Proposal of new genus for Asterocheres mucronipes Stock, 1960 (Copepoda, Siphonostomatoida, Asterocheridae), an associate of the scleractinian coral Astroides calycularis (Pallas, 1766) in the Strait of Gibraltar

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A new genus of Asterocheridae (Copepoda: Siphonostomatoida) **Stockmyzon gen. nov.** is proposed for Asterocheres mucronipes Stock, 1960, and a new, previously misidentified, species **Stockmyzon crassus sp. nov.** from sponge washings in Mauritius. **Stockmyzon gen. nov.** can be differentiated from other asterocherid genera by the annulated mandibular stylet, the atrophied maxillulary palp with large modified lateral seta, the presence of beak-shaped processes on the endopods of legs 1, and the transformation of the outer spine on the first exopodal segment of leg 4 into a seta. **Stockmyzon mucronipes comb. nov.** is the fourth copepod known to utilize the hermatypic coral Astroides calycularis (Pallas, 1766) as its host in the Strait of Gibraltar. A reinterpretation of the original description of Asterocheres stimulans Giesbrecht, 1897 from Naples revealed that it was based on an amalgam of two diffent species, the male being conspecific with S. mucronipes; the illustrated female is formally designated here as the lectotype of A. stimulans. The current symbiotic relationship between S. mucronipes and the gorgonian Eunicella singularis (Esper, 1794) along the French mediterranean coast is reviewed in the light of potential host switching, following the extinction of A. calycularis in the north-western Mediterranean, north of 40°N, during the late Sicilian regression (Rissian age), about 238 000–225 000 years ago. © 2008 The Linnean Society of London, Zoological Journal of the Linnean Society, 2008, **152**, 635–653.

ADDITIONAL KEYWORDS: glaciation - scanning electron microscopy - Scleractinia - symbiosis - taxonomy.

INTRODUCTION

Siphonostomatoid copepods are almost exclusively symbiotic, and utilize a wide range of invertebrate and vertebrate hosts all around the world (Gotto, 1979; Ho, 1982; Humes, 1993; Humes, 1996; Ivanenko & Smurov, 1997; Kim, 1998; Boxshall & Halsey, 2004). Those that live as external or internal symbionts of marine invertebrates primarily utilize sponges, cnidarians, echinoderms, bryozoans, molluscs, and ascidians, but for many members of the families Asterocheridae and Artotrogidae the hosts are still unknown. Substantial gaps remain in our knowledge of symbiotic copepods, even in areas where marine invertebrates have been the subject of comprehensive investigation. For example, in European waters siphonostomatoids are most commonly reported from sponges, but documented associations with scleractinian corals are scarce. This conceivably reflects sampling bias rather than host-phylum preference. Five years ago, an ongoing programme on the biology of the hermatypic scleractinian *Astroides calycularis* (Pallas, 1766) was initiated around Tarifa Island (Strait of Gibraltar), where it represents the most important macrobenthic organism in shallow waters. Although there were no previous records of

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copepods inhabiting A. calycularis, this coral species turned out to be the host of a variety of symbiotic copepods, reinforcing Humes's (1994) hypothesis that virtually any marine macroinvertebrate is a potential host to copepods. Recently, Conradi, Bandera & López-González (2006) described two new species, Doridicola helmuti (Rhynchomolgidae) and Asterocheres astroidicola (Asterocheridae), and listed the first record of Acontiophorus scutatus (Brady & Robertson, 1873) from this coral host. Here, we describe another new asterocherid that exhibits similarities with members of the genus Asterocheres, but also displays some important differences. Comparison of the nearly 70 species currently assigned to the genus revealed that one species. Asterocheres mucronipes Stock, 1960, was morphologically very similar to the specimens recovered from the Astroides colonies. Stock's (1960) description was based on four females obtained from washings of the gorgonian Eunicella verrucosa (Pallas, 1766), found at a depth of 30 m near Cap Béar along the French mediterranean coast (Roussillon). In a later paper, Stock (1966) emended the description based on 19 females in washings of an orange sponge, possibly a species of Oscarella Vosmaer, 1884, from Mauritius, Stock (1966) also corrected the identification of the Roussillon host to Eunicella stricta (Bertoloni, 1810), but the latter is now generally regarded as a junior synonym of the white seafan *Eunicella singularis* (Esper, 1794) (cf. Weinberg, 1976, 1978). A re-examination of Stock's (1960) type material of Asterocheres mucronipes in the Zoological Museum of Amsterdam proved that the specimens from Tarifa were conspecific with the Roussillon population. Contrary to Stock's (1966) opinion, the material from Mauritius differed significantly from both Mediterranean populations, justifying the proposal of a new species. In this paper we establish a new genus, Stockmyzon, to accommodate the type species Stockmyzon mucronipes (Stock, 1960) comb. nov., and a new species Stockmyzon crassus sp. nov. is proposed for Stock's (1966) specimens from Mauritius; detailed descriptions of both species are presented.

MATERIAL AND METHODS

Colonies of *A. calycularis* were individually collected by SCUBA diving at Tarifa Island, and were immediately isolated in separate plastic bags containing a solution of 8-10% formaldehyde in seawater. Symbiotic fauna was obtained by pouring the wash water through a 100-µm net. Copepods were extracted from the filtrate and preserved in 70% ethanol.

