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PHYLOGENETIC ANALYSIS OF THE STOMATOPODA (MALACOSTRACA)

Shane T. Ahyong

ABSTRACT

The stomatopods or mantis shrimps are malacostracan crustaceans of the subclass Hoplocarida. All extant hoplocarids belong to the order Stomatopoda and suborder Unipeltata. The Unipeltata comprises the extinct, stem-lineage sculdids, and the crown-group which includes the 19 extant families with more than 400 species. A cladistic analysis of all 20 families of the Unipeltata, rooted with four fossil outgroups, resulted in a single, fully resolved topology. The results largely support the existing five-superfamily classification. The Squilloidea, not the Bathysquilloidea, were the earliest derived crown-group superfamily. The Lysiosquilloidea and Erythrosquilloidea are derived as sister groups, which together are sister to the gonodactyloids. The Bathysquilloidea and Gonodactyloidea, however, were not monophyletic, supporting the erection of new superfamilies for the extinct Sculdidae and the extant Parasquillidae.

The Bathysquilloidea is restricted to the Bathysquillidae and Indosquillidae, but, owing to incomplete fossil data, a new taxon is not erected for the sculdids. Instead, the Sculdidae is considered incertae sedis until more fossil data become available. The superfamilial affiliation of the Parasquillidae is also considered uncertain pending further research. Monophyly of the Heterosquillidae sensu Manning (1995) was unsupported. *Paracoridon,* presently a heterosquillid, is transferred to the Corononididae. Further study of coronidid relationships is necessary and may support the removal of both *Acoridon* and *Paracoridon.* The Tetrasquillidae and Heterosquillidae, as restricted here, are recognized as sister taxa, but further study may require their synonymy. Characters based on the modified male first pleopod are informative at superfamily level and further study may reveal characters useful down to the specific level.

Stomatopods are among the most aggressive and behaviorally complex crustaceans. All are active predators and mark one of the very few radiations of obligate carnivores within the Crustacea (Schram, 1986). Characteristic features of stomatopods are the large and powerful raptorial appendages. Prey is captured by "spearing" or "smashing," depending on whether the dactyl is extended or kept folded during the strike. The two methods of prey capture distinguish two broad functional groups, the "smashers" and the "spearers" (Caldwell and Dingle, 1976). These two groups comprise the order Stomatopoda, the only living representatives of the subclass Hoplocarida (Schram, 1986).

The phylogenetic status of the hoplocarids has been subject to much speculation (Schram, 1969). Burnett and Hessler (1973) considered the hoplocarids to be eumalacostracans on the basis of "caridoid facies" (Calman, 1909). Many characters, however, also occur in other groups (Kunze, 1981). On the basis of functional morphology, Kunze (1981) concluded that the hoplocarids evolved from a phyllocarid-like ancestor, distinct from the eumalacostracans. Conversely, Schram (1986) proposed that the hoplocarids and eumalacostracans were sister taxa, and included the malacostracan phyllocarids with several non-malacostracan groups in the Class Phyllopoda. Although the sister relationship of the hoplocarids and eumalacostracans is well supported, Schram's concept of Phyllopoda is now discounted (Martin and Christiansen, 1995). Three major radiations from an ancestral malacostracan stock appear to have occurred: the Phyllocarida, the Hoplocarida, and the other Eumalacostraca.

Presently, the fossil record is relatively poor, but apparently the hoplocarid ancestors diverged from other malacostracans during the Devonian. Three hoplocarid orders are recognized by Schram (1986): Aeschronectida, Palaeostomatopoda, and Stomatopoda. Fossil aeschronectids and palaeostomatopods are known from North America and Europe where they occupied near-shore, shallow-water habitats (Schram, 1977). The aeschronectids were the least specialized, whereas the palaeostomatopods possessed small, subchelate, raptorial claws. Two suborders of the Stomatopoda are recognized: Archaeostomatopoda and Unipeltata (containing the extant stomatopods). The archaeostomatopods first appeared in the Carboniferous family Tyrannophontidae and are believed to link the Palaeostomatopoda with the Unipeltata.

The Unipeltata comprises the Jurassic family Sculdidae and the extant superfamilies, usually termed Recent (Manning, 1980, 1995). The term Recent is used variously in different contexts, but usually means Holocene to the present. Since the fossil record suggests that extant superfamilies have Cretaceous origins (Schram, 1986; Reaka and Manning, 1987), they are here referred to as the crown-group (Jeffries, 1979). The Unipeltata is here considered to be the total-group and therefore the extinct sculdids comprise the stem-group or better, the stem lineage (Ax, 1985). The crown-group stomatopods are up to 100 million years old, displaying little morphological divergence since then. All fossil stomatopods since the Cretaceous may be assigned to extant families (Schram, 1986).

Over the past three decades, the taxonomy of the Stomatopoda has been revised extensively, principally through the work of Manning (1963, 1968, 1980, 1995). Prior to his work, only the single family, Squillidae, was recognized for crown-group taxa. Giesbrecht (1910) proposed several subfamilies based on larvae, but his work was largely ignored by those working with adults (Manning, 1968). In the most comprehensive work of its time, Kemp (1913) recognized only 126 species in six genera, in the single family Squillidae. Using larval, maxillipedal, and telson morphology, Manning (1968) recognized 37 genera in four families: Squillidae, Lysiosquillidae, Bathysquillidae, and Gonodactylidae. These four families were considered to represent distinct lineages within the Stomatopoda. Although the general aspect is often sufficient to distinguish the four groups, the telson and maxillipedal morphology appear to be fundamental and conservative characters, appearing also in larvae where known (Manning, 1968). Giesbrecht's subdivisions, based on larvae, correspond to the familial lineages recognized by Manning (1968). Manning (1980), in a further review of stomatopod classification, recognized four superfamilies: Squilloidea, Lysiosquilloidea, Bathysquilloidea, and Gonodactyloidea. Manning and Camp (1993) recognized in a new superfamily, the Erythrosquilloidea, *Erythrosquilla megalops* Manning and Bruce, previously assigned tentatively to the Lysiosquilloidea. Nineteen families and five superfamilies are currently recognized by Manning (1995) for living taxa, containing more than 100 genera and 400 species. The many genera, each containing relatively few species, have been considered to exhibit relict distribution patterns consistent with the antiquity of the Stomatopoda (Reaka and Manning, 1987). Certainly, many apparently closely related taxa exhibit restricted distributions which are consistent with a former Tethyan distribution. To date, however, cladistic biogeographic analyses have not been conducted with stomatopods to test such hypotheses. These, of course, require prior knowledge of phylogeny.

Although stomatopods are remarkably uniform in general structure, much morphological diversity exists within the group. Previous classifications were based on intuitive estimates of phylogeny. Relationships between a few genera or families have been discussed or implied in the classification (e.g., Manning, 1963, 1969c; Manning and Camp, 1993). For more than a century, however, no formal phylogeny of the Stomatopoda has been proposed, and there are no studies based on cladistic principles. This analysis of the Unipeltata, therefore, provides a framework for further study.

MATERIALS AND METHODS

Taxa Included.—All 20 families of the Unipeltata are represented by their respective type genera, or genera regarded as closely related (if material was unavailable or published descriptions were insufficient). The Protosquillidae is thus represented by *Haptosquilla* Manning (formerly *Protosquilla* Brooks) and Parasquillidae by *Faughnia* Serène (formerly a subgenus of *Parasquilla* Manning). Where the family was relatively heterogeneous, several taxa from that family were included to represent morphological diversity. The Squillidae was represented by *Squilla* Fabricius and *Levisquilla* Manning. The Nannosquillidae was represented by *Hadrosquilla* Manning and *Acanthosquilla* Manning. The Heterosquillidae was represented by *Heterosquilla* Manning, *Heterosquilloides* Manning, and *Parăcoridon* Moosa. The Coronididae was represented by *Coronida* Brooks and *Acoridon* Adkison, Heard, and Hopkins. The Tetrasquillidae was represented by *Tetrasquilla* Manning and Chace and *Tectasquilla* Adkison and Hopkins.

Characters were polarized using multiple outgroups (Maddison *et al.*, 1984), thus making no a priori assumptions of plesiomorphy or apomorphy. Insofar as the purpose of this study was to resolve relationships among living stomatopods, only fossil taxa were available as outgroups. Outgroups included four extinct hoplocarid groups outside of the Unipeltata. Whereas the cladogram can be rooted with only a single outgroup, multiple outgroups were selected in order to better represent morphological diversity among the fossil taxa. Three taxa representing the Perimecturidae (Palaeostomatopoda) were included: *Perimecturus* Peach, *Bairdops* Schram, and *Archaeocaris* Meek. The Tyrannophontidae was represented by its type genus *Tyrannophontes* Schram.

Material Examined.—The character states were scored from published descriptions and material in the collections of the Australian Museum, Queensland Museum, Northern Territory Museum of Arts and Sciences, and the Smithsonian Institution. Appendix 1 lists material examined from the genera included in the analysis, but is by no means restricted to the total material examined.

Analytical Methods.—The final character matrix included 30 taxa and 43 characters (Appendix 2). Characters were unordered (nonadditive), missing data were scored unknown, and polymorphic characters were scored as such rather than assuming the plesiomorphic state. Uninformative characters were excluded to avoid artificially inflating the consistency indices. Since character polarity was determined by outgroup comparison and character states were unordered, the number given to each character state (i.e., 0, 1, 2) implies nothing about apomorphy or plesiomorphy. Characters and their states are listed in Appendix 3.

Trees were generated in PAUP 3.1.1 (Swofford, 1993) using the heuristic search option (MULPARS, tree-bisection-reconnection, 10 replications with random input order). In PAUP, analyses were run so that the outgroups formed a basal polytomy with the ingroup, and separate analyses were run with the outgroups constrained as monophyletic (the ingroup topology, of course, remained unchanged). Character changes were studied in MacClade 3.04 (Maddison and Maddison, 1993).

Relative stability of clades was assessed using bootstrap (Felsenstein, 1985) and decay analyses (Bremer, 1988, 1994). Bootstrapping was based on 100 replicates of random input order. Decay analysis was conducted by relaxing parsimony step by step until clades on the most parsimonious tree were no longer unequivocally supported on suboptimal trees.

CHARACTER ANALYSIS

Eyes

Vision in stomatopods has received considerable attention in recent years (e.g., Cronin and Marshall, 1989). Corneal morphology is diverse and exhibits discernible taxonomic trends. Except in bathysquilloids, the cornea is bisected by a central band of ommatidia. The cornea is often bilobed and set transversely or obliquely on the stalk (Fig. 1A). In erythrosquilloids, most squilloids, and lysiosquillids, the cornea is considerably broader than the peduncle and strongly bilobed (Fig. 1B). The broad cornea is thought to increase parallax, thereby improving the precision of stereoscopic rangefinding (Caldwell, 1991). In most gonodactyloids and some lysiosquilloids (e.g., Nannosquillidae), the eyes are subcylindrical or subspherical (e.g., Gonodactylidae and Odontodactylidae) (Fig. 1C, D). The cornea of bathysquilloids, though much reduced, is also subspherical. Many corneal characters are useful at generic and specific level, but at the level of this analysis, fewer characters are informative.

