

PHYLOGENY AND ZOOGEOGRAPHY OF THE PLANKTONIC COPEPOD GENUS *TORTANUS* (CALANOIDA: TORTANIDAE), WITH ESTABLISHMENT OF A NEW SUBGENUS AND DESCRIPTIONS OF TWO NEW SPECIES

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ABSTRACT

Tortanus (*Boreotortanus*), new subgenus, is established to accommodate the North Pacific/northwestern Atlantic species *T. discaudatus* and the taxonomy and ecology of the five subgenera in the genus *Tortanus* are discussed. *Tortanus* sensu stricto occurs in eutrophic waters in the Indo-West Pacific, *Atortus* in oligotrophic waters in the same region, *Eutortanus* in brackish waters in East Asia, *Acutanus* in eutrophic waters in the northwestern Atlantic, and *Boreotortanus* in eutrophic waters in the North Pacific and the northwestern Atlantic. Two new species are described: *T. (Eutortanus) terminalis* and *T. (Acutanus) ecornatus*.

Phylogenetic relationships among the 5 subgenera were constructed based on cladistic and zoogeographical analyses. *Boreotortanus* may have originated in the Sea of Japan; *Eutortanus* in the East China Sea; *Tortanus* sensu stricto in the Indo-Malayan region. The final divergence is represented by the *Atortus-Acutanus* clade, which is characterized by reductions of elements on the antennule, the antenna, legs 2 and 3 of both sexes, and elongation of the left leg 5 of males. The ancestor of *Acutanus* could have colonized the northwestern Atlantic from the Indo-Malayan region through the Isthmus of Panama during the Middle Miocene to Pliocene. It appears that *Atortus* first succeeded in exploiting clear oligotrophic waters and in developing swarming behavior to avoid visual predators in such clear waters. These originally tropical copepods seem to have secondarily adapted to cold waters along the East Asian archipelagoes during the Pleistocene.

The planktonic calanoid copepod genus *Tortanus* Giesbrecht, 1898, comprises four distinct subgenera and *Tortanus discaudatus* (Thompson and Scott, 1897), which cannot be assigned to any of the four subgenera. Although the genus is widely distributed in coastal waters in the Indo-Pacific and the northwestern Atlantic, each subgenus has its own restricted distribution (Ohtsuka, 1992; Ohtsuka *et al.*, 1992). The Indo-Pacific subgenera clearly exhibit habitat segregation; the subgenus *Tortanus* inhabits tropical-temperate eutrophic waters, whereas the subgenus *Atortus* is mainly distributed in tropical/subtropical oligotrophic waters (Ohtsuka, 1992; Ohtsuka and Kimoto, 1989). The subgenus *Eutortanus* is distributed exclusively in subtropical/temperate brackish waters in East Asia (Ohtsuka *et al.*, 1992, 1995). In the northwestern Atlantic, *T. discaudatus* and the subgenus *Acutanus* are contiguously distributed, though they co-occur in North America, and probably have different origins (Ohtsuka, 1992). The present study includes the establishment of a new subgenus to accommodate *T. discaudatus*, and an elucidation of the phylogenetic and zoogeographic relationships among these five subgenera. Two new spe-

cies, belonging to the subgenera *Acutanus* and *Eutortanus*, are also described.

MATERIALS AND METHODS

The dates and localities for the species examined in the present study are summarized in Table 1. Types of the two new species are deposited at the National Museum of Natural History, Washington (USNM), and the Natural History Museum and Institute, Chiba (CBM).

Phylogenetic relationships among the subgenera of *Tortanus* were analyzed using the PAUP software (Version 3.0, Swofford, 1993). The options used in this analysis were BRANCH AND BOUND and DELTRAN. All characters were set IRREVERSIBLE-UP. Morphological terminology follows Huys and Boxshall (1991).

Family Tortanidae Sars, 1902

Genus *Tortanus* Giesbrecht, 1898 (in Giesbrecht and Schmeil, 1898)

Diagnosis (emended).—Rostrum absent. Naupliar eyes well developed. Sclerotized circular structure, with marginal setules, present anterior to labrum, holding tips of long maxillary spiniform setae when not feeding. Cephalosome separate from pediger 1. Pedigers 4 and 5 separate or fused. Urosome of female 2- or 3-segmented (4-segmented in *Tortanus sheni* Hulsemann, 1988) with anal somite usually fused to caudal rami. Urosome

Table 1. Species of *Tortanus* examined in the present study.

Subgenus	Species	Locality	Date
<i>Boreotortanus</i> , new subgenus			
	<i>T. (B.) discaudatus</i>	Maine, U.S.A. Seattle, U.S.A.	26 Jul 1912 16 Nov 1905
<i>Eutortanus</i>			
	<i>T. (E.) derjungini</i>	Mankyong River, Korea	17 Jul 1990
	<i>T. (E.) dextrilobatus</i>	Somjin River, Korea	18 Dec 1991
	<i>T. (E.) terminalis</i> , new species	Tanega Island, Japan	1 Jun 1996
<i>Tortanus</i>			
	<i>T. (T.) barbatus</i>	New South Wales, Australia	30 Oct 1986
	<i>T. (T.) forcipatus</i>	Takehara, Japan	30 Aug 1993
	<i>T. (T.) gracilis</i>	Takehara, Japan	30 Aug 1993
<i>Atortus</i>			
	<i>T. (A.) digitalis</i>	Okinawa, Japan	10, 12 May 1988
	<i>T. (A.) erabuensis</i>	Okinawa, Japan	10, 12 May 1988
	<i>T. (A.) longipes</i>	Okinawa, Japan	10, 12 May 1988
	<i>T. (A.) lophus</i>	Kranket Island, New Guinea	Oct 1969
	<i>T. (A.) recticauda</i>	Arabian Gulf	—
	<i>T. (A.) rubidus</i>	Shijiki Bay, Japan	10–13 May 1984
	<i>T. (A.) ryukyuensis</i>	Okinawa, Japan	10 May 1988
	<i>T. (A.) scaphus</i>	Gilbert Island	6 Jan 1900
<i>Acutanus</i>			
	<i>T. (A.) angularis</i>	Twin Cay, Belize	21 Oct 1985
	<i>T. (A.) compernis</i>	Bahia Fosforescente, Puerto Rico	19 Jul 1957
	<i>T. (A.) ecornatus</i> , new species	Black River, Jamaica	22 Mar 1994
	<i>T. (A.) setacaudatus</i>	Massachusetts, U.S.A.	25 Sep 1925

of male 5-segmented; second urosomite of male often with 1 or 2 spiniform processes posterolaterally. Antenna with basis and first endopod segment almost completely fused. Maxillule with well-developed praecoxal arthrite bearing 11–13 elements and coxal endite having 3 spinulose setae; coxal epipodite, basis, and both rami completely lost. Maxilla with 7 large, serrated stout spiniform setae on second coxal and basal endites and endopod; praecoxal and first coxal endites rudimentary. Maxilliped with syncoxa having 2 or 5 spinulose setae; basis unarmed; endopod bearing 3 inner and 1 outer setae. Leg 1 with 2- or 3-segmented endopod and 3-segmented exopod; legs 2–4 with 2-segmented endopod and 3-segmented exopod. Female leg 5 uniramous, with or without 1-segmented exopod. Male leg 5 uniramous, with both basis and 1-segmented exopod forming stout chela on right side; left leg with 2-segmented exopod as grasping organ.

Remarks.—Although Brady (1883) first established the genus *Corynura*, that generic name was preoccupied. Therefore, Giesbrecht (in Giesbrecht and Schmeil, 1898) substituted the name *Tortanus* and redefined the

genus on the basis of only five species by comparison with the genus *Acartia* belonging to a related family Acartiidae. Because five subgenera and 26 described species, including the new taxa presented here, have been added since, the diagnosis of the genus by Giesbrecht (1898) should be partly revised in order to include the newly added taxa and to define the genus more concretely (Ohtsuka, 1992; present study).

Giesbrecht (in Giesbrecht and Schmeil, 1898) established the genus without designating a type species. Ohtsuka (1992) subsequently designated *Corynura gracilis* Brady, 1883, as the type for the genus and its nominotypical subgenus.

KEY TO SUBGENERA OF *TORTANUS*

1. Right caudal ramus of female bearing large acute outer process; right caudal seta II of male much thicker and longer than left; second endopod segment of leg 4 bearing 7 setae *Tortanus (Boreotortanus)*, new subgenus
- Caudal rami of both sexes not as above; second endopod segment of leg 4 with 6 setae 2
2. Maxilliped syncoxa bearing 5 setae 3
- Maxilliped syncoxa bearing only 2 setae 4
3. In both sexes, dorsal terminal triangular process present on both caudal rami; prosomal corners of

female not produced; caudal rami of male extremely slender, as long as or longer than urosomites combined; second endopod segments of legs 2 and 3 each bearing 7 setae

- *T. (Tortanus)* Giesbrecht, 1898
- In both sexes, dorsal terminal triangular process absent on both caudal rami; prosomal corners of female produced posteriorly into winglike process; caudal rami of male shorter than urosomites combined; second endopod segments of legs 2 and 3 each bearing 8 setae
..... *T. (Eutortanus)* Smirnov, 1935
 - 4. In both sexes, pedigers 4 and 5 separate; female leg 5 with 1-segmented exopod bearing either 4 spines or 3 spines plus 1 process; in right leg 5 of male, exopod arising proximally from basis
..... *T. (Acutanus)* Ohtsuka, 1992
 - In both sexes, pedigers 4 and 5 fused; female exopod of leg 5 either reduced or 1-segmented, tapering distally with spines/processes; in right leg 5 of male, exopod arising distally from basis
..... *T. (Atortus)* Ohtsuka, 1992

**Subgenus *Tortanus* (*Boreotortanus*),
new subgenus**

Diagnosis.—Prosome of female approximately 1.8 times as long as urosome; pedigers 4 and 5 separate in female and incompletely separate in male; posterolateral corners of female pediger 5 produced backward into triangular process. Urosome of female asymmetrical, 3-segmented; second urosomal and anal somites with patch of minute spinules on right side; second urosomal somite of male posterolaterally produced on right side; caudal rami and anal somite fused in female, separate in male; right caudal ramus of both sexes more expanded and longer than left, right seta II modified as large acute process in female, thicker and longer than left one in male.

Ancestral segment I of antennule separate from segment II in both sexes. Maxillular praecoxal arthrite with 11 elements. Maxilliped syncoxa bearing 5 setae. Leg 1 with 3-segmented endopod. Third exopod segments of legs 1 and 2 bearing 2 and 3 outer spines, respectively; second endopod segments of legs 2–4 having 8, 8, and 7 setae, respectively. Both legs 5 of female 3-segmented, left slightly longer than right; exopod 1-segmented, tapering distally, with 3 minute outer spinules, inner margin smooth.

Basis of right leg 5 of male swollen inwardly, with 2 triangular processes along inner margin, each having setule at tip; exopod bearing large inner proximal process. Left leg 5 with basis and first exopod segment relatively short, first exopod segment with long stout outer spine subterminally, second segment with short outer spine at midlength.

Remarks.—The new subgenus is readily discernible from the other subgenera in: (1) remarkably asymmetrical caudal rami of both sexes, with the right ramus expanded and longer than the left, right caudal seta II modified into swollen process in female, thicker and longer than left in male, (2) antennular segmentation and armature elements of both sexes in most primitive state of all subgenera (see Figs. 12, 13), (3) maxillular praecoxal arthrite with 11 elements, (4) 7 setae on second endopod segment of leg 4, and (5) structure of both exopods of male leg 5.

The combination of the following characteristics is also unique to the new subgenus: (1) pedigers 4 and 5 separate in female and incompletely separate in male, (2) pediger 5 of female posterolaterally produced into triangular process, (3) second urosomite of male protruded at right posterolateral corner, (4) terminal endopod segments of legs 1–3 with 6, 8, and 8 setae, respectively, (5) exopod of female leg 5 tapering distally with 3 minute outer spinules, and inner margin smooth, and (6) left leg 5 of male relatively short.

Type Species.—*Corynura discaudata* Thompson and Scott, 1897 (by monotypy).

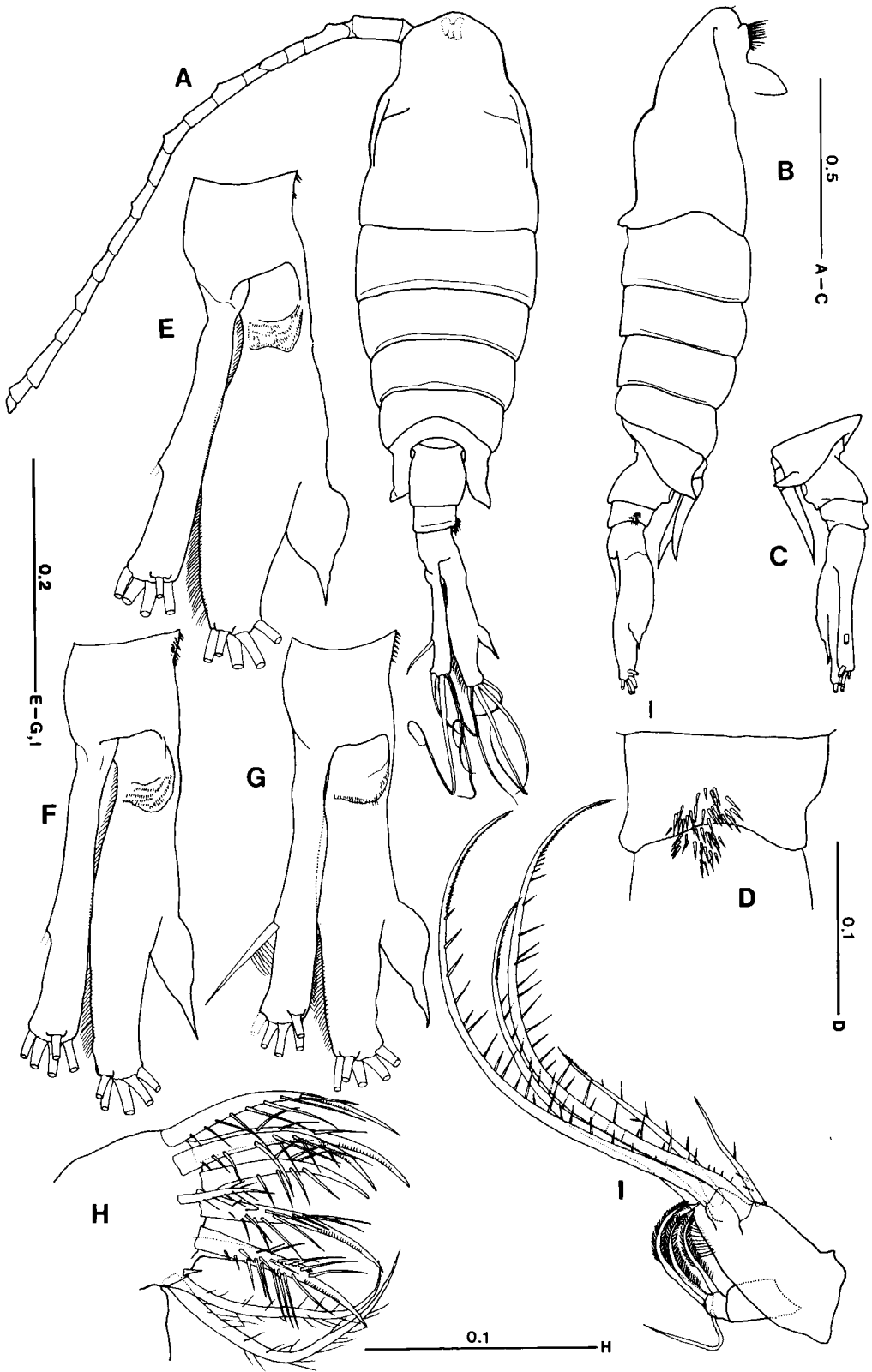
Etymology.—The new subgeneric name *Boreotortanus* is derived from the Latin *borealis* meaning northern, and the generic name *Tortanus*.

***Tortanus* (*Boreotortanus*) *discaudatus*
(Thompson and Scott, 1897)**

Figs. 1–4

Material Examined.—Two adult ♀♀ and 1 adult ♂, Portland Harbor, Maine, surface tow, 26 July 1912 (USNM 73498); 3 adult ♀♀ and 1 adult ♂, Yes Bay to Seattle,

Fig. 1. *Tortanus* (*Boreotortanus*) *discaudatus*, female, from the northwestern Atlantic (A–D,H,I) and the northeastern Pacific (E–G). A, habitus, dorsal; B, habitus, right lateral; C, pediger 5 and urosome, left lateral; D, second urosomite and anal somite, right lateral; E–G, anal somite and caudal rami, dorsal; H, maxillular praecoxal arthrite; I, maxilliped. Scale bars in mm.



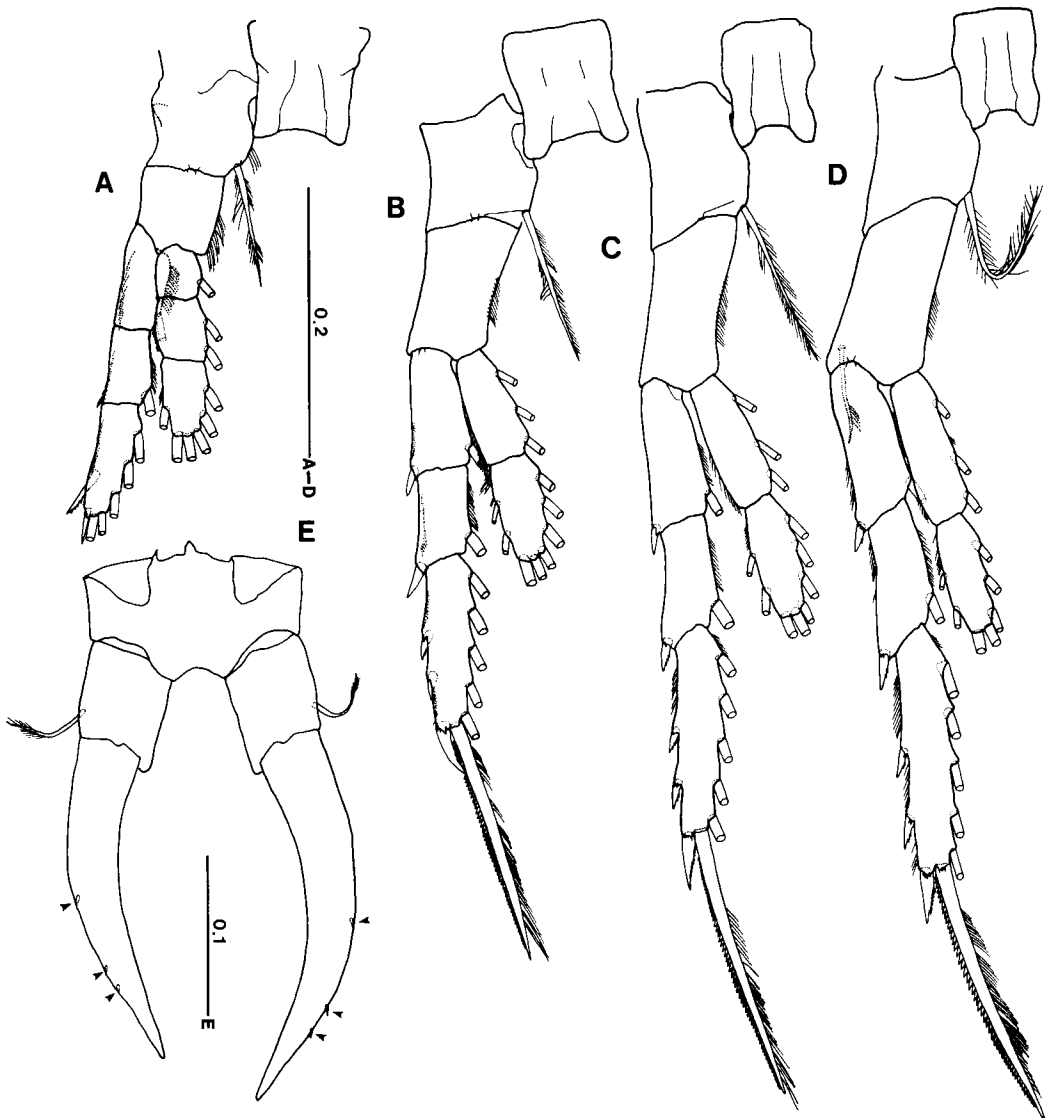


Fig. 2. *Tortanus (Boreotortanus) discaudatus*, female, from the northwestern Atlantic. A, leg 1, anterior; B, leg 2, anterior; C, leg 3, anterior; D, leg 4, anterior; E, leg 5, anterior. Scale bars in mm.

