

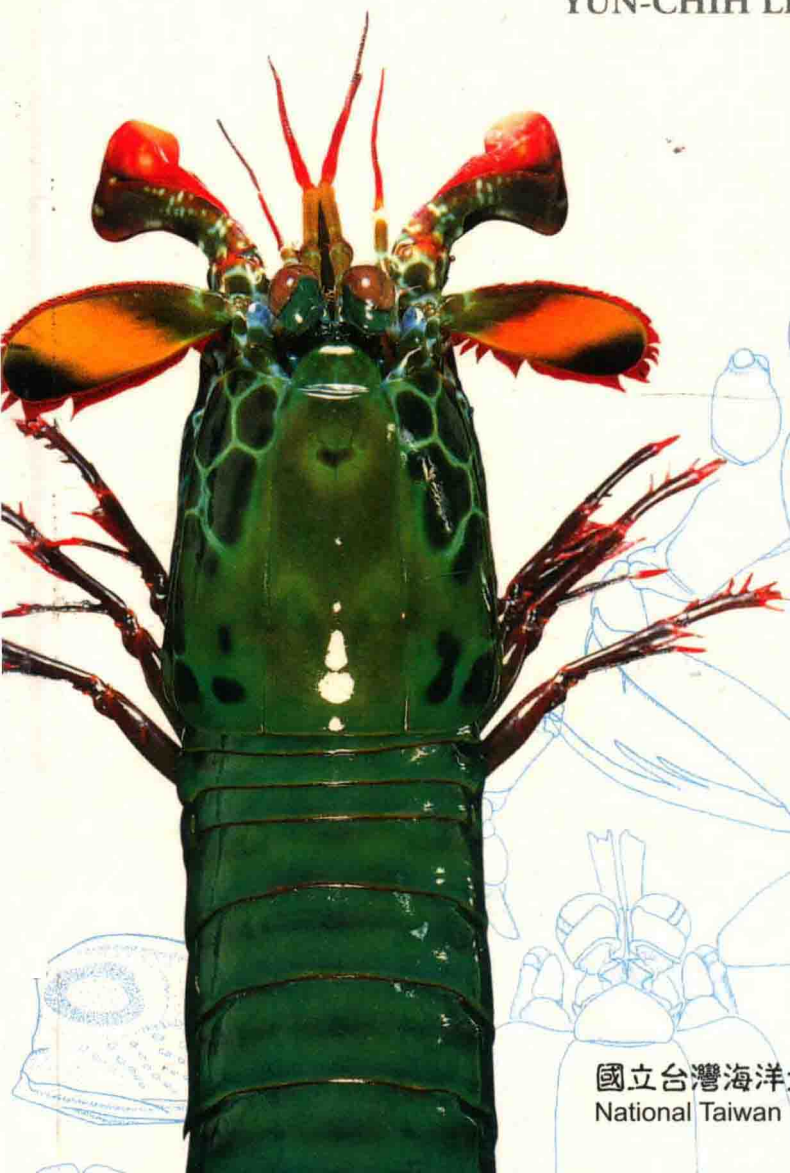
台灣蝦蛄誌

A CATALOG OF THE MANTIS SHRIMPS (STOMATOPODA) OF TAIWAN

SHANE T. AHYONG

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序

大型甲殼類一般是指十足目的蝦蟹和口足目的蝦蛄，十足目的大鉗為步足所特化，而口足目的大鉗則是由第二顎足特化而成，故兩者在演化上有很大的差距。蝦蛄都是棲息在海洋且主要生活於淺海，可在台灣的珊瑚礁及岩礁海岸常見其蹤跡，而不少棲息於沙泥底的蝦蛄更是具有經濟價值的漁獲物，唯蝦蛄因為身體多刺不易處理，除大型的種類之外，價格普遍不高。台灣最早的蝦蛄學術記錄是在1880年，英人 E. J. Miers 根據台灣的標本發表一種圓尾綠蝦蛄 *Clorida rotundicauda*，之後都只有少數國外學者的零散記錄，1966年本土生物學者開始研究台灣蝦蛄，在此之前僅記錄有14種。近年來行政院國家科學委員會大力支持台灣的生物多樣性調查研究，使台灣的學者能積極的在台灣各地採集蝦蛄標本並做深入的研究，再經由行政院國家科學委員會補助的研究計畫『編撰台灣無脊椎動物誌—台灣甲殼類』，邀請國際最著名的蝦蛄分類專家共同編撰台灣蝦蛄誌，共整理出5總科9科28屬63種，其中有1總科1科8屬32種是台灣的新記錄或首次正式的記錄。雖然仍未有台灣特有的種類，但其中6種的正模 (holotype) 或新模 (neotype) 是選自台灣的標本。

