A Guide to, and Checklist for, the Decapoda of Namibia, South Africa and Mozambique (Volume 2)

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By

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INFRAORDER ANOMURA
MCLEAY, 1838

Although this infraorder has been known as the "Anomala" and included various anomalous decapods, McLaughlin & Holthuis (1985) confined only the three superfamilies Paguroidea, Galathoidea and Hippoidea to the Anomura and concluded that the name Anomura MacLeay, 1838 should be used instead of the older, but less-used name "Anomala" Latreille, 1816 (De Grave et al., 2009; Poore, 2016). The "Thalassinidea" (now recognised as two separate infraorders, Gebiidea and Axiidea, Poore, 2016) were once thought to be anomurans (Borradaile, 1903), even relatively recently (Williams, 1984), but Burkenroad (1963) excluded them, which was supported by de Saint Laurent (1979) and Bowman & Abele (1982). There was also a controversial opinion that the Dromioidea were actually anomurans (Williamson, 1992; Spears et al., 1992), but this was disputed by Scholtz & Richter (1995) and not accepted by Davie (2002b).

In an early interpretation, Warner (1977) envisioned that the Anomura emerged from the Glypheoidea during the Triassic, over 200 Mya. This was recently confirmed by Chablais et al. (2011) who found the oldest Anomuran, *Platykotta akaina*, which dated back to the Triassic, more than 200 Mya (Schweitzer & Feldmann, 2015; Table 2-1). The Paguroidea originated during the Early Jurassic, around 180 Mya (Walker, 1988; Lemaitre & McLaughlin, 2009), with hermit crabs in general dating from the Cretaceous around 100 Mya (Williams & McDermott, 2004; Lemaitre & McLaughlin, 2009). Bracken-Grissom et al. (2013), however, estimated an earlier emergence of the Anomura during the Late Permian, 296–224 Mya, with radiations of families during the Jurassic and Early Cretaceous, 180 to 120 Mya.

Various hypotheses have been forwarded for the origin and evolution of the Anomura. Martin & Abele (1986) found that within the Anomura, the Albuneidae-Hippidae branched off first, followed by a clade which had the Aeglidae emerging first followed by the Chirostylidae and the Galatheidae-Porcellanidae, while another clade led to the Lomisidae-Hapalogastridae-Lithodidae and the Pylochelidae-Paguridae-Parapaguridae-Diogenidae-Coenobitidae. In their phylogenetic analysis, Scholtz &

Richter (1995) had the sequence running Polychelidae, Achelata, "Homarida" [*sic*], which was followed by a division into the Astacidea-"Thalassinida" and the "Anomala"-Brachyura. Using spermatozoa data, Tudge (1997) found that *Hippa-Thalassina* branched off after the Astacidae, followed by the Porcellanidae, *Cancellus* and Galatheidae-Chirostylidae, with the rest of the chirostylids, Paguridae, and Parapaguridae on another branch, while the tree terminated in the Diogenidae and Coenobitidae. McLaughlin & Lemaitre (1997), using majority rule consensus, found that the chirostylids and galatheids emerged fairly basally, after *Cheiroplatea-Pylocheles-Mixtopagurus* and the Lomisidae, but before *Albunea-Lophomastrix-Blepharipoda* and *Hippa-Aegla*. Within the chirostylid-galatheid clade, *Galathea* emerged first, followed by *Munida*, *Gastroptychus*, *Munidopsis*, *Uroptychus*, *Euceramus*, *Petrolisthes* and *Petrocheles-Polynyx*. Crandall et al. (2000) placed the Anomura on the Reptantia line before the Brachyura, Astacidea, and "Thalassinidea"-"Palinura". Schram (2001) had the "Thalassinidea" and Brachyura on different branches, with the whole of the Anomura branching off along the Brachyuran line. Morrison et al. (2002) had the Galatheoidea branching off after the Thalassinidea and before the Lomisidae and Hippoidea, while within the Galatheoidea clade, *Lomis-Aegla* branched off first, followed by *Munida-Eumunida* and *Petrolisthes-Pachycheles*. Perez-Losada et al. (2002), found a basal dichotomy, with one branch leading to the Paguroidea, with the Aeglidae and Galatheidae-Chirostylidae-Porcellanidae branching off before and with the Hippoidea, "Thalassinidea" and Brachyura along the other branch. Dixon et al. (2003) also had a basal dichotomy with one branch leading directly to the Brachyura, while the other led to the Paguroidea-Lomisodea and then to the Lithodidea, Hippoidea, Galatheoidea and Aegloidea. Ahyong & O'Meally's (2004) analysis resolved the "Anomala"-Brachyura as having emerged along the "Reptantia" line after the Polychelidae, Achelata, Glypheoidea-Astacidea and "Thalassinidea". Within the Anomura these authors had the Blepharipoda-Albuneidae-Hippidae emerging basally, followed by Pylochelidae, Galatheidae, Chirostylidae-Porcellanidae in one clade and the remaining anomurans in another clade. These authors found good support for the monophyly of the Anomura. Schram & Dixon (2004) had the "Anomala" and Brachyura as sister groups after the "Thalassinidea" and Achelata, with the "Anomala"-Brachyura split occurring during the Triassic, 250–200 Mya, with the Achelata having branched off slightly before in the Triassic, and the deeper division with the "Thalassinidea" going right back to the Devonian, 400–360 Mya. MacPherson et al.'s (2005) anomuran phylogeny had the Hippidae as