47°37'48"N, 122°26'20"W, surface tow, 16 November 1905 (USNM 70712).

Body Length.—The present and previous data are as follows. Adult female: 1.8–3.1 mm (Pacific region: Sato, 1913; Mori, 1937; Davis, 1949; Brodsky, 1950; Kim, 1985; present study); 2–2.25 mm (Atlantic region: Thompson and Scott, 1897; Giesbrecht and Schmeil, 1898; Wilson, 1932; present study). Adult male: 1.36–2.5 mm (Pacific region: Sato, 1913; Mori, 1937; Davis, 1949; Brodsky, 1950; present study); 1.75–2 mm (Atlantic region: Wilson, 1932; present study).

Sato (1913) reported extraordinarily large females (2.5–3.1 mm) from northern Japan (see Remarks also).

Description.—Female.—Body (Fig. 1A, B) with pediger 5 asymmetrically produced posteriorly with tip directed ventrally (Fig. 1B, C); second urosomite with patch of minute spinules on right posterolateral corner; anal somite almost completely coalescing into caudal rami, bearing patch of minute spinules of almost same size as in preceding somite on right posterolateral corner. Caudal rami con-

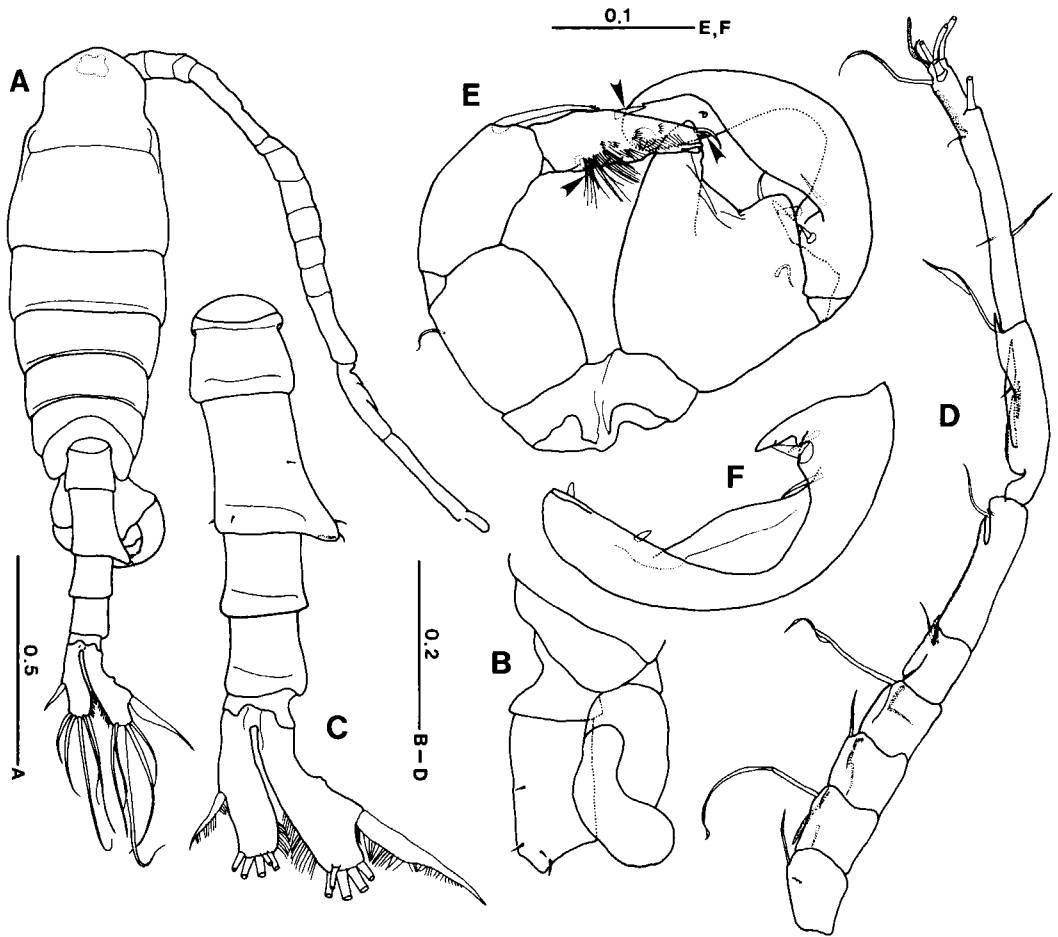


Fig. 3. *Tortanus (Boreotortanus) discaudatus*, male, from the northwestern Atlantic. A, habitus, dorsal; B, pediger 5 to second urosomite, right lateral; C, urosome, dorsal; D, right antennular segments XV–XXVIII; E, leg 5, anterior; F, exopod of right leg 5, posterior. Scale bars in mm.

siderably asymmetrical, right ramus much more expanded and slightly longer than left; seta I rudimentary (not illustrated in Fig. 1E–G); right seta II modified into sharply pointed process with swollen base, left seta II stout, with setules along middle of posterior margin; seta V longest; inner margins of both rami fringed with setules. Caudal rami exhibiting variation, in particular, in relative width of right ramus and its middle outer process (modified seta II) (Fig. 1A, E–G).

Antennular segments II–XIV almost completely or incompletely fused. Armature as follows (see Fig. 12 also): I–1, II–IX–9 (setae) + 2 ae (ae = aesthetasc), X–2, XI–2 + ae, XII–2, XIII–2, XIV–2 + ae, XV–2 + ae, XVI–2 + ae, XVII–2 + ae, XVIII–2 + ae,

XIX–2 + ae, XX–2, XXI–2 + ae, XXII–1, XXIII–1, XXIV–1 + 1, XXV–1 + 1 + ae, XXVI–XXVIII–6 + ae. Antenna and mandible with same armature elements as in other subgenera. Maxillular praecoxal arthrite (Fig. 1H) with 7 spinulose and 2 setulose setae, minute naked seta, and spinous process. Maxilla with 2 setae on first coxal endite. Maxilliped (Fig. 11) with syncoxa having 3 endites bearing 2, 2, and 1 setae, respectively; basis unarmed; endopod 1-segmented, with suture subtly visible anteriorly, bearing 3 plumose setae along anterior margin and 1 posteriorly directed seta.

Seta and spine formula of legs 1–4 (Fig. 2A–D) as follows (spines, Roman numerals; setae, Arabic numerals):

	coxa		basis			exopod			endopod		
	1	2	1	2	3	1	2	3	1	2	3
Leg 1	0-1	0-0	0-1;	0-1;	II, 1, 4	0-1;	0-2;	1, 2, 3			
Leg 2	0-1	0-0	I-1,	I-1;	III, 1, 5	0-3;	2, 2, 4				
Leg 3	0-1	0-0	I-1;	I-1;	III, 1, 5	0-3;	2, 2, 4				
Leg 4	0-1	1-0	I-1;	I-1;	III, 1, 5	0-3;	2, 2, 3				

Leg 5 (Fig. 2E) 3-segmented; both coxae and intercoxal sclerite fused to form common base; basis bearing minute plumose seta at point three-fourths along outer margin; endopod absent; exopod 1-segmented, curved smoothly inwardly, slightly asymmetrical, left longer than right, with inner margin smooth (i.e., not fringed with fine setules) and outer margin with 3 minute spines (indicated by arrows).

Male.—Body (Fig. 3A) much more slender than that of female; pediger 5 (Fig. 3A, B) produced posteriorly into rounded end reaching more than half length of genital somite. Urosome (Fig. 3C) with second urosomite longest, produced laterally at right posterior corner, on which 2 hair-sensilla present; third urosomal and anal somites slightly asymmetrical; anal somite separate from caudal rami; caudal rami asymmetrical, right ramus longer than left, curved outward, having long sclerotized seta II; seta I rudimentary (not illustrated in Fig. 3C); right seta I originating from outer middle knob (not illustrated in Fig. 3C).

Right antennule (Fig. 3D) with segments II–XIV almost completely or incompletely fused. Armature elements as follows (see Fig. 13 also): I-1, II-V-5 + ae, VI-2, VII-2 + ae, VIII-2, IX-2, X-2, XI-2 + ae, XII-2, XIII-2, XIV-2 + ae, XV-2, XVI-2 + ae, XVII-2 + ae, XVIII-2 + ae, XIX-1 + ae + process, XX-1 + ae + process, XXI-XXIII-2 + ae + 2 processes, XXIV-XVIII-10 + 2 ae. Mouthparts and legs 1-4 same as in female.

Leg 5 (Fig. 3E, F) with both coxae completely fused to form compact common base. Right leg with basis greatly expanded inwardly with 2 triangular processes along distal half of inner margin, each bearing minute seta at tip; 1 short seta present on posterior surface of basis; exopod (Fig. 3F) curved inwardly, lamellar, with 2 setae, short spine, and bifurcate process along proximal inner margin, 2 short spiniform setae along distal half of inner margin. Left leg with basis having minute seta at point about three-fourths of outer margin. Exopod 2-segmented; first segment bearing stout spiniform outer subterminal seta; second segment tapering distally,

bearing outer spine at midlength, 1 inner basal seta, and 1 short terminal seta (all indicated by arrows in Fig. 3E), fringed with setules of various length along inner margin, with several longitudinal ridges terminally.

Remarks.—This species was first described by Thompson and Scott (1897) from the northwestern Atlantic, and later redescribed by Sato (1913), Mori (1937), Davis (1949), Brodsky (1950), and Kim (1985) from the North Pacific, and by Wheeler (1901) (as *Corynura bumpusii*) and Wilson (1932) from the Atlantic. No morphological differences between the North Pacific and North Atlantic populations have been reported, which is confirmed on the basis of seven specimens from two sites in the present study. This suggests that speciation has not yet occurred between these populations since the intrusion of the North Pacific population into the North Atlantic in the latest postglacial or interglacial period (Ohtsuka, 1992).

Body lengths of this species, in particular those of females, vary greatly based on the previous data, in which the largest individuals are about 1.7–1.8 times as large as the smallest ones (see Body Length above). Such great variations are found also in other brackish and marine calanoid copepods. For example, the largest known male (1.96 mm) of *Sinocalanus sinensis* (Poppe, 1889) (family Centropagidae) from Japan is approximately 1.8 times as large as the smallest one (1.10 mm) (Hiromi and Ueda, 1987); about 1.7 times in female *Paraeuchaeta barbata* (Brady, 1883) (family Euchaetidae) (Mauchline, 1992). These variations may be caused by different biophysical factors, such as water temperature and food availability (Mauchline, 1992). Although previous data show that the size variation of *T. discaudatus* is greater in the Pacific region than in the Atlantic region, this was not confirmed in the present study because of the small number of individuals examined.

Distribution.—This species is distributed in cold waters on the northwestern and northeastern Pacific coasts, with an extension into the southern part of the Arctic Sea and the northwestern Atlantic (Fig. 4). Although Wilson (1932) mentioned its occurrence in the North Sea, citing Breeman (year not given), Breeman (1908) stated that it was found only on the east coast of North America. There-

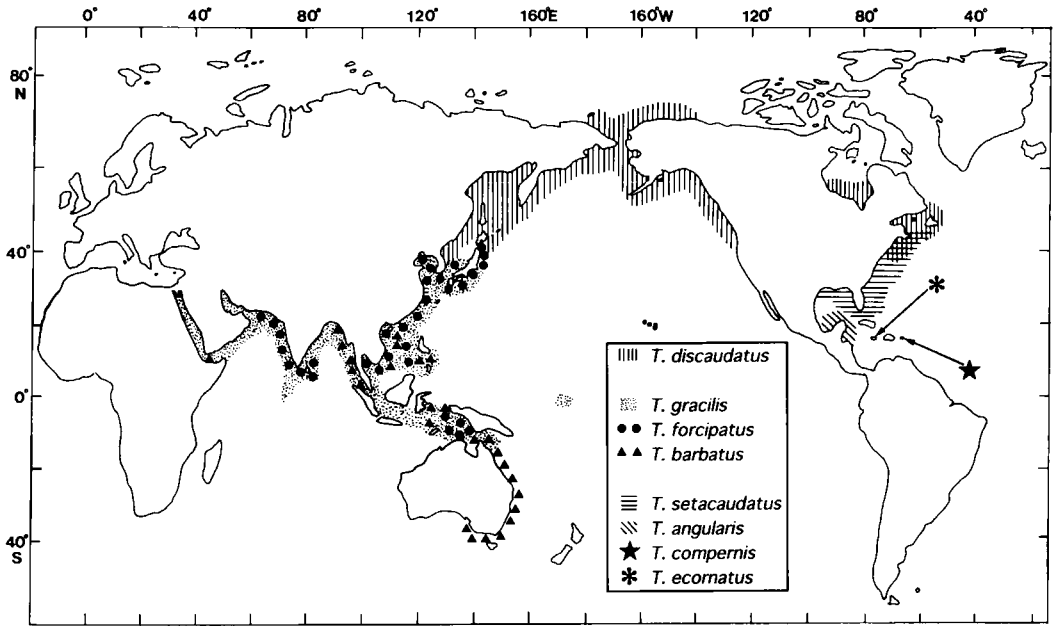


Fig. 4. Horizontal distributions of three subgenera of the genus *Tortanus*, *T. (Boreotortanus)* (= *T. discaudatus*), *T. (Tortanus)* (= *T. barbatus*, *T. forcipatus*, *T. gracilis*), and *T. (Acutanus)* (= *T. angularis*, *T. compernis*, *T. ecomatus*, new species, and *T. setacaudatus*). Based on Brady (1883), Giesbrecht (1892), Thompson and Scott (1897), Williams (1906), Sato (1913), Sewell (1912, 1914, 1932), Früchtl (1924), Steuer (1926), Wilson (1932, 1950), Johnson (1934), Farran (1936), Mori (1937), Davis (1949), Brodsky (1950), Rose (1956), Chen and Zhang (1965), González and Bowman (1965), Tanaka (1965), Hirota (1968a, b, 1979), Rehman (1973), Motoda and Minoda (1974), Greenwood (1978), Zheng *et al.* (1982), Chen (1983), Michel and Herring (1984), Kim (1985), Madhupratap and Haridas (1986), Hattori *et al.* (1991), Ohtsuka (1992), Shih and Young (1995), Drs. H. Ueda and E. Suárez-Morales (personal communication), and S. Ohtsuka (unpublished data).

fore, the North Sea record is doubtful, because the occurrence of *T. discaudatus* in northern Europe has never since been confirmed.

Ecological Note.—Adults of *Tortanus discaudatus* occur in plankton only during warm months (Wilson, 1932; Johnson, 1934, 1967). Johnson (1967) observed that pelagic eggs of *Tortanus discaudatus* hatched at temperatures of -2 to 12.5°C ; at 12.5°C 100% of the eggs hatched in 3–4 days, whereas at -2°C only 5% of the eggs hatched after 30 days. Johnson (1967) suggested that *T. discaudatus* probably produces resting eggs for hibernation, as is the case in *T. forcipatus* (Giesbrecht) (see Kasahara and Uye, 1979). On the other hand, *T. discaudatus* has been recorded in late fall to early spring in northern Japanese waters (Sato, 1913; Hattori and Tsumura, 1990). Since these regions are influenced during summer and fall by the warm Tsushima Current, resulting in water temperatures between 10 and 23°C (Hattori and Tsumura, 1990), the species seems to be intolerant of

warm water. *Tortanus discaudatus* can also withstand water of relatively low salinity (Brodsky, 1950), and in the Bering Strait it occurs at salinities less than 30‰ (Hattori *et al.*, 1991).

The feeding ecology of *T. discaudatus* is well documented. Johnson (1934) cultured adults and nauplii of this species on copepods and tintinnids, respectively. Ohtsuka *et al.* (1996) revealed by gut content analysis that females feed on copepodids, polychaetes, and appendicularians. In the laboratory, the functional response of *T. discaudatus* to types and densities of prey was studied by Anraku and Omori (1963), Ambler and Frost (1974), Mullin (1979), and Landry and Fagerness (1988).

Subgenus *Tortanus* (*Tortanus*)

Remark.—An emended diagnosis of the nominotypical subgenus was proposed by Ohtsuka (1992).

Type Species.—*Corynura gracilis* Brady, 1883.

Other Species.—*Tortanus barbatus* (Brady, 1883); *T. forcipatus* (Giesbrecht, 1892).

Distribution.—The subgenus is broadly distributed in Indo-West Pacific coastal waters (Fig. 4), but does not occur on the eastern African coast (Ohtsuka, 1992). Species tend to occur in eutrophic waters. The three species have overlapping distributions in the Indo-Malayan region, but only *Tortanus barbatus* is recorded in southeastern Australian waters. *Tortanus forcipatus* and *T. barbatus* seem not to be as common in the Indian Ocean as *T. gracilis*.

Ecological Note.—The subgenus *Tortanus* is distributed in warm coastal waters (Steuer, 1926; Hirota, 1968a, b, 1979; Rehman, 1973; Hirota and Uno, 1977; Madhupratap and Haridas, 1986). *Tortanus forcipatus* and probably *T. gracilis* (probably contaminated with *T. forcipatus*) lay resting eggs which overwinter in inlets in central Japan (Kasahara *et al.*, 1974; Hirota and Uno, 1977; Kasahara and Uye, 1979); both species occur in the plankton during warm months and disappear from the plankton during cold months. However, *T. forcipatus* occurs all-year-round without a resting phase in tropical regions (Rehman, 1973; Madhupratap and Haridas, 1986). Water temperature is presumably the most important factor in inducing the production of resting eggs, as is the case for *Acartia omorii* Bradford (see Uye, 1985, as *A. clausi* Giesbrecht).

In contrast to *Tortanus discaudatus* (see Johnson, 1967), subitaneous and diapause eggs of *T. forcipatus* hatched at much higher temperature. Both types hatched at 15–25°C but not at 5–10°C, although they differ substantially in dormancy (Kasahara and Uye, 1979), suggesting that *T. discaudatus* is more adapted to low water temperature than *T. forcipatus*. The diapause eggs of *T. forcipatus* require about a 2–3 month refractory period (Kasahara and Uye, 1979). Four types of eggs were found in *T. forcipatus* (Kasahara *et al.*, 1974), but two closely related species, *T. forcipatus* and *T. gracilis*, must have been contaminated in this report, because these two species have a sympatric distribution in the Seto Inland Sea, Japan (Ohtsuka, 1997), where four types of eggs were found.