本誌之編輯及印刷是行政院國家科學委員會補助，由國立台灣海洋大學出版，是繼“台灣寄居蟹類誌”後第二本台灣甲殼類誌（初版登錄於TaiBNET台灣生物多樣性資訊網<http://www.taibif.org.tw/nbrpp/nbrpp.php>），誌中對台灣目前發現的63種蝦蛄全都有提供型態描述、重要特徵線繪圖和檢索等，其中48種亦附有彩色標本照，以利參考鑑別。本誌之出版獲行政院國家科學委員會及國立台灣海洋大學水產生物科技頂尖研究中心大力支持及補助，謹致上由衷謝意，並感謝林芝君小姐在編輯上的協助。台灣目前記錄的蝦蛄種類已達全世界已知蝦蛄的七分之一，希望能藉本誌讓國內外人士更深入了解台灣豐富的海洋生物多樣性，進而關懷及永續利用這一項得天獨厚的自然資源。

INTRODUCTION

The mantis shrimps (Stomatopoda) are marine, predatory species, characterized by the greatly developed second maxilliped modified as large powerful raptorial appendages. Prey is captured by ‘spearing’ or ‘smashing’, depending on whether the dactyl is extended or held folded during the strike. The two methods of prey capture distinguish two broad functional groups — the ‘smashers’ and the ‘spearsers’ (Caldwell & Dingle, 1976). Stomatopods occur in a wide range of habitats, from the shore down to about 1500 m, being common and conspicuous on coral reefs, and abundant on soft, level substrates less than about 200 m depth. More than 450 described species are known, distributed in seven superfamilies and 17 families (Ahyong, 2001). Many species that inhabit soft bottoms are fished commercially in many countries, though generally as bycatch with low economic value except for those very large species (e.g., *Harpiosquilla raphidea* (Fabricius, 1798) with maximum total length of 33 cm and *Lysiosquillina maculata* (Fabricius, 1793) reaching a total length of 38 cm).

Miers (1880) described the first stomatopod from Taiwan: *Clorida rotundicauda*. Balss (1910a) reported five species from Taiwan [now known as *Acanthosquilla multifasciata* (Wood-Mason, 1895), *Bigelowina phalangium* (Fabricius, 1798), *Pseudosquilla ciliata* (Fabricius, 1787), *Harpiosquilla harpax* (de Haan, 1844), and *Oratosquilla oratoria* (de Haan, 1844)], and Kemp (1913) reported the first Taiwanese record of *Oratosquillina interrupta* (Kemp, 1911). As part of broader studies of Japan and adjacent localities, Komai (1927) recorded additional species from Taiwan, and Schmitt (1927) listed the 14 species then known from the island. Since then, only a few studies have dealt with Taiwanese stomatopods, the most important of which is Lee & Wu (1966), reporting 21 species from Taiwan. Manning (1978b, c; 1980b), Hwang & Yu (1980), Manning & Chan (1997), Jeng (1998), Ahyong *et al.* (1998, 2000), Ahyong & Naiyanetr (2000), Huang & Hsueh (2006) and Ahyong & Chan (2008) reported additional species from Taiwan. Liu & Wang (1999) listed 101 stomatopod species from the China Seas including a preliminary list of 53 species from Taiwan based on our unpublished data (including new records of 1 family, 7 genera and 24 species). Those specimens on which Liu & Wang’s (1999) ‘new’ Taiwanese records were based are formally reported herein.

Through recent projects supported by the National Science Council, Taiwan, R.O.C., extensive surveys on the stomatopods of Taiwan revealed a total of 63 species distributed in 5 superfamilies, 9 families, and 28 genera of which 1 family and superfamily, 8 genera and 32 species are new records for Taiwan. A preliminary version of this catalog is available online at TaiBent (<http://www.taibif.org.tw/nbrpp/nbrpp.php>), supported by the National Science Council, Taiwan, R.O.C. In this printed version the contents of the original catalogue have been revised with supplementary data and illustrations. All stomatopod species known from Taiwan are included herein.

The number of species now recorded from Taiwan represents slightly less than one-seventh of the stomatopod species currently known worldwide. Most specimens studied herein were collected by commercial trawling on soft, level, inshore substrates. As in other Asian countries, stomatopods are common as by-catch in local trawl fisheries and generally of low economic value (about NT\$150/kg retail price and NT\$300/kg retail for large specimens), presumably because of their hard, spiny shells and wide availability of other crustaceans such as penaeid prawns. Squilloids, bathysquilloids, parasquilloids and lysiosquilloids typically burrow in the soft substrata of the seabed. Bathysquilloids and parasquilloids are deepwater species and thus are relatively seldom captured. Lysiosquilloids, although often present in shallow water, occupy deep burrows and rarely forage, and are also seldom captured by trawling. Squilloids actively forage and are most frequently captured by demersal trawls. Interestingly, of the squilloids previously reported from Taiwan, *Clorida rotundicauda* (Miers, 1880), *C. japonica* Manning, 1978, and *Cloridopsis scorpio* (Latreille, 1828) are known only from very few specimens. This apparent ‘rarity’ is probably related to lack of sampling in intertidal and shallow subtidal