Recently, the value of the central band of ommatidia has been recognized as an important taxonomic character (Manning *et al.*, 1984a, b). Bathysquilloids possess no central band of ommatidia. Squilloids possess two bands of central ommatidia. Gonodactyloids and lysiosquilloids possess six bands of ommatidia in the central band but the ommatidial facets differ in shape. The absence of a central band of ommatidia in bathysquilloids may be an artifact of living at considerable depth, since the corneal facets are absent or ill-defined and the neural connections to the eyes are degenerate (Manning *et al.*, 1984b). In contrast, the fundamental differences in the central band in the other superfamilies suggest that the currently recognized lineages were differentiated early in the history of the group (Manning *et al.*, 1984b). The central band ommatidia of *Erythrosquilla* appears to be absent (Manning, 1995).

Character 1: cornea strongly bilobed (0); bilobed (1); subspherical or faintly bilobed (2).

Character 2: central band of ommatidia absent (0); with two rows (1); with six rows (2).

Character 3: central band ommatidia hexagonal (0); rectangular (1); absent (2).

Character 4: facets of the cornea well defined (0); poorly defined or absent (1).

Antennal Protopod

The antennal protopod carries the antenna and the antennal scale (scaphocerite). Several characters are informative at family level and three are considered here. The protopod often bears ventral and mesial papillae. Ventral papillae are present in squilloids, most lysiosquilloids, most bathysquilloids, erythrosquilloids, and some gonodactyloids. Mesial papillae are present in most lysiosquilloids.

An articulated plate (antennal plate), arising from the dorsal margin of the antennal protopod, is present in the gonodactyloid families Pseudosquillidae, Eurysquillidae, Hemisquillidae, and Odontodactylidae (Fig. 1C). The antennal plate is absent in all other stomatopods (Fig. 1A, B). In takuids, gonodactylids, protosquillids, and alainosquillids, a

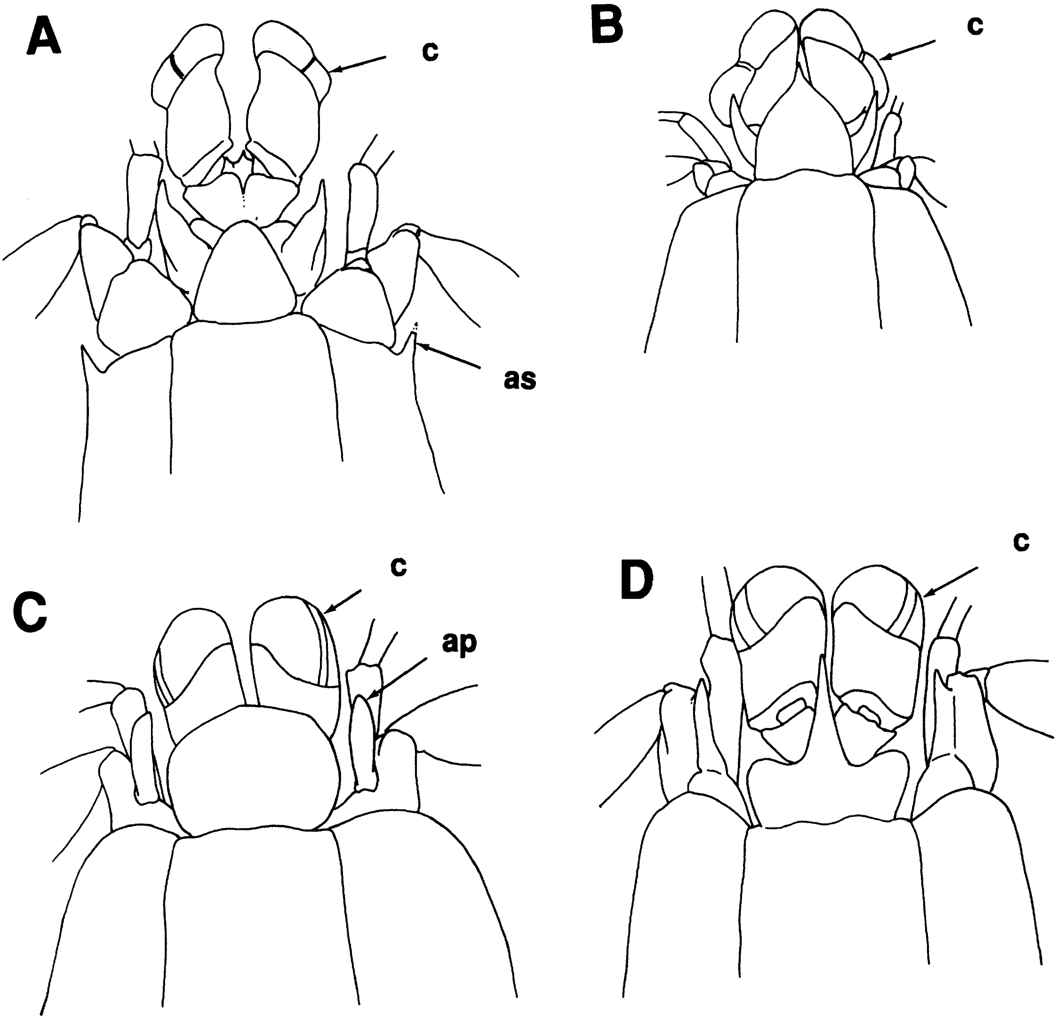

Fig. 1. Anterior region of selected stomatopods. A, *Levisquilla jurichi* (Squillidae); B, *Heterosquilloides insignis* (Heterosquillidae); C, *Pseudosquilla ciliata* (Pseudosquillidae); D, *Gonodactylus platysoma* (Gonodactylidae). ap = antennal plate, as = anterolateral spine, c = cornea.

long, slender, dorsal spine is present (Fig. 1D). In other taxa, a small tooth may be present.

Character 5: ventral papillae absent (0); present (1).

Character 6: mesial papillae absent (0); present (1).

Character 7: dorsal margin of antennal protopod unarmed or with small tooth (0); with articulated plate (1); with slender, fixed spine (2).

Maxillipeds

The structure of the propodi of the third to fifth maxillipeds is recognized as fundamental in delineating the superfamilies (Manning, 1968, 1980, 1995). In bathysquilloids, squilloids, and gonodactyloids, the propodi of the last three maxillipeds are longer than broad (Fig. 2A–C). In contrast, the maxillipedal propodi of lysiosquilloids and erythrosquilloids are broader than long, bearing ventral ribbing or beading (Fig. 2D). In most coronidids, the propodi are broad, but the ventral beading is reduced. These maxillipedal forms are characteristic of both adults and known larvae (Manning, 1963).

In most stomatopods, the distal margin of the propodus of the fifth maxilliped bears a dense brush of grooming setae (Bauer, 1987). This setal brush is vestigial in some gonodactyloids and present, but reduced, in bathysquilloids.

In the Archaeostomatopoda and Palaeostomatopoda, the relative lengths of the max-

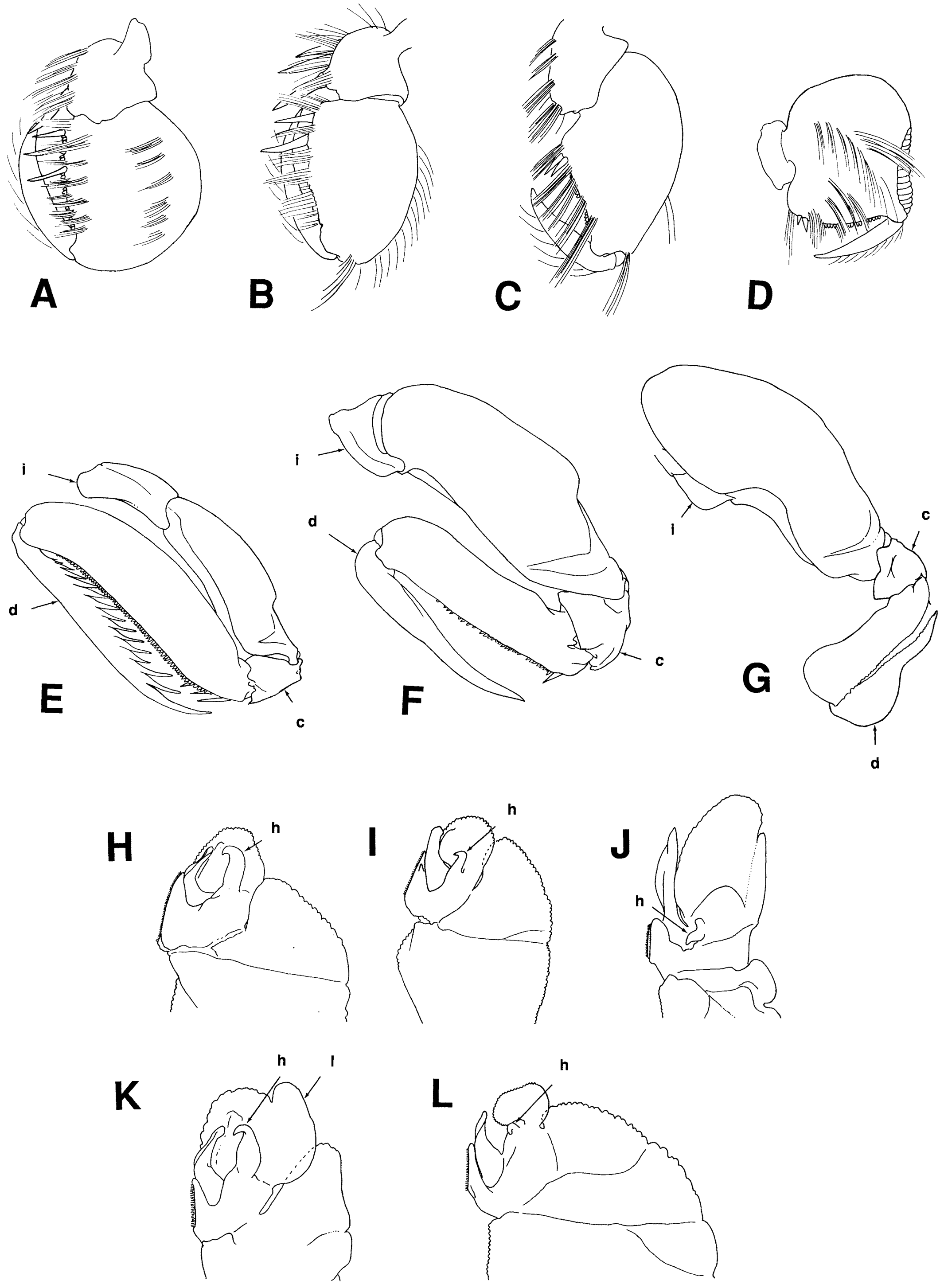

Fig. 2. Stomatopoda. A–D, Propodi of maxilliped 3: A, *Oratosquillina stephensoni* (Squillidae); B, *Bathysquilla crassispinosa* (Bathysquillidae); C, *Gonodactylus platysoma* (Gonodactylidae); D, *Lysiosquilla hoevenii* (Lysiosquillidae). E–G, raptorial claw: E, *Heterosquilla tricarinata* (Heterosquillidae); F, *Hemisquilla ensigera australiensis* (Hemisquillidae); G, *Gonodactylus platysoma* (Gonodactylidae). H–L, endopod of the first male pleopod (A, B, D, E, right anterior, C, left anterior): H, *Faughnia serenei* (Parasquillidae); I, *Oratosquillina stephensoni* (Squillidae); J, *Bathysquilla crassispinosa* (Bathysquillidae); K, *Gonodactylus platysoma* (Gonodactylidae); L, *Lysiosquilla* sp. (Lysiosquillidae). c = carpus, d = dactylus, i = ischium, h = hooked process, l = lateral lobe. (J redrawn after Bruce (1988)).

illipedal segments differ from those of crown-group stomatopods. The propodi of maxillipeds 3–5 are all relatively large, elongate, and similar in size (Schram, 1969). This contrasts with the crown-group stomatopods, where most maxillipeds are reduced, compared to the outgroups, and the second maxilliped is specialized as a large raptorial claw.

