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EASTERN PACIFIC SPECIES OF *TRAPEZIA* (CRUSTACEA, BRACHYURA: TRAPEZIIDAE), SIBLING SPECIES SYMBIOTIC WITH REEF CORALS

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ABSTRACT

Trapezia corallina Gerstaecker, *T. digitalis* Latreille, *T. ferruginea* Latreille and *T. formosa* Smith are trapeziid crabs that live sympatrically on reef corals of the genus *Pocillopora* in the tropical eastern Pacific. They differ from each other only in color and small morphological characters and thus represent a complex of sibling species.

Species of *Trapezia* are common symbionts of pocilloporid corals in the Indo-west Pacific and the tropical eastern Pacific regions. Heterosexual pairs of several species typically inhabit single coral colonies, where they secure food and shelter (reviews by Castro, 1976, 1988). Species of *Pocillopora* are hosts in the eastern Pacific.

Four species of *Trapezia* have been recorded from the eastern Pacific. Two (*T. digitalis* Latreille, 1828 and *T. ferruginea* Latreille, 1828) are widely distributed across the Indian and Pacific oceans, while the other two (*T. corallina* Gerstaecker, 1857 and *T. formosa* Smith, 1869) seem to be endemic to the eastern Pacific. The small morphological differences among the four species, however, led taxonomists who worked with preserved material, where live color had been destroyed, to restrict the number of species to two. The placement of *T. corallina* and *T. formosa* in synonymy with *T. digitalis,* while being commonly grouped with *T. ferruginea* in practice, resulted in considerable confusion (Castro, 1982).

In addition to these four species, *T. rufopunctata* (Herbst), was once recorded from a single specimen from the Revillagigedo Islands, Mexico (Stimpson, 1860). It was identified as *T. maculata* (MacLeay). *T. rufopunctata* is an Indo-west Pacific species found as far east as French Polynesia and the Hawaiian Islands. The specimen may have been collected elsewhere or it may have been the result of a rare, long-distance dispersal of larvae.

Morphology is traditionally used to separate the many species of *Trapezia.* These differences, however, are very small. The many color varieties, traditionally treated as subspecies or varieties, may actually represent complexes of sibling species where color is the most reliable means of identification. Sibling species, the groups of species that are difficult to distinguish using conventional morphological characters, are not uncommon among decapod crustaceans and marine species in general (reviews by Knowlton, 1986, 1993).

MATERIALS AND METHODS

Most of the preserved material examined is deposited in the Allan Hancock Foundation, University of Southern California, Los Angeles (AHF) (now at the Natural History Museum, Los Angeles), Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Mazatlán, Mexico (EM), Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ), Muséum National d'Histoire Naturelle, Paris (MNHN), The Natural History Museum, London (BMNH), Smithsonian Institution, and Nationaal Natuurhistorisch Museum, Leiden, The Netherlands (RMNH).

Mate-choice trials were carried out at the Naos laboratory of the Smithsonian Tropical Research Institute, Panamá (June–August 1979). Colonies of *Pocillopora damicornis* (Linnaeus) and their crabs were collected from patch reefs at Urabá and Taboga islands, Gulf of Panamá. Four crabs of approx-

imately the same size, one female and one male each from two of three species (*T. corallina, T. ferruginea* and *T. formosa*), were placed in one of four small (10–15 cm) colonies of *Pocillopora damicornis*. The two crabs of the same species used in each trial were collected from separate coral colonies. Crabs were never used in more than one trial. The colonies were placed about 10–15 cm apart to form a square in the center of large containers provided with running seawater. The location of each crab was recorded overnight, 15–17 hours after the start of each trial.

Color descriptions of live crabs from the eastern Pacific follows the nomenclature of Kornerup and Wanscher (1967). The spelling of geographical names follows, whenever possible, the 1993 edition of *The Times Atlas of the World* (Time Books, London). The following abbreviations are used throughout the text: cl, carapace length; cw, carapace width.

Trapezia corallina Gerstaecker, 1857
Figure 1A–E

Trapezia corallina Gerstaecker 1857: 126 (type locality: "Veragua," Gulf of Chiriquí, Panamá).—Miers 1886: 165 (list).—Borradaile 1902: 265.—Serène 1959: 129 (in key), 131 (list).—Castro 1982: 12 (Colombia: Gorgona island).—Huber 1985b: 23 (Panamá: gulfs of Chiriquí and Panamá).—Prahl and Alberico 1986: 98, 104 (list).—Lemaitre and Alvarez-León 1992: 59 (list).

Trapezia coralina—Serène 1971: 148 (erroneous spelling; in key).

Trapezia digitalis—Ortmann 1897: 208 (part).—Rathbun 1930: 559 (part). (not *Trapezia digitalis* Latreille)

Trapezia cymodoce ferruginea—Rathbun 1930: pl. 228, fig. 1, 2 (part).—Finnegan 1931: 610, 645 (Colombia: Gorgona island; Panamá: Taboga and Coiba islands) (part).—Garth 1946a: 491 (Galápagos Islands) (part).—Garth 1946b: 624 (list) (part).—Garth 1948: 51 (Ecuador: La Plata island) (part).—Garth 1960: 116 (Mexico: Isabel island) (part). (not *Trapezia ferruginea* Latreille)

Trapezia ferruginea—Garth 1965: 24 (Clipperton Island) (part).—Garth, 1974: 401 (list) (part).—Prahl et al. 1978: 89 (Colombia: Gorgona island) (part).—Holthuis 1979: 4 (Galápagos Islands) (part).—Prahl et al. 1979: 43, 50 (Colombia: Gorgona island) (part).—Prahl and Alberico 1986: 98, 104 (list) (part).—Garth 1991: 127, 128, 136, 140 (list) (part).—Garth 1992: 2, 3, 5 (Mexico: Clarión and Socorro islands, Revillagigedo Islands) (part). (not *Trapezia ferruginea* Latreille)

Material Examined.—Neotype herein designated: Urabá island (8°46′57″N, 79°32′23″W), Taboga Islands, Gulf of Panamá, Panamá, from *Pocillopora damicornis,* 2–3 m, coll. by P. Castro, 2.v.1979, male (cw 10.8 mm, cl 9.1 mm) (MNHN-B22723). MEXICO: west of Acapulco, outside Acapulco Bay, leg. Dora Henry, 12.v.1961, 3 females, 2 males, 3 juveniles (RMNH 23651); material identified by J. S. Garth as *Trapezia ferruginea*: San Gabriel Bay, Espíritu Santo island, Gulf of California, VELERO, station 1110-40, 2–4 m, 14.ii.1940, 9 females (cw 11.6–14.6 mm), 9 males (cw 10.0–13.8 mm) (AHF VELERO 1110-40); material identified by J. S. Garth as *Trapezia cymodoce ferruginea*: Isabel island, Sinaloa, VELERO, station 125-33, 2 m, 19.iii.1933, 5 females, 3 males (AHF VELERO 125-33); Tangola-Tangola Bay, VELERO, station 161-34, 1.iii.1934, 11 females, 14 males (AHF VELERO 161-34). CLIPPERTON ISLAND: material identified by J. S. Garth as *Trapezia ferruginea*: Scripps Expedition, 30.viii.1958, 1 female (cw 14.3 mm, cl 11.9 mm), 2 males (cw 13.5, 14.4 mm, cl 11.5, 12.6 mm) (AHF); Scripps Expedition, 14.ix.1958, 2 females, 2 males (AHF). COSTA RICA: material identified by J. S. Garth as *Trapezia cymodoce ferruginea*: Port Culebra, VELERO, station 258-34, 25.ii.1934, 24 females, 26 males (AHF VELERO 258-34). PANAMA: Uva island (7°48′46″N, 81°45′35″W), Gulf of Chiriquí, reef flat, coll. by P. Castro, 31.i.1979, 12 females (cw 6.0–13.9 mm), 9 males (cw 6.7–11.9 mm) from 9 *Pocillopora* spp. colonies; Uva island, Gulf of Chiriquí, reef flat and inner and outer reef slope, coll. by P. Castro and M. Huber, 22–25.vii.1979, 76 females (cw 3.3–11.1 mm), 73 males (cw 3.2–10.6 mm), 4 juveniles from 25 *Pocillopora damicornis,* 12 *P. robusta* Verrill and 1 *P. eydouxi* Milne Edwards and Haime colonies; Contadora island, Gulf of Panamá, coll. by P. Castro, 21.iii.1979, 5 females (cw 10.1–13.7 mm), 6 males (cw 8.9–11.9 mm) from 10 *Pocillopora* spp. colonies; Tabogilla island, Gulf of Panamá, coll. by P. Castro, 13.vi.1979, 5 females, 4 males from 3 *Pocillopora robusta* and 2 *P. damicornis* colonies; Urabá island (8°46′57″N, 79°32′23″W), Gulf of Panamá, from *Pocillopora* spp., coll. by P. Castro, 2.v.1979, 5 females, 4 males (1 male, neotype MNHN-B22723; 1 female, 1 male MNHN-B22724); Urabá island, Gulf of Panamá, coll. by P. Castro, vi.1979, 12 females (cw 6.5–13.9 mm), 8 males (cw 8.8–13.6 mm) from *Pocillopora* spp; Urabá island, Gulf of Panamá, coll. by P. Castro, vii.1979, 20 females, 16 males from 30 *Pocillopora damicornis* and 3 *P. robusta* colonies; Tabogilla island, Gulf of Panamá, coll. by P. Castro and M. Huber, 27.viii.1979, 9 females, 6 males from 5 *Pocillopora damicornis* and 2 *P. robusta* colonies. PANAMA-COLOMBIA: material identified by S. Finnegan as *Trapezia cymodoce* var. *ferruginea*: Coiba island, Panamá and Gorgona island, Colombia, ST. GEORGE Pacific Expedition, 1924–25, 29 females (cw 6.7–19.0 mm, cl 5.4–15.8 mm), 25 males (cw 6.7–16.0 mm, cl 5.3–14.0 mm), 7 juveniles (cw 4.4–6.4 mm, cl 3.2–5.1 mm) (BMNH 1932.12.19.178–187). COLOMBIA: Gorgona island, La

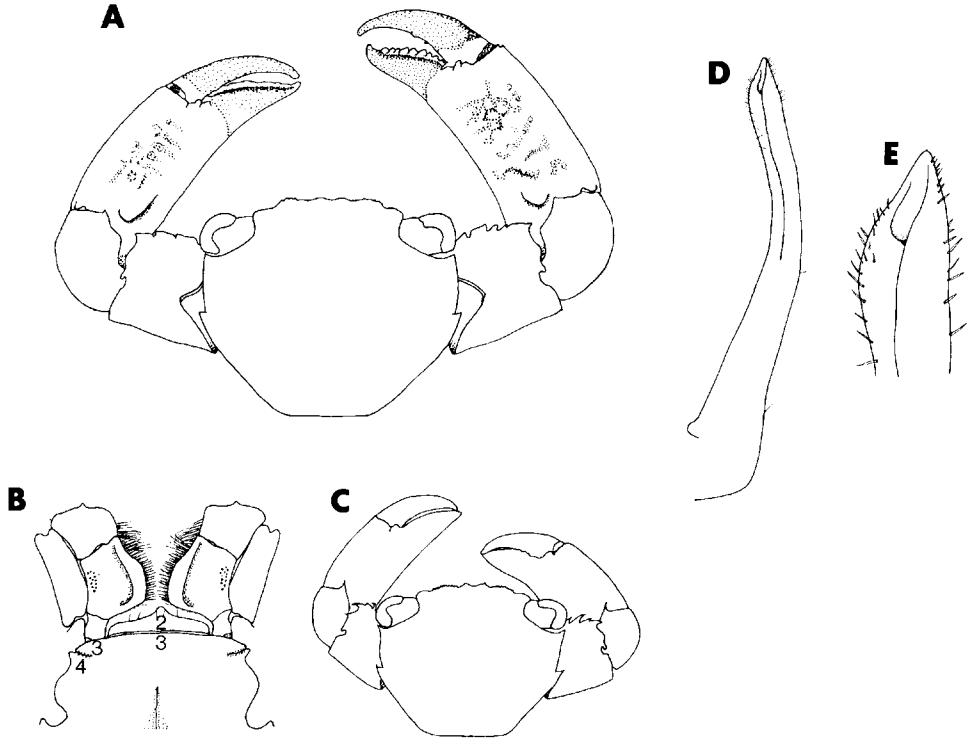

Figure 1. *Trapezia corallina* Gerstaecker. A–B, neotype, adult male (cw 10.8 mm, cl 9.1 mm), Panamá (MNHN-B22723): A, dorsal view (×4.5); B, anterior sternal region (×9). C, juvenile (cw 7.7 mm, cl 6.4 mm), Panamá or Colombia (BMNH 1932.12.19.178–187) (×4.5). D–E, male pleopod, adult male (cw 11.8 mm, cl 10.3 mm), Panamá (MNHN-B22724): D, lateral view (×25); E, apex (×65).

