ISRAEL JOURNAL OF ZOOLOGY, Vol. 32, 1983, pp. 1–12

A NEW SUBSPECIES OF *TRIPNEUSTES GRATILLA* FROM THE NORTHERN RED SEA (ECHINODERMATA: ECHINOIDEA: TOXOPNEUSTIDAE)

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ABSTRACT

Tripneustes gratilla elatensis n. ssp. from the northern Red Sea, is significantly different from the Indo-Pacific *T.g. gratilla*. It is more compressed, and has a larger peristome aperture, fewer interambulacral plates, lesser spine tuberculation, and more vivid colors than its Indo-Pacific conspecific. The typical habitats of *T.g. elatensis* are mainly rocky shores and coral reefs. Specimens of *T.g. elatensis* and the Indo-Pacific *T.g. gratilla* occur together in the southern Red Sea.

INTRODUCTION

Tripneustes gratilla (Linnaeus, 1758) was originally described as *Echinus gratilla* from the Indian Ocean. Although the type specimens were lost, Loven (1887) assigned it to the genus *Tripneustes* Agassiz. The many nominal species of *Tripneustes* which have been described from various parts of the Indo-Pacific region were considered by Mortensen (1943) to be synonyms of *T. gratilla*. In this paper, northern Red Sea specimens of this species are compared with material from the Indo-Pacific Ocean, made available by the British Museum (Natural History), and with detailed descriptions by Mortensen (1943). Observations and measurements of living animals and skeletons are aimed at describing a new subspecies unique to the Red Sea, whereas the typical Indo-Pacific *T. gratilla* is defined here as *T.g. gratilla* (L.).

METHODS

Measurements, taken with vernier calipers (with a precision of 0.1 mm), and counts of the plates and spine tubercles, were related through the allometric equation (Ricker, 1979) for both subspecies. Covariance analysis (Snedecor & Cochran, 1967) was applied to compare the regression lines for the difference between the slopes and adjusted means for each set of measurements. The shape of test, degree of tuberculation and other morphological features were recorded. Color variation was evaluated for the new subspecies using an arbitrary light-dark ranking of three components – color shades of spines, tubefeet and pedicellaria. The five grades of darkness were:

Received 4 July 1982 and in revised form 24 December 1982

(1) white or colorless; (2) purplish-light green; (3) reddish or green; (4) dark red, brown or gray; (5) black. A combined 3-digit number marks the individual darkness pattern. The darkness index (DI), the arithmetic mean of these grades, is used to specify the average darkness, whereas SD, the sum of absolute deviations of the individual grades from the mean, is a measure of monochromy ($SD \leqslant 1.33$) or heterochromy ($SD \geqslant 2$). Thus, for a sea urchin whose spines are black, with dark red tube-feet and gray pedicellaria, the darkness index (DI) is $(5 + 4 + 4)/3 = 4.33$ and $SD = 1.33$. Secondary discoloration of the primary spines is ignored in this analysis and only the original spine color or shade shown at their bases considered.

THE NEW SUBSPECIES

Tripneustes gratilla elatensis n. ssp.

Material

Description is based on a type series of 8 sea urchins, one whole animal, designated as holotype and 7 skeletons designated as paratypes (Table I), deposited in the Hebrew University of Jerusalem and the British Museum (Natural History) (BMNH). Numerous (> 150) living sea urchins and denuded tests were used for the comparative biometrical analyses. To avoid deleterious effects on sea urchins by industrial and urban pollution in the northern tip of the Gulf (Dafni, 1980, 1983), collections were made on a 10-km stretch of pollution-free shore in the vicinity of Wadi Tweibe, NW Gulf of Elat (= Gulf of 'Aqaba) (29°29'N, 34°52'E), 15 km south of Elat. The habitat and population dynamics of these sea urchins were studied for 4 years and will be published elsewhere (Dafni, in prepn.). Seventeen *T.g. gratilla* tests on loan from the British Museum, and data on additional tests (Mortensen, 1943: table on p. 503), represent the following locations (Fig. 1A):

