RESEARCH ARTICLE

Establishment of a new subfamily for *Shenius anomalus* (Shen, 1935) (Crustacea: Decapoda: Brachyura: Dotillidae)

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Abstract

Shenius anomalus (Shen, 1935) has previously been assigned to the Macrophthalmidae Dana, 1851, and the Camptandriidae Stimpson, 1858. However, a close examination of adult and first stage zoeal morphology confirms some previous suggestions that *S. anomalus* is actually an anomalous member of the Dotillidae Stimpson, 1858. However, because a number of distinctive features distinguish it from *Dotilla* Stimpson, 1858, *Ilyoplax* Stimpson, 1858 and *Scopimera* de Haan, 1833, a new subfamily Sheniinae is established.

Key words: Crustacea, Brachyura, new subfamily, Dotillidae, Sheniinae, new subfamily, systematics

Introduction

Shen (1935) described an unusual thoracotreme crab species from China, *Camptandrium anomalum*. He noted that although its carapace closely resembled the known species of *Camptandrium* Stimpson, 1858, it nevertheless had many atypical features such as a unique shape of the male abdomen and unusually structured male first gonopods. The assignment of this species to *Camptandrium* was challenged by Serène (1968) and he eventually established a new genus to accommodate it, *Shenius* Serène, 1971. Although Serène (1974), Serène & Kumar (1971) and Serène & Moosa (1974) formally recognised the Camptandriinae Stimpson, 1858, as a distinct subfamily in the Ocypodidae Rafinesque, 1815, these authors were uncertain with regard to the placement of *Shenius*. Later, Tan & Ng (1999) commented that *Shenius* was merely an anomalous member of the Dotillinae Stimpson, 1858 (Ocypodidae). Recently, Ng et al. (2008a) considered that *Shenius* should be referred to its own subfamily within the Dotillidae, but deferred from formally doing so.

The purpose of this paper is to review the adult and first zoeal characters of *Shenius* and formally assigned the genus to a new dotillid subfamily.

Methods

Adult material. Dissected appendages were dissected under a Leica MZ16 and mounted in polyvinyl lactophenol on glass slides and drawn using Leica DM 5000 B microscope each with DIC.

Zoeal material. Dissections of appendages were carried out under a Leica MZ16 and placed in glass slides in polyvinyl lactophenol and allowed to clear for 24 hrs before examination. Cover-slips were sealed with clear nail varnish. Appendages were drawn using Leica DM 5000 B microscope each with DIC. The sequence of the zoeal descriptions was based on the malacostracan somite plan and described from anterior to posterior. Setal armature of appendages was described from proximal to distal segments and endopod first, then exopod (Clark et al., 1998). The long antennular aesthetascs and the long plumose natatory setae of the first and second maxillipeds were drawn truncated. The dorsal spines of all the *S. anomalus* first stage zoeas examined for the present study were damaged and consequently this character is drawn truncated too. The mandible is not fully described or illustrated because the only significant character of this appendage is the appearance of the palp in the zoeal phase. The approximate measurement of the antennal endopod (for its ratio with the protopod) was made from its base to the tip.

Measurements of adults provided, in millimeters, are of the maximum carapace widths and lengths, respectively.

Abbreviations used: Institute of Zoology, Chinese Academy of Sciences, Beijing = CAS; The Natural History Museum, London = NHM; the Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore = ZRC; coll. = collected by; pres. = presented by; P2-P4 = first to fourth ambulatory legs, respectively; G1 = male first gonopod; G2 = male second gonopod; ovig. = ovigerous.

Taxonomy

Family DOTILLIDAE Stimpson, 1858

Sheniinae, new subfamily

Type Genus

Shenius Serène, 1971

Diagnosis

Carapace hexagonal, dorsal surface not convex with regions well defined, covered with short stiff setae. Buccal cavity broad, covering most of face; third maxillipeds with merus and ischium large, squarish, not forming any gape when closed. Ambulatory legs long, positioned laterally on thorax; meri of P2-P4 with dorsal margins armed with distinct spines; outer surface with submarginal carina. Male and female sternoabdominal cavity reaching to base of buccal cavity. Male abdomen with somite 5 shaped like hour-glass. G1 sinuous, slender, with several short and long spines distally.