Azufrada fringing reef, coll. by P. Castro, 18–22.v.1979, 37 females (cw 5.7–15.4 mm), 56 males (3.8–13.8 mm), 5 juveniles from 12 *Pocillopora damicornis*, 6 *P. elegans* Dana and 2 *P. eydouxi* colonies; 7 females (cw 7.9–19.2 mm), 6 males (cw 7.6–15.0 mm) from *Pocillopora* spp.; material identified by J. S. Garth as *Trapezia cymodoce ferruginea*: Port Utria, VELERO, station 414-35, 5 m, 23.i.1935, 11 females, 13 males (AHF VELERO 414-35). MAINLAND ECUADOR: material identified by J. S. Garth as *Trapezia cymodoce ferruginea*: La Plata island, 5 m, ASKOY, station 80, 13.iv.1941, 11 females, 9 males (AHF *ASKOY* 80). GALAPAGOS ISLANDS: north of Baltra island near Seymour island, leg. M. Azzaroli, 29.xii.1971, 1 female (RMNH 21947); Santa Cruz island, coll. by P. Castro and M. Huber, 1–4.ix.1979, 4 females, 4 males from 46 *Pocillopora* spp. colonies.

Description of Neotype.—Carapace (Fig. 1A) smooth and shiny, microscopically granular behind frontal border, slightly broader than long, slightly convex dorsally and not divided in regions. Anterolateral borders of carapace shorter than posterolateral borders and almost parallel to each other. Epibranchial teeth in form of acute tooth. Posterolateral borders converging posteriorly.

Frontal border wide and slightly arched, equal to over half greatest width of carapace and cut into rounded supraorbital angles and four lobes. Two median lobes smallest; rounded, unequal, each with three barely noticeable, rounded teeth. Submedian lobes longest, with 11-12 minute teeth, of which only triangular middle six are clearly discernible. Supraorbital angles rounded with barely noticeable teeth. Orbits large and slightly quadrate. Postorbital angles prominent. Inner suborbital teeth acute.

Third maxillipeds (Fig. 1B) subrectangular, with columnar exognath slightly

tapered distally. Ischium of endognath with scattered punctae and cluster of small granulations on distal inner region; shallow sulcus parallel to inner margin. Merus of endognath granulate, outer distal angle produced and rounded and inner angle obliquely truncate. Conspicuous and complete suture (sternal suture 2/3) between second and third thoracic sternites (Fig. 1B). Small, incomplete lateral groove (sternal suture 3/4) between third and fourth thoracic sternites. Abdomen narrow and consisting of five segments. First pleopod long, slender and slightly curved at tip (first pleopod of specimen from same locality of neotype illustrated in Fig. 1D, E).

Chelipeds well developed, polished and moderately unequal. Merus quadrate with round, shallow tubercles on dorsal and ventral surfaces; anterior border crest-like and cut into serrulate teeth, seven on right merus and five on left merus. Anterior distal margin of carpus with obtuse tooth, anterior proximal margin with more rounded tooth. Few microscopic setae along outer margin. Propodus massive, smooth outer and inner surfaces, and subcylindrical, with slight and shallow crest along upper margin. Lower margin cristate, with sparse and minute teeth. Proximal inner region with prominent node-like tubercle. Fingers short, curved, and crossing at tips, with blunt teeth on dactylus and immovable finger of large (right) cheliped and cutting edges on fingers of other.

Merus of walking legs laterally flattened with cristate dorsal margin. Slender long setae on upper margins of carpus (distal portion) and entire length of propodus. Some setae plumose. Outer (anterior) margin with numerous slender setae, some plumose, others thick and horny. Inner (posterior) margin with six thick, horny setae and four transversal, comb-like rows of shorter setae proximally. Distal end curved with series of horny ridges at tip.

Variation in Morphology.—Epibranchial teeth of juveniles (Fig. 1C) and small adults acute; anterolateral borders of carapace parallel to each other. Epibranchial teeth obtuse and anterior portion of anterolateral borders slightly arched with increasing size of carapace. Arching of anterolateral borders slightly more pronounced in large females, with dorsal surface of carapace slightly more inflated than males. Epibranchial teeth developing into notches or even disappearing in very large adults. Postorbital angles acute in juveniles, obtuse with increasing size. Inner suborbital teeth also grow progressively more obtuse.

Frontal border, which consists of two rounded supraorbital angles and four lobes, always appearing six-lobed. Median lobes rounded or triangular. Teeth on lobes and supraorbital angles minute and decreasing in number and becoming barely noticeable or disappearing in larger adults. Always well-developed suture between second and third thoracic sternites. One fully grown female from Panamá (MNHN-B22724), however, with suture fused in the middle.

Merus of chelipeds ornamented with teeth showing much variation in size and number, even right and left meri of one individual. Teeth more acute in juveniles and small adults. Tooth on anterior distal margin of carpus more prominent and spine-like in juveniles but growing less acute with age. Setae along outer margins of carpus and propodus. Short tomentum may be present on proximal and distal joints of carpus in large individuals, rarely on outer surface. Propodus may have very slight crest along upper margin but typically rounded in fully grown individuals. Chelipeds varying in size and development of teeth but typically unequal, with largest heavier in males than females.

Horny setae on inner (posterior) margin of dactyli vary from six to eight. Transversal rows of setae better developed on last pair; vary from three in small individuals to eight in large ones.

First pleopod of male long and slender, with asymmetrical apex and short spines along both distal surfaces (Figs. 1D, E).

Color in Life.—Carapace and walking legs brownish orange. Eyes dark gray. Chelipeds with dark brownish orange and irregular reticulations that extend through outer and inner surface of propodus (Fig. 1A and photo labelled as *T. ferruginea* in Glynn, 1976). Thin, light brownish orange band sometimes along anterior border of carapace, anterior and distal borders of merus of chelipeds and borders of third maxillipeds. Antennules, antennae, maxillipeds and gonopods may have small brownish orange spots. Finger and dactylus of chelipeds dark brownish orange.

Color in Alcohol.—Carapace, walking legs and chelipeds reddish brown. Lighter band along anterior edges of carapace, merus of chelipeds and third maxillipeds sometimes visible. Finger and dactylus of chelipeds dark reddish brown. Reticulations on outer and inner surface of propodus of chelipeds may show as irregular spots.

Remarks.—Trapezia corallina was described by Gerstaecker (1857) from "Veragua," which is assumed to be on the Gulf of Chiriquí coast of Veraguas Province, Panamá. No illustrations of the species have been published, except in photos where it is erroneously identified as *T. ferruginea* Latreille (Rathbun, 1930 and Glynn, 1976). The type material, several specimens, was originally at the Zoologisches Museum, Berlin but "eliminated because it was completely destroyed" (H. E. Gruner, *in litt.,* June 12, 1979). The original description agrees well with the available material of *T. corallina.* Specimens were described as "blass korallenroth" (pale coral red) with dark brown fingers, the color shown by dried specimens of *T. corallina.* The description, however, does not give any comparisons with other eastern Pacific species.

Miers (1886) included *T. corallina* in a list of four *Trapezia* species having a uniformly colored carapace. These species were suggested to be identical with one or more of six other species that included *T. digitalis* Latreille. Ortmann (1897) followed this suggestion by relegating *T. corallina* as a color variety of *T. digitalis.* Rathbun (1930) examined the type material but kept the species, together with *T. formosa* Smith, as synonyms of *T. digitalis.* Evidence of Rathbun's confusion is her use of a photograph of *T. corallina* from the Revillagigedo Islands, Mexico to illustrate *T. ferruginea* (pl. 228, figs. 1, 2). Only Serène (1959, 1971) kept *T. corallina* as a distinct species characterized by its color ("rouge corail"). His conclusion, however, appears not to have been based on the examination of specimens. Subsequent authors followed Rathbun and, like Rathbun herself, identified specimens of *T. corallina* as *T. ferruginea* since preserved specimens of both species show various shades of orange in sharp contrast to the smaller, dark brown specimens of *T. digitalis.*

As a result, only two eastern Pacific species of *Trapezia* were traditionally recognized: an orange *T. ferruginea* and a dark brown *T. digitalis.* Specimens of *T. corallina* and *T. formosa* are commonly found among specimens identified as *T. ferruginea* by Garth and others, even when Garth (1965) refers to several specimens of *T. ferruginea* as having a "reticulate chela," a characteristic of *T. corallina.* Live specimens may also be difficult to distinguish to the untrained eye. References to *T. ferruginea* in the work of Abele (1976), Abele and Patton (1976), Glynn (1976), Castro (1978) and Finney and Abele (1981) most probably included *T. corallina.*

Castro (1982) reinstated *T. corallina* and separated it from *T. digitalis, T. fer-*

Table 1. Results of mate-choice trials among three species of *Trapezia*. Each trial traced the movement overnight (after 15–17 h) or crabs among four colonies of *Pocillopora damicornis* after four crabs (one female and one male each from two *Trapezia* species) were placed on one of the four coral colonies.