estuarine and mangrove habitats, and also to habitat loss or degradation in many parts of coastal Taiwan. Although Squilloidea is the most speciose of stomatopod superfamilies (Ahyong, 2005b), the high proportion of squilloids in the known Taiwanese fauna (66.7%) probably also reflects sampling bias. Most specimens were collected by commercial trawlers which employ the method most likely to capture squilloids. In contrast to species of the aforementioned superfamilies, gonodactyloids occupy hard substrates on coral and rocky reefs, habitats that require different methods of sampling. Gonodactyloidea is also a very diverse superfamily, but only 11 species are presently known from Taiwan. Numbers of gonodactyloids from neighbouring waters, however, are considerably higher with at least 40 species occurring in Japanese waters (Hamano, 2005; Ahyong, unpublished), and at least 30 in the northern South China Sea and Philippines (Kemp 1915; Liu & Wang 1999; Ahyong 2004). When more intensive sampling is conducted in coral and rocky habitats, particularly on the coral reefs of southern Taiwan, the known gonodactyloid fauna will also certainly increase. The percentage composition of the fauna according to superfamily is given below in Table 1. Currently, no known Taiwanese stomatopods are endemic, and most are widespread in the western Pacific. Nevertheless, 6 species, namely *Alima orientalis* Manning, 1978, *Busquilla quadraticauda* (Fukuda, 1911), *Clorida rotundicauda* (Miers, 1880), *Faughnia formosae* Manning & Chan, 1997, *Oratosquilla manningi* Ahyong, Chan & Liao, 2000, and *O. nordica* Ahyong & Chan, 2008, have their respective holotypes or neotypes based on Taiwanese specimens. *Oratosquilla megalops* (Manning, 1980) and *Harpisquilla ocellata* Ahyong, Chan & Liao, 1998, which are junior synonyms of *O. inornata* (Tate, 1883) and *H. sinensis* Liu & Wang, 1998, respectively, were also described from Taiwan. Of the known Taiwanese stomatopods, only *Clorida japonica* Manning, 1978, and *Quollastria imperialis* (Manning, 1965) are restricted to the northwestern Pacific, both being known only from Japan and Taiwan.

	No. species in Taiwan	% of fauna
Bathysquilloidea	1	1.6%
Gonodactyloidea	11	17.5%
Lysiosquilloidea	6	9.5%
Parasquilloidea	3	4.8%
Squilloidea	42	66.7%

Table 1. Percentage composition of Taiwanese stomatopod fauna according to superfamily.

The majority of specimens reported herein are housed in the collections of the National Taiwan Ocean University, Keelung (NTOU). Other specimens studied are deposited in the Australian Museum, Sydney (AM); Academia Sinica Institute of Zoology, Taipei (ASIZ); Muséum national d'Histoire naturelle, Paris (MNHN); National Institute of Water and Atmospheric Research, Wellington, New Zealand (NIWA); Natural History Museum, London (NHM); Raffles Museum of Biodiversity Research, National University of Singapore (ZRC); Taiwan Museum, Taipei (TMCS); National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM); Zoological Museum, Hamburg (ZMH); and Zoologische Staatsammlung, Munich (ZSM).

For each species in the catalog, restricted synonymies are presented that cover the original citation, primary synonyms, major works, and references relevant to Taiwan. Each species, genus, family and superfamily is diagnosed. Line drawings illustrating distinguishing characters are given for all the species based on Taiwanese specimens except for one species, *Cloridina verrucosa* (Hansen, 1926), for which the Taiwan specimen could not be located during the preparation of the catalog. The diagnosis and line drawings of this species are based on a specimen from Australia (AM). Color photographs are provided for 48 species, all based on Taiwanese

material. Coloration is often very useful in distinguishing species, particularly the color markings on the tailfan.

Terminology and size descriptors generally follow Ah Yong (2001) and general morphology is illustrated in Morphological Terms. All specimen measurements are in millimeters (mm). The size measure given for most specimens is total length (TL), which is measured along the midline from the apex of the rostral plate to the apices of the submedian teeth of the telson. For broken or damaged specimens, carapace length (CL) is indicated, measured along the midline excluding the rostral plate. Relative eye size is a useful taxonomic feature and is measured by the corneal index (CI). The CI is given as $100CL$ divided by corneal width. Other abbreviations: antennule (A1), antenna (A2), abdominal somite (AS), and thoracic somite (TS).

Moose specimens were collected by commercial trawlers. For specimens collected by the "TAIWAN 2001" and "2002" cruises, gear types are abbreviated as CP and CH and indicated before the station number. The abbreviations for gear types CP and CH refer to the four-meter French beam trawl, and the otter trawl used by commercial trawlers, respectively.