Remarks

From his choice of the species name (*anomalum*), Shen (1935) clearly had doubts as to placing the species in *Camptandrium* Stimpson. 1858. In his Prodromus of the Indo-Pacific Brachyura, Serène (1968) retained the species in *Camptandrium* but later (Serène, 1971) established a new genus *Shenius* within the Ocypodidae Rafinesque, 1815, for the species, commenting that it differed markedly from the known species of *Camptandrium*. Serène & Umali (1972) elaborated on the problematic status of *Shenius*, by illustrating more characters. In his review of *Camptandrium*, Serène (1974) reappraised the status of the Camptandriidae Stimpson, 1858. He resurrected the Camptandriinae as a subfamily within the Ocypodidae, and also recognised the Scopimerinae Alcock, 1900 (= Dotillidae Stimpson, 1858). Nonetheless, Serène

(1974) was unsure of the systematic status of *Shenius*. In defining the various ocypodid subfamilies, he placed *Shenius* with the group of genera that constitute the Dotillinae (as Scopimerinae), noting that they all had similar G1 structures (Serène, 1974: 60). But in his provisional key to the Camptandriinae, Serène (1974: 66) treated *Shenius* as if it was a member of the subfamily.

In an unpublished thesis, Harminto (1986) had argued that while *Shenius* had many dotilline features, it was nevertheless so unusual that it merited its own subfamily within the Ocypodidae. Tan & Ng (1999: 195), in their revision of *Camptandrium*, noted "Serène (1974) had in fact transferred *Shenius* (with some doubt) to the Dotillinae Stimpson, 1858. *Shenius* is certainly more closely affiliated to the Dotillinae as the male abdomen has all seven segments free (segments two and three always immovable in camptandriines). In addition to this, the G1 structure (slender and bent at tip), as well as the form of the mouthparts and orbital regions of *Shenius* differ significantly from that typically found in the Camptandriidae" (see also Tan & Ng, 1995).

Kitaura et al. (2002) proposed that the Dotillinae should be recognised as a family, and this was followed by Ng et al. (2008a), who also placed *Shenius* in the Dotillidae. Ng et al. (2008a), however, commented that, "The position of *Shenius anomalus* (Shen, 1935) has not been settled. Shen (1935: 32, Figure 9A, B) originally placed it in *Camptandrium* because the carapace and legs are similar, but his figures of the suborbital margin, male abdomen and G1 (Shen, 1935: Figure 8B, 9C, D) do not indicate a close relationship. Realising this, Serène (1971) established a new genus, *Shenius*, for it. Serène (1974) then transferred *Shenius* to Dotillinae Stimpson, 1858 (present Dotillidae), albeit with some doubt, probably because the carapace and pereiopod structures of *Shenius*, when compared to dotillids, are extremely different.

Manning & Holthuis (1981) agreed that *Shenius* was not a camptandriid. In an unpublished thesis, Harminto (1988) re-examined *Shenius* and agreed with Serène (1974) about its relationships to the Dotillidae. As in dotillids the male abdomen has all segments freely articulating, the G1 is slender and bent at the tip, and the mouthparts and orbital regions are of the same form. The different carapace and periopod features, however, suggest that it should be placed in its own subfamily" (Ng et al., 2008a: 235).

With the exception of *Shenius*, the eight known genera of dotillids, *Dotilla* Stimpson, 1858, *Dotilloplax* Tweedie, 1950, *Dotillopsis* Kemp, 1919, *Ilyoplax* Stimpson, 1858, *Potamocypoda* Tweedie, 1938, *Pseudogelasimus* Tweedie, 1937, *Scopimera* De Haan, 1833, and *Tmethypocoelis* Koelbel, 1897, have similar carapace and periopod structures. The atypical external morphology of *Shenius* (see below) strongly suggests it should be placed it its own subfamily.

Shenius Serène, 1971

Shenius Serène, 1971: 903, 916; Serène & Umali, 1972: 92; Ng et al., 2008a: 235.

Type species

Camptandrium anomalum Shen, 1935, by original designation; gender masculine.

Diagnosis

As for subfamily.

Remarks

With regards to the gender of *Shenius*, Serène (1971) named the genus after C. J. Shen but gave no indication of the gender. Under such cases, the gender should be treated as masculine. In the introduction of his paper, Serène (1971: 903) listed the species as "*Shenius anomalus*". However, in his diagnosis and discussion of the genus (Serène, 1971: 917), he referred to the species as "*Shenius anomalum*", treating the new genus as neuter. As *Shenius* is masculine, the species name should be "*anomalus*".