KEY TO SPECIES OF *TORTANUS* (*TORTANUS*)

1. Left exopod of female leg 5 with inner middle margin serrate; in right leg 5 of male, inner mid-

- dle process on basis one-half as long as basis *T. (T.) barbatus* (Brady, 1883)
- Left exopod of female leg 5 without serration along inner margin; in right leg 5 of male, inner middle process on basis less than one-third as long as basis 2
 - 2. Female exopods asymmetrical, left leg about twice as long as right; in right leg 5 of male, exopod without distinct inner process at midlength; body length 1.09–1.35 mm in female, 1.00–1.05 mm in male *T. (T.) forcipatus* (Giesbrecht, 1889)
 - Female exopods nearly symmetrical; in right leg 5 of male, exopod with distinct inner process at midlength; body length 1.61–1.80 mm in female, 1.35–1.40 mm in male *T. (T.) gracilis* (Brady, 1883)

Subgenus *Tortanus* (*Acutanus*) Ohtsuka, 1992

Diagnosis (emended).—Anal somite partly fused to caudal rami, usually with acute dorsal process. Leg 2 bearing 0 or 1 outer spine on second exopod segment; third exopod segment bearing 2 or 3 outer spines. Leg 3 with or without outer spine on second exopod segment; third exopod segment bearing 2 or 3 outer spines. Leg 4 with 2 or 3 outer spines on third exopod segment. Right leg 5 of male with contorted exopod arising from inner proximal margin of basis.

Remarks.—The new species described below lacks the dorsal median process on the anal somite which is found in the rest of the subgenus. Perhaps this process has been secondarily lost due to miniaturization. Nevertheless, the new species is assignable to this subgenus as discussed below in detail.

Tortanus angularis Ohtsuka from Mexico bears 3 outer spines on the third exopod segment of leg 2, instead of the 2 spines in specimens originally described from Belize (Ohtsuka, 1992).

Type Species.—*Tortanus angularis* Ohtsuka, 1992.

Other Species.—*Tortanus setacaudatus* Williams, 1906; *T. compernis* González and Bowman, 1965; *T. ecornatus*, new species, described below.

Distribution.—The subgenus is distributed exclusively in northwestern Atlantic waters (Fig. 4).

Ecological Note.—The ecology of this subgenus is little known. Robertson (1983) examined feeding by adult females of *Tortanus*

setacaudatus on two species of tintinnids. This species ingested a larger tintinnid, *Favella panamensis* Kofoid and Campbell (265 μm lorica length), but not the smaller *Tintinnopsis lobiancoi* Daday (as *Tintinnopsis tubulosa* Levander) (148 μm).

KEY TO SPECIES OF *TORTANUS* (*ACUTANUS*)

1. Legs 2 and 3 with second exopod segment lacking outer spine; 2 outer spines on third exopod segment of leg 4; both sexes lacking acutely pointed anal operculum *T. (A.) ecornatus*, new species
- Legs 2 and 3 with second exopod segment bearing outer spine; 3 outer spines on third exopod segment of leg 4; both sexes with acutely pointed anal operculum 2
2. Exopod of female leg 5 with 3 spines terminally; in male, right posterolateral process on second urosomite minute *T. (A.) setacaudatus* Williams, 1906
- Exopod of female leg 5 with 2 spines plus 1 process terminally; in male, right posterolateral process on second urosomite well developed 3
3. In exopod of leg 5 of female, terminal 2 spines widely separate from innermost process; in right leg 5 of male, basis concave along inner margin *T. (A.) compernis* González and Bowman, 1965
- In exopod of leg 5 of female, terminal 2 spines not widely separated from innermost process; in right leg 5 of male, basis bulblike *T. (A.) angularis* Ohtsuka, 1992

Tortanus (Acutanus) ecornatus, new species Figs. 5, 6

Material Examined.—1 adult ♀, cephalosome partly damaged; 1 adult ♂, Black River Morass, Jamaica, 22 March 1994, collected by W. Janetzky.

Types.—Holotype, adult ♀, dissected and mounted on glass slides, USNM 239271; paratype, adult ♂, dissected and mounted on glass slides, USNM 239272.

Body Length.—Adult ♀ 0.94 mm (holotype). Adult ♂ 0.79 mm (paratype).

Description.—Female (holotype). Body (Fig. 5A) with both prosome and urosome slightly damaged; similar to that of *Tortanus angularis*, but urosome relatively shorter than in latter, approximately two-fifths as long as prosome. Cephalosome without marginal prominences such as those found in *T. angularis*. Urosome 3-segmented with anal somite partly fused with caudal rami; genital compound somite slightly asymmetrical, more swollen on left side than on right; anal somite lacking dorsomedial process. Left caudal ramus longer than right.

Antennule (Fig. 5B, C) resembling that of *T. angularis* in segmentation and setation. Segments I–XIV almost completely or incompletely fused; segments X and XI partly

fused; segments XI and XII almost completely fused; segments XII–XIV fused with suture line visible posteriorly. Armature of segments as follows (see Fig. 12 also): I–1, II–IX–9 + 2 ae, X–2, XI–2 + ae, XII–1, XIII–2, XIV–2, XV–1, XVI–2 + ae, XVII–1, XVIII–2 + ae, XIX–1 + ae, XX–2, XXI–2 + ae, XXII–1, XXIII–1, XXIV–1, XXV–1 + 1 + ae, XXVI–XXVIII–6 + ae. Antenna as in *T. angularis*. Mandibular palp (Fig. 5D) similar to that of *T. angularis*, but distal endopod segment with only 5 setae terminally. Maxillule, maxilla, and maxilliped with same segmentation and setation as in *T. angularis*.

Leg 1 (Fig. 5E) with same seta and spine formula as in *T. angularis*. Leg 2 (Fig. 5F) with slender basis; second exopod segment bearing 1 outer distal process instead of spine. Leg 3 (Fig. 5G) with slender basis as in leg 2; second exopod segment without outer spine, third segment bearing only 2 outer spines. Leg 4 (Fig. 5H) with coxa and basis slender, elongated; second exopod segment with outer spine, third segment with only 2 outer spines. Leg 5 (Fig. 5I) symmetrical, similar to that of *T. angularis*, but different from latter in having terminal segment relatively shorter than in latter, outer spine located at midlength, terminal inner process swollen basally.

Male (paratype). Body (Fig. 6A, B) much more slender than that of female. First urosomite (= genital somite) asymmetrical with left lateral margin swollen; second somite (Fig. 6C) with long process at right distal corner reaching midlength of next somite and bearing 1 terminal and 1 proximal setule. Anal somite without acute dorsal process as in female, bearing tuft of long setules only on right side. Caudal rami asymmetrical, left ramus slightly longer than right; right ramus with tuft of long setules laterally along anterior half of outer margin.

Right antennule (Fig. 6D) geniculate. Segments I–XIV almost completely or incompletely fused. Armature of segments as follows (see Fig. 13 also): I–1, II–V–5 + ae (probably 1 seta missing in Fig. 6D), VI–1, VII–2 + ae, VIII–2, IX–2, X–2, XI–2 + ae, XII–1, XIII–1, XIV–2, XV–1, XVI–2 + ae, XVII–2, XVIII–2 + ae, XIX–1 + process, XX–1 + process, XXI–XXIII–2 + ae + 2 processes, XXIV–XXVIII–9 + 2 ae; anterior process on segment XIX relatively long, reaching beyond base of anterior process on segment XX. Anterodistal process on compound segment XXI–XXIII relatively short.

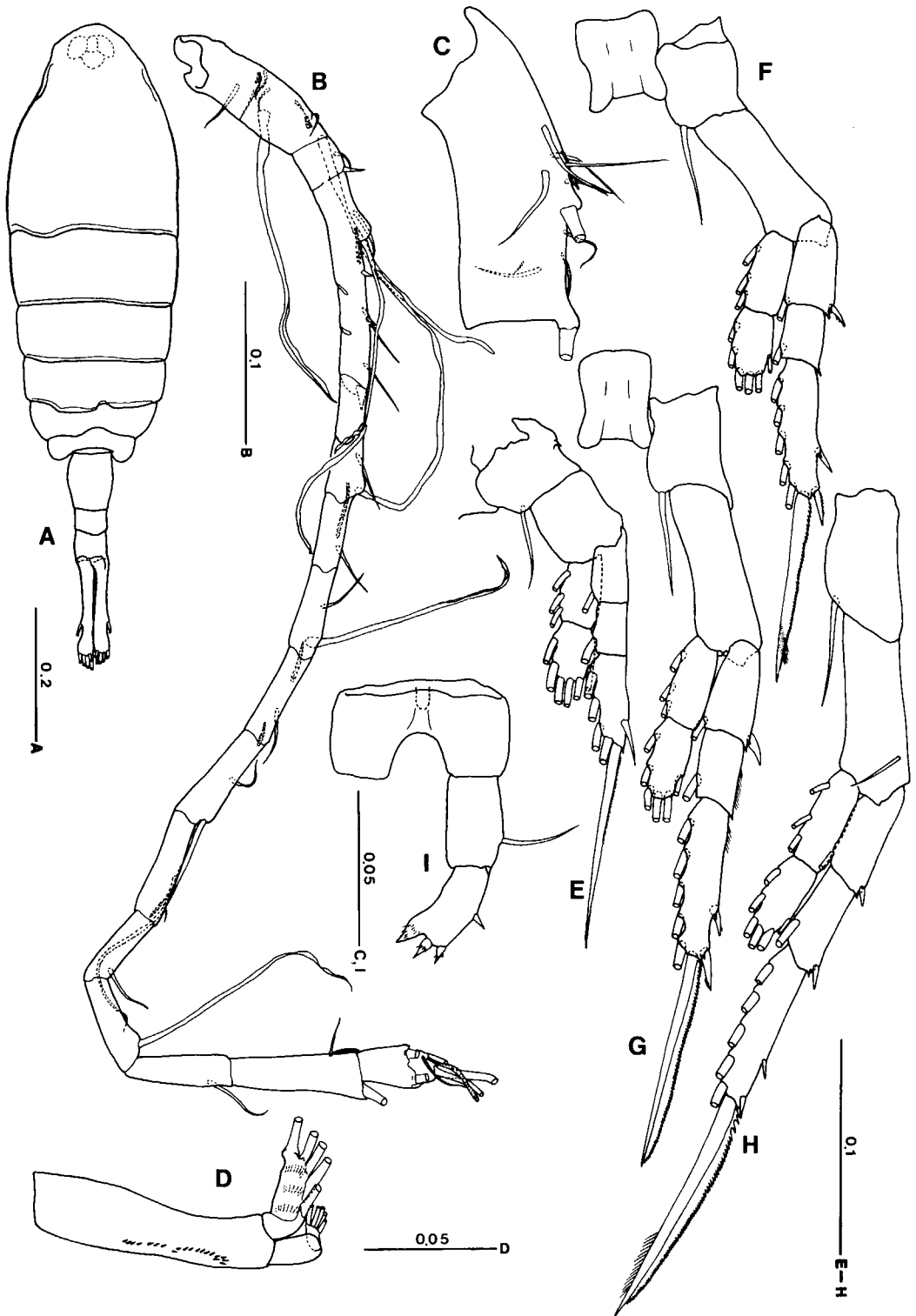


Fig. 5. *Tortanus (Acutanus) ecornatus*, new species, female (holotype). A, habitus, dorsal; B, antennule; C, first segment of antennule; D, mandibular palp; E, leg 1, posterior; F, leg 2, anterior; G, leg 3, anterior; H, leg 4, posterior; I, leg 5, right basis and exopod omitted, anterior. Scale bars in mm.

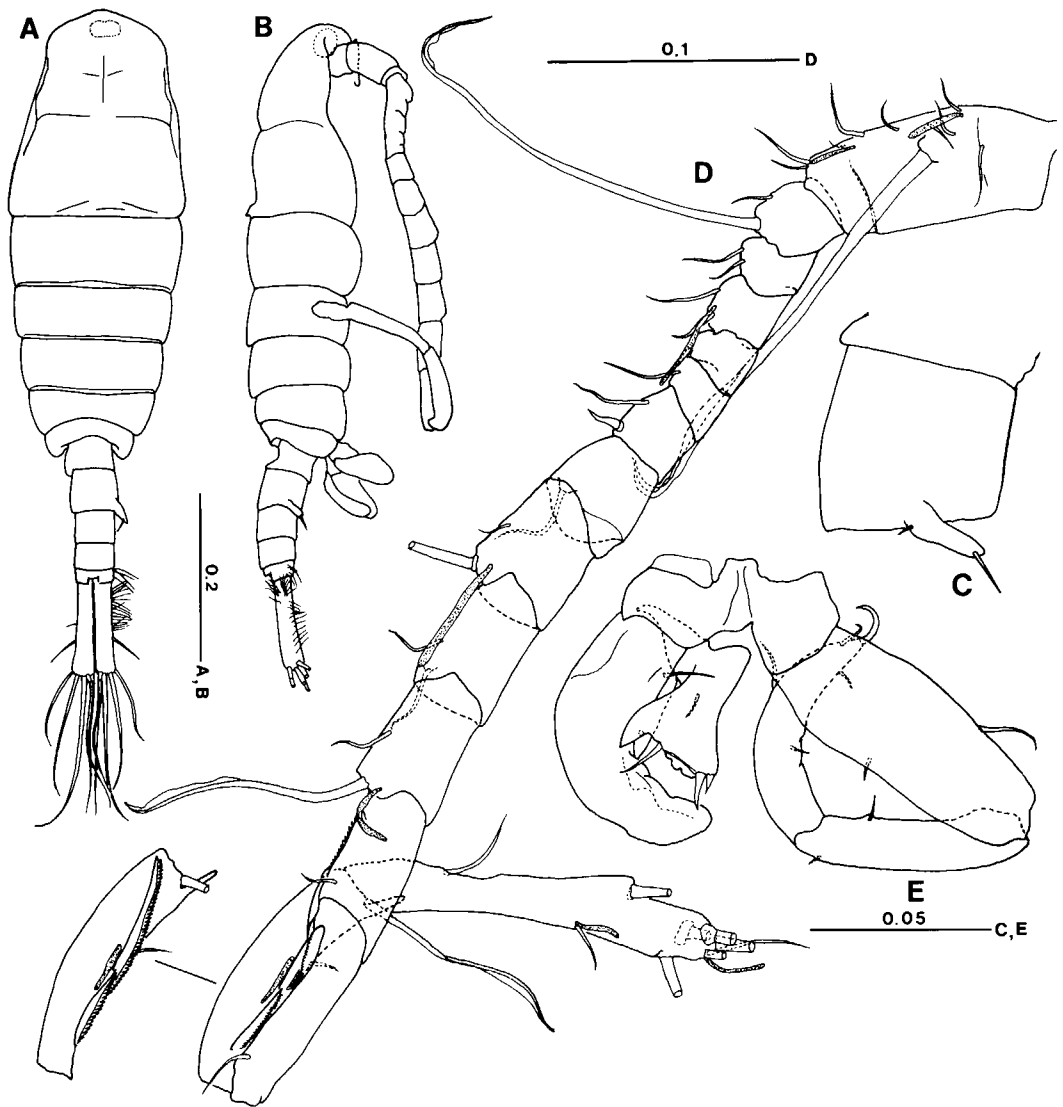


Fig. 6. *Tortanus (Acutanus) ecornatus*, new species, male (paratype). A, habitus, dorsal; B, habitus, right lateral; C, first abdominal somite, right lateral; D, right antennule; E, leg 5, anterior. Scale bars in mm.

Antenna to leg 4 with the same segmentation and armature of elements as in female.

Leg 5 (Fig. 6E) with both coxae completely fused to form common base. Left leg similar to that of *T. angularis*, but first exopod segment with small inner knob bearing setule. Right leg with basis expanded, curved inward, bearing 1 proximal seta and 1 medial seta along inner concave margin; joint of exopod located at proximal part of basis, expanded anteriorly with truncate tip bearing 2 spines, 1 seta and 1 acute process.

Remarks.—This new species can be easily distinguished from the other three members of the subgenus as follows: (1) the absence of outer spines on the second exopod segments of legs 2 and 3; (2) only 2 outer spines on the third exopod segment of leg 4; and (3) the lack of a median dorsal process on the anal somite. Despite its uniqueness, the new species can be assigned to the subgenus *Acutanus* by the following features: (1) the male right leg 5 with a small, contorted exopod arising from the inner proximal margin

of the basis (strict synapomorphy of *Acutanus*), and (2) the female leg 5 with 3 terminal and 1 outer distinct elements on the exopod (symplesiomorphy).

The new species is most closely related to *T. compernis*, and shares the following features: (1) the female with the innermost terminal spine of the terminal segment of leg 5 fused to form a process, (2) the male with a tuft of setules on the right side of the anal somite, and (3) the structure of the right leg 5 of the male. The first character is shared also by *T. angularis*. In addition, the long process on the right side of the second urosomite of the male is found solely in the new species and in *T. angularis*, although the structures of the male leg 5 differ remarkably. Compared with the apomorphic states in the mandibular palp and legs of the new species, its antennular armature is relatively plesiomorphic. The armature is basically similar to that of *T. angularis*, with the following differences in the female: X-2 (1 in *T. angularis*), XIII-2 (1), XVI-2 + ae (1 + ae), XVII-1 (0), XIX-1 + ae (0), XXV-1 + 1 + ae (1); in the male: X-2 (1). One terminal seta on the compound segment XXVI-XXVIII of *T. angularis* is probably missing in fig. 1E of Ohtsuka (1992).

Distribution.—The new species is known only from the type locality. No specimens of the new species were present in other plankton samples from Oyster Bay, Falmouth, Jamaica (26–27 February 1963).

Etymology.—The new specific name *ecornatus* (Latin *e-* meaning without, *cornatus* meaning horned) refers to the lack of a median dorsal process on the anal somites of both sexes.

Subgenus *Tortanus* (*Atortus*) Ohtsuka, 1992

Remarks.—Because Sewell (1932) established a new subgenus *Atortus* in the genus *Tortanus* without designating a type species, the subgenus name was unavailable (ICZN Art. 13(b)). Therefore, Ohtsuka (1992) proposed a new subgenus *Atortus*, the same name as that given by Sewell (1932).

Type Species.—*Tortanus scaphus* Bowman, 1971 (by designation).

Other Species.—*Tortanus recticauda* (Giesbrecht, 1892); *T. brevipes* Scott, 1909; *T. murrai* Scott, 1909; *T. tropicus* Sewell, 1932; *T. longipes* Brodsky, 1948; *T. rubidus* Tanaka, 1965; *T. giesbrechti* Jones and Park, 1968; *T. lophus* Bowman, 1971; *T. capensis* Grindley, 1978; *T. erabuensis* Ohtsuka, Fukuura, and Go, 1987; *T. digitalis* Ohtsuka and Kimoto, 1989; *T. ryukyensis* Ohtsuka and Kimoto, 1989; *T. sinicus* Chen, 1983; *T. bonjol* Othman, 1987; *T. bowmani* Othman, 1987; *T. sp.* from Yemen.

Distribution.—The distribution of the subgenus is restricted to the Indo-West Pacific, with one species off southernmost Africa (Ohtsuka and Kimoto, 1989, figs. 10, 11). Recently a variant form of *Tortanus scaphus* was recorded in Australian waters (McKinnon, 1993).

Ecological Note.—In contrast to the other subgenera, this subgenus seems to be exclusively distributed in oligotrophic waters (Chen, 1983; Ohtsuka and Kimoto, 1989). Swarming behavior is unique to *Atortus* (see Ohtsuka and Kimoto, 1989; S. Ohtsuka *et al.*, personal observation), which seems to be related to antipredation in clear waters.