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SYSTEMATICS

Order STOMATOPODA

The mantis shrimps belong to subclass Hoplocarida and Order Stomatopoda. The phylogenetic position of the hoplocarids has been widely debated (Schram, 1969), with controversy largely surrounding the interrelationships of the major malacostracan subclasses: Hoplocarida, Eumalacostraca, and Phyllocarida. Burnett & Hessler (1973) and Hessler (1983) regarded hoplocarids as eumalacostracans on the basis of the 'caridoid facies' (Calman, 1909). Using functional morphology, Kunze (1981, 1983) concluded that the hoplocarids evolved from a phyllocarid-like ancestor, separate from the eumalacostracans. Schram (1986) proposed that the hoplocarids and eumalacostracans were sister taxa, but included the malacostracan phyllocarids with several non-malacostracan groups in the Class Phyllopoda. Currently, the hoplocarids are widely accepted as the sister to eumalacostracans, which together are sister to the phyllocarids (Martin & Davis, 2001; Richter & Scholtz, 2001).

The fossil record suggests that the hoplocarid ancestors diverged from other eumalacostracans during the Devonian (Hof, 1998b). Until recently, three hoplocarid orders were recognized: Aeschronectida,

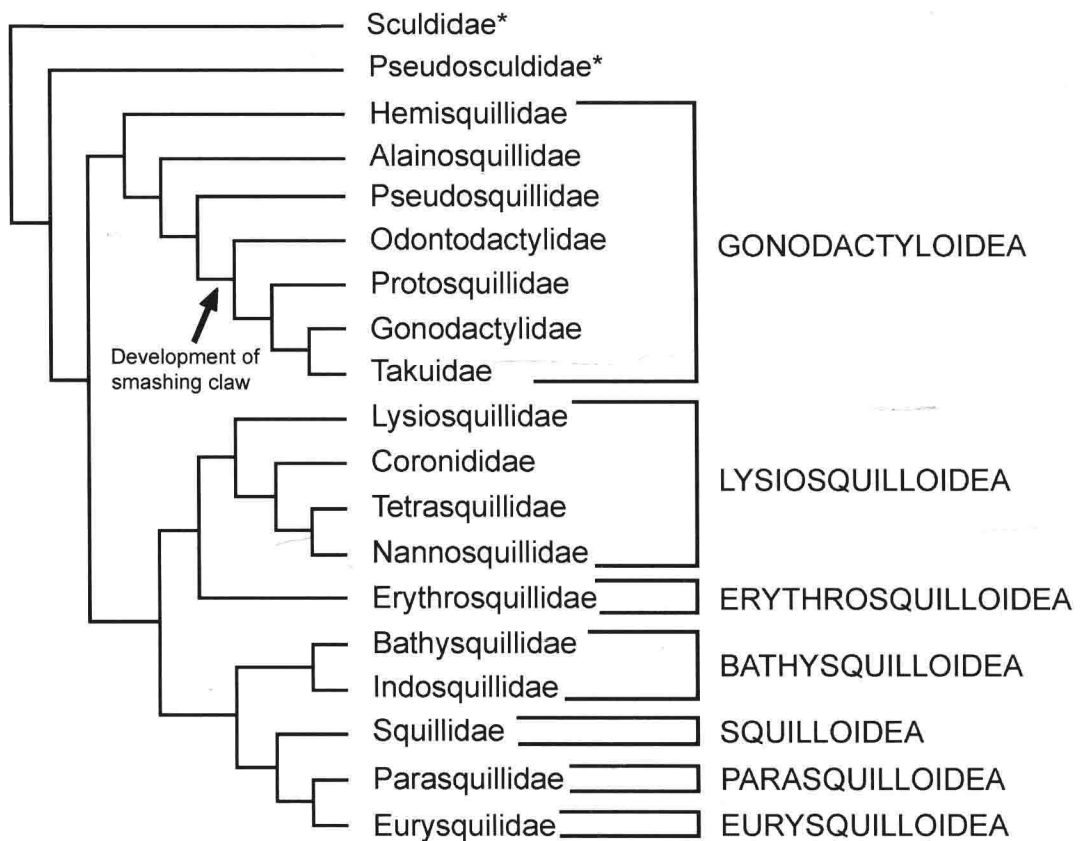


Fig. 1. Phylogenetic relationships of the unipeltatan stomatopod families; * extinct. Based on Ahyong & Harling (2000).

Palaeostomatopoda and Stomatopoda. Recent detailed analysis of the palaeozoic forms, however, showed that the palaeostomatopods form a paraphyletic grade leading to Stomatopoda (Jenner *et al.*, 1998; Schram, 2007). Thus, the most appropriate classification recognizes two orders, Aeschronectida and an expanded Stomatopoda which includes the paleostomatopods. The aeschronectids were shrimp-like and the least specialized. Stomatopoda, on the other hand witnessed the evolution of the massive raptorial claw (Schram, 2008). The palaeostomatopods and archaeostomatopodeans form a paraphyletic 'transition series' with increasing differentiation of the second maxilliped as a powerful raptorial claw, which reaches maximum development in the Unipeltata. Unipeltata includes all modern stomatopods, the 'true' mantis shrimp. The archaeostomatopodeans first appeared in the Carboniferous families, Daidalidae Schram, 2007, Gorgonophontidae Schram, 2007, and Tyrannophontidae Schram, 1969. Of the three known archaeostomatopodean families, Tyrannophontidae is the likely sister group of the Unipeltata (see Schram, 2007).

