fossil species, those with very distinctive morphologies, have not been referred to *Hoploparia*. (For example, fossil *Oncopareia* Bosquet, 1854, bear a very distinctive abdomen and major claw and are confidently related to Recent *Thaumastochelodes* Wood-Mason, 1874 / *Thaumastochelopsis* Bruce, 1988. Similarly, fossil *Metanephrops*

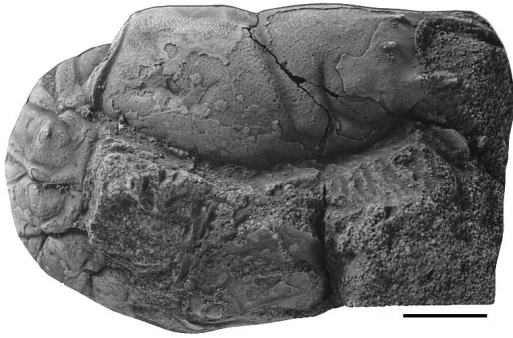


Fig. 1. Clawed lobster (Nephropidae), *Hoploparia gabbi* Pilsbry, 1901, Late Coniacian Bad Heart Formation, Alberta, Canada (Royal Tyrell Museum TMP 2001.9.2). Scale bar equals 1 cm.

Jenkins, 1972, bear distinctive ridges and spines that show their obvious relationship to Recent *Metanephrops*.) The inclusion of 50 other fossil species in *Hoploparia* has, in *de facto* fashion, variously stretched and expanded the definition of *Hoploparia* to accommodate this or that spine, this or that carina, etc., to the point that, at this time, nobody is certain what “*Hoploparia*” really means. Currently, there is so much variation among lobster species referred to *Hoploparia* that the genus is difficult to characterize. Tshudy (1993) encountered this while attempting to write an updated diagnosis of the genus. His diagnosis (pp. 71, 72), by necessity, is rife with descriptions of how character states “typically” occur. Moreover, some of his other statements, such as “thoracic region lacks carinae,” are invalidated by one or a few species (e.g., presence of thoracic carinae on *Hoploparia antarctica* Wilckens, 1907, and *Hoploparia bearpawensis* Feldmann, 1977).

A “wastebasket” taxon is a paraphyletic group in which the constituent taxa are united by the absence of synapomorphies that distinguish other groups. In other words, a “wastebasket” taxon is an unnatural, default receptacle for taxa excluded from other higher groupings. Objectively, all paraphyletic taxa are “wastebasket” taxa, but it seems a matter of degrees of parphyly and of taxonomic history that determine “wastebasket” status in practical terms.

A good example of a “wastebasket” taxon is the Family Pongidae Simpson, 1945, which, to the traditional (non cladistic) systematist, includes all apes that are not human (Prothero, 1998: 50). Cladistically, apes, both nonhuman and human, form a monophyletic group defined by synapomorphies. Pongidae is defined not

by synapomorphies but instead by the lack of synapomorphies that define humans (Hominiidae). Therefore, Pongidae is a paraphyletic, “wastebasket” taxon.

Prior to the present study, two separate issues raised the suspicion that *Hoploparia* is a “wastebasket” genus—one that has served as a receptacle for fossil species lacking truly distinctive morphologies (e.g., bizarre, pectinate claws, as on fossil *Oncopareia*, or thoracic carinae as on fossil and extant *Metanephrops*). One issue is the aforementioned variability within the genus and the resulting difficulty in characterizing its morphology, e.g., coding the genus for cladistic analysis. A second issue is that morphologic comparisons between some recent genera (e.g., *Nephropides* Manning, 1969, and *Eunephrops* Smith, 1885) and fossil *Hoploparia* lead us to ask, “If this Recent lobster were found in fossil form, wouldn’t it fit into the wide range of morphologies referred to *Hoploparia*?” *Nephropides* and *Eunephrops*, if found in fossil form, would very likely be referred to *Hoploparia*.

Nephropides, a monospecific genus known from slope depths in the Caribbean Sea, is noteworthy for the rigidity of its carapace and for the uniformly dense coverage of its carapace by large tubercles. However, carapace rigidity is indeterminate in the lobster fossil record, and there is nothing in the definition of *Hoploparia* that excludes coverage by tubercles. In fact, many *Hoploparia* are well covered by granules or tubercles. So, again, the question is, “Why would anyone not refer a fossil *Nephropides* to *Hoploparia*?”

Eunephrops, a genus known by three Recent species (Holthuis, 1974), very strongly resembles *Hoploparia*. In fact, there are no consistent differences between the two genera. Unlike most *Hoploparia*, *Eunephrops* possess a gastrolateral spine on the cephalothorax. Also, the gastric tubercle (a small projection located dorsomedially on the cephalothorax, approximately midway between the orbit and the postcervical groove) is present on most *Eunephrops* but absent on *Hoploparia*. In the absence of consistent differences, why would anyone not refer a fossil *Eunephrops* to *Hoploparia*?

In summary, it is wide morphologic variation among the many fossil species referred to *Hoploparia*, and also morphologic similarity between fossil *Hoploparia* and some Recent genera, that have led us to hypothesize that *Hoploparia* is a “wastebasket” genus for any

