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A NEW SPECIES OF *TMETHYPOCOELIS* (CRUSTACEA: BRACHYURA: OCYPODIDAE) FROM JAPAN

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ABSTRACT. - A new species of *Tmethypocoelis*, *T. choreutes*, is described from the Ryukyu Islands, Japan. It was previously known from Japanese waters under the name *T. ceratophora* (Koelbel), but this species is restricted to the mainland coasts of China and Vietnam, and eastwards to Taiwan. It is reliably separated from *T. ceratophora* by the distinctive ornamentation of the tip of the male first gonopod, by adult male cheliped characters; and by marked differences in the male waving display.

INTRODUCTION

Tmethypocoelis Koelbel, 1897, was originally described as a subgenus of *Ilyoplax* (then known under the preoccupied name *Dioxippe* de Man). Indeed, *Tmethypocoelis* and *Ilyoplax* share many characters in common which separate them from other dotilline genera: subequal chelipeds; a similar type of second maxilliped without the penultimate segment expanded, and with the last segment attached terminally; and, the upper surface and lateral walls of the carapace not conspicuously sculptured.

Until Davie (1990), *Tmethypocoelis* was considered to be monotypic, and represented by only the wide-ranging type-species, *T. ceratophora* Koelbel, 1897. This species was described from near Hong Kong, but was also identified from Japan, and recorded from as far south as Lombok, Indonesia. Davie (1990) described two new species, *T. koelbeli*, from the Northern Territory, Australia, and *T. odontodactylus* from Madang, Papua New Guinea. The knowledge that there were several species in the genus, led the second author (TK) to send to the first author (PD) some Japanese specimens to confirm their identity. Close examination with topotypic material of *T. ceratophora* collected from Hong Kong, suggested that there were differences in the male first gonopods which seemed possible grounds to separate the Japanese populations as a distinct taxon. This was corroborated by TK after comparing the male waving displays between his Japanese and Taiwanese study populations. Subsequent close examination

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of a series of specimens collected from a number of localities in Indonesia, has shown that an additional three species remain to be described, and this will form the subject of a later paper by PD.

Specimens examined are in the collections of the Queensland Museum (QM), or the Zoological Reference Collection (ZRC), Department of Zoology, National University of Singapore; c.b. = carapace breadth.

TAXONOMY

OCYPODIDAE RAFINESQUE, 1815

DOTILLINAE STIMPSON, 1858

Tmethypocoelis Koelbel, 1897

Tmethypocoelis Koelbel, 1897: 715. [Not seen, pagination follows Shen (1935) and others, although Tesch (1918) gives p. 573]. (Type species: Dioxippe (*Tmethypocoelis*) *ceratophora* Koelbel, 1897, by original designation, subsequently elevated by Shen, 1935).

Diagnosis. - Dotillinae with ocular peduncle prolonged beyond cornea as long styliform projection. Sub-orbital margin cut into two parts by deep groove running obliquely and medially downwards; inner part with two transverse granular ridges separated by a groove. Endopod of second maxilliped with ovate palp. Chelipeds subequal. Second maxilliped with penultimate segment not expanded; with last segment attached terminally. Carapace with upper surface and lateral walls not conspicuously sculptured. Ambulatory legs with large tympana. [After Davie, 1990].

Tmethypocoelis choreutes, new species
(Figs. 1B, D, F, 2C, D, 3B, 4B)

Material examined. - Holotype - male (6.0 x 3.7 mm) (QM W20461), Yuhi River, Okinawa, Ryukyu Islands, coll. T. Kosuge, Mar.1992.

Paratypes - 7 males (3.7 x 2.5 - 6.3 x 3.6 mm), 5 females (4.5 x 3.1 - 5.4 x 3.3 mm) (QM W20462), Yuhi River, Okinawa, Ryukyu Islands, coll. T. Kosuge, Mar.1992. — 4 males (4.6 x 3.0 - 5.8 x 3.6 mm) (QM W20463), Gabui, Okinawa Island, Ryukyu Islands, coll. T. Kosuge, Mar.1992. — 3 males (5.1 x 3.3 - 6.5 x 3.8 mm), 1 female (5.5 x 3.6 mm) (ZRC 1995.555), Ohara, Iriomote Island, Ryukyu Islands, coll. T. Kosuge, Feb.1990. — 1 male (5.0 x 3.0 mm), 1 female (4.8 x 2.9 mm) (QM W10957), Fukido-Gawa, Ryukyu Islands, coll. T. Sakai, date not recorded.