KEY TO SPECIES OF *TORTANUS* (*ATORTUS*)

1. Exopod of female leg 5 1-segmented, bearing 2–4 distinct spines/processes; in male, second urosomite without right posterolateral process (*recticauda* complex sensu Ohtsuka and Kimoto, 1989) 2
 - Exopod of female leg 5 either absent or, if rarely present, slender, 1-segmented with 1 or 2 terminal spines or processes; in male, second urosomite with right posterolateral process (*brevipes* complex sensu Ohtsuka and Kimoto, 1989) 9
2. Exopod of female leg 5 bearing 1 middle or proximal inner spine or process; in male, basis of right leg 5 with inner distal or middle process 3
 - Exopod of female leg 5 bearing 2–4 terminal or subterminal processes, without inner spine or process; in male, basis of right leg 5 without inner distal or middle process 4
3. Female genital compound somite with anterolateral swellings; exopod of female leg 5 with 1 inner middle and 2 or 3 terminal processes; in male, basis of right leg 5 with inner process at mid-length *T. (A.) recticauda* (Giesbrecht, 1889)
 - Female genital compound somite without lateral process; exopod of female leg 5 with inner proximal spine and serrate terminal process; in male, basis of right leg 5 with inner distal process *T. (A.) capensis* Grindley, 1978
4. Exopod of female leg 5 shorter than or as long as basis; in male, basis of right leg 5 without large inner proximal process 5

- Exopod of female leg 5 longer than basis; in male, basis of right leg 5 with large triangular or round inner proximal process 6
- 5. Female caudal rami asymmetrical with right ramus expanded distally; exopod of female leg 5 with 1 large terminal and 1 bifurcate outer process; in male, basis swollen inward, exopod smoothly curved
T. (A.) erabuensis Ohtsuka, Fukuura, and Go, 1987
- Female caudal rami slightly asymmetrical, with right ramus longer than left; exopod of female leg 5 with bifurcate terminal process; in right leg 5 of male, basis not swollen, exopod abruptly curved inward *T. (A.) sinicus* Chen, 1983
- 6. Left caudal ramus of female with outer distal swelling; in male, basis of right leg 5 with round inner process arising from near inner proximal margin *T. (A.) bonjol* Othman, 1987
- Left caudal ramus of female without outer distal swelling; in male, basis of right leg 5 with triangular inner processes 7
- 7. Female genital compound somite with acute ventral posterior process on each side; in right leg 5 of male, terminal end of exopod not reaching inner proximal process of basis
..... *T. (A.) lophus* Bowman, 1971
- Female genital compound somite without process or with round prominence on left side; in right leg 5 of male, terminal end of exopod reaching inner proximal process of basis 8
- 8. Female genital compound somite without process; in male, middle inner basal process of right leg 5 acutely pointed
..... *T. (A.) scaphus* Bowman, 1971
- Female genital compound somite with round prominence on left side; in male, middle inner basal process of right leg 5 bluntly pointed *T. (A.) murrayi* Scott, 1909
- 9. In female, both distal corners of prosome and caudal rami almost symmetrical; in male, basis of right leg 5 bearing square platelike inner process distally
..... *T. (A.) ryukyuensis* Ohtsuka and Kimoto, 1989
- In female, distal corners of prosome and/or caudal rami asymmetrical; in male, basis of right leg 5 without such process 10
- 10. Exopod of female leg 5 1-segmented, with 1 inner spine at midlength; in male, coxa of left leg 5 with triangular process at inner distal corner *T. (A.) giesbrechti* Jones and Park, 1968
- Exopod of female leg 5 either 1-segmented, without inner spines, or completely absent; in male, coxa of left leg 5 without process 11
- 11. Exopod of female leg 5 1-segmented; in right leg 5 of male, basis with large round inner process, exopod elongate and curved strongly inward *T. (A.) tropicus* Sewell, 1932
- Female leg 5 lacking exopod; right leg 5 of male, basis with minute or large bilobed or small simple inner process, exopod relatively short, weakly curved inward 12 (female only; skip to 13 in male)
- 12. Right prosomal corner much more produced posteriorly than left *T. (A.) brevipes* Scott, 1909
- Left prosomal corner more produced posteriorly than right, or both corners almost equally produced posteriorly 13
- 13. In female, both prosomal corners almost equally produced posteriorly; in male, right posterolateral process on second urosomite short, not reaching one-half midlength of next somite (terminal spine not included) *T. (A.) bowmani* Othman, 1987
- In female, left prosomal corner more produced posteriorly than right; in male, right posterolateral process on second urosomite relatively long, reaching beyond midlength of next somite 14
- 14. Female genital compound somite with large right lateral process posterior to midlength; in male, basis of left leg 5 with large triangular process along inner proximal margin *T. (A.) longipes* Brodsky, 1948
- Female genital compound somite with large right lateral process at midlength; in male, basis of left leg 5 without large proximal inner process 15
- 15. Genital compound somite of female with 3 lateral processes anteriorly on right side; left leg 5 of male with inner proximal process on first exopod segment about one-half as long as segment *T. (A.) digitalis* Ohtsuka and Kimoto, 1989
- Genital compound somite of female with 1 lateral process anteriorly on right side; left leg 5 of male with inner proximal process on first exopod segment at most one-fifth as long as segment *T. (A.) rubidus* Tanaka, 1965

Subgenus *Tortanus* (*Eutortanus*) Smirnov, 1935

Diagnosis.—Although the diagnosis of the subgenus was provided in Ohtsuka *et al.* (1992), one character must be emended: leg 1 with 2- or 3-segmented endopod.

Remarks.—The zoogeography of the subgenus was elucidated by Ohtsuka *et al.* (1992). However, the finding of the new species described below is important in considering the evolution of this subgenus, and may verify some morphological and zoogeographical features. It is evident that fusion of segments in some appendages has occurred convergently in the genus *Tortanus*. For example, a 2-segmented endopod of leg 1 has occurred independently at least twice in the genus *Tortanus*, i.e., within the subgenus *Eutortanus* and after the offshoot of *Eutortanus* (see Discussion).

Type Species.—*Tortanus derjugini* Smirnov, 1935.

Other Species.—*Tortanus vermiculus* Shen, 1955; *T. spinicaudatus* Shen and Bai, 1956; *T. dextrilobatus* Chen and Zhang, 1965; *T. sheni* Hulsemann, 1988; *T. terminalis*, new species, described below.

Distribution.—The subgenus is distributed exclusively in East Asian brackish waters (Ohtsuka *et al.*, 1992, fig. 6). Based on the present-day distributional pattern, the origin of the subgenus may have been in a huge low-salinity gulf of the ancient East China Sea (Fig. 10B), existing during the Miocene-Pleistocene (Nishimura, 1980, 1981; Ohtsuka *et al.*, 1992, 1995). It is surprising that only the new species described below is distributed in high-salinity waters (34.5‰), at the northern part of Tanega Island (arrowed in Fig. 10A), southwestern Japan. These waters are strongly influenced by the warm Kuroshio Current. If the occurrence of the new species at this locality has not been caused by artificial transport (cf. Cordell *et al.*, 1992), there is a possibility that the brackish/neritic ancestor of the new species was broadly distributed throughout the ancient East China Sea and then the population around Tanega Island was isolated from the main continental populations by transgression(s) and evolved into the new species occurring in high-salinity waters (see Discussion).

The presence of a population of the brackish-water species *T. derjugini* in the Ariake Sea, Kyushu, isolated from the Asian continental populations, suggests that this species was distributed widely in the ancient East China Sea during the Middle Miocene to the Pleistocene (Ohtsuka *et al.*, 1992, 1995). The gulf might have been partially closed by the land bridge of the Nansei Islands, with an entrance between Okinawa and Miyako Islands or between Amami and Yaku Islands (Kizaki and Oshiro, 1977; Nishimura, 1980, 1981). The present find indirectly suggests that low-salinity waters of the ancient East China Sea may have extended entirely throughout the gulf, and that the ancestor of this subgenus may have had a broad distribution in the sea.

Ecological Note.—The subgenus is highly adapted to brackish waters, except for the new species described below (Brodsky, 1950; Ohtsuka *et al.*, 1992, 1995; present study).

KEY TO SPECIES OF *TORTANUS* (*EUTORTANUS*)

1. First 2 urosomites of female each with high posterodorsal projection; right leg 5 of male with basis having proximal inner process as long as exopod of left leg 5 *T. (E.) terminalis*, new species
- First 2 urosomites of female without high posterodorsal projection; right leg 5 of male with ba-

- sis having proximal inner process much shorter than exopod of left leg 5 2
2. Female anal somite with serrate margin anterolaterally on right side; right leg 5 of male with inner proximal process of basis having broad base, exopod with acutely pointed process along inner proximal margin *T. (E.) vermiculus* Shen, 1955
- Female anal somite without serrate margin anterolaterally on right side; right leg 5 of male with inner proximal process of basis having narrow base, exopod without acutely pointed process along inner margin 3
3. Female anal somite with spiniform process on posterolateral corner on right side; right leg 5 of male with exopod not extending beyond inner proximal process on basis *T. (E.) spinicaudatus* Shen and Bai, 1956
- Female anal somite without process, or with anterolateral process on right side; right leg 5 of male with exopod extending beyond inner proximal process on basis 4
4. Female urosome 4-segmented; right leg 5 of male with exopod acutely pointed at tip *T. (E.) sheni* Hulsemann, 1988
- Female urosome 3-segmented; right leg 5 of male exopod rounded at tip 5
5. Female anal somite with developed anterolateral process; right leg 5 of male relatively small, with basis about 0.1 mm at maximum width *T. (E.) dextrilobatus* Chen and Zhang, 1965
- Female anal somite without anterolateral process; right leg 5 of male relatively large with basis about 0.2 mm at maximum width *T. (E.) derjugini* Smirnov, 1935

Tortanus (*Eutortanus*) *terminalis*, new species Figs. 7–9

Material Examined.—Four adult ♀♀ and 8 adult ♂♂. 1 June 1996 (local time 2200), Nishino-omote Pier, Tanega Island, Kagoshima Prefecture. Towing around underwater light with a NORPAC net (mesh size 0.1 mm).

Types.—Holotype, adult ♀, dissected and mounted on glass slides, body in vial. CBM ZC-4538; paratypes, 1 adult ♀ and 1 adult ♂, appendages dissected and mounted on glass slides, bodies in vials, CBM ZC-4539, and 2 adult ♀♀ and 7 adult ♂♂, whole specimens, CBM ZC-4540.

Body Length.—Adult ♀: range 1.94–2.12 mm (average \pm SD = 2.04 \pm 0.09 mm, $N = 4$); adult ♂: range 1.86–2.10 mm (1.97 \pm 0.09 mm, $N = 8$).

Description.—Female. Body (Fig. 7A, B) widest in first pediger; fourth and fifth pedigers almost coalescent, with suture visible dorsolaterally and dorsomedially; prosomal end (Fig. 7C–H) asymmetrical, right end longer and more prominent than left, reaching half length of genital compound somite, left end produced into rounded process. Uro-

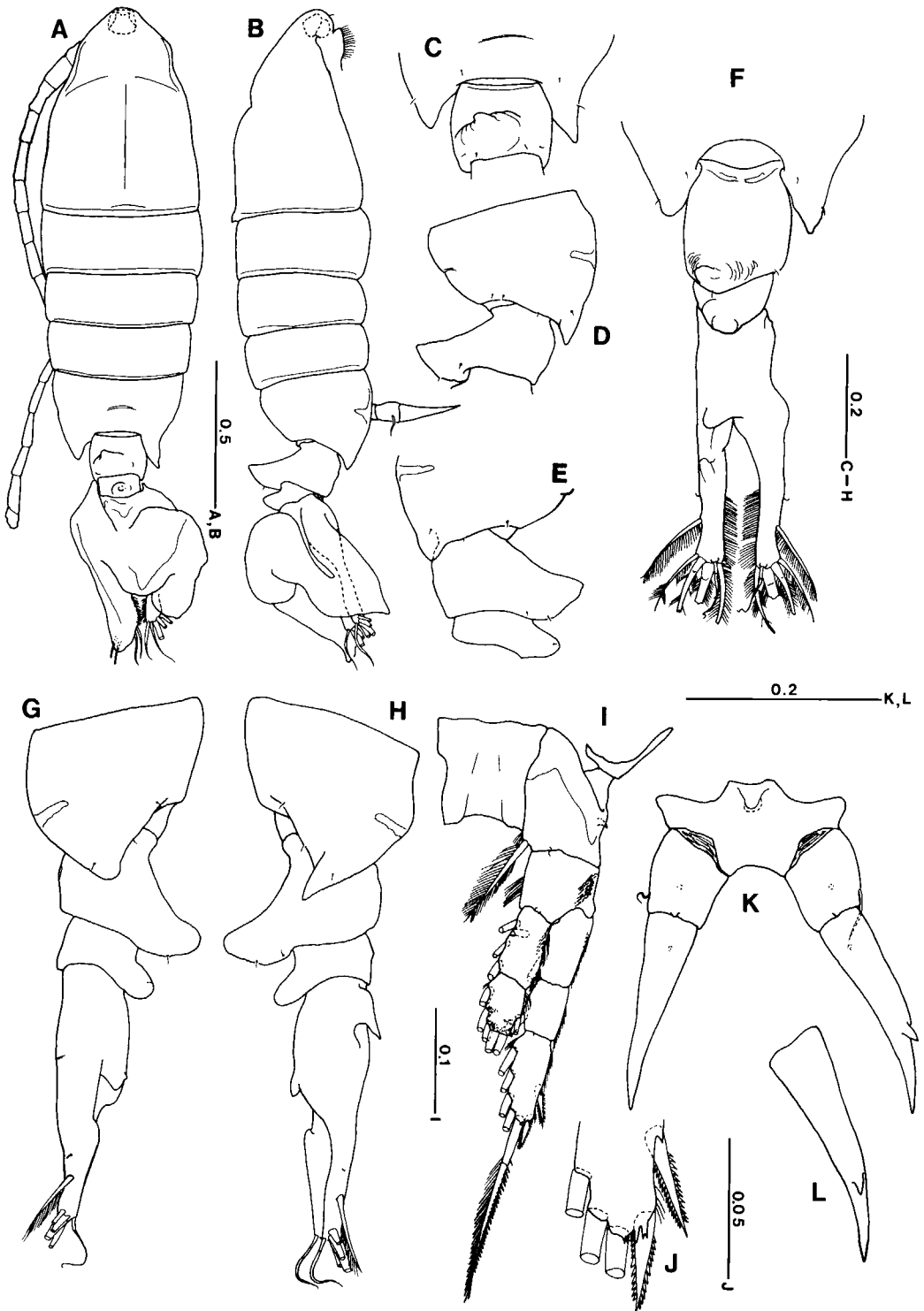


Fig. 7. *Tortanus (Eutortanus) terminalis*, new species, female (A–E, I–K: holotype; F–H, L: paratype). A, habitus, dorsal; B, habitus, right lateral; C, distal corner of prosome and genital compound somite, dorsal; D, distal corner of prosome and genital compound somite, right lateral; E, distal corner of prosome and genital compound somite, left lateral; F, distal corner of prosome and urosome, dorsal; G, posterior corner of prosome and urosome, left lateral; H, posterior corner of prosome and urosome, right lateral; I, leg 1, anterior; J, terminal portion of third exopod segment of leg 1, anterior; K, leg 5, anterior; L, left exopod of leg 5, anterior. Scale bars in mm.

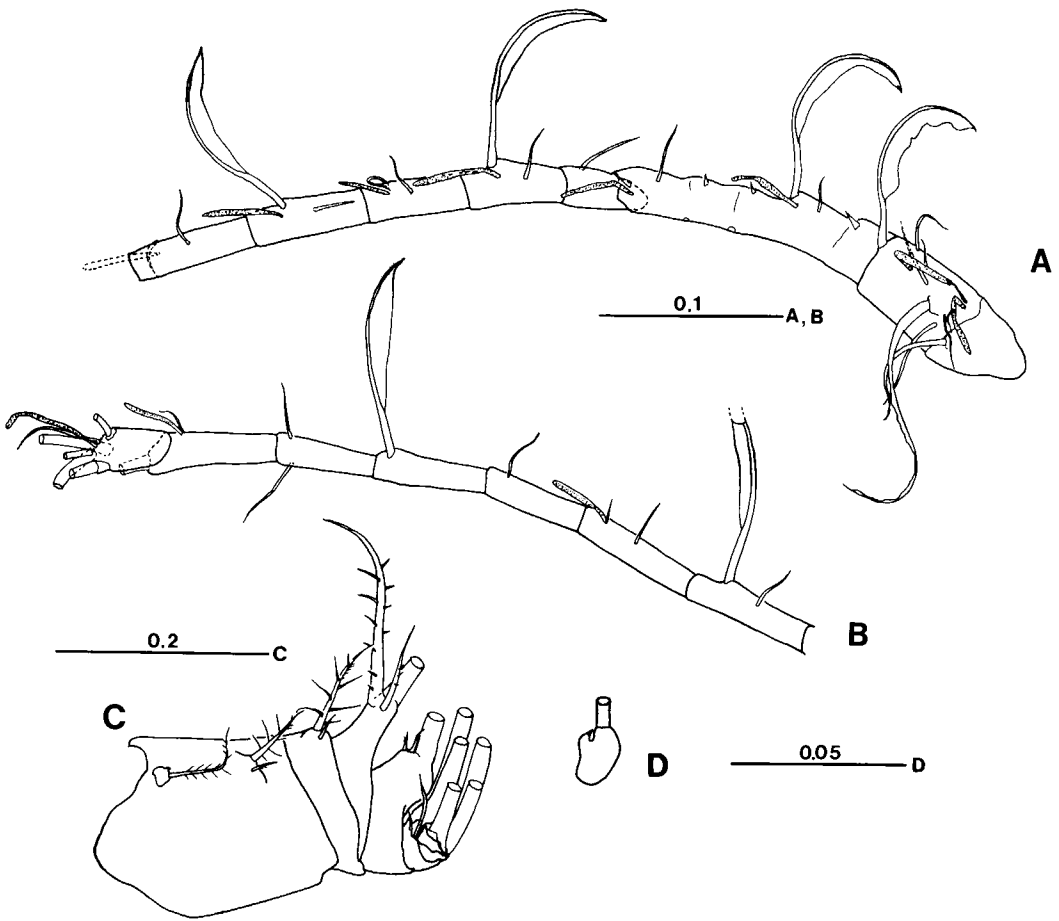
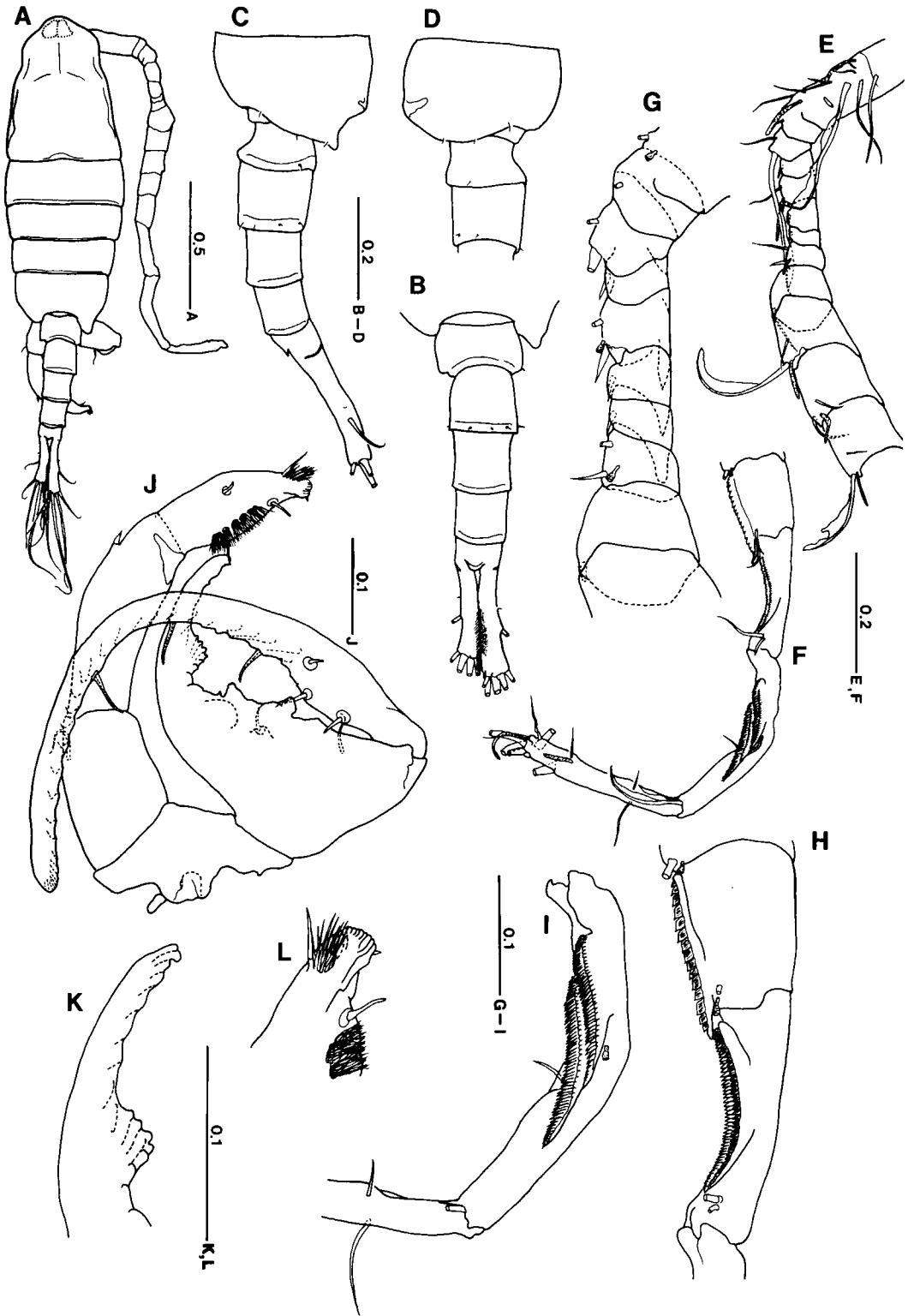