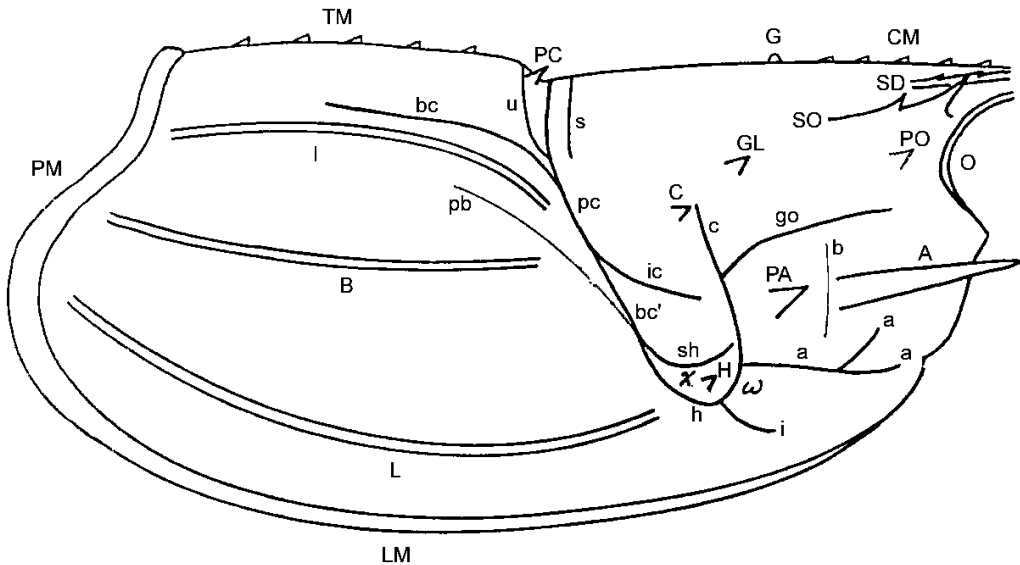


Fig. 2. Schematic line drawing of nephropid lobster cephalothorax, showing positions of grooves, spines, etc. (modified from Holthuis, 1974). a, antennal groove; A, antennal spine; b, buccal groove; B, branchiocardiac groove; bc, branchiocardiac groove; bc', ventral extension of branchiocardiac groove; CM, cephalic median carina; G, gastric spine; go, gastro-orbital groove; h, hepatic groove; H, hepatic spine; i, inferior groove; I, intermediate carina; ic, intercervical groove; L, lateral carina; LM, lateral margin; O, orbit; PA, postantennal spine; pb, parabranchial groove; pc, postcervical groove; PC, postcervical groove; PO, postorbital spine/carina; PM, posterior margin; s, sellar groove; SD, subdorsal carina; sh, suprahepatic groove; SO, supraorbital spine/carina; TM, thoracic median carina; u, urogastric groove; χ , prominence chi; ω , prominence omega. Discussion of these features in Tshudy, (1993: 453–472).

fossil lobster with a mainstream morphology. In this study, we test the hypothesis with species-level cladistic analysis of morphology. *Hoploparia* will be demonstrated here to be a “wastebasket” genus if cladistic analyses indicate it to be paraphyletic.

MATERIALS AND METHODS

The first author has examined all known fossil and Recent nephropid species (122 total; 70 fossil and 52 Recent), directly whenever possible, but otherwise through the literature, in an attempt to understand the nature and range of morphologic variation in nephropid lobsters (Tshudy, 1993). In the present study, the master data matrix (Appendix II) produced for cladistic analysis consists of 35 characters, mostly external hardparts. Emphasized are carapace grooves (characters 1–10) and ornamentation (11–25), but the abdomen (26), telson (27–29), claws (30, 31), other appendages (33–35), and a fusiform plate in the cephalothorax (32) are also considered. We used all known characters in the analysis but, nonetheless, express the following opinions and preferences about them. Carapace grooves, being expressions of internal anatomy (at least as sites of muscle attachment (Albrecht, 1981; de Saint Laurent,

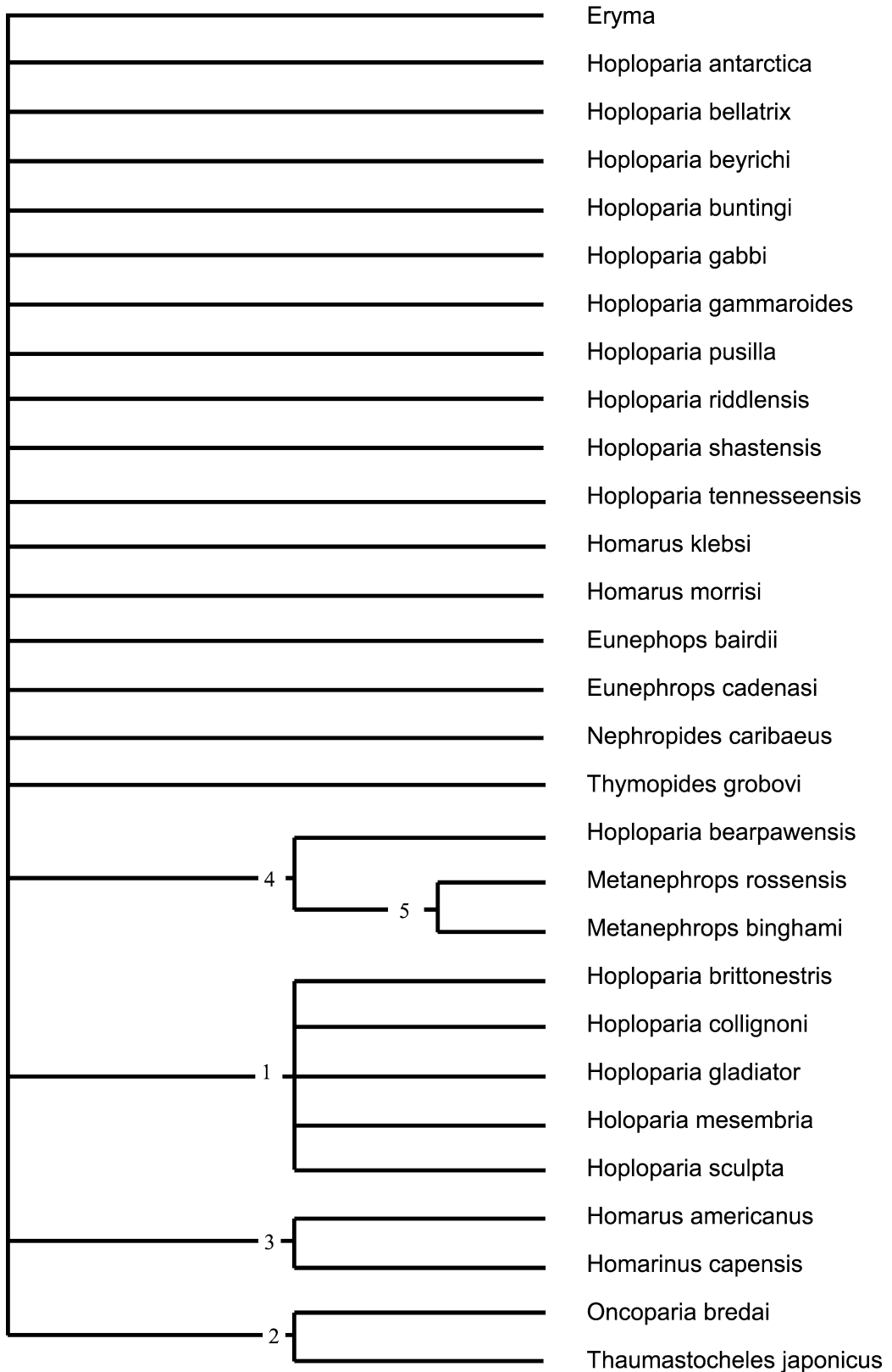
personal communication, 1990) but maybe even body segmentation (Secretan, 1960, others; Glaessner, 1969)), would seem to be more conservative, i.e., less subject to homoplasy, than other, structurally simpler characters such as carapace spines. Ornamentation is still well represented in the data matrix because these features—spines, ridges, etc.—are numerous and well preserved on fossils. The abdomen is less commonly preserved than the cephalothorax (Tshudy *et al.*, 1989). Claws are relatively well calcified and therefore commonly preserved; however, they are especially subject to homoplasy (Tshudy and Sorhannus, 1998). Characters 33–35 are rarely, if ever, observable on fossil lobsters.