Character 8: propodi of third to fifth maxillipeds very elongate (0); slender (1); broad and ventrally ribbed (2); broad with ribbing reduced (3).

Character 9: propodus of maxilliped 5 with setal brush present (0); vestigial (1); reduced (2).

Raptorial Claw

Unlike the archaeostomatopods and palaeostomatopods, the second maxilliped of crown-group stomatopods is specialized as a raptorial claw. Apparently, in crown-group stomatopods, maxillipeds 3–5 have become reduced in size, while maxilliped 2 has become specialized. The condition in the sculdids is presently unknown.

In all squilloids, bathysquilloids, erythrosquilloids, most lysiosquilloids, and some gonodactyloids, the dactylus is armed with a series of serrated teeth used to impale prey. On the basis of ontogeny, fossil evidence, and behavior, the spearing claw (Fig. 2E) is probably plesiomorphic (Caldwell, 1991).

In smashers, the dactyl is basally inflated and heavily calcified (Fig. 2F, G). The inner margin of the dactyl is unarmed in the Protosquillidae, Gonodactylidae, and Hemisquillidae (Gonodactyloidea). In Coronididae (Lysiosquilloidea) and Odontodactylidae (Gonodactyloidea), the inner margin of the dactylus is armed with teeth.

The dorsal surface of the raptorial carpus bears a stout tooth in most crown-group taxa. In the squilloids, however, the carpus is carinate (which may be tuberculate) or unadorned.

The raptorial propodus in most spearers is pectinate and armed proximally with a series of up to four movable spines. In most coronidids, the propodus is pectinate only for the proximal two-thirds, except in *Acoridon.* In *Acoridon,* the propodus is pectinate for nearly its full length, as in *Tectasquilla,* for example. In the bathysquilloids and harpiosquillids, the propodus is also armed with a series of evenly spaced, erect spines, presumably to aid prey retention. Two rows are present in bathysquillids (one on each side of the propodus) and one row is present in harpiosquillids (on the outer side only). Manning (1969a) and Bruce (1988) considered the spined propodus in bathysquillids and harpiosquillids to be convergent, since the major spines arise on different sides of the propodus. In contrast, the outer row of spines in harpiosquillids and bathysquillids may be homologous despite their size, and the inner row a bathysquillid synapomorphy. In the gonodactyloid smashers, the ventral margin of the propodus is smooth or faintly pectinate, except in the Hemisquillidae.

The ischiomeral articulation of the raptorial claw relates to the type of raptorial appendage and may be terminal or subterminal. In spearers, the ischiomeral articulation is terminal (Fig. 2E, F). In most lysiosquilloids the ischium is relatively long in proportion to the merus. In *Heterosquilla tricarinata,* for example, the ischium is approximately half the merus length (Fig. 2E). The relatively long ischium in the lysiosquilloids appears to facilitate increased reach of the raptorial claw from the burrow entrance.

The subterminal ischiomeral articulation (Fig. 2G) appears to be a specialization for smashing and is present in the most specialized smashers (Protosquillidae, Odontodactylidae, Gonodactylidae, and Takuidae). This condition may have arisen from enlargement of the muscle blocks in the merus, allowing a more powerful smashing strike. The ischiomeral articulation is terminal in all outgroups.

Character 10: maxillipeds subequal in size (0); second maxilliped considerably larger than others (1).

Character 11: raptorial dactylus with long serrated teeth (0); teeth small, triangular (1); teeth absent (2).

Character 12: raptorial dactylus basally uninflated (0); inflated (1).

Character 13: raptorial carpus unadorned (0); carinate (1); with obsolete projection or tooth (2); with stout tooth, usually acute (3).

Character 14: number of movable spines on propodus absent (0); 1 (1); 2 (2); 3 (3); 4 (4).

Character 15: outer inferior propodal margin with fixed spines (0); pectinate (1); smooth (2); pectinate for part of length (3).

Character 16: fixed spines on inner inferior margin of propodus present (0); absent (1).

Character 17: ischiomeral articulation of raptorial claw terminal (0); subterminal (1).

Character 18: ischium length relative to merus very short (0); long (1).

Carapace

The carapace of crown-group stomatopods is broad and shieldlike. In most squilloids, the carapace bears anterolateral spines (Fig. 1A). A well-defined cervical groove is present across the dorsum of the carapace in squilloids, bathysquilloids, and parasquillids. In other taxa, the cervical groove is absent or only faintly indicated laterally on or near the gastric grooves.

In all crown-group stomatopods, the carapace lacks ventrally produced lateral margins, permitting free movement and accommodating the massive raptorial claws. In the outgroups, the lateral margins of the carapace continue ventrally, partially enclosing the oral field.

In the Tyrannophontidae and all crown-group stomatopods, the last three thoracic somites are fully exposed. In the Palaeostomatopoda, the thoracic somites are largely concealed by the carapace.

Character 19: carapace largely concealing thoracic somites (0); posterior thoracic somites fully exposed (1).

Character 20: carapace lateral margins produced ventrally (0); lateral margins not produced ventrally (1).

Character 21: anterolateral spines present (0); absent (1).

Character 22: cervical groove present (0); absent (1).

Male First Pleopod

Stomatopods possess five pairs of gill-bearing pleopods. The distal segment of the endopod of the first male pleopods undergoes secondary sexual modification (Fig. 2H–L). The precise function of the petasma is unclear, but it appears to have reproductive utility as in other malacostracans. The morphology of the petasma may be used to broadly delineate lineages at a superfamilial level. Further study may indicate generic and specific level differences, although Manning (1969b) found no specific differences in *Gonodactylus*. Ingle (1963) believed that the form of the petasma bears useful generic characters. Specifically, he identified the form of the "hook" process as useful for separating lysiosquillids from pseudosquillids. The genera of Ingle (1963), however, now correspond to families and superfamilies. Thus, the assertions of Ingle still hold when interpreted at a higher taxonomic level.

Two characters are used in this study: the structure of the hooked process and the presence or absence of a large, lateral lobe on the distal margin of the endopod (Fig. 2K). In lysiosquilloids, the hooked process is usually short and the apex is always produced to a blunt, round hook (Fig. 2L). The hooked process in bathysquilloids resembles the lysiosquilloid condition (Fig. 2J). In squilloids and gonodactyloids, the hooked process is elongate terminating in a sharp, crochet hook (Fig. 2H, I, K). A broad, nonsetose lobe is present distolaterally on the endopod of gonodactyloids (Fig. 2K) and absent in other taxa, including *Faughnia* (Parasquillidae) (Fig. 2H). Some bathysquilloids bear a notch in the margin, but no lobe or evidence of a lateral expansion, as in the gonodactyloids, is present.

Character 23: endopod of male first pleopod lacking lateral lobe (0); with lobe (1); margin with a notch (2).

Character 24: hook process elongate (0); short (1).

Pereiopods

Malacostracans typically walk on the endopods of the thoracic pereiopods. In stomatopods, the pereiopods consist of a 3-segmented protopod, a 2-segmented outer branch and a 1- or 2-segmented inner branch. Stomatopods walk on the outer branch. The outer branch is usually termed the exopod and the inner branch the endopod on the basis of spatial position (Holthuis and Manning, 1969). Nevertheless, the endopod and exopod of the stomatopods may not be homologous with the caridoid endopod and exopod (Kunze, 1983).

The shape of the pereiopodal endopods is used as a diagnostic character in lysiosquilloids. The endopods vary from elongate (lysiosquillids) (Fig. 3A) to oval (tetrasquillids, coronidids, and heterosquillids) (Fig. 3B) to subcircular (nannosquillids) (Fig. 3C). The roundness of the pereiopodal endopods correlates with body size. Lysiosquillids, in which the pereiopodal endopods are elongate, are also the largest. The nannosquillids, which mature at the smallest sizes, have subcircular pereiopodal endopods.

Character 25: 1,2 pereiopodal endopods elongate (0); ovate (1); subcircular (2).

Abdomen and Thorax

The dorsal ornamentation, structure, and articulation of the thoracic and abdominal somites are particularly informative at superfamily and family levels. The squilloid body form is typically dorsoventrally depressed and longitudinally carinate (Fig. 3E). The degree of carination varies and is a useful generic character. Bathysquilloids also have dorsoventrally depressed, carinate bodies, though the carinae are much reduced. All lysiosquilloids have flattened, noncarinate abdomens (Fig. 3D) and somites are usually loosely articulated. In the Coronididae, Tetrasquillidae, and Heterosquillidae, the thoracic and abdominal somites are more closely articulated, referred to as compact (although diagnosed as "loosely articulated" by Manning (1995), the articulation in all heterosquillids examined appears to be compact). In eurysquillids and erythrosquillids, the body resembles *Lysiosquilla*.

In the gonodactyloids, the abdomen is usually subcylindrical and compact (Fig. 3F). This condition is typical of the Gonodactylidae, Odontodactylidae, Protosquillidae, and Pseudosquillidae. The abdominal form may relate to the habitat that most species of these families occupy, namely, rock and coral crevices (Reaka and Manning, 1981). Hemisquillids and parasquillids are more dorsoventrally flattened and depressed.

The fusion of the anterolateral plates of the first abdominal somite unites bathysquillids. In the outgroups, the anterolateral plates are absent and, in most ingroup taxa, they are articulated.

Character 26: abdomen depressed (0); subcylindrical (1); flattened (2).

Character 27: abdomen dorsally carinate (0); noncarinate (1).

Character 28: abdominal articulation compact (0); loose (1).

Character 29: anterolateral plates articulated (0); fused (1); absent (2).

