TORTANUS (ACUTANUS) ANGULARIS, NEW SUBGENUS AND NEW SPECIES (COPEPODA: CALANOIDA), FROM THE CARIBBEAN SEA, WITH REMARKS ON THE SUBGENERA IN THE GENUS TORTANUS

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Abstract.—Tortanus (Acutanus) angularis, new subgenus and new species (Copepoda: Calanoida), is described from Belize. The new subgenus Acutanus which accommodates three northwestern Atlantic species, T. angularis, n. sp., T. setacaudatus Williams, 1906 and T. compernis González & Bowman, 1965, is defined and compared with the other subgenera, Tortanus Giesbrecht, 1898 and Atortus, new subgenus. Diagnoses for these three subgenera are presented with remarks on species distributions. The type species of the genus Tortanus Giesbrecht, 1898 and its nominotypical subgenus is newly designated.

During taxonomical and phylogenetic studies on the pelagic calanoid copepod Tortanus by the author (Ohtsuka et al. 1987, Ohtsuka & Kimoto 1989), a new species of the genus was found in a plankton sample from the Caribbean Sea, which Dr. F. D. Ferrari (Smithsonian Institution) collected and kindly sent me. This new species is the fourth species from the Atlantic Ocean, and shares morphological characters with two previously known species from the northwestern Atlantic, T. setacaudatus Williams, 1906 and T. compernis González & Bowman, 1965. All three species cannot be assigned to the subgenera Tortanus, Eutortanus and Atortus from the Indo-Pacific region, hence a new subgenus is established to accommodate these three species.

A type species has never been fixed for the genus *Tortanus* Giesbrecht, 1898 and its nominotypical subgenus. Moreover, Sewell (1932) established the Indo-West Pacific subgenus *Atortus* without the fixation of a type species. Therefore the subgenus name *Atortus* is not available based on Art. 13(b) of the International Code of Zoological Nomenclature and must be published

here as a new subgenus along with the designation of a type species. In the present paper, the type species of these two subgenera are newly designated, and the two new and the nominotypical subgenera are defined in detail.

Materials and Methods

Specimens of the new species of *Tortanus* were included in a plankton sample collected from shallow-water channels (100 cm in depth) of a mangrove cay (Twin Cays) off Belize (16°50′N, 88°05′W, 21 Oct 1985) with a plankton net (mesh size: 110 μm) by Dr. F. D. Ferrari. The new species was compared with *T. setacaudatus* collected from Waquoit Bay, Falmouth, Massachusetts (25 Sep 1925; Dr. C. B. Wilson leg.) and *T. compernis* from Bahía Fosforescente, Puerto Rico (19 Jul 1957; Dr. R. E. Coker leg.), specimens of which I received from Dr. T. E. Bowman in exchange for specimens of other species of *Tortanus*.

All types of the new species are deposited in the National Museum of Natural History, Smithsonian Institution. Tortanus (Acutanus), new subgenus

Diagnosis. - Body slender. Prosome of female about twice as long as urosome. Pedigers 4 and 5 separate; pediger 5 symmetrical. Urosome of female 3-segmented; genital somite nearly symmetrical; genital operculum crescent-shaped; anal somite with acute dorsal process medially, and incompletely fused with caudal rami; 2nd-to-innermost caudal setae of both rami normally thickened and not so swollen as in subgenus Atortus, new subgenus (diagnosis of the new subgenus given below). Urosome of male 5-segmented; right posterior margin of 2nd somite produced into spine-like process posteriorly; anal somite separated from caudal rami and having acute dorsal process as in female. Fused segments 19-21 of right antennule of male not so produced terminally as in Atortus. Maxillule with 11 setae on arthrite. Basipod 1 of maxilliped bearing 2 large spinulose setae. Legs 1-4 with 2-segmented endopod and 3-segmented exopod; terminal exopod segment of leg 1 with 1 outer spine; terminal exopod segment of leg 2 with 2 outer lateral spines; terminal endopod segments of legs 1-4 each having 6 setae. Leg 5 of female uniramous, 3-segmented; terminal segment bearing 1 outer lateral and 3 terminal spines, innermost of which may be fused to terminal segment. Proximal exopod segment of right leg 5 of male swollen; distal exopod segment originating from near inner base of proximal exopod segment; inner lateral margin of proximal segment facing outer lateral margin of distal exopod segment to form chela.

Type species.—Tortanus angularis, new species, by original designation, described below.

