

The genus *Telmatactis* Gravier, 1916 (Actiniaria: Acontiaria: Isophelliidae) in Greece and the eastern Mediterranean

J.C. den Hartog

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J.C. den Hartog, National Museum of Natural History, P.O. Box 9517, 2300 RA Leiden, The Netherlands.

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Three species of the actinian genus *Telmatactis* Gravier, 1916, viz. *T. forskalii* (Ehrenberg, 1834), *T. solidago* (Duchassaing & Michelotti, 1864) and *T. cricoides* (Duchassaing, 1850), occurring in Greece and the eastern Mediterranean, are described and discussed. Detailed data on the cnidom of the three species are provided.

The characteristic penicilli of members of the genus *Telmatactis* are discussed. These penicilli were classified by Schmidt (1969, 1972) as p-rhabdoids (= penicilli) B1b, but it is here claimed that they actually belong in Schmidt's B2 group (provisionally as penicilli B2c). They correspond in general form and as to their distribution in the actinian polyp with the more usual penicilli B2a sensu Schmidt (1969), but unlike these, they lack a terminal tube (= amastigophores sensu stricto) and a folded portion of the shaft. So far, the presence of these nematocysts has exclusively been established with certainty in species of *Telmatactis* but presumably this presence is shared with other members of the family Isophelliidae.

Telmatactis forskalii basically has a subtropical East Atlantic/Mediterranean distribution penetrating also in the tropical Cape Verde Islands. *Telmatactis solidago* and *T. cricoides* are species of the amphiatlantic subtropical/tropical warm water fauna, but they are apparently absent in the mid-Atlantic Azores. *T. solidago* is here reported for the first time from the relatively warm eastern part of the Mediterranean, and the occurrence of *T. cricoides*, recently recorded for the first time from the Central Mediterranean (Ates, 1990), is confirmed and supplemented with records from the eastern Mediterranean. Present-day winter temperatures in the western Mediterranean, although possibly not being lethal, would at least seem unfavourable to these two species, but it is obvious that they can not have survived the considerably lower temperatures in this region during the last glacial period, 18,000 years B.P. Hence, the isolated eastern Mediterranean populations of both species probably represent interglacial relicts.

Introduction

According to the most recent review, by Schmidt (1972: 42), the actinian fauna of the Mediterranean is thought to include only a single species of *Telmatactis*, viz., *T. forskalii* (Ehrenberg, 1834). Doumenc et al. (1985: 521) confirmed this idea for the northern Aegean Sea, although their data are somewhat controversial (cf. p. 160). Ates (1990: 91-92, fig. 5) subsequently reported beyond doubt another species, *Telmatactis cricoides* (Duchassaing, 1850), from the mainland coast of NW Greece at the border of the northern Ionian Sea.

Bearing this in mind, I paid some special attention to members of the genus *Telmatactis* in the period 1989-1994 during short visits to three Greek islands in the

southern Aegean, viz., Kreta (1989), Samos (1993) and Rhodos (1994). Surprisingly, my collecting efforts in each of these three islands yielded a different species. Samos in the eastern Aegean yielded *Telmatactis forskalii* (Ehrenberg, 1834), whereas Kreta and Rhodos, both situated in the boundary region of the Aegean and the Levantine Basin, yielded *T. cricoides* and *T. solidago* (Duchassaing & Michelotti, 1864), the last-named species being a new record for the (eastern) Mediterranean.

Additional material of *Telmatactis forskalii* (1 sample) and *T. cricoides* (2 samples) proved to be present in the collection of the Zoological Museum of Tel-Aviv University, Israel, whereas one more sample of *T. cricoides* collected in S Turkey was found among unidentified Mediterranean material in the RMNH collection.

Abbreviations and symbols

RMNH = Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands.

ZMA = Zoologisch Museum, Amsterdam, The Netherlands.

ZMB = Zoologisches Museum, Berlin, Germany.

ZMTAU = Zoological Museum, Tel-Aviv University, Tel Aviv, Israel.

The following codes and abbreviations are used in the nematocyst surveys of the species (tabs 1-3): a = absent; - - - = sporadic; - - = rare; - = uncommon; + = rather common; ++ = common; +++ = very common; -/+ = uncommon to rather common, etc.; ? = data insufficient to even suggest frequency, due to the condition of the material or otherwise; (inc.) = inconspicuous and easily overlooked.

Descriptive part

In the present paper I will restrict myself mainly to descriptive notes on the present eastern Mediterranean material, adding data on general distribution and zoogeography. In anticipation of a revision of the genus *Telmatactis* (Ocaña & den Hartog, in prep.) I refrain from presenting full references, and from proposing any (formally necessary) changes in nomenclature.

Isophelliidae Stephenson, 1935

Telmatactis Gravier, 1916

Telmatactis Gravier, 1916: 236 [type species: *Telmatactis vallefiori* Gravier, 1916 (by monotypy), a subjective junior synonym of *T. cricoides* (Duchassaing, 1850)].

Capneopsis Duchassaing & Michelotti, 1864: 128 [34] [type species: *C. solidago* Duchassaing & Michelotti, 1864, by monotypy; accepting that *Telmatactis cricoides* and *Capneopsis solidago* belong in the same genus, the generic name *Capneopsis* formally has priority over *Telmatactis*].

Diagnosis.— Base adherent. Column divided into a large scapus covered by a distinct investment, and a narrow, naked scapulus. Scapus without cinclides and generally without distinct tenaculi. General plan basically hexamerous, but slight irregularities, especially in the younger cycles of tentacles and mesenteries are not uncommon. Tentacles 24 to 96, entacmaceous, rather short to moderately long with acute to distinctly clavate tips, those of the primary cycle often considerably larger

than the rest. Sphincter mesogloal, elongate, with two separate more strongly developed parts, one distally and one considerably lower. Stomodaeum with two siphonoglyphs supported by two pairs of directives. Mesenteries arranged in two to the directives included, with strong, generally circumscribed to kidney-shaped retractors and well-developed unilobed filaments. Other cycles microcnemic, sterile; in exceptional cases some of the mesenteries of cycle II also macrocnemic, but always less developed than those of cycle I. Acontia usually profusely present; mesenteries of the primary cycle always with a single well-developed acontium, emerging proximally of the gonads and filaments; younger mesenteries generally with more than one acontium.

