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Stomatopod Interrelationships: Preliminary Results Based on Analysis of three Molecular Loci

Shane T. Ahyong [1] & Simon N. Jarman [2]

[1] Marine Biodiversity and Biodescurity, National Institute of Water and Atmospheric Research, Private Bag 14901, Kilbirnie, Wellington, New Zealand [s.ahyong@niwa.co.nz]
[2] Australian Antarctic Division, 203 Channel Highway, Kingston, Tasmania 7050, Australia [simon.jarman@aad.gov.au]

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> Abstract

The mantis shrimps (Stomatopoda) are quintessential marine predators. The combination of powerful raptorial appendages and remarkably developed sensory systems place the stomatopods among the most efficient invertebrate predators. High level phylogenetic analyses have been so far based on morphology. Crown-group Unipeltata appear to have diverged in two broad directions from the outset – one towards highly efficient 'spearing' with multispinous dactyli on the raptorial claws (dominated by Lysiosquilloidea and Squilloidea), and the other towards 'smashing' (Gonodactyloidea). In a preliminary molecular study of stomatopod interrelationships, we assemble molecular data for mitochondrial 12S and 16S regions, combined with new sequences from the 16S and two regions of the nuclear 28S rDNA to compare with morphological hypotheses. Nineteen species representing 9 of 17 extant families and 3 of 7 superfamilies were analysed. The molecular data reflect the overall patterns derived from morphology, especially in a monophyletic Squilloidea, a monophyletic Lysiosquilloidea and a monophyletic clade of gonodactyloid smashers. Molecular analyses, however, suggest the novel possibility that Hemisquillidae and possibly Pseudosquillidae, rather than being basal or near basal in Gonodactyloidea, may be basal overall to the extant stomatopods. In this context, it is significant that in many respects, hemisquillids resemble the stem-lineage condition more so than any other extant forms.

> Key words

Hoplocarida, Stomatopoda, molecular phylogeny.

1. Introduction

The mantis shrimps (Stomatopoda) are quintessential marine predators and are the most accomplished in the Crustacea. Their powerful raptorial appendages, adapted to 'spearing' or 'smashing' are trademark adaptations (Caldwell & Dingle 1976). The raptorial strike is one of the fastest known animal movements and the force of the blow from the most powerful 'smashers' may approach that of a small calibre bullet (Patek & Caldwell 2005). An equally important adaptation enabling the stomatopod to track prey and engage with its environment is acute vision, which is possibly the most complex of any invertebrate. Not only is each eye capable of binocular vision, but many species can detect polarised light and wavelengths well beyond that visible to humans (Marshall et al. 2007). The combination of powerful raptorial appendages and remarkably developed sensory systems place the stomatopods among the most efficient invertebrate predators.

The evolution of such a potent hunting system is of considerable interest. The fossil record suggests that the hoplocarid ancestors diverged from other eumalacostracans during the Devonian, but it was not until the Carboniferous that signs of differentiation of the subchelate maxillipeds first appeared (Schram 2007). These proto-mantis shrimp groups essentially form a 'transition series' with increasing differentiation of the second maxilliped as a raptorial claw. The

claw reaches maximum development in the Unipeltata, which includes all modern stomatopods, the 'true' mantis shrimp.

Unipeltata comprises the Jurassic–Cretaceous stem-lineage families Sculdidae Dames, 1886, and Pseudosculdidae Dames, 1886 (see HOF 1998; AHYONG et al. 2007), and the seven extant, crown-group superfamilies (MANNING 1980, 1995; AHYONG & HARLING 2000; AHYONG 2001, 2005). Of these seven superfamilies, the bulk of the almost 500 known species is contained in three major superfamilies: Gonodactyloidea Giesbrecht, 1910, Lysiosquilloidea Giesbrecht, 1910, and Squilloidea Latreille, 1802. The fossil record indicates that these three major superfamilies diverged by the late Cretaceous, remaining clearly recognisable since then.