Description. - Carapace approximately pentagonal; convex along mid-dorsal line, slightly convex laterally; c. 1.5-1.7 times broader than long, broadest in large specimens. Regions semi-defined; epigastric lobes just visible. Cervical groove dividing gastric and cardiac regions, well marked; cardiac region with slight central depression. Branchial region sloping, with small, well-spaced, low, tubercles, each bearing a seta. Sub-branchial region bulging, bearing regular setae, separated from branchial region by sinuous lateral border fringed with short setae. Front at base c. 0.2 distance between exorbital angles; lateral borders moderately converging; frontal angles rounded; anterior margin with small central blunt prominence. Supra-orbital borders sinuous, sloping backward, microscopically beaded. Exorbital angle

with outer margin convex; posteriorly followed by broad U-shaped sinus. Distance between epibranchial angles subequal or slightly less than between exorbital angles. Hind margin slightly concave, c. 0.6 distance between exorbital angles; fine ridge parallel with hind margin forming broad rim. Infra-orbital border with medial notch, below which, on pterygostome, runs inwardly directed oblique channel. Inner part of infra-orbital border consisting of two granular ridges separated by shallow channel. Outer part of infra-orbital border granular, concave, ending in broad notch below exorbital angle. Eyestalks widen distally; cornea bulging; medial thickening gives twisted appearance; usually reach level of exorbital angle. Eyestalk projecting beyond cornea in form of long style, which in adult males is equal to, or longer than cornea, but shorter in younger specimens. Tip with 7-8 stiff setae. Style absent in female.

External maxillipeds do not close buccal cavern, slightly vaulted. Ischium subquadrate; antero-internal angle produced as narrow, rounded lobe. Merus slightly larger than ischium; lateral margins converge distally; inner margin straight with long feathered setae, outer margin convex. Merus and ischium covered with surface smooth and shiny; some very short scattered setae. Dactylus slender, twice length of propodus; long stiff setae apically.

Male abdomen with telson rounded, c. 1.4 times wider than long. Sixth segment c. 1.3 times wider than long; c. 1.25 times longer than fifth segment; with slightly concave, parallel sides. Fifth segment markedly constricted at base; c. 1.6 times wider than long (measured at widest point).

Male chelipeds stout, subequal. Merus trihedral with serrulate margins; reaching only to about level of exorbital angles; oval tympanum on inner surface; outer face with tympanum smaller, elongate. Carpus not only slightly elongated, c. 1.3 times longer than wide; unarmed except for fine serrulation of inner and outer borders. Palm bulky, length (excluding fixed finger) c. 1.3-1.4 times height; outer surface granulate over dorso-distal half; smooth ventrally. Inner surface coarsely granulate over upper half, extending over dorsal curve to sharply cut superior border of outer surface. Lower border with supra-marginal groove extending for most of length of fixed finger. Fingers gaping at base; curved inwards, expanded distally to form spooned tip. Cutting margins evenly serrated, dactyl with broad, convex, serrated lobe proximo-medially; fixed finger slightly convex over entire length, but without larger tooth or lobe differentiated. Dactyl with band of fine granules on dorsal surface; outer surface with median row of granules culminating in strong, broad, triangular, outwardly directed tooth two-thirds towards tip. Inner margin at tip of both fingers with short row of stout setae. Spooned tips with corneous edge. Chelipeds of females small and simple.

Walking legs slender, elongate. Merus of third leg c. 3.0 times longer than broad, slightly longer than carpus and propodus together; upper and lower margins convex; with oval tympana on both sides. Tympani large and of same relative size on anterior face of all meri, but on posterior faces becoming progressively smaller from 1st to 4th legs. Second pair of legs slightly the longest. Carpi and propodi with fine bristles. Dactyli nearly straight, pointed, slightly shorter than propodi. Thick tufts of long setae, extending to bases of meri, present between bases of first and second, and second and third walking legs.

First male pleopod long, recurved, very slender; apex with 12 large, stout, serrated setae (see Fig. 2C, D).