Etymology. — The subgeneric name "Acutanus" is derived from the Latin acutus, meaning acute and anus, meaning anus, and refers to the acute dorsal process on the anal somites of both sexes.

Remarks.—The new subgenus comprises only three species, T. angularis, n. sp., T.

setacaudatus and T. compernis. T. angularis is selected as type species since the oldest species, T. setacaudatus, was not fully illustrated in the original description by Williams (1906).

Tortanus (Acutanus) angularis, new species Figs. 1-4, 6

Material examined. -29 99 (body length 1.04 (mean) \pm 0.03 mm (standard deviation), range 0.98–1.09 mm); 80 88 (body length 0.83 \pm 0.02 mm, range 0.77–0.88 mm).

Types. —Holotype: ♀, dissected and mounted on glass slides, USNM 251273. Allotype: ♂, dissected and mounted on glass slides, USNM 251274. Paratypes: 2 ♀♀ & 3 ♂♂, dissected and mounted on glass slides, 20 ♀♀ & 20 ♂♂, whole specimens, USNM 251275.

Description. - Female (holotype). Body (Fig. 1A, B) slender, 1.01 mm in length. Eye large, tinged with red. Cephalosome, dorsal side of cephalosome with middle transverse groove and protrusion on middle posterior end; both lateral sides fringed with minute prominences. Pediger 5, both posterior corners symmetrical, rounded. Urosome relatively slender, 3-segmented; genital somite (Fig. 1C) about 1.4 times as long as wide, having crescent-shaped genital operculum; anal somite (Fig. 1D) with strong acute process posterodorsally, fused dorsally with caudal rami; caudal rami (Fig. 1D) slender, nearly symmetrical, bearing minute sensillum in middle of outer margin, with 1 subterminal outer, 1 dorsal and 4 terminal plumose setae; posterior half of inner margin of caudal ramus fringed with hairs. Antennule (Fig. 1E) reaching middle of caudal ramus, consisting of 17 free segments, since segments 1-7, 9-12 and 24-25 are fused (segmentation based on Giesbrecht (1892)); armament on segments 13-23 similar to that of Tortanus scaphus (see Table 1, Bowman 1971) except for segments 17 and 19; seg-

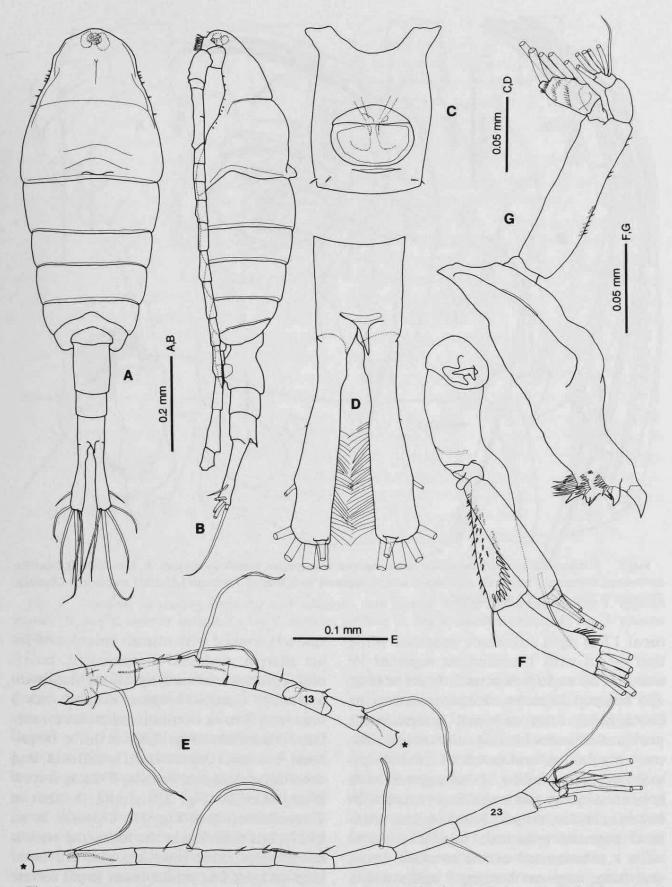


Fig. 1. Tortanus (Acutanus) angularis, new subgenus, new species, female (holotype). A, Habitus, dorsal view; B, Habitus, lateral view; C, Genital somite, ventral view; D, Anal somite and caudal rami, dorsal view; E, Right antennule; F, Antenna; G, Mandible.