Phylogenetic analyses of the modern stomatopods have been conducted only in the last decade or so (e.g., AHYONG 1997; HOF 1998; AHYONG & HARLING 2000; BARBER & ERDMANN 2000; AHYONG 2005), most of which were based on morphology. AHYONG & HARLING's (2000) comprehensive morphological analysis indicated that Unipeltata diverged in two broad directions from the outset – one towards highly efficient 'spearing' with multispinous dactyli on the raptorial claws, and the other towards 'smashing'. Although stomatopods have often been included in wider studies of arthropod interrelationships (e.g., GIRIBET et al. 2001; CARAPELLI et al. 2007), only BARBER & ERDMANN (1998), using COI sequences to study species and genera within the Gonodactylidae, have directly applied molecular data to estimate stomatopod phylogeny. Thus, the high-level phylogeny of the Stomatopoda has not been specifically approached using molecular data. As a prelude to more extensive molecular analyses of the stomatopods, the present study assembles available molecular data for mitochondrial 12S and 16S regions, combined with new sequences from the 16S and two regions of the 28S rDNA.

2. Materials and methods

2.1. Taxon sampling and outgroup selection

Nineteen species spanning nine families and the largest three superfamilies were included as terminals (Tab. 1). Sequences were derived from GenBank or newly gathered. Specimens sequenced for this study were initially preserved in 85–95% ethanol prior to DNA extraction. Muscle tissue was sampled from the merus of the raptorial claw or from the abdomen. Voucher specimens are deposited in the Australian Museum, Sydney (AM), National Institute of Water and Atmospheric Research, Wellington, New Zealand (NIWA), and Queensland Museum, Brisbane (QM). Taxonomic authorities of all terminal taxa are given in Tab. 1.

The position of Hoplocarida in relation to the other major malacostracan clades, Leptostraca and Caridoida (= Eumalacostraca of some authors; see MARTIN & DAVIS 2001 for summary) has been subject to some debate. Most recent analyses, however, regard hoplocaridans as closer to Caridoida than to Leptostraca (e.g., RICHTER & SCHOLTZ 2001; JENNER et al. 2009) with Eumalacostraca comprising hoplocaridans and caridoidans. Although significant amounts of sequence data are available for both leptostracans and putatively near-basal caridoidans (such as euphausiaceans and anaspidaceans), only in the case of the leptostracans was sequence data available for all loci studied herein. Therefore, the analysis was rooted to Leptostraca based on concatenated sequences of *Nebalia* sp. (28S: AY859590), *Nebalia hessleri* (12S: AF107606) and *Paranebalia longipes* (16S: AY744909).

2.2. DNA extraction and analysis

DNA was extracted using a modified Chelex rapid-boiling procedure (WALSH et al. 1991). Approximately 0.5 mg of tissue was placed in a 1.5 ml microcentrifuge tube containing 200 µl of 6% Chelex® 100 resin in 50 mM Tris pH 8.0, 0.5 mM EDTA. The tube was placed in a 100°C heating block for 5 minutes, vortexed, incubated for a further 5 minutes at 100°C, and then centrifuged at 20,000 × G for 10 minutes. The resulting supernatant was then removed to a fresh 1.5 ml centrifuge tube and was ready as a template for PCR amplifications.

Two regions of the 28S rDNA (df and vx) were amplified. The df region was PCR amplified using the primers 28Sdd (5'-gtcttgaaacagggaccaaggagt ct-3') and 28Sff (5'-ggtgagttgttacacactccttagtcgg at-3') (HILLIS & DIXON 1991). The vx region was PCR amplified using the primers 28Sv (5'-aaggtagccaaa tgcctcgtcatc-3') and 28Sx (5'-gtgaattctgcttcacaatga taggaagagcc-3') (HILLIS & DIXON 1991). An approximately 530 bp region from the 5' end of the mitochondrial 16S rDNA was amplified using the primers 16Sar-L (5'-cgcctgtttatcaaaaacat-3') and 16Sbr-H (5'-ccggtctgaactcagatcacgt-3') (PALUMBI et al. 1991).

PCR conditions were identical for all primer sets and took place in 50 µl reactions containing 5 µl of Chelex-extracted DNA solution as a template, 0.1% Triton® X-100, 50 mM KCl, 10 mM Tris-HCl pH 9.0, 2.5 mM $MgCl_2$, 0.25 mM dNTPs, and 2 units *Taq* DNA Polymerase (Promega). Cycle conditions were 94°C, 30 seconds; 50°C, 1 minute; 72°C, 1.5 minutes for 40 cycles followed by 72°C, 6 minutes. Complet-

Tab. 1. Terminal taxa, classification, voucher catalogue numbers, and GenBank accession numbers. Voucher specimens for new sequences were deposited in the Australian Museum, Sydney (AM), National Institute of Water and Atmospheric Research (NIWA) and Queensland Museum (QM). New sequences are indicated*. Note that *Chorisquilla tweediei* sequences (AF107609, AF 107598) are incorrectly listed on GenBank as *C. trigibbosa*, and *Hemisquilla californiensis* (AF107597, AF107616) as *H. ensigera*.