Type and number of trials	Crabs in heterosexual pairs of same species (no)	Crabs in heterosexual pairs between two species (no)	Crabs in heterosexual pair of a second species (no)	Crabs alone in a colony (no)
Trapezia corallina + *Trapezia formosa* 8 (32 crabs)	24*	0	1	7
Trapezia corallina + *Trapezia ferruginea* 10 (40 crabs)	28*	2	1 (dead)	9
Trapezia ferruginea + *Trapezia formosa* 7 (28 crabs)	22*	0	2	4

* $P < 0.001$ (significance of difference among observed frequencies and that obtained at random: χ^2 test).

ruginea and *T. formosa* based on the color of live specimens from Panamá, Gorgona island and the Galápagos Islands and on the results of mate-choice experiments in Panamá (Table 1). The status of *T. corallina* as a separate species was confirmed by a study of relative growth of the carapace among eastern Pacific species (Huber, 1985a) and by electrophoretic analysis of eastern and Indo-west Pacific species of *Trapezia* (Huber, 1985b). Work on the ecology of *Trapezia* and its coral host in Panamá (Gotelli and Abele, 1983; Abele, 1984; Gotelli et al., 1985), the apparent role of crabs in the defense and increase in survivorship of corals (Glynn, 1980, 1983), the relationship of lipid content in crabs and corals (Glynn et al., 1985), mate-choice behavior (Huber, 1985c) and the effects of high temperature stress (Glynn and D'Croz, 1990) identified *T. corallina* as one of four eastern Pacific species of *Trapezia*. Garth (1991), however, continued to recognize only two eastern Pacific species, *T. digitalis* and *T. ferruginea*.

Trapezia digitalis Latreille, 1828
Figure 2A–E

Records limited to eastern Pacific locations:

Trapezia digitalis Latreille, 1828: 696 (type locality: Red Sea).—Miers 1886: 164.—Ortmann, 1897: 203 (in key, as *Trapezia digitalis typica*), 208, 213.—Borradaile 1902: 265 (as *Trapezia digitalis* var. *typica*).—Rathbun 1910: 586 (list) (part).—Rathbun 1930: 559, pl. 228, figs. 5, 6 (Mexico: María Madre Island; Clarión and Socorro islands, Revillagigedo Islands; Panamá: Veraguas, Pearl Islands) (part).—Schmitt 1933: 22 (Galápagos Islands).—Glassell 1934: 301 (list).—Crane 1937: 49, 73 (Mexico: from *Pocillopora ligulata* Dana, Arena Bank, Gulf of California).—Garth 1946a: 493, pl. 81, fig. 6 (Galápagos Islands).—Garth 1946b: 624 (list).—Crane 1947: 83 (Mexico: Clarión island, Revillagigedo Islands; Zihuantenejo; Costa Rica: Uvita Bay; Panamá: Bahía Honda).—Garth 1948: 13, 51 (Colombia: Gorgona island; Ecuador: La Plata island).—Hertlein and Emerson 1957: 5 (Clipperton Island).—Serène 1959: 128 (key), 129, figs. 1, 2A, pl. 1.—Garth 1960: 116 (Mexico: Espíritu Santo island, Gulf of California; Isabel island, Nayarit).—Garth 1965: 23 (Clipperton Island).—Serène 1971: 148 (in key).—Garth 1974: 401 (list).—Luke 1977: 51 (Mexico: Cabo San Lucas, Baja California).—Prahl et al. 1978: 89 (Colombia: Gorgona island).—Holthuis 1979: 5 (Galápagos Islands)—Prahl et al. 1979: 43, 50 (Colombia: Gorgona island).—Castro 1982: 14 (Colombia: Gorgona island).—Serène 1984: 270, 271 (in keys), 277 (synonymy), fig. 185; pl. 38, fig. D.—Huber 1985b: 23 (Panamá: gulfs of Chiriquí and Panamá).—Hernández-Aguilera et al. 1986: 195 (Mexico: Islas Marías, Bahía Chamela, Jalisco).—Prahl and Alberico 1986: 98, 104 (list).—Rodríguez de la Cruz-Ramírez 1987: 164 (Mexico: San José del Cabo, Baja California; Mazatlán).—Galil 1988: 163 (synonymy), fig. 2.—Nates-Rodríguez 1989: 34, table 1, fig. 12 c–d; pl. 5, fig. B (Mexico: Bahía Chamela, Jalisco).—Villalobos-Hiriart et al. 1989: 90 (Mexico: Cerralvo Island).—Correa-Sandoval 1991: 89 (list).—Garth 1991: 127, 128, 136, 140 (list).—Garth 1992: 2, 3, 5 (Mexico: Clarión and Socorro islands, Revillagigedo Islands).—Hernández-Aguilera and Martínez-Guzmán 1992: 5 (Mexico: Islas Marías).—Lemaitre and Alvarez-León 1992: 59 (list).—Lira-Fernández 1992: 84, 134, tables 3, 5, 7, fig. 11; pl. 5,

fig. a (Mexico: Cerralvo island, Baja California).—Hendrickx 1992: 9 (list).—Villalobos-Hiriart et al. 1992: 6 (list).—Hendrickx 1993: 314 (list).

Trapezia nigro-fusca Stimpson 1860: 219 (type locality: Cabo San Lucas, Baja California, Mexico).—Miers 1886: 165.—A. Milne Edwards 1881: 343 (Mexico: Cabo San Lucas, Baja California).

Material Examined.—MEXICO: San Gabriel Bay, Espíritu Santo island, Gulf of California, VELERO, station 1110-40, 2–4 m, 14.ii.1940, 4 females (cw 12.0–12.3 mm), 6 males (cw 5.5–13.4 mm) (AHF VELERO 1110-40); Braithwaite Bay, Socorro island, Revillagigedo Islands, VELERO, station 131-34, 3.i.1934, 20 females (cw 6.1–11.0 mm), 25 males (cw 6.1–10.3 mm) (AHF VELERO 131-34); Sulphur Bay, Clarión island, Revillagigedo Islands, VELERO, station 298-34, shore, 10.vi.1934, 7 females (cw 9.8–12.0 mm), 7 males (cw 8.5–12.1 mm) (AHF VELERO 298-34). PANAMA: Uva island (7°48′46″N, 81°45′35″W), Gulf of Chiriquí, reef flat and inner and outer reef slope, coll. by P. Castro and M. Huber, 22–25.vii.1979, 4 juveniles from 25 *Pocillopora damicornis, P. robusta* and *P. eydouxi* colonies; Contadora island, Gulf of Panamá, coll. by P. Castro, 29.iv.1979, 2 females (cw 9.8 mm, 14.4 mm), 2 males (cw 9.2 mm, 13.1 mm) from 2 *Pocillopora robusta* colonies; Urabá island (8°46′57″N, 79°32′23″W), Gulf of Panamá, coll. by P. Castro, vii.1979, 1 female, 1 male from 30 *Pocillopora damicornis* and 3 *P. robusta* colonies. COLOMBIA: Gorgona island, La Azufrada fringing reef, coll. by P. Castro, 18–22.v.1979, 2 females (cw 9.5 mm, 10.8 mm), 2 males (cw 7.9 mm, 9.9 mm), 3 juveniles from 12 *Pocillopora damicornis*, 6 *P. elegans* and 2 *P. eydouxi* colonies; 6 females (cw 6.2–15.3 mm), 7 males (cw 5.8–12.8 mm) from *Pocillopora* spp. (1 female, 1 male BMNH 1994.3373–3374; 1 female, 1 male MNHN-B22727). GALAPAGOS ISLANDS: Academy Bay, Santa Cruz island, leg. M. Azzaroli, 23.xii.1971, 1 male, 1 juvenile (RMNH 31945); Santa Cruz island, coll. by P. Castro and M. Huber, 1–4.ix.1979, 68 females, 74 males, 32 juveniles from 46 *Pocillopora* spp. colonies. RED SEA: unknown location, CALYPSO, 1952, 1 female, 2 males (MNHN-B13926, B-13927). SEYCHELLES: Mahé, Ste. Anne Bay, coll. by A. J. Bruce, 19.ii.1972, 4 females, 4 males (MNHN-B8266); unknown location, ORSTOM Reves 2, 8.ix.1980, 1 female (MNHN-B20654); Farquhar Islands, Manihine, coll. by A. J. Bruce, 26.ii.1972, 2 females, 1 male (MNHN-B8265). MADAGASCAR: Iles Glorieuses, coll. by A. Crosnier, 16.ix.1958, 1 male (MNHN-B8264). MAURITIUS: Le Chaland, coll. by P. Carié, x.1911, 1 male (MNHN-B16909); Grand Port, coll. by P. Carié, 1913, 1 female (MNHN-B16907); coll. by P. Carié, 1 male (MNHN-B16908). REUNION: La Saline, from *Pocillopora*, coll. by S. Ribes, 1976, 1 male (MNHN-B8267); La Saline, from *Pocillopora*, 5 m, coll. by S. Ribes, 1976, 3 females, 4 males (MNHN-B13325, B-13326, B-13328); La Saline, from *Pocillopora eydouxi*, 5 m, coll. by S. Ribes, 1976, 1 female, 1 male (MNHN-B13324); La Saline, from *Pocillopora*, 10 m, coll. by S. Ribes, 1976, 1 female, 1 male (MNHN-B13329); La Saline, from *Stylophora*, 1 female, 2 males (MNHN-B13327); unknown location, from *Pocillopora*, coll. by C. Vadon, 3 females, 3 males (MNHN-B9746-9748).

Description.—Anterolateral borders of carapace always parallel in fully grown individuals (Fig. 2A) and juveniles (Fig. 2C). Epibranchial tooth as acute tooth in juveniles but eventually reduced to notch until disappearance in most adults. Posterolateral borders converging posteriorly slightly more abruptly than in other eastern Pacific species of *Trapezia*. Postorbital angles and inner suborbital teeth acute in juveniles but growing progressively less pronounced with age.

Frontal border consisting of supraorbital angles and four lobes, all cut from each other by slight emarginations. In many fully grown individuals separation between supraorbital angles and submedian lobes absent. Entire frontal border always bearing numerous minute teeth.

Third maxillipeds (Fig. 2B) subrectangular. Ischium of endognath with scattered punctae but no granulations. Suture (sternal suture 2/3) between second and third thoracic sternites only in juveniles and smallest adults. Suture always absent in fully grown individuals (Fig. 2B) although junction of sternites may be marked by light-color scar in some.