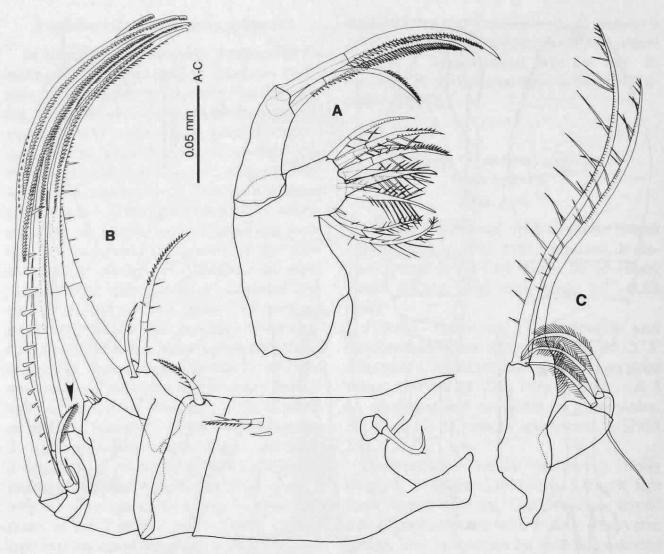


Fig. 2. Tortanus (Acutanus) angularis, new subgenus, new species, female (holotype). A, Maxillule; B, Maxilla, arrowhead meaning a relatively developed seta, compared with that of Tortanus (Atortus) erabuensis Ohtsuka, Fukuura & Go, 1987; C, Maxilliped.

ment 17 of right antennule unarmed while that of left with 1 aesthetasc; segment 19 with 2 setae and 1 aesthetasc. Antenna (Fig. 1F), basipod 2 fused with endopod, bearing subterminal seta; endopod 2-segmented, proximal segment bearing subterminal seta, row of spinules, and patch of minute spinules on outer surface, apical segment with 6 terminal setae and small inner knob with tuft of spinules; exopod 3-segmented, proximal segment unarmed, middle segment with 1 subterminal and 2 terminal setae, and distal segment bearing 2 apical setae. Mandible (Fig. 1G), mandibular cutting edge with 5 cusped teeth; 2 ventral teeth monocuspid with crown; basipod elongate,

sparsely fringed with minute spinules on inner margin; endopod 2-segmented, proximal segment unarmed, apical segment with 6 setae of unequal lengths; exopod with 5 setae and 3 rows of minute spinules on surface. Maxillule (Fig. 2A), arthrite developed, bearing 10 setae and 1 small seta; 2nd inner lobe elongate, bearing 3 thick, serrate setae. Maxilla (Fig. 2B) similar to that of T. erabuensis (see Fig. 2B, Ohtsuka et al. 1987), but differing in the following points: no spinules along inner margin; 3rd inner lobe without fine setule; inner small serrate seta (indicated by an arrowhead in Fig. 2B) relatively well-developed; inner terminal seta with large spinules along inner basal

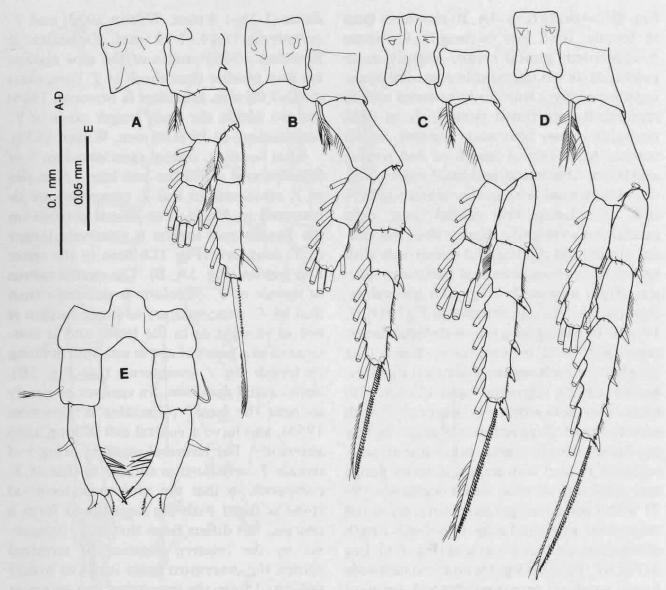


Fig. 3. Tortanus (Acutanus) angularis, new subgenus, new species, female (holotype). A, Leg 1, anterior surface; B, Leg 2, anterior surface; C, Leg 3, anterior surface; D, Leg 4, anterior surface; E, Leg 5, anterior surface.