Taxon	Voucher	12S	16S	28Sdf	28Svx
Hoplocarida Calman, 1904					
Stomatopoda Latreille, 1817					
Gonodactyloidea Giesbrecht, 1910					
Hemisquillidae Manning, 1980					
Hemisquilla australiensis Stephenson, 1967	AM P56794	—	FJ871141*	FJ871156*	FJ871148*
Hemisquilla californiensis Stephenson, 1967		AF107597	AF107616	—	—
Gonodactylidae Giesbrecht, 1910					
Gonodactylaceus graphurus (Miers, 1884)	AM P56972	—	AF133678	FJ871157*	FJ871149*
Gonodactylus chiragra (Fabricius, 1781)		AF107594	AF107614	—	—
Gonodactylus smithii Pocock, 1893		AF107595	AF107615	—	—
Neogonodactylus sp.		AF107596	AF107612	—	—
Protosquillidae Manning, 1980					
Chorisquilla tweediei (Serène, 1952)		AF107609	AF107598	—	—
Haptosquilla glyptocercus (Wood-Mason, 1875)		AF107599	AF107610	—	—
Pseudosquillidae Manning, 1977					
Pseudosquilla ciliata (Fabricius, 1787)	QM W21730	AY947836	FJ871142*	FJ871158*	FJ871149*
Takuidae Manning, 1995					
Taku spinosocarinatus (Fukuda, 1909)		AF107600	AF107613	—	—
Lysiosquilloidea Giesbrecht, 1910					
Lysiosquillidae Giesbrecht, 1910					
Lysiosquillina maculata (Fabricius, 1793)	AM P58558	AF107603	AF107618	FJ87155*	FJ871147*
Nannosquillidae Manning, 1980					
Alachosquilla vicina (Nobili, 1904)					
Austrosquilla tsangi Ahyong, 2001	NIWA 48492	—	FJ871139*	FJ871153*	FJ871145*
Pullosquilla thomassini Manning, 1978		AF107602	AF107611	—	—
Tetrasquillidae Manning & Camp, 1993					
Heterosquilla tricarinata (Claus, 1871)	Not retained	—	FJ871140*	FJ871154*	FJ871146*
Squilloidea Latreille, 1802					
Squillidae Latreille, 1802					
Alima sp.		AF107604	AF107607	—	—
Harpiosquilla harpax (de Haan, 1844)	AM	—	FJ871137*	FJ871151*	FJ871143*
*Kempina mikado (*Kemp & Chopra, 1921)	AM P55585	—	FJ871138*	FJ871152*	FJ871144*
Squilla empusa Say, 1818		AF107605	AF107617	AY210842	AY210842
Leptostraca Claus, 1880					
Nebaliidae Baird, 1850					
Nebalia sp.		—	—	AY859590	AY859590
Nebalia hessleri Martin et al., 1996		AF107606	—	—	—
Paranebalia longipes (Willemoes-Suhm, 1875)		—	AY744909	—	—

ed PCR reactions were electrophoresed through a 1% agarose gel for 40 min at 80 V and 50 mA. The DNA band was excised from the gel under UV illumination and then extracted from the gel slice using a Quiaex II Gel Extraction kit (Qiagen). Final PCR-product DNA concentration was measured using a TKO-400 Fluorimeter (Hoefer Scientific Instruments).

Both strands of each PCR product were sequenced using BigDye Terminator sequencing reactions (ABI) in which 5 ng of respective primers were used to prime the amplification, and 30–40 ng of PCR product was sequenced. The resulting sequencing reactions were analysed on an ABI 310 or 377 automated DNA sequencer. Sequence data for both strands of each sample were initially analysed and aligned using Sequence Navigator (ABI) software. Multiple alignments were then conducted using the Clustal X (default settings) and checked by eye. Gaps were treated as missing data. Regions of ambiguous alignment were excluded.