Chelipeds slender and relatively short and slightly unequal. Meri fringed with teeth that vary in size and number. Teeth more acute in juveniles and small adults. Tooth on anterior distal margin of carpus also more acute in juveniles while tooth on anterior proximal margin always obtuse. Short setae, sometimes as short and sparse tomentum, along outer margins of carpus and propodus. Upper margin of propodus rounded; lower margin cristate with few microscopic and flattened teeth. Light-colored, node-like tubercle at distal end of inner surface of propodus at base

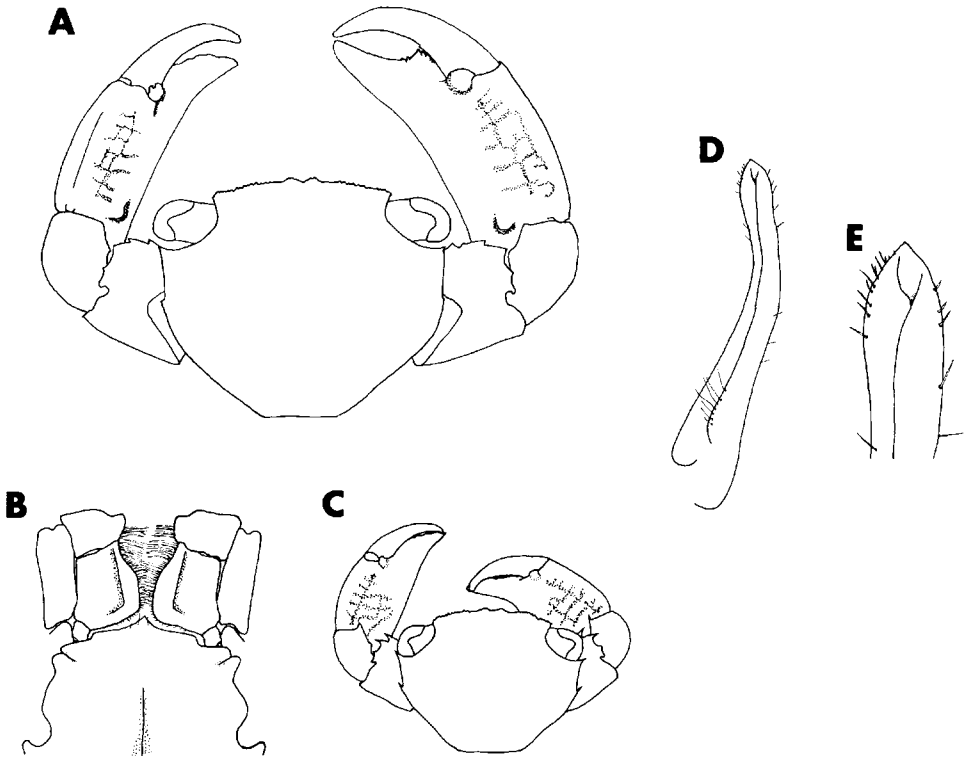

Figure 2. *Trapezia digitalis* Latreille. A–B, D–E, adult male (cw 10.2 mm, cl 8.4 mm), Colombia (MNHN-B22727): A, dorsal view (×4.5); B, anterior sternal region (×9); D, male pleopod, lateral view (×25); E, male pleopod, apex (×65). C, juvenile (cw 6.4 mm, cl 5.2 mm), Galápagos Islands (RMNH 31945) (×4.5).

of dactyli. Fingers short and curved. Dactylus and immovable finger of largest cheliped typically armed with sharp teeth that decrease in size distally; fingers of smallest cheliped armed with cutting edges.

Walking legs thick and stocky. Few slender, short setae on upper margins of carpus (distal portion only) and propodus. Setae more numerous along upper margin of dactyli. Inner (posterior) margin of dactyli with three pairs of horny setae and three transversal rows of shorter setae proximally.

First pleopod of male relatively short, with stout, symmetrical apex. Short distal spines along both surfaces and simple setae near base (Fig. 2D, E).

Color in Life.—Carapace, upper surface of chelipeds and eyes dark brown. Thin, light brown band often along anterior border of carapace and anterior and distal borders of merus of chelipeds. Ventral portion of chelipeds, fingers and dactyli orange-white (cream). Dark body in contrast to light tips of chelipeds thus represents "negative" of the color pattern of other three eastern Pacific species. Dorsal portion of chelipeds may bear light brown reticulations, usually square and rectangular in shape (Fig. 2A). Node-like tubercle at distal end (base of dactylus) of inner surface of propodus of chelipeds orange-white (cream). Walking legs light to reddish brown. Postlarvae and juveniles often show broad orange-white (cream) band across posterior border of carapace.

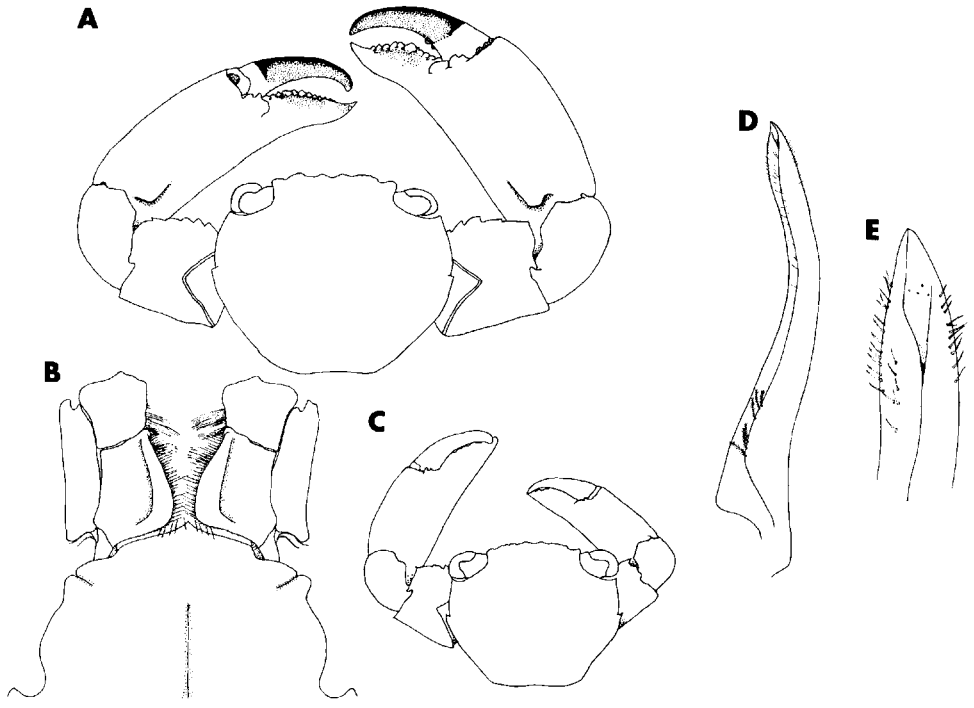

Figure 3. *Trapezia ferruginea* Latreille. A–B, D–E, adult male (cw 15.5 mm, cl 12.8 mm), Panamá (MNHN-B22725): A, dorsal view (×3); B, anterior sternal region (×9); D, male pleopod: lateral view (×25); E, male pleopod, apex (×65). C, juvenile (cw 7.9 mm, cl 6.4 mm), Panamá or Colombia (BMNH 1932.12.19.188–202) (×4.5).

Color in Alcohol.—Carapace, dorsal surface of chelipeds and walking legs brown to dark reddish brown. Ventral portion of chelipeds, fingers and dactyli off-white or cream. Square and rectangular reticulations on chelipeds usually visible.

Remarks.—None of the material from the Red Sea, the type locality, at the Muséum National d'Histoire Naturelle in Paris corresponds to the specimen used by Latreille (1828) in his description.

T. digitalis is widely distributed throughout the Indo-west Pacific and eastern Pacific regions. It was more common at Gorgona island in Colombia and the Galápagos Islands than in Panamá, where it is rare (Castro, 1982). No significant morphological differences were observed between Indo-west Pacific and eastern Pacific specimens. The notch between the outer and median lobes of the frontal border of the carapace, however, was weak or even absent in more eastern Pacific specimens than in Indo-west Pacific specimens. Another difference was observed in the retention by adults of the acute spine at the outer distal end of the carpus of the chelipeds of juveniles and small individuals. It was more common among fully grown Indo-west Pacific specimens than in those from the eastern Pacific. Some specimens from the western Indian Ocean (MNHN-B9746–9748 from Réunion, for example) showed short but conspicuous tomentum on the outer margin of the chelipeds and walking legs. Color of specimens in alcohol, which is preserved relatively well in this species, did not show noticeable variations.

Trapezia ferruginea Latreille, 1828
Figure 3A–E

Records limited to eastern Pacific locations:

Trapezia ferruginea Latreille 1828: 695 (type locality: Red Sea).—Ortmann 1897: 203 (in key, as *Trapezia ferruginea typica*), 205. Borradaile 1902: 264 (as *Trapezia ferruginea* var. *typica*).—Buitendijk 1950: 278 (Mexico: Acapulco).—Serène 1959: 138, fig. 2B.—Garth 1965: 24 (Clipperton Island) (part).—Serène 1971: 146 (in key), figs. 27, 29, 31, 33.—Brusca 1973: 278, fig. 7.79 (Mexico: Cabo San Lucas).—Garth 1974: 401 (list) (part).—Sakai 1976: 506 (in key), 507, pl. 182, fig. 2.—Prahl et al. 1978: 89, fig. 4 (Colombia: Gorgona island) (part).—Holthuis 1979: 4 (Galápagos Islands) (part).—Prahl et al. 1979: 43, 50, fig. 18 (Colombia: Gorgona island) (part).—Brusca 1980: 297 (in key), 312, fig. 20.33 (Mexico: from *Pocillopora elegans*, Cabo San Lucas, Bahía Los Frailes and Bahía Pulmo, Gulf of California).—Castro 1982: 13 (Colombia: Gorgona island).—Van der Heiden and Hendrickx 1982: 62 (Mexico: Mazatlán, Sinaloa).—Hendrickx and van der Heiden 1983: 278 (Mexico: Punta Raza, Nayarit).—Serène 1984: 270, 271 (in keys), 273 (synonymy), fig. 180; pl. 38, fig. C.—Huber 1985b: 23 (Panamá: gulfs of Chiriquí and Panamá).—Hernández-Aguilera et al. 1986: 195 (Mexico: Islas Marías; Bahía Chamela, Colima).—Prahl and Alberico 1986: 98, 104 (list).—Galil 1988: 164 (synonymy), fig. 3.—Nates-Rodríguez 1989: 34 (in key), 35, table 1, fig. 12a–b; pl. 6, fig. A (Mexico: Bahía Chamela, Jalisco).—Villalobos-Hiriart et al., 1989: 90 (Mexico: Santa Catalina, Santa Cruz, San José, Espiritu Santo and Cerralvo islands).—Correa-Sandoval 1991: 90 (list).—Dai and Yang 1991: 380 (in key), 382, fig. 186(1), pl. 51, fig. 6.—Garth, 1991: 127, 128, 136, 140 (list) (part).—Garth 1992: 2, 3, 5 (Mexico: Clarión and Socorro islands, Revillagigedo Islands) (part).—Hernández-Aguilera and Martínez-Guzmán 1992: 5 (Mexico: Islas Marías).—Lemaitre and Alvarez-León 1992: 59 (list).—Lira-Fernández 1992: 84 (in key), 86, 134, tables 2, 3, 5, 7, fig. 11; pl. 5, fig. b (*T. corallina* ?) (Mexico: Santa Catalina, Santa Cruz, San José, Espíritu Santo and Cerralvo islands, Baja California).—Hendrickx 1992: 9 (list) (part).—Villalobos-Hiriart et al. 1992: 6 (list).—Hendrickx 1993. 314 (list).

