ABSTRACT: The tetractlid fauna at Elat, Israel, on the Gulf of Aqaba, Red Sea, consists of three morphologically distinct species. *Tetraclita rufotincta* Pilsbry, 1916 was reported previously from this region and may have been confounded with *T. achituvi* n.sp., and *T. barnesorum* n.sp. Although these species occur sympatrically, according to previous studies, and recent observations, they apparently occupy different levels in the narrow intertidal zone (~50 cm) of this area. Cirral morphology suggests that each differs in the manner by which they capture and manipulate prey. Little is known about the occurrence of these new species elsewhere in the Red Sea and adjoining Arabian Sea.

KEY WORDS: *Tetraclita achituvi* n.sp., *T. barnesorum* n.sp., zonation, cirral morphology, feeding.

INTRODUCTION

*Tetraclita rufotincta* was first described by Pilsbry (1916: 253) from Aden, South Arabia near the entrance to the Red Sea. It has been reported subsequently from within the Red Sea, East Africa, Pakistan, west coast of India and islands of the western Indian Ocean (Newman and Ross, 1976: 48). Among the specimens that Pilsbry (1916: 254) studied, those from Prison Island, Zanzibar and tentatively referred to *T. rufotincta*, differ morphologically from those found at Aden and likely represent an undescribed species. Nilsson-Cantell (1932: 11) described *T. alba* from Dar-es-Salaam, Tanzania, and Ren (1989: 452) described *T. africana* from Madagascar; neither of these are known to range north into the Arabian or Red Sea, and they are not represented in the present collections from Elat, Israel.

Only one species, *T. rufotincta*, has been reported from the Gulf of Aqaba, Red Sea, although there has long been circumstantial evidence for the presence of at least one or possibly two other species of *Tetraclita* (Achituv and Borut, 1975: 105; Achituv and Mizrahi, 1987: 185). At Elat, on the Gulf of Aqaba, in addition to *T. rufotincta*, which may be undergoing a population decline due to pollution (Fishelson, 1995), there is one tetractlid that is "red", has a relatively large orifice and a thin wall, and occurs low in the intertidal zone. A third has a relatively small orifice, a thick wall, and occurs in the upper reaches of the *Tetraclita* belt (Achituv and Borut, 1975: 105). Both of these are previously undescribed species that are readily distinguished from *T. rufotincta* and from one another on the basis of their morphology, intertidal position and by a different mode of feeding.

There have been numerous studies on what was assumed to be *T. rufotincta* in the Red Sea and elsewhere. These are not cited in the synonymy that follows, and they may
need to be reevaluated in light of the present findings.

SYSTEMATICS

Family Tetraclitidae Gruvel, 1903
Subfamily Tetraclitinae Gruvel, 1903
Genus Tetraclita Schumacher, 1817
Tetraclita rufotincta Pilsbry, 1916
(Fig. 1)

Tetraclita squamosa rufotincta Pilsbry, 1916: 253, Pl. 58, figs. 5-5b only (Aden, South Arabia, type locality); Zullo, 1968: 227; Newman and Ross, 1976: 48 (distribution).

DIAGNOSIS: Wall large, massive, conic to cylindroconic; adductor ridge of scutum long, angular, deeply undercut, separated from articular ridge, contiguous with rostral depressor muscle crests; 12-16 rostral depressor muscle crests; rami of cirrus II and III moderately long, stout, not antenniform.