2.3. Phylogenetic analysis

The 12S, 16S and 28S sequences were analysed simultaneously following the principle of 'total evidence' (e.g., NIXON & CARPENTER 1996; PRENDINI et al. 2003). Maximum parsimony analyses (MP) were conducted in PAUP*4.0b10 (SWOFFORD 2002) (heuristic search, TBR, random addition sequence, 500 replicates). Topological robustness was assessed using parsimony jackknifing (FARRIS et al. 1996). Jackknife frequencies (JK) were calculated in PAUP* using 1000 pseudoreplicates under a heuristic search with 30% character deletion. Maximum likelihood (ML) analyses were conducted in PAUP* (heuristic search, TBR, random addition sequence, 50 replicates). MODELTEST 3.7 (POSADA & CRANDALL 1998) was used to select the most appropriate model of nucleotide evolution of the combined dataset. Topological robustness was assessed by 100 jackknife replicates.

3. Results

Twenty-two new sequences were collected for eight species (6 for 16S, 8 for 28S df and 8 for 28S vx; Tab. 1). The alignment comprised 20 terminals and 1975 positions of which 283 are parsimony informative. The aligned 16S rRNA dataset comprised 462 positions of which 136 were parsimony informative (29%); the 12S rRNA comprised 375 positions of which 119 were parsimony informative (32%); and the 28S dataset (df + vx) comprised 1138 positions of which 28 were parsimony informative (2%). The 12S and 16S fragments are relatively AT rich compared to the two 28S fragments. Overall mean nucleotide composition is as follows: A 0.315, C 0.168, G 0.234, T 0.282. MODELTEST selected the TVM+I+G as the optimal model of nucleotide evolution under the Akaike Information Criterion (AIC). Parameters were as follows: A = 0.31260, C = 0.17920, G = 0.24340, T = 0.26480; proportion of invariant sites 0.4668; shape parameter 0.3488.

Maximum parsimony analysis retrieved a single, fully resolved minimal length tree (length 1483, consistency index less uninformative characters 0.4588, retention index 0.4201; Fig. 1A). Squilloidea and Lysiosquilloidea were reciprocally monophyletic sister clades (79% and 92% JK support, respectively). Gonodactyloidea, however, was paraphyletic. Within Squilloidea, *Harpiosquilla* was sister to the remaining three squilloids. Within Lysiosquilloidea, the lysiosquillid, *Lysiosquillina*, was sister to the remaining genera comprising the tetrasquillid, *Heterosquilla*, and three nannosquillids. A clade of gonodactyloids, comprising 'smashers' of the families Gonodactylidae, Protosquillidae and Takuidae (85% JK) was sister to Squilloidea + Lysiosquilloidea. Within this clade of 'smashers,' Gonodactylidae was paraphyletic. The two other gonodactyloid terminals representing Hemisquillidae and Pseudosquillidae were basal and near-basal to the remaining stomatopods, respectively, though their positions were only weakly supported. Maximum likelihood results (lnL = –9076.07077) (Fig. 1B) broadly resembled the MP topology, differing in relationships within the major clades, most notably in a monophyletic Gonodactylidae, and a *Pseudosquilla* + *Hemisquilla* clade.

4. Discussion

The overall cladistic pattern recovered here (Fig. 1A,B) corroborates the most recent morphological analyses (HOF 1998; AHYONG & HARLING 2000) in finding squilloids and lysiosquilloids to be closer to each other than either is to the gonodactyloids.

The traditional concept of Gonodactyloidea included those groups having a telson with a median carina and two intermediate denticles, and ovate propodi of maxillipeds 3–5 (all plesiomorphies). Under this concept of Gonodactyloidea, MANNING (1995) united nine families: Alainosquillidae Moosa, 1991, Eurysquillidae Manning, 1977, Gonodactylidae Giesbrecht, 1910, Hemisquillidae Manning, 1980, Odontodactylidae Manning, 1980, Parasquillidae Manning, 1995, Protosquillidae Manning, 1980, Pseudosquillidae Manning, 1977, and Takuidae Manning, 1995. AHYONG & HARLING (2000) showed that Gonodactyloidea sensu MANNING (1980, 1995) was polyphyletic and removed Eurysquillidae and Parasquillidae to their own superfamilies in proximity to Squilloidea. SCHRAM & MÜLLER (2004) also recognised the squillid + (eurysquillid + parasquillid) relationship but favoured an expanded concept of Squilloidea to contain all three clades (see AHYONG 2005 for discussion).