Unipeltata comprises the Jurassic–Cretaceous stem-lineage families Sculdidae and Pseudosculdidae (see Hof, 1998b, Ah Yong *et al.*, 2007), and the extant, crown-group superfamilies (Manning, 1980b, 1995, Ah Yong & Harling, 2000, Ah Yong, 2001, 2005b). The major crown-group superfamilies, Gonodactyloidea, Lysiosquilloidea and Squilloidea, are known to have diverged by the late Cretaceous and have displayed little major morphological divergence since then.

The taxonomy of the Stomatopoda has been extensively revised over the past four decades, e.g., Manning (1963b, 1968c, 1980b, 1995) and Ah Yong (2001). Prior to Manning's work, only the single family, Squillidae was recognized for crown-group taxa. Giesbrecht (1910) proposed several subfamilies based on larval morphology, but his work was largely ignored by those working with the adults. Using larval, maxillipedal and telson morphology, Manning (1968c) recognized 37 genera in four families: Squillidae; Lysiosquillidae; Bathysquillidae; and Gonodactylidae. Giesbrecht's subdivisions, based on larvae, correspond to the families recognized by Manning (1968c). Manning (1980b) further reviewed stomatopod classification and recognized four superfamilies: Squilloidea, Lysiosquilloidea, Bathysquilloidea, and Gonodactyloidea. Manning & Camp (1993) recognized Erythrosquilloidea for *Erythrosquilla megalops* Manning & Bruce, 1984, previously assigned tentatively to the Lysiosquilloidea. Manning (1995) recognized 19 families and 5 superfamilies for living taxa, containing more than 100 genera and 450 species.

Phylogenetic analyses of the modern stomatopods have been conducted only in the last decade or so (e.g., Ah Yong, 1997; Hof, 1998b; Ah Yong & Harling, 2000; Barber & Erdmann, 2000; Ah Yong, 2005). Interrelationships of the genera of the largest stomatopod superfamily, Squilloidea, were studied by Ah Yong (2005b). Relationships among the selected gonodactyloids were studied by Barber & Erdmann (2000), and are the subject of more extensive studies currently underway by Barber, Erdmann and Ah Yong. The most comprehensive overall study of stomatopod interrelationships recognized 7 superfamilies and 17 families (Ah Yong & Harling, 2000).

The Unipeltata appears to have 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'. These two major stomatopod lineages also correlate broadly with habitat type. The gonodactyloid clade, members of which primarily occupy cavities and crevices on hard substrates, have become the dominant stomatopods on coral reefs. Most are small species, with body size apparently constrained by available hard substrate domiciles. The largest gonodactyloids (*Hemisquilla* spp. and *Odontodactylus* spp.) live in burrows in sand or sandy-mud. Almost all gonodactyloids are 'Smashers', and within this clade, the smashing claw attains its greatest development, ideal for preying on molluscs and crabs that are common on reefs. The other major lineage, comprising the remaining superfamilies, developed large, efficient spearing claws, occupying burrows in soft

substrates (note that a few lysiosquilloids and squilloids both ‘Spear’ and ‘Smash’). Prey is typically soft bodied, such as shrimp, cephalopods and fish. Habitat is apparently a lesser constraint on body size than for gonodactyloids, for the largest known stomatopods are all ‘Spearers’. Of this group, the parasquilloids and squilloids are generalist foraging predators, the bathysquilloids are restricted to deep water, and the eurysquilloids, lysiosquilloids and erythrosquilloids are specialized for burrow habitation in soft substrata. Members of five of seven stomatopod superfamilies are presently known from Taiwan.

Key to Superfamilies of the Stomatopoda from Taiwan

- | | |
|---|-------------------------|
| 1. Propodi of maxillipeds 3–4 ovate, usually longer than broad, without distal ribbing. | 2 |
| - Propodi of maxillipeds 3–4 subquadrate, broader than long, usually with distal ribbing. | |
| | Lysiosquilloidea |
| 2. All primary teeth of telson with articulated apices | Bathysquilloidea |
| - At most, submedian teeth of telson with articulated apices | 3 |
| 3. Telson with 4 or more closely spaced intermediate denticles arranged in regular row | Squilloidea |
| - Telson with no more than 3 (usually 2) 'intermediate' denticles | 4 |
| 4. Uropodal protopod with three primary spines. Cornea asymmetrically bilobed, with outer margin of eye longer than inner margin; with 2 or 3 rows of hexagonal ommatidia in the mid-band | Parasquilloidea |
| - Uropodal protopod with two primary spines. Cornea subglobular or symmetrically bilobed, with 6 rows of rectangular ommatidia in mid-band | Gonodactyloidea |