Uropodal Articulation

The uropods of stomatopods are broad and massive relative to those of other malacostracans. The tail fan of the crown-group stomatopods is far more elaborate than in the outgroups. It typically consists of a forked, elongate protopod, unsegmented endopod, and 2-segmented exopod. Unlike caridoids, stomatopods do not use the telson and uropods for backward propulsion as in the "caridoid escape reaction." Rather, the uropods and telson usually function to support the abdomen and hold the pleopods (bearing gills) off the substrate (Tirmizi and Kazmi, 1984). A secondary use of the telson and uropods is in offense and defense, particularly among gonodactylids. The uropods are rich in diagnostic characters below family level but are less similar between families. Three characters are considered here. The segmentation of the uropodal exopod is significant. The uropodal exopod may be 1- or 2-segmented. In most crown-group taxa, the exopod is 2-segmented. In most fossil taxa, such as the Sculdidae, the exopod is 1-segmented. In *Tyrannophontes* the segmentation is scored as polymorphic because of variation in the family and uncertainty in one species (Schram, 1984). In the bathysquilloid *Indosquilla manihinei* Ingle and Merrett the distal segment is reduced and separated from the proximal segment only by an indistinct diaeresis. Although it has been speculated that the exopod of *Indosquilla* marks affinity with the sculdids, I believe that the resemblance is superficial, reflecting neoteny as seen in several other stomatopod larvae (Manning, 1991). Where the exopod is 2-segmented, the articulation of the uropodal exopod may be terminal (Fig. 3G) or subterminal (Fig. 3H).

The uropodal endopod of the lysiosquilloids bears a dorsolateral fold. In nannosquillids, the fold is strong (Fig. 3I). In other lysiosquilloids, the fold is weak (Fig. 3J) and in other taxa, the fold is absent (Fig. 3K).

Character 30: uropodal exopod unsegmented (0); with diaeresis (1); 2-segmented (2).

Character 31: articulation of uropodal exopod segments terminal (0); subterminal (1); absent (2).

Character 32: dorsolateral endopod fold absent (0); weak (1); strong (2).

Telson

The telson bears diagnostic characters at all taxonomic levels. In all groups except the lysiosquilloids, a distinct dorsal median carina is present (Fig. 4A, B, D, E). The median carina is present in fossil groups and is proba-

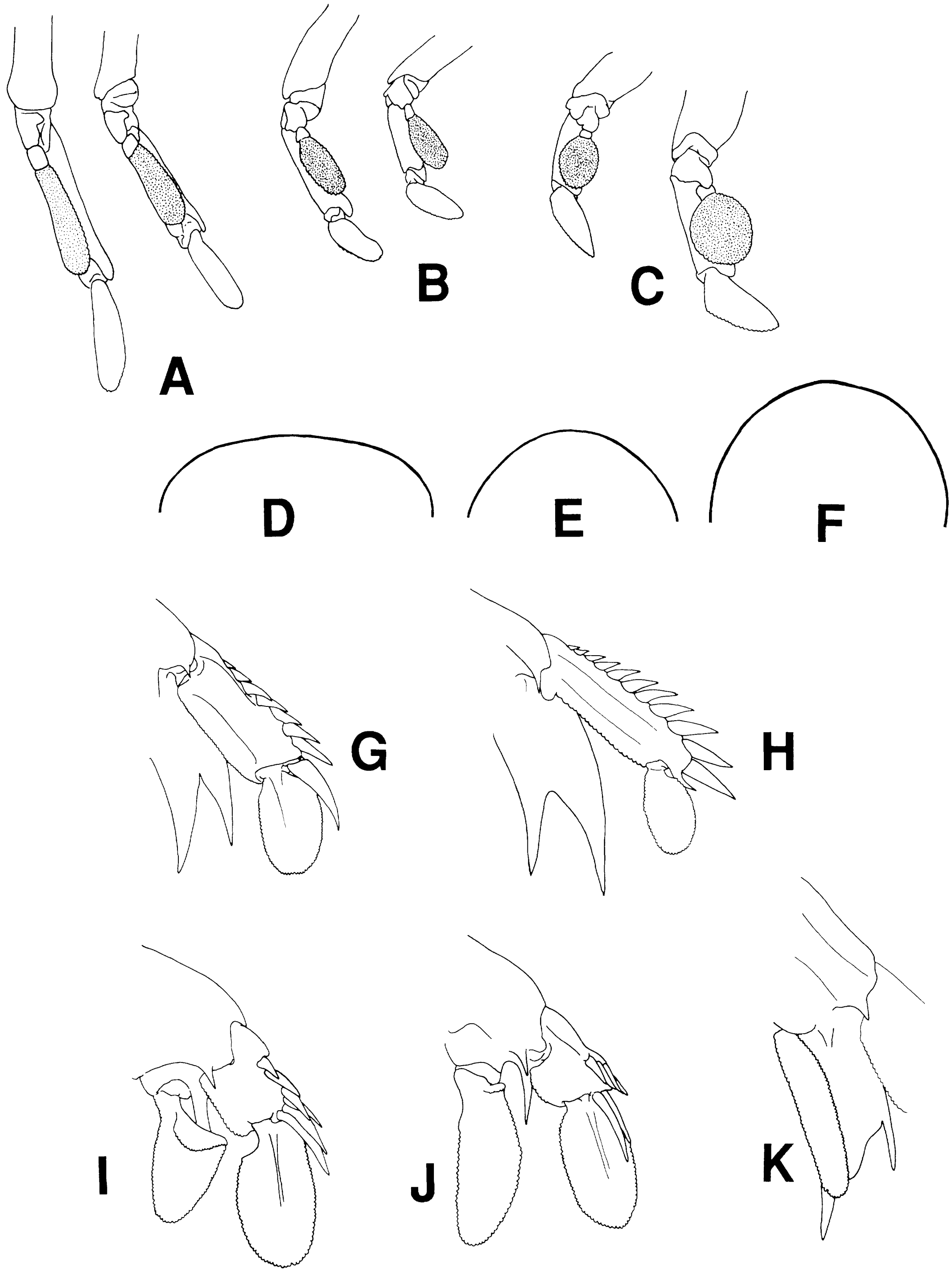

Fig. 3. Stomatopoda. A–C, first and second pereiopodal endopods (indicated by stippling): A, *Lysiosquilla hoevenii* (Lysiosquillidae); B, *Heterosquilloides insignis* (Heterosquillidae); C, *Acanthosquilla acanthocarpus* (Nannosquillidae). D–F, abdominal cross-sectional form: D, flattened; E, depressed, F, subcylindrical. G–H, uropodal exopod: G, *Pseudosquilla ciliata* (Pseudosquillidae); H, *Gonodactylus platysoma* (Gonodactylidae). I–K, uropodal endopod: I, *Acanthosquilla acanthocarpus* (Nannosquillidae); J, *Lysiosquilla hoevenii* (Lysiosquillidae); K, *Levisquilla jurichi* (Squillidae).

bly plesiomorphic. In lysiosquilloids, a low median boss may be present (Fig. 4C). In most taxa other than squilloids, a pair of low, distinct submedian carinae or bosses is present on the dorsal surface, though the submedian ornamentation is highly reduced or absent in many nannosquillids. In coronidids, the entire surface of the telson is strongly sculptured or covered with closely spaced tubercles (Fig. 4F). An unusual squilloid character is the presence of a curved ventrolateral carina originating behind the base of each uropod. The function of the ventral carinae may be associated with sound production via stridulation of the dorsal surface of the uropod with the ventral surface of the telson (personal observation; Kemp, 1913; Tirmizi and Kazmi, 1984).

Most lysiosquilloids bear additional dorsal ornamentation in the form of a false eave or additional rows of marginal spines. Such additional marginal ornamentation may obscure the true marginal armature and effectively thickens the telson. In heterosquillids and tetrasquillids, a rounded to subquadrate, raised, median prominence is present on the posterior margin.

In most crown-group stomatopods, the telson has three pairs of marginal teeth (more in bathysquilloids) and the apices of these teeth may be fixed or mobile. In gonodactyloids and erythrosquilloids, the submedian teeth are mobile (Fig. 4D, E). In bathysquilloids, all marginal teeth bear movable apices (Fig. 4B), but, in squilloids, the apices are usually fixed (in more than half the genera, and certainly in the majority of species) (Fig. 4A). In lysiosquilloids, the submedian teeth may bear movable apices. In the outgroups, marginal teeth are absent. In sculdids, marginal teeth appear to be mobile (Holthuis and Manning, 1969).

The intermediate marginal denticles are important characters separating the current superfamilies (Manning and Camp, 1993). Intermediate denticles are absent in bathysquilloids and the number varies in lysiosquilloids. In squilloids, four or more intermediate denticles are always present (Fig. 4A). In gonodactyloids and erythrosquilloids, two intermediate denticles, at most, are present (Fig. 4D, E).

Small caudal furcae are present in all outgroups except the Tyrannophontidae. Caudal furcae are the paired rami of the telson and occur in some phyllocarids and eumalacostracans, but are considered absent in the Stomatopoda (Kunze, 1983). A note of caution is appropriate here in interpretation of the caudal furcae, since further study of the fossil record may suggest that the caudal furcae and marginal spines are homologous. Until such data become available, however, the interpretation of Kunze (1983) is followed here in considering the caudal furcae absent in the Unipeltata. Nevertheless, the ingroup topology is unaffected even if the caudal furcae are scored as homologous with the marginal spines of the telson in unipeltatans. In *Perimecturus* and *Bairdops,* the telson terminates in a long, median spine.

Character 33: ventrolateral carinae of telson absent (0); present (1).

Character 34: median carina of telson present (0); absent (1); with raised posterior median prominence (2).

Character 35: dorsal surface of telson relatively unadorned (0); entirely tuberculate or strongly sculptured (1).

Character 36: submedian ornamentation absent (0); carina present (1); boss present (2).

Character 37: additional marginal armature absent (0); present (1).

Character 38: marginal teeth of telson absent (0); all apices fixed (1); submedian teeth movable (2); all teeth movable (3).

Character 39: marginal intermediate denticles 4 or more (0); 2 or fewer (1); absent (2).

Character 40: caudal furca present (0); absent (1).

Character 41: telson with long terminal median spine present (0); absent (1).