Most characters are coded as binary, with most character states being “absent” or “present.” One (4) is described as “absent” or, arbitrarily, “short” or “long.” Claw form (30), likewise, is coded arbitrarily. Telson shape (27) is described as “longer than wide” or “wider than long.” In all analyses, characters were unordered *a priori*.

Despite coding mainly in “presence/absence” form, the first author encountered some “gray areas” for which judgements had to be made. This was most true for carapace grooves, which sometimes are neither plainly evident nor plainly absent. As a test on the reproducibility of character coding, the first author reexamined the matrix one year after its construction. In the 35 character by 29 taxon matrix

→

Fig. 3. Cladogram produced by unweighted analysis is strict consensus of 696 most parsimonious trees, has length = 86, retention index of 0.61, consistency index of 0.40, and is unresolved with regard to monophyly of *Hoploparia*.



(1015 character states), eight states (0.8%) were changed (recoded) in the reanalysis. Seven of the eight changes concerned fossil taxa.

For the master data matrix, we selected 28 nephropid taxa for cladistic analysis. We used 16 of the better known (better preserved) *Hoploparia* species that represented the range of morphologic variation in the genus. We also included genera that resemble *Hoploparia*—including *Homarus* (the distinction between *Hoploparia* and *Homarus* has been much debated (Tshudy, 1993, p. 57)), *Homarinus* Kornfield, 1995 (only recently removed from *Homarus*), *Nephropides*, *Eunephrops*, and, finally, *Metanephrops*, a genus that is morphologically very different from *Hoploparia*. The lobster *Eryma* Von Meyer, 1840, representing the family Erymidae, was selected as the outgroup and used to root the trees.

The three cladistic analyses discussed herein were performed with PAUP* 4.0 (Swofford, 1998). The first was an unweighted heuristic search using random addition of sequences (100 replicates) and tree-bisection-reconnection branch swapping.

In the second analysis, which had the same heuristic search settings as the first analysis, the data were reweighted successively, as specified by Farris's (1969) successive weighting approach to character weighting, until the weights stabilized. The characters were reweighted based on the rescaled consistency index (base weight = 1000). Through successive weighting, the phylogenetic signal in the original matrix can be enhanced, even when cladistically reliable characters are heavily outnumbered by unreliable ones (Farris, 1969).

In the third analysis, we reduced the number of taxa in the hopes of producing a more resolved cladogram. Eleven fossil species, including eight *Hoploparia* and two *Homarus*, were removed from the master matrix, leaving eight well-preserved species representing the range of morphologic variation in *Hoploparia*. This reduced matrix (Appendix III) was analyzed unweighted as in the first analysis.

TreeView (Page, 1996) was used to draw the phylogenetic trees. Rescaled weighted and 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 in the program TreeRot (Version 2.0) (Sorenson, 1999).

RESULTS

In the master matrix of 35 characters, three are constant, and five variable characters are autapomorphous. This leaves 27 characters as parsimony informative. In the taxon-reduced matrix, also of 35 characters, three are constant, and four variable characters are autapomorphous, leaving 28 as parsimony informative.

Unweighted analysis of the master matrix (the first analysis) produced a cladogram that is unresolved with regard to monophyly of *Hoploparia* (Fig. 3). The cladogram represents the strict consensus of 696 most parsimonious trees, and has a length = 86, retention index = 0.61, and consistency index = 0.40. Unweighted

Bremer support values are shown for resolved clades (Fig. 3).

Successive weighting analysis of the master matrix (the second analysis) produced a cladogram that is the strict consensus of 20 most parsimonious trees, has a length = 21,701, retention index = 0.84, consistency index = 0.70, and is well resolved but with poorly supported groups (Fig. 4). *Hoploparia* is shown to be paraphyletic. Rescaled, weighted Bremer support values for the resolved nodes are shown on the cladogram.

Unweighted analysis of the reduced matrix (the third analysis) produced a cladogram that is resolved sufficiently to show that *Hoploparia* is paraphyletic (Fig. 5). The cladogram represents the strict consensus of 33 most parsimonious trees, and has a length = 68, retention index = 0.60, and consistency index = 0.50. Unweighted Bremer support values are shown on the cladogram. Reduction in the number of taxa improved the support values as compared to those on the cladogram (Fig. 4) produced by weighted analysis of the master matrix.

DISCUSSION

We hypothesized prior to this study that *Hoploparia* is a "wastebasket" genus, one that has served as a receptacle for fossil species lacking truly distinctive morphologies. We reasoned that, in being such a "wastebasket," *Hoploparia* has been expanded in *de facto* fashion to an extent that, today, it is difficult to characterize its morphology, and is easily broad enough to include morphologies of several Recent genera (e.g., *Eunephrops*, *Nephropides*). We tested the hypothesis that *Hoploparia* is a paraphyletic, "wastebasket" taxon in a cladistic analysis.

Cladistic analysis herein shows that *Hoploparia* is a paraphyletic group, and, therefore, we failed to reject the hypothesis. Cladistic analysis, therefore, supports the intuitive judgement that *Hoploparia* is a "wastebasket" taxon.