Trapezia cymodoce—Smith 1869: 287 (Panamá: Pearl Islands).—Miers 1886: 165, 166.—Lockington 1877: 105 (list).—A. Milne Edwards 1881: 342 (Panamá: Pearl Islands).—Faxon 1895: 22 (Mexico: Acapulco).—Odinetz 1983: 30, photo 2.—Odinetz 1984: 432, figs. 1, 2 (part). [not *Trapezia cymodoce* (Herbst)]

Trapezia cymodoce ferruginea—Ortmann 1893: 483 (as *Trapezia cymodoce* var. *ferruginea*).—Rathbun 1910: 586 (list).—Boone 1927: 240, fig. 88 (Cocos island; Galápagos Islands).—Rathbun 1930: 557, pl. 228, figs. 1, 2 (*T. corallina*) (Mexico: María Madre island; Clarión and Socorro islands, Revillagigedo Islands; Acapulco; Panamá: Taboga and Tabogilla islands; Pearl Islands) (part).—Finnegan 1931: 610, 645 (Colombia: Gorgona island; Panamá: Taboga and Coiba islands) (part).—Schmitt 1933: 22 (Galápagos Islands).—Crane 1937: 73 (Mexico: from *Pocillopora ligulata*, Arena Bank, Gulf of California).—Hult 1938: 13 (Galápagos Islands).—Garth 1946a: 491, pl. 81, fig. 4 (Galápagos Islands) (part).—Garth 1946b: 624 (list) (part).—Crane 1947: 83 (Mexico: Clarión island, Revillagigedo Islands; Zijuantenejo, Acapulco, Guatulco; Costa Rica: Culebra, Port Parker, Gulf of Nicoya, Uvita Bay; Panamá: Bahía Honda).—Garth 1948: 13, 51 (Panamá: Pearl Islands, Guayabo Chiquito; Colombia: Utria Bay, Gorgona island; Ecuador: La Plata island) (part).—Hertlein and Emerson 1957: 5 (Clipperton Island).—Garth 1960: 116 (Mexico: Espíritu Santo and Isabel islands, Gulf of California) (part).—Parker 1964: 164 (Mexico: María Cleofas island, Islas Marías).—Luke 1977: 51 (Mexico: Socorro island, Revillagigedo Islands; Panamá: Jicarón, Ladrones and Callada islands, Gulf of Chiriquí).—Rodríguez de la Cruz-Ramírez 1987: 164 (Mexico: Bahía de La Paz, Espíritu Santo island, Baja California; Mazatlán).

Material Examined.—MEXICO: Bahía Candeleros, Gulf of California, coll. by A. Villalobos, 13.viii.1965, 2 females, 2 males (RMNH 21744); San Gabriel Bay, Espíritu Santo island, Gulf of California, VELERO, station 1110-40, 2–4 m, 14.ii.1940, 35 females (cw 8.5–14.7 mm), 28 males (cw 8.0–13.8 mm) (AHF VELERO 1110-40); Isabel island, Sinaloa, VELERO, station 125-33, 4 m, 19.iii.1933, 4 females, 8 males (AHF VELERO 124-33); Rincón de Guayabitos, Nayarit, 25.i.1980, 1 female (EM 0638); Sulphur Bay, Clarión island, Revillagigedo Islands, VELERO, station 298-34, 10.vi.1934, 3 females (cw 10.4–12.0 mm), 6 males (cw 10.6–13.0 mm) (AHF VELERO 298-34); Acapulco, coll. by M. Cárdenas, 15.xii.1941, 1 male (RMNH 21744); west of Acapulco, outside Acapulco Bay, leg. Dora Henry, 12.v.1961, 2 females, 1 male (RMNH 23651); Tangola-Tangola Bay, VELERO, station 161-34, 1.iii.1934, 21 females, 20 males, 2 juveniles (AHF VELERO 161-34). CLIPPERTON ISLAND: Scripps Expedition, 30.viii.1958, 9 females (max cw 16.0 mm), 4 males (max cw 17.0 mm) (AHF). COSTA RICA: Port Culebra, VELERO, station 258-34, 25.ii.1934, 17 females, 17 males (AHF VELERO 258-34). PANAMA: Guayabo Chiquito, ASKOY, station 104, sample 410, 8–9 m, 20–21.v.1941, 3 females (cw 8.8–15.3 mm), 4 males (cw 5.2–12.0 mm) (AHF); Uva island (7°48′46″N, 81°45′35″W), Gulf of Chiriquí, reef flat, coll. by P. Castro, 31.i.1979, 21 females (cw 6.2–13.6 mm), 26 males (cw 5.5–13.6

mm) from 9 *Pocillopora* spp. colonies; Uva island, Gulf of Chiriquí, reef flat and inner and outer reef slope, coll. by P. Castro and M. Huber, 22–25.vii.1979, 95 females (cw 2.9–15.6 mm), 87 males (cw 2.3–16.6 mm), 17 juveniles from 25 *Pocillopora damicornis,* 12 *P. robusta* and 1 *P. eydouxi* colonies; Contadora island, Gulf of Panamá, coll. by P. Castro, 21.iv.1979, 6 females (cw 7.4–15.2 mm), 5 males (cw 12.0–15.8 mm) from 10 *Pocillopora* spp. colonies; Tabogilla island, Gulf of Panamá, coll. by P. Castro, 13.vi.1979, 2 females, 4 males from 3 *Pocillopora robusta* and 2 *P. damicornis* colonies; Urabá island (8°46′57″N, 79°32′23″W), Gulf of Panamá, coll. by P. Castro, vi.1979, 12 females (cw 9.5–17.6 mm), 14 males (cw 7.6–19.7 mm) from *Pocillopora* spp.; Urabá island, Gulf of Panamá, coll. by P. Castro, vii.1979, 6 females, 8 males from 30 *Pocillopora damicornis* and 3 *P. robusta* colonies; Urabá island, Gulf of Panamá, from *Pocillopora damicornis,* coll. by P. Castro, 1979, 8 females, 2 males (2 females, 1 male MNHN-B22725); Taboga island, Gulf of Panamá, coll. by P. Castro, vi.1979, 1 female, 1 male from *Pocillopora damicornis*; Tabogilla island, Gulf of Panamá, coll. by P. Castro and M. Huber, 27.viii.1979, 5 females, 4 males from 5 *Pocillopora damicornis* and 2 *P. robusta* colonies. PANAMA-COLOMBIA: Coiba island, Panamá and Gorgona island, Colombia, *ST. GEORGE* Pacific Expedition, 1924–25, 16 females (cw 6.7–22.4 mm, cl 5.3–18.0 mm), 19 males (cw 7.1–20.6 mm, cl 5.8–16.9 mm), 6 juveniles (cw 4.5–5.5 mm, cl 3.6–4.3 mm), 1 female (Coiba island), 26 unidentifiable juveniles, post-larvae and megalopae that probably included other species (BMNH 1932.12.19.188–202). COLOMBIA: Port Utria, VELERO, station 414-35, 5 m, 23.i.1935, 28 females, 18 males; Gorgona island, La Azufrada fringing reef, coll. by P. Castro, 18–22.v.1979, 23 females (cw 5.2–16.2 mm), 36 males (cw 3.7–15.3 mm), 10 juveniles from 12 *Pocillopora damicornis,* 6 *P. elegans* and 2 *P. eydouxi* colonies; 5 females (cw 10.4–16.2 mm) and 4 males (cw 11.2–15.4 mm) from *Pocillopora* spp. MAINLAND ECUADOR: La Plata island, ASKOY, station 80, 5 m, 13.iv.1941, 8 females, 10 males, 1 juvenile (AHF ASKOY 80). GALAPAGOS ISLANDS: north of Baltra island, near Seymour island, leg. M. Azzaroli, 29.xii.1971, 1 female, 1 male (RMNH 31947); Academy Bay, Santa Cruz island, leg. M. Azzaroli, 23.xii.1971, 1 male (RMNH 31946); Santa Cruz island, coll. by P. Castro and M. Huber, 1–4.ix.1979, 150 females, 191 males, 41 juveniles from 46 *Pocillopora* spp. colonies. RED SEA: Marmar island, CALYPSO, 19.i.1952, 1 female, 1 male (MNHN-B16518); Abu Latt, CALYPSO, 1952, 4 females, 7 males (MNHN-B13925); unknown location, CALYPSO, 1952; 1 female (MNHN-B16523); unknown location, coll. by J. Bonnier and C. Pérez, 1901, 1 male (MNHN-B16544); unknown location, coll. by Clot-Bey, 1 male (MNHN-B2940); unknown location, coll. by Quartin, Dillon and Petit, 2 females (MNHN-B4343); unknown location, coll. by Beaudouin, 1 male (MNHN-B2947); unknown location, 1 male (MNHN-B10832). SEYCHELLES: Mahé, Ste. Anne Bay, coll. by A. J. Bruce, 19.ii.1972, 2 females, 5 males, 1 juvenile (MNHN-B8236, B-8945); ORSTOM Reves 2, 8.ix.1980, 3 males (MNHN-B12806); ORSTOM Reves 2, 8.ix.1980, 5 females, 2 males (MNHN-B116518); Remise islands, coll. by A. J. Bruce, 12.ii.1972, 5 females, 2 males (MNHN-B8944); Astove Island, from *Stylophora,* coll. by A. J. Bruce, 27.ii.1972, 1 female, 4 males (MNHN-B8942); Farquhar Islands, coll. by A. J. Bruce, 26.ii.1972, 3 females, 4 males (MNHN-B8235). COMORO ISLANDS: Mayotte, coll. by A. Crosnier, ix.1959, 1 female (MNHN-B8234). MADAGASCAR: Iles Glorieuses, coll. by A. Crosnier, 16.ix.1958, 2 females, 2 males (MNHN-B8233); Nosy Bé, coll. by M. Chavane, vii.1958, 1 male (MNHN-B8231); Tuléar, coll. by R. Plante, 1 female, 1 male (MNHN-B8232); unknown location, coll. by de Lartigues, 1 female (MNHN-B16520). REUNION: La Saline, from *Pocillopora,* coll. by S. Ribes, 1977, 8 females, 9 males (MNHN-B8237, B-16088-16091). MAURITIUS: coll. by P. Carié, ix.1912, 1 female, 1 male (MNHN-B16521); coll. by P. Carié, 2 males (MNHN-B16516). MALDIVE ISLANDS: Addu atoll, from *Seriatopora,* XARIFA Expedition, coll. by S. Gerlach, 30.xii.1957, 1 male (MNHN-B16517). GUAM: Luminao, from *Pocillopora,* coll. by O. Odinetz, vi.1981, 1 female, 1 male (MNHN-B9678); Luminao, from *Pocillopora,* coll. by O. Odinetz, iii.1982, 1 female, 1 male (MNHN-B9676); Luminao, from *Pocillopora,* coll. by O. Odinetz, vi.1982, 1 female, 1 male (MNHN-B9677). FRENCH POLYNESIA: Takapoto atoll, Tuamotu Archipelago, from *Pocillopora,* coll. by O. Odinetz, ii.1982, 3 females, 2 males (MNHN-B9673-9674); Moorea, from *Pocillopora,* coll. by O. Odinetz, iii.1982, 1 female, 1 male (MNHN-B9670); Moorea, from *Pocillopora,* coll. by O. Odinetz, iv.1982, 1 female, 2 males (MNHN-B9672); Tahiti, Mission Ranson, 1952, 1 female, 1 male (MNHN-B16543); Tahiti, from *Pocillopora,* coll. by O. Odinetz, iii.1982, 2 females, 2 males (MNHN-B9671, B-9673). UNKNOWN LOCATIONS: coll. by E. Bouvier, 1 female (MNHN-B16525); French Polynesia (?) 3 females, 3 males (MNHN-B8898).

Description.—Anterolateral borders of carapace curved in fully grown individuals (Fig. 3A) and nearly parallel to each other in juveniles (Fig. 3C) but curving with increasing size. Epibranchial tooth as acute tooth or notch in juveniles and adults but may be absent in largest individuals. Postorbital angles acute in juveniles and obtuse in adults. Inner suborbital teeth showing similar development.

Frontal border wide, arched and clearly cut into two rounded supraorbital angles

and four lobes. Median lobes typically triangular but sometimes rounded. In juveniles and small adults four lobes and supraorbital angles ornamented with variable number of minute teeth, which decrease in number and become barely noticeable or disappear in larger individuals.