Selected specimens were dissected in lactic acid and examined as temporary mounts in lactophenol. For scanning electron microscopy, a specimen of each species was dehydrated in a graded series of ethanol, critical-point dried, mounted on stubs, coated with a gold-palladium alloy, and examined in a Phillips XL30 SEM. All figures were drawn with the aid of a camera lucida mounted on a Zeiss Axioskop differential interference contrast microscope. All appendage segments and setation elements are named and numbered using the terminology introduced by Huys & Boxshall (1991).

Material from Tarifa was deposited in the Zoological Museum of Amsterdam (ZMA), and in the collection of the research team Biodiversidad y Ecología de Invertebrados Marinos of the University of Seville (BEIM).

SYSTEMATICS

Order Siphonostomatoida Burmeister, 1835 Family Asterocheridae Giesbrecht, 1899 Genus **Stockmyzon gen. nov.**

Diagnosis: Asterocheridae. Body: cyclopiform, comprising dorsoventrally flattened prosome and cylindrical urosome. Siphon of medium size, reaching to or slightly beyond rear margin of cephalothorax. Sexual dimorphism present in prosome width, urosomal segmentation, antennules, maxillipeds, and leg 6.

Urosome: four-segmented in female; five-segmented in male. Antennule: 20-segmented in female, with large aesthetasc on segment 18; 18-segmented in male, with large aesthetasc on segment 17 and geniculation located between segments 16 and 17. Antenna: with large one-segmented exopod and threesegmented endopod with terminal claw. Mandibular palp: two-segmented, second segment with two plumose setae; stylet with annulation in middle part and denticulate margin subapically. Maxillule: bilobed, with a rectangular praecoxal endite, and atrophied palp bearing large characteristically plumose seta and two or three accessory setae. Maxilla: two-segmented, with aesthetasc-like tubular extension on praecoxal portion of syncoxa, and a claw-like basis recurved towards the apex. Maxilliped: comprising short syncoxa, long basis, and threesegmented endopod; male basis with spinous process close to syncoxa-basis joint. Legs 1-4: biramous with three-segmented rami; middle and distal endopodal segments with beak-shaped spiniform processes. Outer element on proximal exopodal segment of leg 4: setiform. Leg 5: with protopod incorporated into somite (represented by dorsal surface seta) and onesegmented exopod bearing three setae.

Etymology: The genus is named in honour of the late Prof. Jan Hendrik Stock (Zoölogisch Museum, Amsterdam) who described its type species. The

Greek suffix *-myzon* ($\mu\nu\zeta\omega$), meaning to suck, is commonly used in the formation of siphonostomatoid generic names, and refers to the sucking oral cone or siphon. Gender: male.

Type species: Asterocheres mucronipes Stock, 1960 = Stockmyzon mucronipes (Stock, 1960) comb. nov.

Other species: Stockmyzon crassus sp. nov.

Remarks

Stock (1960) placed his new species A. mucronipes in Asterocheres, but expressed some reservations about his generic assignment. Although he recognized a superficial similarity in the enlarged prosome with some other Asterocheres species, such as Asterocheres lilljeborgi Boeck, 1859 and Asterocheres ovalis Sewell, 1949, certain other characters exhibited by A. mucronipes were considered more significant and potentially of 'valeur générique'. In particular, Stock (1960) mentioned the characteristic endopodal spinous processes on legs 1-4, the unusual armature of leg 4 (proximal exopod segment with outer seta), the 'biarticulated' mandibular stylet, and the presence of only two setae (instead of four) on the maxillulary palp, one of which being enlarged ('aspect gonflé'). Stock also noted that the male of Asterocheres stimulans Giesbrecht, 1897 has similar spinous processes on legs 1-4 (Giesbrecht, 1899: plate 3). He also claimed that the maxillulary palp of Asterocheres canui Giesbrecht, 1897 [= A. lilljeborgi sensu Canu (1892); cf. Giesbrecht (1897): 11)] displays a transitionary state, between the typical Asterocheres condition and that in A. mucronipes, having retained the typical number of four terminal setae, with one of them being gonflate. Based on these observations, Stock (1960) maintained a tentative assignment of A. mucronipes to Asterocheres was warranted. However, our reinterpretation of Giesbrecht's (1899) illustrations of male A. stimulans revealed that it is conspecific with A. mucronipes (see the Discussion), and comparison of Canu's (1892) figure of the maxillule showed it to be quite different from the A. mucronipes condition, but remarkably similar to that of other typical Asterocheres species, such as Asterocheres reginae Boxshall & Huys, 1994 (Boxshall & Huys, 1994: fig. 3F). The palp in A. canui is not atrophied, and the lateral seta is not enlarged, excessively plumose, or typically recurved and concealed under the gnathobasal endite, as it is in A. mucronipes.

Although *A. mucronipes* resembles species of *Asterocheres* in several aspects, such as the long, multisegmented antennule, the antenna with one-segmented exopod and three-segmented endopod, the segmentation of the maxilla and maxilliped, and the

one-segmented leg 5 bearing three setae, it differs in a number of characters, warranting the proposal of a new genus.

The mandible of *Stockmyzon* has a two-segmented palp, which is shared by over two-thirds of the species of *Asterocheres*; however, none of these exhibits the distinctly annulated stylet. This character is regarded here as an autapomorphy of the new genus. In some asterocherids the mandibular stylet shows a thinning of the cuticle halfway along its length, but never a strong annulation. Johnsson (1998) illustrated a long 'segmented' stylet in his description of *Asterocheres crenulatus* Johnsson, 1998, but a re-examination of a female paratype (NHM reg. no. 1997.185) revealed this to be an observational error, possibly as a result of excessive squashing during the mounting process.