East Africa
Mombasa, Kenya (4 specimens)
Zanzibar, Tanzania (4)
Delagoa Bay, Mozambique (2)
Durban, South Africa (4)

Central Indian Ocean
Aldabra Island (3)
Montebello, NW Australia (2)

Western Pacific Ocean
Banda, Indonesia (5)
Port Jackson, SE Australia (1)
Great Barrier Reef, Australia (1)
Puerto Galera, Philippines (4)
Solomon Islands (2)
Tonga Island (1)
Samoan Islands (1)
Guam Island (1)
Hawaiian Islands (8)

Data of a further 18 specimens from various parts of the Red Sea proper, the Gulf of Aden and the adjacent East African shores (Fig. 1B) provided by E. Tortonese and J. Roman, or measured from specimens borrowed from the Rijksmuseum van Natuurlijke Historie, Leiden, and one specimen collected during the Israel South Red Sea Expedition, 1962 (Table IV), were used to establish the distribution pattern of *T.g. elatensis.*

TABLE I
Type series of *T.g. elatensis*[1]

Status and No.[2]	*Diameter (HD)*	*Height (VD)*		*Apical system*		*Peristome*		*No. of plates*		*Oculars insert*
		Size	*% of HD*	*Size*	*% of HD*	*Size*	*% of HD*	*A*	*IA*	
Holotype (HUJ EC 1)	68.9	35.1	50.9	13.4	19.4	23.7	34.4	?	24–25	I, V
Paratype (HUJ EC 2)	74.3	40.2	54.1	15.2	20.5	24.2	32.6	73	27	I, IV, V
(HUJ EC 3)	108.0	61.8	57.2	16.0	14.8	29.0	26.9	117	34–35	I, V
(HUJ EC 4)	94.0	52.2	55.9	17.5	18.6	26.5	28.2	90	29–30	I, V
(HUJ EC 5)	50.0	28.5	57.0	10.0	20.0	18.5	37.0	57	21–22	I, V
(HUJ EC 6)	69.0	38.0	55.1	13.5	19.6	24.0	24.8	77	26	I, V
(HUJ EC 7)	67.0	41.7	62.2	12.0	17.9	22.0	32.8	73	25	I, IV, V
(BMNH/1981.11.30.13)	103.0	57.7	54.0	16.8	16.3	28.5	27.7	106	34–35	I, IV, V

[1] Leg. J. Dafni, all from NW Gulf of Elat (29°29′N, 34°52′E) (measurements in mm).
[2] Holotype is entire animal preserved in alcohol, paratypes are dry tests.

Fig. 1. Distribution map of *T. gratilla*, showing origin of analyzed specimens. A. Indo-Pacific distribution of specimens. B. Location of Red Sea specimens (cf. Table IV). ◆ – *T.g. elatensis* type locality; ● – British Museum specimens; + Data from Mortensen, 1943.

Description of the Type Series (n = 8)

Sea urchins of medium size, diam rarely over 110 mm, inhabiting hard-bottomed habitats in the subtidal region and coral reefs of the northern Gulf of Elat.

Shape semiglobular with a flat apical region. Vertical diam (VD) is 0.51–0.62 of the horizontal diam (HD), average 0.559 ± 0.031. Ambitus round to subpentagonal. Oral side flat, peristome rim somewhat elevated. Ambulacral plates narrow, trigeminate, pores in three vertical series along the ambulacral plate row. Interambulacral (IA) plates larger, densely covered with globiferous pedicellaria. Primary spines short, thin and sparse in the aboral half, altogether missing from some IA plates. In the oral half spines are numerous in the IA and ambulacral plates. Peristome 0.25–0.37 of horizontal diam with small gill slits. Apical system is 15–20% of HD and 2–3 ocular plates are inserted. Coloration of the holotype uniformly mauve; spines pale. Paratypes are bare tests, yellowish in color.