basal, followed by the Lithodidae-Hapalogastridae in one branch, the Aeglidae in another branch and the Kiwaoidea, Galatheidae, Chirostylidae-Porcellanidae in a third branch. Porter et al. (2005) showed the Brachyura branching off basally followed by the Hippoidea, Aeglidae-Lomisidae-Chirostylidae-Galatheidae-Lithodidae, the Achelata and the Astacidea-"Thalassinidea". McLaughlin et al. (2007) found that the Dromiidae and Dynomenidae (Brachyura) branched of basally, followed by the Paguroidea, Kiwaoidea, Lomisoidea, then the Galatheoidea, followed by the Aegloidea, Lithodoidea and Hippoidea. These authors also showed the Anomura were a monophyletic infraorder. Tsang et al. (2008) had the phylogenetic sequence running "Thalassinidea", Hippoidea, Lomisoidea, with the anomuran families Lithodidae-Paguridae-Diogenidae-Coenobitidae forming one clade and the Galathoidea (*Petrolisthes-Paramunida-Munida*) and the Pylochelidae forming another clade. Lemaitre & McLaughlin (2009) reviewed research on anomuran phylogeny and found that different views have emerged from different workers using different techniques such as morphology, molecular data, larval information, spermatophore data and the fossil record itself. Bracken et al. (2009a) found that the Anomura emerged after the "Thalassinidea", followed by the Polychelida, after which there was a dichotomy, with one branch leading to the Polychelida and another to the Brachyura and Glypheidea and Achelata. Within the Anomura one branch led from *Munidopsis* to *Munida* and *Petrolisthes*.

Superficially this group of decapods are diverse, with some looking like crabs, some like hermit crabs, some like lobsters, while others are not easily categorised, but the small fifth thoracic leg is the only character which unites them (Poore, 2004). As all these forms could not be placed in the three superfamilies Paguroidea, Galathoidea or Hippoidea, more superfamilies had to be introduced. Martin & Davis (2001) had a four superfamily system with regard to the Anomura, while McLaughlin et al. (2007) extended this to a seven superfamily system. New molecular evidence has aided in unravelling the relationships between known anomuran families and its superfamilies. Perez-Losada et al. (2002) reviewed ideas based on traditional taxonomy with new molecular evidence and confirmed the accepted composition of the Galathoidea (Porcellanidae, Chirostylidae, Galatheidae and Aeglidae) and only differed in the relative positions of families from previous research (Martin & Abele, 1986; Tudge, 1997; see Schnabel & Ahyong, 2010, in later discussion). They also found that the Galathoidea and Paguroidea were more closely related to each other than to the Hippoidea, whereas Morrison et al. (2002) found the Hippoidea were closest to the Paguroidea.

Boas (1880) first suggested that lithodids evolved from pagurid ancestors, followed by Bouvier (1894), with the crab-like lithodid shape evolving from a shell inhabiting hermit crab. Cunningham et al's (1992) and Richter & Scholtz's (1994) data appeared to support this hypothesis. Furthermore, the larvae of the crab-like lithodids look similar to the pagurid crabs, and Cunningham et al's (1992) molecular-based work actually put two lithodid genera into *Pagurus*. However, McLaughlin & Lemaitre (1997, 2000) showed the reverse from adult and larval morphology: that hermit crabs developed from a lithodid-like ancestor (Davie, 2002b). It appears that carcinisation to a crab-like form has evolved independently several times in the Anomura, a phenomenon debated by McLaughlin & Lemaitre (1997), with McLaughlin et al. (2004) disagreeing with Cunningham et al's (1992) conclusions. Nuclear gene work by Tsang et al. (2011) found that not only do the hermit crabs have a single origin, but that most anomuran body forms and clades can be derived from within the hermit crabs, with the squat lobster form and crab-like form having evolved at least twice from different hermit crab ancestors (symmetrical) via intermediate forms. In addition, dextral shell habitation also evolved at least twice, once in a deep water clade and once in a common ancestor of all asymmetrical hermit crabs. Such parallelism is remarkable and exhibits phenotypic flexibility in hermit crab form. Using both molecular and morphological data, Schnabel et al. (2011) found that the Anomura fell into two major clades, one which included the Munididae sensu stricto, Galatheidae sensu stricto, Porcellanidae and Munidopsidae and another which included the Hippoidea, Paguroidea, Lomisidae, Aeglidae, Kiwaidae and Chirostylidae. A recent reconstruction of anomuran evolution by Bracken-Grissom et al. (2013) using molecular and morphological methods coupled with fossil evidence for divergence times has also revealed that most superfamilies and families are monophyletic. However, they found that three families, namely Diogenidae, Paguridae and Munididae, were either paraphyletic or polyphyletic. Using outgroups, they also found the Brachyura to be a sister taxon to the Anomura, from which they diverged during the Permian, 296 to 224 Mya. The earliest branching clade was the Blepharipodidae-Albuneidae-Hippae during the Late Triassic, 220 Mya, with the most recent split, between the Lithodidae and Hapalogastridae, estimated to be around 18 Mya. Carcinisation was shown to have occurred independently three times. Speciation rates were found to be low for the Lomisidae and high for the Chirostylidae. Bracken-Grissom et al's (2013) work also confirmed the "hermit to king" hypothesis and also found a close relationship between the pagurid