Shenius anomalus (Shen, 1935)

(Figures 1-10)

Camptandrium anomalum Shen, 1935: 31, text figures 8B, 9; Tweedie, 1937: 162.

? *Camptandrium anomalum* - Serène, 1968: 1010.

Shenius anomalum - Serène, 1971: 917, Plate 5C; Serène & Umali, 1972: 94, plate 9, figures 5-7, text figures 124, 125; Serène, 1974: 66; Tan & Ng, 1994: 84; Ng et al., 2008b: 126.

Shenius anomalus - Serène, 1971: 903; Yang, 1979: 42; Manning & Holthuis, 1981: 200; Dai et al., 1986: 441, figure 247 (1–3); Dai & Yang, 1991: 483, figure 247 (1–3); Ng et al., 2008a: 235.

Material examined

Type: Da Pu Xu (= Taipo), Guangdong Province, (= Canton), southern China, coll. 2 Jun. 1932; holotype ♂ (4.5 × 3.5 mm) (CAS CB-02060a); paratype ♀ (3.8 × 2.9 mm) (CAS CB-02060b).

Others: 9 ♂, 4 ovig. ♀ (NHM 1937.11.15.132-141), Kranji River, Singapore; pres Raffles Museum; 2 ♂, 1 ovig. ♀, 5 ♀ (ZRC 1965.7.15.1–8), Kranji, Singapore, coll.

M. W. F. Tweedie, Jun. 1935; 1 ♀ (ZRC 1993.488), Sungei Buloh Nature Reserve, Singapore, coll. D. Wee, 10 Aug. 1992; 1 ♂ (5.5 × 4.9 mm), 1 ♀ (6.8 × 5.5 mm) (NHM, ex ZRC 1987.338–339), Lim Chu Kang, Singapore, coll. P. K. L. Ng, Mar. 1986; 1 ♂, 1 ♀ (ZRC 1999.1176), Lim Chu Kang, Singapore, coll. P. K. L. Ng, Apr. 1995; 1 ♀ (ZRC 2000.1111), Lim Chu Kang, Singapore, coll. P. K. L. Ng, 23 Mar. 2000; 2 ♀ (larger 5.0 × 4.0 mm) (ZRC 1987.333–334), Mandai, Singapore, coll. P. K. L. Ng, 21 Feb. 1987; 2 ♂ (3.0 x 2.8 mm, 2.6 x 2.4 mm), 1 ♀ (4.3 × 3.5 mm) (ZRC 1987.335–337), Lim Chu Kang, Singapore, coll. P. K. L. Ng, 19 Mar. 1987; 1 ♀ (4.7 × 4.1 mm) (ZRC 1987.1181), Lim Chu Kang, Singapore, coll. S. Harminto, 30 Jul. 1987; 1 ♀ (ZRC 2002.611), Sungei Buloh Nature Reserve, Singapore, coll. P. K. L. Ng, Aug. 2002; 2 ♀ (ZRC 1993.486–487), Sungei Buloh Nature Reserve, Singapore, coll. D. Wee, 28 Jul. 1992; 2 ♂, 1 ovig. ♀, 1 ♀ (ZRC 1965.7.9.18–20), Johore Straits, coll. M. W. F. Tweedie, Oct. 1934; 1 ♀ (ZRC 1965.7.15.9), Muar, Johor, Peninsular Malaysia, coll. M. W. F. Tweedie, Feb. 1935; 5 ♂ (largest 4.6 × 3.8 mm), 11 ♀ (ZRC 1965.7.15.14–23), Mersing, Johor, Peninsular Malaysia, coll. M. W. F. Tweedie, Nov. 1938; 1 ♂, 1 ovig. ♀, 2 ♀ (ZRC 1965.7.15.10–13), Prai, Province Wellesley, Peninsular Malaysia, coll. M. W. F. Tweedie, Dec. 1938.

Diagnosis

Carapace hexagonal, dorsal surface not convex with regions well defined, covered with short stiff setae. Outer surface of chelipeds covered with short stiff setae; dactylar finger of adult male chela with prominent sub-basal tooth; distal parts of cutting margins of fingers spatuliform. Ambulatory legs with dorsal margin of P2 meri armed with 2 spines, those of P3 and P4 with 3 spines, that of P4 with 1 spine; outer surface with submarginal carina; outer surfaces of meri with numerous short

stiff setae; propodus and dactylus long, slender, unarmed. Male and female sternoabdominal cavity reaching to base of buccal cavity Male abdomen with somite 5 hour-glass shaped. G1 sinuous, slender, with several short and long spines distally.