Comparisons

Tripneustes gratilla elatensis differs from the Indo-Pacific *T.g. gratilla* in the following:

Horizontal diameter. The largest specimen of *T.g. elatensis* that came to my knowledge is one of 130 mm, living in the Coral World Underwater Observatory and Aquarium at Elat for > 5 years (D. Friedman, pers. commun.). The largest specimen observed in the field measured ca. 120 mm, compared with records of 145 mm attained by *T.g. gratilla* on the South African coast (Clark & Courtman-Stock, 1976), Australia (Clark, 1946) and Hawaii (Mortensen, 1943). Dollfus and Roman's (1981) description of Red Sea *T. gratilla* is mainly based on Mortensen (1943), therefore their stated record of 145 mm is questionable.

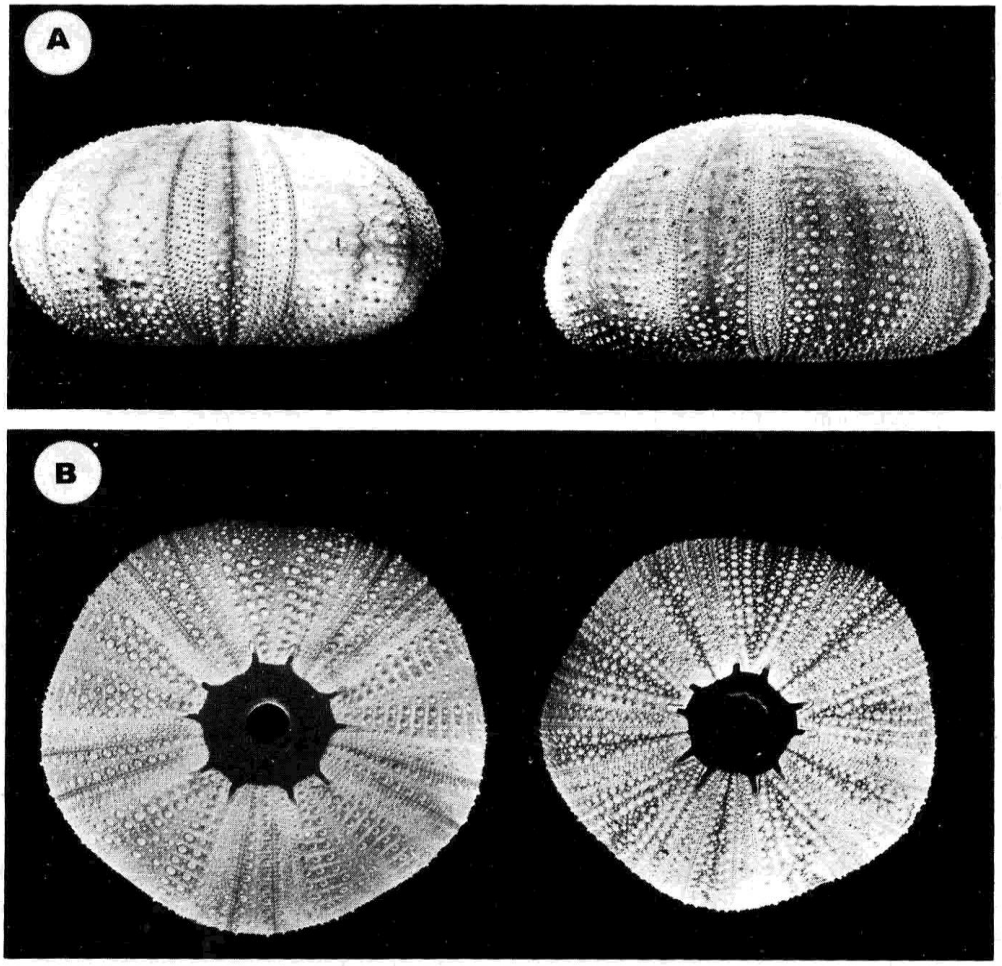

Fig. 2. *Tripneustes gratilla elatensis* n. ssp. and Indo-Pacific *T.g. gratilla* tests. A. Side view of a 69 mm HD specimen from Elat (left), compared with an equal sized test from Mombasa, Kenya. B. Oral view of a 94 mm HD specimen from Elat (left) and an 83 mm HD test from Mombasa. Note the flatter appearance and relatively larger peristome in *T.g. elatensis*.