Discorsopagurus and the Lithodidea, suggesting a *Discorsopagurus*-like precursor leading to the lithodids, 29 to 18 Mya.

Although Davie (2002b) did not include any superfamilies, Poore (2004) included the Paguroidea, Galatheoidea and Hippoidea as well as *Lomis*, which was based on McLaughlin's (1983) phylogenetic reappraisal supported by Martin & Abele (1986). The Lomisidae appeared to be highly derived hermit crabs, possibly related to the Lithodidae, while the Coenobitidae were included with the Paguroidea (Poore, 2004). In their review of the Anomura, McLaughlin et al. (2007) subsequently gave a seven superfamily system—Aegloidea, Galatheoidea, Hippoidea, Kiwaoidea, Lithodoidea, Lomisoidea and Paguroidea—which was followed by De Grave et al. (2009). Schnabel & Ahyong (2010) raised the Chirostylidae to superfamily status, Chirostyloidea. Schnabel et al., (2011) then showed that the Galatheoidea were not monophyletic and defined the superfamilies Chirostyloidea and Galatheoidea. This evidence led to the new classification of the Galatheoidea in which the Munidopsidae were basal, followed by the Munididae, with the Galatheidae and Porcellanidae emerging lastly as sister groups (Ahyong et al., 2010). This eight superfamily system is used here. Based on both morphological and molecular methodologies the Anomura and Brachyura are monophyletic sister clades (Lemaitre & McLaughlin, 2009; Bracken-Grissom et al., 2013); the "Thalassinidea" are out of the Anomura as the infraorders Axiidea and Gebiidea (Robles et al., 2009; Poore, 2016); the Lomisoidea and Hippoidea are monophyletic; the Aeglidae are out of the Galatheoidea; the Lithodidae have their own superfamily (McLaughlin et al., 2007) although this has been contested (see De Grave et al., 2009); and there is polyphyly or paraphyly in the Diogenidae, Paguridae and Munididae (Bracken-Grissom et al., 2013). Although polyphyly was found for the Pylochelidae previously (Richter & Scholtz, 1994; Lemaitre & McLaughlin, 2009), Bracken-Grissom et al. (2013) found this family to be monophyletic. Tsang et al. (2011) showed that the symmetrical pylochelids were intermediate in two crab-like pathways, one leading via the squat lobsters to the porcellanids and another via asymmetrical hermit crabs such as the Diogenidae and Paguridae to the lithodids, which changes Cunningham et al's (1992) "Hermit to King" theory to "Hermit to All".

SUPERFAMILY CHIROSTYLOIDEA ORTMANN, 1892

Body symmetrical, carapace with or without transverse striae; rostrum, variable, but usually prominent and well-developed; supraocular spines can be present or absent. Antenna, peduncle made up of 5 segments, acicle may be present or absent. Mandible has toothed cutting edge. Maxilliped 1, with or without epipod. Pereiopods, P1 always chelate, P2 to P4 as walking legs. Maxilliped 3 and pereiopods have no epipods. Gills are phyllobranchiate. Sternal plastron made up of 3 to 7 sternites, thoracic sternite 8 without sternal plate. Abdomen, well-developed with all somites sclerotised and articulating; tail-fan well-developed and folded against preceding somite; telson and uropods laminar, telson divided transversely by a suture. This superfamily is made up of three families, Chirostylidae, Eumunididae and Kiwaidae (Schnabel & Ahyong, 2010; Schnabel et al., 2011).

The Chirostylids were previously considered part of the Galatheoidea, but this group was found to be polyphyletic which necessitated the removal of the Chirostylidae and Kiwaidae to a separate superfamily (Ahyong et al., 2010; Schnabel & Ahyong, 2010; Schnabel et al., 2011). Tsang et al. (2011), using nuclear genes, found a similar grouping with a *Uroptychus-Eumunida-Kiwa* clade which corresponds to the Chirostyloidea. Bracken-Grissom et al. (2013) have recently shown the Chirostyloidea to be monophyletic. These authors showed that after the Hippoidea, radiation during the Late Triassic led to emergence of the Chirostyloidea from squat-lobster ancestors around 205 Mya, with a split with the Lomisoidea around 122 Mya, which coincides with recent fossil evidence from this period in the form of *Platykotta akaina*, the oldest known anomuran fossil (Chablais et al., 2011). Only the Chirostylidae and Eumunididae are represented in southern African waters.