Hoploparia is shown to be paraphyletic in both (the second and the third) analyses showing resolution for *Hoploparia*; i.e., *Hoploparia* species are positioned in clades that include other, non-*Hoploparia* species, both fossil and Recent. Fossil non-*Hoploparia* have been excluded from *Hoploparia* by traditional systematists because of autapomorphies and synapomorphies that make them distinctive from "*Hoploparia*." By traditional systematic methods, this made sense. Nevertheless, these

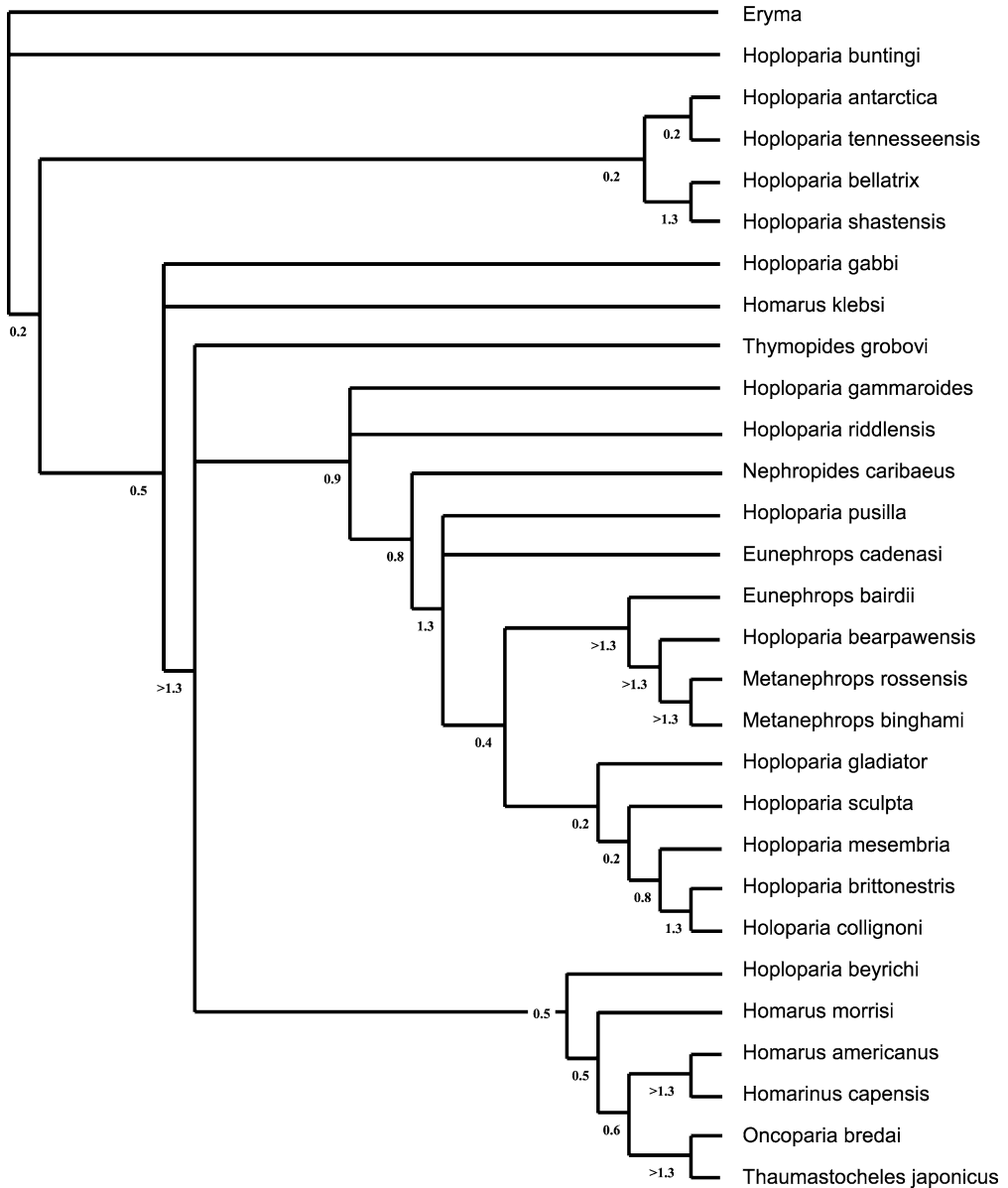


Fig. 4. Cladogram produced by successive weighting analysis is strict consensus of 20 most parsimonious trees and has a length of 21,701, retention index = 0.84, and consistency index of 0.70. Cladogram is well resolved but with poorly supported groups. Rescaled, weighted Bremer support values for the resolved nodes are shown on the tree. *Hoploparia* is shown to be paraphyletic.

fossil genera are part of what makes *Hoploparia* a paraphyletic group.

Monophyletic groups in our cladograms also mix *Hoploparia* and Recent non-*Hoploparia*. Note, for example, the positions of the Recent genera *Nephropides* and *Eunephrops* (Figs. 4, 5), which make *Hoploparia* paraphyletic. From a traditional, systematic standpoint, this sug-

gests either that both *Nephropides* and *Eunephrops* should be made junior synonyms of *Hoploparia*, or that *Hoploparia* should be rediagnosed in a more restricted fashion, one congruent with ranges of morphologic variation in Recent genera. We favor the latter; nevertheless, it should be pointed out that traditional systematic specialists on Recent lobsters have