Relative height and test shape. T.g. elatensis is, relative to HD, shorter in its VD and has a flatter apical region, while *T.g. gratilla* is more domed (Fig. 2). Allometric relations between HD and VD (Table IIA) show isometry. GM, the functional regression slope (slope of regression divided by the correlation coefficient (Ricker, 1979)), is 1.003 for *T.g. elatensis* and 1.024 for *T.g. gratilla*; not significantly different, although differing in the adjusted means.

Peristome size. T.g. elatensis has a relatively larger peristome than *T.g. gratilla*, which further increases with diam (GM = 0.840 and 0.756, respectively). Regression slopes and adjusted means are significantly different between the two subspecies (Table IIB).

TABLE II

Allometric equations for the relationship between: (A) Horizontal and vertical diameter; (B) Peristome size and horizontal diameter, and (C) The number of IA plates and horizontal diameter for *T. gratilla elatensis* n. ssp. and *T.g. gratilla*[1]

A. *Relation between diameter size (HD) and height (VD)*		
T.g. elatensis	$VD = 0.501\ HD^{1.021}$	($r = 0.997$, $N = 101$)
T.g. gratilla	$VD = 0.603\ HD^{0.994}$	($r = 0.991$, $N = 44$)
	$F_{slopes} = 1.816$	(ns)
	$F_{adjusted\ means} = 40.25$	($p < 0.001$)
B. *Relations between peristome (P) and horizontal diameter (HD)*		
T.g. elatensis	$P = 0.679\ HD^{0.835}$	($r = 0.994$, $N = 62$)
T.g. gratilla	$P = 0.856\ HD^{0.739}$	($r = 0.978$, $N = 42$)
	$F_{slopes} = 14.31$	($p < 0.01$)
	$F_{adjusted\ means} = 66.26$	($p < 0.001$)
C. *Relations between number of interambulacral plates (IA) and horizontal diameter (HD)*		
T.g. elatensis	$IA = 7.44 \ln HD - 4.316$	($r = 0.973$, $N = 76$)
T.g. gratilla	$IA = 12.68 \ln HD - 20.77$	($r = 0.917$, $N = 41$)
	$F_{slopes} = 56.38$	($p < 0.001$)
	$F_{adjusted\ means} = 65.07$	($p < 0.001$)

[1] N – number of specimens; F = coefficient of covariance analysis; r = coefficient of correlation.

Number of interambulacral and ambulacral plates. Interambulacral (IA) plate counts for *T.g. elatensis* and *T.g. gratilla* are shown in Fig. 3 and the allometric relations, in Table IIC. Large *T.g. elatensis* have significantly fewer IA plates than *T.g. gratilla*. The number of ambulacral plates was related to the number of IA plates. For *T.g. elatensis* it is 2.08 per IA plate whereas for *T.g. gratilla* it is 2.14 (insignificant difference, T-test).

Spine tubercles. No adult *T.g. elatensis* ($\geqslant 30$ mm) possessed complete IA spine tuberculation. In the aboral half of each interambulacrum, 2–5 plates lacked primary spine tubercles (Fig. 4). In many cases primary tubercles appear only on every second plate in the superambital region. In *T.g. gratilla* (BMNH material, Mortensen's illustrations and observations offered by E. Tortonese), the array of tubercles is always complete ($\geqslant 1$ tubercle per each IA plate). Young *T.g. elatensis* (< 10 mm), however, show complete tuberculation. No difference is shown in ambulacral tuberculation between the subspecies.