Larvae

Unfortunately, our knowledge of stomatopod development is nowhere near as complete as our understanding of the adults. The larval stages of many stomatopods are still unknown or at least unrecognized. Known lysiosquilloid larvae hatch at an early stage of development (Manning, 1963). Early larvae of lysiosquilloids are antizoeae, bearing five pairs of biramous thoracic appendages but no abdominal appendages. The antizoea develops into the erichthus, with two or fewer intermediate denticles on the telson and pleopods appearing from front to rear. Squilloids and gonodactyloids hatch as pseudozoeae with two pairs of uniramous thoracic appendages and four or five pairs of pleopods,

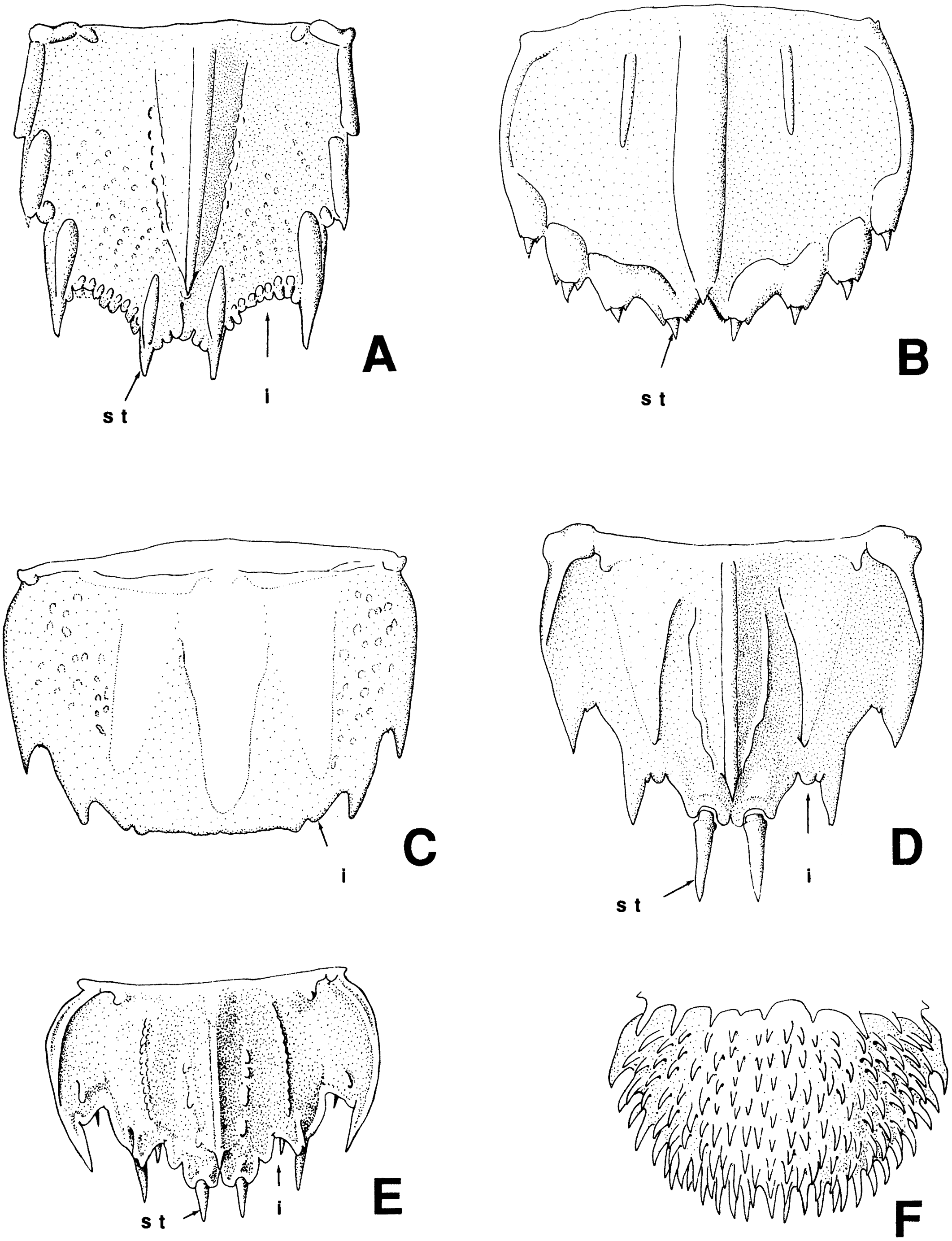

Fig. 4. Dorsal surface of the telson in Stomatopoda: A, *Oratosquillina stephensoni* (Squillidae); B, *Bathysquilla crassispinosa* (Bathysquillidae); C, *Lysiosquilla hoevenii* (Lysiosquillidae); D, *Pseudosquilla ciliata* (Pseudosquillidae); E, *Eurysquilla galatheae* (Eurysquillidae); F, *Coronida bradyi* (Coronididae). i = intermediate denticles, st = submedian tooth. (E, F, redrawn after Manning (1977)).

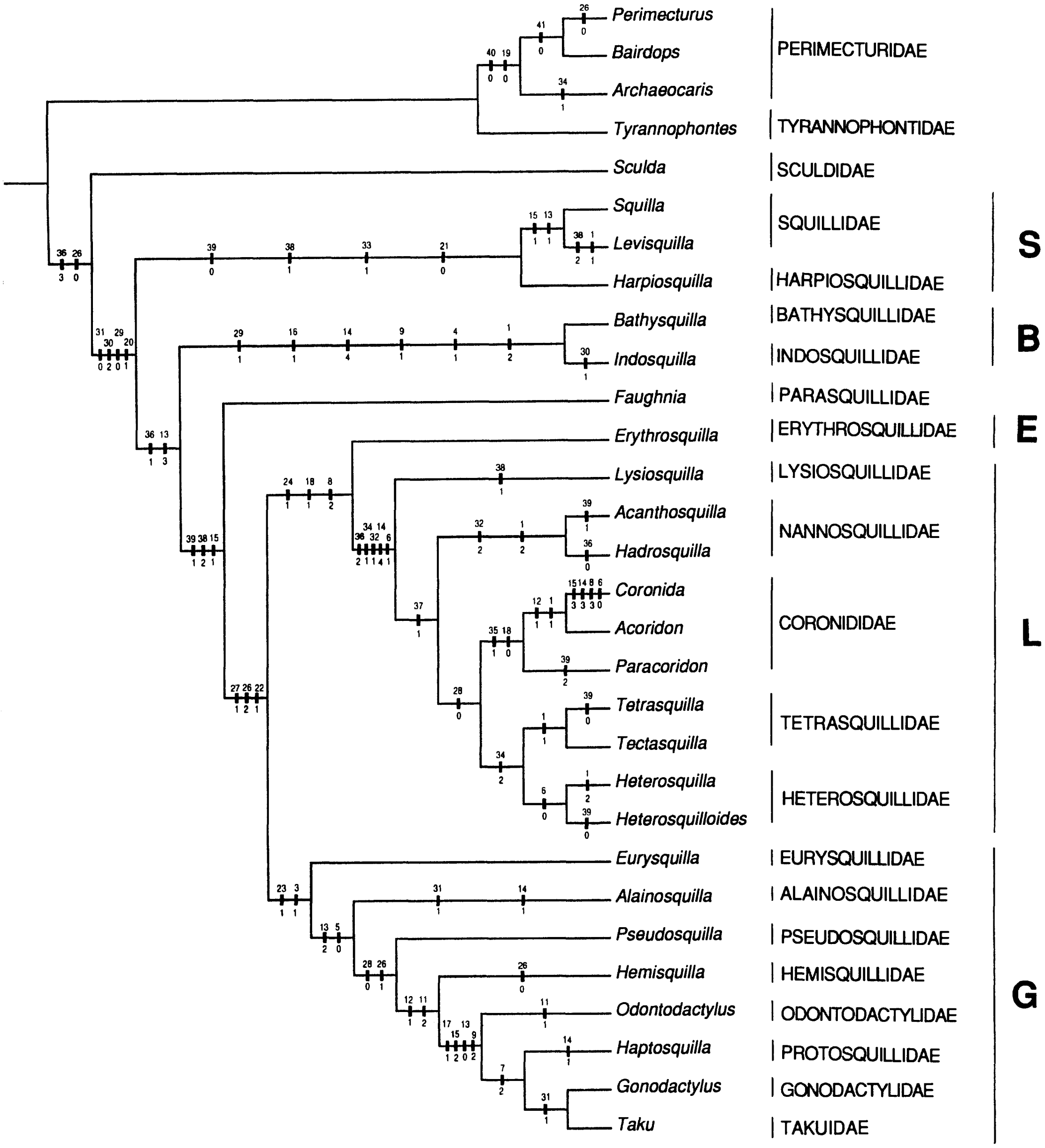

Fig. 5. Single most parsimonious cladogram of the Stomatopoda. Length 118, Consistency Index 0.66, Homoplasy Index 0.41, Retention Index 0.85. Outgroups (*Perimecturus, Archaeocaris, Bairdops, Tyrannophontes*) constrained as monophyletic with respect to the ingroup. B, Bathysquilloidea; E, Erythrosquilloidea; G, Gonodactyloidea; L, Lysiosquilloidea; S, Squilloidea. Unambiguous character changes are indicated. Character number is indicated above the branch. Character state is indicated below the branch.

respectively. Squilloid pseudozoeae develop into an alima larva with four or more intermediate denticles on the telson, whereas gonodactyloid pseudozoeae develop into an erichthus larva (Tirmizi and Kazmi, 1984).

Character 42: early larva a pseudozoea (0); antizoea (1).

Character 43: late larva an alima (0); erichthus (1).

RESULTS

Analysis of the data produced a single most parsimonious cladogram of length 118, consistency index (CI) 0.66 and retention index (RI) 0.85 (Fig. 5). The CI is the ratio between the theoretical minimum number of steps and the actual number. Because the CI is inversely related to the number of extra steps, it is a good measure of homoplasy (Goloboff, 1991). Homoplasy was thus relatively low.

The monophyly of the crown-group is supported in 96% of bootstrap replicates. The bootstrap statistics were relatively low at the bases of some major clades, ranging from 60–96%. The bootstrap values at the bases of the gonodactyloid (G) and erythrosquilloid+lysiosquilloid (E+L) clades were 60% and 62%, respectively. The squilloid (S) clade was supported in 81% of bootstrap replicates. The bathysquilloid (B) and lysiosquilloid (L) clades were the most highly supported of major clades with bootstrap values of 96% and 94%, respectively. In view of the relatively small data set and conservatism of the bootstrap, the upper bootstrap values indicate robust clades. The E and L clades were less well supported by the bootstrap and should be viewed more cautiously if only bootstrapping is considered.

The base of the ingroup clade decayed with two extra steps, but was retained in 99% of suboptimal trees. The decay values for the bases of the crown-group and major ingroup clades (S, B, G, E+L, L) were all at least three extra steps. These decay values may well exceed three steps, but the "+3" run was aborted owing to excessive processing time. Unlike some of the bootstrap values, the decay values indicate well-supported clades giving confidence to the topology produced.

The Squilloidea is unambiguously united by four characters of which only two (Characters 33, 39; Appendix 3) are never reversed—the presence of lateroventral carinae and four intermediate denticles on the telson. The early derivation of squilloids implies early derivation of the strong dorsal carination of the body (Char. 27) and less specialized central ommatidia of the cornea (Chars. 2, 3). The polarization of Char. 27 clearly indicates a reduction in dorsal carinae in successive clades.

The Bathysquilloidea, sensu Schram (1986), comprising extant and Jurassic families, was polyphyletic. The Jurassic sculdids were optimized as the earliest derived unipeltatans, while extant bathysquilloid families were derived after the squillids. The monophyly of extant bathysquilloids was well supported by six synapomorphies.

The Erythrosquilloidea is derived as the sister to the Lysiosquilloidea. The close relationship between these superfamilies is consistent with Manning and Bruce (1984) who originally described the Erythrosquillidae in the Lysiosquilloidea. The broad maxillipedal propodi (Char. 8), elongated ischium of the raptorial claw (Char. 18), and similar male pleopod structures (Char. 24) unite erythrosquilloids and lysiosquilloids. According to the analysis, the appearance of mesial papillae (Char. 6), the presence of four proximal movable spines on the raptorial propodus (Char. 14), the variously folded margin of the uropodal endopod (Char. 32), and the absence of a distinct median carina of the telson (Char. 34) are synapomorphies of the Lysiosquilloidea.