The bilobate maxillule of *Stockmyzon* is unique in its marked size disparity between the outer (palp) and the inner lobe (gnathobase). The palp is atrophied and has two or three small setae, in addition to a large, densely plumose lateral seta. Furthermore, within the Asterocheridae a somewhat similar condition is only found in *Acontiophorus* Brady, 1880 (e.g. Kim & Je, 2000), but this genus represents a completely different lineage in the family, deviating from all others in the morphology of the antennule, antenna, and mandible. The primitive leg 5 and swimming leg armature formula also indicate a very basal position in the Asterocheridae.

The spine and seta formula of the swimming legs in the new genus is similar to that of Asterocheres, except for leg 4, which has an outer seta on the first exopodal segment in *Stockmyzon*, instead of an outer spine. The transformation of this element into a seta is a unique apomorphy within the Asterocheridae. A similar transformation on the basis of leg 1 (seta replaced by spine) in *A. crenulatus* and *Asterocheres spinopaulos* Johnsson, 1998 [and three other species described by Johnsson (1998)] was recently considered potential justification for their removal to a distinct genus (Kim, 2004b).

Perhaps the most conspicuous feature of *Stock-myzon* is the presence of large beak-shaped spiniform processes on the endopodal segments of legs 1–4. This character has been recorded in some genera previously allocated to the Coralliomyzontidae (e.g. Humes & <u>Stock, 1991; Humes, 1997)</u>, which coincidently also utilize scleractinian corals as hosts. Within the speciose genus *Asterocheres*, currently encompassing 67 valid species (Kim, 2004a, b, 2005; Bandera, Conradi & López-González, 2005; Bispo, Johnsson & Neves, 2006; Conradi *et al.*, 2006), only *Asterocheres tubiporae* Kim, 2004 exhibits similar modifications on leg 1. In every other aspect this species is a typical representative of the genus *Asterocheres*, and consequently the spinous processes on the leg-1 endopod are likely

to have resulted from convergence. Also note that Kim (2004b) erroneously described and illustrated the female antennule of *A. tubiporae* as 22-segmented; no other extant siphonostomatoid has more than 21 segments. Comparison with *A. reginae* (Boxshall & Huys, 1994: fig. 3A–E) suggests Kim (2004b) had inadvertently intercalated a supernumerary segment between the spine-bearing segment XIV and the aesthetasc-bearing segment XXI.

Stockmyzon is related to a group of genera that exhibit a tubular extension of the opening of the maxillary gland. Although some reports have suggested that this character may be widely distributed within the Asterocheridae (Boxshall & Huys, 1994), it has thus far been found only in Asterocheres (e.g. Ho, 1984; Boxshall & Huys, 1994; Ivanenko & Smurov, 1997; Ivanenko, 1997; Kim, 2004a, b), Inermocheres Boxshall, 1990 and Sinopontius Boxshall, 1990 (Boxshall, 1990), Dermatomyzon Claus, 1889 (Ivanenko & Ferrari, 2003), and, to a lesser extent, Laperocheres Ivanenko, 1998.

STOCKMYZON MUCRONIPES (STOCK, 1960) COMB. NOV.

Synonyms: Asterocheres mucronipes Stock, 1960; Asterocheres stimulans Giesbrecht, 1897 (\bigcirc only; see the Discussion).

Original description: Stock (1960: 224-228, figs 4, 5).

Type locality: France, Roussillon; off Cap Béar (near Banyuls-sur-Mer); washings of *E. singularis* collected at a depth of 30 m.

Material examined: (a) Holotype female and one paratype female (deposited in ZMA) from type locality; collected by J.H. Stock, 17 June 1959; (b) five females and nine males (deposited in ZMA) associated with *A. calycularis* off Tarifa Island (southern Spain) at a depth of 10–20 m; collected September 1999, by SCUBA diving; (c) additional specimens from Tarifa Island deposited in BEIM.

Description

Female: Body (Fig. 1A–B): cyclopiform, consisting of dorsoventrally flattened prosome and cylindrical urosome. Total length from anterior margin of rostrum to posterior margin of caudal rami, 603μ m; maximum width, 465μ m measured at 4/5 length of cephalothorax. Prosome: comprising cephalothorax (fully incorporating first pedigerous somite) and three free pedigerous somites. Cephalothorax (Fig. 1B) with posterolateral angles produced into backwardly directed processes. Rostrum completely fused to cephalothorax, forming triangular ventrally deflected

lobe. Somites bearing legs 2–3, broad; epimeral areas with posterolateral angles rounded (leg 2) or pointed (leg 3) (Fig. 1B). Somite bearing leg 4: much smaller and narrower than preceding ones. Dorsal cephalothoracic shield and free pedigerous somites ornamented with numerous integumental pores and sensilla.

Urosome: four-segmented, comprising leg-5-bearing somite, genital double somite, and two free abdominal somites. Except for leg-5-bearing somite, all other urosomites ornamented with large, flattened epicuticular scales, arranged in irregular overlapping pattern dorsally (Fig. 1D) and ventrally (not shown in Fig. 1C); scales occasionally with incised distal margin. Posterior hvaline frills of urosomites with serrate free margins (Fig. 1C). Leg-5-bearing somite: narrow, largely concealed under pleurotergite of leg-4-bearing somite. Genital double somite (Fig. 1C-D): laterally produced; about 1.65 times wider than long; paired genital apertures bipartite, each comprising lateroventral copulatory pore and dorsolateral gonopore (oviduct opening); lateral margins with setular tufts in distal third (posterior to genital apertures).