margin. Maxilliped (Fig. 2C), basipod 1 produced anteriorly, and bearing 2 spinulose setae terminally; basipod 2 unarmed; endopod with 3 thick, plumose inner setae and 1 seta directed posteriorly. Legs 1–4 each with 2-segmented endopod and 3-segmented exopod. Leg 1 (Fig. 3A), basipod 1 with inner distal plumose seta and acute outer prominence; terminal exopod segment bearing middle outer spine and terminal seta serrate along proximal part of outer margin. Leg 2 (Fig. 3B), terminal exopod segment with 2 outer serrate spines. Leg 3 (Fig. 3C), terminal exopod segment bearing 3 outer

spines. Leg 4 (Fig. 3D), basipod 2 with seta on posterior surface; terminal exopod segment having 3 outer spines. Leg 5 (Fig. 3E) nearly symmetrical; 1st basipods completely fused with intercoxal plate to form common base; basipod 2 with fine seta at a point of about two-thirds outer margin; exopod 1-segmented, longer than basipod 2; exopod bearing 3 serrate terminal spines, innermost fused with segment; outer spine at a point of one-third margin from base; relatively long spinules along distal half of inner margin.

Male (allotype: Figs. 4A-E, 6A; paratype:

Fig. 4F).—Body (Fig. 4A, B) slenderer than in female, 0.85 mm in length. Urosome 5-segmented; genital somite slightly more produced on left lateral side at genital opening than on right side; 2nd urosomal somite remarkably protruded posteriorly at right posterior corner into acute process, which reaches to one-third length of 3rd somite and bears subterminal and basal setules (Fig. 4C); anal somite with acute mid-dorsal process, articulating with caudal rami; right caudal ramus slightly shorter than left caudal ramus, and right caudal ramus only with tuft of hairs along proximal half outer margin. Right antennule (Fig. 4D) geniculate; segments 1-5 (a seta missing in Fig. 4D), 7, 14, and 16 having long seta with distal flange; segments 7-12 incompletely fused (the number for each segment is based on Giesbrecht (1892)); segments 9 and 12 each with thick, short seta anteriorly; segment 17 with serrate flange along anterior margin slightly produced distally, and subterminal seta; segment 18 also with serrate anterior flange and subterminal seta; fused segments 19-21 with 2 serrate ridges anteriorly, proximal ridge short and distal ridge two-thirds length of segment, and terminal seta (Fig. 6A). Leg 5 (Fig. 4E, F), right leg: 1st and 2nd basipods fused, swollen; proximal exopod segment expanded, with plumose seta near the base on anterior surface and 2 fine setae distally; apical exopod segment spatulate, bearing 2 minute setae along concave outer margin and terminal setule, and its outer distal tip corrugate. Left leg: basipod 1 unarmed; basipod 2 elongate, bearing seta at a point of two-thirds of outer margin and inner seta at midlength; proximal exopod segment with subterminal outer and middle inner setae; distal exopod segment having 2 inner and 2 outer setae and relatively long terminal seta.

Etymology.—The specific name "angularis" refers to the acute ventrolateral process on the right posterior margin of the second urosomal somite of the male.

Comparison.—Females of the new species are smaller than those of T. setacau-

datus (1.25–1.4 mm, Wilson 1932) and *T. compernis* (1.14.–1.19 mm, González & Bowman 1965); males of the new species are also smaller than those of *T. compernis* (1.02–1.08 mm, González & Bowman 1965) but are within the body length range of *T. setacaudatus* (0.75–0.95 mm, Wilson 1932).

Anal somites, caudal rami and legs 5 of females, and urosomes and legs 5 of males of T. setacaudatus and T. compernis are illustrated in Fig. 5. The dorsal process on the female anal somite is relatively longer in T. angularis (Fig. 1D) than in the other two species (Fig. 5A, B). The caudal ramus of female of T. angularis is slenderer than that of T. setacaudatus; its inner margin is not as straight as in the latter and is constricted at a point of about one-fourth along its length. In T. compernis (see Fig. 5B), both caudal rami are "in contact or nearly so near the base" (González & Bowman 1965), and have a ventral tuft of long hairs anteriorly. The terminal segment of leg 5 of female T. angularis is similar to that of T. compernis in that the innermost terminal spine is fused with the segment to form a process, but differs from that of T. compernis by the relative position of terminal spines: the innermost spine is not as widely separated from the remaining two spines in T. angularis as in T. compernis (Figs. 3E, 5D). The innermost spine of T. setacaudatus is articulated with the segment (Fig. 5C).