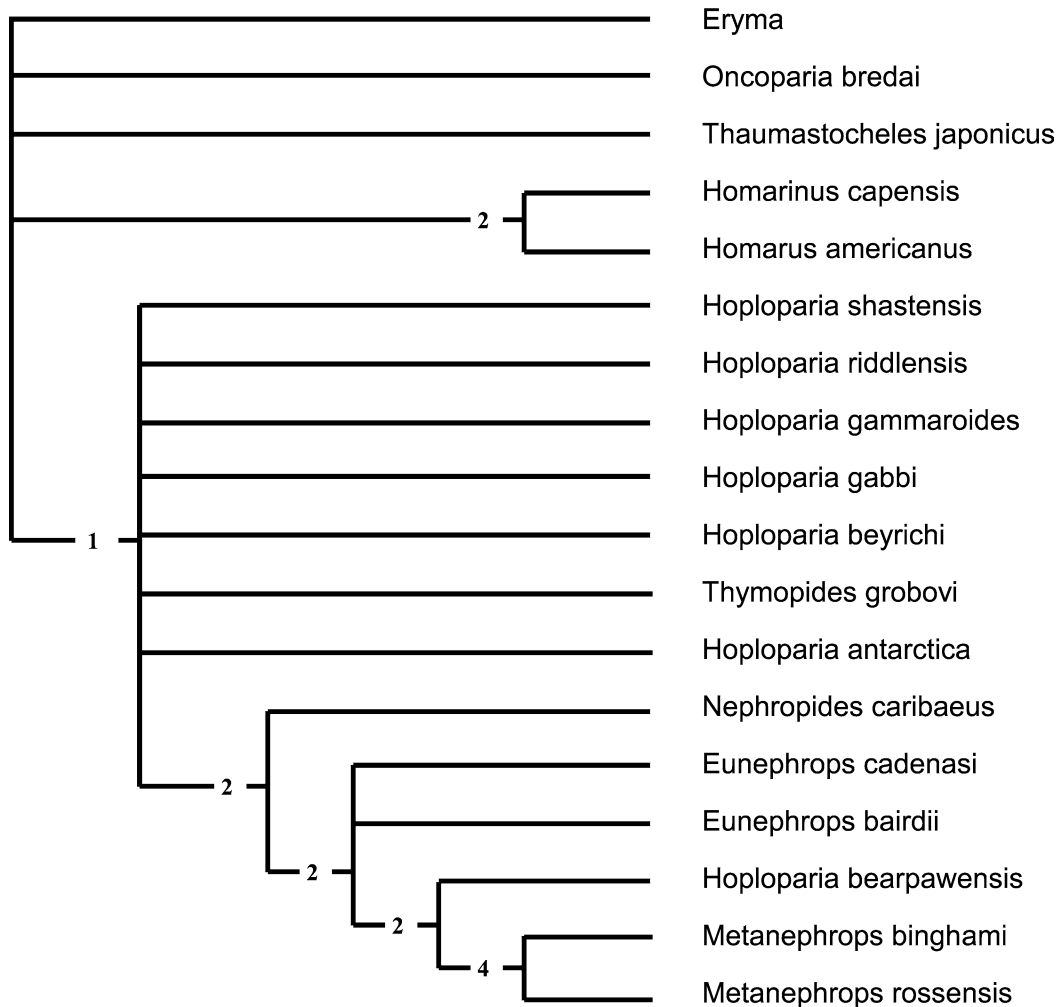


Fig. 5. Cladogram produced by unweighted analysis of reduced matrix is strict consensus of 33 most parsimonious trees, and has a length = 68, retention index = 0.60, and consistency index = 0.50, and shows *Hoploparia* to be paraphyletic.

generally ignored fossil taxa. For example, Manning (1969) made no mention of fossil taxa when erecting *Nephropides*, even though *Nephropides* seems easily accommodated within *Hoploparia*. If the authors of some Recent genera had considered fossil taxa, then some of these Recent genera might never have been erected.

Not all of the cladograms is in opposition to the existing, intuitively derived systematic classification. Several aspects of the cladograms reconcile well with the existing classification:

a. In Figs. 3 and 4, *Oncoparia* and *Thaumastocheles* form a monophyletic group, as they have in previous analyses (Tshudy and Babcock, 1997; Tshudy and Sorhannus, 1998).

On the basis of morphologic similarity and stratigraphic occurrence, the fossil *Oncoparia* has been confidently considered as ancestral to the Recent *Thaumastocheles*.

- b. In Figs. 3, 4, and 5, one fossil and one Recent *Metanephrops* species form a monophyletic group.
- c. In Figs. 3, 4, and 5, *Homarus americanus* H. Milne-Edwards, 1837, and *Homarinus* form a monophyletic group. *Homarinus* was known as *Homarus capensis* (Herbst, 1792), until Kornfield *et al.* (1995) removed it as *Homarinus* on the basis of both morphologic and molecular differences.

What is the remedy for the paraphyly of *Hoploparia*? In acknowledging that *Hoploparia*

is paraphyletic, the traditional systematist might narrow the diagnosis of *Hoploparia*, creating new genera for species thereby excluded. Ranges of morphologic variation in Recent genera would be used as a guide to drawing generic boundaries in fossils. Also, some Recent genera would become junior synonyms of *Hoploparia*. Alternatively, a cladistic approach, which we prefer, would abandon the existing taxa and propose new, monophyletic groupings. We do not, however, believe that proposing a new, formal classification is prudent at this time. Instead, this paper is intended as a first step toward a more meaningful taxonomy. This is the first published species-level cladistic analysis of *Hoploparia*, or of a data matrix for same. It is hoped that this publication will generate discussion among lobster specialists and bring forth additional characters for cladistic analysis and other new insights that may lead to better support in cladograms addressing lobster taxonomy.

CONCLUSION

While it is true that any genus is merely an opinion about how to group similar species, and that there is no biological basis, or even any standard, objective basis, for the genus concept, the case of *Hoploparia* is worse, having been variously stretched and expanded through time in *de facto* fashion by various workers to the point that, today, nobody really knows what *Hoploparia* means. *Hoploparia* McCoy, 1849, was erected for a single species and, by modern standards, was ambiguously diagnosed on the basis of just a few characters. Since that time, the genus has received almost all fossil lobsters with a mainstream nephropid morphology. "Wastebasket" status for *Hoploparia* seemed intuitively reasonable prior to the present study. In this study, cladistic analyses indicate that *Hoploparia* is not a natural group but is, instead, paraphyletic and lacking defining synapomorphies. Thus, we now conclude on both intuitive and cladistic bases that *Hoploparia* is a "wastebasket" genus.