FAMILY CHIROSTYLIDAE
ORTMANN, 1892
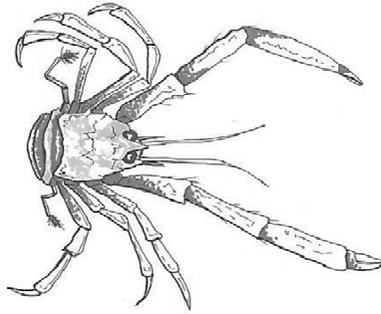
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Uroptychus foulisi

Carapace, smooth, tuberculate or spinose, with no transverse striae, posterolateral border not defined or inflated; rostrum, varying in shape; supraocular spines absent. Eyes, well-developed. Antennule, basal segment with distolateral spines. Antenna, peduncle made up of 5 segments, acicle may be present or absent. Mandibles, cutting edge calcified and strongly serrated. Maxilliped 1, has no epipod, exopod flagellum may be present and not annulated or absent. Maxilliped 3, arthrobranchs may be vestigial or well-developed, but pereiopods 1 (P1) to P4, each with 2 arthrobranchs. P5 with only one arthrobranch. P2 to P4 with pleurobranch. Sternum, sternite 3 not strongly produced towards the anterior. Abdomen: anterolateral margin of somite 2 with no prominent anterolaterally directed spine; pleopods 1 and 2 present in males, but pleopods 3 to 5 may be vestigial to absent (Schnabel & Ahyong, 2010). Type genus, *Chirostylus*.

The chirostylids emerged during the Cretaceous some 95 Mya (Bracken-Grissom et al., 2013). MacPherson et al. (2005) showed the Hippidae as basal in the Anomura, followed by the Lithodidae-Haplogastridae; Aeglidae; and Kiwaiidae, Galatheidae, Chirostylidae-

Porcellanidae as sister groups. An analysis by McLaughlin et al. (2007) had the Pylochelidae, Coenobitidae, Diogenidae, Parapaguridae-Paguridae-Pylojacquesidae in one clade, with Kiwaidae, Lomisidae and Chirostylidae, Galatheidae-Porcellanidae in one branch of another clade and the Aeglidae, Lithodidae-Hapalogastridae, Blepharipodidae and Albuneidae-Hippidae in another branch of this second clade. Phylogenetically Tsang et al.'s (2008) molecular analysis placed the Anomura between the "Thalassinidea" and Brachyura. Bracken-Grissom et al. (2013) showed this family to have a high speciation rate; currently this family contains 7% of all anomuran species with many new species awaiting description. The chirostylids have a fossil record with the extinct genus *Pristinaspina* (De Grave et al., 2009; Schweitzer et al., 2010; Fossilworks). *Pristinaspina gelasina* was described from the Cretaceous, 140 Mya, of Alaska and seemed to die out around the start of the Palaeocene around 65 Mya (Schweitzer & Feldman, 2000a). This early occurrence of this family member along the North Pacific Rim suggests that this family could have had its origins there.

Chirostylids are a marine family of often small, inconspicuous shrimp-like anomurans, which are found in a variety of habitats, from shallow subtidal reefs to the deep sea (Davie, 2002b) and even around hydrothermal vents. Superficially they resemble the galatheids, but generally occur in deeper shelf or slope waters. They are often associated with soft corals, antipatharians and gorgonians (Le Guilloux et al., 2010). Baba (1988) recognised 5 genera (*Eumunida*, *Chirostylus*, *Gastroptychus*, *Pseudomunida* and *Uroptychus*) and over 100 species worldwide, most of which occur in the Indo-West Pacific (Poore, 2004). However, in the newly defined chirostylid family the genera are limited to *Chirostylus*, *Gastroptychus*, *Hapaloptyx*, *Uroptychodes* and *Uroptychus* (Schnabel & Ahyong, 2010). Barnard (1950) gave two genera and species under the family Uroptychidae, namely *Uroptychus nitidus* and *Hapaloptyx difficilis*. Kensley (1981a) gave five species of *Uroptychus* (*U. edwardi*, *U. foulisi*, *U. nitidus*, *U. simiae* and *U. undecimspinosa*) and one species of *Eumunida* (*E. picta*) for southern African waters. Although *U. nitidus* is accepted by WoRMS, according to Baba et al. (2008) this is a new species and needs to be re-examined. *Uroptychus edwardi* is now synonymised with *U. scambus*, while *U. insignis*, *U. nigricapillis* and *U. remotispinatus* are new to the area (Baba et al., 2008). *Eumunida picta* has been moved from the chirostylids to the Eumunididae, and *Hapaloptyx difficulis* has been moved from the Uroptychidae (Stebbing, 1920; Barnard, 1950) and Incertae Sedis (Kensley, 1981a) into the Chirostylidae (Baba et al., 2008;

Schnabel & Ahyong, 2010), so currently there are 9 species of chirostylid in southern African waters (see checklist).