Description of male

Carapace hexagonal, regions well defined, separated by broad depressions, prominently raised, peaks with tubercle (Figures 1, 2a, c, 3a, b); dorsal surface covered with very short black setae, denser near raised parts of regions (Figure 2a, c). Carapace margins, including front, lined with small, fine rounded granules (Figures 1, 2a, c, 3a, b). Front sinuous, weakly bilobed, each lobe rounded with broadly concave median depression; separated from low inner orbital tooth by shallow cleft, without fissure (Figures 1. 2a, c, 3a, b). Supraorbital margin sinuous, without cleft (Figures 1, 3a, b). External orbital tooth prominent, triangular, directed obliquely outwards (Figures 1, 3a, b). Anterolateral margin with 2 distinct triangular teeth, first tooth smaller than second tooth (Figures 1, 3a, b). Posterolateral margin sinuous, median part with low raised lobe on posterolateral region (Figures 1, 2a, c, 3a, b). Posterior carapace margin almost straight (Figures 1, 3a, b). Pterygostomial, subhepatic and suborbital regions smooth but covered with numerous short setae (Figure 3c). Suborbital margin distinctly sinuous, finely granulated, with 2 large, broad rounded lobes (Figure 3c). Orbits complete; eyestalk relatively short, stout; cornea large (Figure 3c). Basal antennal segment mobile, flagellum relatively short, only reaching to external orbital tooth (Figure 3c). Antennules folding obliquely (Figure 3c). Posterior margin of epistome with large triangular median lobe and a small triangular lobe on each side (Figure 3c). Buccal cavity wide, occupying most of face; third maxillipeds short, broad, without any gape when closed (Figures 3c, 5a); merus and

ischium almost squarish; merus larger than ischium, antero-external margin rounded; ischium without teeth or grooves; palp (carpus, propodus and dactylus) relatively short, inserted submedially on distal margin of merus; exopod long, reaching just beyond distal edge of merus, with long flagellum (Figure 5a).

Outer surfaces of cheliped segments covered with short, stiff setae; with very small granules (Figures 1b, d, 4e). Merus relatively short, with blunt subdistal angle on dorsal margin; distal part of ventral margin with denticulated margin. Carpus longer than broad with low inner angle. Chela with fingers shorter than palm; fingers with distal third of cutting margin spatuliform (Figure 4e), inside surface of distal third of fingers with numerous long plumose setae; dactylus with prominent subtruncate basal tooth, cutting edge lined with numerous denticles; fingers forming small gape when closed (Figure 4e).

Ambulatory legs inserted laterally on thorax, distinctly unequal in length; P2 shortest; P3 and P4 longest (Figures 2a, c, 4a-d). Coxa with outer margins denticulated; ventral surface of base of coxa without setae. Basis-ischium with distal margin finely granulated. Merus broadest medially; outer surfaces of meri finely granulated, with numerous short, stiff setae, with low but distinct subdorsal granulated ridge which spans proximal two-thirds length, not reaching distal margin; with distinct, blunt distal tooth on dorsal margin; dorsal and ventral margins lined with numerous low but outwardly directed granules; dorsal margin of P2 merus with 1 small submedian spine and 1 large subdistal spine, dorsal margins of P3 and P4 meri each with 3 prominent spines on distal two-thirds, dorsal margin of P5 merus with 1 small subdistal tooth. Carpus, propodus and dactylus smooth, glabrous; propodus longest; dactylus gently curved.

Thoracic sternum transversely broad; sternites 1-3 completely fused, just visible between bases of ischia of third maxillipeds; sternoabdominal cavity reaching to base of buccal cavity (Figure 2b); part of sterno-abdominal cavity covered by hour-glass like abdominal somite 4 exposed. Press button present as low rounded knob on distal edge of sternite 5. Male abdomen relatively slender, all somites and telson mobile; somite 1 mostly hidden under posterior edge of carapace; somite 2 transversely narrow; somites 1 and 2 not wider than somite 3, not reaching coxae of P5; somite 3 subrectangular with gently convex lateral margins; somite 4 trapezoidal, as long as somite 3; somite 5 hour-glass shaped with prominent median constriction which exposes sterno-abdominal cavity and G1 beneath; somite 6 trapezoidal, lateral margins gently concave; telson triangular in general shape but with median part of lateral margin prominently concave and edges convex, structure appears almost trilobite in form (Figure 5b). G1 slender, sinuous, S-shaped, distal part with several small and large spines; tip open (Figure 6a-d). G2 very short, tip without flagellum (Figure 6e).