Fig. 8. *Tortanus (Eutortanus) terminalis*, new species, female (holotype). A, antennule, segments I–XIX; B, antennule, segments XX–XXVIII; C, maxilla, large setae on coxa, basis, and endopod omitted; D, first endite of maxilla, seta omitted. Scale bars in mm.

some (Fig. 7F–H) 3-segmented, last somite incompletely coalescent with caudal rami; genital compound somite with large dorsodistal projection bearing at least 3 hair sensilla; in holotype, complex spermatophore covering entire urosome except for dorsal sides of genital compound somite and second urosomite; second urosomite also bearing dorsodistal projection, this projection, in lateral view, not as high as that of genital compound somite; third urosomite elongate,

bearing acute process ventrolaterally on right side, with right lateral margin sinuate and left straight, almost fused to caudal rami; anal operculum round at tip, directed leftward and posteriorly. Caudal rami (Fig. 7F) asymmetrical, right ramus slightly longer than left, fringed with long setules along posterior half of inner margin; in lateral view, right ramus (Fig. 7H) tapering distally, while left ramus (Fig. 5G) expanded medially; rudimentary caudal seta I located at midlength of outer

Fig. 9. *Tortanus (Eutortanus) terminalis*, new species, male (paratype). A, habitus, dorsal; B, distal corner of prosome and urosome, dorsal; C, posterior corner of prosome and urosome, right lateral; D, posterior corner of prosome and genital and first abdominal somites, left lateral; E, right antennule, segments I–XVIII; F, right antennule, segments XIX–XXVIII; G, right antennule, segments VIII–XV; H, right antennule, segments XIX and XX; I, right antennule, segments XXI–XXIV; J, leg 5, anterior; K, inner projection of basis of right leg 5, anterior; L, terminus of second exopod segment of left leg 5, anterior. Scale bars in mm.



margin; seta II longer than seta III; seta V thick at base.

Antennule (Fig. 8A, B) reaching nearly to anus. Segments II–XIV almost completely or incompletely fused. Segments X, XII, XIII, and XIV each bearing spiniform seta. Armature as follows (see Fig. 12 also): I–1, II–IX–9 + 2 ae, X–1, XI–2 + ae, XII–1, XIII–1, XIV–2 + ae, XV–1, XVI–2 + ae, XVII–2 + ae, XVIII–2 + ae, XIX–2 + ae, XX–2, XXI–2 + ae, XXII–1, XXIII–1, XXIV–1 + 1, XXV–1 + 1 + ae, XXVI–XXVIII–6 + ae. Antenna to maxillule and maxilliped with same segmentation and setation as in *Tortanus dextrilobatus*, redescribed by Ohtsuka *et al.* (1992). Maxilla (Fig. 8C) differing from that of *T. dextrilobatus* in the presence of, presumably, rudimentary element on first praecoxal endite (Fig. 8D) and of minute seta on first coxal endite.

Leg 1 (Fig. 7I) with 2-segmented endopod and 3-segmented exopod; suture present between original first and second segments of endopod; distal endopod segment with patches of minute spinules terminally and subterminally; distal exopod segment with mono- or bicuspid prominences distally (Fig. 7J). Legs 2–4 with same armature as in *T. dextrilobatus* (see Ohtsuka *et al.*, 1992).

Leg 5 (Fig. 7K, L) uniramous, slightly asymmetrical with left leg slightly longer than right, with both coxae and intercoxal sclerite fused to form common base; basis as long as wide, bearing fine seta at posterior one-fifth of outer margin and minute integumental pore on posteromedial surface; exopod 1-segmented; left exopod curved slightly inward, bearing pointed process at distal one-third of its length; right exopod barely curved, tapering distally.

Male. Body (Fig. 9A) more slender than that of female; fourth and fifth pedigers almost fused, with suture visible only ventrolaterally; prosomal corners asymmetrical with right longer than left; right corner, in lateral view, having posteriorly directed, round prominence, whereas left corner smoothly rounded. Urosome (Fig. 9B–D) 5-segmented, with anal somite incompletely fused to caudal rami; genital somite slightly asymmetrical, with left distal corner protruded posteriorly; second urosomite carrying relatively long hair sensilla along distal margin; anal operculum round at tip; caudal rami asymmetrical, right longer than left.

Right geniculate antennule (Fig. 9E–I): segments II–VII, XXI–XXIII, and XXIV–XXVIII almost completely fused; segments I and II–VII, II–VII and VIII, and IX–XII incompletely fused (Fig. 9E, G); segments X–XIV each with spiniform seta; segment XV with sheathlike extension. Armature of segments as follows (see Fig. 13 also): I–1, II–V–5 + ae, VI–2, VII–2 + ae, VIII–1, IX–2, X–1, XI–2 + ae, XII–1, XIII–1, XIV–2 + ae, XV–1, XVI–2 + ae, XVII–2 + ae, XVIII–2 + ae, XIX–1 + ae + process, XX–1 + ae + process, XXI–XXIII–2 + ae + 2 processes, XXIV–XXVIII–10 + 2 ae. Segments XIX, XX, and XXI–XXIII bearing 1, 1, and 2 serrate processes along anterior margin, respectively (Fig. 9F, H, I); compound segment XXIV–XXVIII bearing round prominence distally.

Legs 1–4 as in female except for distal monocusped prominences on third exopod segment of leg 1. Leg 5 (Fig. 9J–L) stout; both coxae and intercoxal sclerite fused to form common base. Right leg 5 heavily sclerotized; basis expanded inward into stout, sinuate projection (Fig. 9K), with 3 prominences along outer margin of projection and 2 low protuberances and 2 setules on posterior surface; exopod slender, longer than entire length of left leg, smoothly curved inward, sinuate along inner margin, bearing 6 setae, all of which except proximal one having minute pore at tip. Left leg 5 with basis having fine outer seta at distal one-third of length; exopod incompletely 2-segmented, first segment elongate with subterminal outer spine, second segment bearing 6 tufts of fine setules and 2 setae along inner margin and tuft of long spinules and 2 setae along outer margin, with sinuate tip bearing minute subterminal spine (Fig. 9L).

Variation.—Although the posterior ends of the female prosome are always asymmetrical with the right longer than the left, the shape of the tips is slightly variable (Fig. 7C–H). The subterminal pointed process on the left exopod of the female leg 5 is directed slightly outward (Fig. 7K) or distally (Fig. 7L).

Remarks.—The new species is readily distinguishable from the other species of the subgenus *Eutortanus* in having: (1) leg 1 with 2-segmented endopod, (2) the urosome of the female with dorsal swellings on the genital compound somite and the second urosomite, and a ventrolateral pointed process on the last

urosomite, (3) leg 5 of the female with a sub-terminal prominence on the left exopod, and (4) the right exopod of the male leg 5 with a strongly developed inner process on the basis and an extremely elongated exopod. The complex spermatophores of the new species may also be a diagnostic character in the subgenus, because the other species of the subgenus have a relatively simple, sausage-like spermatophore (Ohtsuka *et al.*, 1995). Complicated spermatophores are common in the subgenus *Atortus* (Tanaka, 1965; Othman, 1987; Ohtsuka and Kimoto, 1989), but rare in the other subgenera.

The new species has characters unique in the subgenus. All other species of the subgenus *Eutortanus* have a 3-segmented endopod of leg 1, while only the new species has a 2-segmented one. However, it is clear that the new species is a member of the subgenus *Eutortanus* because of the following synapomorphies: (1) the fourth and fifth pedigers are almost completely fused; (2) the right caudal ramus is longer than the left; (3) the second endopod segments of legs 2 and 3 have 7 setae; (4) the exopod of the female leg 5 bears no element along the outer margin; and (5) the developed chelate structure is formed by the basal process and the elongate exopod of the right leg 5 of the male. The unique characters of the new species obscure its relationship to other members of the subgenus. The distinctly produced prosomal corners of the female and the chelate structure of the right leg 5 of the male are indicative of its close relationship to *T. derjugini* and *T. dextrilobatus*.

Etymology.—The specific name *terminalis* (Latin, meaning terminal) alludes to its isolated occurrence in Japanese waters compared with the distribution of most other species of the subgenus in brackish waters on the East Asian continental coasts (Ohtsuka *et al.*, 1992).

Distribution.—The new species has so far been recorded only from the type locality (arrowed in Fig. 10A), Shibushi Bay, Kagoshima (H. Ueda, personal communication), and Tanabe Bay, Wakayama (S. Ohtsuka, personal observation) (Fig. 10A). In contrast to the fact that most members of the subgenus *Eutortanus* are restricted to brackish waters along the East Asian continent, the new species occurs only in neritic waters of high salinity (Fig. 10A).

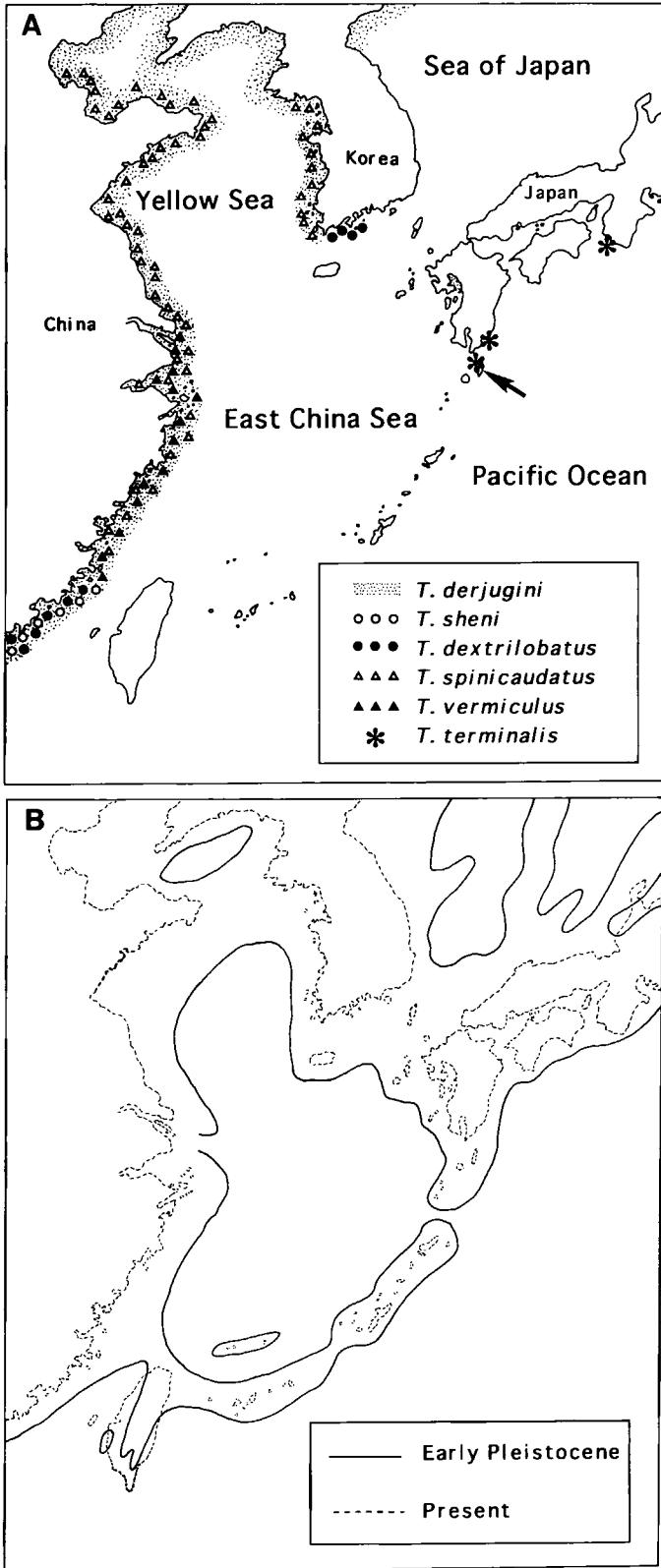
Discussion

The morphology, phylogeny, and zoogeography of the genus *Tortanus* are discussed. First, the structure of the right leg 5 of the male is taken into account. This leg is modified into a grasping organ, and the explanation of Giesbrecht (1892) of the segmentation was subsequently followed by Ohtsuka *et al.* (1987, 1992, 1995), Ohtsuka and Kimoto (1989), and Ohtsuka (1992). However, the system of Giesbrecht is reconsidered in the present study. Second, some distinct evolutionary trends found in the bodies and appendages of the five subgenera of *Tortanus* are pointed out. Third, a cladistic analysis is employed in order to infer their phylogenetic relationships, origins, and dispersal patterns.

Male Leg 5

The structure of the adult male leg 5 of *Tortanus*, in particular the right leg, has not been clearly understood. Giesbrecht (1892) thought that the right leg was composed of a coxa, basis, and 2-segmented exopod, the exopod forming a chela. This system was wholly or partly followed by Bowman (1971), Ohtsuka *et al.* (1987, 1992, 1995), Ohtsuka and Kimoto (1989), and Ohtsuka (1992). Through observations of the fifth copepodid stages of males of *T. (Tortanus) gracilis* (Fig. 11C, D), *T. (Eutortanus) derjugini* (Fig. 11A, B), *T. (Boreotortanus) discaudatus* (see Johnson, 1934), and *T. (Atortus) capensis* (Grindley, 1978), we have concluded that this system is incorrect.

The most important tool to trace the homology of segments and elements through development is to examine the newly formed appendage under the cuticle of the preceding stage (cf. Hulsemann, 1991). The second segments of the adult male leg 5, with an outer (or posterior) seta on each side, are referred to as the basis. Both coxae and the intercoxal sclerite are completely fused to form a common base in the fifth and sixth (adult) copepodid stages of the above four species. The segment(s) distal to the basis were called the exopod (Giesbrecht, 1892; Ohtsuka and Kimoto, 1989; Ohtsuka, 1992; Ohtsuka *et al.*, 1992, 1995) or endopod (Jones and Park, 1968; Bowman, 1971). Presumably the process on the right basis of the fifth copepodid stages of *T. (B.) discaudatus* and *T. (E.) derjugini* corresponds to the vestigial endopod. *Labidocera tasmanica* Nyan, 1974, of the



closely related family Pontellidae, apparently bears a 1-segmented rudimentary endopod and 2-segmented well-developed exopod on each side of leg 5 of the fifth copepodid stage male, and the endopod is absent in the adult male (Nyan, 1974). This observation supports the conclusion that the segment distal to the common base (fused coxae) of the right leg 5 of male *Tortanus* should be referred to as the basis.

The fifth copepodid stage has a 2-segmented exopod in *T. (E.) derjugini* (Fig. 11A), and a 1-segmented one in *T. (B.) discaudatus* (see Johnson, 1934) and *T. (T.) gracilis* (Fig. 11C). *Tortanus (A.) capensis* bears a 2-segmented exopod on the left side and a 1-segmented one on the right in this stage, judging from the illustration of Grindley (1978). The 1-segmented exopod of the adult *T. (E.) derjugini* is formed in the 2-segmented exopod of the preceding stage (Fig. 11A). On the other hand, a proximal spiniform seta (arrowed in Fig. 11D) on the exopod of adult *T. (T.) gracilis* can be seen from the fifth copepodid stage onward (arrowed in Fig. 11C). These present observations strongly support the assumption that the distal two segments of the right leg 5 forming a chela are the basis and 1-segmented exopod, respectively. The separation of the left exopod and the secondary fusion of the right exopod at the final molt may be heterochronically controlled in the ontogeny of each genus or species.

The chelate structure of the right leg 5 of the male in the Tortanidae is unique. The closely related families Pontellidae and Acartiidae form a chela consisting of the two distal exopod segments, whereas the genus *Candacia* of another related family, the Candaciidae, may be similar to the Tortanidae in the structure of the right leg 5 of the male (cf. Giesbrecht, 1892).

Morphological Transformation

Transformations of the somites and appendages occur in the five subgenera of *Tortanus*, making a phylogenetic analysis of the subgenera possible. Before the analysis, we discuss these transformations among the subgenera and autapomorphic characters of each

subgenus. The autapomorphic characters are excluded from the phylogenetic analysis.

1. Pedigers 4 and 5. The fourth and fifth pedigers of both sexes are separate in the subgenera *Acutanus* and *Tortanus* and fused in *Boreotortanus*, *Eutortanus*, and *Atortus*. Although in the Calanoida the fusion of these somites is commonly a result of convergence, we assume that this separation is a symplesiomorphy accompanied by the symmetrical and not posteriorly produced fifth pediger. The asymmetrical winglike expansions of pediger 5 of the female are conspicuous in *Boreotortanus* and *Eutortanus*, but their homology is unknown. Some species of *Atortus* have an asymmetrical and posteriorly produced pediger 5, while others bear a symmetrical rounded one.

2. Urosome of the female. The number of urosomites is consistently 2 or 3. The only exception is *T. (E.) sheni* (= *T. denticulatus* Shen and Lee, 1963) with a 4-segmented urosome. Although Shen and Lee (1963) stated that the type specimens of the species are deposited at the Institute of Zoology, Academia Sinica, Beijing, it was impossible to borrow these from the institute in spite of several attempts. We had to abandon examining this species directly and have excluded it from the phylogenetic analysis. This species has never been encountered in Chinese waters since the original description in 1963 (C. Haung, personal communication).