Chirostylids such as *Gastroptychus* have been observed to repeatedly oscillate their chelipeds from the surface of the deep water coral *Leiopathes* to their mouthparts and collect prey and detritus in their first maxillipeds, suggesting that they feed off these corals (Le Guilloux et al., 2010).

CHIROSTYLIDAE
Uroptychus foulisi **Kensley, 1977b**

Synonymy. Nil (Baba, 2005).

Common Name. Nil.

Description. Carapace, triangular, with narrow front which rapidly diverges posteriorly, with maximum width about 0.75 of carapace length posteriorly roughly around level of P2, unarmed dorsally, wider than mid-dorsal length (excluding rostrum), adorned with numerous fine, silky hairs and with numerous pits, rostrum reaching beyond eyestalks with an entire margin; anterolateral corner a forward projecting triangular spine, carapace sides with ridge-like tubercle anteriorly, a spinose tubercle midway followed by tubercles of decreasing size towards the posterior, supra-ocular spines absent. Sternum, with V-shaped margin and no median notch. Eyes, well developed, cornea, narrower than setose eyestalk.

Antennule, basal segment with crest and blunt at tip with a spine on each corner distally. Antenna, peduncle with 5 segments or articles and an antennal scale. Mandible, cutting edge calcified, strongly serrate. Maxilliped 1, no epipod. Third maxilliped, dactyl and propodus with a pad of setae, ischium finely denticulate on inner margin. Exopod of maxilliped 1 with flagellum. Mandible serrate. Chelipeds long and slender, with joint 5 elongated, cutting edge of dactyl finely denticulate with triangular tooth at proximal third of finger, finger and thumb half the length of the palm, carpus shorter than palm, outer surface with low tubercles, merus with spine on inner angle distally, the rest with scattered small tubercles, iscium with small spine ventrodistally and hook-like spine dorsodistally, with similar shaped spine on basis. Pereiopods: P2 as broad as P3, the dactyls curved, with 8 strong spines on ventral edge; P2–P4 with pleurobranch. The last thoracic somite is lacking. Abdomen, symmetrical and folded on itself; telson, fissured transversely and folded against preceding segments. In males, pleopods 1 and 2 are present, but pleopods 3–5 are vestigial (Kensley, 1977b; Baba, 1989, 2005; Baba et al., 2008; Schnabel & Ahyong, 2010). *Size*, 7.5mm CL (rostrum included), 6.9mm CW (male), 8.2mm CL, 7.9mm CW (female). *Colour*, pale pink. *Type locality*, off St Lucia, KZN, S Africa (Kensley, 1977b; Baba et al. 2008).

A well represented genus with 124 species world-wide, mainly from the Pacific Ocean (79 species), 36 from the Indian Ocean and 18 from the Atlantic (Baba et al., 2008). De Grave et al. (2009) gave 134 species for *Uroptychus*. Six species of *Uroptychus* are known from southern African waters: *U. foulisi*, *U. nitidus* (off KZN and East London; Kensley, 1977b, 1981a), *U. remotispinatus* (from off KZN and Mozambique Baba, 2005; Baba et al., 2008), *U. scambus* (=*U. edwardi*, caught off Port Edward at 900m, hence the specific name; Kensley, 1981b), *U. simiae* (off St Lucia, KZN) and *U. undecimspinosus* (off Richards Bay between 360–420m; see checklist). *Uroptychus insignis* is also known from the Prince Edward Islands (Baba et al., 2008). The joint MNHN-IOE Mainbaza Cruise off Mozambique has yielded another species, *Uroptychus nigricapillis* (Chan, pers. comm.), which was previously known from off Kenya (Baba, 2005), bringing the total to eight species. *Uroptychus mauritius* is found off Mauritius, while *U. brevipes*, *U. crosnieri*, *U. crassor* and *U. longioculus* occur off Madagascar. *Uroptychus dentatus* also occurs off E Africa (Baba et al., 2008).

Distribution. An endemic chirostylid, which is only known from off St Lucia, KZN, South Africa (Kensley, 1981a).

Zonation & Habitat. This small chirostylid occurs on the shelf in depths between 1000 and 1200m (Kensley, 1981a). Members of this family are generally associated with octocorallarian corals as commensals in deep water habitats (Baba, 1973).