Third maxillipeds (Fig. 3B) subrectangular. Ischium of endognath smooth with scattered punctae but no granulation. Juveniles and small adults showing suture between second and third thoracic sternites (sternal suture 2/3). Suture absent in adults (Fig. 3B). Some with faint scar or suture remaining on one or on two opposite outer margins of sternite.

Chelipeds massive, particularly in males, and almost always unequal. Merus of chelipeds armed with well-developed teeth that vary in size and number, often between right and left meri of individual. Teeth more acute in juveniles and small adults. Distal and proximal angles along anterior margin of carpus of juveniles and adults with two rounded, acute teeth. Short setae along outer margins of carpus and propodus. Short or moderately long tomentum sometimes present on proximal and distal joints of carpus or even on outer surface of carpus of large individuals. Upper margin of propodus rounded; lower margin cristate with few microscopic teeth. Fingers short and curved. Development of teeth on fingers varying. Dactylus and immovable finger of largest cheliped armed with large teeth in some; cutting edges or teeth on fingers of smaller cheliped.

Merus of walking legs laterally flattened with cristate dorsal margin. Upper margins of carpus, propodus and dactylus with many slender, long setae. Some setae plumose. Distal end of dactylus curved with horny ridges at tip; inner (posterior) margin with eight to 10 thick, horny setae and, proximally, four to eight transversal rows of shorter setae. Transversal rows of setae decreasing in development from last pair of legs.

First pleopod of male long and slender. Apex slender and symmetrical (Fig. 3D, E). Short spines along both distal surfaces; proximal plumose setae.

Color in Life.—Carapace and walking legs orange to brownish orange. Thin, light orange band often along anterior border of carapace, anterior and distal borders of merus of chelipeds and borders of third maxillipeds. Eyes dark brown, almost black. Ventral portion of inner surface of chelipeds light orange or orange-yellow. Finger and dactylus of chelipeds dark brown to black. Antennules, antennae, maxillipeds and gonopods may have small brownish orange spots. Post-larvae and juveniles with blue spot on inner junction of carpus and merus of chelipeds.

Color in Alcohol.—Carapace, walking legs and chelipeds orange to brownish orange. Lighter band along anterior edges of carapace, merus of chelipeds and third maxillipeds often visible. Finger and dactylus of chelipeds dark brown, usually darker than in *T. corallina.*

Remarks.—The species has been recorded from locations across the Indo-west Pacific and from the tropical eastern Pacific (Boone, 1934). A record of "one mutilated specimen from Colon" on the Caribbean Sea coast of Panamá (Finnegan, 1931) is most probably an error.

None of the Red Sea material at the Muséum National d'Histoire Naturelle, Paris corresponds to the specimen used by Latreille (1828) in his description. Serène (1984) concluded that the type material had been lost.

Although two other eastern Pacific species, *T. corallina* and *T. formosa,* were placed in synonymy with *T. digitalis* by Rathbun (1930), others erroneously identified these two species as *T. ferruginea* due to similarities in morphology and

color. Consequently, many collections of *T. ferruginea* included *T. corallina* and *T. formosa* as well. Work on the ecology (Abele, 1976; Abele and Patton, 1976), behavior (Castro, 1978) and allometric growth (Finney and Abele, 1981) of *T. ferruginea* from Panamá most probably included these two other species. Castro (1982) distinguished among the four eastern Pacific species of *Trapezia.* Other work on the ecology of *Trapezia* and its coral host in Panamá (Gotelli and Abele, 1983; Abele, 1984; Gotelli et al., 1985) and on the nature of its relationship with the coral (Glynn, 1980, 1983; Glynn et al., 1985; Glynn and D'Croz, 1990) treat *T. ferruginea* as one of four eastern Pacific species. Garth (1991), however, continued to recognize only two species.

A comparison between eastern Pacific specimens of *T. ferruginea* and those from the Indo-west Pacific failed to show any morphological differences. A comparison between the relative growth of the carapace of Panamanian and Hawaiian populations of the same species did not show any significant differences either (Huber, 1985a). Genetic differentiation between Panamanian and Indo-west Pacific populations was also very small (Nei's standard genetic distance of 0.1694 $\pm$ 0.0996 between Panamanian and Marshall Islands populations and 0.0004 $\pm$ 0.0004 between Panamanian and Hawaiian populations) which suggests that *T. ferruginea* may be a recent immigrant to the tropical eastern Pacific (Huber, 1985b).

The separation between *T. ferruginea* Latreille and *T. cymodoce* (Herbst), a close Indo-west Pacific species, has been much debated. Descriptions of the two species were too brief and the type specimen of *T. cymodoce,* like that of *T. ferruginea,* was "displaced or destroyed" (H. E. Gruner, *in litt.,* June 6, 1994). A photograph of the type of *T. cymodoce* in Rathbun (1906) is of little help. Disagreements as to the validity of the characters used to separate the two species led to misidentifications and to the description of separate species and varieties, even when de Man (1880) clearly outlined the differences between the two species, as did Boone (1934) and Galil and Clark (1990). Ortmann (1893) relegated *T. ferruginea* to a variety of *T. cymodoce* but treated them as separate species in a subsequent review (Ortmann, 1897). Rathbun (1910, 1930) reduced *T. ferruginea* to subspecies status under *T. cymodoce.* Many subsequent identifications of eastern Pacific material followed Rathbun (1930) and continued to treat *T. ferruginea* as a subspecies.

Both species have been recorded as sympatric through most of the Indo-west Pacific. *T. cymodoce,* however, is absent from the eastern Pacific. Specimens from Panamá referred by Smith (1869) as *T. cymodoce* were probably *T. ferruginea,* even when most of the characters given by Smith also apply to *T. corallina.* Faxon (1895) examined Smith's specimens as well as additional material from Mexico and Panamá and concluded that they were similar to *T. cymodoce* (in fact *T. ferruginea*) from the Hawaiian Islands. Rathbun (1930) examined Smith's and Faxon's specimens and refers to them *T. cymodoce ferruginea.* Galil and Clark (1990) agreed that the eastern Pacific material referred to as *T. cymodoce* by Smith (1869), Lockington (1877), A. Milne Edwards (1881) and Faxon (1895) is actually *T. ferruginea.*

Examination of numerous Indo-west Pacific specimens previously identified as *T. ferruginea* or *T. cymodoce* confirmed that several morphological characters separate the two species (Castro, in press). The upper and outer margin of the chelipeds of *T. ferruginea* may have microscopic setae or, rarely, a conspicuous tomentum restricted to the carpus, while in *T. cymodoce* a tomentum is always well developed and present along the entire upper and outer surface of the chelipeds (Galil, 1988: fig 1). The upper edge of the propodus of the chelipeds is

rounded in fully grown *T. ferruginea* but subacute in *T. cymodoce*. The second and third thoracic sternites are fused in adult *T. ferruginea*, while in *T. cymodoce* there is a conspicuous suture in the same location. A rounded tooth is present on the distal margin of the carpus of the chelipeds in juvenile and adult *T. ferruginea*, while most specimens of *T. cymodoce* show a tooth that is often acute. The epibranchial tooth of the carapace is obtuse and located slightly more anterior in fully grown *T. ferruginea*, while it is typically acute and slightly more posterior in *T. cymodoce* (Serène, 1971: figs. 26, 27). The anterolateral borders of the carapace are curved (convex) in fully grown *T. ferruginea* but less curved and almost parallel to each other at the base (although not much so in the largest specimens) in *T. cymodoce*. The apex of the first male pleopod is clearly more slender in *T. ferruginea* than in *T. cymodoce* (Serène, 1971: figs. 30–33). The merus of the fourth pair of walking legs is slightly shorter in *T. ferruginea* than in *T. cymodoce*. Assumed variations in diagnostic characters, a claim that morphological differences previously used were not valid and the finding of seemingly intermediate specimens from Guam and French Polynesia led Odinetz (1984) to consider *T. ferruginea* a junior synonym of *T. cymodoce*.

Of all the diagnostic characters, the absence or restricted development of tomentum on the chelipeds and the absence of a suture between the second and third thoracic sternites are the most reliable in separating fully grown individuals of *T. ferruginea* from *T. cymodoce*. The absence of tomentum and the presence of a blunt tooth on the carpus of the chelipeds are most useful in juveniles and small adults. The development of tomentum varies in *T. ferruginea*, which explains the "intermediate" individuals of Odinetz (1984). In most eastern Pacific specimens it consists of microscopic setae restricted to the carpus and the proximal portion of the propodus. Some, however, have a well developed tomentum restricted to the joints of the carpus. One large male from Panamá or Colombia (BMNH 1932.12.19.188–202) showed conspicuous tomentum on the outer margin of the carpus and the proximal portion of the propodus. Another male from the Galápagos Islands (RMNH 31945) had even more conspicuous tomentum on the same region but only on the left cheliped. The specimen also had conspicuous tomentum on the walking legs. The nature of the thoracic sternites is also a useful character.

Color is an additional complication. Color differences have been recorded for *T. ferruginea* throughout its range: "bright orange red, with brownish black eyes and wood brown fingers" in live specimens from French Polynesia and Bali (Boone, 1934), "uniformly yellowish or light brownish" from southern Japan but illustrated in a plate as light orange-brown with darker reticulations on the chelipeds (Sakai, 1976), "yellowish bluish-grey" carapace and walking legs "ocher-yellow with red dot distally on propod" in live specimens from the Red Sea (Galil, 1988), "uniform orange yellow" in the western Indian Ocean (Serène, 1984) and "yellowish" with brown carapace borders and cheliped joints in a preserved specimen form the South China Sea (Dai and Yang, 1991). It is possible, however, that some of these records were the result of erroneous identifications.