Color variation. There is a large range of color variation in *T.g. elatensis* and no typical pattern is shown. The darkness index (DI) for 127 specimens ranged from 1.0, "albino" (5.5%), to the darkest form (3.9%), with many intermediate forms (Table III). Variations were unevenly distributed (χ^2, $p < 0.01$), having a dominance of intermediate forms (48% had DI = 2.33–3.66). However, 85% were monochromatic

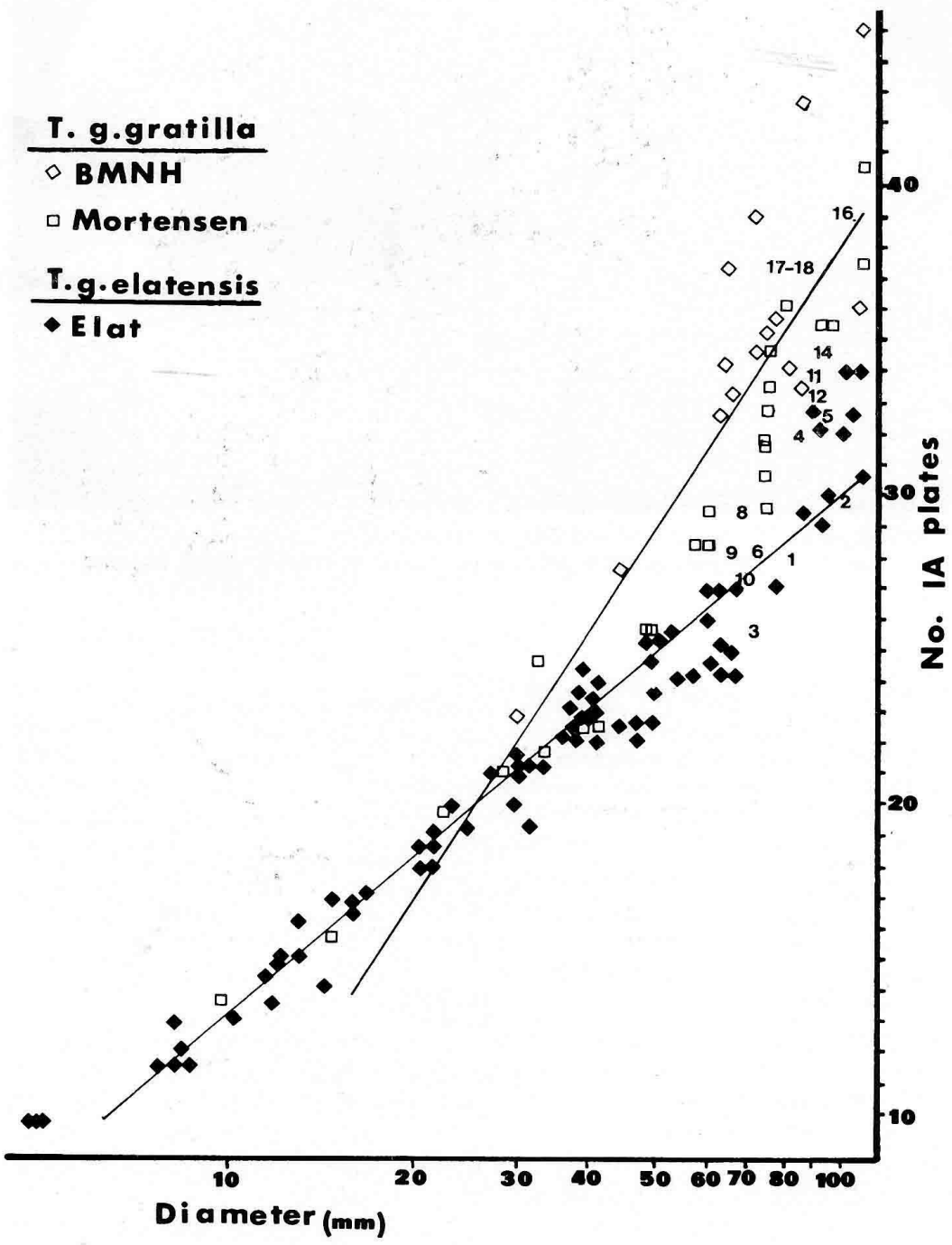

Fig. 3. Counts and regression lines of interambulacral plates vs. horizontal diameter for *T.g. elatensis* n. ssp. and *T.g. gratilla* from the British Museum (BMNH) and cited by Mortensen (1943). 1–18, specimens from the Red Sea proper and adjacent African coasts (cf. Table IV).