The paraphyly of the gonodactyloids, or more accurately, lack of molecular support for its monophyly, reflects the difficulty in identifying morphological synapomorphies for Gonodactyloidea (even as restricted by AHYONG & HARLING 2000). Unity of other stomatopod superfamilies is supported by suites of synapomorphies. In the case of Gonodactyloidea, however, the only recognised synapomorphies are in the presence and features of the articulated plate of the inner margin of the antennal protopod (becoming fused or immobile in Gonodactylidae, Protosquillidae and Takuidae) and, potentially, the unique presence of rectangular facets in the ommatidial mid-band (though

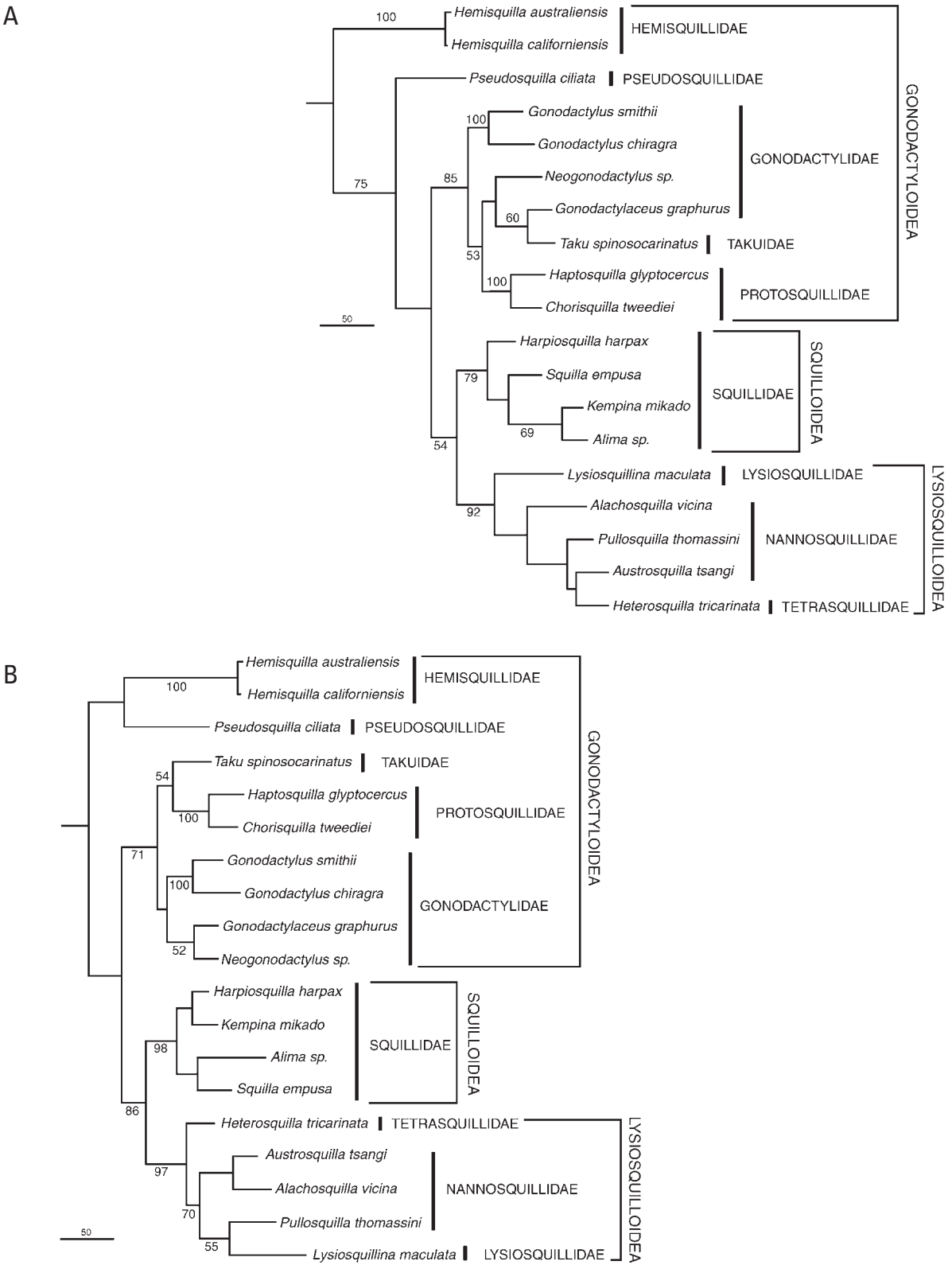

Fig. 1. Phylogenetic relationships of Stomatopoda. **A**: Maximum parsimony phylogram (length 1483, consistency index less uninformative characters 0.4588, retention index 0.4201). **B**: Maximum likelihood phylogram based on TVM+I+G model (lnL = -9076.07077). Jackknife proportions indicated at nodes.