Cnidom: spirocysts; spirulae; penicilli A in stomodaeum and filaments, relatively uncommon and inconspicuous; penicilli B1 only in filaments; penicilli B2c (shaft without folded portion and without a terminal tube; for a discussion on these penicilli, see p. 156) in all parts of the body; their presence in the ectoderm of the tips of at least the older tentacles, although sparse or sporadic, a characteristic feature of most species. Acontia with dominating, somewhat asymmetrical, bottle-shaped spirulae and large penicilli B2c, in some species supplemented with sparse non-bottle-shaped spirulae. Massive numbers of relatively large, usually somewhat curved spirulae in tentacle tips.

Always without zooxanthellae (see, however, "Remarks" below). Asexual reproduction by transverse fission established in the type species but possibly a common feature of the genus.

Distribution.— A genus of tropical to subtropical species, distributed world-wide. Number of species in the Atlantic three or four, world-wide almost certainly less than ten. Three species occur in the Mediterranean, one of which, *Telmatactis solidago* (Duchassaing & Michelotti, 1864) is here reported for the first time.

Remarks.— Carlgren (1949: 90-91) listed more than 30 nominal species which he considered to belong in *Telmatactis*. No doubt, a considerable number of these is conspecific, and several names applied to Atlantic species are actually synonymized in the present paper. Also, some of the species listed by Carlgren probably belong in other genera. On the other hand, it must be noted that most genera of Isophelliidae are ill-defined, and some species placed in these genera may in fact belong in *Telmatactis*.

In an attempt to review the genus, Doumenc et al. (1989) made a useful compilation of the available, often rather incomplete, information of 24 species, adding the description of one new species. Unfortunately the authors omitted a critical appraisal of these species, and did neither re-examine any existing types, nor study topotypical and other material in order to check and/or supplement the available data. As a consequence, they failed to recognize the conspecificity of several nominal Atlantic/Mediterranean species, e.g. *Telmatactis vallefiori* Gravier, 1916, *T. americana* Verrill, 1869, and *T. pseudoroseni* Pax, 1924 (see the synonymy of *T. cricoides*, p. 166), whereas not listing *T. solidago*.

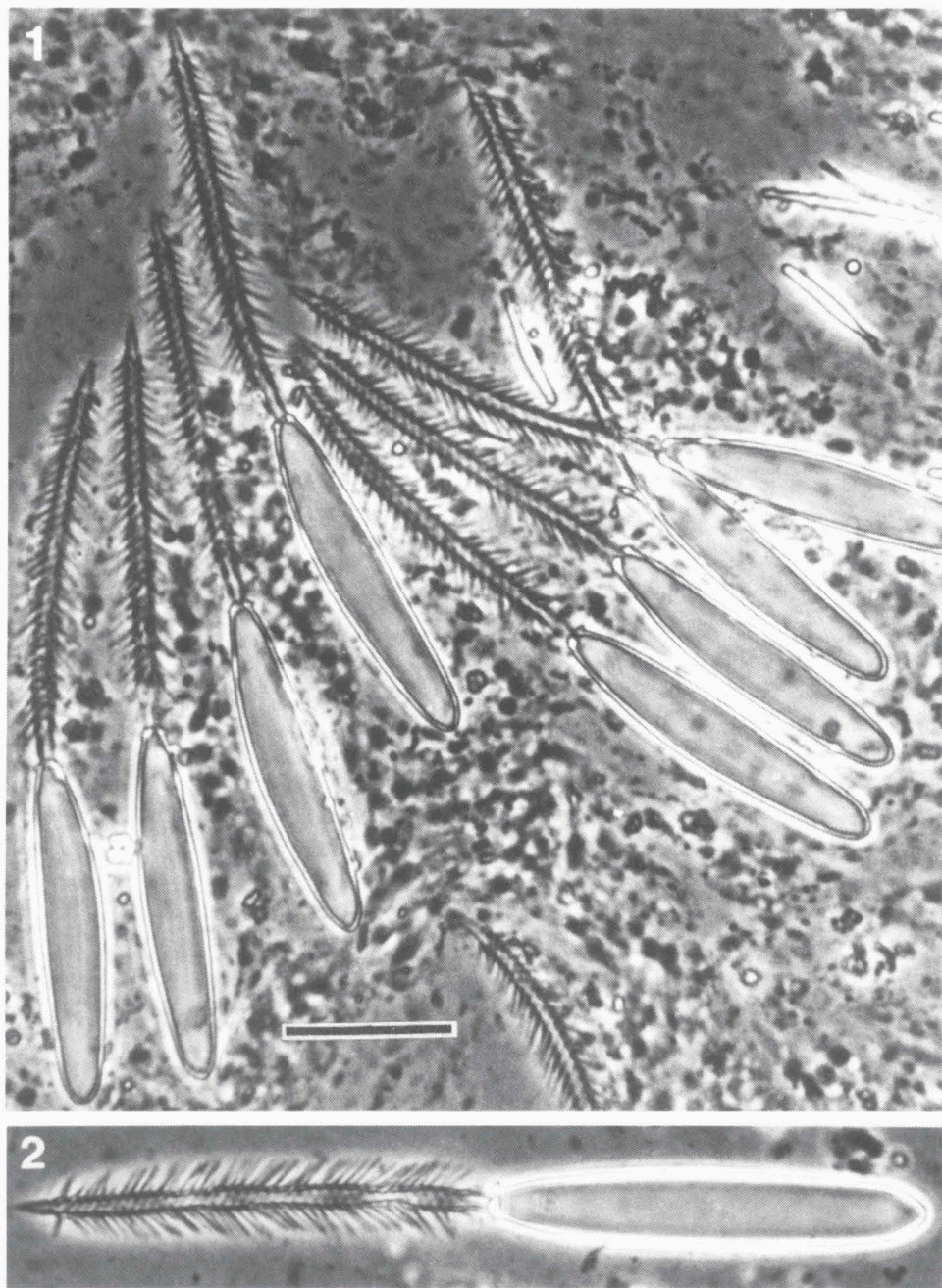
Most interesting is their description of the new species *Telmatactis carlgreni*, claimed to be zooxanthellate. This character would be unique within the genus and the family, and therefore needs verification. The presence of zooxanthellae is definitely not shared with *Telmatactis ambonensis* (Kwietniewski, 1897), as suggested by

the authors (cf. Doumenc et al., 1989: 14); Kwietniewski (1897: 399) actually stated explicitly that zooxanthellae are absent in *T. ambonensis* ("Die zooxanthellen, welche oft so massenhaft im Entoderm vorkommen habe ich bei *Phellia ambonensis* gänzlich vermisst").