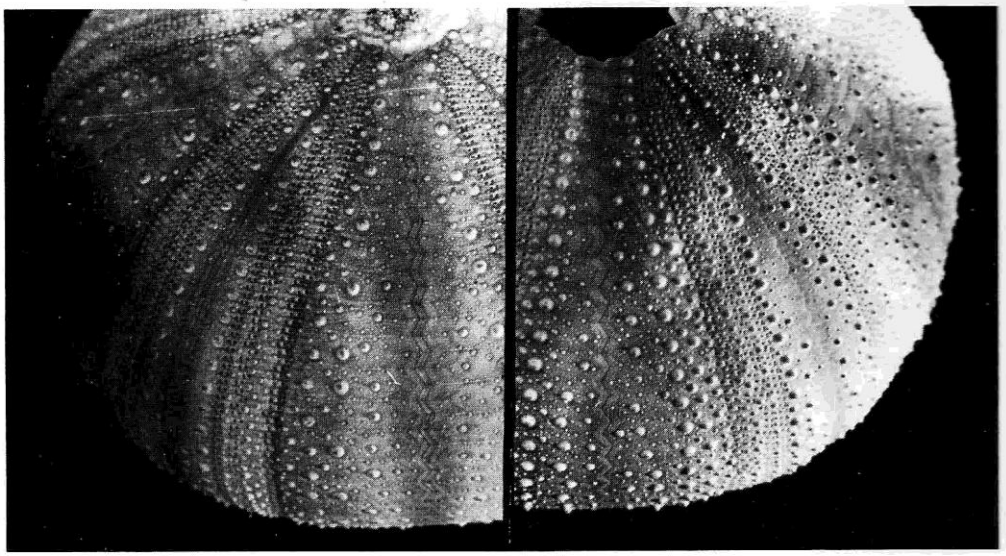

Fig. 4. Oblique aboral view of a 94 mm HD *T.g. elatensis* n. ssp. (left), compared with a *T.g. gratilla* (77 mm). Note the lack, in the former, of primary spine tubercles from some IA plates.

TABLE III

Classification of 158 *Tripneustes g. elatensis* specimens by color index (average grade of three color components on a darkness scale, 1–5) and by the measure of heterochromy (SD – sum of deviations from this mean): main values, percentages of 127 adults; values in parentheses, percentages of 31 juveniles (up to 15 mm HD)

Darkness index	*Measure of heterochromy (SD)*			
(DI)	*0.0*	*1.33*	*2.00*	*> 2.66*
1.00	5.5 (29.0)	–	–	–
1.33	–	5.5 (29.0)	–	–
1.66	–	3.9 (9.7)	–	(6.5)
2.00	5.5 (6.5)	–	3.1 (3.2)	–
2.33	–	11.0 (16.1)	–	–
2.66	–	8.7	–	–
3.00	11.0	–	5.5	–
3.33	–	7.9	–	–
3.66	–	3.1	–	0.8
4.00	6.3	–	4.7	–
4.33	–	7.1	–	0.8
4.66	–	5.5	–	–
5.00	3.9	–	–	–
Total	32.2 (35.5)	52.7 (54.8)	13.3 (3.2)	1.6 (6.5)

(SD $\leqslant$ 1.33). Most young animals ($\leqslant$ 15 mm) were uniformly greenish (DI = 1.33–2.33).