LITERATURE CITED

- Albrecht, H. 1981. Zur Deutung der Carapaxfurchen der Asataceida (Crustacea, Decapoda).—*Zoologica Scripta* 10: 265–271.
- Bosquet, H. 1854. Les crustacés fossils du terrain Crétacé du Duché Limbourg.—*Verhandelingen van de Commissie van de Geologische Beschrijving en Kaart van Nederland, Deel II*: 10–371.
- Bremer, K. 1994. Branch support and tree stability.—*Cladistics* 10: 295–304.
- Bruce, A. J. 1988. *Thaumastocheles wardi*, gen. et sp. nov., a new blind deep-sea lobster from the Coral Sea (Crustacea: Decapoda: Nephropidae).—*Invertebrate Taxonomy* 2: 903–914.
- Farris, J. S. 1969. Successive approximations approach to character weighting.—*Systematic Zoology* 18: 374–385.
- Feldmann, R. M., G. S. Bishop, and T. W. Kammer. 1977. Macrurous decapods from the Bearpaw Shale (Cretaceous; Campanian) of northeastern Montana.—*Journal of Paleontology* 51: 1161–1180.
- Glaessner, M. F. 1969. Decapoda. Pp. R399–R651 in R. C. Moore, ed. *Treatise on Invertebrate Paleontology, Part R, Arthropoda 4 (2)*, Geological Society of America and University of Kansas Press, Lawrence.
- Herbst, J. F. W. 1791–1796. Versuch einer Natureschichte der Krabben und Krebse nebst einer systematischen Beschreibung ihrer verschiedenen Arten, 2. 226 pp. [Not seen.]
- Holthuis, L. B. 1974. The lobsters of the Superfamily Nephropidae of the Atlantic Ocean (Crustacea: Decapoda).—*Bulletin of Marine Science* 24: 723–884.
- Jenkins, J. F. 1972. *Metanephrops*, a new genus of late Pliocene to Recent lobsters (Decapoda, Nephropidae).—*Crustaceana* 22: 161–177.
- Kornfield, I., A. B. Williams, and R. S. Steneck. 1995. Assignment of *Homarus capensis* (Herbst, 1792), the Cape lobster of South Africa, to the new genus *Homarinus* (Decapoda: Nephropidae).—*Fishery Bulletin (U.S.)* 93: 97–102.
- Manning, R. M. 1969. A new genus and species of lobster (Decapoda, Nephropidae) from the Caribbean Sea.—*Crustaceana* 17: 303–309.
- McCoy, F. 1849. On the classification of some British fossil Crustacea, with notices of new forms in the University Collection at Cambridge.—*The Annals and Magazine of Natural History* 2: 161–179.
- Mertin, H. 1941. Decapode Krebse aus dem subhercynen und Braunschweiger Emscher und Untersen sowie Bemerkungen über einige verwandte Formen in der Oberkreide. *Nova Acta Leopoldina, N.F.* 10. 264 pp.
- Milne-Edwards, H. 1837. *Histoire Naturelle des Crustacés; comprenant l'anatomie, la physiologie et la classification de ces animaux*, 2. Paris. 532 pp.
- Page, R. D. M. 1996. TREEVIEW: an application to display phylogenetic trees on personal computers.—*Computer Applications in the Biosciences* 12: 357, 358.
- Pilsbry, H. A. 1901. Crustacea of the Cretaceous formation of New Jersey.—*Proceedings of the Academy of Natural Sciences of Philadelphia* 53: 111–118.
- Prothero, D. R. 1998. *Bringing Fossils To Life: An Introduction to Paleobiology*. WCB/McGraw-Hill, Boston. 457 pp.
- Secretan, S. 1960. Observations relatives au processus d'évolution des sillons chez les Crustacés Décapodes Macroures.—*Comptes Rendus des Séances de l'Académie des Sciences* 251: 1551–1553.
- . 1964. Les crustacés décapodes du Jurassique Supérieur et du Crétacé de Madagascar.—*Mémoires du Muséum National d'Histoire Naturelle* 19. 223 pp.
- Simpson, G. G. 1945. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History* 85: 1–35.
- Smith, S. I. 1885. Description of a new crustacean allied to *Homarus* and *Nephrops*.—*Annals and Magazine of Natural History, London, series 5*, 16: 233–236.

- Sorenson, M. D. 1999. TreeRot, Version 2.0. Boston University.
- Sowerby, G. B. 1826. Description of a new species of *Astacus*, found in a fossil state at Lyme Regis.—*Zoological Journal* 2: 293–494.
- Swofford, D. L. 1998. PAUP* 4.0.—Phylogenetic Analysis Using Parsimony (*and Other Methods). Sinauer Associates, Sunderland, Massachusetts.
- Tshudy, D. 1993. Taxonomy and Evolution of the Clawed Lobster Families Chilenophoberidae and Nephropidae.—Unpublished Ph.D. Thesis, Kent State University, Kent, Ohio. 472 pp.
- , and L. Babcock. 1997. Morphology-based phylogenetic analysis of the clawed lobsters (family Nephropidae and the new family Chilenophoberidae).—*Journal of Crustacean Biology* 17: 253–263.
- , R. M. Feldmann, and P. D. Ward. 1989. Pectinate claws in decapod crustaceans: convergence in four lineages.—*Journal of Paleontology* 74: 474–486.
- , and U. Sorhannus. 1998. *Jagtia kunradensis*, a new genus and species of clawed lobster (Decapoda: Nephropidae) from the Upper Cretaceous (Upper Maastrichtian) Maastricht Formation, The Netherlands.—*Journal of Paleontology* 74: 224–229.
- Von Meyer, H. 1840. Neu Gattungen fossiler Krebs aus Gebilden von bunten Sandstein bis in die Kreide. Publisher unknown, Stuttgart, Germany. 28 pp. [Not seen.]
- Weber, F. 1795. *Nomenclator entomologicus secundum Entomologiam systematicam ill. Fabricii adjectis species recens detectis et varietatibus*. 171 pp. [Not seen.]
- Wilckens, O. 1907. Die Lamellibranchiaten, Gastropoden etc. der oberen Kreide Südpatagoniens. *Berichte der Naturforschenden Gesellschaft zu Freiberg*.
- Wood-Mason, J. 1874. Blind Crustacea.—*Proceedings of the Asiatic Society of Bengal*, 42: 230–232. [Not seen.]

RECEIVED: 8 August 2002.

ACCEPTED: 22 January 2003.

APPENDIX I

Pre-Quaternary stratigraphic distribution of species of *Hoploparia sensu* Tshudy, 1993; 49 species total.