Trapezia formosa Smith, 1869
Figure 4A–F

Trapezia formosa Smith 1869: 286 (type locality: Pearl Islands, Panamá, from *Pocillopora capitata* Verrill).—Miers 1886: 164 (list).—Lockington 1877: 105 (list).—A. Milne Edwards 1881: 343, pl. 58, figs. 1, 1a, 1b (Panamá: Pearl Islands).—Serène 1959: 129 (in key), 131 (list).—Garth 1971: 188 (list).—Serène 1971: 148 (in key) (list).—Castro 1982: 12 (Colombia: Gorgona is-

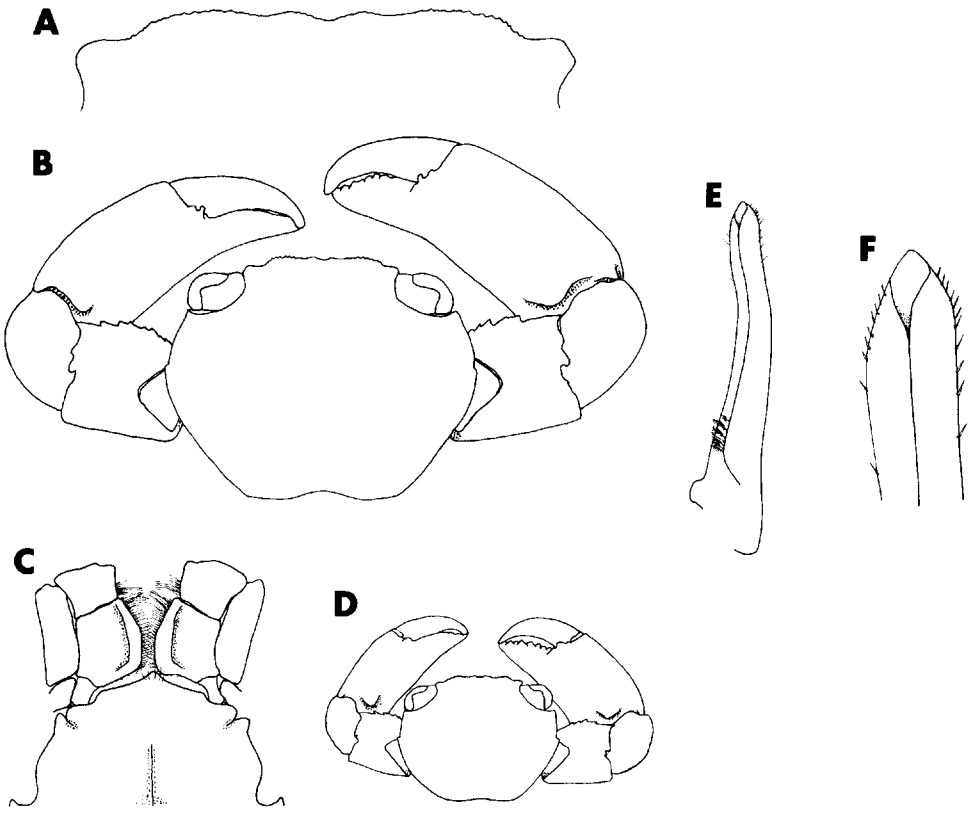

Figure 4. *Trapezia formosa* Smith. A–B, lectotype, female (cw 8.5 mm, cl 6.5 mm), Panamá (MCZ 4834): A, anterior border of carapace (×20); B, dorsal view (×6). C, E–F, male (cw 10.1 mm, cl 8.4 mm), Panamá (MNHN-B22726): C, anterior sternal region (×9); E, male pleopod, lateral view (×25); F, male pleopod, apex (×65). D, small female (cw 6.2 mm, cl 4.7 mm), Colombia (MNHN-B22728) (×4.5).

land).—Huber 1985b: 23 (Panamá: gulfs of Chiriquí and Panamá).—Prahl and Alberico 1986: 98, 104 (list).—Lemaitre and Alvarez-León 1992: 59 (list).

Trapezia digitalis—Ortmann 1897: 208 (part).—Rathbun 1910: 586, 618 (list) (part). (not *Trapezia digitalis* Latreille)

Trapezia digitalis var. *formosa*—Borradaile 1902: 265.

Trapezia cymodoce var. *ferruginea*—Finnegan 1931: 610, 645 (Colombia: Gorgona island; Panamá: Taboga and Coiba islands) (part).—Garth 1946a: 491 (Galápagos Islands) (part).—Garth 1946b: 624 (list) (part).—Garth 1948: 51 (Ecuador: La Plata island) (part).—Garth 1960: 116 (Mexico: Isabel island) (part). (not *Trapezia ferruginea* Latreille)

Trapezia ferruginea—Garth 1965: 24 (Clipperton Island) (part).—Garth 1974: 401 (list) (part).—Prahl et al. 1978: 89 (Colombia: Gorgona island) (part).—Holthuis 1979: 4 (Galápagos Islands) (part).—Prahl et al. 1979: 43 (Colombia: Gorgona island) (part).—Prahl and Alberico 1986: 98, 104 (list) (part).—Garth 1991: 127, 128, 136, 140 (list) (part).—Garth 1992: 2, 3, 5 (Mexico: Clarión and Socorro islands, Revillagigedo Islands) (part). (not *Trapezia ferruginea* Latreille)

not *Trapezia formosa*—Ribes 1978: 14 (Réunion) = *T. bella* Dana, (*fide* Serène 1984).

not *Trapezia formosa*—Kropp and Birkeland 1981: 629 (Takapoto atoll, French Polynesia).—Dai et al. 1983: 252, 261, pl. 4, fig. 8 (Xisha Islands = Paracel Islands, South China Sea).—Odinetz 1983: 31, photo 4 (Moorea, Tahiti and Takapoto atoll, French Polynesia).—Delesalle 1985: 289 (Mataiva, French Polynesia).—Guinot 1985: 452 (list).—Odinetz-Collart and Richer de Forges 1985: 201 (Moorea, Tahiti and Takapoto atoll, French Polynesia).—Dai et al. 1986: 359, fig. 187(3), pl. 52, fig. 4 (Xisha Islands = Paracel Islands, South China Sea).—Dai and Yang 1991: 380 (in key), 387, fig. 187(3); pl. 52, fig. 4 (Xisha Islands = Paracel Islands, South China Sea).

?*Trapezia formosa*—Huber 1985b: 23 (Marshall Islands).—Chang et al. 1987: 214 (Taiwan).

Material Examined.—Lectotype herein designated: Pearl Islands, Gulf of Panamá, Panamá, coll. by F. H. Bradley, female (cw 8.5 mm, cl 6.5 mm) (MCZ 4834); Paralectotype: Pearl Islands, Gulf of Panamá, Panamá, female (cw 11.2 mm, cl 9.1 mm), male (cw 9.0 mm, cl 7.4) (MNHN-B16542).

MEXICO: Bahía Candeleros, Gulf of California, coll. by A. Villalobos, 13.viii.1965, 1 female, 1 male (RMNH 21744); Rincón de Guayabitos, Nayarit, 25.i.1980, 1 male (EM 0638); material identified by J. S. Garth as *Trapezia ferruginea*: San Gabriel Bay, Espíritu Santo island, Gulf of California, VELERO, station 1110-40, 2–4 m, 14.ii.1940, 36 females (cw 5.0–10.0 mm), 35 males (cw 3.8–9.3 mm) (AHF VELERO 1110-40); material identified by J. S. Garth as *Trapezia cymodoce ferruginea*: Isabel island, Sinaloa, VELERO, station 125-33, 4 m, 19.iii.1933, 3 females, 2 males (AHF VELERO 125-33); Sulphur Bay, Clarión island, Revillagigedo Islands, VELERO, station 298-34, 10.vi.1934, 28 females (cw 6.7–9.6 mm), 27 males (cw 6.5–8.8 mm) (AHF VELERO 298-34); Tangola-Tangola Bay, VELERO, station 161-34, 1.iii.1934, 2 females, 3 males (AHF VELERO 161–34). CLIPPERTON ISLAND: material identified by J. S. Garth as *Trapezia ferruginea*: Scripps Expedition, 30.viii.1958, 4 females (cw 5.6–8.0 mm), 2 males (cw 6.4–6.6 mm) (AHF). COSTA RICA: material identified by J. S. Garth as *Trapezia cymodoce ferruginea*: Port Culebra, VELERO, station 258-34, 25.ii.1934, 7 females, 8 males (AHF VELERO 258-34). PANAMA: Uva island (7°48′46″N, 81°45′35″W), Gulf of Chiriquí, reef flat, coll. by P. Castro, 31.i.1979, 7 females (cw 7.2–10.1 mm), 5 males (cw 7.5–9.5 mm) from 9 *Pocillopora* spp. colonies; Uva island, Gulf of Chiriquí, reef flat and inner and outer reef slope, coll. by P. Castro and M. Huber, 22–25.vii.1979, 12 females (cw 3.9–8.1 mm), 12 males (cw 2.9–7.6 mm), 2 juveniles from 25 *Pocillopora damicornis*, 12 *P. robusta* and 1 *P. eydouxi* colonies; Tabogilla island, Gulf of Panamá, coll. by P. Castro, 13.vi.1979, 4 females, 5 males from 3 *Pocillopora robusta* and 2 *P. damicornis* colonies; Urabá island (8°46′57″N, 79°32′23″W), from *Pocillopora damicornis*, Gulf of Panamá, coll. by P. Castro, 2.v.1979, 7 females, 3 males (1 female, 1 male MNHN-B22726); Urabá island (8°46′57″N, 79°32′23″W), Gulf of Panamá, coll. by P. Castro, vi.1979, 5 females (cw 9.8–11.6 mm), 5 males (cw 8.0–11.0 mm) from *Pocillopora* spp.; Urabá island, Gulf of Panamá, coll. by P. Castro, vii.1979, 4 females, 3 males from 30 *Pocillopora damicornis* and 3 *P. robusta* colonies; Tabogilla island, Gulf of Panamá, coll. by P. Castro and M. Huber, 27.viii.1979, 6 females, 4 males from 5 *Pocillopora damicornis* and 2 *P. robusta* colonies. PANAMA-COLOMBIA: material identified by S. Finnegan as *Trapezia cymodoce* var. *ferruginea*: Coiba island, Panamá and Gorgona island, Colombia, *ST. GEORGE* Pacific Expedition, 1924–25, 8 females (cw 5.4–12.4 mm, cl 4.3–9.0 mm), 8 males (cw 7.2–11.6 mm, cl 5.7–8.7 mm), 1 juvenile (cw 3.7 mm, cl 2.9 mm) (BMNH 1932.12.19.173–177). COLOMBIA: Gorgona island, La Azufrada fringing reef, coll. by P. Castro, 22.v.1979, 24 females (cw 3.8–10.7 mm), 22 males (cw 4.2–9.4 mm) from 12 *Pocillopora damicornis*, 6 *P. elegans* and 2 *P. eydouxi* colonies; 2 females (cw 7.0 mm, 9.9 mm), 2 males (cw 8.3 mm, 7.8 mm) from *Pocillopora* spp., 2 females, 2 males (MNHN-B22728); material identified by J. S. Garth as *Trapezia cymodoce ferruginea*: Port Utria, *VELERO*, station 414-35, 5 m, 23.i.1935, 15 females, 11 males (AHF *VELERO* 414-35). MAINLAND ECUADOR: material identified by J. S. Garth as *Trapezia cymodoce ferruginea*: La Plata island, ASKOY, station 80, 5 m, 13.iv.1941, 4 females, 1 male (AHF ASKOY 80). GALAPAGOS ISLANDS: Academy Bay, Santa Cruz island, leg. M. Azzaroli, 23.xii.1971, 1 female (RMNH 31946); Santa Cruz island, coll. by P. Castro and M. Huber, 1–4.ix.1979, 31 females, 26 males from 46 *Pocillopora* spp. colonies.

Description.—Anterolateral borders of carapace markedly curved in all individuals (Fig. 4B) except juveniles and small adults, where they are less curved (Fig. 4D). Anterior branchial region slightly inflated so carapace has conspicuous globular appearance. Epibranchial tooth as small obtuse tooth in juveniles and slight notch in small adults; absent or barely noticeable in most fully grown individuals. Postorbital angles acute in juveniles and obtuse in adults.

Frontal border wide, arched and cut by shallow emarginations into two rounded supraorbital angles and four lobes. Median lobes typically rounded. The four lobes and supraorbital angles of juveniles and adults armed with numerous irregular, minute teeth, more noticeable on submedian lobes, barely noticeable on supraorbital angles (Fig. 4A).

Third maxillipeds (Fig. 4C) subrectangular. Ischium of endognath smooth, with scattered punctae but no granulation. Suture between second and third thoracic sternites (sternal suture 2/3) of juveniles and smallest adults but absent in adults (Fig. 4C).