Lysiosquilla is derived earliest in the L clade, followed by several subsequent clades. *Hadrosquilla* and *Acanthosquilla* form a discrete clade united unambiguously by the corneal morphology (Char. 1) and form of the uropodal endopod (Char. 32), corresponding to the Nannosquillidae. The other clades are united by the compact abdominal articulation (Char. 28). Most heterosquillid genera (*Heterosquilla* and *Heterosquilloides*) are derived as the sister to the tetrasquillids (*Tetrasquilla* and *Tectasquilla*). *Paracoridon,* originally described as a coronidid (Moosa, 1991) and tentatively transferred to the Heterosquillidae by Manning (1995), is derived as the sister to the coronidids, represented by *Acoridon* and *Coronida.* The analysis supports the monophyly of the Coronididae and the Tetrasquillidae.

The morphology of the pereiopodal endopods is supported as a strong phylogenetic character. The pereiopodal endopods are slender and elongate in the Lysiosquillidae, less slender in the coronidid+tetrasquillid+heterosquillid clade, and least slender among nannosquillids. The polarization of Char. 25 clearly indicates that the styliform pereiopodal endopod is plesiomorphic.

The Gonodactyloidea sensu Manning (1995) are polyphyletic in this analysis. Excluding *Faughnia* (Parasquillidae), the gonodactyloids are derived as the sister to the E+L clade. *Faughnia,* which appears to bear both squilloid and gonodactyloid characters, is derived as the sister to the E+L+G clade. In *Faughnia,* the dorsal carinae and male pleopod form resemble the condition in squilloids. Furthermore, in material that I have examined, the number of ommatidial rows in the central band of the cornea appears to resemble squilloids. The ommatidial characters, however, were scored unknown, because the preservation of available material made the ommatidia difficult to observe. Although the corneal characters were scored as unknown, the topology remains unchanged regardless of whether they are scored as squilloid, gonodactyloid, or absent. Manning (1963, 1969b) regarded the dorsal carination as convergent. The exclusion of that character from the analysis has no effect on the topology.

The remaining gonodactyloids are united by two synapomorphies (Chars. 3, 23). Eurysquillids, derived first, exhibit the flattened abdomen which typifies lysiosquilloids and erythrosquilloids. Higher in the clade, taxa progressively become more subcylindrical in body form. A corresponding trend is also present with the narrowing of the cornea and derivation of the smashing claw. *Hemisquilla,* with a raptorial claw intermediate between the spearing and smashing taxa, is derived as such, between *Pseudosquilla* and *Odontodactylus.*

The gonodactyloid smashers are united by four unambiguous characters, most relating to the raptorial claw. *Gonodactylus* and *Taku* (formerly in the Gonodactylidae) are most closely related and together form a sister clade to the protosquillids.

DISCUSSION

Bathysquillids were considered to be the most ancient of crown-group stomatopods on the basis of their apparent relict, upper-slope distributions paralleling various ancient fish species, and the segmentation of the uropodal exopod (Manning and Struhsaker, 1976). All known bathysquillids are restricted to upper-shelf habitats, but new distribution records are regularly appearing (e.g., Bruce, 1985, 1988; Manning *et al.,* 1990; Moosa, 1986; and unpublished Australian records, Ahyong, in preparation). The segmentation of the uropodal exopod (Char. 30) and its relation to the condition in the Sculdidae (discussed in the character analysis) may not be homologous or derived. *Indosquilla* bears characters that closely resemble last-larval characters of *Bathysquilla crassispinosa* reported by Manning (1991). The unsegmented uropod and more pronounced dorsal and lateral spines in *Indosquilla* imply neoteny, as postulated by Ingle and Merrett (1971). Little a priori justification exists for considering bathysquilloids to be the earliest derived crown-group taxa. The earliest reported fossil attributed to *Bathysquilla* is from the lower Eocene (Quayle, 1987), whereas squilloids are known from the Cretaceous (Holthuis and Manning, 1969). Furthermore, the material of *B. wetheralli* Woodward studied by Quayle (1987) is incomplete and may not even represent *Bathysquilla.* Nevertheless, caution must be exercised when interpreting incomplete fossil specimens. The derivation of bathysquilloids after squillids suggests that bathysquilloids formerly possessed good vision and occupied shallow-water habitats.

The Bathysquilloidea, sensu Schram (1986), comprising extant and Jurassic families, was derived as polyphyletic. The Bathysquilloidea is restricted to the Bathysquillidae and the Indosquillidae, and the Sculdidae is here considered incertae sedis.

The squilloid clade is unambiguously united by four characters, two of which are never reversed. Stronger apomorphic support for squilloids will probably result from complete data in surrounding clades. Larval characters, for instance, are unknown in the outgroups, sculdids and bathysquillids. The maxillipedal morphology and number of intermediate denticles in larvae are conserved in adults. If larval types can be predicted from adult characters, the larvae of the aforementioned taxa may be dissimilar to the squillids. Although the monophyly of the squilloid families is supported, the present analysis is not sufficiently detailed to suggest trends within the superfamily. More than 40 genera are presently included in two families. The relationships within the superfamily will be studied in an analysis of the squilloid genera (Ahyong, in preparation).

Kemp (1913) considered the squilloids to represent the most ancient lineage of extant stomatopods, a view supported here. It should, however, be noted that the earliest known crown-group fossil, *Palaeosquilla brevicoxa* Schram, from the Middle Cretaceous, is believed to be a gonodactyloid (Schram, 1968). With few exceptions, squilloids burrow in level, soft substrates and forage nocturnally for all types of soft-bodied prey. They are the most cosmopolitan of known stomatopods.

Manning (1995) separated the Heterosquillidae from the Tetrasquillidae, based on abdominal articulation (loose and compact, respectively) and the number of teeth on the raptorial claw (four in tetrasquillids and more than four in heterosquillids). The abdominal articulation in taxa of both families, however, is compact. When *Paracoridon* is excluded from the Heterosquillidae, the absence of mesial papillae (Char. 6) becomes a heterosquillid synapomorphy. The genera of the two families are otherwise very similar. Characters distinguishing heterosquillids from tetrasquillids vary within genera of other families. Most species of both families were included in the single genus *Heterosquilla* by Manning (1963, 1969b). The independent status of the Heterosquillidae (excluding *Paracoridon*) and the Tetrasquillidae is not disputed in this analysis, but the absence of strong characters for their separation may favor their synonymy. The Heterosquillidae is presently restricted to *Acaenosquilla* Manning, *Heterosquilla* Manning, *Heterosquilloides* Manning, *Heterosquillopsis* Moosa, and *Kasim* Manning.

The analysis supports the removal of *Paracoridon* from the Heterosquillidae and supports the original inclusion by Moosa (1991) of *Paracoridon* in the Coronididae. *Paracoridon* is derived as the sister to the coronidids, principally on the basis of the dorsal ornamentation of the telson (Char. 35). Manning (1995) recognized five coronidid genera: *Acoridon* Adkison, Heard, and Hopkins, *Coronida* Brooks, *Neocoronida* Manning, *Parvisquilla* Manning, and *Mortensenenus* Manning. *Acoridon* is atypical among the coronidids in bearing mesial papillae, the maxillipedal propodi are strongly beaded ventrally, and there are four instead of three movable spines proximally on the raptorial propodus which is pectinate for most of its length. All of these characters are also found in *Paracoridon.* Therefore, the most important character excluding *Paracoridon* from the Coronididae is the uninflated raptorial dactylus (Char. 12). That character, however, is an unreliable coronidid synapomorphy. For instance, the raptorial dactylus in *Parvisquilla* is relatively uninflated. *Parvisquilla* is otherwise a "typical" coronidid (Chars. 6, 8, 14, 15) suggesting the definition of the Coronididae requires review. Pending further research, however, *Paracoridon* is included in the Coronididae. Presently, the elaborate dorsal ornamentation (Char. 35) will distinguish the Coronididae from other lysiosquilloids. In many respects, *Acoridon* appears to be more similar to *Paracoridon* than to other coronidids. Further study may support the removal of *Acoridon* and *Paracoridon,* in which case the Coronididae could be defined by at least four strong synapomorphies (Chars. 6, 8, 14, 15).

Lysiosquilloids are well adapted for life in burrows. The flattened, lightly sclerotized body permits great flexibility within the burrow confines. The elongated ischium of the raptorial claw may be an adaptation for increasing reach from the burrow entrance. Coronidids are the only lysiosquilloids which may also occupy preformed coral cavities (Reaka and Manning, 1981). Based on field observations, lysiosquilloids rarely leave their burrows and often live in colonies (Caldwell, personal communication). According to Reaka and Manning (1987), rates of morphological evolution inversely relate to body size. More than 40 species of nannosquillids are known, compared with fewer than 15 species of lysiosquillids. The smaller lysiosquilloids appear to be undergoing active radiation (Reaka and Manning, 1987). Lysiosquilloids appear to have evolved in conjunction with soft substrates and are specialized for life in burrows unlike the well-armored squillids which actively forage.

The close relationship between lysiosquilloids and gonodactyloids has been implied in the literature through the discovery of the eurysquillids (e.g., Ingle, 1963) and *Erythrosquilla* (e.g., Manning and Camp, 1993). The eurysquillids bear the flattened habitus of lysiosquilloids and *Erythrosquilla* bears characters considered diagnostic of both lysiosquilloids and gonodactyloids. Members of the G clade are readily distinguished from the E+L clade by male pleopod characters.

The taxonomic significance of the endopod of the male first pleopod is mentioned by various workers (e.g., Ingle, 1963; Brooks, 1886), but has hardly been used to study relationships within the Stomatopoda. The lateral lobe on the endopod was previously unrecognized and appears to be an extremely useful gonodactyloid synapomorphy. Further, male pleopod characters are useful in distinguishing the superfamilies and further study of the pleopods will likely yield several more informative characters which may be useful down to the specific level.