Discussion on the characteristic penicilli B of the genus *Telmatactis* (figs 1, 2).—The term penicillus (Stephenson, 1928: 62) as consistently used in my papers, is synonymous with the term p-rhabdoid sensu Schmidt (1969, 1972, 1974, etc.). It covers the combined classic terms p-mastigophore (Carlgren, 1940: 4) and amastigophore (Weill, 1934). The term became obsolete when the nematocyst classification of Weill (1934) was generally adopted. Obviously, it has escaped the notice of most authors that the prefix "p-" in p-mastigophore actually stands for "penicillus" [just like the prefix "b-" in b-mastigophore was used by Carlgren to indicate the close similarity of this type with Weill's "basitrichs"] (cf. Carlgren, 1940: 4).

Schmidt (1969: 299-303) correctly distinguished between two main categories of p-rhabdoids, A and B. In addition he recognized a category C, which occurs exclusively in the Boloceroidaria (Schmidt, 1969: 303-305). He further subdivided the p-rhabdoids B into four categories: B1a, B1b, B2a, and B2b. It is beyond the scope of this paper to discuss these categories in full detail and for the definitions I refer to Schmidt's publication. Here, I restrict myself to observing that Schmidt's category B1b (without folded portion and terminal tube), typical of the genus *Telmatactis*, was chosen somewhat unfortunate. Apparently attributing too much importance to the absence of a folded portion ("Faltstück"), he wrongly classified this nematocyst type in the category B1, i.e. suggesting a close similarity with the radially symmetrical, ovate to ovate-elongate category B1a (also without folded portion, but unlike the B1b category with a long terminal tube), characteristic of the filaments of most Actiniaria. However, considering their general morphology, bilateral symmetry and distribution in the actinian body, these penicilli B of *Telmatactis* obviously substitute and are fully homologous with Schmidt's penicilli B2a, which predominate in species of Boloceroidaria and Acontiaria. Therefore, this type, presumably typical of all Isophelliidae, definitely belongs in the B2 category, and is here provisionally referred to as penicillus B2c (instead of B1b). The disposal of Schmidt's indication B1b further implies that the category B1a may henceforth be simply referred to as category B1.

Another unfortunate mistake by Schmidt concerning this nematocyst type is his statement that a (vestigial) terminal tube always stays behind in the discharged capsule (Schmidt, 1969: 291). This phenomenon may be true for the penicilli B2a of many Boloceroidaria, Aiptasiidae, Diadumenidae and Sagartiidae, but certainly not for the (corresponding) penicilli B2c of *Telmatactis*. In these, the terminal tube beyond the cone-shaped tip of the shaft is completely reduced (and the same presumably holds for other Isophelliidae), stamping them as the only true "amastigophores" known thus far (cf. figs 1-2). The fact that Schmidt never observed an everted terminal tube is of course correct, because there is no terminal tube. His own photographs (Schmidt, 1969: figs 4b, 7f), showing an unripe undischarged capsule with the cone-shape tip of the shaft and a discharged capsule, respectively, certainly do not support his statement. To illustrate that the tube always stays behind in the discharged capsule, Schmidt (1969: 291, fig. 7g) actually mistakenly referred to a penicillus B2a of *Cereus pedunculatus* (Pennant, 1777) (Sagartiidae). Persisting in this error, he subse-



Figs 1-2. Discharged penicilli B2c in squash preparations of unpreserved fragments of acontia of *Telmatactis solidago* (fig. 1) and *T. cricoides* (fig. 2) (phase contrast); specimens from Curaçao, Netherlands Antilles.

Note absence of folded portion and terminal tube in discharged capsules. Scale bar to both figs = 20 μm .

quently (Schmidt, 1972: fig. 10a) presented a faulty drawing of a penicillus from the acontia of *Telmatactis forskalii*, both in undischarged and discharged condition, showing a non-existent vestigial tube in the aboral part of the capsule.

The three species of *Telmatactis* occurring in the Mediterranean

Telmatactis forskalii (Ehrenberg, 1834) (figs 3, 4)

Actinia elongata Delle Chiaje, 1825: ? [Not (yet) consulted, but according to several authors, e.g. Jourdan (1880: 39) Delle Chiaje presented this name in combination with a figure of the species, which constitutes a valid description (ICZN, 1985: art. 12 (7)). Formally therefore the specific epithet *elongata* Delle Chiaje, 1825, has priority over *forskalii* Ehrenberg, 1834]; Delle Chiaje, 1841: ? [not (yet) consulted]; Jourdan, 1880: 39-40, 97-102, pl. 1 fig. 2-2b, pl. 10 figs 70-72, pl. 11; Pax & Müller, 1962: 221, fig. 110.

Actinia Chamaeleon Grube, 1840: 8-9 [Two fragments from Palermo, Sicily, examined, presumably belonging to Grube's original type material, ZMB 151].

Actinia Entacmaea forskalii Ehrenberg, 1834: 37.

Telmatactis forskalii; Doumenc et al., 1985: 521-522; Ates, 1990: 89-91, figs 3, 4, 6.

Telmatactis forskallii; Doumenc et al., 1989: 15-16 [misspelling].