The last compound somite of the 3-segmented urosome is probably homologous to the original anal somite and its preceding somite in the calanoid Bauplan (cf. Huys and Boxshall, 1991). In the case of the 2-segmented urosome, the original first free abdominal somite is presumably incorporated in the genital double-somite. A 3-segmented urosome is consistently found in the subgenera *Boreotortanus*, *Eutortanus* (except *T. sheni*), *Tortanus*, and *Acutanus*. Although the 2-segmented condition is usual in the subgenus *Atortus*, *T. (A.) erabuensis* has an indistinctly 3-segmented urosome, in which the second urosomite is incompletely fused to the genital double-somite.

Fig. 10. A, horizontal distribution of the subgenus *Tortanus (Eutortanus)* modified from Ohtsuka *et al.* (1992), Tanega Island (type locality of *T. (E.) terminalis*) arrowed; B, paleogeography of the East China Sea and its neighboring regions during the Early Pliocene, the dotted line indicating the present coastline (redrawn after Kizaki and Oshiro, 1977, with permission of Kaiyou Shuppan Co., Ltd.).

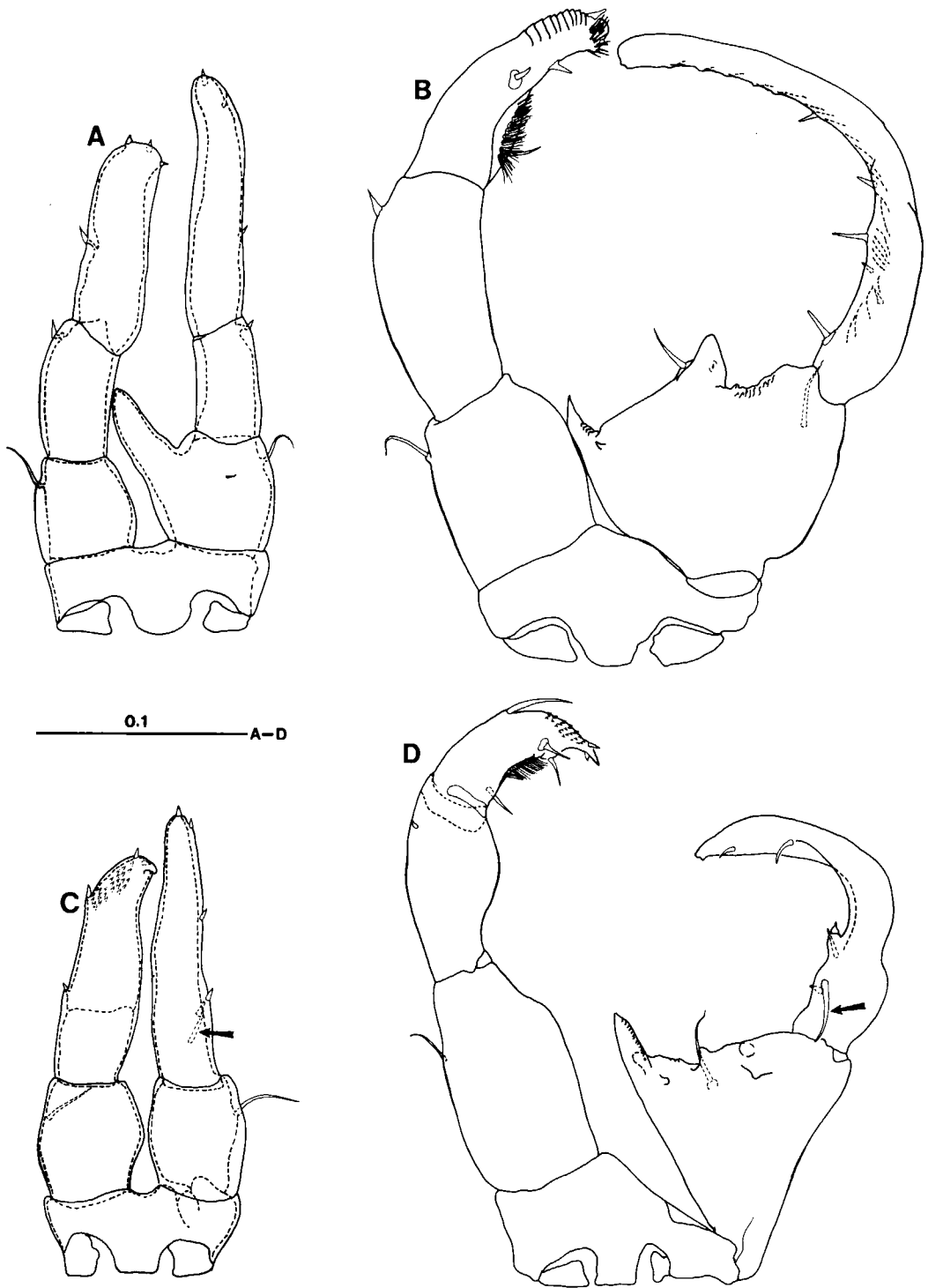


Fig. 11. Leg 5 of fifth (A, C) and sixth (B, D) copepodid stages of males. *Tortanus (Eutortanus) derjugini* (A, B); *Tortanus (Tortanus) gracilis* (C, D). Note newly formed leg 5 of adult stage within preceding stage (thick dotted line in A, C). Arrows in C, D indicate a presumed homologous seta. Scale bar in mm.

The anal somite and caudal rami are diagnostic for each subgenus. In females these are completely or incompletely fused, and usually asymmetrical. The anal somite usually possesses dorsal, ventral, or lateral projection(s) or swelling(s). An acute dorsomedial process (anal operculum) on the anal somite is found only in *Acutanus*, except for the new species, *T. (A.) ecornatus*.

The degree of asymmetry of the caudal rami varies in the genus. In *Atortus* and *Acutanus*, they are symmetrical or nearly so. In *Eutortanus* and *Tortanus*, the rami are always asymmetrical with the right ramus longer than the left. The caudal rami of *Boreotortanus* are considerably asymmetrical, with the right ramus being longer and much wider than the left ramus, and with seta II modified as a stout process solely on the right side.

Both sexes of all three species of the subgenus *Tortanus* possess a triangular terminal prominence on the dorsal side of each caudal ramus, a feature unique to the subgenus.

3. Urosome of the male. All species of *Eutortanus* and *Tortanus* lack a process or swelling on the right distal corner of the second urosomite (first abdominal somite), which is probably the plesiomorphic state. In some taxa, this somite is furnished with such a structure on the right distal corner. Some species of the subgenus *Atortus* (= *Tortanus*) (*Atortus*) *brevipes* complex sensu Ohtsuka and Kimoto, 1989) have a distinct acute process on the somite, while those of the *T. (A.) recticauda* complex sensu Ohtsuka and Kimoto (1989) lack it. In *Boreotortanus*, the right distal corner of the somite is produced laterally into a round swelling (Fig. 3B, C). In *Acutanus*, the shape of the right distal corner of the somite is variable. *Tortanus angularis* and *T. ecornatus* possess a distinct acute, posteriorly directed process as in the *T. (Atortus)* *brevipes* complex, whereas *T. compernis* and *T. setacaudatus* bear a relatively simple, laterally produced small prominence (Ohtsuka, 1992). Judging from microstructures such as integumental hair sensilla on the somite, these seem not to be homologous. For example, the *T. (Atortus)* *brevipes* complex has one large acute and one minute process, each bearing a sensillum at its tip (Jones and Park, 1968; Othman, 1987; Ohtsuka and Kimoto, 1989), while *T. (Acutanus)* *angularis* and *T. (A.) ecornatus* bear one large acute process with one subterminal and one basal sensillum

(see Fig. 6C). Therefore, the presence of a process or swelling on the second urosomite is unavailable for the cladistic analysis.

The anal somite is separate from the caudal rami in *Boreotortanus*, while in *Atortus* these are incompletely fused. These are separate in some species of *Eutortanus*, *Tortanus*, and *Acutanus*, but fused in others. Hence, fusion of the anal somite and the caudal rami seems to have occurred independently within each of these three subgenera. In *Boreotortanus*, the caudal rami are considerably asymmetrical, with the right seta II heavily sclerotized and larger than the left seta II. In the subgenus *Tortanus*, each caudal ramus is very slender and possesses a triangular process dorsodistally as in the female.

4. Antennule of the female. Many transformations are found in the antennules (Fig. 12). The most primitive states of the segmentation and armature elements are exhibited by *Boreotortanus* (see Tables 2, 3; Fig. 12). Reduction of elements is found in the ancestral segments X, XII, XIII, XIV, XV, XVII, XIX, XXI, and XXIV in the other subgenera. The fusion pattern and armature elements are the same in both the *brevipes* and *recticauda* complexes of *Atortus*.

5. Right antennule of the male. As in the female antennule, the most plesiomorphic states are retained by *Boreotortanus* (Fig. 13). The other subgenera show reductions in the number of elements on the ancestral segments VI, VIII, X, XII, XIII, XIV, XV, XVII, XIX, XX, and XXIV (Fig. 13).

The fusion pattern and armature elements are the same in both the *brevipes* and *recticauda* complexes of *Atortus* as in the female.

6. Antenna. The only difference between the subgenera is the number of setae on the coxa and basis. Both *Eutortanus* and *Tortanus* have primitive conditions (1 coxal and 2 basal setae), while the other subgenera show more advanced states (no coxal seta in *Acutanus* and *Atortus*; 1 basal seta in *Boreotortanus*, *Acutanus*, and *Atortus*).

7. Maxillule. The praecoxal arthrite shows different conditions. The most primitive state is retained by *Eutortanus* and *Atortus*, with 13 elements in all. These elements are easily identified based on their relative size and position (Fig. 14). The subgenus *Tortanus* lacks only one posterior seta, whereas both *Boreotortanus* and *Acutanus* lack 2 setae (see Fig. 14).

Table 2. Characters used in cladistic analysis for five subgenera of the genus *Tortanus*. Codes 0–3 refer to transformation series of multistate characters. 0 = plesiomorphic.

Characters	States	Score
1. Pedigers 4 and 5 in female	separate/fused	0/1
2. Pedigers 4 and 5 in male	separate/fused	0/1
3. Numbers of setae on segment X of female antennule	2/1	0/1
4. Number of setae on segment XII of female antennule	2/1	0/1
5. Number of setae on segment XIII of female antennule	2/1	0/1
6. Aesthetasc on segment XIV of antennules of both sexes	present/absent	0/1
7. Elements on segment XV of female antennule	2 + aesthetasc/1	0/1
8. Elements on segment XVII of female antennule	2 + aesthetasc/1 + aesthetasc/1/0	0/1/2/3
9. Elements on segment XIX of female antennule	2 + aesthetasc/1 + aesthetasc/aesthetasc	0/1/2
10. Number of setae on segment XXIV of female antennule	1 + 1/1	0/1
11. Segments I and II of right antennule of male	separate/fused	0/1
12. Number of setae on segment VI of right antennule of male	2/1	0/1
13. Number of setae on segment VIII of right antennule of male	2/1	0/1
14. Number of setae on segment X of right antennule of male	2/1	0/1
15. Number of setae on segment XII of right antennule of male	2/1	0/1
16. Number of setae on segment XIII of right antennule of male	2/1	0/1
17. Elements on segment XV of right antennule of male	2/1	0/1
18. Aesthetasc on segment XVII of right antennule of male	present/absent	0/1
19. Aesthetasc on segment XIX of right antennule of male	present/absent	0/1
20. Aesthetasc on segment XX of right antennule of male	present/absent	0/1
21. Number of setae on segment XXIV of right antennule of male	1 + 1/1	0/1
22. Seta on antennal coxa	present/absent	0/1
23. Number of setae on antennal basis	2/1	0/1
24. Number of setae on maxillular praecoxal arthrite	13/12/11	0/1/2
25. Number of setae on maxilliped syncoxa	5/2	0/1
26. Number of endopod segments of leg 1	3/2	0/1
27. Number of outer spines on third exopod segment of leg 1	2/1	0/1
28. Number of setae on second endopod segment of leg 2	8/7/6	0/1/2
29. Number of setae on second endopod segment of leg 3	8/7/6	0/1/2
30. Number of setae on second endopod segment of leg 4	7/6	0/1
31. Inner basal seta of left leg 5 of male	present/absent	0/1
32. Inner seta on first exopod segment of left leg 5 of male	present/absent	0/1
33. Elongation of basis and first exopod segment of left leg 5 of male	no/yes	0/1

Table 3. Character data matrix (see Table 2). 0 = ancestral state; 1 = derived state; 2 and 3 = more derived states.

Subgenus	Character state																																		
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Boreotortanus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	1	0
<i>Eutortanus</i>	1	1	1	1	0	1	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	
<i>Tortanus</i>	0	0	1	1	0	1	1	1	0	1	0	1	1	1	1	0	1	1	0	0	0	1	0	1	0	1	0	1	0	1	1	1	1	0	
<i>Atortus</i>	1	1	0	1	1	1	3	2	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	2	2	1	0	0	1	1	
<i>Acutanus</i>	0	0	0	1	0	1	1	2	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	2	2	1	0	0	1

8. Maxilla. The first coxal endite primitively bears two setae of unequal length, but the rudimentary seta is absent in *Acutanus* and some species of *Eutortanus*.

9. Maxilliped. There are two types of armature on the syncoxa: (1) three endites with 2, 2, and 1 spinulose setae, respectively; (2) two endites each carrying one spinulose seta. The former is found in *Boreotortanus*, *Eu-*

tortanus, and *Tortanus*, and the latter in *Acutanus* and *Atortus*. Based on the relative position of these endites and the size of the spinulose setae, the whole first (proximal) endite with two setae and a smaller seta on the second (middle) endite of the former group are absent in the latter group. According to Johnson (1934), the proximal endite of the syncoxa appears first in the second copepodid

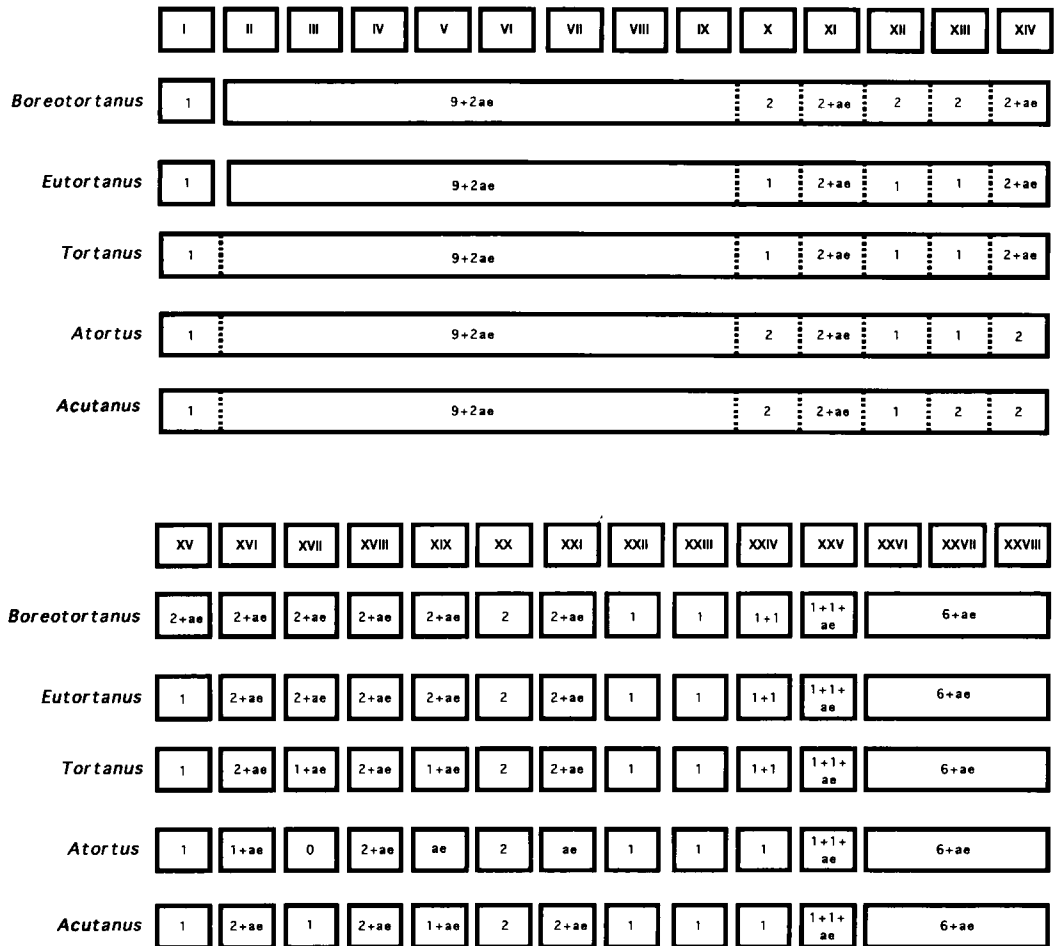


Fig. 12. Schematic illustration of fusion pattern and armature of female antennule of each subgenus of *Tortanus*. Roman and Arabic numerals indicate numbers of ancestral segments and of setae, respectively. ae = aesthetasc.

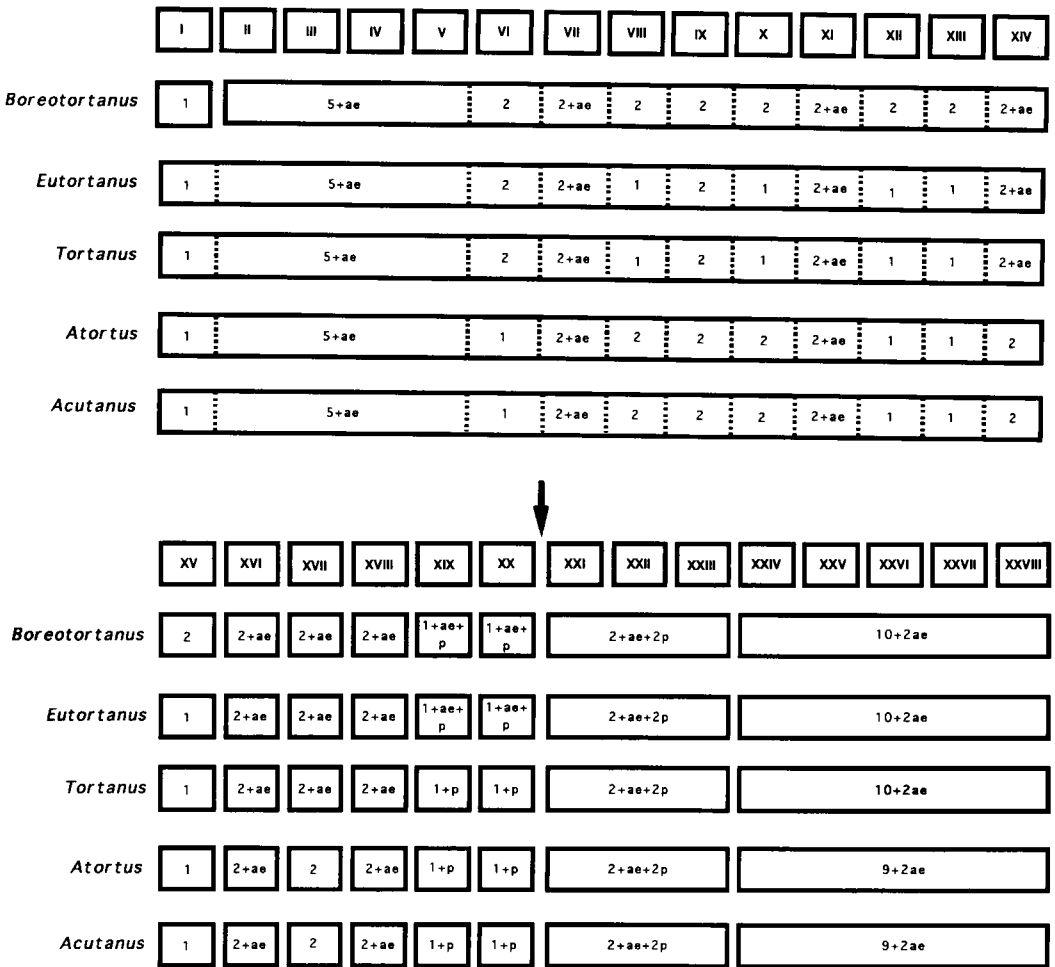


Fig. 13. Schematic illustration of fusion pattern and armature of right antennule of male of each subgenus of *Tortanus*. Roman and Arabic numerals indicate numbers of ancestral segments and of setae, respectively. ae = aesthetasc; p = process modified from element. Arrow indicates position of hinge.

stage. The advanced state of both *Acutanus* and *Atortus* may be regarded as a suppressed state of the first copepodid stage.