SUPPLEMENTARY DESCRIPTION: Wall grey, to 60 mm in rostrocarinal diameter, thick; radii lacking, sutures obscure to obsolete; secondary filling of parietal tubes grey, commonly suffused with hydrangea pink; sheath about 1/2 height of wall, appressed. Basis calcareous, thin. Scutum as high as, or higher than wide; occludent margin with 6-10 oblique teeth on lower half or teeth poorly defined; basal margin evenly convex, terminating below mid-height of plate; articular margin more than 1/2 height of plate; articular ridge evenly curved to slightly angular; adductor ridge sinuous to angular, extending almost to basal margin, apically paralleling articular ridge; secondary pitted filling present between articular and adductor ridges; adductor muscle pit ovate, deep, lower border above mid-height of plate; rostral depressor muscle crests erect, long, extending medially along basal margin to basal termination of adductor ridge; 4-6 long primary, and numerous secondary lateral depressor muscle crests extending almost to adductor ridge. Tergum about twice as high as wide; external longitudinal furrow open, shallow; scutal margin weakly inflected in small individuals, strongly inflected in large; spur terminally separated from basiscutal angle by less than 1/2 its own width; carinal portion of plate narrow, 5-7 inclined crests. Labrum with shallow medial sulcus; crest lacking teeth; clothed with short, slender, acicular spines. Mandible with 4 unequally spaced teeth; tooth 2 and 3 with 1 subsidiary cusp; tooth 4 with 2-3 subsidiary cusps; basal comb with 10-15 short, stout spines; inferior angle with 1-3 longer, stout spines poorly differentiated from comb. Maxilla I with 5 long, stout spines, and 2-3 shorter, more slender spines above subapical notch; 20-35 long, slender spines in medial cluster; basal cluster with 12-15 shorter, slender spines. Anterior ramus of cirrus I about 1/4 longer than posterior ramus; basal and intermediate articles of both rami wider than high. Rami of cirrus II subequal, intermediate articles more than twice as wide as high. Rami of cirrus III subequal, intermediate articles twice as wide as high. Rami of cirri IV-VI essentially equal in length; setation of intermediate articles of cirrus VI ctenopod, 4 pairs, rarely 3; cirral
Ross: *Tetraclita* from the Red Sea.

Fig. 1. *Tetraclita rufotincta* Pilsbry, 1916. a, internal view of scutum. b, internal view of tergum. c, internal view of scutum from large individual. d, crest of labrum. e, mandible. f, enlarged portion of basal comb and inferior angle of mandible. g, maxilla I. h, cirrus I. i, cirrus II. j, cirrus III. k, intermediate segment of cirrus VI. SIO C-7186.
counts are (a/p, right side, r-c diam. 43.1mm): 31/19, 18/14, 18/17, 24/27, 31/31, 31/32. Intromittant organ slightly longer than cirrus VI.

MATERIAL: One km north of H. Steinitz Marine Laboratory, Elat, Israel, Red Sea, approx. 29°33'N, 34°57'E, intertidal, Y. Achituv coll., 1994. Scripps Institution of Oceanography, Benthic Invertebrates (SIO), C-7186; 10 spec.

_Tetraclita achituvi_ n. sp.
(Fig. 2)

DIAGNOSIS: Wall low, conic; adductor ridge of scutum moderately long, evenly curved, undercut, separated from articular ridge and from rostral depressor muscle crests; 20-25 rostral depressor muscle crests; rami of cirrus II and III long, slender, delicate, somewhat antenniform.

DESCRIPTION: Wall white to cream, relatively thin, to 40mm in rostrocarinal diameter; compartments commonly discrete, radii narrow to broad, summits horizontal; secondary filling of parietal tubes pink-vinaceous; sheath adpressed, about 1/2 height of wall. Basis calcareous, thin. Scutum higher than wide; occludent margin with 5-10 oblique teeth along lower 1/2; basal margin terminating at 1/3 height of plate and below level of lower edge of adductor muscle depression; articular margin approximately 2/3 height of plate; articular ridge low, evenly curved; adductor ridge low, thick, slightly undercut, well separated from basal margin of plate; adductor muscle pit elongate-oval, exceedingly deep, occupying supramedial portion of plate; rostral depressor muscle crests thin, relatively short, erect, irregular; 8-12 lateral depressor muscle crests, irregular, thin, shorter than rostral crests. Tergum about 1/3 higher than wide; external longitudinal furrow broad, shallow, open; scutal margin weakly inflected; spur separated from basiscutal angle by less than 1/2 its own width, distal end bluntly rounded; 6-7 erect, primary depressor muscle crests, and numerous intercalated secondary crests. Labrum with shallow, medial sulcus; crest armed with 2-3 teeth on each side of sulcus and 2 teeth in sulcus; crest and sulcus densely clothed with short, stiff, acicular spines. Mandible with 4 subequally spaced teeth; tooth 2 and 3 with 1 subsidiary cusp; tooth 4 with 2-3 subsidiary cusps; basal comb with 23-25 teeth; inferior angle with 2-5 short, stout spines, poorly differentiated from comb. Maxilla I with 2 long, stout, and 7-8 shorter, slender spines above narrow, subapical notch; 18-21 stout spines in medial cluster; 15-18 short, slender spines in basal cluster. Anterior ramus of cirrus I about 1/4 longer than posterior ramus; intermediate articles of anterior ramus higher than wide; wider than high on posterior ramus. Rami of cirrus II subequal; intermediate articles wider than high. Rami of cirrus III equal in length, long, slender, somewhat antenniform; intermediate articles higher than wide. Rami of cirri IV-VI equal in length; setation of intermediate articles of cirrus VI ctenopod, 3 pairs; cirral counts are (a/p, right side, holotype): 21/15, 18/16, 23/24, 26/30, 31/29, 32/32. Intromittant organ same as to 1/2 again as long as cirrus VI.