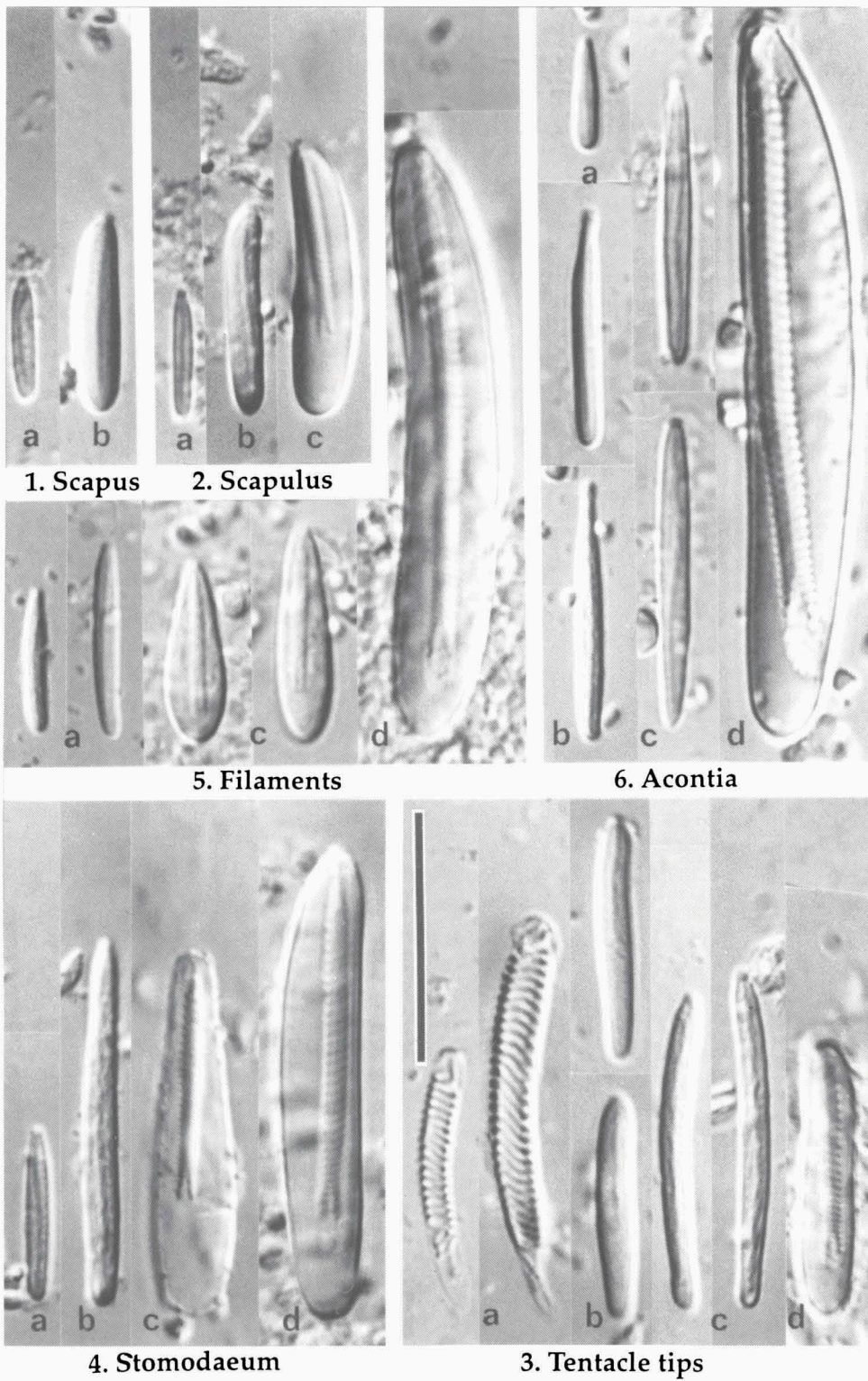
For the further synonymy of this species, see Schmidt, 1972: 42, 44-45.

Material.— **GREECE:** RMNH Coel. 18843 (Samos, NW coast, Georgiou Bay/Ormos Armenaki, on rock among encrusting red algae, ca 0.5-2 m, 5.ix.1993, leg. J.C. den Hartog; 6 specimens); RMNH Coel. 18844 (Samos, SW tip, Agiou Ioanni, S side of sandy cove, on rocks among calcareous algae, ca 1 m, 7.ix.1993, leg. J.C. den Hartog; 2 specimens). — **ISRAEL:** ZMTAU NS 21576 (Tantura, 0-3 m, 17-20.ix.1979, leg. Lewinsohn; 2 specimens).

Descriptive notes and remarks.— The Greek specimens are semi- to fully contracted and rather small, the largest specimen being ca 12 mm high and 15 mm in cross-section; tentacles of this last-named specimen difficult to count due its state of contraction, more than 80, but not exceeding 96. Due to the presence of numerous more or less well developed tenaculi, the investment shows the typical minutely papillate character (well visible under low magnification) so characteristic of the species. The internal structure and the mesenterial arrangement are difficult to study due to the contracted state of the specimens. Two transversely dissected specimens show 3 cycles of mesenteries, but in relation to the number of tentacles a fourth cycle is presumably present distally in at least the largest specimen. Cycle I macrocnemic with well-developed gonads, the directives included, and with strong, circumscribed retractors. Other cycles microcnemic and sterile. Acontia present but their number and distribution could not be verified.

Fig. 3. *Telmatactis forskalii*. Pictorial survey of the cnidom of a specimen from Samos (RMNH Coel. 18844). Numerals and letters correspond to table 1.

1. Scapus: a. Spirula; b. Spirula. **2. Scapulus:** a. Spirula; b. Spirula; c. Penicillus B2c. **3. Tentacle tips:** a. Spirocysts, b. Spirulae; c. Spirulae; d. Penicillus B2c. **4. Stomodaeum:** a. Spirula; b. Spirula; c. Penicillus A; d. Penicilli B2c. **5. Filaments:** a. Spirula; c. Penicilli B1; d. Penicilli B2c. **6. Acontia:** a. Spirula; b. spirulae (bottle-shaped); c. spirulae; d. Penicilli B2c. Scale bar = 20 µm.



For a detailed description of the species I refer to Schmidt (1972: 42-45). Not however without a remark on the number of acontia, one per mesentery according to Schmidt. This is certainly true for the mesenteries of cycle I, but in my experience (based on Atlantic material) the mesenteries of cycles II and III may each have up to at least eight well developed acontia, attached proximally and distally of separate fragments of discontinuous trilobed filament.

The Israel specimens are fully contracted and in bad condition, being rather tough and rigid due to previous desiccation. However, the character of the cuticle, the arrangement of the mesenteries, and the small size of the spirulae in the tentacles [$23.0(21.3-24.0) \times 2.2-2.7 \mu\text{m}$; $N = 10$] leave no doubt about the identity of the specimens (cf. tab. 1.3c; tab. 2.3c and tab. 3.3b).

Doumenc et al. (1985: 521, fig. 1) reported the species from various localities in the northern Aegean. However, the data of these authors on the cnidom do not fully fit *Telmatactis forskalii*. It seems that they overlooked some of the less common types, but more striking are the dimensions given for the spirulae ("microbasic b-mastigophores") of the acontia. The usual values for the penicilli and spirulae of the acontia of *T. forskalii* range from ca $55-70 \times 8-10 \mu\text{m}$ and $18-23 \times 1.8-2.3 \mu\text{m}$, respectively [data based on several specimens from the Mediterranean (including Schmidt's material), and the eastern Atlantic]. The dimensions given by Doumenc et al. (1985: 522) are: penicilli $59.3(52.9-70.6) \times 5.8-8.1 \mu\text{m}$, and spirulae $46(37.0-47.4) \times 3-4.6 \mu\text{m}$. This would suggest that at least the specimen(s) from which these measurements were taken belong to another species. Yet, considering that these dimensions also do not fit any other Atlantic species of *Telmatactis*, they are presumably just erroneous. The authors actually did observe the discrepancy of their measurements and those given by Schmidt, but attributed this difference to confusion of "microbasic b-mastigophores" (spirulae) with "microbasic p-mastigophores" (penicilli B2c). This explanation however, is unacceptable as these two nematocyst categories simply cannot be confused (cf. e.g. fig. 3.6b and d of the present paper). Unfortunately these same faulty data were repeated in a subsequent publication (Doumenc et al., 1989: 15-16).