In the male, the posterolateral process on the right side of the second urosomal somite is species-specific. In *T. angularis*, the process is strongly produced posteriorly to reach one-third the length of the third urosomal somite (Fig. 4A, B). In *T. setacaudatus* (Fig. 5E, F), the process is relatively small and produced outward, while in *T. compernis* (Fig. 5G–I) the process is irregularly produced outward and more developed than in *T. setacaudatus*. A tuft of hairs on the right lateral side of the anal somite is present only in *T. compernis*. The location of a tuft of hairs on the right caudal ramus of the male is different among these three species. In *T.*

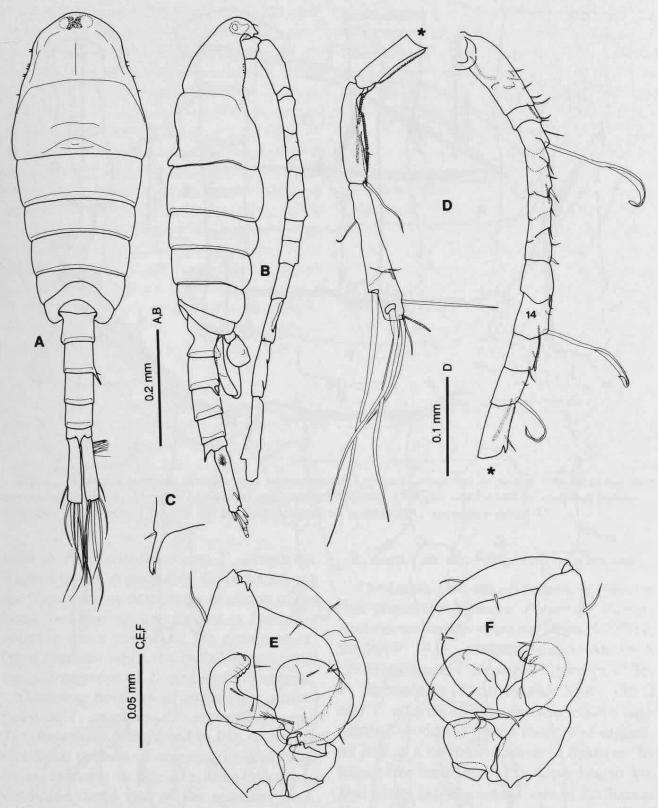


Fig. 4. Tortanus (Acutanus) angularis, new subgenus, new species, male (allotype: A-E; paratype: F). A, Habitus, dorsal view; B, Habitus, lateral view; C, Posterolateral process of second urosomal somite, ventral view; D, Right antennule; E, Leg 5, anterior surface; F, Leg 5, posterior surface.

angularis and T. setacaudatus, the tuft is found within the anterior half, whereas in T. compernis it is present along the posterior half of the outer margin. Legs 5 of males of

T. setacaudatus and T. compernis are shown in Fig. 5J and K, respectively. A subterminal outer seta of basipod 1 of left leg 5 is relatively longer in T. angularis (Fig. 4E, F)