TYPE LOCALITY: About 200m south of H. Steinitz Marine Laboratory, Elat, Israel, approx. 29°33'N, 34°57'E, intertidal, Y. Achituv coll., 2 Feb., 1995.
Fig. 2. *Tetraclita achituvi* n. sp. a, internal view of scutum. b, internal view of tergum. c, mandible. d, enlarged portion of basal comb and inferior angle of mandible. e, crest of labrum. f, maxilla I. g, cirrus I. h, cirrus II. i, cirrus III. j, intermediate segment of cirrus VI. Holotype, CAS no. 107401.
MATERIAL: Holotype, California Academy of Sciences (CAS) no. 107401 (rostrocarinal diameter 27.85mm, orifice 10.4mm, height 20.4mm); 1 paratype, CAS no. 107402; 13 paratypes, SIO C-9957.

ETYMOLOGY: Named in honour of Yair Achituv, in recognition of his numerous contributions on the Cirripedia of Israel and adjoining seas, and who first alerted me some 25 years ago that there may be more than one species of Tetraclita in the Gulf of Aqaba, and lastly who provided the specimens from Elat upon which this study is based.

REMARKS: Pilsbry (1916) relied on Ridgeway colour charts where colour was of paramount importance. In proposing the specific epithet, "rufotincta", he was alluding to the tinted or suffused hydrangea pink of the secondary filling of the parietal tubes. There is no indication that the name refers to the intensely pigmented secondary filling of the parietal tubes that occur in this species.

Tetraclita barnesorum n. sp. (Fig. 3)

DIAGNOSIS: Wall low, parabolic to conic; adductor ridge of scutum short, evenly curved, shallowly undercut, well separated from rostral depressor muscle crests; 9-12 rostral depressor muscle crests; rami of cirrus II and III short, stout, not antenniform.

DESCRIPTION: Wall white to cream, thick, to 40mm in rostrocarinal diameter; compartments either discrete or sutures obsolete; secondary filling of parietal tubes usually white to cream, commonly suffused with pink along basal margin; sheath adpressed, about 1/2 height of wall. Basis calcareous, thin. Scutum as wide as to slightly wider than high; occludent margin with 6-10 oblique teeth along lower 2/3 of plate; basal margin curving angularly, terminating above mid-height of plate at level above basal edge of adductor muscle depression; articular margin about 2/3 height of plate; articular ridge low, evenly curved; adductor ridge short, low, deeply undercut, well separated from articular ridge; adductor muscle pit elongate-oval, shallow, occupying supra-medial portion of plate; rostral depressor muscle crests short, inclined, with subsidiary crests; 4-5 crests for lateral depressor muscle, short, with subsidiary crests. Tergum more than twice as high as wide; external longitudinal furrow open, shallow; scutal margin not inflected; spur separated from basi-scutal margin by less than 1/3 its own width, distal end acuminated; 6-7 crests for depressor muscle, thick, inclined, commonly lacking secondary crests. Labrum with relatively shallow, medial sulcus; crest armed with 3-4 teeth on each side of sulcus; crest and sulcus densely clothed with short, stiff acicular spines. Mandible with 4 unequally spaced teeth; tooth 2 and 3 with 1 subsidiary cusp; tooth 4 with 2-4 subsidiary cusps; basal comb with 15-18 teeth; inferior angle with 2 long, stout spines and 3-4 shorter, slender spines. Maxilla I with 2 long, stout and 4-5 shorter spines above subapical notch; 12-14 stout spines in medial cluster; 5-8 short, slender spines in basal cluster. Anterior rami of cirrus I about 1/4 longer than posterior rami; intermediate articles of anterior ramsusas high as wide, wider than high on posterior rami. Rami of cirrus II subequal; intermediate articles of both rami wider than high, those of anterior...
Ross: *Tetraclita* from the Red Sea.