Cnidom.— A detailed survey of the cnidom of one of the specimens from Samos is presented in table 1. These data are largely in accordance with those given by Schmidt (1972: 44) and also with those obtained from specimens from various localities in the south-eastern part of the North Atlantic (unpublished). Penicilli B2 present in the tentacles (tab. 1.3d) are easily overlooked due to their sporadic occurrence and may not always be present. They were not found in some other specimens examined for comparison.

One more detail, viz., the presence of a few homotrichs in the mesenterial filaments (tab. 1.5e) calls for notice. I would have been inclined to consider this presence the result of contamination, if I had not previously found these same nematocysts abundantly in a tentacle tip of rather soft texture (catch tentacle?) of a specimen from Flores, Azores (RMNH Coel. 18800), and if Dr O. Ocaña (La Laguna, Tenerife) had not informed me that he also observed them to be numerous in some tentacles of a specimen from Ceuta, Strait of Gibraltar (RMNH Coel. 19953).

The cnidom of the Israel specimens could be studied only very fragmentary due to the poor condition of these specimens (see above: "Descriptive notes and remarks").

Table 1 (cf. fig. 3). *Telmatactis forskalii*, survey of the cnidom of a specimen from Samos, RMNH Coel. 18844.

| Body part | Nematocyst type | Mean and range (in parentheses) of length and width of nematocyst capsules in μm | N | Frequency |
|------------------|------------------|---------------------------------------------------------------------------------------------|----|------------|
| 1. Scapus | a. Spirulae | $8.5(7.1 - 9.8) \times 1.6(1.3 - 1.8)$ | 6 | ---?(inc.) |
| | b. Spirulae | $15.5(14.2 - 17.8) \times 3.2(2.9-3.6)$ | 50 | + / ++ |
| | c. Penicilli B2c | $24.9 - 25.9 \times 5.3 - 6.2$ | 2 | --- |
| 2. Scapulus | a. Spirulae | $10.2(8.9 - 11.6) \times 1.6(1.3 - 1.8)$ | 20 | - |
| | b. Spirulae | $15.4(14.2 - 16.5) \times 2.6(2.4 - 2.9)$ | 20 | + / ++ |
| | c. Penicilli B2c | $19.4(16.9 - 22.7) \times 4.0(3.6 - 4.7)$ | 20 | + / ++ |
| 3. Tentacle tips | a. Spirocysts | $17.8 - 36.5 \times 2.7 - 4.2$ | — | +++ |
| | b. Spirulae | $19.1(16.0 - 21.4) \times 2.6(2.2 - 3.1)$ | 20 | - |
| | c. Spirulae | $27.2(24.0 - 30.3) \times 2.5(2.4 - 2.7)$ | 25 | + / ++ |
| | d. Penicilli B2c | $23.7(22.3 - 24.9) \times 5.2(4.9 - 5.3)$ | 4 | --- |
| 4. Stomodaeum | a. Spirulae | $15.0(13.4 - 17.8) \times 2.0(1.8 - 2.0)$ | 20 | + |
| | b. Spirulae | $27.9(25.8 - 29.4) \times 2.5(2.4 - 2.7)$ | 20 | + |
| | c. Penicilli A | $27.3(24.0 - 31.2) \times 5.7(4.9 - 6.5)$ | 40 | + |
| | d. Penicilli B2c | $37.4(32.9 - 41.8) \times 6.5(5.8 - 7.1)$ | 20 | + |
| 5. Filaments | a. Spirulae | $15.6(12.0 - 19.6) \times 2.0(1.8 - 2.4)$ | 60 | + / ++ |
| | b. Penicilli A | $24.7(21.4 - 28.5) \times 5.3(4.9 - 5.6)$ | 11 | --- |
| | c. Penicilli B1 | $16.4(14.2 - 18.2) \times 3.9(3.6 - 4.5)$ | 30 | + |
| | d. Penicilli B2c | $43.2(31.2 - 49.8) \times 7.2(6.0 - 8.5)$ | 30 | -- / - |
| | e. Homotrichs | $\text{ca } 37.5 - 40.0 \times 3.6 - 4.0$ | 5 | ? |
| 6. Acontia | a. Spirulae | $10.7(9.8 - 13.4) \times 1.7(1.5 - 1.9)$ | 15 | -- / --- |
| | b. Spirulae | $20.1(18.7 - 22.3) \times 1.9(1.8 - 2.0)$ | 20 | +++ |
| | c. Spirulae | $22.5(19.6 - 26.7) \times 2.2(2.0 - 2.4)$ | 25 | -- |
| | d. Penicilli B2c | $60.1(57.9 - 65.9) \times 8.6(8.0 - 8.9)$ | 20 | ++ |

Habitat.— All specimens collected in Samos were found in shallow water, about 0.5-2 m deep, exposed to moderate light conditions, and attached in holes in calcareous rock or among concretions of coralline algae. In the same niche was found the solitary coral *Balanophyllia europaea* (Risso, 1826).

Distribution (fig. 4).— Throughout the Mediterranean (cf. Schmidt, 1972: 44; Doumenc et al., 1985: 521-522), except maybe in the northernmost parts of the Adriatic and the Aegean. Outside the Mediterranean the species ranges from the surroundings of the Strait of Gibraltar, via the coast of the Iberian Peninsula northward to at least Biarritz in SW France (Ramil & Pulpeiro, 1990: 24; RMNH collection). Published records from the continental coast of NW and W Africa are not available. During two visits to the Cap Vert Peninsula, Senegal, in 1982 and 1983, I failed to find the species, which, although no definite proof of its absence there, indicates that it must at least be rare. The species occurs throughout the Macaronesian Islands, being common in Madeira, the Azores and the Canary Islands, but less so in the tropical Cape Verdes (RMNH collection).