the plesiomorphic condition is not yet known owing to lack of data from stem-lineage fossils) (Ahyong & Harling 2000). Other features used to recognise Gonodactyloidea are combinations of plesiomorphies (see Ahyong 2001). Thus, the paucity of gonodactyloid synapomorphies already points to potential non-

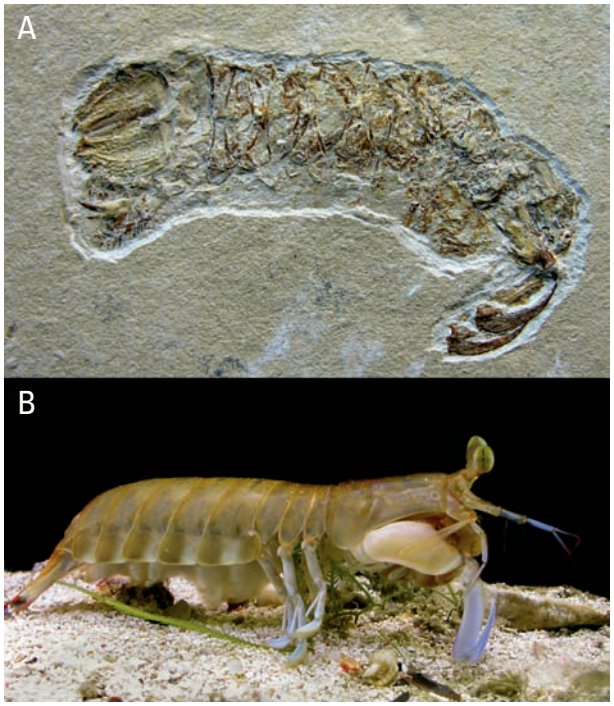

Fig. 2. A: *Archaeosculda phoenicia* Ahyong, Garassino & Gironi, 2007, Pseudosculdidae (Upper Cretaceous, Lebanon). **B**: *Hemisquilla australiensis* Stephenson, 1967, Hemisquillidae (Broken Bay, New South Wales, Australia).

monophyly, which is consistent with current molecular results.

The possibility that Hemisquillidae and Pseudosquillidae might not be true gonodactyloids (Fig. 1A,B), but instead basal or near-basal crown-group clades is the most interesting aspect of present findings. The morphology of *Hemisquilla* is certainly consistent with this possibility. The subcylindrical body-form of *Hemisquilla* (as with other gonodactyloids and parasquilloids) reflects the plesiomorphic stem-lineage condition. The raptorial claw in *Hemisquilla* is neither highly specialised for 'smashing' nor 'spearing', though it can use both feeding modes effectively. The dactylus is simple, without additional teeth on the occlusal margin for more effective 'spearing', and without an inflated heel on the outer margin for enhanced 'smashing'. The merus is not enlarged proximally to accommodate additional muscle mass as in the most highly derived hard substrate 'smashers' (Odontodactylidae, Protosquillidae, Gonodactylidae and Takuidae). The relatively unspecialised raptorial claw of *Hemisquilla* contrasts with those of the more highly modified claws of specialised 'smashers' and 'spearers' that are adapted to specific prey types (hard and soft bodied, respectively). As observed by AHYONG et al. (2007), the raptorial claw of *Hemisquilla* is structurally very similar to the stem-lineage Pseudosculdidae, the differences essentially being morphometric (Fig. 2A,B).