Caudal rami (Fig. 1C–D): about as long as wide (measured along outer margin); trapezoid with inner margin much shorter than outer one; entirely covered by overlapping epicuticular scales; armed with six setae; seta I absent, setae II–VII all arranged around posterior margin, with setae II and VII slightly displaced onto dorsal surface.

(Fig. 1E–G): 20-segmented, Antennule about 250-µm long, lengths of segments (measured along posterior nonsetiferous margin) 16 (30-µm along anterior margin), 7, 8, 8, 7, 7, 6, 11, 11, 1, 7, 13, 16, 14, 14, 13, 13, 13, 8, and 14 µm, respectively. Segmental fusion pattern as follows (Roman numerals indicating ancestral segments): 1(I), 2(II), 3(III), 4(IV), 5(V), 6(VI), 7(VII), 8(VIII), 9(IX-XII), 10(XIII), 11(XIV), 12(XV), 13(XVI), 14(XVII), 15(XVIII), 16(XIX), 17(XX), 18(XXI), 19(XXII-XXIII), 20(XXIV-XXVIII). Segments 1-8, each with two setae, one of which is plumose; segment 9, with seven setae and a small spine; segments 10-11, each with one seta and one small spine at anterodistal corner; segments 12-17, each with two setae; segment 18, with two setae plus an aesthetasc; segment 19, with one anterior, one ventral, and one posterior seta; segment 20, with ten setae (Fig. 1G). Segment 10(XIII): reduced, forming incomplete sclerite, partly overlapped by distal expansion of compound segment 9(IX-XII) (Fig. 1F).

Antenna (Fig. 2A–B): biramous. Coxa unarmed, with few spinules. Basis unarmed, with fine spinule rows as shown in Figure 2A. Exopod: one-segmented, slender, about 2/5 length of proximal endopod segment; with one small lateral seta and two terminal setae. Endopod: three-segmented; proximal segment



Figure 1. *Stockmyzon mucronipes* (Stock, 1960) **comb. nov.** (female). A, habitus, dorsal; B, habitus, lateral; C, urosome (excluding leg-5-bearing somite), ventral; D, urosome, dorsal; E, antennule, ventral; F, detail of antennulary segments IX–XII, XIII, and XIV; G, detail of antennulary segments XXI, XXII–XXIII, and XXIV–XXVIII.

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Figure 2. *Stockmyzon mucronipes* (Stock, 1960) comb. nov. (female). A, antenna; B, detail of second and third endopodal segments of antenna; C, mandible; D, maxillule, dorsal (posterior); E, detail of praecoxal gnathobase of maxillule, dorsal (posterior); F, maxilla; G, maxilliped.

elongated, ornamented with lateral and distal rows of fine spinules, as illustrated; middle segment produced distally on medial side, but articulating with distal segment proximally on lateral side (Fig. 2B), bearing one distal seta; distal segment with large distal claw, one well-developed pinnate seta, and two short, smooth setae; outer margin of distal segment with few coarse spinules and surface with long setules. Siphon (Figs 3B, D): long and slender, reaching nearly to the posterior margin of the intercoxal sclerite of leg 2 (Fig. 1B).

Mandible (Fig. 2C): comprising stylet-like gnathobase and slender two-segmented palp. Proximal segment of palp: longest, ornamented with rows of spinules; distal segment minute, with two plumose, unequal apical setae. Stylet located in oral cone, formed by anterior labrum and posterior labium (Fig. 3D). Stylet: with annulation (not a genuine articulation) at about halfway along its length; basal part relatively more chitinized, distal part flexible with denticulate margin subapically (Fig. 3D).

Maxillule (Figs 2D–E, 3E): bilobed; praecoxal gnathobase (inner lobe) distinctly larger than palp (outer lobe). Praecoxal endite: rectangular, ornamented with long setules proximally and spinules distally on the lateral margin, and with a row of long setules medially (Fig. 2E); armed with one short and four long but unequal setae, latter ornamented with short spinules proximally and setules distally. Palp strongly reduced, atrophied, with one elongate strongly plumose (Fig. 3E) and three shorter pinnate setae.

Maxilla (Fig. 2F): two-segmented, but with partial transverse surface suture on syncoxa (proximal segment), possibly marking the plane of the praecoxacoxa fusion; praecoxal portion bearing flaccid aesthetasc-like element medially, representing tubular extension of external opening of maxillary gland; coxal portion unarmed, but ornamented with a row of spinules medially. Basis: claw-like, more or less straight, but recurved towards the apex; armed with two vestigial setae in middle third; distal inner margin of claw provided with a double row of minute spinules.

Maxilliped (Figs 2G, 4C): five-segmented, comprising short syncoxa, long basis, and three-segmented endopod. Syncoxa: with one short seta distally. Basis: with a row of spinules on distal outer margin. First endopodal segment: bearing two short distal setae; second endopodal segment compound, partial suture marking original separation of two ancestral segments, with (0,1) armature formula; third endopodal segment bearing recurved terminal claw plus additional apical seta. Distal margin of claw provided with rows of minute spinules; apex with pore (Fig. 4C).

Swimming legs 1–4 (Fig. 5A–D): biramous, with three-segmented protopods (praecoxa not shown in Fig. 5A–D, but see Fig. 4A for complete protopod) and three-segmented rami. Intercoxal sclerite present in legs 1–4, ornamented with patches of spinules in legs 1–2.