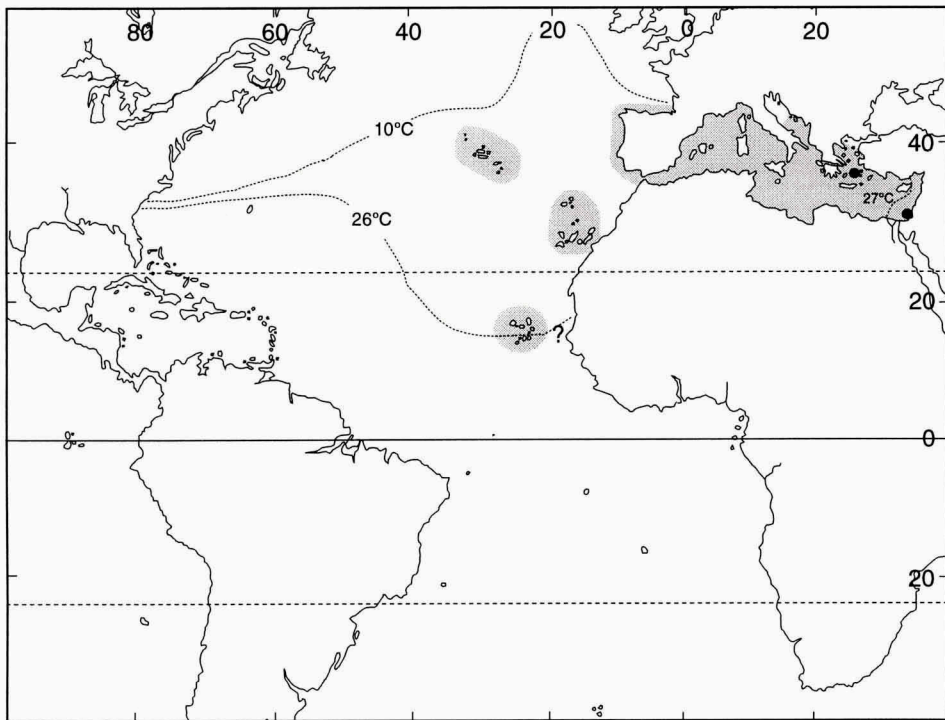


Fig. 4. *Telmatactis forskalii*. Distribution (shaded), based on the literature and RMNH collections. Dots indicate localities of eastern Mediterranean material examined. The dotted lines represent the isotherms of the mean temperature of the coldest and the warmest month (February, 10°C; August, 26 and 27 °C) as related to the limits of the known distributional range of the species. Temperature data after Gorshkov, 1978, and Thiede, 1980.

Telmatactis solidago (Duchassaing & Michelotti, 1864)
(figs 1, 5, 6)

Capneopsis solidago Duchassaing & Michelotti, 1864: 128-129 [34-35] [type locality: St Thomas, Virgin Islands, Caribbean].

Phellia solidago; Andres, 1883: 340-341 [132-133]; 1884: 128-129.

Phellia simplex Verrill, 1901: 48-49 [type locality sensu lato: Bermuda].

Telmatactis solidago; Cairns et al., 1986: 175, pl. 50.

Edwardsia horstii Pax, 1924: 94 (pro parte) [type series from Curaçao (ZMA Coel. 2531) examined, consisting of 3 specimens of an *Edwardsia* species and 36 specimens of *Telmatactis solidago*].

Probably not *Capneopsis solidago*; Duerden, 1898: 459.

Material.— **GREECE**: RMNH Coel. 19662 (Rhodos, SW coast, small bay with stony beach at Fourni, bottom with large algae-covered boulders, 2-3 m, under stones and boulders, 5.vi.1994, leg. J.C. den Hartog; 2 minute specimens); RMNH Coel. 19663 (Rhodos, E coast, in small protected "harbour" for small boats and dinghies, exactly down the road from Asklipio, ca 0.5-1 m, under stones and boulders in greyish sand with the base attached to buried stones or pebbles, 8/9.vi.1994, leg. J.C. den Hartog; 10 specimens).

Morphology.— Body elongate to vermiformous, somewhat *Edwardsia*-like, up to at least 6 cm long by 6 mm wide in fully expanded living individuals. Preserved specimens in various stages of contraction, varying in size from ca 10 × 3 mm to 22 × 9 mm. Investment distinct, in some specimens not of uniform appearance, showing a more or less distinctly demarcated paler and thinner zone in the distal and/or basal part of the scapus.

Base small, exceeded by the diameter of the column.

Oral disc small, of about the same diameter as the column. Tentacles entacmaeous, rather short with round, never capitate tips; their number in most specimens exactly 24, but up to about 36 in the largest specimens.

Colour.— Scapus sand-coloured to rusty-ochre. Base and scapulus opaque-white to creamy. Oral disc with a pattern of white to cream and brown. Tentacles also whitish to creamy, proximally with conspicuous brown W-marks.

Anatomy.— Mesenteries very thin and membranaceous, 12-18 pairs, arranged in two cycles, and, in the larger specimens, part of a third cycle. Cycle I macrocnemic with rather strong, kidney-shaped retractors and well-developed filaments and gonads; filaments proximally with a single well-developed acontium. Mesenteries of cycles II and III microcnemic, without filaments or with a trace of triple cord only, but each with a well-developed acontium, its place of junction strongly varying per mesentery, even in mesenteries of the same pair. Number of mesenteries proximally and distally equal.

Variation.— Examination of Atlantic material showed that the species may develop up to 48 tentacles and 24 pairs of mesenteries. The primary mesenteries are invariably provided with a single acontium emerging proximally of the unilobed filament, but more than one acontium may spring from the secondaries and tertiaries, usually proximally of small, separate fragments of trilobed filament (unpublished data).

Cnidom.— For a survey of the cnidom, see table 2 and fig. 5.

Penicilli B2, although not found in the scapus of the specimen examined, are not always fully absent from this part of the body (material examined for comparison from the Caribbean, Bermuda, Senegal, Canary and Cape Verde Islands). However, unlike in *Telmatactis forskalii* and *T. cricoides*, it seems that these nematocysts are invariably absent in the tentacle tips.