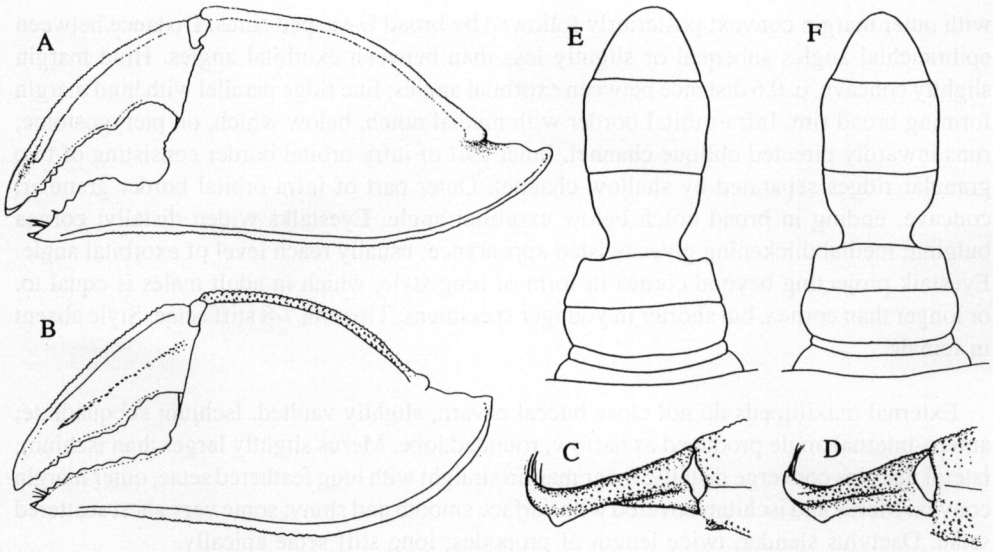

Fig. 1. A, C, E, *Tmethypocoelis ceratophora*, male (6.3 mm c.b.) (QM W20465), Hoi Ha Wan, Hong Kong, coll. P.Davie, (17 Apr. 1989); B, D, F, *Tmethypocoelis choreutes*, new species, holotype male. A, B, left chela; C, D, dorsal view of dactyl of male left cheliped; E, F, male abdomen.

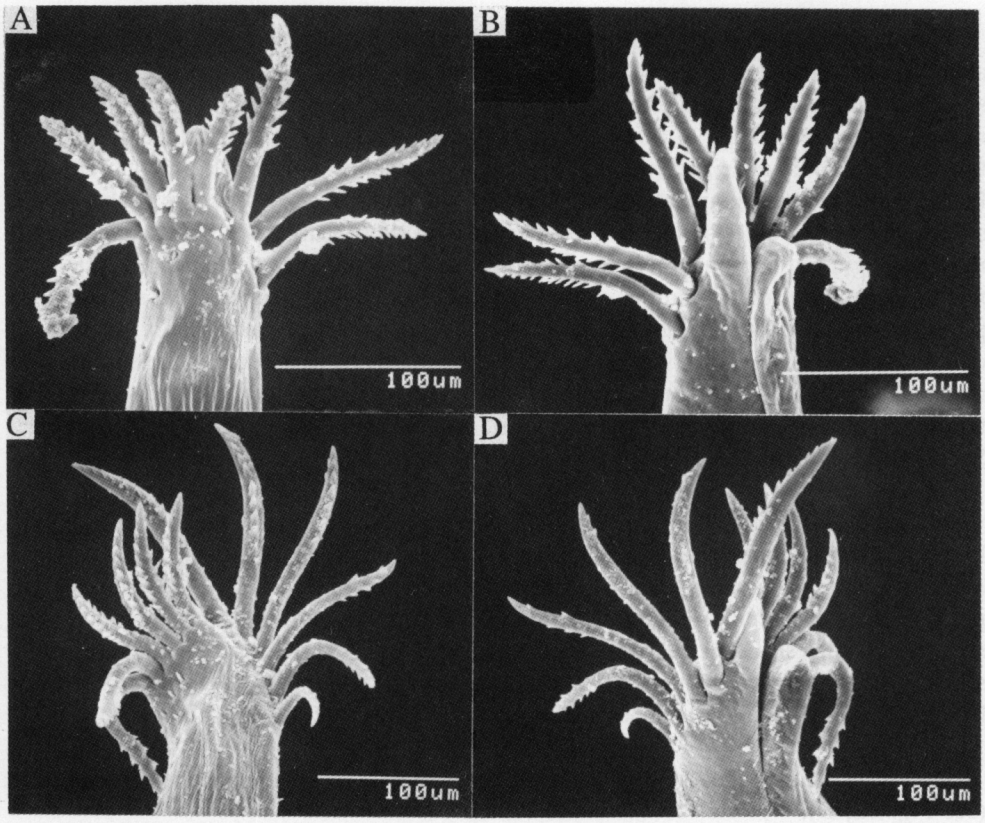

Fig. 2. Scanning Electron Micrographs of the apex of the male first gonopods of: A, B, *T. ceratophora* (6.1 mm c.b.) (QM W20465), Hoi Ha Wan, Hong Kong, coll. P.Davie, (17 Apr. 1989); C, D, *Tmethypocoelis choreutes*, new species, holotype (QM W20461).