See Table 1 for the spine and seta formula.

Coxae ornamented with spinule rows around outer margin; inner coxal sets short and bare in leg 1, long and plumose in legs 2–3, and absent in leg 4. Bases of P1–P3: with spinules around inner margin; outer seta

Table 1. Spine and seta formula of Stockmyzonmucronipes (Stock, 1960) comb. nov.

	Coxa	Basis	Exopod	Endopod
Leg 1	0-1	1-1	I-1; I-1; III,2,2	0-1; 0-2; 1,2,3
Leg 2	0-1	1-0	I-1; I-1; III,I+1,3	0-1; 0-2; 1,2,3
Leg 3	0-1	1-0	I-1; I-1; III,I+1,3	0-1; 0-2; 1,1+I,3
Leg 4	0-0	1-0	1–1; I-1; III,I+1,3	0-1; 0-2; 1,1+I,2

plumose in leg 2, but smooth in other legs, and extremely long in leg 1. Outer spines of exopodal segments in legs 2–4 bilaterally serrate; in leg 1, smooth with subapical tubular extension. Lateral margins of exopodal segments: with minute serrations or spinular rows; those of endopodal segments with rows of setules. Middle and distal endopodal segments in legs 1–4: with a beak-shaped spiniform process distally (Fig. 4B). Outer element on proximal exopodal segment of leg 4: setiform instead of spiniform (as in legs 1–3).

Fifth leg (Fig. 1D): with protopod incorporated into somite; outer basal seta displaced to laterodorsal surface. Free segment (exopod): elongate-oval, with three smooth setae distally; outer and inner margins with spinules.

Sixth leg represented by paired opercular plates closing off gonopores on genital double somite; each armed with one plumose seta and one spiniform element.

Male: Mean body length, 463 μ m (450–480 μ m), and greatest width, 323 μ m (320–430 μ m) (N = 3). Sexual dimorphism present in prosome width, urosomal segmentation, antennules, maxillipeds, and leg 6. Prosome (Fig. 6A): broader than in female, about 1.05 times wider than long. Urosome (Fig. 6B): five-segmented, comprising leg-5-bearing somite, genital somite, and three free abdominal somites. Dorsal surface of genital somite, and dorsal and ventral surfaces of free abdominal somites, ornamented with large, epicuticular scales arranged in an irregular overlapping pattern; scales occasionally with serrate distal margin. Posterior margin of urosomites: ornamented with hyaline frills with serrate free margins. Genital somite about 1.4 times wider than long.

Antennule (Figs 3C, 6D–F): 18-segmented, geniculate with geniculation positioned between segments 16(XIX–XX) and 17(XXI–XXIII). Segmental fusion pattern as follows (Roman numerals indicating ancestral segments): 1(I), 2(II), 3(III), 4(IV), 5(V), 6(VI), 7(VII), 8(VIII), 9(IX–XII), 10(XIII), 11(XIV), 12(XV), 13(XVI), 14(XVII), 15(XVIII), 16(XIX–XX), 17(XXI–XXIII), 18(XXIV–XXVIII). Segments 1–8, each with two setae; segment 9, with eight setae; segment 10,



Figure 3. *Stockmyzon mucronipes* (Stock, 1960) **comb. nov.** SEM micrographs. A, rostral area (female); B, oral cone (female); C, antennulary segments XVIII and XIX–XX (male); D, apical part of labrum and stylet-like gnathobases of mandibles (female); E, large plumose seta on maxillulary palp (female).



Figure 4. *Stockmyzon mucronipes* (Stock, 1960) **comb. nov.** SEM micrographs (female). A, protopodal segmentation of leg 1, anterior; B, spinous process on proximal endopod segment of leg 4; C, tip of maxillipedal claw.

with one seta and one small spine; segments 11–15, each with two setae; segment 16, with four setae; segment 17, with three setae plus an aesthetasc; segment 18 with nine setae. Segment 10 reduced, partly covered by distal expansion of compound segment 9 (Fig. 6E). Proximal seta on ancestral segments XVIII– XX: rudimentary (Figs 3C, 6D).

Maxilliped (Fig. 6C): indistinctly six-segmented; comprising short syncoxa, long basis, and indistinctly four-segmented endopod. Syncoxa with one short seta distally, incompletely separated from basis. Basis: with one small tooth-like process along medial margin near syncoxa-basis joint; with spinules along outer margin. First endopodal segment not completely separated from basis; with two setae and a few spinules near the distal margin. Second endopodal segment: with one terminal seta. Third endopodal segment: compound, showing membranous insert marking plane of fusion between ancestral segments 3–4; with recurved terminal claw plus short accessory apical seta.

Fifth legs (Fig. 6B): not markedly different from those of female.

Sixth legs (Fig. 6B): represented by opercula closing off genital apertures; each with two smooth setae.