Tertiary species = 9 (8 new species + continuation of *H. stokesi*)

- Hoploparia alpinus* (van Straelen, 1936) (Auversien)
H. buntingi (Feldmann and Holland, 1971) (Paleocene)
H. corneti van Straelen, 1921 (Upper Ypresien)
H. gammaroides McCoy, 1849 (Lower Eocene)
H. gadzicki Feldmann and Crame, 1998, (Lower Miocene)
H. groenlandica Ravn, 1903 (Lower Eocene)
H. johnsoni Rathbun, 1935 (Middle Eocene)
H. stokesi (Weller, 1903) (Campanian–Paleocene)
H. wardi Quayle, 1987 (Lower Eocene)

Upper Cretaceous species = 27 (26 new species + continuation of *H. tshudyi*)

- Hoploparia antarctica* Wilckens, 1907 (Campanian–Maastrichtian)
H. arbei Aguirre-Urreta, 1989 (Turonian–Coniacian)
H. bearpawensis Feldmann, 1977 (uppermost Campanian)
H. bennetti Woodward, 1900 (K–Upper)
H. beyrichi (Schlüter, 1862) (Maastrichtian)
H. biserialis Fritsch, 1887 (Turonian)
H. blossomana Rathbun, 1935 (Coniacian)
H. brittonestrus (Stenzel, 1945) (lower Turonian)
H. davisii (Stenzel, 1945) (lower Turonian)
H. fraasi (Böhm, 1891) (Senonian)
H. gabbi Pilsbry, 1901 (lower Campanian)
H. georgeana Rathbun, 1935 (Maastrichtian)
H. gladiator Pilsbry, 1901 (Maastrichtian)
H. hakelensis (Fraas, 1878) (Cenomanian)
H. hemprichi (Mertin, 1941) (Coniacian or lower Santonian)
H. mcnairyensis Rathbun, 1929 (Maastrichtian)
H. mickelsoni Bishop, 1985 (lower Campanian)
H. miyamotoi Karasawa, 1998 (Campanian–Maastrichtian)
H. muncki Pelseneer, 1886 (Senonian)
H. pusilla Secretan, 1964 (lower Campanian)
H. schluteri Tribolet, 1874 (Cenomanian)
H. senonensis Forir, 1887 (Senonian)
H. shastensis (Rathbun, 1929) (upper Coniacian–lower Campanian)
H. stokesi (Weller, 1903) (Campanian–Paleocene)
H. tennesseensis Rathbun, 1926 (Maastrichtian)
H. trigeri (A. Milne-Edwards, 1886) (upper Cenomanian)
H. tshudyi Schweitzer and Feldmann, 2001 (upper Albian–upper Cenomanian)

Lower Cretaceous species = 17

- Hoploparia aspera* Harbort, 1905 (Valanginian)
H. collignoni (van Straelen, 1949) (Albian)
H. columbiana Beurlen, 1938 (Neocomian)
H. dentata (Roemer, 1841) (Valangian–Urgonian)
H. dentonensis Rathbun, 1935 (upper Albian)
H. edwardsi (Robineau-Desvoidy, 1849) (lower Neocomian)
H. intermedia Secretan, 1964 (Albian)
H. kamuy Karasawa and Hayakaya, 2000 (lower Santonian–upper Turonian)
H. longimana (Sowerby, 1862) (Aptian, Albian)
H. mesebria Etheridge, Jr., 1917 (upper Albian)
H. minima Tribolet, 1876 (Neocomian)
H. pelseeneeri (van Straelen, 1936) (Albian)
H. riddlensis Feldmann, 1974 (Hauterivian)
H. sculpta Secretan, 1964 (Albian)
H. travisensis (Stenzel, 1945) (middle Albian)
H. triboleti Borissjak, 1904 (Neocomian)
H. tshudyi Schweitzer and Feldmann, 2001 (upper Albian–upper Cenomanian)

APPENDIX II

Master data matrix for cladistic analysis.

<i>Eryma</i>	10020	11100	00100	00000	00000	00001	00???
<i>Hoploparia antarctica</i>	11000	11111	?0010	11110	00011	00011	01???
<i>Hoploparia bearpawensis</i>	11020	01001	01??0	01?1?	110?1	0????	?1???
<i>Hoploparia bellatrix</i>	1????	11011	??110	00100	0001?	0????0	01???
<i>Hoploparia beyrichi</i>	10010	01001	00?10	00100	00010	00??1	01???
<i>Hoploparia brittonestrus</i>	00020	01011	10110	01100	00011	0????0	01???
<i>Hoploparia buntingi</i>	10020	11001	00?00	00110	00011	00??1	01???
<i>Hoploparia collignoni</i>	00020	01111	00110	01100	00011	0????0	01???
<i>Hoploparia gabbi</i>	10000	11001	00110	00100	00010	00??1	01???
<i>Hoploparia gammaroides</i>	10000	01001	00110	00100	00010	000?0	01???
<i>Hoploparia gladiator</i>	10020	011?1	10110	00100	00011	0????0	11???
<i>Hoploparia mesebria</i>	1?020	01011	??110	01100	00011	0?????	01???
<i>Hoploparia pusilla</i>	10000	01011	00110	00000	00011	00???	?1???
<i>Hoploparia riddlensis</i>	10000	01001	1?110	00000	00010	00??0	01???
<i>Hoploparia sculpta</i>	11020	???.11	10110	01100	00011	00??0	11???
<i>Hoploparia shastensis</i>	10020	11011	00110	00100	00010	0????0	01???
<i>Hoploparia tennesseensis</i>	10020	11111	00110	00100	00011	0???.1	01???
<i>Homarus americanus</i>	01020	01001	00000	00100	00010	01011	01111
<i>Homarus klebsi</i>	10000	111?1	1?110	00110	0?010	0????1	01???
<i>Homarus morrisi</i>	10010	01001	00000	00?10	000?0	0????1	01???
<i>Eunephrops bairdii</i>	10020	01011	00110	00011	01011	00110	11111
<i>Eunephrops cadenasi</i>	11000	01011	00110	00010	00011	00010	11111
<i>Nephropides caribaeus</i>	11010	01001	00100	00010	00010	00010	11011
<i>Homarinus capensis</i>	01020	0????1	00100	00100	00000	01011	01111
<i>Metanephrops rossensis</i>	10000	01000	11011	11110	1?111	00??0	01???
<i>Metanephrops binghami</i>	10000	01000	01011	11111	11111	00010	11101
<i>Oncoparia bredai</i>	10020	01001	00010	00100	00010	11??2	01???
<i>Thaumastocheles japonicus</i>	10020	01001	00000	00000	00000	11002	01011
<i>Thymopides grobovi</i>	11100	01001	00111	00000	00010	00011	01011

APPENDIX III

Reduced data matrix for cladistic analysis.