Female characters. Females are similar to males but the chelipeds are relatively weaker, smaller; manus not inflated; fingers with sub-basal dactylar tooth smaller, spatuliform margin extending most of length. Abdomen rounded, with all somites and telson free, completely covering thoracic sternal surface, telson reaching base of buccal cavity; telson broad, tip gently rounded, margins sinuous; somites 1 and 2 very broad, longitudinally narrow, somite 2 with granulated median transverse ridge. Vulva simple, subovate, between thoracic sternites 5 and 6, submedian in position, without cover or ridges. Eggs small.

Remarks

Shen (1935) described *Camptandrium anomalum* on the basis of one male measuring 4.5 × 3.5 mm, and one female from Taipo, near Canton in southern China. The specimens were from muddy flats. The two type specimens in CAS were examined by N. K. Ng at our request. Both specimens are in an extremely poor condition, with only the carapace still present, and the male abdomen has been detached. The holotype male agrees well with Shen's (1935) original descriptions and figures.

Biology

The species is a wholly mangrove species and has been found outside this habitat. They prefer areas nearer the edge of the mangroves but only those that have substantial shade and are flooded only by the highest tides. They are often found under planks, wood or rafts of decaying vegetation, the substrate usually been sandy-mud. They are also not uncommon among the mangrove pneumatophores where the mud is soft and moist (see Ng et al., 2008b). Tweedie (1937: 162) commented that at Kranji mangroves in Singapore, numerous individuals can be found "… inhabiting burrows in soft mud …". They have been observed foraging during the day. Their movements on the mud are similar to those of grapsoids and camptandriids, with the carapace generally close to the ground. The dart about when disturbed but usually not moving very far. In life, they are always covered with mud that is trapped by the numerous short setae all over their carapace and pereopods. This makes them difficult to spot in the low light conditions of the covered mangrove forest.

Distribution

Shenius anomalus is known thus far only from southern China (type locality), Peninsular Malaysia and Singapore (Tweedie, 1937; Serène & Umali, 1972; Yang,

1979; Tan & Ng, 1994). It is almost certainly also found in mangroves in many other parts of Southeast Asia; but because of its small size and cryptic habitats, it is rarely encountered.

Shenius anomalus zoea I

(Figures 7–10)

Material examined Shenius anomalus: 1 ♀ (ZRC 1988.792), Mandai, Singapore, coll. P. K. L. Ng, 21 Feb. 1987, Z1 hatched 23 Feb. 1987; *Baruna trigranulum* (Dai & Song, 1986): 1 ♀ (ZRC 1988.791), Pandan mangroves, Singapore, coll. S. Harminto, 3 Oct. 1986, Z1 hatched 7 Oct. 1986; *Dotilla myctiroides* (H. Milne Edwards, 1852): 1 ♀ (ZRC 1988.789), Punggol Point, Singapore, coll. S. Harminto, 31 Oct. 1986, Z1 hatched 1 Nov. 1986.

Description

Carapace (Figure 7a, b): dorsal spine present; rostral spine present and much longer than antennal protopod and with distal spinulation; lateral spines absent; anterodorsal setae absent; 1 pair of posterodorsal setae; ventral margin without setae; eyes sessile.

Antennule (Figure 7c): uniramous, endopod absent; exopod unsegmented with 3 (1 broad, 2 slender) terminal aesthetascs of unequal length and 1 terminal seta.

Antenna (Figure 7d): long protopod with spinulation, shorter than rostral spine; endopod absent; exopod minute with 1 terminal seta.

Mandible: palp absent.

Maxillule (Figure 8a): epipod seta absent; coxal endite with 4 setae; basial endite with 5 setal processes and 2 small setal buds; endopod 2-segmented, proximal

segment without setae; distal segment with 4 terminal (subterminal setae absent); exopod seta absent.

Maxilla (Figure 8b): coxal endite not bilobed with 6 setae; basial endite bilobed with 5+4 setae; endopod bilobed, with 2+ 3 terminal (subterminal setae absent) setae; exopod (scaphognathite) margin with 4 setae and 1 long distal stout process.