Remarks

Comparison with Stock's (1960) text and illustrations revealed a number of discrepancies, which may be attributed to imperfect dissection and/or observation: (1) Stock (1960) described the female antennule as 19-segmented and stated that segments 18–19 were indistinctly separated; re-examination showed that the minute tenth segment (XIII) was overlooked by Stock, and that the terminal segments are divided by a clear articulation; (2) the antennary exopod has not two, but three elements; Stock missed the lateral exopodal seta, as well as the two smaller setae on the distal endopod segment; (3) the mandibular palp is not indistinctly two-segmented, as stated by Stock; (4) Stock's illustration of the maxillule shows four terminal setae on the praecoxal endite (the shorter one was overlooked), and only two instead of four on the palp; (5) the maxilla has an aesthetasc-like extension on the proximal part of the syncoxa, which was not illustrated by Stock [nor in any other asterocherid descriptions prior to Ho (1984); cf. Asterocheres aesthetes Ho, 1984); (6) Stock described and illustrated the maxillipedal endopod as distinctly threesegmented, but his segment boundaries do not coincide with the pattern we observed - his proximal segment is a composite of the genuine first segment and the proximal half of the middle segment (compare Fig. 2G), whereas his middle segment corresponds to only the distal half of that segment - this reinterpretation explains the difference between our endopodal setal formula [2, (0,1), 1+claw] and Stock's [1, 1, 1]1+claw]; (7) Stock overlooked the inner basal seta on P1, and erroneously illustrated the outer basal seta as plumose; (8) the epicuticular scales on the urosomited were not illustrated in Stock's description.

Slight morphological variations occur between the Tarifa specimens and the Roussillon population. In



Figure 5. *Stockmyzon mucronipes* (Stock, 1960) **comb. nov.** (female). A, leg 3, anterior; B, leg 4, anterior; C, leg 2, anterior; D, leg 1, anterior.



Figure 6. *Stockmyzon mucronipes* (Stock, 1960) **comb. nov.** (male). A, habitus, dorsal; B, urosome, ventral; C, maxilliped; D, antennule; E, detail of antennulary segments VIII, IX–XII, XIII, XIV, and XV; F, detail of antennulary segments XX–XXII and XXIII–XXVIII.

the Roussillon population: (1) the oral cone is slightly shorter, reaching only as far as the bases of leg 1; (2) the proximal outer process on the middle endopod segment of leg 1 is markedly shorter, whereas the apical process and outer seta on the distal endopod segment are distinctly longer; (3) the apical spine and seta on the distal endopod segment of leg 3 are longer than the segment (but shorter in the Tarifa population); (4) the caudal rami are slightly longer; and (5) the body length is smaller (551–589 μ m).

STOCKMYZON CRASSUS SP. NOV.

Synonym: Asterocheres mucronipes Stock, 1960 sensu Stock (1966).

Original description: Stock (1966: 146-147, fig. 1a-c).

Type locality: Mauritius, Chenal du Trou d'Eau Douce; associated with "small flabby orange sponges", without skeleton (*Oscarella* sp.), in small "grottos" in the reef at 6–10 m depth'.

Material examined: Holotype female and 16 paratype females (originally identified as *A. mucronipes*) (ZMA Co. 100.955) from type locality; collected by J.H. Stock, 7 February 1964.

Description: Restricted to differences with the type species.

Female: Body (Fig. 7A): cyclopiform, consisting of dorsoventrally flattened prosome and cylindrical urosome. Total length measured from rostral margin to posterior margin of caudal rami, 652 µm [564–664, N = 6 according to Stock (1966)]; maximum width, 440 µm measured at 4/5 length of cephalothorax. Ratio of length to width of prosome: 1.08 : 1. Ratio of length of prosome to that of urosome: 2.5 : 1. Genital double somite and free abdominal somites: covered with large epicuticular scales arranged in an overlapping pattern (Fig. 8E); scales larger than in S. mucronipes. Somite bearing leg 5 (Fig. 7B): wider than long, with some spinules around bases of outer basal setae. Genital double somite (Fig. 7B-C): narrower and less laterally produced than in S. mucronipes, about 1.2 times wider than long; with lateral postgenital setular tufts.

Caudal rami (Figs 7B–C, 8E): slightly longer than wide (measured along outer margin), ornamented with epicuticular scales all over. Caudal setae IV–V: distinctly swollen in proximal half.

Antennule (Fig. 7D): 20-segmented, about $312-\mu m$ long; segmental fusion pattern as in *S. mucronipes*. Segments 1–8, each with two setae; segment 9, with six setae and a small spine; segment 10, with two

setae; segment 11, with one seta and one small spine; segments 12–17, each with two setae; segment 18, with two setae plus an aesthetasc; segment 19, with three setae; segment 20, with nine setae. Segment 10(XIII), reduced, forming incomplete sclerite partly overlapped by distal expansion of compound segment 9(IX–XII). All setae smooth.

Antenna (Fig. 7E): biramous, 186-µm long. Coxa and basis: without spinule rows. Exopod: as in *S. mucronipes*. Endopod: three-segmented; proximal segment with spinular ornamentation as illustrated; middle segment with one smooth seta; distal segment with one naked seta and one distal claw, and with few spinules along margin and long setules on anterior surface.

Siphon (Fig. 8A): long and slender, reaching to intercoxal sclerite of leg 1.

Mandible (Fig. 9A): comprising stylet-like gnathobase and slender two-segmented palp. Proximal segment of palp unarmed; distal segment with two plumose, unequally long, apical setae. Stylet: as in *S. mucronipes*.

Maxillule (Figs 8C, 9B): bilobed. Praecoxal gnathobase four times longer than palp; ornamented with a row of long spinules distally, and a row of shorter spinules laterally; armed with five distal setae (one of them smooth and short). Palp strongly reduced; with one elongate, strongly plumose seta, and two short pinnate setae.

Maxilla (Figs 8B, 9C): essentially as in *S. mucronipes*, but coxal part of syncoxa without surface spinule row. Vestigial element on claw-like basis: not discernible.