<i>Eryma</i>	10020	11100	00100	00000	00000	00001	00????
<i>Hoploparia antarctica</i>	11000	11111	?0010	11110	00011	00011	01????
<i>Hoploparia bearpawensis</i>	11020	01001	01??0	01?1?	110?1	0?????	?1????
<i>Hoploparia beyrichi</i>	10010	01001	00?10	00100	00010	00??1	01????
<i>Hoploparia gabbi</i>	10000	11001	00110	00100	00010	00??1	01????
<i>Hoploparia gammaroides</i>	10000	01001	00110	00100	00010	000?0	01????
<i>Hoploparia riddlensis</i>	10000	01001	1?110	00000	00010	00??0	01????
<i>Hoploparia sculpta</i>	11020	????11	10110	01100	00011	00??0	11????
<i>Hoploparia shastensis</i>	10020	11011	00110	00100	00010	0???0	01????
<i>Homarus americanus</i>	01020	01001	00000	00100	00010	01011	01111
<i>Eunephrops bairdii</i>	10020	01011	00110	00011	01011	00110	11111
<i>Eunephrops cadenasi</i>	11000	01011	00110	00010	00011	00010	11111
<i>Nephropides caribaeus</i>	11010	01001	00100	00010	00010	00010	11011
<i>Homarus capensis</i>	01020	0????1	00100	00100	00000	01011	01111
<i>Metanephrops rossensis</i>	10000	01000	11011	11110	1?111	00??0	01????
<i>Metanephrops binghami</i>	10000	01000	01011	11111	11111	00010	11101
<i>Oncoparia bredai</i>	10020	01001	00010	00100	00010	11??2	01????
<i>Thaumastocheles japonicus</i>	10020	01001	00000	00000	00000	11002	01011
<i>Thymopides grobovi</i>	11100	01001	00111	00000	00010	00011	01011

APPENDIX IV

Explanation of characters and character states used in data matrix. Characters are discussed in Tshudy (1993: 453–472).

Carapace Grooves

1. Ventral extension of branchiocardiac groove (bc') (part of the postcervical groove *sensu* Holthuis, 1974): 0 = absent, 1 = present. This is the ventral extension of the postcervical groove *sensu* Holthuis (1974). The homology of this groove on various clawed lobsters is discussed in detail in Tshudy (1993: fig. 3, 461–464).
2. Urogastric groove (u): 0 = absent, 1 = present.
3. Sellar groove (s): 0 = absent, 1 = present.
4. Branchiocardiac groove (bc) (horizontal portion on thoracic region): 0 = absent, 1 = short (extending less than halfway to posterior margin), 2 = long (extending greater than halfway to posterior margin). Judgements about this groove can be especially difficult to make, as we ask "is it a groove, or just the lower surface bordering an intermediate carina?".
5. Parabranchial groove (pb): 0 = absent, 1 = present.
6. Inferior groove (i): 0 = absent, 1 = present.
7. Hepatic groove (h): 0 = absent, 1 = present.
8. Suprahepatic groove (sh): 0 = absent, 1 = present.
9. Buccal groove (b): 0 = absent, 1 = present.
10. Intercervical groove (ic): 0 = absent, 1 = present.

Carapace Ornamentation

Note: "carina" herein refers to a ridge, with or without ornamentation, or a row of projections (spines, spinules, or rounded "tubercles"). There is, among nephropids, a continuum between ornamented ridges that are topographically high, topographically low, and simple, unelevated rows of projections. Any divisions of this continuum would be arbitrary.

11. Cephalic median carina (CM): 0 = absent, 1 = present.
12. Thoracic median carina (TM): 0 = absent, 1 = present.
13. Subdorsal carina (SD): 0 = absent, 1 = present.
14. Supraorbital carina (SO): 0 = absent, 1 = present.
15. Lateral carina (L): 0 = absent, 1 = present.
16. Branchial carina (B): 0 = absent, 1 = present.
17. Intermediate carina (I): 0 = absent, 1 = present. Judgements on this character can be especially difficult to make. Taphonomic effects are a real possibility, and, also, we sometimes ask, "Is it a ridge, or just the higher surface bordering a branchiocardiac groove?".
18. Postorbital spine (PO): 0 = absent, 1 = present.
19. Gastrolateral spine (GL): 0 = absent, 1 = present.
20. Gastric tubercle (G): 0 = absent, 1 = present.
21. Cervical spine (C): 0 = absent, 1 = present.
22. Postcervical spine (PC): 0 = absent, 1 = present.
23. Hepatic spine (H): 0 = absent, 1 = present.
24. Supraorbital spine (SO): 0 = absent, 1 = present.
25. Postantennal spine (PA): 0 = absent, 1 = present.

Abdomen

26. Abdominal pleura quadrate (as on *Thaumastocheles*): 0 = absent, 1 = present.

Telson

27. Telson shape: 0 = longer than wide, 1 = wider than long (as on *Thaumastocheles*).
28. Telson with lateral spine on each side: 0 = absent, 1 = present.
29. Telson with spine on each posterior corner: 0 = absent, 1 = present.

Claws

30. Claw palm shape: 0 = elongate (palm length medially / maximum palm width > 2), 1 = broad (palm length medially / maximum palm width = 2), as on *Homarus americanus*, 2 ≤ bulbous (as on *Thaumastocheles*), 3 = cylindrical (as on *Acanthacaris*).
31. Claws with longitudinal carinae (either as ridge, row of obvious spines, or both) on upper and/or lower surfaces: 0 = absent, 1 = present.

Fusiform Plate as on *Eryma*

32. Fusiform plate on median of gastric region: 0 = present, 1 = absent.

Appendages (other than first pereopods or "claws")

33. Podobranch on maxilliped 2: 0 = absent, 1 = present.
34. Exopod on maxilliped 2: 0 = absent or reduced, 1 = present.
35. Exopod on maxilliped 3: 0 = absent or reduced, 1 = present.