First Maxilliped (Figure 9a): coxa with 1 seta; basis with 10 setae arranged 2,2,3,3; endopod 5-segmented with 2,2,1,2,5 (1 subterminal, 4 terminal) setae, respectively; exopod 2-segmented, distal segment with 4 long terminal plumose natatory setae.

Second Maxilliped (Figure 9b): coxa without setae; basis with 3 setae arranged 1,1,1; endopod 3-segmented, with 1,1,6 (3 subterminal, 3 terminal) setae, respectively; exopod 2-segmented, distal segment with 4 long terminal plumose natatory setae.

Third Maxilliped: absent.

Pereiopods: absent.

Abdomen (Figure 10a, b): 5 somites; somite 2 with 1 pair of dorsolateral processes directed anteriorly; somite 3 with 1 pair of dorsolateral processes directed ventrally; somites 1 and 2 each with rounded posterolateral processes and 3–5 each with short posterolateral spinous processes; somite 1 without setae; somites 2–5 each with 1 pair of posterodorsal setae and small spinules on posterior margin of somites 3–5; pleopod buds absent.

Telson (Figure 10a, b, c): each fork long, gradually curved distally, not spinulate with 1 lateral spine and 2 smaller dorsomedial spines; posterior margin with 3 pairs of stout spinulate setae.

Remarks

All the dorsal spines of the first stage zoeas examined for the present study were damaged as the original material is relatively old and not sufficiently well preserved. However, the authors had access to an old figure by Sundowo Harminto which illustrated the first stage zoea of *Shenius anomalus*. Although his larval illustration (figure 12a) lacks many details, it does figure the carapace spines. By using the scale bar provided by Harminto, the rostral spine measured ca. 0.52 mm and the dorsal ca. 0.25 mm. Therefore it appears that the rostral spine length is approximately twice that of the dorsal.

Brachyuran first stage zoeas of congeneric species appear to have identical setotaxy (Christiansen, 1973; Clark, 1983, 1984; Ng & Clark, 2000). This similarity provides a degree of predictability within a taxon. Conversely, setal differences (incongruence) within a group suggest incorrect assignment of taxa and lack of systematic compatibility. Consequently the first stage zoeal morphology described in the present study may provide addition information regarding the classification of *S. anomalus*.

Shenius anomalus was previously assigned to Macrophthalmidae Dana, 1851. However when comparing its zoea I morphology with that of a typical macrophthalmid such as *Macrophthalmus* (*Mareotis*) *depressus* Rüppell, 1830, as described by Rice (1975), several important differences can be observed: macrophthalmids possess a “spine” or “tooth” (Figure 11a) on the ventral margin of the carapace (vs. absent in *S. anomalus*, Figure 7a); the antennal exopod to propodus percentage (Figure 11b) is ca. 39% (vs. ca. 1% in *S. anomalus*, Figure 7d); the

antennal exopod is a spine (vs. exopod terminates as seta in *S. anomalus*, Figure 7d); the maxillule endopod has a setal formula of 1, 5 (one subterminal, 4 terminal) setae (vs. 0, 4 terminal setae in *S. anomalus*, Figure 8a); the bilobed endopod of the maxilla has 2+2 setae (vs. 2+3 setae in *S. anomalus*, Figure 8b); 9 setae on the basis of the first maxilliped arranged 2,2,3,2 (vs. 10 arranged 2,2,3,3 in *S. anomalus*, Figure 9a); 4 setae on the basis of the second maxilliped arranged 1,1,1,1 (vs. 3 arranged 1,1,1,0 in *S. anomalus*, Figure 8b); a telson without lateral spines (vs. 1 present in *S. anomalus*, Figure 10c) and the shape of the telson (Figure 11c) is straight (vs. medially with a waist in *S. anomalus*, Figure 10a, c). Moreover, these morphological incongruences between the first stage zoeal of *M.* (*M.*) *depressus* and *S. anomalus* indicate that assignment of the latter species to the Macrophthalmidae is not well supported (see Table 1).