Morphological Terms

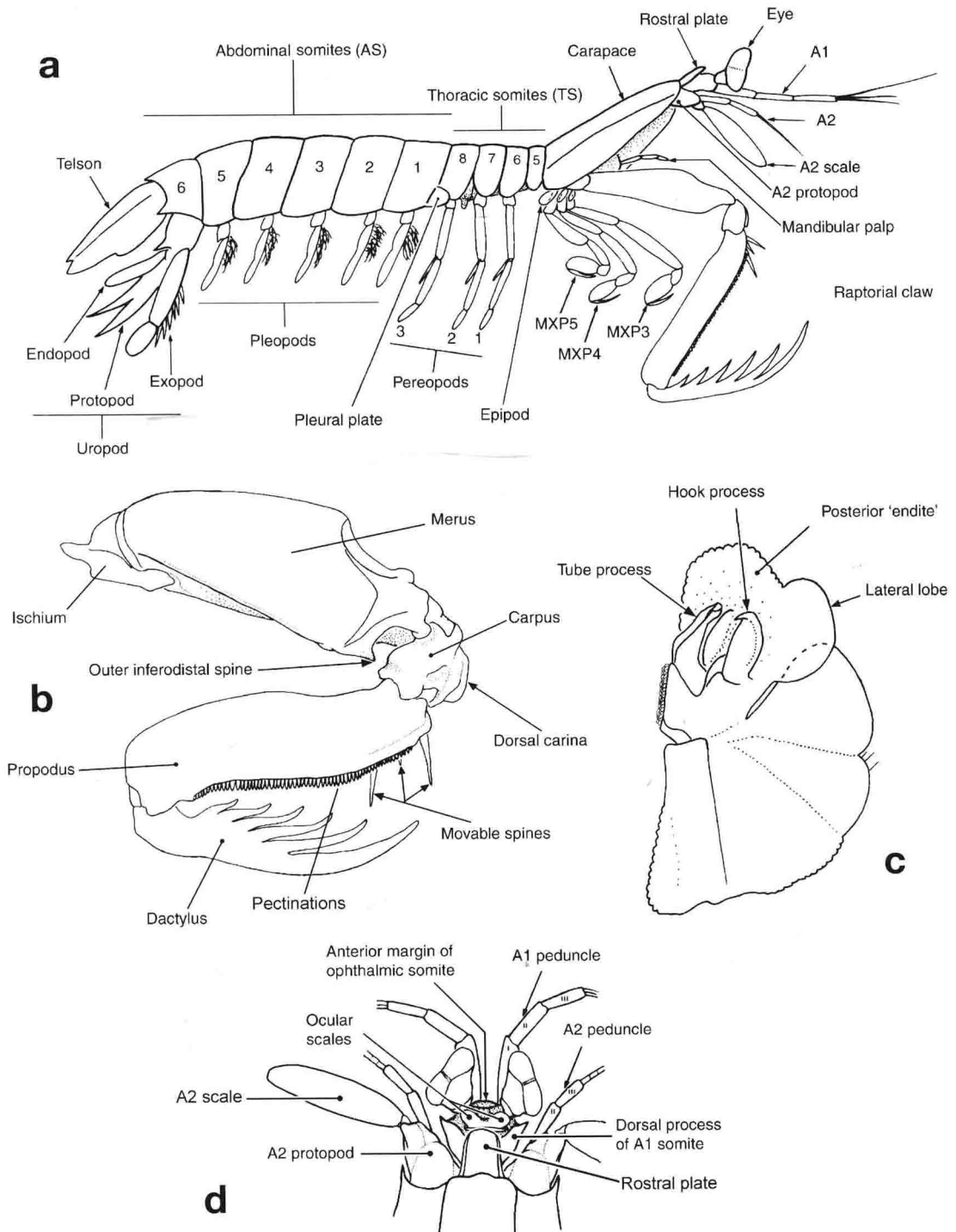


Fig. 2. Morphology: **a**, general; **b**, right raptorial claw; **c**, right male pleopod 1 endopod, anterior view; **d**, anterior.