Maxilliped (Fig. 9D): as in *S. mucronipes*, but basis and endopod relatively more slender; endopod segments 1–2 separated by suture on anterior side only.

Swimming legs 1–4 (Figs 8D, 10A–D): intercoxal sclerite present in legs 1-4, ornamented with patches of spinules in legs 1–3. Spine and seta formula: as for S. mucronipes. Coxae ornamented with spinule rows laterally, as illustrated. Middle and distal endopodal segments in legs 1-4: with a beak-shaped spiniform process distally (e.g. Fig. 8D). Leg 1 differs from that of S. mucronipes in the following characteristics: outer basal seta shorter; inner coxal seta pinnate instead of bare; proximal outer spinous process on middle endopod segment shorter; outer seta of distal endopod segment extending just beyond distal spinous process. Legs-2-3 inner coxal seta and outer basal seta: much shorter than in S. mucronipes. Proximal inner seta of middle endopod segment of leg 4: much longer than in S. mucronipes and approaching the length of the distal inner seta.

Fifth leg (Fig. 7B): as in *S. mucronipes* except for lateral exopodal seta being distinctly shorter. Sixth legs (Fig. 7B): represented by paired opercular plates



Figure 7. *Stockmyzon crassus* (Stock, 1966) **sp. nov.** (female). A, habitus, dorsal; B, urosome, dorsal; C, urosome (excluding leg-5-bearing somite), ventral; D, antennule, ventral; E, antenna.

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Figure 8. *Stockmyzon crassus* (Stock, 1966) sp. nov. SEM micrographs (female). A, oral cone; B, maxilla; C, maxillary palp; D, P4 endopod, anterior; E, surface scales on urosomites, ventral.

closing off gonopores on genital double somite; armed with one short, smooth seta, and one spiniform element.

Male: Unknown.

Etymology: The specific name is derived from the Latin *crassus*, meaning thick, and refers to the swollen caudal setae.

Remarks

Stock's (1966) redescription of *A. mucronipes* from Mauritian sponges is concise and limited to illustrations of the urosome, leg 4, and the maxillule. Stock confirmed several similarities with the Mediterranean type population, such as the annulated structure of the mandibular stylet and the presence of beak-shaped processes on the swimming legs; however, he also claimed that the maxillule differed slightly in the shape of the 'outer ramus' or palp, being gonflate basally, and distinctly narrower distally (Stock (1966: fig. 1b). This could not be confirmed in the Mauritian material or in the types of S. mucronipes (Stock doubted his original observation) (Figs 2D, 9B); instead, our re-examination revealed that Stock (1966) had overlooked a seta on both the maxillulary endite and palp. His illustration of leg 4 also shows minor discrepancies with our Figure 10D, such as proportional length differences in the outer seta of the proximal exopodal segment and the inner proximal seta of the middle endopodal segment, and the apparent slenderness of the outer



Figure 9. Stockmyzon crassus (Stock, 1966) sp. nov. (female). A, mandible; B, maxillule; C, maxilla; D, maxilliped, posterior.

exopodal spines (as a result of omitting the membranous flanges). Stock (1966) illustrated the swollen caudal ramus setae IV–V, but did not remark on this character in the text.

DISCUSSION

SPECIES DISCRIMINATION

Stockmyzon mucronipes and S. crassus are morphologically very similar in most aspects, but the latter can be distinguished from the former by the following suite of characters: (1) epicuticular scales on genital double somite and free abdominal somites, larger; (2) genital double somite, narrower and less laterally produced (width: length ratio 1.2 vs. 1.7 in S. mucronipes); (3) caudal ramus setae IV-V distinctly swollen in proximal half; (4) all antennulary setae smooth; (5) siphon slightly shorter, reaching to intercoxal sclerite of leg 1; (6) maxillulary palp with one elongate, strongly plumose seta, and only two short pinnate setae; (7) coxal part of maxillary syncoxa without surface spinule row; (8) maxilliped basis and endopod relatively more slender; (9) leg-1 outer basal seta shorter, and inner coxal seta pinnate instead of bare; proximal outer spinous process on middle endopod segment, shorter; outer seta of distal endopod segment extending just beyond distal spinous process; (10) legs-2–3 inner coxal seta and outer basal seta, much shorter; (11) proximal inner seta of middle endopod segment of leg 4, much longer, approaching the length of the distal inner seta; and (12) leg-5 lateral exopodal seta, distinctly shorter.

TAXONOMIC POSITION OF ASTEROCHERES STIMULANS GIESBRECHT, 1897

Giesbrecht (1897) named three new species of Asterocheres, all of which were collected in the Gulf of Naples: Asterocheres dentatus, Asterocheres parvus, and A. stimulans. Although no illustrations or formal diagnoses were given, Giesbrecht did cite the new species in his identification key. Such a citation can be considered the equivalent of a differential diagnosis, and is sufficient to make the new species names available. Illustrated descriptions were given in a subsequent report on the Asterocheridae of the Gulf of Naples (Giesbrecht, 1899). Stock (1960) recognized the similarity in swimming leg morphology between



Figure 10. *Stockmyzon crassus* (Stock, 1966) **sp. nov.** (female). A, leg 1, anterior; B, leg 2, anterior; C, leg 3, anterior; D, leg 4, anterior.