Table 2 (cf. fig. 5). *Telmatactis solidago*, survey of the cnidom of a medium size specimen from Rhodes (RMNH Coel. 19663).

| Body part | Nematocyst type | Mean and range (in parentheses) of length and width of nematocyst capsules in μm | N | Frequency |
|------------------|------------------|---------------------------------------------------------------------------------------------|----|-----------|
| 1. Scapus | a. Spirulae | 9.5(8.0 - 11.6) × 1.6(1.3 - 1.8) | 10 | ? |
| | b. Spirulae | 20.4(18.7 - 22.3) × 3.1(2.9 - 3.3) | 30 | + |
| | c. penicilli B2c | Not observed | — | — |
| 2. Scapulus | Spirulae | 10.0(8.5 - 11.1) × 1.7(1.6 - 1.8) | 10 | -- (inc.) |
| | Spirulae | 14.8(13.4 - 16.5) × 2.5(2.2 - 2.7) | 30 | 30 |
| | Penicilli B2c | 16.7(14.2 - 18.7) × 4.4(3.8 - 4.9) | 20 | -- /- |
| 3. Tentacle tips | a. Spirocysts | 15.1 × 41.8 × 2.2 - 4.0 | — | +++ |

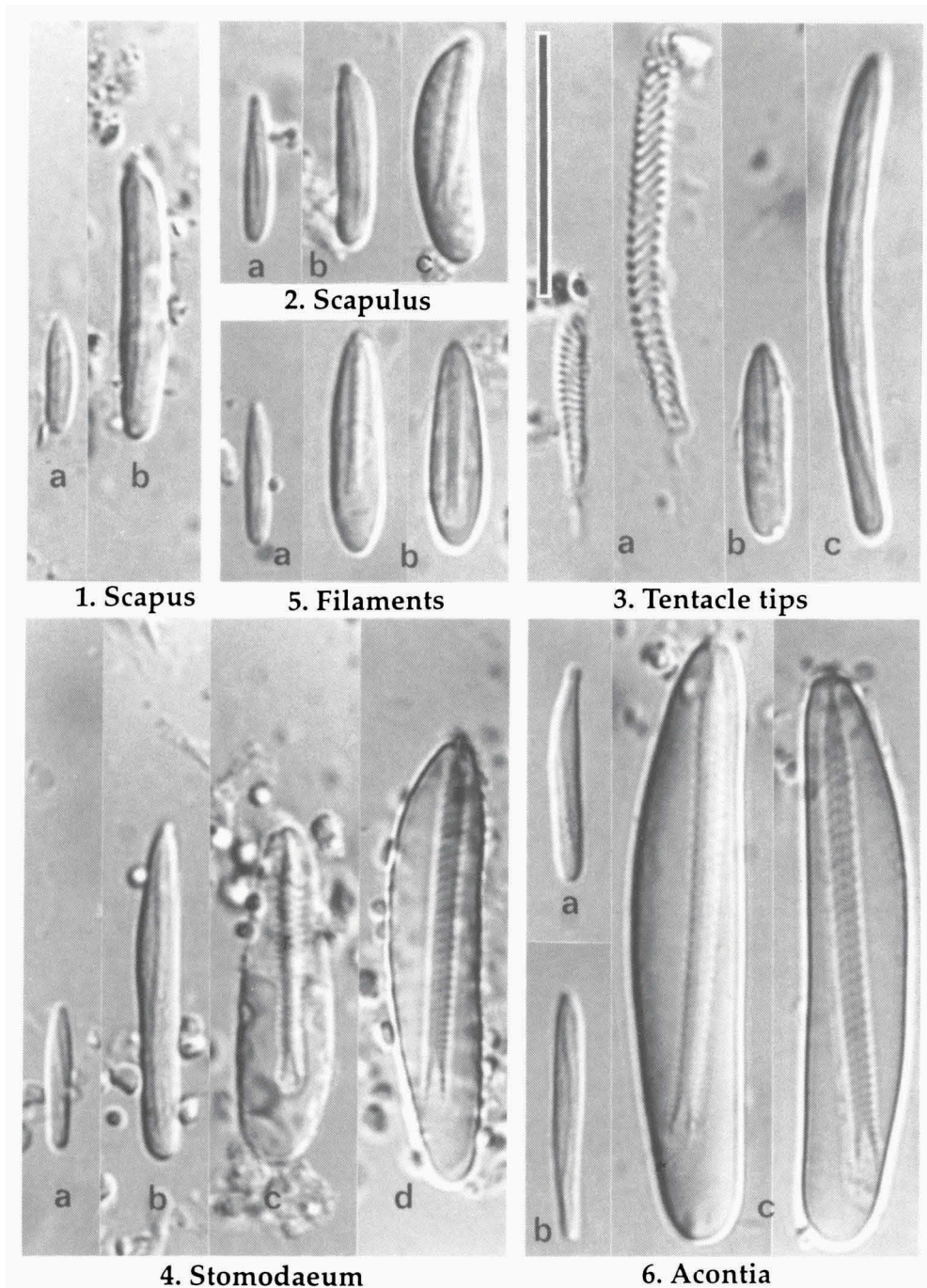


Fig. 5. *Telmatactis solidago*. Pictorial survey of the cnidom of a medium size specimen from Rhodes (RMNH Coel. 19663). Numerals and letters correspond to table 2.

1. Scapus: a. Spirula; b. Spirula. **2. Scapulus:** a. Spirula; b. Spirula; c. Penicillus B2c. **3. Tentacle tips:** a. Spirocysts, b. Spirula; c. Spirula. **4. Stomodaeum:** a. Spirula; b. Spirula; c. Penicillus A; d. Penicillus B2c. **5. Filaments:** a. Spirula; b. Penicilli B1. **6. Acontia:** a. Spirula (bottle-shaped); b. Spirula; c. Penicilli B2c. Scale bar = 20 μ m.

| | | | | |
|---------------|------------------|------------------------------------|----|----------|
| | b. Spirulae | 14.3(13.4 - 15.1) × 2.8(2.7 - 2.9) | 20 | - |
| | c. Spirulae | 33.6(28.5 - 39.6) × 2.8(2.7 - 2.9) | 25 | +++ |
| | d. Penicilli B2c | not observed | — | a |
| 4. Stomodaeum | a. Spirulae | 13.8(12.0 - 15.6) × 1.8(1.6 - 2.0) | 20 | - / + |
| | b. Spirulae | 26.4(24.0 - 28.5) × 2.7(2.5 - 2.9) | 30 | + / ++ |
| | c. Penicilli A | 27.9(25.8 - 30.3) × 6.5(5.8 - 7.6) | 20 | + / ++ |
| | d. Penicilli B2c | 35.8(33.8 - 38.3) × 7.3(6.2 - 8.5) | 8 | --- |
| 5. Filaments | a. Spirulae | 12.0(9.8 - 13.8) × 1.6(9.8 - 13.4) | 20 | ++ / +++ |
| | b. Penicilli B1 | 15.0(13.8 - 16.9) × 3.9(3.6 - 4.5) | 30 | ++ / +++ |
| 6. Acontia | a. Spirulae | 16.0(14.7 - 17.8) × 2.0(1.8 - 2.3) | 20 | +++ |
| | b. Spirulae | 20.0(18.2 - 21.4) × 1.9(1.6 - 2.0) | 10 | -(inc.) |
| | c. Penicilli B2c | 45.8(40.9 - 49.8) × 7.5(7.1 - 8.0) | 20 | +++ |

Habitat.— The specimens from Rhodos were found in shallow water, in muddy sand under and between stones; two of the specimens were found under a single stone together with a specimen of *Scolanthus callimorphus* Gosse, 1853 (RMNH Coel. 19686).