Etymology. - *Choreutes* is Greek meaning "dancer", and refers to the characteristic raising of the second pair of walking legs during the male waving display. It is used as a noun in apposition.

Remarks. - *Tmethypocoelis choreutes*, new species, can be separated from *T. ceratophora* by a number of adult male cheliped characteristics, as well as a distinctively different male first gonopod. The merus of the cheliped is much shorter in *T. choreutes*: when held against the body it does not reach noticeably higher than the exorbital angle, whereas in *T. ceratophora* the merus is very long and stands much higher than the top of the carapace. The palm of the cheliped (cf. Figs 1A, B) is relatively shorter in relation to its length (length: breadth ratio, excluding fixed finger, c. 1.3) than for *T. ceratophora* (length: breadth ratio c. 1.7). The cheliped dactylus differs by having a medial granular row on its outer face ending distally in a strongly projecting flat broad tooth; in *T. ceratophora* there is no clear median row of granules, but a similar shaped subdistal tooth is formed by a projection of the supramarginal crest (cf. Figs. 1C, D). Also on the cheliped the dentition of the cutting margins differs: on *T. choreutes* the fixed finger is slightly convex throughout its length, bearing low serrations only; on *T. ceratophora* there is a broadly raised serrated tooth. The dactylus also differs in the degree and shape of development of the sub-median tooth between the two species (cf. Figs. 1A, B).

The male first gonopods differ in the number and disposition of the terminal setae. In *T. choreutes* there are 11 setae, three of which are conspicuously longer and distally projecting, while the others become strongly recurved laterally, and flared away from the terminal aperture (Fig. 2C, D). In *T. ceratophora* there are only eight terminal setae, none are particularly longer than the others, and they are arranged in a simple fan (Fig. 2A, B).

The male abdomen of *T. choreutes* is slightly narrower than in *T. ceratophora*, and in particular segment 6 is c. 1.25 times longer than segment 5 versus 1.1 times for the latter species (c.f. Figs. 1E, F).

Distribution. - *Tmethypocoelis choreutes* has only been found within the confines of the Ryukyu Islands, from Amami Island in the north, south to Iriomote Island.

BEHAVIOUR

Material and methods. - Male waving displays were recorded in the field using a video camera (SONY CCD-V800). *Tmethypocoelis choreutes* was filmed at the Yuhi River, Okinawa Island, Japan on April 6 1992 and *T. ceratophora* at Kuwantu, Taipei, Taiwan on 31 March 1992. Air temperatures were 22°C at the Yuhi River and 21°C at Kuwantu. Crabs performing waving displays were commonly observed at both sites. Waving displays were recorded for 11 individuals of *T. ceratophora* and 12 individuals of *T. choreutes*. Four to 16 bouts of waving were analyzed for each crab.

To describe the individual components of the waving displays, each crab posture was figured from viewing the tapes, and the duration of each component was measured to the nearest 0.001 second by using a digital timer superimposed on video replays of the behaviour.

Results. - Male waving displays of *Tmethypocoelis choreutes* and *T. ceratophora* are clearly distinct (Fig. 3). At the beginning, *T. ceratophora* folds both chelipeds in front of the buccal