10. Leg 1. The most plesiomorphic state is found in *Boreotortanus* and *Eutortanus* except for *T. (E.) terminalis*, with 3-segmented rami, and two outer spines on the third exopod segment. The most derived state occurs in *Acutanus* and *Atortus*: 2-segmented endopod, and one outer spine on the third exopod segment. *Tortanus (E.) terminalis* and the subgenus *Tortanus* have the combination of a 2-segmented endopod and two outer spines on the third exopod segment. Apparently the fusion of segments occurred independently within *Eutortanus* and the *Tortanus-Atortus-Acutanus* clade (see Fig. 15). Based on the position of outer spines on the third exopod

segment, the terminal spine is lost in *Acutanus* and *Atortus*. It is worth noting that this reduction is not a suppression of the “youngest” spine during development (cf. Ferrari, 1991). It may be that dedifferentiation of elements occurs during development.

11. Leg 2. The most primitive states of the armature elements are found in *Boreotortanus* and *Eutortanus*, with three outer spines on the third exopod segment, and eight setae on the second endopod segment. The number of setae on the second endopod segment is seven in *Tortanus* and six in both *Acutanus* and *Atortus*. Perhaps the proximal outer seta is absent in the former and both one inner and one outer proximal setae are lacking in the latter. These “youngest” setae (cf. Ferrari, 1991) seem to be suppressed during the develop-

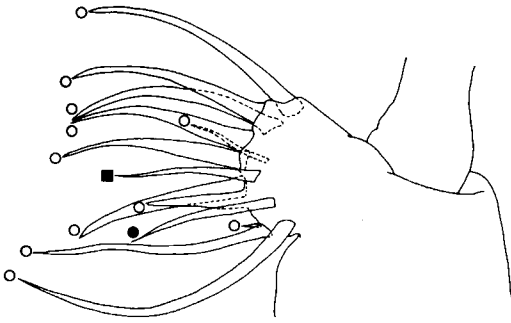


Fig. 14. Maxillular praecoxal arthrite of *Tortanus*. Open circles indicate elements found in all subgenera of the genus *Tortanus*; closed square indicates that the subgenus *Tortanus* lacks this seta; closed circle indicates that the subgenera *Boreotortanus* and *Acutanus* lack this element in addition to the element symbolized by the closed square.

ment of legs between the last and penultimate copepodid stages.

In *Acutanus*, the outer spines on the exopod are variably changed. *Tortanus* (*A.*) *ecornatus* has a minute outer prominence on the second segment instead of an outer spine, while other species of *Acutanus* have a distinct outer spine. *Tortanus* (*A.*) *angularis* shows intraspecific variation in the number of outer spines on the third exopod segment, with two in specimens from Belize and three in those from Mexico. It is not certain whether this difference is consistent between these two localities, because only a few individuals from Mexico have been examined.

12. Leg 3. Evolutionary trends are the same as in leg 2. In *T.* (*Acutanus*) *ecornatus*, the same extreme reduction of elements is found as in leg 2, with no outer spine on the second exopod segment, and the proximal spine on the third exopod segment being absent. Since the reduced elements of legs 2 and 3 in *T.* (*A.*) *ecornatus* correspond to the youngest and second youngest elements of *T.* (*B.*) *discaudatus* (see plate IV, Johnson, 1934), the double suppression may occur through the second to the fifth copepodid stages.

13. Leg 4. There are differences between the subgenera in the numbers of setae on the second endopod segment and of the outer spines on the third exopod segment. Seven setae are present on the former segment in *Boreotortanus* and six in the other subgenera. The outer proximal (youngest) seta of *Boreotortanus* is presumably suppressed in the other subgenera. The exception is *T.* (*A.*)

ecornatus, in which there are two outer proximal spines on the third exopod segment (three in the other species). In contrast to legs 2 and 3, leg 4 exhibits reduction of only the youngest outer spine, but not the second youngest spine.

14. Leg 5 of the female. The fifth leg shows a wide variety of transformations. The most primitive state is found in *T.* (*Acutanus*) *setacaudatus* with a 1-segmented exopod with four distinct spines whose bases are separate from the segment. The most reduced state is found in some species of *Atortus*, in which coxae, intercoxal sclerite, and basis coalesce, with a basal seta on each side, and the exopod is completely lost. It is difficult to trace evolutionary trends, in particular, of elements on the exopod among the subgenera. *Boreotortanus*, *Eutortanus*, and *Tortanus* bear three rudimentary spines along the outer margin of the exopod (see Fig. 2E, arrowed) which may be homologous to an outer and two terminal spines of *T.* (*A.*) *setacaudatus* (cf. fig. 5C, Ohtsuka, 1992). The innermost spine of the latter species may be modified in a process extending beyond the terminal outer spine of the former subgenera. In fact, the remaining species of *Acutanus* have an innermost process instead of a spine (Ohtsuka, 1992; present study). However, there is another possibility that these are not homologous, because the exopod of the fifth copepodid stage of female *Boreotortanus* bears four minute outer spines (Johnson, 1934). *Eutortanus*, except for *T.* (*E.*) *terminalis*, has neither outer spines nor processes.

In the *brevipes* complex of *Atortus*, only *T.* *giesbrechti* and *T.* *tropicus* have exopods. The exopod of *T.* *giesbrechti* has one inner and one outer spine on the right leg and only one inner spine on the left leg, while in *T.* *tropicus* there is one terminal spine on both sides with an additional terminal spinous prominence only on the left leg. In the *recticauda* complex there are one to four terminal and subterminal spinelike processes on the exopod. Only *T.* *capensis* and *T.* *recticauda* have one or two inner elements on the exopod. Although the development of the female leg 5 of *Atortus* is partly described (Grindley, 1978), the homology of these elements is unknown.

Some distinct evolutionary trends are found among species of a subgenus. In *Tortanus*, the most primitive condition is retained by *T.* *gra-*

cilis with almost symmetrical exopods, while derived states are found in *T. forcipatus* and *T. barbatus* with remarkably asymmetrical exopods. In the *brevipes* complex of *Atortus*, the loss of the exopod is usual except for the above-mentioned two species.

15. Leg 5 of the male. The torsion of the right exopod segments is unique to *Acutanus*. This subgenus forms a chela with the exopod segment attached to the inner proximal portion of the basis. In *Acutanus* and *Atortus*, the elongation of the basis and the first exopod segment of the left leg seems to be a synapomorphy, while the presence of an inner setule on these segments is a symplesiomorphy. Since the right leg is remarkably modified as a grasping organ in each species, it is difficult to trace the homology of elements. The sinuate distal margin of the exopod of the left leg is shared by *Boreotortanus* and *Eutortanus*. However, this character was not included in the cladistic analysis in the present study.

Phylogeny and Zoogeography of *Tortanus*

For the phylogenetic analysis, 33 characters are compared among the five subgenera of *Tortanus* (Tables 2, 3). States of all characters are identical in both complexes of *Atortus*. A single most parsimonious cladogram was obtained, in which 10 convergences (characters 1, 2, 3, 5, 13, 14, 23, 24, 31, 32) become apparent (Fig. 15). The tree length and consistency index are 54 and 0.72, respectively. The tree shows that *Boreotortanus* is the first offshoot, subsequently followed by *Eutortanus*, *Tortanus*, and the *Acutanus-Atortus* clade. The *Eutortanus-Tortanus-Acutanus-Atortus* clade is well defined by the following synapomorphies: (1) reduced numbers of elements of antennular segments XII, XIII, and XV in both sexes, (2) the fusion of antennular segments I and II in the male, and (3) a reduced number of setae on the second endopod segment of leg 4. The *Tortanus-Acutanus-Atortus* clade shares the incomplete and almost complete fusion of antennular segments I and II in the female (not included in Table 2) and the loss of an aesthetasc on antennular segment XIX in the male. The *Acutanus-Atortus* clade is characterized by the following derived character states: (1) reduced numbers of elements on antennular segments XIV, XVII, and XXIV in the female and VI, XIV, XVII, and XXIV in the male, (2) reduced numbers of setae on the an-

tennal coxa and basis, (3) reduced numbers of elements in legs 1–3, and (4) the elongation of the basis and first exopod segment of left leg 5 of the male. It is interesting to note that reduction of elements simultaneously occurs on the same antennular segments (X, XII, XIII, XIV, XV, XVII, XXIV) in both sexes.

Taking into account the present distribution and species-diversity of the genus *Tortanus*, with the center of species richness in the Indo-Malayan region, the ancestor may have been an originally coastal, tropical plankter. *Boreotortanus* must have then secondarily adapted to cold waters. The genus *Tortanus* is presently distributed in both the Indo-West Pacific and the northwestern Atlantic, with an extension to the northeastern Pacific Ocean. The origin of *Acutanus* in the Caribbean Sea and its neighboring seas presents a problem. There are the following two possibilities: (1) relatively recent dispersal from the Indo-Malayan region through the Panama passage (cf. van der Spoel, 1983; van der Spoel and Heyman, 1983), or (2) a Tethyan relict. If we adopt the latter hypothesis, the origin of the pre-*Tortanus* form might date as far back as the late Middle Jurassic, when the Tethys Sea existed as a seaway between the present Caribbean, the Mediterranean, and the Indo-Malayan, Australian, and Antarctic regions. However, since we firmly believe that the first offshoot of *Boreotortanus* (Fig. 15) was after the Middle Miocene, the final divergence of the *Acutanus-Atortus* clade must have been later. According to the latter hypothesis, *Acutanus-Atortus* could not have evolved over a long period from the late Middle Jurassic to the Early Tertiary. It is most unlikely that its evolution was in stasis so long because the Caribbean Province in the Tethys Sea was a distinct biotope even in the Cretaceous (cf. Kaufman, 1973). Therefore, *Acutanus* must have originated from the Indo-Malayan ancestral stock and subsequently dispersed to the Caribbean. Since the present distribution of most species of the subgenera *Tortanus*, *Atortus*, and *Acutanus* is restricted to the tropical/subtropical zone, their origin may date back to the Middle Miocene or, less likely, as far back as the Middle Eocene to the Cretaceous before severe cooling of surface waters in the tropics occurred during the Oligocene glaciation. Surface temperatures in the tropical regions in the Middle Miocene are inferred to have been similar to or higher

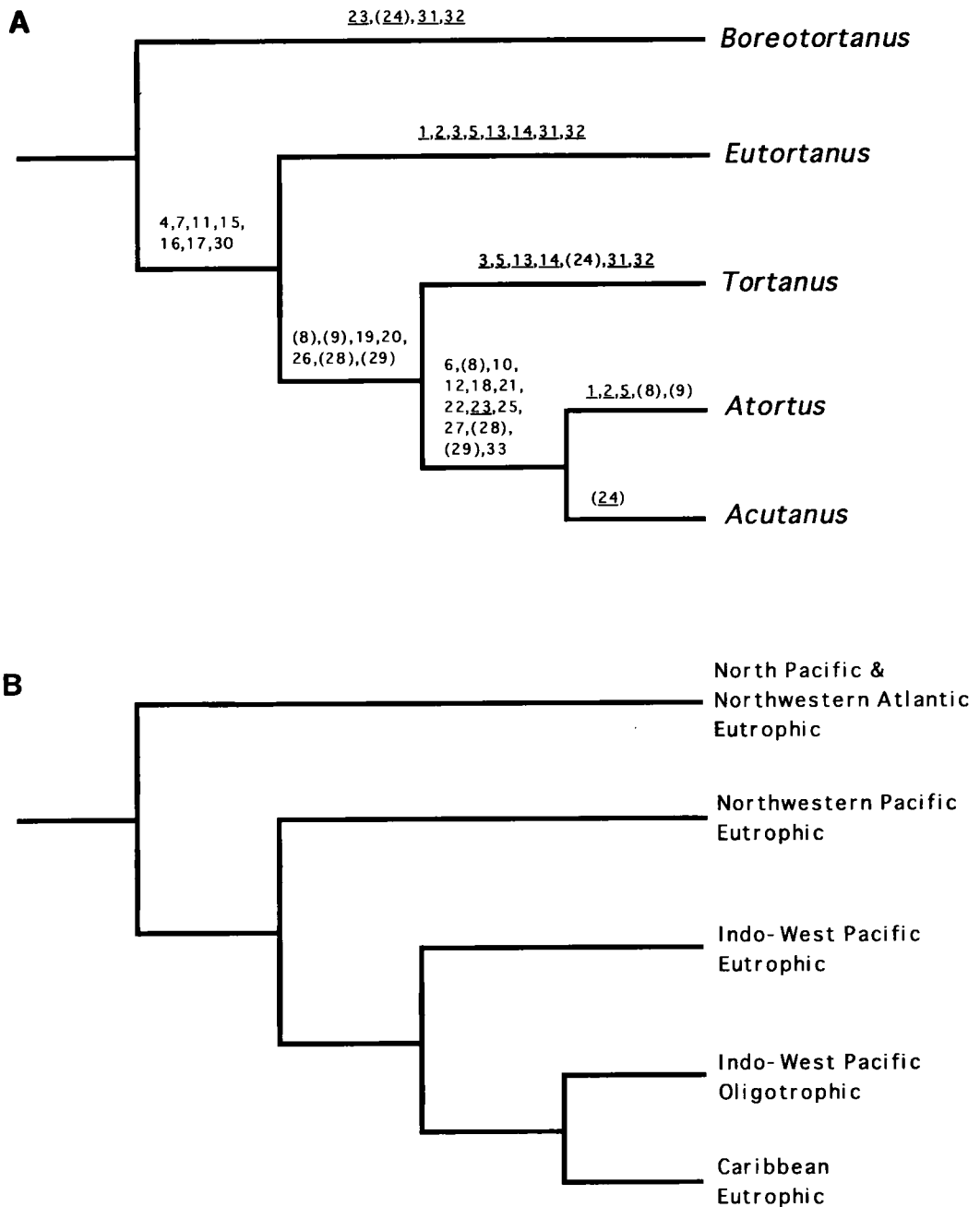


Fig. 15. Phylogenetic relationship between five subgenera of the genus *Tortanus*. A, cladogram; B, geocladogram. Numbers in A refer to characters listed in Table 2. Underlined numbers indicate convergence; numbers in parentheses indicate multiscored characters.

than temperatures of the present day (cf. Savin *et al.*, 1975).

Was it possible for the originally coastal copepods to have been transported the long distance from the Indo-Malayan region to the Caribbean? The hypothesized long journey of

the ancestor of *Acutanus* before the closure of the Panama isthmus is strongly supported by the fact that present species such as *T. (T.) gracilis* (see Fig. 4), *T. (A.) giesbrechti*, and *T. (A.) scaphus* occur as isolated populations in the central Pacific far from the distribu-

tional centers of the subgenera *Tortanus* and *Atortus* (Ohtsuka and Kimoto, 1989). These must have become dispersed recently in geological time. The much more recent dispersal of *T. (E.) terminalis*, probably by the Kuroshio Current, extends at least 500 km (see below). In addition, such a long dispersal from the Indo-West Pacific to the Caribbean is supported by the hypothetical history of another neritic zooplankter. According to van der Spoel (1983), the pelagic shrimp *Acetes*, which is now distributed in the Indo-Pacific (the Indian Ocean and both the western and eastern Pacific) and the western Atlantic (from the North American to the Brazilian coasts) regions, was of Indo-West Pacific origin. The ancestors of the western Atlantic species penetrated through either the Panama passage or pre-Amazonia into the western Atlantic. Although van der Spoel (1983) mentioned that the crossing of the Panama passage by *Acetes* may date back as far as pre-Miocene or earlier periods, he insisted in the same reference that the dispersal direction of plankton changed from westward to eastward in the oceans after the Miocene. Therefore, it is more likely that their crossing occurred after the Miocene epoch. Recently, Miya and Nishida (1997) suggested, based on a molecular phylogenetic study on the deep-sea fish *Cyclothone alba* Brauer, that tropical Pacific and Atlantic waters had been connected via the Panama passage until the isthmus completely closed about 3.2–3.8 million years ago.

The history of *Boreotortanus* and *Eutortanus* can be reconstructed from the zoogeographic hypothesis of Nishimura (1980, 1981). Both subgenera prefer low-salinity waters, and *Boreotortanus* and some species of *Eutortanus* also adapt to cold waters (cf. Mori, 1937; Brodsky, 1950; Chen and Zhang, 1965; Kim, 1985; Ohtsuka *et al.*, 1992, 1995). The complex eastern Asian archipelagoes and gulfs were formed since the Early Miocene, where pre-*Tortanus* became isolated from Indo-West Pacific populations and then adapted to cold low-salinity waters in the gulfs of East Asia (cf. Nishimura, 1980, 1981; Ohtsuka *et al.*, 1992). The ancestor of *Boreotortanus* and *Eutortanus* might have invaded the Sea of Japan and the East China Sea in the Early to Middle Miocene (approximately 19–13 MYA), when these seas became connected to the Pacific and were

characterized by warm waters (Kizaki and Oshiro, 1977; Kaseno, 1989). Isolation from the mother population in these gulfs during the Pliocene to Pleistocene resulted in the almost simultaneous evolution of *Boreotortanus* and *Eutortanus* in the ancient gulfs of the Sea of Japan and the East China Sea, respectively. Probably *Boreotortanus* and at least the northern populations of *Eutortanus* also adapted to cold waters in the Pleistocene (cf. Nishimura, 1980, 1981). The northwestern Atlantic population of *Boreotortanus* was formed secondarily from the North Pacific population. It migrated from the North Pacific to the northwestern Atlantic in a postglacial or interglacial period in the Pleistocene, without subsequent speciation (Ohtsuka *et al.*, 1992).

The extension of *T. (E.) terminalis* to the Pacific coasts of Kyushu and Honshu Islands is noteworthy (see Fig. 10A). Supposedly, this species evolved in the Early Pleistocene (cf. Kizaki and Oshiro, 1977) in the relatively high-salinity waters near the mouth of the gulf of the East China Sea (see Fig. 10B), i.e., the Tokara Strait between Tanega and Amami Islands. Its distribution may have been extended eastward by transportation via the Kuroshio Current, since the Jomonian Transgression ($\pm 10,000$ –6,000 years ago). Since this species is adapted to high-salinity waters, such transportation via oceanic waters may have been possible. The absence of this species from the islands south of Tanega Island, such as Amami, Okinawa, and Ishigaki Islands, supports this hypothesis (S. Ohtsuka, personal observation).