The eyes of *Hemisquilla* are also less specialised than those of other gonodactyloids in having fewer classes of photoreceptive pigment and only a single intrarhabdomal filter in rows two and three (CRONIN & MARSHALL 1989b; CRONIN et al. 1994). The less specialised ommatidia are more likely to be a plesiomorphy than an environmental adaptation to reduced ambient light because other 'smashers' also live at depth (AHYONG & HARLING 2000). Moreover, hemisquillids, in common with several other stomatopod groups, exhibit what appears to be a Tethyian distribution pattern (EKMAN 1953) and exist in widely separate populations in the Western Atlantic (*H. braziliensis* (Moreira, 1903)), the Eastern Pacific (*H. ensigera* (Owen, 1832) and *H. californiensis* Stephenson, 1967) and the Tasman Sea (*H. australiensis* Stephenson, 1967). This strongly disjunct distribution pattern is consistent with a formerly widely distributed group that has experienced extinction over much of its range. Thus, the molecular similarity (in terms of branch lengths) between the two species of *Hemisquilla* (< 2% divergence) is striking in comparison to the two *Gonodactylus* species (9% divergence) (Fig. 1A,B). Although the analysis is based on limited sequence data, the apparently slow molecular evolution of hemisquillids is consistent with their retention of a phenotypically plesiomorphic body plan. Unfortunately, the fossil record of Hemisquillidae is sparse, being known positively only from the Middle Miocene of North America in *Hemisquilla adelaidensis* (see AHYONG et al. 2007). Irrespective of whether Hemisquillidae is basal in the Gonodactyloidea, or basal overall, hemisquillids appear to reflect the unipeltatan stem-lineage condition more so than other extant stomatopods.

The non-gonodactyloid position of *Pseudosquilla* is more anomalous than that of *Hemisquilla*. Like *Hemisquilla*, *Pseudosquilla* possesses the plesiomorphic subcylindrical body form superficially resembling pseudosculdids, but unlike *Hemisquilla*, *Pseudosquilla* has well-developed 'spearing' claws and highly specialised vision similar to that of other coral reef gonodactyloids (CRONIN & MARSHALL 1989a,b). Thus, when raptorial claw morphology, visual architecture, and nodal support are considered, the resolution of *Pseudosquilla* as sister to *Hemisquilla* under ML can be regarded as probably spurious. The 'higher' position of *Pseudosquilla* as recovered under MP, with significantly higher nodal support (75%) than that recovered under ML (< 50%) (Fig. 1A,B) is more plausible. Nevertheless, that pseudosquillids probably represent an ancient radiation is consistent with their apparent Tethyian distribution, in which three of the four recognised genera occur in both the Atlanto-East Pacific and Indo-West Pacific regions. The palaeontological record of Pseudosquillidae presently includes

only three species dating back to the lower Eocene (De Angeli & Garassino 2008).

Ahyong & Harling (2000) suggested that crown-group Unipeltata diverged in two broad directions from the outset, with one major clade evolving highly efficient 'smashing' claws (Gonodactyloidea), and the other becoming specialized for 'spearing' (remaining superfamilies). Even with the possible basal and near-basal positions of Hemisquillidae and Pseudosquillidae implied by present results, the present topologies are consistent with the scenario proposed by Ahyong & Harling (2000). That stem-lineage unipeltatans could strike forcefully is demonstrated by the presence in fossils of the meral 'saddle' – a key adaptation involved in energy storage and transfer during the raptorial strike (Patek et al. 2004). The question arises, however, as to the primary hunting mode in the stem-lineage – 'spearing' or 'smashing'? Detailed comparative and functional analysis will be required to robustly address this issue. If the behaviour of *Hemisquilla* can be taken as a guide, however, then pseudosculdids could be inferred to have used both modes, though the proportionally longer raptorial dactyli of pseudosculdids probably indicates 'spearing' as the more common. Note that 'smashing' or 'spearing' in stem-lineage taxa, as with *Hemisquilla*, is possibly better considered in the simpler context of striking with either a closed or open dactyl rather than being directly compared to that of highly specialised 'smashers' or 'spearers' in which the efficiency of the raptorial strike has been optimised by further structural adaptations for handling very different types of prey.

The phylogenetic signal in the molecular data reflects the overall patterns derived from morphology, especially in relation to well supported clades recovered by both data sources – namely a monophyletic Squilloidea, a monophyletic Lysiosquilloidea and a monophyletic clade of gonodactyloid 'smashers'. Important questions are raised, however, about the position of Hemisquillidae and monophyly or limits of Gonodactyloidea. These are significant issues, having major implications for the higher classification of the Stomatopoda and for models of unipeltatan evolution. Also, the present data cannot address the positions of other stomatopod clades such as Bathysquilloidea, Eurysquilloidea and Parasquilloidea. These issues are beyond the reach of present data and will be addressed in future studies using much wider taxon sampling and more appropriate markers.

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