Fig. 3. *Tetraclita barnesorum* n.sp. a, internal view of scutum. b, internal view of tergum. c, mandible. d, enlarged portion of basal comb and inferior angle. e, maxilla I. f, crest of labrum. g, cirrus I. h, cirrus II. i, cirrus III. j, intermediate segment of cirrus VI. Holotype, CAS no. 107403.
about 1/3 wider than those of posterior ramus. Rami of cirrus III subequal, articles wider than high; protuberant articles of anterior about 1/3 wider than those of posterior ramus. Rami of cirri IV-VI equal in length; setation of intermediate articles of cirrus VI ctenopod, 4 pairs; cirral counts are (a/p, right side, holotype): 19/11, 13/13, 15/15, 24/25, 26/24, 28/28. Intromittant organ annulated, ranging from 2/3 to 1 1/2 times length of cirrus VI.

TYPE LOCALITY: About 200m south of H. Steinitz Marine Laboratory, Elat, Israel, approx. 29°33'N, 34°57'E, intertidal, Y. Achituv coll., 2 Feb 1995.

MATERIAL: Holotype, California Academy of Sciences, no. 107403 (rostrocarinal diameter 27.6mm, orifice 5.4mm, height 17.1mm); 1 paratype, CAS no. 107404; 7 paratypes, SIO C-9958.

ETYMOLOGY: Named in honour of Harold Barnes (1908-1978), and his wife Margaret, whose collaborative efforts are unprecedented in the history of studies on the Cirripedia. Their published works span some 25 years, during which time they coauthored more than 50 papers on a wide range of topics. For a review of the life and works of Harold Barnes see Anonymous (1979).

COMPARATIVE MORPHOLOGY

Large individuals of *rufotincta* have a massive, conic to cylindroconic wall with numerous rows of large parietal tubes. The radii are lacking, and the sutures, discernible near the apex in smaller individuals, may be absent in larger ones. Alternatively, the relatively thin, eroded wall of *achituvi* is a truncated cone, with a large, irregular orifice, discrete compartments with remnants of the radii and/or sutures visible, and relatively few rows of small parietal tubes. Individuals of *bamesorum* have a thick, low spreading or parabolic wall with numerous rows of small, parietal tubes, obl same radii, and sutures discernible only on the upper portion of the wall; individuals higher in the intertidal may have a conic wall. Ren (1989: 453) noted that eroded specimens of *africana* lack remnants of the radii, have obliterated sutures, and a thick wall with a few rows of parietal tubes, the secondary filling of which is densely pigmented, much like that of *achituvi*. Based on available specimens (SIO C-6060; Dar-es-Salaam, Tanzania), *alba* is a relatively small species with a white to cream, distinctly ribbed, thin, conic to cylindroconic wall and only a few rows of parietal tubes which, when eroded, have a pink to pink-vinaceous filling. It also has a distinctly subtrigonal to pentagonal orifice, that is also apparent in *bamesorum*. The ratio of basal diameter to that of the orifice averages 3.24: 1 (n=6) in *rufotincta*, 2.21: 1 (n=6) in *achituvi* and 4.39:1 (n=7) in *bamesorum*.

External morphology of the opercular plates appears to be of little value in discriminating the species described here (cf. Yamaguchi, 1987: 342). Pilsbry (1916) placed much reliance on the number of "oblique teeth" found on the occludent margin of the scutum, but this feature is seemingly more variable among eroded individuals than previously reported, and thus may prove to be of questionable taxonomic value (see Foster, 1982: 215).
The adductor ridge of *rufotincta* extends angularly from the basal margin near the rostral depressor muscle crests to above the adductor muscle depression. In large (old) individuals a secondary, commonly pitted, callous develops between the adductor and articular ridges. The ridge of *achituvi* is shorter than in *rufotincta*, and it extends curvilinearly to well above the adductor muscle depression. In *barnesorum*, the ridge is shorter than in *achituvi*, evenly curved, and it does not extend to the upper limits of the adductor muscle depression. The thin, deeply undercut adductor ridge of *alba* extends from near the basioccludent angle, gradually rising angularly almost to the apex of the plate. In *africana* the adductor ridge is short, shallowly undercut, and extends to the lower limits of the adductor muscle depression much like that of *barnesorum*.