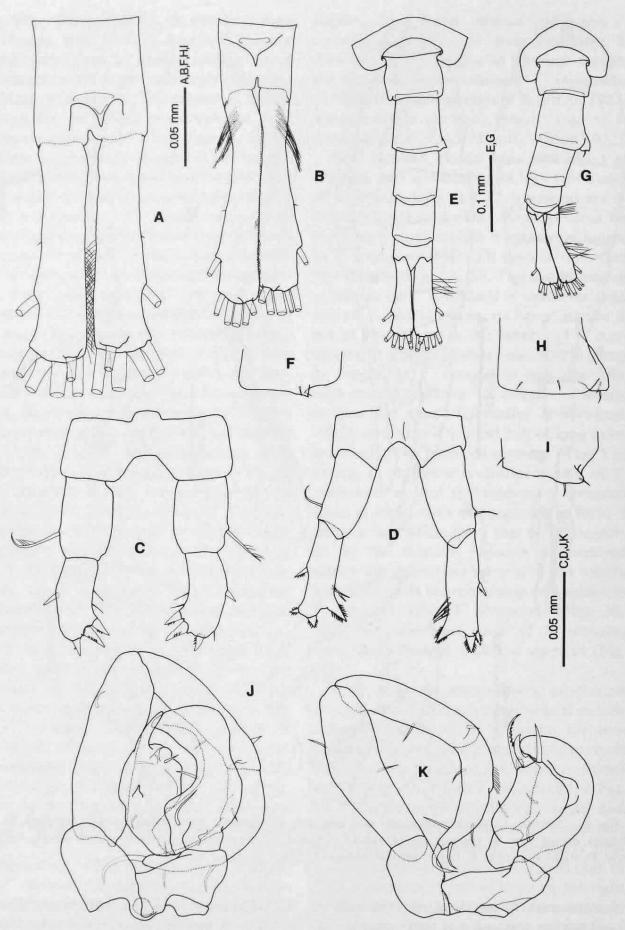


Fig. 5. Tortanus (Acutanus) setacaudatus Williams, 1906 (A, C, E, F, J) and Tortanus (Acutanus) compernis González & Bowman, 1965 (B, D, G-I, K). A, B, Anal somites and caudal rami of females, dorsal view; C, Leg

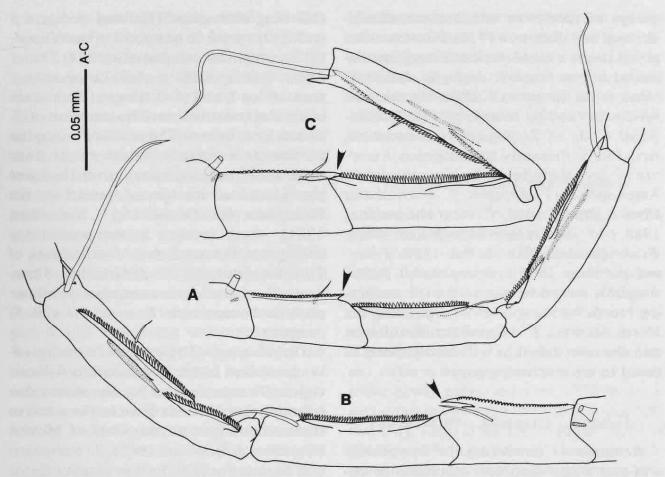


Fig. 6. Grasping portions of male right antennules of *Tortanus* (*Acutanus*) angularis, new subgenus, new species (allotype) (A), *Tortanus* (*Acutanus*) setacaudatus Williams, 1906 (B), and *Tortanus* (*Acutanus*) compernis González & Bowman, 1965 (C). An arrowhead means an anterodistal process of segment 17.

than in *T. setacaudatus* and *T. compernis*. Right legs are remarkably different among the three species. Structures of chelae of the latter two species are similar in having a concave inner margin of the proximal exopod segment while the bulb-like proximal exopod segment of *T. angularis* is unique.

Grasping portions of male right antennules of *T. angularis*, *T. setacaudatus* and *T. compernis* are depicted in Fig. 6. An anterodistal process of segment 17 (indicated by arrowheads in Fig. 6) is long enough to reach the distal end of the segment in *T. setacaudatus* (Fig. 6B) and *T. compernis* (Fig. 6C), while that of *T. angularis* is short (Fig. 6A).

Remarks on the Subgenera of Tortanus

The genus *Tortanus* presently comprises four nominal subgenera, *Tortanus*, *Atortus*, *Eutortanus*, and *Acutanus* (Sewell 1932, Smirnov 1935, present study). Smirnov (1935) assigned *T. derjugini* Smirnov, 1935, *T. discaudatus* (Thompson & Scott, 1897) and *T. setacaudatus* to the less known subgenus *Eutortanus* whose name was suggested first in a communication to Smirnov by Steuer (see Smirnov 1935). According to Art. 8(a) of the International Code of Zoological Nomenclature, Smirnov (1935) is responsible for the subgeneric name. *Eutortanus* corresponds to the first of Steuer's (1926)

^{5,} anterior surface; D, Leg 5, posterior surface; E, G, Urosomes of males, dorsal view; F, I, Posterolateral processes of second urosomal somites, lateral view; H, Posterolateral process of second urosomal somite, dorsal view; J, K, Legs 5, anterior surface.

groups of species or setacaudatus-discaudatus-group (Smirnov 1935). However, this group is not a monophyletic lineage as discussed below. Since T. derjugini should be alone in the subgenus Eutortanus, the type species is fixed by monotypy (the International Code of Zoological Nomenclature, Art. 13(c)). Presently the subgenus Eutortanus accommodates five northeastern Asian species (T. derjugini, T. dextrilobatus Chen & Zhang, 1965, T. sheni Hulsemann, 1988, (=T. denticulatus Shen & Lee, 1963), T. spinicaudatus Shen & Bai, 1956, T. vermiculus Shen, 1955) (present study). A new subgenus should be erected for the remaining North Pacific species incorporating the North Atlantic, T. discaudatus. Eutortanus and the new subgenus will be discussed in detail in a forthcoming paper.