The origin and history of the remaining subgenera are, however, not so easily inferred as those of *Boreotortanus-Eutortanus*. Since the divergences of *Boreotortanus* and *Eutortanus* from the ancestral stock probably took place sometime during the Middle Miocene to Pliocene, the branchings of more advanced genera must have occurred later. The offshoot of *Atortus* and *Acutanus* after the divergence of *Tortanus* (Fig. 11) may have occurred after the formation of the isthmus of Panama. According to van der Spoel and Heyman (1983), the Panama passage was presumably closed in the Pliocene (± 3.5 MYA). Collins *et al.* (1996) suggested that a jet of the Pacific North Equatorial Countercurrent-Equatorial Undercurrent flowed via the passage into the Caribbean at 6 MYA. It may be that the incursion of pre-*Acutanus* from the Indo-

Malayan stock into the Caribbean was accelerated by these strong currents. There is another possibility that the pre-*Acutanus* stock had colonized the Caribbean earlier than 8 MYA. At that time, the Caribbean-Pacific surface waters may have been mixed by the opening of another strait in the Atrato Basin, northwestern Colombia (Collins *et al.*, 1996). After the corridor closed at 3.5 MYA, the Caribbean populations of pre-*Acutanus* may have diversified during the Pleistocene, while the eastern Pacific populations became extinct, as suggested by van der Spoel (1983).

All subgenera other than *Atortus* occur in highly productive brackish/neritic waters. *Atortus* tends to occur in more or less oligotrophic high-salinity (up to 34.5–40‰) waters, sometimes strongly influenced by warm currents or in coral reefs (cf. Wilson, 1932; González and Bowman, 1965; Jones and Park, 1968; Greenwood, 1978; Grindley, 1978; Chen, 1983; Ohtsuka and Kimoto, 1989; Ohtsuka, 1992; McKinnon, 1993; S. Ohtsuka, personal observation). Therefore, the present cladogram shows that the ancestor of the genus conceivably preferred eutrophic waters and that the occurrence of the genus in oligotrophic waters is an ecological apomorphy.

The northwestern Pacific populations of *Tortanus* (*T.*) *forcipatus* and *T.* (*T.*) *gracilis* and probably *Boreotortanus* produce diapause eggs for hibernation (cf. Johnson, 1967; Kasahara *et al.*, 1974; Kasahara and Uye, 1979; S. Ohtsuka, personal observation). This phenomenon indicates that these taxa must have convergently developed a tolerance for cold waters in the Sea of Japan and the East China Sea during the Pleistocene. Presumably some northern populations of *T.* (*E.*) *derjugini* occurring in the Sea of Japan, the Yellow Sea, and the Sea of Okhotsk may produce resting eggs to overwinter. This speculation is supported by the fact that the occurrence of the species was reported in the Yellow Sea only in warm months when water temperature ranges from 14.3–27.6°C (as *T. spinicaudatus*; Suh *et al.*, 1991) and in the Amur River in July and August (Smirnov, 1935).

Speciation in each subgenus (*Eutortanus*, *Tortanus*, *Atortus*, and *Acutanus*) may have occurred separately, mainly during the Pleistocene, *Eutortanus* within the East China Sea, *Tortanus* and *Atortus*, presumably, in Wallacea and its neighboring seas (cf. Fleminger, 1986), and *Acutanus* in the Caribbean Sea and

its adjacent waters. Fleminger (1986) proposed that speciation of the calanoid family Pontellidae took place in Wallacea and its adjacent waters during the Pleistocene. These vicariant events may also apply to speciation in *Tortanus* and some species of *Atortus*.

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LITERATURE CITED

- Ambler, J. W., and B. W. Frost. 1974. The feeding behavior of a predatory planktonic copepod, *Tortanus discaudatus*.—*Limnology and Oceanography* 19: 446–451.
- Anraku, M., and M. Omori. 1963. Preliminary survey of the relationship between the feeding habit and the structure of the mouth-parts of marine copepods.—*Limnology and Oceanography* 8: 116–126.
- Bowman, T. E. 1971. *Tortanus scaphus* and *Tortanus lo-phus*, new Pacific planktonic copepods, with notes on *Tortanus murrayi* (Calanoida, Tortanidae).—*Pacific Science* 25: 521–528.
- Brady, G. S. 1883. Report on the Copepoda collected by H.M.S. Challenger during the years 1873–76.—Report on the Scientific Results of the Voyage of H.M.S. Challenger, *Zoology* 8: 1–142.
- Brodsky, K. A. 1950. Calanoida of polar and far-eastern seas of the U.S.S.R.—*Opredeliteli po Faune S.S.S.R.* 35: 1–442. [In Russian.]
- Chen, Q.-C. 1983. The pelagic copepods of the South China Sea. III.—Contributions on Marine Biological Research of the South China Sea 1: 133–138. [In Chinese with English abstract.]
- , and S.-Z. Zhang. 1965. The planktonic copepods of the Yellow Sea and the East China Sea. I. Calanoida.—*Studia Marina Sinica* 7: 20–131. [In Chinese with English abstract.]
- Collins, L. S., A. G. Coates, W. A. Berggren, M.-P. Aubry, and J. Zhang. 1996. The Late Miocene Panama isthmian strait.—*Geology* 24: 687–690.
- Cordell, J. R., C. A. Morgan, and C. A. Simenstad. 1992. Occurrence of the Asian calanoid copepod *Pseudodiaptomus inopinatus* in the zooplankton of the Columbia River estuary.—*Journal of Crustacean Biology* 12: 260–269.
- Davis, C. C. 1949. The pelagic Copepoda of the north-eastern Pacific Ocean.—University of Washington Publications in Biology, New Series 14: 1–117.
- Farran, G. P. 1936. Copepoda.—Scientific Reports of the Great Barrier Reef Expedition 1928–29, British Museum (Natural History) 5: 73–142.
- Ferrari, F. D. 1991. Using patterns of appendage development to group taxa of *Labidocera*, Diaptomidae and Cyclopidae (Copepoda).—*Bulletin of Plankton Society of Japan*, Special volume, pp. 115–128.

- Fleminger, A. 1986. The Pleistocene equatorial barrier between the Indian and Pacific Oceans and a likely cause for Wallace's Line.—In: A. C. Pierrrot-Bults, S. van der Spoel, B. J. Zahuranc, and R. K. Johnson, eds., Pelagic biogeography. UNESCO Technical Papers in Marine Science 49: 84–97.
- Früchtl, F. 1924. Die Cladoceren- und Copepoden-Fauna des Aru-Archipels.—Arbeiten aus dem zoologischen Institut der Universität Innsbruck 2(2): 1–114.
- Giesbrecht, W. 1892. Systematik und Faunistik der pelagischen Copepoden des Golfes von Neapel.—Fauna und Flora des Golfes von Neapel und der angrenzenden Meeres-Abschnitte 19: 1–831.
- , and O. Schmeil. 1898. Copepoda I. Gymno-plea.—Das Tierreich 6: 1–169.
- González, J. G., and T. E. Bowman. 1965. Planktonic copepods from Bahía Fosforescente, Puerto Rico, and adjacent waters.—Proceedings of the United States National Museum 117: 241–303.
- Greenwood, J. G. 1978. Calanoid copepods of Moreton Bay (Queensland) III. Families Temoridae to Tortanidae, excluding Pontellidae.—Proceedings of the Royal Society of Queensland 89: 1–21.
- Grindley, J. R. 1978. A new species of *Tortanus* (Crustacea, Copepoda) from South Africa.—Annals of the South African Museum 74: 219–228.
- Hattori, H., and K. Tsumura. 1990. Seasonal change in zooplankton distribution off Haboro, Japan Sea.—Proceedings of Hokkaido Tokai University Science and Engineering 3: 115–128. [In Japanese with English abstract.]
- , A. Tanimura, M. Fukuchi, and O. Matsuda. 1991. Distribution of copepods in the northern Bering Sea and the Chukchi Sea in October 1988.—Proceedings of the NIPR Symposium on Polar Biology 4: 175–177.
- Hiromi, J., and H. Ueda. 1987. Planktonic calanoid copepod *Sinocalanus sinensis* (Centropagidae) from estuaries of Ariake-kai, Japan, with a preliminary note on the mode of introduction from China.—Proceedings of the Japanese Society of Systematic Zoology 35: 19–26.
- Hirota, R. 1968a. Zooplankton investigations in the Setonaikai (Inland Sea of Japan), I. Occurrence of zooplankton in the western half of the Setonaikai in June, 1963.—Journal of the Oceanographical Society of Japan 24: 203–211.
- . 1968b. Zooplankton investigations in the Setonaikai (Inland Sea of Japan), II. Occurrence of zooplankton in the eastern half of the Setonaikai in September, 1963.—Journal of the Oceanographical Society of Japan 24: 212–219.
- . 1979. Seasonal occurrence of zooplankton at a definite station off Mukaishima from July of 1976 to June of 1977.—Publications from the Amakusa Marine Biological Laboratory 5: 9–17.
- , and S. Uno. 1977. Seasonal abundance of the pelagic eggs of Copepoda in the vicinity of Amakusa-Matsushima, western Kyushu.—Bulletin of Plankton Society of Japan 24: 77–84. [In Japanese with English abstract.]
- Hulsemann, K. 1991. Tracing homologies in appendages during ontogenetic development of calanoid copepods.—Bulletin of Plankton Society of Japan Special volume, pp. 105–114.
- Huys, R., and G. A. Boxshall. 1991. Copepod evolution.—The Ray Society 159: 1–468.
- Johnson, M. W. 1934. The life history of the copepod *Tortanus discaudatus* (Thompson and Scott).—Biological Bulletin 67: 182–200.
- . 1967. Some observations on the hatching of *Tortanus discaudatus* eggs subjected to low temperatures.—Limnology and Oceanography 12: 405–410.
- Jones, E. C., and T. S. Park. 1968. A new species of *Tortanus* (Calanoida) from Pago Pago Harbor, American Samoa.—Crustaceana, supplement 1: 152–158.
- Kasahara, S., and S. Uye. 1979. Calanoid copepod eggs in sea-bottom muds. V. Seasonal changes in hatching of subitaneous and diapause eggs of *Tortanus forcipatus*.—Marine Biology 55: 63–68.
- , ———, and T. Onbé. 1974. Calanoid copepod eggs in sea-bottom muds.—Marine Biology 26: 167–171.
- Kaseno, Y. 1989. The origin of the Sea of Japan.—Aokishoten Ltd., Tokyo, Japan. Pp. 1–148. [In Japanese.]
- Kaufman, E. G. 1973. Cretaceous Bivalvia.—In: A. Hallam, ed., Atlas of paleobiogeography. Pp. 353–383. Elsevier Scientific Publishing Company, Amsterdam, The Netherlands.
- Kim, D.-Y. 1985. Taxonomical study on calanoid copepod (Crustacea: Copepoda) in Korean waters.—D. Sc. thesis. Hanyang University, Seoul, Korea. Pp. 1–187.
- Kizaki, K., and I. Oshiro. 1977. Paleogeography of the Ryukyu Islands.—Marine Science 9: 542–549. [In Japanese with English abstract.]
- Landry, M. R., and V. L. Fagerness. 1988. Behavioral and morphological influences on predatory interactions among marine copepods.—Bulletin of Marine Science 43: 509–529.
- McKinnon, A. D. 1993. A variant form of *Tortanus scaphus* Bowman, 1971 from Davies Reef, North Queensland.—Proceedings of the Royal Society of Queensland 103: 1–3.
- Madhupratap, M., and P. Haridas. 1986. Epipelagic calanoid copepods of the northern Indian Ocean.—Oceanologica Acta 9: 105–117.
- Mauchline, J. 1992. Taxonomy, distribution and biology of *Euchaeta barbata* (= *E. farrani*) (Copepoda: Calanoida).—Sarsia 77: 131–142.
- Michel, H. B., and D. C. Herring. 1984. Diversity and abundance of Copepoda in the northwestern Arabian Gulf.—Crustaceana, supplement 7, Studies on Copepoda II: 326–335.
- Miya, M., and M. Nishida. 1997. Speciation in the open ocean.—Nature 389: 803–804.
- Mori, T. 1937. Pelagic Copepoda from the neighbouring waters of Japan.—Yokendo Ltd., Tokyo, Japan. Pp. 1–150.
- Motoda, S., and T. Minoda. 1974. Plankton of the Bering Sea.—In: D. W. Hood and E. J. Kelley, eds., Oceanography of the Bering Sea. Pp. 207–241. Institute of Marine Science, University of Alaska, Fairbanks, Alaska.
- Mullin, M. M. 1979. Differential predation by the carnivorous marine copepod, *Tortanus discaudatus*.—Limnology and Oceanography 24: 774–777.
- Nishimura, S. 1980. The origin of the Sea of Japan. Second edition.—Chikuji-shokan, Tokyo, Japan. Pp. 1–288. [In Japanese.]
- . 1981. Seas and organisms on the earth: an introduction to marine zoogeography.—Kaimei-sha, Tokyo, Japan. Pp. 1–284. [In Japanese.]
- Nyan, T. 1974. A new species of *Labidocera* (Copepoda: Calanoida) from Tasmania and its postnaupliar developmental stages.—Australian Journal of Marine and Freshwater Research 25: 261–272.
- Ohtsuka, S. 1992. *Tortanus (Acutanus) angularis*, new subgenus and new species (Copepoda: Calanoida), from the Caribbean Sea, with remarks on the subgen-

- era in the genus *Tortanus*.—Proceedings of the Biological Society of Washington 105: 255–267.
- . 1997. Family Tortanidae.—In: M. Chihara and M. Murano, eds., An illustrated guide to marine plankton in Japan. Pp. 924–931. Tokai University Press, Tokyo, Japan. [In Japanese.]
- , and K. Kimoto. 1989. *Tortanus* (*Atortus*) (Copepoda: Calanoida) of southern Japanese waters, with description of two new species, *T. (A.) digitalis* and *T. (A.) ryukyuensis*, and discussion on distribution and swarming behavior of *Atortus*.—Journal of Crustacean Biology 9: 392–408.
- , Y. Fukuura, and A. Go. 1987. Description of a new species of *Tortanus* (Copepoda: Calanoida) from Kuchinoerabu Island, Kyushu, with notes on its possible feeding mechanism and in-situ feeding habits.—Bulletin of Plankton Society of Japan 34: 53–63.
- , H. Ueda, and G.-S. Lian. 1995. *Tortanus derjugini* Smirnov (Copepoda: Calanoida) from the Ariake Sea, western Japan, with notes on the zoogeography of brackish-water calanoid copepods in East Asia.—Bulletin of Plankton Society of Japan 42: 147–162.
- , Y.-H. Yoon, and Y. Endo. 1992. Taxonomic studies on brackish copepods in Korean waters. I. Redescription of *Tortanus dextrilobatus* Chen and Zhang, 1965 from Korean waters, with remarks on zoogeography of the subgenus *Eutortanus*.—Journal of the Oceanological Society of Korea 27: 112–122.
- , A. M. Shimozu, A. Tanimura, M. Fukuchi, H. Hattori, H. Sasaki, and O. Matsuda. 1996. Relationships between mouthpart structures and in situ feeding habits of five neritic calanoid copepods in the Chukchi and northern Bering Seas in October 1988.—Proceedings of the NIPR Symposium on Polar Biology 9: 153–168.
- Othman, B. H. R. 1987. Two new species of *Tortanus* (Crustacea, Copepoda) from Sabah, Malaysia.—Malayan Nature Journal 41: 61–73.
- Rehman, F.-U. 1973. Observations on variation in a planktonic copepod, *Tortanus forcipatus* (Giesbrecht, 1889) from the inshore waters of the Karachi coast, Pakistan.—Crustaceana 25: 113–118.
- Robertson, J. R. 1983. Predation by estuarine zooplankton on tintinnid ciliates.—Estuarine, Coastal and Shelf Science 16: 27–36.
- Rose, M. 1956. Les copépodes pélagiques de la Baie de Cauda (Viet-Nam).—Bulletin du Muséum National d'Histoire Naturelle, Paris, ser. 2, 28: 458–465.
- Sato, C. 1913. Pelagic Copepoda.—Journal of Hokkaido Fisheries Experimental Station 1: 1–79. [In Japanese.]
- Savin, S. M., R. G. Douglas, and F. G. Stehli. 1975. Tertiary marine paleotemperatures.—Geological Society of America Bulletin 86: 1499–1510.
- Scott, A. 1909. The Copepoda of the Siboga Expedition 1. Free-swimming, littoral, and semi-parasitic Copepoda.—Siboga Expedition, Monograph 29a: 1–323.
- Sewell, R. B. S. 1912. Notes on the surface-living Copepoda of the Bay of Bengal, I and II.—Records of the Indian Museum 7: 313–382.
- . 1914. Notes on the surface Copepoda of the Gulf of Mannar.—Spolia Zeylanica 9: 191–262.
- . 1932. The Copepoda of Indian Seas. Calanoida.—Memoirs of the Indian Museum 10: 223–407.
- Shen, C.-J., and F.-S. Lee. 1963. The estuarine Copepoda of Chiekong and Zaikong Rivers, Kwangtung Province, China.—Acta Zoologica Sinica 15: 571–596. [In Chinese with English abstract.]
- Shih, C.-T., and S.-S. Young. 1995. A checklist of free-living copepods, including those associated with invertebrates, reported from the adjacent seas of Taiwan.—Acta Zoologica Taiwanica 6: 65–81.
- Smirnov, S. S. 1935. K faune Copepoda Amurskoga limana. Zur Copepodenfauna des Amur-Limans.—Issledovaniia morei S.S.S.R. 22: 41–53.
- Steuer, A. 1926. Revision der Copepodengattung *Tortanus* Giesbr.—Bollettino della Società Adriatica di Scienze Naturali, Trieste 29: 49–69.
- Suh, H.-L., H. Y. Soh, and S. S. Cha. 1991. Salinity and distribution of zooplankton in estuarine system of Monkong River and Dongjin River.—Journal of the Oceanological Society of Korea 26: 181–192. [In Korean with English abstract.]
- Swofford, D. L. 1993. Phylogenetic analysis using parsimony. Version 3.0s.—Illinois Natural History Survey, Champaign, Illinois.
- Tanaka, O. 1965. The pelagic copepods of the Izu region, Middle Japan. Systematic account XIII. Parapontellidae, Acartiidae and Tortanidae.—Publications of the Seto Marine Biological Laboratory 12: 379–408.
- Thompson, I. C., and A. Scott. 1897. Notes on new and other Copepoda.—Proceedings and Transactions of the Liverpool Biological Society 12: 71–82.
- Uye, S. 1985. Resting egg production as a life history strategy of marine planktonic copepods.—Bulletin of Marine Science 37: 440–449.
- van Breeman, P. J. 1908. Copepoden.—Nordisches Plankton 4(8): 1–264.
- Van der Spoel, S. 1983. Pattern in plankton distribution and the relation to speciation: the dawn of pelagic biogeography.—In: R. W. Sims, J. H. Price, and P. E. S. Whalley, eds., Evolution, time and space: the emergence of the biosphere. Pp. 291–334. Academic Press, London, England.
- , and R. P. Heyman. 1983. A comparative atlas of zooplankton.—Springer-Verlag, Berlin, Germany. Pp. 1–186.
- Wheeler, W. M. 1901. The free-swimming copepods of the Woods Hole region.—Bulletin of the United States Fish Commission, 1899, 19: 157–192.
- Williams, L. W. 1906. Notes on marine Copepoda of Rhode Island.—American Naturalist 40: 639–660.
- Wilson, C. B. 1932. The copepods of the Woods Hole region, Massachusetts.—Bulletin of the United States National Museum 158: 1–635.
- . 1950. Copepods gathered by the United States Fisheries Steamer "Albatross" from 1887 to 1909, chiefly in the Pacific Ocean.—Bulletin of the United States National Museum 100: 141–441.
- Zheng, Z., S. Li, S.-j. Li, and B. Chen. 1982. Marine planktonic copepods of China. Volume 2.—Shanghai Scientific and Technological Press, Shanghai, China. Pp. 1–162. [In Chinese.]

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