Manning (1962) noted that parasquillids were morphologically intermediate between squillids and gonodactylids. In all subsequent higher classifications, parasquillids were

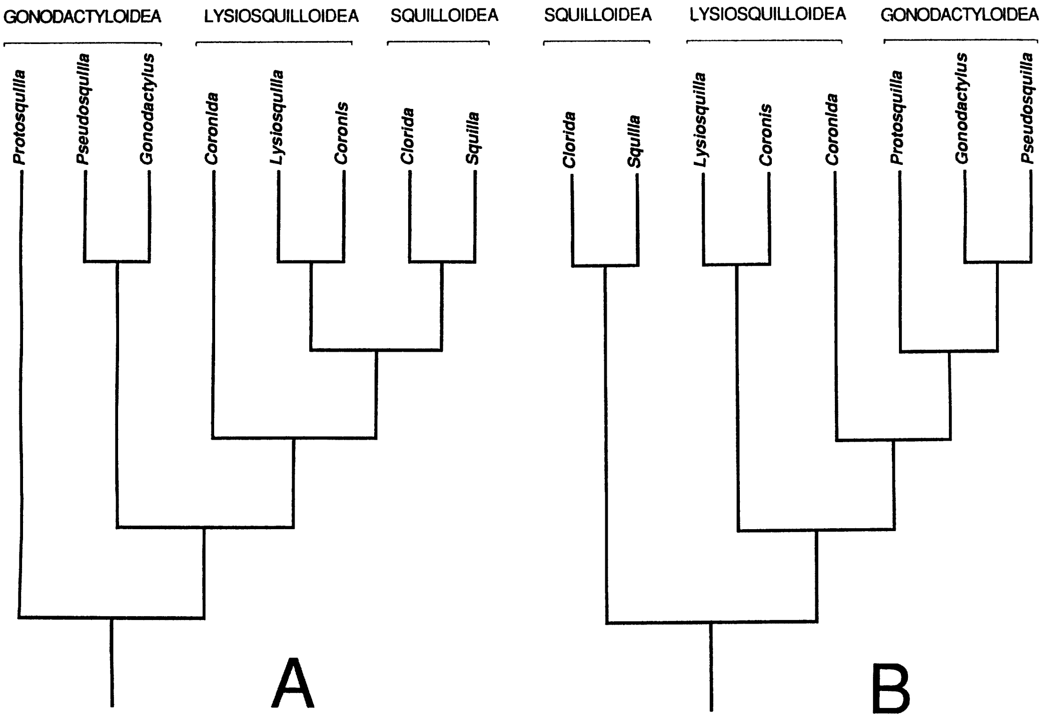

Fig. 6. Phylogeny of Brooks (1886): A, reinterpreted as a cladogram; B, re-rooted using the squilloids.

aligned with the gonodactyloids, with the squilloid characters considered convergent. The present analysis optimizes parasquillids outside of the Gonodactyloidea and suggests that a new superfamily should be erected for the Parasquillidae. The pleopod structure and the number of ommatidial rows suggests that the squilloid facies of parasquillids may mark squilloid affinity. Whether or not the squilloid facies are in fact homologous must be determined by further study and the present result should be accepted with caution. Therefore, superfamilial affinity of the parasquillids is presently considered uncertain. This analysis nevertheless supports the familial status of parasquillids recently recognized by Manning (1995); parasquillids were previously included with the pseudosquillids (Manning, 1977, 1980).

My analysis strongly supports the view that the smashing claw (Odontodactylidae, Gonodactylidae, and Protosquillidae) is derived from a spearing ancestor (Caldwell, 1991). Hemisquillid raptorial claws are morphologically intermediate between the spearers and smashers, and the analysis optimizes them as such. In gonodactyloids, the change in body form from flattened to subcylindrical correlates with increased dorsal armor and the development of the smashing claw. Thus, the general trends in gonodactyloid phylogeny are consistent with specialization corresponding to increasing exploitation of hard-bodied prey and coarse substrates, such as rock and coral reefs.

The only overall phylogenetic scheme to be explicitly proposed (other than that implied by classifications) was that of Brooks (1886), when fewer than 10 genera were recognized. The topology of Brooks (1886) differs markedly from the present analysis and is interpreted as a cladogram in Fig. 6A. The weaknesses of his scheme were reviewed by Manning (1963). Though the classifications of Manning (1968, 1980, 1995) and this cladogram lend no support to Brooks (1886), some points are noteworthy. If Fig. 6A is rerooted with the squillids (*Squilla* and *Clorida*), the topology resembles the present analysis and differs chiefly in the position of *Coronida* (Fig. 6B). Thus, the most important difference between the present analysis and that of Brooks is in his identification of *Protosquilla* as the earliest derived group. This result points to some broader issues in phylogenetic systematics—the importance of identifying reliable characters and distinguishing between plesiomorphies and apomorphies. According to this analysis, Brooks misinterpreted his characters. Brooks (1886) was confident of his phylogeny and probably never imagined the diversity in the Stomatopoda. Our knowledge of stomatopods has vastly increased in the century since Brooks, but it is always possible that future discoveries, particularly from the fossil record, may significantly alter our concepts of stomatopod relationships.

From the cladogram, a broad picture of stomatopod evolution may be drawn. The earliest of the crown-group stomatopods were probably dorsally carinate, generalist spearers with a broad flat telson. Squillids and bathysquillids appeared earliest and both now occupy soft, level substrates. Bathysquillids were restricted to deep water leading to degenerate vision, while the cosmopolitan squillids exploited shallower waters. The E+L+G clade, derived as the sister to parasquillids, has diverged in two broad directions. In the E+L clade, dorsal armature is lightly calcified, the elongated ischium facilitates spearing prey from the vertical burrow entrance, and the flattened body form permits maximum flexibility in the burrow confines. Taxa appear well adapted to a sedentary habit on soft, level substrates.

In the G clade, the general reduction in body size, stronger dorsal body armor, and development of the subcylindrical body form and smashing claw appear more suited to occupy and forage on coarse substrates. Perhaps the most extreme specialization is the smashing claw which permits exploitation of the hard-bodied prey common on coarse substrates. Thus, today there are the cosmopolitan squilloids, deep-water bathysquilloids, lysiosquilloids occupying vertical burrows in soft substrates, and gonodactyloids occupying hard substrates.

The analysis supports the monophyly of the Unipeltata and largely supports the current five superfamily classification of Manning (1968, 1980, 1995). The purported ancient derivation of the Bathysquillidae (Manning *et al.*, 1990), however, was unsupported. Rather, the Squilloidea is the earliest derived crown-group superfamily. The analysis is not sufficiently detailed to suggest trends within the Squilloidea, but a more detailed study of the squilloid genera is in progress.

The Erythrosquilloidea, Lysiosquilloidea, and Squilloidea are each supported as monophyletic. Monophyly of the Gonodactyloidea and Bathysquilloidea was unsupported and the analysis supports erection of new superfamilies for the Sculdidae and Parasquillidae. The sculdids are excluded from the Bathysquilloidea. Owing to incomplete fossil data, however, the Sculdidae are considered incertae sedis until more fossil data are available. The superfamilial affinity of the Parasquillidae is also considered uncertain pending further research.

The Heterosquillidae sensu Manning (1995) is polyphyletic. *Paracoridon* is removed from the Heterosquillidae and transferred to the Coronididae. The Coronididae requires reevaluation and more detailed analyses may support the removal of *Acoridon* and *Paracoridon* to new taxa. Characters separating the Heterosquillidae, as restricted here, from the Tetrasquillidae are weak, varying within genera of other families. Further analysis will likely favor their synonymy.

The E+L clade forms the sister group to the G clade. Lysiosquilloids show a trend toward general reduction in body size, which correlates with the shape of the pereiopodal endopods and increasing numbers of species. Apparently they have diverged to exploit soft, level substrates. Evolution of gonodactyloids correlates with exploitation of coarse substrates.

Characters derived from the pleopods, especially the first male pleopod, appear to be extremely useful phylogenetic characters. Further study of pleopod morphology is in progress and will likely yield further informative characters.

CLASSIFICATION OF THE STOMATOPODA

Extinct taxa are indicated (*).

- Phylum, Subphylum, or Superclass Crustacea
  - Class Malacostraca
    - Subclass Phyllocarida Packard, 1879
    - Subclass Eumalacostraca Grobben, 1892
    - Subclass Hoplocarida Calman, 1904
      - Order Aeschronectida Schram, 1969 (*)
      - Order Palaeostomatopoda Brooks, 1962 (*)
        - Family Perimecturidae Peach, 1908
      - Order Stomatopoda Latreille, 1817
        - Suborder Archaeostomatopoda Schram, 1969 (*)
          - Family Tyrannophontidae Schram, 1969
        - Suborder Unipeltata Latreille, 1825

- Superfamily Lysiosquilloidea Giesbrecht, 1910
    - Family Tetrasquillidae Manning and Camp, 1993
    - Family Heterosquillidae Manning, 1995
    - Family Coronididae Manning, 1980
    - Family Nannosquillidae Manning, 1980
    - Family Lysiosquillidae Giesbrecht, 1910
- Superfamily Erythrosquilloidea Manning and Bruce, 1984
    - Family Erythrosquillidae Manning and Bruce, 1984
- Superfamily Gonodactyloidea Giesbrecht, 1910
    - Family Takuidae Manning, 1995
    - Family Gonodactylidae Giesbrecht, 1910
    - Family Protosquillidae Manning, 1980
    - Family Odontodactylidae Manning, 1980
    - Family Hemisquillidae Manning, 1980
    - Family Pseudosquillidae Manning, 1977
    - Family Alainosquillidae Moosa, 1991
    - Family Eurysquillidae Manning, 1977
- Superfamily Bathysquillidoidea Manning, 1967
    - Family Bathysquillidae Manning, 1967
    - Family Indosquillidae Manning, 1995
- Superfamily Squilloidea Latreille, 1803
    - Family Harpiosquillidae Manning, 1980
    - Family Squillidae Latreille, 1803
- Superfamily uncertain
    - Family Sculdidae Dames, 1886 (*)
    - Family Parasquillidae Manning, 1995

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Address: Centre for Evolutionary Research, Australian Museum, 6 College Street, Sydney, New South Wales, Australia 2000 and School of Biological Sciences, University of New South Wales, Sydney, Australia 2052. (e-mail: s.ahyong@unsw.edu.au)

Appendix 1. Material examined from genera included in the analysis. AM (Australian Museum), NTM (Northern Territory Museum of Arts and Sciences), QM (Queensland Museum), SI (Smithsonian Institution).