Morphological Terms

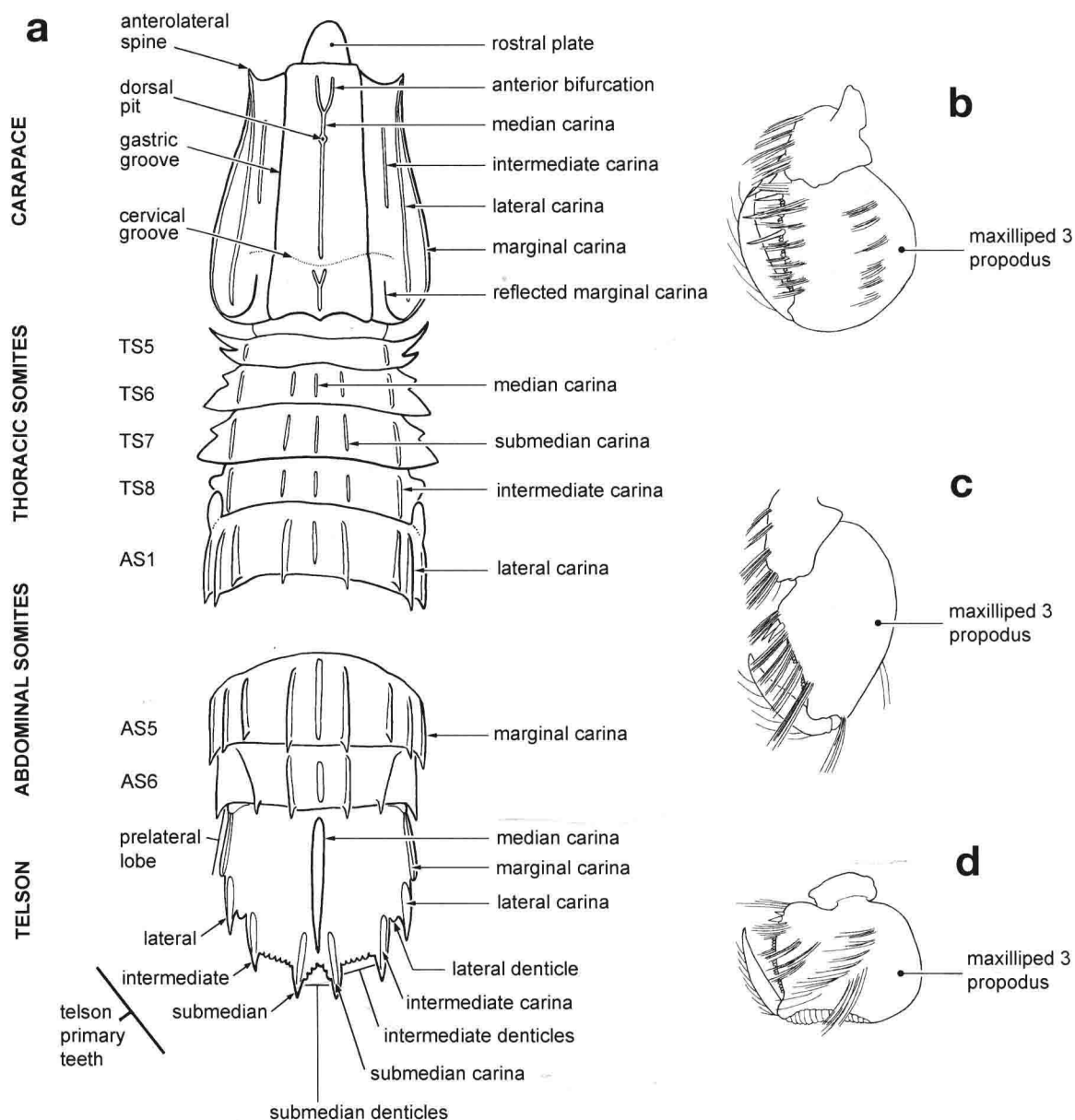


Fig. 3. Morphology: **a**, dorsal carinae; **b**, maxilliped 3 (Squilloidea); **c**, maxilliped 3 (Gonodactyloidea); **d**, maxilliped 3 (Lysiosquilloidea).