Phylogeny. There do not appear to be any fossil species of *Uroptychus* (De Grave et al., 2008; Schweitzer et al., 2010). In their phylogeny of the decapods, Porter et al. (2005) showed that *Uroptychus parvulus* grouped with *Munida subrugosa* within the "Anomala", which branched off after the Brachyura and before the Achelata, "Thalassinidea" and Astacidea. Within the "Anomala" these authors had the Hippidae emerging basally, followed by the Lomisidae-Aeglidae, Lithodidae, and Chirostylidae-Galatheidae. This result placed the divergence between *Uroptychus* and *Munida* over 200 Mya during the Triassic, with the deeper branching off of the Anomala during the Carboniferous around 320 Mya. Bracken et al. (2009a), researching the Decapod tree of life, found that *Uroptychus* grouped with *Eumunida* in the Anomura, which was positioned after the Stenopodidea and "Thalassinidea", but before the Polychelidae, Astacidea and Brachyura-Achelata. Ahyong et al. (2009) thoroughly investigated Anomuran phylogeny using molecular methods and found that the Galatheidae-Porcellanidae formed one clade, with the Diogenidae-Coenobitidae, the Lepidopidae-Hippidae-Blepharipodidae and the remainder of the Anomura as sister groups. Within this "remainder" clade, the Pylochelidae emerged first, followed by the Paguridae-Lithodidae-Haplogastridae, Pylochelidae-Parapaguridae, Aeglidae, Lomisidae, Kiwaidae, Eumunididae and Chirostylidae. *Uroptychus* grouped with *Gastroptychus* and *Chirostylus* within the Chirostylidae, after having branched off from *Eumunida*. In this analysis, the Chirostylidae is excluded from the Galathoidea to warrant its own superfamily, which was subsequently published by Schnabel & Ahyong (2010) and Schnabel et al., (2011). These last three works show that the chirostylids have emerged independently of the galatheids-porcellanids, which differs from previous analyses, which have nested these three groups closely. *Kiwa* grouped within the Chirostylidae, so that the Kiwaidae could be incorporated into the Chirostylidae. Clark & Ng (2008) showed that the larval characters of *Chirostylus* are quite different from those of *Galathea*, while chirostylid sperm morphology is more closely akin to hermit crab sperm than to the galathoids (Tudge, 1997), so chirostylids could be closer to the non-galatheids than the galatheids or porcellanids (Ahyong, 2009). The internal relationships within the Anomura are still far from being settled, with polyphyly in the Pylochelidae, so some alliances will undoubtedly change

with future anomuran phylogenetic studies (Ahyong et al., 2009). Schnabel et al. (2011) found that the Anomura divided into two major clades, the second of which had the Hippoidea as basal, followed by a division into the Paguroidea on one hand, while on the other, the Lomisidae and Aeglidae branched off first, followed by the Kiwaidae and Chirostylidae, which included *Eumunida*, *Gastroptychus*, *Uroptychus*, *Uroptychodes* and *Chirostylus*. Eight species of chirostylid (*Chirostylus novaecaledoniae*, *Gastroptychus novaezealandiae*, *G. rogeri*, *G. spinifer*, *Uroptychus nitidus*, *U. parvulus*, *U. scambus* and *U. spinirostris*) were used in a molecular and morphological analysis of the Anomura by Bracken-Grissom et al. (2013) and the positioning of them differed according to methodology. Using molecular methods they grouped the Chirostyloidea in with the Kiwaidae and Eumunididae after the Galathoidea, but using combined molecular and morphological methods the chirostylids tested grouped in a clade which sequenced Aeglidae, Lomisidae, Eumuninidae, Kiwaidae, Chirosytlidae, with the Galathoidea as a sister clade. However, *Gastroptychus* and *Uroptychus* were found to be polyphyletic/paraphyletic.

Etymology. *Uroptychus*, *Uro-* Gr. *oura*, tail, *-ptych* Gr. *ptych*, a fold, in reference to the tail being folded under, *-us*, maculine suffix; *foulisi*, Kensley named this species for Captain George Foulis, Master of the CSIR Research Vessel *Meiring Naude*, which undertook numerous research cruises along the South African coastline.

FAMILY EUMUNIDIDAE A. MILNE-EDWARDS & BOUVIER, 1900
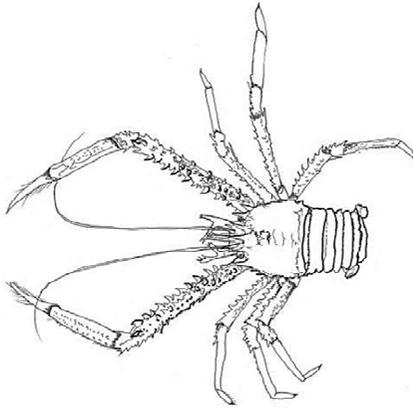
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Eumunida squamifera