Shenius anomalus has also been assigned to the Camptandriidae. This family can be represented by the first stage zoeas of *Baruna trigranulum* (Dai & Song, 1986), figured for the present study from the unpublished material of the present authors as part of an eventual larger study of the Ocypodoidea. There are a number of incongruent characters when the ZI morphology of the two species is compared: for example in *B. trigranulum* the dorsal carapace spine (Figure 11d) is absent (vs. present in *S. anomalus*, Figure 7a, b); a plumose seta is present of the ventral (Figure 11d) carapace margin (vs. absent in *S. anomalus*, Figure 7a); the antennal exopod to propodus percentage (Figure 11b) is ca. 42% (vs. ca. 1% in *S. anomalus*, Figure 7d), antennal exopod is distally spinulate (vs. not spinulate in *S. anomalus*); antennal exopod with 1 subterminal seta (vs 1 terminal seta in *S. anomalus*); abdominal somite 4 (Figure 11f) with 1 pair of lateral spines (vs. absent in *S. anomalus*, Figure 9a-b); fifth abdominal somite is distinctly wider than other somites and telson (vs. somite 5

is not distinctly wider in *S. anomalus*); in the furcal arms are "short" (vs. much longer in *S. anomalus*) and the shape of the telson (Figure 11f) is straight (vs. medially wasted in *S. anomalus*, Figure 10a, c). Although *B. trigranulum* and *S. anomalus* share the same setal formula for the maxillule endopod, the bilobed endopod of the maxilla, and the basial setation of the first and second maxillipeds; the larval differences cited here, especially the morphology of the antenna and abdomen, suggest that *S. anomalus* is not a camptandrid (Table 1).

Significantly, the general morphology of *S. anomalus* first stage zoea resemble those of the known larval stages of Dotillidae species including the setal formula of the maxillule and maxilla endopods, and the basial setation of the first and second maxillipeds. With respect to the zoeas of *Dotilla* Stimpson, 1858, the morphology of two species is known, namely that *D. blanfordi* Alcock, 1900, by Rajabai, 1958 (which maybe considered a little dated) and unpublished data on *D. myctiroides* (H. Milne Edwards, 1852) (Figure 12a-f). The antennal morphology of both these zoeas is more camptandrid-like in that the exopod is well developed (ca. 90% of protopod) with a subterminal seta, however the exopod is not distally spinulate. But with regard to the morphology of the abdomen, both first stage zoeas are similar to *S. anomalus* in that somite 5 is not broad and the telson is medially wasted. Furthermore, the first stage zoeal descriptions are available for other Dotillidae genera, *Ilyoplax pingi* Shen, 1932, by Jang et al. (1991), *Ilyoplax tansuensis* Sakai, 1935, by Ko & Kim (1991) and *Scopimera crabricauda* Alcock, 1900, by Rice (1976). The rostral spine is relatively long in all four species including *S. anomalus* compared with the other first stage zoeas examined for the present study. Moreover, the considered rostral spine/dorsal spine ratio of 2:1 for *S. anomalus* compares well with that of *I. pingi* (see Figure 13a). Carapace lateral spines are present in *I. pingi* and *S. crabricauda* (Figure 13a, g

respectively) but absent for *I. tansuensis* and *S. anomalus* (Figures 13d, 7a, b respectively). The antennal protopod morphology is similar for all four species including *S. anomalus* in being relatively long and spinulate for the distal three quarters. While absent in *S. crabricauda* (Figure 13h) the exopod is minute in the other three species, with one terminal seta in *I. tansuensis* and *S. anomalus* (Figures 13e, 7d) and two in *I. pingi* (Figure 13b) The telson appears to be elongated and wasted in all zoeas illustrated (Figures 13c, f, i, 10a, b). For the present study the first stage zoeas of *I. tansuensis* and *S. anomalus* are remarkably similar, but can be distinguished from *I. pingi* and *S. crabricauda*. The zoeas of the latter two species can be on the presence and absence of an antennal exopod respectively and the former processing two terminal exopod setae (Table 1).

In summary, the first stage zoea of *S. anomalus* appear to have more characters in common with the dotillids *I. tansuensis*, *I. pingi* and *S. crabricauda* than those of *D. blanfordi* and *D. myctiroides*, but there is enough support from zoeal morphology to suggest that *S. anomalus* be classified in the Dotillidae with perhaps assignment to its own subfamily emphasising the incongrences with the other dotillid genera.