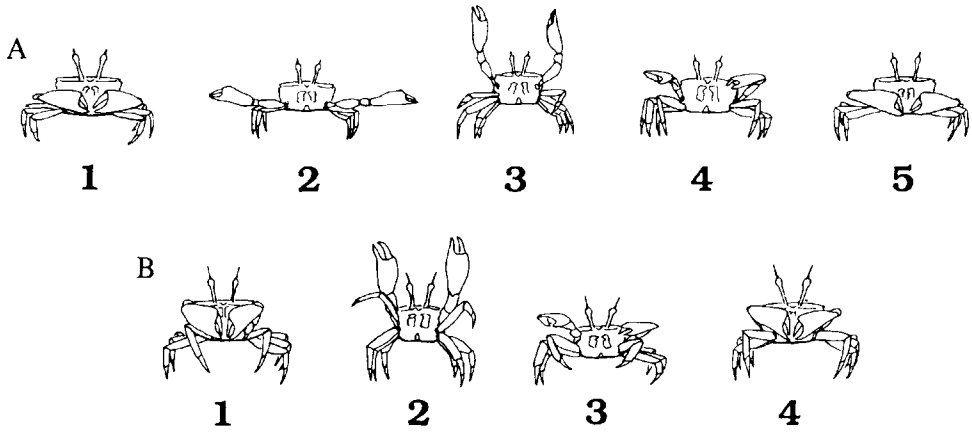

Fig. 3. Successive postures of waving displays of: A, *Tmethypocoelis ceratophora*; and B, *T.choreutes*, new species

region; they are then unfolded laterally (Figs. 3A(2), 4A); and then raised such that the chelipeds are pointing upwards, this posture is held at the apex for a moment, before they are lowered frontally.

Unlike *T. ceratophora*, the wave of *T. choreutes* does not contain any static postures. Starting from the position where the chelipeds are folded in front of the buccal region, the crab unfolds the chelipeds frontally up to their maximum height (Figs. 3B(2), 4B), but they are then re-folded promptly. At the apex of the wave the body is raised up and the second legs are lifted off the ground.

Each component of the wave performed by *T. ceratophora* took more time than for *T. choreutes* (Table 1). The differences in wave patterns between *Tmethypocoelis ceratophora* and *T. choreutes* means that the different species can be easily recognised in the field by observing their waving displays. The same pattern of waving that was recorded at the Yuhi River for *T. choreutes* was also observed at the following localities: Sumiyo river, Amami Island, 30 July 1987; Gabui, Okinawa Island, 8 July 1988; Gesashi River, Okinawa Island, 12 July 1992; Miyara River, Ishigaki Island, 23 March 1993; Ohara, Iriomote Island, 20 June 1993; and Shiira River, Iriomote Island, 22 June 1993.

Table 1. Comparison of temporal patterns in the waving display of *Tmethypocoelis choreutes*, new species, in Okinawa Island, Japan and *T. ceratophora* in Taipei, Taiwan.

Species	Sample size	Mean duration ± SD (sec.)			
		Initial-apex	Apex	Apex-final	Initial-final
T. choreutes	104	0.57± 0.16	0	0.17±0.10	0.74±0.16
T. ceratophora	78	0.80± 0.06	0.14±0.03	0.28±0.10	1.23±0.14