Tortanus (Acutanus), new subgenus

Remarks.—Considering the morphological and zoogeographical relationships between species of the genus Tortanus, Steuer (1926) proposed three distinct groups within the genus, (1) setacaudatus-discaudatusgroup, (2) gracilis-forcipatus-barbatusgroup, and (3) murrayi-brevipes-recticaudagroup. Later, Sewell (1932) regarded the latter two groups classified by Steuer (1926) as two subgenera, namely, Tortanus and Atortus (see Bowman 1971). Although T. discaudatus and T. setacaudatus have parapatric distributions in the northwestern Atlantic Ocean (e.g., Steuer 1926, Wilson 1932, Brodsky 1950), Steuer's (1926) setacaudatus-discaudatus-group is incorrect, because of the following morphological differences between these two species: the number of endopod segments of leg 1 is 2 in T. setacaudatus, but 3 in T. discaudatus; pedigers 4 and 5 are separate in T. setacaudatus, but fused in T. discaudatus (Wilson 1932, Mori 1937). By contrast, T. discaudatus is more closely related to the five northeastern Asian species mentioned above (T. derjugini, T. dextrilobatus, T. sheni, T. spinicaudatus, T. vermiculus) in sharing the following characters, (1) fused pedigers 4 and 5, (2) 5 setae on basipod 2 of maxilliped, (3) 3-segmented endopod of leg 1, (4) 2 outer lateral spines of the terminal exopod segment of leg 1, and (5) 5th legs of both sexes of similar construction. The intrusion of T. discaudatus from the North Pacific into the northwestern Atlantic Ocean might have originated from migration during the latest post-glacial or interglacial period in the Pleistocene (cf. Ekman 1953, Nishimura 1981), which resulted in the present-day contiguous but secondary distributions of T. discaudatus and T. setacaudatus. However, T. setacaudatus comprises a monophyletic lineage with T. angularis and T. compernis.

Distribution. — The subgenus is exclusively distributed in the northwestern Atlantic region. T. setacaudatus has the widest distribution from Woods Hole in the north to the northern part of the Gulf of Mexico (González & Bowman 1965). T. compernis was recorded only in the type locality, Bahía Fosforescente, Puerto Rico. T. angularis is reported only from off Belize (present study).

According to Fleminger (1957), the northern neritic region of the Gulf of Mexico is characterized by a warm temperate water indicator, Labidocera aestiva Wheeler, 1901, while the remaining neritic waters of the Gulf are dominated by a subtropical/ tropical water indicator, L. scotti Giesbrecht, 1897. Hence, supposing a strict allopatry of T. angularis and T. setacaudatus, a habitat partition of both species appears not unlikely: T. setacaudatus is likely to be distributed in the northern warm temperate region of the Gulf, while the subtropical/ tropical T. angularis may occupy the southern part of the Gulf as its northernmost occurrence.

Tortanus (Tortanus) Giesbrecht, in Giesbrecht & Schmeil, 1898

Type species.—Corynura gracilis Brady, 1883, by subsequent designation.

Remarks. — The subgenus consists of three

species, *T. gracilis* (Brady, 1883), *T. barbatus* (Brady, 1883) and *T. forcipatus* (Giesbrecht, 1889). Based on Art. 69(a) of the International Code of Zoological Nomenclature, *T. gracilis* is selected as the type species of the genus and its nominotypical subgenus. Although *T. barbatus* is one of the originally included nominal species, the original illustrations of *T. gracilis* are more detailed than those of *T. barbatus* (see Brady 1883) and *T. gracilis* is hereby designated as the type species.

Diagnosis. - According to Steuer (1926) and Sewell (1932), the subgenus is defined as follows: prosome of female approximately 1.5 times as long as urosome; pedigers 4 and 5 separate; urosome elongate, 3-segmented in female; both right and left caudal rami of female fused with anal somite; endopod of leg 1 2-segmented; terminal endopod segments of legs 3 and 4 having 7 and 6 setae, respectively (according to my observation of T. forcipatus and T. gracilis, Sewell's (1932) statement that the terminal endopod segments of both legs 3 and 4 have 7 setae was not correct). In addition, both sexes of these three species have a terminal dorsal process on each caudal ramus unique to this subgenus (see Chen & Zhang 1965, Greenwood 1978). Moreover, although I have not examined T. barbatus yet, both T. forcipatus and T. gracilis share the following characters: terminal exopodal segments of legs 1 and 2 with 2 and 3 lateral spines, respectively; terminal endopodal segment of leg 2 with 7 setae; maxillulary arthrite with 12 setae; basipod 1 of maxilliped having 5 setae.