Habitat

T.g. elatensis mainly inhabits rocky substrates in the sublittoral fringe and coral reef and rubble, where the newly metamorphosed young settle, and larger specimens occupy holes and crevices in the coral reef. It is totally absent from seagrass beds, the main habitat of *T.g. gratilla* in the Indo-West Pacific region (Mortensen, 1943; MacNae & Kalk, 1958; Herring, 1972). I have also found it living among mangrove (*Avicennia marina*) pneumatophores in the southern Gulf of Elat.

Distribution

Specimens collected elsewhere along the Gulf of Elat conform to the above description. Data of examined specimens from other parts of the Red Sea and adjacent African coasts (Table IV and Fig. 3) show that specimens found north of the Dahlak Archipelago may belong to *T.g. elatensis*. Their shape, peristome size, number of IA plates and tuberculation fit this description. Dahlak specimens (nos. 12 and 14, Table IV), on the other hand, have complete tuberculations and domed shapes, which resemble those of specimens from the Indian Ocean coast (nos. 16–18). One specimen (no. 14) has the banded color pattern typical of *T.g. gratilla* (Mortensen, 1943).

DISCUSSION

Fifteen specific names have been given to Indo-Pacific *Tripneustes*, all considered synonyms of *T. gratilla* by Mortensen (1943). Although he admitted to a certain amount of local variation, he concluded that none was sufficiently characterized to deserve distinction as a variety. *T.g. elatensis* is proposed as an exception. Without challenging Mortensen's conclusion, it is my opinion that the significant difference between the Indo-Pacific and Red Sea *T. gratilla* justifies the distinction of the latter on the subspecific level. The distinction of *T.g. elatensis* was also recognized by T.A. Ebert (pers. commun.) and Dollfus and Roman (1981), whose specimens (nos. 1 and 2 in Table IV) conform to my description.

Open sea conditions throughout the Indo-Pacific Ocean favor a continuous gene flow due to long-living pluteus larvae. Under these conditions significant local variation is expected only in the most isolated and remote sites, such as the nearly landlocked Red Sea. A gradual northward change in the environmental conditions forms a cul-de-sac situation in the Red Sea, characterized by depletion of animal inventory and increase in endemism (Por, 1975). It is, therefore, not surprising to find forms here which are different from those inhabiting the open ocean. Some of the differences between the Red Sea *T. gratilla* and its Indo-Pacific conspecific are probably adaptations to the different habitats. For example, experimentally transferring rock-dwelling *T.g. elatensis* into sandy substrates results in an increase in their relative height (Dafni, in prepn.). Some of the subspecific characteristics described above, however, such as reduced tuberculation, number of plates and the different color patterns, are presumably genetic.