Chelipeds, especially larger one, distinctively thick and bulky, with short and stubby fingers. Merus of chelipeds with teeth varying in size and number, even

between right and left meri of same individual. Teeth more acute in juveniles. Distal and proximal angles along anterior margin of carpus of juveniles and adults with two rounded, obtuse teeth. Few scattered and short setae may be present along outer margins of carpus and propodus. Upper margin of propodus rounded or with very slight crest; lower margin slightly rounded. Dactylus and immovable finger of largest cheliped typically shorter and thicker, armed with large teeth. Smaller cheliped with more slender fingers armed with cutting edges.

Walking legs thick and stocky. Upper margins of carpus and propodus with only few setae, except first pair, where few long setae may be found on distal portion of carpus. Setae more numerous along upper margin of dactyli. Few plumose setae. Inner (posterior) margin of dactyli with five or six horny setae and three to four transversal rows of shorter setae proximally.

First pleopod of male relatively short and with stout, symmetrical apex similar to that of *T. digitalis* (Figs. 4D, E). Short distal spines along both surfaces and proximal plumose setae.

Color in Life.—Carapace and walking legs reddish orange. Eyes greenish gray. Dorsal portion of chelipeds dark reddish orange in sharp contrast with ventral portion of inner surface, which is orange-yellow to deep orange. Reddish orange reticulations may be present on outer and inner surface of propodus of chelipeds. Finger and dactylus of chelipeds brown to dark brown.

Color in Alcohol.—Carapace, walking legs and chelipeds bright orange. Dark orange reticulations may show on outer and inner surface or propodus of chelipeds. Finger and dactylus of chelipeds light brown.

Remarks.—The extant type material consists of specimens referred to as "cotypes" and "syntypes." A female (MCZ 4834) is here designated as the lectotype; two damaged specimens apparently from the same material, a male and a female (MNHN-B16542), are designated as paralectotypes.

Miers (1886) included *T. formosa* in a list of *Trapezia* species having no lateral spines or teeth and suggested that it was not "specifically distinct" from *Trapezia digitalis* Latreille. Borradaile (1902) placed the species as a distinct variety of *T. digitalis* but stated that it "differs . . . sharply from the dark-brown true *digitalis*."

Rathbun (1930) placed the species, together with *T. corallina* Gerstaecker, in synonymy with *T. digitalis*. Other workers followed Rathbun but confused *T. formosa* with *T. ferruginea* Latreille because of their similar color. Serène (1959, 1971), however, kept *T. formosa* as a distinct species in his keys. The characters given, however, were not specific enough. As a result, further confusion was created when other species were erroneously identified as *T. formosa* when Serène's keys were used (see below). Garth (1971) listed Borradaile's *T. digitalis* var. *formosa* Smith, as a valid species but did not apply it to eastern Pacific material. References to *T. ferruginea* from Panamá (Abele, 1976; Abele and Patton, 1976; Glynn, 1976, Castro, 1978 and Finney and Abele, 1981) most probably included *T. formosa* and *T. corallina*.

Castro (1982) provided evidence of the validity of *T. formosa* and separated it from the other three eastern Pacific species of *Trapezia*. Further evidence was provided by Huber (1985a). Other work on the eastern Pacific *Trapezia* (Glynn, 1980; Gotelli and Abele, 1983; Gotelli et al., 1985; Huber, 1985b) treats *T. formosa* as a distinct species. Garth (1991), however, did not recognize the validity of the species, not even as a subspecies, in his list of Galápagos crabs.

The material from French Polynesia identified as *T. formosa* by Odinetz (1984) belongs to a different species, possibly a new one. Like *T. formosa*, it is char-

acterized by a rounded and inflated carapace, uniform color and small size. The reexamination of all 39 specimens collected by Odinetz (1983) (MNHN-B9739–9744), however, shows clear differences from *T. formosa.* The frontal border is nearly straight and finely denticulate and the lateral borders of the carapace are never provided with a tooth or notch, not even in juveniles. Live specimens were described as very light brown in color (Odinetz, 1984) but those preserved in alcohol are very light orange.

Specimens from the South China Sea identified as *T. formosa* (Dai et al. 1983, 1986; Dai and Yang, 1991) are most probably the result of an erroneous identification. The carapace is small, rounded and marked by a shallow notch on each side. The anterior border, however, was described as divided into two lobes by a shallow depression in contrast with the six lobes present in *T. formosa.* The color in alcohol was described as orange "outlined by dark orange lines" and the chelipeds and legs are "marked with an obscure [dark?] meshwork pattern." These specimens may belong to *T. cheni* Galil, 1983, which was described from Taiwan (Galil, 1983). *T. cheni* also has a small, rounded carapace and a finely denticulate frontal border marked only by a shallow emargination in the middle. Unlike the South China Seas form, however, there is no lateral notch. The carapace of specimens preserved in glycerin and sugar had "magenta-red lines [that] circumscribe irregular pale orange areolae." The same pattern was observed on the chelipeds but the lines were dark purple. It is possible that in alcohol this pattern turns into the orange and darker meshwork pattern described in the South China Seas form.

The identity of *T. formosa* from Enewetak, Marshall Islands (Huber, 1985b) is questionable. Genetic variability as measured by starch-gel electrophoresis suggested that the Panamanian and Enewetak populations represent different species. This is the only record of *T. formosa* from Enewetak (Garth et al., 1987). *T. formosa* has also been reported from Taiwan (Chang et al., 1987) but, like the Enewetak record, it is probably an erroneous identification that resulted from the use of the key given by Serène (1971). It thus appears that *T. formosa,* as *T. corallina,* is restricted to the tropical eastern Pacific.

Key to the Eastern Pacific Species of Trapezia

1a. Live color of body reddish orange; chelipeds with lower margin of propodus yellow. Adults small (cw rarely above 10 mm), with anterolateral sides of the carapace strongly curved (inclination up to 45°) and anterior portion inflated, which give carapace distinct globose appearance. Chelipeds thick and bulky. Juveniles with anterolateral sides of carapace only slightly curved and few or no setae on carpus and propodus of walking legs . . . . . *T. formosa*

1b. Live or preserved color brownish orange or dark brown. Anterolateral borders of carapace partially or mostly parallel; if carapace rounded, size large (cw more than 10mm). Chelipeds slender. Adults and juveniles with long setae on carpus and propodus of walking legs 2

2a. Body dark brown, with white or cream tubercle at distal end of propodus of chelipeds. Anterolateral borders of carapace always parallel . . . . . *T. digitalis*

2b. Body orange or orange brown, with no white tubercle at distal end of propodus of chelipeds. Anterolateral borders of carapace of adults curved, not distinctively parallel to each other . . 3

3a. Body dark orange-brown, with brown reticulations on propodus of chelipeds. Complete suture between second and third thoracic sternites (see Fig. 1B). Ischium of endognath of third maxillipeds with middle portion of inner margin rough (easily felt with blunt point). Juveniles with acute tooth on anterior distal margin of carpus of chelipeds (Fig. 1C) . . . . . *T. corallina*

3b. Body orange to orange-brown, with no distinct dark reticulations. Adults with fused second and third thoracic sternites. Ischium of endognath of third maxillipeds without clearly rough inner margin. Juveniles and adults with obtuse tooth on anterior distal margin of carpus of chelipeds . . . . . *T. ferruginea*

Table 2. Summary of color, morphological and size differences among the four eastern Pacific species of *Trapezia*

Character	*Trapezia corallina*	*Trapezia digitalis*	*Trapezia ferruginea*	*Trapezia formosa*
Live color	Brownish orange; brown reticulations on lower margin of propodus of chelipeds; eyes dark gray	Dark brown; white or cream tubercle at distal end of propodus of chelipeds; eyes dark brown	Orange to brownish orange; eyes dark brown	Reddish orange; lower margin of propodus of chelipeds yellow; eyes greenish gray
Dactylus and finger of chelipeds	Dark brownish orange	Orange-white	Dark brown to black	Brown to dark brown
Anterolateral borders of carapace of adults	Nearly parallel to slightly curved	Parallel	Curved	Strongly curved
Suture between second and third thoracic sternites of adults	Present	Absent	Absent	Absent
Epibranchial tooth of adults	Acute, obtuse, or notch-like	Notch-like or absent	Obtuse, notch-like or absent	Notch-like or absent
Frontal border	6 lobes; teeth barely noticeable	4–6 lobes; many minute teeth	6 lobes; teeth barely noticeable	6 lobes; minute teeth
Chelipeds	Slender	Slender	Slender	Thick and bulky
Tooth on anterior distal margin of carpus of chelipeds	Acute in juveniles, obtuse in adults	Obtuse	Obtuse	Obtuse
Granulations on inner margin of endognath of ischium of third maxillipeds	Present	Absent	Absent	Absent
Setae on upper margin of carpus and propodus of walking legs	Long	Few	Long	Few or none
Rows of setae on inner margin of dactyli of walking legs	3–8	3	4–8	3–4
First male pleopod	Slender; apex asymmetrical	Short; apex stout and symmetrical	Slender; apex symmetrical	Short; apex stout and symmetrical
Maximum recorded size (carapace width in mm)	Female: 19.2 Male 16.0	Female: 15.3 Male: 13.4	Female: 22.4 Male: 20.6	Female: 12.4 Male: 11.6
Minimum ovigerous size (carapace width in mm)	4.8	5.4 (small sample)	4.6	3.9

Discussion

Small but consistent differences in color and morphology distinguish the four eastern Pacific species of *Trapezia* (Table 2). The separation of these species using morphology followed their recognition by color in live specimens and the formation of species-specific heterosexual pairs under laboratory conditions (Table 1). One of these morphological characters, the nature of the thoracic sternites, is used for the first time in the systematics of *Trapezia.* The discovery of separate species by the use of non-morphological traits and the existence of a long-standing debate among taxonomists on the validity of these species are criteria used by Knowlton (1993) to characterize sibling species.

Although the four species are seemingly sympatric, there are possible differences in microhabitat. *Trapezia formosa,* characterized by its small size, is more frequent in small coral colonies and live fragments. In large colonies, which are invariably inhabited by large individuals of *T. ferruginea* and *T. corallina, T. formosa* is found in the deeper spaces among branches (Castro, 1982). *Trapezia formosa* is also noticeably less aggressive when handled than the other species.

Differences in the morphology of the male gonopods in all four species are indicative of reproductive isolation. Differences in growth patterns are also evident. Females of *T. formosa,* one of the two small species, become ovigerous at a size smaller than in the other species (Table 2).

The apparent presence of color variants throughout the wide geographic distribution of *T. ferruginea* suggests the existence of more than one species. Nevertheless, there is no morphological or genetic evidence to regard the eastern Pacific populations of *T. ferruginea* as a different species. Similarly, there are no morphological differences between Indo-west Pacific and eastern Pacific populations of *T. digitalis.* Color variants, however, appear to occur in this species. Significant variations in the reticulation of the dorsal surface of the carapace were observed in the Hawaiian populations (Huber, 1987). Individuals were shown to prefer mates of the same color pattern, which suggests that in *Trapezia* phenotypic assortative mating associated with color variations may ultimately result in sympatric speciation.

A careful analysis of not only morphology but of live color, agonistic interactions among color variants, microhabitat, genetic structure and even host specificity and feeding habits is needed to better define species of *Trapezia,* particularly those with a wide geographical distribution such as *T. ferruginea, T. digitalis* and *T. cymodoce.*

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