A. mucronipes and the male of A. stimulans, in particular the beak-shaped processes on the endopods. Examination of Giesbrecht's detailed illustrations of both sexes of A. stimulans casts severe doubts on their conspecificity. His figures of the male include the habitus, antennule, maxilliped (note the position of the spinous process on the basis), leg 1, and endopods of legs 2-4 (note the short proximal inner seta on the middle endopod segment of leg 4), all of which conform exactly to S. mucronipes. The only exception is the illustration of the mouth cone area, which shows a slightly longer siphon (extending to the intercoxal sclerite of leg 3), and only three small setae on the maxillulary palp. The first difference is probably caused by excessive squashing of the specimen, which results in a slightly posterior displacement of the siphon in the foreshortened in situ view (also note the distorted position of the mandibular palp). The significant aspect in the second difference is the absence of the large, gonflate seta. This seta is typically medially directed, and could easily be concealed by the praecoxal gnathobase and oral cone in a squashed preparation (compare Figs 2D and 3E). The palp (even though Giesbrecht's illustration is small) shows the atrophied facies that is characteristic for Stock*myzon*. The description of the female of A. stimulans is concise, and includes figures of the habitus, antennule, maxillule, maxilliped, and urosome. The antennule is 20-segmented, as in S. mucronipes, but the segmental homologies are different. In female A. stimulans there are three segments distal to the aesthetasc-bearing segment XXI, and the vestigial segment XIII represents the ninth segment; in S. mucronipes only two segments are expressed distal to the ancestral segment XXI, and segment XIII is homologous with the tenth segment. The maxillule bears no resemblance to that in S. mucronipes, being similar to the typical Asterocheres condition. The female maxilliped is atypical in that it differs significantly from the male in its general slenderness and the length of the endopodal claw; such sexual dimorphism is extremely rare among asterocherids and makes the conspecificity of the two sexes highly questionable. We strongly believe that Giesbrecht (1899) based his description of A. stimulans on an amalgam of two different species. No holotype was designated by Giesbrecht and the original type series no longer exists (Kölmel, 1980; confirmed during a visit to the Stazione Zoologica in Naples by RH, October 2003). In order to preserve the stability of nomenclature, we designate the female specimen illustrated by Giesbrecht (1899: plate 3; figs 1, 3, 6, 7, 12, 14) (as the lectotype of A. stimulans (ICZN Art. 74.4). The male illustrated in Giesbrecht (1899: figs 2, 4, 5, 8–11, 13) is considered here as conspecific with S. mucronipes. Although its host was unknown to Giesbrecht (1897, 1899), we suspect that it was *A. calycularis*; Giesbrecht's material was collected in the vicinity of Naples, which virtually coincides with the northernmost limit of distribution of this host in Italy (Zibrowius, 1995). The identity of Canu's (1898) record of *A. stimulans* from algal washings in Maisy (Normandy coast) requires confirmation. The only female collected shows a 21-segmented antennule, but the similarity in siphon size, shape of the genital double somite, and length of the caudal ramus indicates that conspecificity cannot be ruled out.

Host switching in the north-western Mediterranean?

Astroides calycularis is an azooxanthellate dendrophylliid colonial coral, typically inhabiting shallow waters down to a depth of about 30 m, and preferring shaded places and strong water movement (Zibrowius, 1980, 1995). It is protected by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), and since 1999 has been listed by the Spanish Government as a vulnerable species in the National Catalogue of Endangered Species (Catálogo Nacional de Especies Amenazadas) (Anonymous, 1999). Astroides calycularis is essentially endemic to the south-western Mediterranean, with a few outliers beyond the Straits of Gibraltar in the west and the Straits of Sicily in the east. Its distribution is presently limited at 37°38'N (Cape Palos) on the coast of Spain and 40°48'N (Gulf of Gaeta) on the coast of Italy (Zibrowius, 1980, 1983). More recent research based on fossil evidence has demonstrated that A. calycularis lived on the mediterranean coast of France at 43°42'-43°44'N during part of the Pleistocene, taking advantage of the slightly higher surface water temperatures than those prevailing now in the northern Mediterranean (Zibrowius, 1995). Field experiments with colonies transplanted from Italy showed that present-day temperatures allow short-term survival, but fail to sustain successful reproduction. Stock (1960) found S. mucronipes in washings of the gorgonian E. singularis in the Banyuls-sur-Mer area, which is south of the northernmost limit of distribution of A. calycu*laris* during the Upper Sicilian and Upper Tyrrhenian (interstages of the Riss and Würm glaciations). We postulate that the symbiotic association between A. calycularis and S. mucronipes was already established before the Pleistocene and in the entire former distribution range of the host, i.e. the western mediterranean basin. When climatic conditions changed during the late Sicilian regression (Rissian age), about 238 000-225 000 years ago, the drop in temperature caused the extinction of A. calycularis along the French Mediterranean coast, and the northern

coastal waters of Spain and Italy, but did not necessarily wipe out the symbionts that depended on it. Switching to suitable hosts that reside in deeper waters, and are less susceptible to ambient temperature changes, offers a solution for symbionts that are at the risk of extinction. It appears that S. mucronipes maintained its presence in the north-western Mediterranean by switching to alternative hosts, such as the gorgonian E. singularis; however, the authenticity of Stock's (1960) record requires confirmation by additional sampling over a wider geographical scale before this hypothesis can be supported. Stock (1966) himself failed to collect additional S. mucronipes specimens from *E. singularis* in subsequent years, and therefore suggested the real host may well be a sponge, as in the case of S. crassus.

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