TABLE IV

Examined specimens from the Red Sea proper and along the African adjacent coasts

Locality[1]	*Source*[3]	*HD*	*VD*	*Peristome*	*IA plates*	*Test shape*	*Tuberculation*	*Coloration*
1. Gulf of Suez (27°50′N)	Roman[2] (MNHN 0510)	90.5	48.0	26.0	28	Flat	Incomplete	No record
2. As above	Roman[2] (MNHN 0511)	98.5	53.0	25.0	30	Flat	Incomplete	No record
3. Red Sea (location unknown)	(BMNH 40.3.23.19)	73.3	40.5	23.0	25–26	Flat	Incomplete	Test uniform reddish
4. As above	(RMNH 180-1889)	90.8	50.5	25.2	32	Flat	Incomplete	No record
5. Hurgada, Egypt (27°N)	(BMNH 1924.10.1.2)	87.0	53.0	24.0	32–33	Semi-domed	Incomplete	Whitish
6. Sharm Obhor, Jeddah (22°N)	Tortonese[2] 1978	72.0	31.0	24.0	28	Depressed	Incomplete	White with green median bands
7. As above	As above	60.0	32.0	20.0	?	Depressed	No record	Median area grey
8. Jeddah, Saudi Arabia (22°N)	(RMNH 998-1880)	67.3	41.0	20.5	29–30	Semi-domed	Incomplete	No record
9. Suakin, Sudan (18°N)	(BMNH 1951.5.7.48)	66.0	35.0	23.0	28	Flat	Incomplete	Whitish
10. As above	As above	72.0	39.2	23.0	27	Flat	Incomplete	Uniform dark
11. Nocra, Dahlak Archipelago (15°30′)	Tortonese[2] 1953	90.0	48.0	24.0	34	Depressed	Incomplete	Yellowish
12. As above	As above	90.0	76.0	24.0	33	Sub-conical	Complete	Yellowish, median zone darker
13. As above	As above	80.0	65.0	22.0	?	Depressed	No record	Yellowish
14. Cundabilu, Dahlak	ISRSE, E62/177	91.0	58.5	24.5	34–35	Domed	Complete	White with dark median bands
15. Djibouti, Gulf of Aden (12°N)	Tortonese[2] 1980	90.0	41.0	22.0	?	Depressed	No record	Clear brown
16. As above	Roman[2] (MNHN 0513)	100.0	74.0	22.5	39	Conical	Complete	No record
17. Mogadiscio, Somalia (2°N)	Tortonese[2] 1951	75.0	60.0	22.0	37	High conical	Complete	Radial dark bands
18. As above	As above	75.0	53.0	20.0	37	High conical	Complete	Radial dark bands

[1] Numbers correspond to Fig. 1B.

[2] Data obtained through pers. commun.

[3] Abbreviations: MNHN – Museum Nationale d'Histoire Naturelle, Paris; BMNH – British Museum (Natural History), London; RMNH – Rijksmuseum Natuurlijke Historie, Leiden; ISRSE – Israel South Red Sea Expedition, 1962.

Mortensen (1943) defines the color patterns of *T. gratilla* as highly variable. Nevertheless, he describes a common typical pattern: ". . . The mid-areas of both ambulacra and interambulacra are generally very dark, due to the accumulation there of (mainly globiferous) pedicellaria, which are usually black. . . . The not denuded test, thus has a markedly radiating appearance, the dark mid-areas, separated sharply by white spines and tube feet." This color pattern, illustrated by Faulkner and Smith (1970) from Japan, may be classified in our arbitrary darkness index as DI = 2.33, with an SD of 5.7. Such a color pattern is entirely absent from the northern Red Sea, but may correspond with the banded pattern found in Dahlak and Somali specimens (nos. 12, 14, 17 and 18 in Table IV). A color illustration, presented by Bemert and Ormond (1981) from Sharm Obhor, Saudi Arabia, shows one of the many *T.g. elatensis* color variants.

It is possible that separation of *T.g. elatensis* from *T.g. gratilla* may not be merely geographical. *T.g. elatensis* reproduces mainly in winter, whereas *T.g. gratilla* breeds throughout the summer (Pearse, 1974 and pers. commun.). The mixing of *T.g. elatensis* phenotypes with *T.g. gratilla* phenotypes in the southern Red Sea may result either from an inflow of larvae entering from the south, or from a morphological gradient from the oceanic to the Red Sea form.

ACKNOWLEDGEMENTS

I wish to thank Prof. F.D. Por and Dr. J. Erez for their interest and guidance throughout this study; Prof. T.A. Ebert for information and advice; Miss A.M. Clark of the British Museum (Nat. Hist.) for providing material and advice; Dr. J.C. den Hartog (Rijksmuseum van Natuurlijke Historie, Leiden), Dr. J. Roman (Museum National l'Histoire Naturelle, Paris), Dr. M. Goren (Tel Aviv University) and Prof. E. Tortonese (Museo Zoologico, Via Romana 17 50125 Firenze, Italy) for kindly advising and for supplying specimens and data. Help provided by Miss I. Ferber and the H. Steinitz Marine Biology Laboratory staff is highly appreciated. Mr. A. Niv prepared the photographs. Dr. L. Montgomery is thanked for reviewing the manuscript.

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