Morphological Terms

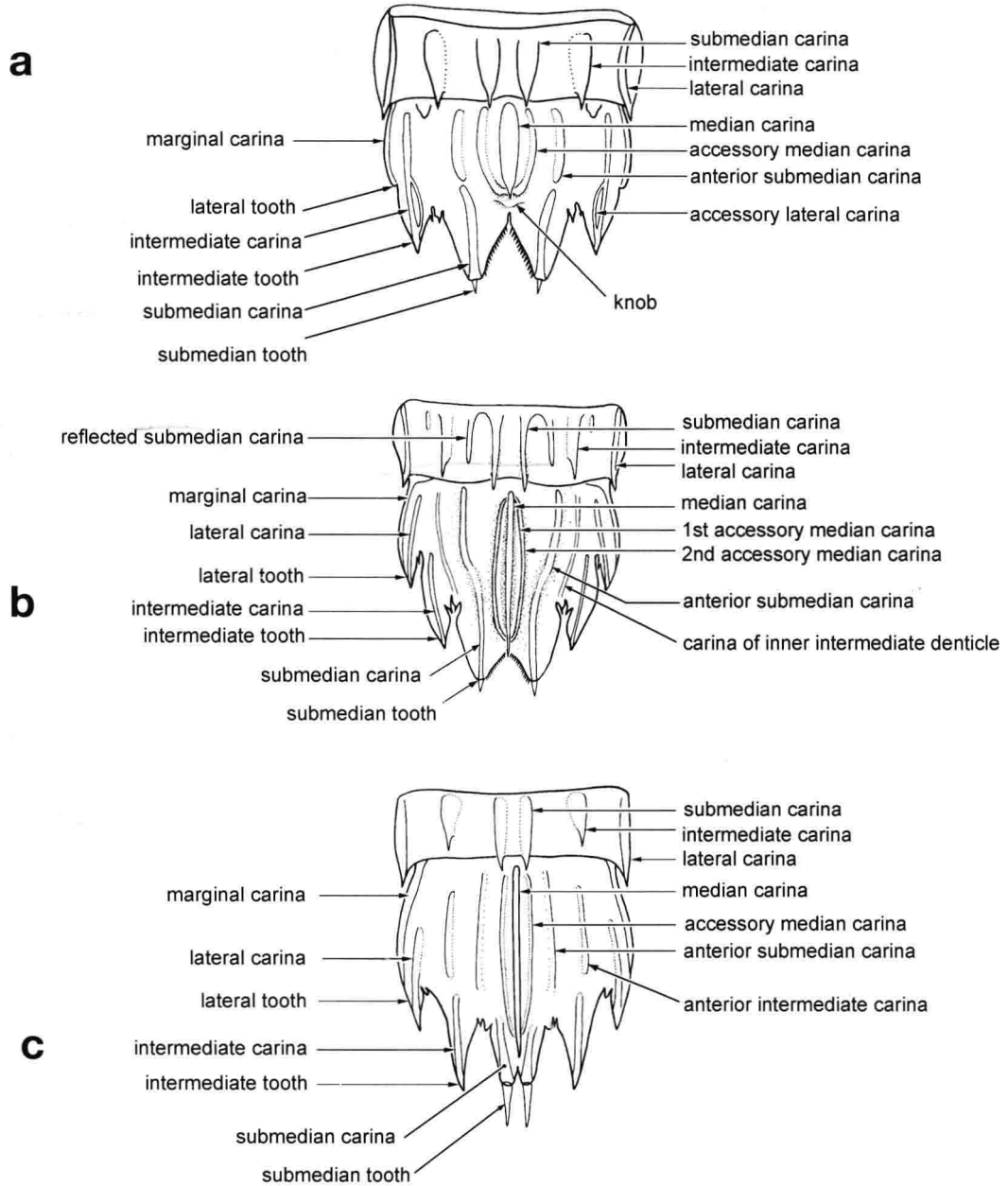


Fig. 4. Telson morphology: **a**, Gonodactylidae; **b**, Odontodactylidae; **c**, Eurysquilloidea, Parasquilloidea, Pseudosquillidae.

BATHYSQUILLOIDEA Manning, 1967

Diagnosis.— Cornea without rows of midband ommatidia. Corneal facets hexagonal, but poorly defined. Propodi of maxillipeds 3–4 ovate, not ribbed or beaded ventrally. Body depressed, articulation compact. Raptorial claw with terminal ischiomerar articulation, dactylus not inflated basally. Telson with distinct median carina; all primary teeth with articulated apices; intermediate denticles absent. Uropodal protopod with two primary spines; exopod segments articulated or separated by diaeresis.

Remarks.— Whereas stomatopods are known for their excellent vision, the bathysquilloids are the exception because of their reduced or degenerate eyes. The bathysquilloids live in deep water on the outer continental shelf and slope, with *B. microps* occurring to about 1500 m (Manning, 1991). Bathysquilloids further differ from all other extant stomatopods by having articulated apices of all primary teeth on the telson. In other stomatopods the primary teeth are either all fixed or have articulated apices of only the submedian primary telson teeth. Bathysquilloidea includes two families, Indosquillidae Manning, 1995, and Bathysquillidae Manning, 1967, of which the latter is represented in Taiwan.

Family BATHYSQUILLIDAE Manning, 1967

Bathysquillidae Manning, 1967a: 238.

Diagnosis.— AS5 without long, posteriorly directed median spine. Telson broader than long; dorsum rugose, tuberculate. Segments of uropodal exopod fully articulated; distal segment longer than proximal segment.

Remarks.— Of the two known bathysquillid genera, only *Bathysquilla* is found in Taiwan.

Genus *Bathysquilla* Manning, 1963

Bathysquilla Manning, 1963b: 323–324. Type species *Lysiosquilla microps* Manning, 1961, by original designation. Gender feminine.

Diagnosis.— Carapace with cervical groove distinct across dorsum. Male pleopod I endopod with lateral lobe on posterior 'endite'. Telson posterior margin with 4 pairs of primary teeth, each with movable apex.

Remarks.— *Bathysquilla* includes two species, *B. microps* (Manning, 1961) and *B. crassispinosa* (Fukuda, 1909), of which the latter occurs in Taiwan.