Carapace, elongate, cordiform, with transverse striae, posterolateral margin not excavated, entire; rostrum, spiniform, with mesial and usually lateral supra-ocular spines, lateral supra-ocular spine well-developed in *Eumunida* and obsolete to minute in *Pseudomunida*; cervical groove distinct. Eyes, well-developed. Ocular peduncular basal segment obscured by rostral and supra-ocular spines dorsally. Anterior border of sternite 3 transversely sinuous to irregular and not strongly produced anteriorly. Antennules, basal article unarmed. Antennae, peduncle made up of 5 segments, with acicle present. Mandibles, cutting edge calcified, tridentate, with a tooth at each end and a single median tooth. Maxilliped 1, has well-developed epipod, and exopod flagellum is only annulated in distal part. Maxilliped 3 to pereiopod 4 (P4) with 2 arthrobranchs each, but vestigial on maxilliped 3. Pereiopods, P5 only has one arthrobranch, P2 to P4 with pleurobranchs. Abdomen, anterolateral margin of somite 2 has prominent anterolaterally directed spine. In males, pleopod 1 is missing,

pleopod 2 vestigial or missing, while pleopods 3 to 5 may be present or missing (Schnabel & Ahyong, 2010). Type genus, *Eumunida*, by monotypy.

This family has a fossil representative in *Eumunida pentacantha* from the Late Eocene of Hungary around 55 Mya (Schweitzer & Feldmann, 2000a; De Grave et al., 2009; Schweitzer et al., 2010). The eumunidids were given their own family in 1900 by Milne-Edwards & Bouvier, but it was not subsequently used, so they were part of the Chirostylidae (Kensley, 1981a; Davie, 2002b; Poore, 2004; Baba, 2005; Baba et al., 2008). Both Ahyong et al. (2009) and Schnabel et al. (2011) gave the chirostylid clade (*Kiwa*, *Eumunida* and *Pseudomunida*) which was paraphyletic outside a "Dypticiens" clade, but while *Eumunida* was strongly supported, *Kiwa* and *Pseudomunida* were ambiguous. Although *Pseudomunida* was not analysed, both Chu et al. (2009) and Tsang et al. (2011) found good support for a *Eumunida* plus *Kiwa* clade which was sister to the main chirostylid clade. Thus, the Chirostylidae sensu lato were not monophyletic, with the old "Eumunidiens" group closer to the Kiwaidae than the other chirostylids. Thus Schnabel & Ahyong (2010) reinstated the eumunidids to family status for the two genera *Eumunida* and *Pseudomunida* (Schnabel et al., 2011).

Presently there is only one eumunidid species in southern African waters, *Eumunida squamifera* (=*E. picta*) from off Namibia (Kensley, 1981a; de Saint Laurent & Macpherson, 1990; Macpherson, 1991; Baba et al., 2008). Squat lobsters in general feed on algae, deposits, particulate organic matter and suspensions, as well as being scavengers and predators (Loverich & Thiel, 2011), but *Eumunida picta*, which occurs in the N Atlantic, is a mesopelagic omnivore, feeding on diatoms, radiolarians, foraminiferans, particulate organic matter, marine snow, copepods, euphausiids, chaetognaths and small fish (Quattrini et al., 2012).

EUMUNIDIDAE
Eumunida squamifera **de Saint Laurent & Macpherson, 1990**

Synonymy. *Eumunida picta* (Kensley, 1980b; de Saint Laurent & Macpherson, 1990; Baba et al., 2008).

Common Name. Squat lobster.

Description. The body is shrimp-like. Carapace, about as long as wide with tapered front leading to the rostrum, which projects 0.75 the way to the tips of the maxilliped 3; three anterolateral spines on each side of the carapace, with the first as long as supraorbital external spine; the lateral and mesial supra-ocular spines (two pairs) are well developed; 5 pairs of lateral spines on posterior carapace decreasing in size with small spinules between; 3 pairs of hepatic spines in an oblique row, hepatic spine 1 is half the size of the external supraorbital spine; posterior carapace has raised striations, with 6 main, transverse striations, interrupted, with segments of variable lengths in the median zone and in short semicircles laterally. Antennular peduncles, extend past antennal peduncle extremities. Antennal peduncles, reach close to external supraorbital spines, antennal flagella long and slender, antennal scale, scaphocerite present, reaches mid-article 2. Maxilliped 3, has short spine on distal third of mesial merus border. Mandible, smooth to feebly dentate on incisor margin. No sternal plate on last thoracic somite. Chelipeds, elongate and slender, 3.7 times CL, the arms, especially the inner surfaces, with numerous sharp spines,

the hand upper surfaces with 2 longitudinal lines of spines, 10–12 mesiodorsal spines and 5–6 mesioventral ones. Pereiopods, elongated, possess spinose meri and carpi on leading edges, but last joints including the dactyls without spines. Abdomen, telson with transverse suture and folds beneath the preceding abdominal somites with the tail fan. Easily recognised by the combination of 5 rostral and supra-ocular spines and oblique rows of 3 spines prior to these (de Saint Laurent & Macpherson, 1990; Poore, 2004). *Size*, not known, but *E. australis* reaches 25mm CL (Poore, 2004). *Colour*, adults, bright orange, lateral carapace spines more pinkish, sternum and dorsal abdomen whitish, legs, orange dorsally, colour more pronounced at base of spines, legs and anterior abdomen lighter in colour. *Type locality*, Tripp Seamount, S Namibia, 152–390m (Baba et al., 2008).