The lower edge of the adductor muscle depression in *rufotincta* and *barnesorum* occurs at a level slightly below the basal limits of the articular furrow, but above it in *achituvi*, *alba* and *africana*. The articular margin in *rufotincta* and *africana* is about 3/5 the height of the plate but only 1/2 in *barnesorum* and *achituvi* and 2/3 in *alba*.

The apical angle of the scutum is about 60° in *rufotincta*, 50° in *achituvi*, 70°-75° in *barnesorum*, 63° in *africana* and 55° in *alba*. The angle formed by the intersection of the basal margin and the rostral side of the tergal spur is about 130° in *rufotincta*, 150° in *achituvi*, 125°-135° in *barnesorum*, 130°-140° in *africana*, and 170° in *alba*.

The labrum has a shallow medial sulcus that is devoid of teeth in *rufotincta*. However, the specimens from Oman that Nilsson-Cantell (1928: 36) attributed to this species have 2 or 3 teeth on each side of the sulcus as well as fine hairs along the crest. The crest in all of those from Elat is covered with short acicular spines, not "fine hairs", which appear to be best suited for trituration.

The cutting edge of the mandible is armed with 4 teeth in all except *alba*, which has 5 teeth. The basal mandibular comb has 10-15 teeth in *rufotincta*, 23-25 in *achituvi*, 18-25 in *barnesorum*, 11-12 in *alba*, and 6-8 in *africana*.

The medial cluster of spines of maxilla I contains 20-35 spines in *rufotincta*, 18-23 in *achituvi*, 12-14 in *barnesorum*, 9 in *alba* and 12 in *africana*. The basal cluster in *rufotincta* contains 12-15 spines, 15-18 in *achituvi*, 5-10 in *barnesorum*, 3 in *alba*, and 8-9 in *africana*.

The ctenopod setation of the intermediate articles of cirrus VI are similar in *rufotincta*, *barnesorum* and *alba*, all of which have 4 pairs as opposed to 3 pairs in *achituvi* and *africana*, although some specimens of *rufotincta* may have only 3 pairs. All of the species have cirrus II and III armed with bipectinate setae, but none are armed with setae such as illustrated for *africana* by Ren (1989: Fig. 12o). Aside from significant differences in cirral counts, the maxillipeds of *rufotincta* and *barnesorum* are fundamentally short and stout, whereas those of *achituvi* are long, slender, and relatively delicate. The maxillipeds, especially II and III, are pigmented along the lesser curvature in *achituvi*, *barnesorum* and *alba* but those of *rufotincta* seemingly lack pigmentation.

**DISCUSSION**

Based on various features of the wall (Achituv and Borut, 1975: 104; Achituv and Mizrahi, 1987: 182), and relative electrophoretic mobilities of certain proteins, Achituv and Mizrahi (1987: 183) concluded that there are two or three local races or subspecies of *Tetraclita* at Elat (cf. Ford and Mitton, 1993: 151). The morphological distinctions in
the preceding sections confirm the observations of these and other workers, but contrary
to their findings, because of the totality and magnitude of these differences, the new
forms warrant recognition as full species as Yamaguchi (1987: 342) found when evaluat­
ing the infraspecific structure of *Tetraclita* in Japan based on similar data, and later con­
firmed by mitochondrial DNA sequencing (Hasegawa et al., 1996).

*Tetraclita* preferentially settles where exposed to waves or water turbulence
at Elat occupy different levels in a relatively narrow intertidal zone (=50 cm; Achituv,
1972: 75; Achituv and Mizrahi, 1987: 182). Elsewhere it is not uncommon to find differ­
tent *t*etraclitid genera similarly occupying distinct zones on the same shore (Denley and
Underwood, 1979: 270; Anderson and Buckle, 1983: 645; Anderson and Anderson,
1985: 89). However, there is apparently no vertical zonation of the sympatric Japanese
species of *Tetraclita* (see Yamaguchi, 1987: 344).