Conclusion

While the male abdomen, G1 and first stage zoeal characters of *Shenius* places this genus within the Dotillidae as currently defined (Ng et al., 2008a), the carapace and ambulatory leg characters of *Shenius* are so atypical, that it cannot be suitably assigned with any of the known dotillid genera. Therefore a new subfamily, Sheniinae, it is established to accommodate *Shenius*. Unlike dotillines which have a more ovate and swollen carapace, with the ambulatory legs positioned more

vertically; sheniines have a flattened and more quadrate carapace, with the ambulatory legs positioned laterally.

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CAPTIONS

Figure 1. *Shenius anomalus* (Shen, 1935). a, holotype ♂ (4.5 × 3.5 mm) (CAS CB-02060a), China; b, paratype ♀ (3.8 × 2.9 mm) (CAS CB-02060b), China.

Figure 2. *Shenius anomalus* (Shen, 1935). a, b, ♂ (3.9 × 3.4 mm) (NHM 1937.11.15.132); c, d, ovigerous ♀ (5.6 × 4.7 mm) (NHM 1937.11.15.133). a, c, dorsal view; b, d, ventral views. Scale bar in mm.

Figure 3. *Shenius anomalus* (Shen, 1935). a, ♂ (4.6 × 3.8 mm) (ZRC 1965.7.15.14), Singapore; b, c, ♂ (4.1 × 3.6 mm) (ZRC 1965.7.15.15), Singapore. a, b, carapace showing details of dentition and regions (denuded); c, frontal view showing front, antennules, orbits and epistome.

Figure 4. *Shenius anomalus* (Shen, 1935), ♂ (4.1 × 3.6 mm) (ZRC 1965.7.15.15). a-d, left P2-P5, respectively; e, outer view of left chela.

Figure 5. *Shenius anomalus* (Shen, 1935), NHM, ex ZRC 1987.338–339; a. ♀ third maxilliped; b. ♂ abdomen somite 3–6 and telson.

Figure 6. *Shenius anomalus* (Shen, 1935), NHM, ex ZRC 1987.338–339; ♂; right first gonopod ventral view; a. entire; b. tip; dorsal view; c. tip; d. entire; right second gonopod ventral view; e. entire.

Figure 7. *Shenius anomalus* (Shen, 1935), zoea I; a. lateral view of carapace; b. anterior view of carapace; c. antennal; d. antenna.

Figure 8. *Shenius anomalus* (Shen, 1935), zoea I; a. maxillule; b. maxilla.

Figure 9. *Shenius anomalus* (Shen, 1935), zoea I; a. first maxilliped; b. second maxilliped.

Figure 10. *Shenius anomalus* (Shen, 1935), zoea I; a. dorsal view of abdomen; b. lateral view of abdomen; c. telson.

Figure 11. *Macrophthalmus* (*Mareotis*) *depressus* Rüppell, 1830; zoea I modified from Rice (1975); a. lateral view of carapace; b. antenna; c. dorsal view of abdomen; *Baruna trigranulum* (Dai & Song, 1986); zoea I; d. lateral view of carapace; e. antenna; f. dorsal view of abdomen.

Figure 12. Zoea I; *Dotilla blanfordi* Alcock, 1900 (modified from Rajabai, 1959); a. lateral view of carapace; b. antenna; c. dorsal view of abdomen; *D. myctiroides* (H. Milne Edwards, 1852); d. lateral view of carapace; e. antenna; f. dorsal view of abdomen.

Figure 13. Zoea I. Lateral view of carapace, antenna and dorsal view of abdomen. a-c. *Ilyoplax pingi* Shen, 1932; d-f. *Ilyoplax tansuensis* Sakai, 1935; g-i. *Scopimera crabricauda* Alcock, 1900 (after Jang et al., 1991; Ko & Kim, 1991; Rice, 1976, respectively).

Table 1. Mouthpart setation pattern and telson armature of the zoeal stages of the families Macrophthalmidae, Camptandriidae, Dotillidae and the species *Shenius anomalus*. Abbreviations: (–), absent; (+), present;

Species/character	Maxillule (endopod)	Maxilla (endopod)	First Maxilliped (basis)	Second Maxilliped (basis)	Telson spines
Macrophthalmidae	1,5	2,2	2,2,3,2	1,1,1,1	-
Camptandriidae	0,4	2,3	2,2,3,3	1,1,1,0	– / +
Dotillidae	0,4	2,3	2,2,3,3	1,1,1,0	– / +
Shenius anomalus	0,4	2,3	2,2,3,3	1,1,1,0	+