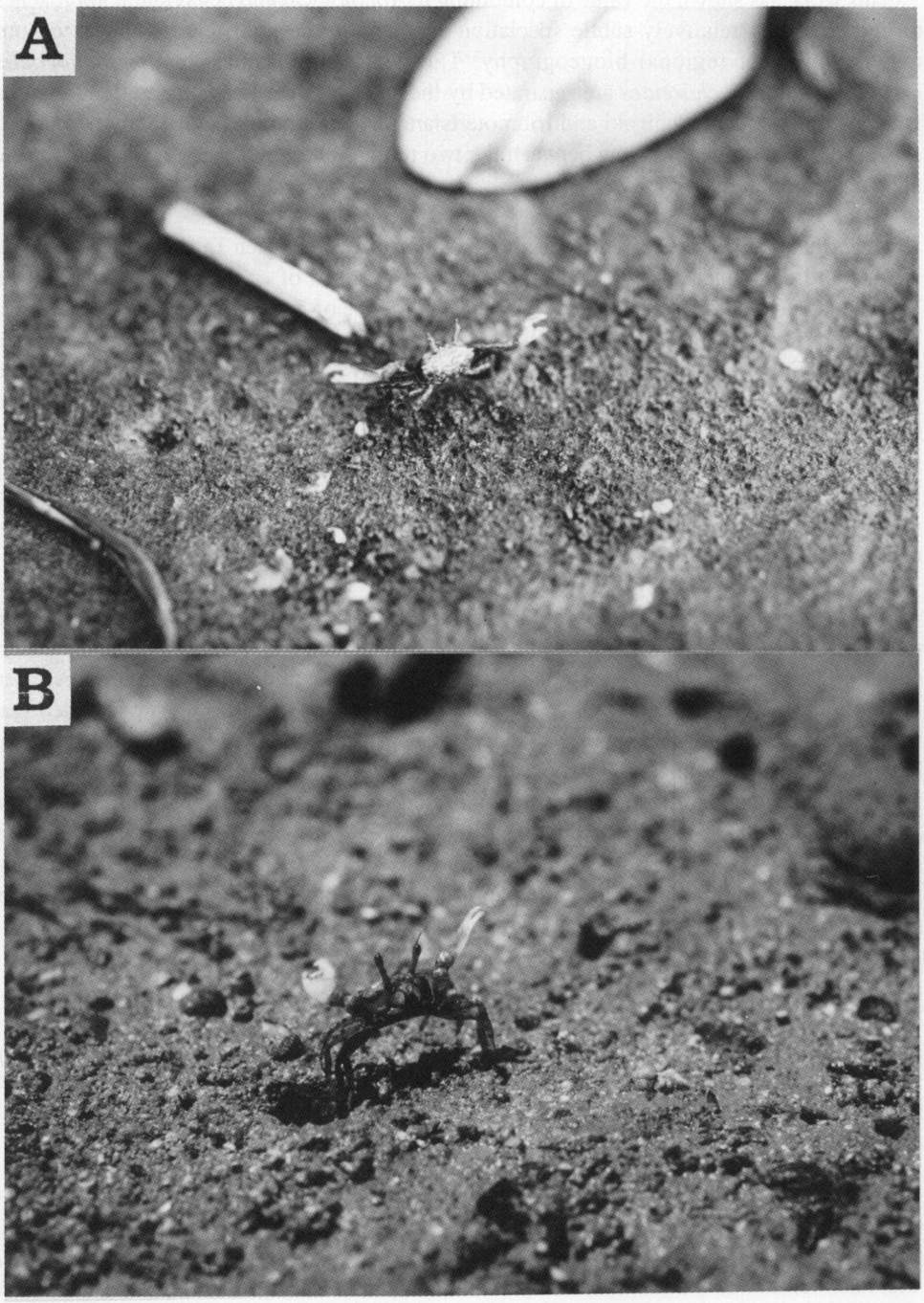

Fig. 4. A: Dorsal view of a waving male of *Tmethypocoelis ceratophora* at Kuwantu, Taipai, Taiwan, 19 April 1993. This posture with the chelipeds extended laterally never appears in the waving of *T. choreutes*, new species. B: A waving male of *T. choreutes* at the Gesashi River, Okinawa, Japan, 12 July 1992.

DISCUSSION

This work has shown the value of combining morphological and behavioural approaches to understanding relatively subtle speciation events, and the light this can throw on our understanding of regional biogeography. The distribution ranges of *Tmethypocoelis ceratophora* and *T. choreutes* are separated by the strait between Taiwan and the Yaeyama Islands (which include Ishigaki and Iriomote Islands). This strait has apparently functioned as a barrier against genetic flow between the two regions, and thus been responsible for the allopatric speciation of the two taxa.

Huang et al. (1989) compared species composition of *Uca* between Taiwan and the Ryukyu Islands and concluded that the Taiwan fauna is comprised of continental species but the Ryukyu Islands region is characterized by the occurrence of more typically oceanic species. Recent new records of *Uca arcuata* in Okinawa Island (Hosoya et al., 1930), *U. lactea perplexa* in Taiwan (Fukui et al., 1989) and *U. tetragonon* in Taiwan (Ho et al., 1993) means that the explanation by Huang et al. (1989) is perhaps a little too simplified. However, the separate but closely adjacent distribution ranges of *Tmethypocoelis ceratophora* and *T. choreutes* support the belief that the ocypodid faunas of the two regions have had separate evolutionary histories. Interestingly Davie (1993) has shown that the grapsid crab, *Parasesarma acis* Davie, 1993, has been able to span the strait between Japan and Taiwan, but apparently does not occur on the mainland.

Tmethypocoelis species are essentially estuarine animals, living abundantly on estuarine mud flats, and able to tolerate low salinities. Lack of suitable habitat, combined with a short larval life, may be partly the cause of the north-south discontinuity in distribution between Iriomote Is. and Taiwan, and thus to separate speciation. Davie (1984) has postulated that these same factors may have also led to the high degree of endemicity seen in the intertidal crabs of tropical Australia. However it seems more likely that local hydrological factors are responsible for maintaining the separation of these two taxa, especially considering the large gaps between islands over the known distribution of *T. choreutes*. Studies of survivorships of pelagic larvae under various salinity regimes, and analyses of genetic structure among different island populations would provide further insight for understanding the distribution patterns of these coastal crabs.

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