Wall strength, architecture and relative shell hardness, among other factors, play an
important role in the shape of the wall (Murdock and Currey, 1978: 184; Pentcheff,
1991: 405). However, barnacles occupying the lower reaches of the intertidal are com­
monly subject to more constant erosion/corrosion in contrast to those higher in the inter­
tidal, and this is readily apparent in *achituvi*.

The effects of temperature and dessication on the *Tetraclita* at Elat, relative to orifi­
cesize, wall thickness and tidal position were described by Achituv and Borut (1975:
104). Similar findings have been reported for the species occurring in Hong Kong (Liu
and Morton, 1994: 334). In general, barnacles having a small orifice and a relatively tall,
moderately thick wall occupy the higher reaches of the intertidal whereas those with a
large orifice, and a relatively thin wall occur low in the intertidal (Moore, 1935: 266;
Achituv and Borut, 1975: 104). Although the ratio of orifice size to basal diameter is sig­
nificant in the three species at Elat, there may not be an obvious progression in orifice
size relative to the tidal position occupied by each species. This is because *barnesorum*,
which has the smallest orifice and thickest wall of the three species, commonly occurs in
a zone above *rufotincta*, whereas in the absence of *rufotincta* it occurs above *achituvi*, or
it may even occur by itself as *may rufotincta* (Y. Achituv, in litt.). The ability to segre­
gate specimens into distinct groups solely on the basis of orifice size or wall thickness, as
did Achituv and Borut (1975, figs. 8, 9) may not prove useful for field identification,
largely because of variations arising from crowding and growth of one individual upon
another, the effects of erosion/corrosion as well as admixture at the transition to each
zone. Similarly, wall colour is highly variable among these species, and it too may not be
useful for identification.

*Tetraclitids* are suspension-feeding captorial planktivores (Barnes, 1959: 232;
Anderson and Buckle, 1983: 649), and some display a dichotomy in feeding. In all tetra­
clitids cirri IV-VI are employed in normal captorial planktivory whereas in some the
maxillipeds (cirri I-III) tend to supplement what is caught in the cirral net by setal filtra­
tion of mantle currents (Hunt and Alexander, 1991: 8). Nonetheless, among tetraclitids
the dietary intake is remarkably similar, consisting largely of small crustaceans, mainly
copepods, barnacle nauplii and cyprids, diatoms and filamentous algae (Barnes, 1959:
233; Anderson and Buckle, 1983: 649).

The oligotrophic waters of Elat are relatively low in nutrients, and consequently
plankton content (Achituv and Barnes, 1978: 321). Therefore, different feeding strategies relative to the emergence/submergence regime should be apparent in the captorial appendages. However, cirri IV-VI are fundamentally similar in the three species despite major differences in cirral counts, but there are even more pronounced differences in the form and relative proportions of the maxillipeds. It is doubtful that these correlate with overall wall size or orifice size, but likely to differences in the prey captured and the ability to manipulate it as well as the manner by which the maxillipeds clean the posterior cirri (IV-VI) and reject inedible particles, rather than other cirral activities that correlate with rate of water flow (Anderson and Southward, 1987: 135). Unfortunately, little is known about cirral morphology relative to tidal level, especially in sympatric species.

The endopod of cirrus I, largely responsible for sorting and rejecting inedible particles (Anderson and Anderson, 1985: 98; Anderson and Southward, 1987: 166), is considerably longer and has more segments in rufotincta than the other two species. But, the rami of cirrus II and III are short and stout in this species, although more so in barnesorum, suggesting that both feed in oscillatory or turbulent flow where there may be a considerable number of inedible particles. In contrast, the maxillipeds of achituvii are long, slender, clothed with fine setae, and appear to be somewhat more delicate, suggesting that it feeds on smaller prey and fine particles in more gentle currents. Obviously, this is an area for further study.

The sympatric occurrence of three species of Tetraclita at Elat, although unexpected, is not without precedent (Yamaguchi, 1987: 341). What is perhaps unusual, is that taxonomists have not appreciated the diversity of species in the Arabian and Red Sea as well as oceanic islands of the western Indian Ocean where there appears to be several other undescribed species of Tetraclita.

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REFERENCES


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