This species was originally thought to belong to *Eumunida picta* (Kensley 1980b, 1981a), but de Saint Laurent & Macpherson (1990) separated it as a new species. A total of 28 species of *Eumunida* are known in the world, with most (23) coming from the Pacific, followed by three from the Indian Ocean and three from the Atlantic (Baba et al., 2008). This species can be distinguished from *E. bella* by the scaley striations on the carapace. This closely related species from off NW Africa is also closely related to the typical western Atlantic form, *E. picta*. *Euminida bispinata* and *E. similior* are known from Madagascar (Baba, 2005).

Distribution. A relatively large chirostylid with a restricted distribution from S Namibia to off the mouth of the Orange River, NW Cape (de Saint Laurent & Macpherson, 1990).

Zonation & Habitat. This squat lobster occurs in a depth zone on the shelf varying from 152 to 390m (de Saint Laurent & Macpherson, 1990; Baba et al., 2008), while Kensley (1980b, 1981a) recorded it from 800m off Lüderitz and over the seamount Tripp. Decapod community structure research of Namibia by Macpherson (1991) showed that *E. squamifera* was found on the southern slope between 300 and 500m. *Eumunida picta* lives over soft bottoms in which it can burrow, so this species could have similar habits. *E. picta* has also occasionally been found as a vagrant in cold-seep sites on the Louisiana Slope, USA (Cheveldonne & Olu, 1996), and has also been associated with deep water corals (Le Guilloux et al., 2010).

Although not much is known on the ecology of *E. squamifera*, the closely related species *E. picta* is quite well known and is also often associated with deep water gorgonians. Off Nova Scotia, Canada, it occurs

on the gorgonians *Primnoa resedaeformis* and *Paragorgonia arborea* (Buhl-Mortensen & Mortensen, 2004; Metaxas & Davis, 2005). This species is also a conspicuous and dominant megafaunal associate of the *Lophelia pertusa* reefs on the mid-continental slope (300–700m) off N Carolina on the SE coast of the USA (Nizinski et al., 2004).

This species probably has lots of small eggs as work on *E. picta* from the Middle Atlantic Bight has shown that females produce large numbers of small dispersive eggs (producing planktotrophic larvae), compared with *Munida* or *Munidopsis* which produce a few large eggs with lecithotrophic larvae (Wenner, 1982).

Phylogeny. Tudge (1997), investigating the phylogeny of the Anomura found that spermatologically *Eumunida* was more closely related to the paguroids than the galatheoids and could represent a link between these two superfamilies. In a graphic representation of galatheoid phylogeny, Schweitzer & Feldmann (2000a) showed that *Eumunida* branched off from the Galatheidae sensu stricto around 200 Mya before branching off from the Munididae spp. during the Upper Cretaceous around 80 Mya. Ahyong & O'Meally (2004) found that *Eumunida* nested with *Petrolisthes* in the Anomura, with *Munida* branching off earlier. However, Ahyong et al. (2009) later found that *Eumunida* nested with the Chirostylidae between *Pseudomunida* and *Uroptychus-Gastroptychus-Chirostylus*. Both Machordom & Macpherson (2004) and Cabezas et al. (2008) found that *Eumunida sternomaculata* was basal in their analyses. Using combined data Bracken et al. (2009a) showed *Eumunida* nested with *Petrolisthes*, with *Pylocheles* and *Munida* having branched off first. Using molecular data Ahyong et al. (2009) found that in the Kiwaidae-Chirostylidae clade, *Pseudomunida* was basal, followed by *Kiwa*, *Eumunida*, *Chirostylus*, *Gastropthychus* and finally *Uropthychus*. As *Kiwa* nested within the Chirostylidae, this questioned the validity of the Kiwaidae. Both *Kiwa* and the chirostylids have lost the last thoracic sternite, which was originally interpreted as parallelism (MacPherson et al., 2005; McLaughlin et al., 2007), but is now regarded as a synapomorphy. The chirostylids could be closer to the non-galatheids as the larval characters of *Chirostylus* are different from that of galathea, and chirostylid sperm is more like that of hermit crabs than of galatheoids (Tudge, 1997; Ahyong et al., 2009). Tsang et al. (2011) found that *Eumunida funambulus* nested with *Kiwa hirsuta*, with *Uroptychodes grandirostris* more basal, while Toon et al. (2009) similarly found *E. funambulus* emerging with *Kiwa hirsuta*, after *Pomatocheles*, *Munidopsis*, *Lomis* and *Aegla*.

Etymology. *Eu-* Gr. *eu-* prefix for true, *-munida*, a galatheid genus, L. *munitas*, armed, as members of this genus are usually well armed with spines; *squamifera*, L. *squamus*, pavement, *ferus*, to carry, i.e., named for its pavement-like ornamentation of the dorsal carapace (de Saint Laurent & Macpherson, 1990).