- Squillidae
  - *Levisquilla jurichi* (Makarov, 1979) AM
  - *Levisquilla inermis* (Manning, 1965) NTM
  - *Squilla mantis* (Linnaeus, 1758) AM
- Harpiosquillidae
  - *Harpiosquilla harpax* (de Haan, 1844) AM
  - *Harpiosquilla annandalei* (Kemp, 1911) AM
- Bathysquillidae
  - *Bathysquilla crassispinosa* (Fukuda, 1911) QM
  - *Bathysquilla microps* (Manning, 1961) AM
- Parasquillidae
  - *Faughnia haani* Holthuis, 1959 AM
  - *Faughnia serenei* Moosa, 1982 AM, QM
- Lysiosquillidae
  - *Lysiosquilla sulcirostris* Kemp, 1911 SI
  - *Lysiosquilla tredecimdentata* Holthuis, 1941 AM, QM
  - *Lysiosquilla hoevenii* (Herklots, 1851) SI
- Nannosquillidae
  - *Acanthosquilla acanthocarpus* (Claus, 1871) AM
  - *Acanthosquilla multifasciata* (Wood-Mason, 1895) AM
  - *Hadrosquilla perpasta* (Hale, 1924) AM
- Heterosquillidae
  - *Heterosquilla tricarinata* (Claus, 1871) AM
  - *Heterosquilloides insignis* (Kemp, 1911) NTM
- Pseudosquillidae
  - *Pseudosquilla ciliata* (Fabricius, 1787) AM
- Hemisquillidae
  - *Hemisquilla ensigera australiensis* Stephenson, 1967 AM
- Odontodactylidae
  - *Odontodactylus scyllarus* (Linnaeus, 1758) AM
  - *Odontodactylus japonicus* (de Haan, 1844) AM
- Gonodactylidae
  - *Gonodactylus chiragra* (Fabricius, 1781) AM
  - *Gonodactylus platysoma* (Wood-Mason, 1895) AM
  - *Gonodactylus smithii* Pocock, 1893 AM
- Takuidae
  - *Taku spinosocarinatus* (Fukuda, 1909) AM
- Protosquillidae
  - *Haptosquilla glyptocercus* (Wood-Mason, 1875) AM
  - *Haptosquilla trispinosa* (Dana, 1852) AM

Appendix 2. Input data matrix of 43 characters and 30 taxa. Multistate characters are indicated by (/) and missing data (?). Outgroups are the last four listed (*Perimecturus, Archaeocaris, Bairdops,* and *Tyrannophontes*).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43
Levisquilla	1	1	0	0	0	0	0	1	0	1	0	0	1/2	3	1	0	0	0	1	1	0/1	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	2	0	1	1	0	0
Squilla	0	1	0	0	1	0	0	1	0	1	0	0	1	3	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	1	0	1	1	0	0
Harpiosquilla	0	1	0	0	1	0	0	1	0	1	0	0	0	3	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	1	0	1	1	0	0
Bathysquilla	2	0	2	1	1	0	0	1	1	1	0	0	3	4	0	1	0	0	1	1	1	0	2	1	0	0	0	1	1	2	0	0	0	0	0	1	0	3	2	1	1	?	?
Indosquilla	2	0	2	1	0	0	0	1	1	1	0	0	3	4	0	1	0	0	1	1	1	0	?	?	0	0	0	1	1	1	0	0	0	0	0	1	0	3	2	1	1	?	?
Erythrosquilla	0	0	2	0	1	0	0	2	0	1	0	0	3	3	1	0	0	1	1	1	1	1	0	1	0	2	1	1	0	2	0	0	?	0	0	1	0	2	1	1	1	?	?
Lysiosquilla	0	2	0	0	1	1	0	2	0	1	0	0	3	4	1	0	0	1	1	1	1	1	0	1	0	2	1	1	0	2	0	1	0	1	0	2	0	1	1	1	1	1	1
Acanthosquilla	2	2	0	0	1	1	0	2	0	1	0	0	3	4	1	0	0	1	1	1	1	1	0	1	2	2	1	1	0	2	0	2	0	1	0	2	1	2	0	1	1	1	1
Hadrosquilla	2	2	0	0	1	1	0	2	0	1	0	0	3	4	1	0	0	1	1	1	1	1	0	1	2	2	1	1	0	2	0	2	0	1	0	0	1	2	1	1	1	1	1
Coronida	1	2	0	0	1	0	0	3	0	1	0	1	3	3	3	0	0	0	1	1	1	1	0	1	1	2	1	0	0	2	0	1	0	1	1	2	1	2	1	1	1	1	1
Acoridon	1	?	0	0	1	1	0	2	0	1	0	1	3	4	1	0	0	0	1	1	1	1	?	?	1	2	1	0	0	2	0	1	0	1	1	2	1	2	1	1	1	?	?
Paracoridon	0	?	0	0	1	1	0	2	0	1	0	0	3	4	1	0	0	0	1	1	1	1	?	?	1	2	1	0	0	2	0	1	0	1	1	2	1	2	2	1	1	?	?
Tetrasquilla	1	2	0	0	1	1	0	2	0	1	0	0	3	4	1	0	0	1	1	1	1	1	0	1	1	2	1	0	0	2	0	1	0	2	0	2	1	2	0	1	1	?	?
Tectasquilla	1	2	0	0	1	1	0	2	0	1	0	0	3	4	1	0	0	1	1	1	1	1	0	1	1	2	1	0	0	2	0	1	0	2	0	2	1	2	1	1	1	?	?
Heterosquilla	2	2	0	0	1	0	0	2	0	1	0	0	3	4	1	0	0	1	1	1	1	1	0	1	1	2	1	0	0	2	0	1	0	2	0	2	1	2	1	1	1	1	1
Heterosquilloides	0	?	0	0	1	0	0	2	0	1	0	0	3	4	1	0	0	1	1	1	1	1	0	1	1	2	1	0	0	2	0	1	0	2	0	2	1	2	0	1	1	1	1
Alainosquilla	2	2	1	0	0	0	2	1	0	1	0	0	2	1	1	0	0	0	1	1	1	1	?	?	0	2	1	1	0	2	1	0	?	0	0	1	0	2	1	1	1	?	?
Eurysquilla	1	2	1	0	1	0	0	1	0	1	0	0	3	3	1	0	0	0	1	1	1	1	1	0	0	2	0/1	1	0	2	0	0	0	0	0	1	0	2	1	1	1	?	?
Gonodactylus	2	2	1	0	0	0	2	1	2	1	2	1	0	0/1	2	0	1	0	1	1	1	1	1	0	0	1	1	0	0	2	1	0	0	0	0	1	0	2	1	1	1	0	1
Haptosquilla	2	2	1	0	0	0	2	1	2	1	2	1	0	1	2	0	1	0	1	1	1	1	1	0	0	1	1	0	0	2	0	0	0	0	0	1	0	2	1	1	1	0	1
Hemisquilla	2	2	1	0	0	0	1	1	0	1	2	1	2	2	1	0	0	0	1	1	1	1	1	0	0	0	1	0	0	2	0	0	0	0	0	1	0	2	1	1	1	0	1
Odontodactylus	2	2	1	0	0	0	1	1	2	1	1	1	0	0	2	0	1	0	1	1	1	1	1	0	0	1	1	0	0	2	0	0	0	0	0	1	0	2	1	1	1	0	1
Faughnia	0	?	?	0	1	0	0	1	0	1	0	0	3	3	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1	0	2	1	1	1	?	?
Pseudosquilla	2	2	1	0	0	0	1	1	0	1	0	0	2	3	1	0	0	0	1	1	1	1	1	0	0	1	1	0	0	2	0	0	0	0	0	1	0	2	1	1	1	0	1
Taku	2	2	1	0	0	0	2	1	2	1	2	1	0	0	2	0	1	0	1	1	1	1	1	0	0	1	1	0	0	2	1	0	0	0	0	1	0	2	1	1	1	?	?
Sculda	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	1	0	1	0	?	?	?	2	0	0	2	0	2	0	0	0	0	0	0	3	?	1	1	?	?
Perimecturus	?	?	?	?	?	?	0	0	?	0	0	0	0	?	?	0	0	?	0	0	1	?	?	?	?	2	0	0	2	0	2	?	?	0	0	0	0/1	0	2	0	0	?	?
Bairdops	?	?	?	?	?	?	0	0	?	0	0	0	0	?	0/2	0	0	?	0	0	1	?	?	?	?	1	0	0	2	0	2	?	?	0	0	0	1	0	2	0	0	?	?
Archaeocaris	?	?	?	?	?	?	0	0	?	0	0	0	0	?	0	0	0	?	0	0	1	?	?	?	?	1	1	0	2	0	2	?	?	1	0	0	0	0	2	0	1	?	?
Tyrannophontes	?	?	?	?	?	?	0	0	?	0	0	0	0	?	0	0	0	?	1	0	1	?	?	?	?	1	1	0	2	0/1	0/2	?	?	0	0	0	0	0	2	1	1	?	?

Appendix 3. Characters and states used in the cladistic analysis.

Character 1: cornea strongly bilobed (0); bilobed (1); subspherical or faintly bilobed (2).
Character 2: central band of ommatidia absent (0); with two rows (1); with six rows (2).
Character 3: central band ommatidia hexagonal (0); rectangular (1); absent (2).
Character 4: facets of cornea well defined (0); poorly defined or absent (1).
Character 5: ventral papillae absent (0); present (1).
Character 6: mesial papillae absent (0); present (1).
Character 7: dorsal margin of antennal protopod unarmed or with small tooth (0); with articulated plate (1); with slender, fixed spine (2).
Character 8: propodi of third to fifth maxillipeds very elongate (0); slender (1); broad and ventrally ribbed (2); broad with ribbing reduced (3).
Character 9: propodus of maxilliped 5 with setal brush present (0); vestigial (1); reduced (2).
Character 10: maxillipeds subequal in size (0); second maxilliped considerably larger than others (1).
Character 11: raptorial dactylus with long serrated teeth (0); teeth small, triangular (1); teeth absent (2).
Character 12: raptorial dactylus basally uninflated (0); inflated (1).
Character 13: raptorial carpus unadorned (0); carinate (1); with obsolete projection or tooth (2); with stout tooth, usually acute (3).
Character 14: number of movable spines on propodus absent (0); 1 (1); 2 (2); 3 (3); 4 (4).
Character 15: outer inferior propodal margin with fixed spines (0); pectinate (1); smooth (2); pectinate for part of length (3).
Character 16: fixed spines on inner inferior margin of propodus present (0); absent (1).
Character 17: ischiomeral articulation of raptorial claw terminal (0); subterminal (1).
Character 18: ischium length relative to merus very short (0); long (1).
Character 19: carapace largely concealing thoracic somites (0); posterior thoracic somites fully exposed (1).
Character 20: carapace lateral margins produced ventrally (0); lateral margins not produced ventrally (1).
Character 21: anterolateral spines present (0); absent (1).
Character 22: cervical groove present (0); absent (1).
Character 23: endopod of male first pleopod lacking lateral lobe (0); with lobe (1); margin with notch (2).
Character 24: hook process elongate (0); short (1).
Character 25: 1,2 pereiopodal endopods elongate (0); ovate (1); subcircular (2).
Character 26: abdomen depressed (0); subcylindrical (1); flattened (2).
Character 27: abdomen dorsally carinate (0); noncarinate (1).
Character 28: abdominal articulation compact (0); loose (1).
Character 29: anterolateral plates articulated (0); fused (1); absent (2).
Character 30: uropodal exopod unsegmented (0); with diaeresis (1); 2-segmented (2).
Character 31: articulation of uropodal exopod segments terminal (0); subterminal (1); absent (2).
Character 32: dorsolateral endopod fold absent (0); weak (1); strong (2).
Character 33: ventrolateral carinae of telson absent (0); present (1).
Character 34: median carina of telson present (0); absent (1); with raised posterior median prominence (2).
Character 35: dorsal surface of telson relatively unadorned (0); entirely tuberculate or strongly sculptured (1).
Character 36: submedian ornamentation absent (0); carina present (1); boss present (2).
Character 37: additional marginal armature absent (0); present (1).
Character 38: marginal teeth of telson absent (0); all apices fixed (1); submedian teeth movable (2); all teeth movable (3).
Character 39: marginal intermediate denticles 4 or more (0); 2 or fewer (1); absent (2).
Character 40: caudal furca present (0); absent (1).
Character 41: telson with long terminal median spine present (0); absent (1).
Character 42: early larva a pseudozoea (0); antizoea (1).
Character 43: late larva an alima (0); erichthus (1).