Distribution.—The distributions of the three species are partly overlapping in the Indo-West Pacific. However, only T. barbatus occurs in South Australian waters, but has hitherto not been reported from Japanese and Chinese waters (Greenwood 1978). T. forcipatus and T. gracilis have a sympatric distribution in the Indo-West Pacific region (Giesbrecht 1892, Giesbrecht & Schmeil 1898, Scott 1909, Steuer 1926, Mori 1937, Chen & Zhang 1965, Tanaka 1965,

Madhupratap & Haridas 1986) but no occurrence of these two species has been reported from the East African coast. In the Red Sea all three species were recorded (Giesbrecht 1892, Giesbrecht & Schmeil 1898, Scott 1909, Steuer 1926, Tanaka 1965, Greenwood 1978).

Tortanus (Atortus), new subgenus

Type species.—*Tortanus murrayi* Scott, 1909, by original designation.

Remarks. - Sewell (1932) newly established the subgenus Atortus in which four species, T. recticauda (Giesbrecht, 1889), T. brevipes Scott, 1909, T. murrayi Scott, 1909 and T. tropicus Sewell, 1932 were included. However, Sewell (1932) did not designate any of them as type species. A genus-group name newly published after 1930 must be accompanied with the fixation of a type species (Art. 13(b) of the International Code of Zoological Nomenclature). Hence the subgenus name Atortus dissatisfies the criteria of availability. By the fixation of the type species, a new subgenus Atortus whose name is the same as Sewell (1932) proposed before becomes available in the present paper. Since T. murrayi is one of the well illustrated species in the subgenus and the lectotype and four paralectotypes Bowman (1971) designated are preserved at the University of Amsterdam, Zoological Museum at present, it is designated as type species. 16 species and one undescribed species which are discussed in Ohtsuka & Kimoto (1989) are assigned to the new subgenus: T. recticauda, T. brevipes, T. murrayi, T. tropicus, T. longipes Brodsky, 1950, T. rubidus Tanaka, 1965, T. giesbrechti Jones & Park, 1968, T. lophus Bowman, 1971, T. scaphus Bowman, 1971, T. capensis Grindley, 1978, T. sinicus Chen, 1983, T. bonjol Othman, 1987, T. bowmani Othman, 1987, T. erabuensis Ohtsuka, Fukuura & Go, 1987, T. digitalis Ohtsuka & Kimoto, 1989, T. ryukyuensis Ohtsuka & Kimoto, 1989, T. sp. from South Yemen.

Diagnosis. —By reference to the previous

works by Sewell (1932), Bowman (1971), Ohtsuka et al. (1987) and Ohtsuka & Kimoto (1989), the new subgenus is defined as follows. Prosome of female about 3 times as long as urosome; pedigers 4 and 5 fused; urosome of female 2- or 3-segmented; caudal rami not as elongate as in subgenus *Tortanus*; maxillulary arthrite with 13 setae; basipod 1 of maxilliped with 2 long setae; endopod of leg 1 2-segmented; terminal endopod segments of legs 3 and 4 with 6 setae.

An additional study of the morphology of *Atortus* revealed that the following characters combined are also unique to this subgenus: terminal exopod segment of leg 1 and leg 2 bearing 1 and 3 outer spines, respectively; terminal endopod segment of leg 2 with 6 setae.

Distribution. — The distributions of the 17 species within the subgenus were discussed in detail in my previous work (Ohtsuka & Kimoto 1989). All the species are exclusively distributed in the Indo-West Pacific region (Ohtsuka & Kimoto 1989).

Acknowledgments

I express my sincere thanks to Dr. F. D. Ferrari for loaning the specimens of *Tortanus angularis* and critical reading of the manuscript and to Dr. T. E. Bowman for giving me specimens of *T. setacaudatus* and *T. compernis*. I am grateful to Drs. K. Hülsemann and A. Fosshagen and Prof. J. H. Stock and two anonymous reviewers for their comments on the International Code of Zoological Nomenclature. Indebtedness is also expressed to Miss J. Clark for deposition of the type specimens of *T. angularis* in the National Museum of Natural History, Smithsonian Institution.

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