Distribution (fig. 6).— The present records of the species are the first from the Mediterranean. So far, it had exclusively been reported from the Caribbean and Ber-

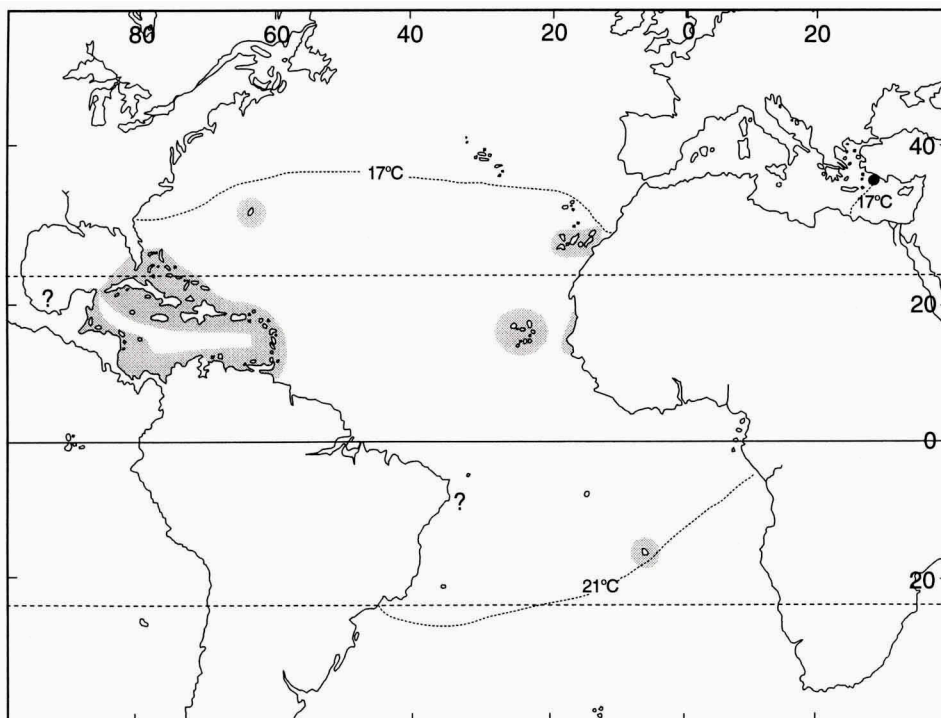


Fig. 6. *Telmatactis solidago*. Distribution (shaded), based mainly on RMNH collections. The dot indicates the new eastern Mediterranean records from Rhodos. The dotted lines represent the isotherms of the mean temperature of the coldest months (17°C in the N Atlantic and the Mediterranean, 21°C in the S Atlantic) as related to the limits of the known distributional range. Temperature data after Gorshkov, 1978, and Thiede, 1980.

muda (Duchassaing & Michelotti, 1864: 128 [34]; Pax, 1924: 94, as *Edwardsia horstii* spec. nov.; Verrill, 1901: 48-49; Cairns et al.: 175; RMNH collection), but in recent years it has also been found in the eastern and Central Atlantic: Canary and Cape Verde Islands, on the Cap Vert Pensinsula (Senegal), and in St Helena (RMNH collection).

Telmatactis cricoides (Duchassaing, 1850)
(figs 2, 7, 8)

Entacmaea cricoides Duchassaing, 1850: 10 [type locality: Antilles, presumably Guadeloupe, see next line].

Dysactis cricoides; Duchassaing & Michelotti, 1860: 316 [40], pl. 6 fig. 4 [Guadeloupe].

Telmatactis cricoides; Cairns et al., 1986: 175, pl. 50; Ates, 1990: 91-92, fig. 5.

Paractis clavata Duchassaing & Michelotti, 1860: 316 [40], pl. 6 figs 7, 8 [type locality: St Thomas, Caribbean].

?*Phellia clavata*; Duerden, 1898: 459.

Phellia americana Verrill, 1869: 327 [replacement name for *Phellia clavata* (Duchassaing & Michelotti, 1864), a junior homonym of *Phellia clavata* (Stimpson, 1855)].

Phellia rufa; Verrill, 1901: 49; Verrill, 1907: 254-256, figs 107, 108; Pax, 1924: 104-105, pl. 9 fig. 8.

Telmatactis rufa; Corrêa, 1964: 108-112, pl. 13 fig. 34, pl. 14 fig. 35; Belém & Schlenz, 1989: 343-353, figs 1-9; Pires et al., 1992: 9.

Telmatactis Vallefiori Gravier, 1916: 234-236; 1918: 16-21, figs 8-13, pl. 2 figs 12-13 [type locality: São Thomé, Gulf of Guinea].

Phellia pseudoroseni Pax, 1924: 105-106, fig. 11, pl. 9 fig. 7 [typeseries (ZMA Coel. 3056), consisting of two specimens from Curaçao, examined].

Not *Phellia rufa* Verrill, 1900: 557, pl. 68 fig. 2; Verrill, 1907: 266 fig. 108a [= *Capnea vernonia* Duchassaing & Michelotti, 1864].

Material.— GREECE: RMNH Coel. 18842 (Ionian Sea, NW coast of continental Greece, opposite Corfu, Igoumenitsa, Sivota, under large stones, depth ca 3-4 m, 28.vii.1988, leg. R.M.L. Ates; 5 specimens); RMNH Coel. 19661 (Kreta, N coast, narrow bay on NW side of Akrotiri peninsula, attached to the underside of a large stone, depth ca 2 m, 1.vi.1989, leg. J.C. den Hartog; 1 specimen). — ISRAEL: ZMTAU NS 21577 (Tantura, 15.x.1975; 1 specimen); ZMTAU Co 29227 (Mediterranean coast of Israel, no further data; 2 specimens), RMNH Coel. 17704 (same data; 1 specimen). — TURKEY: RMNH Coel. 19676 (S coast, 36°45'N 31°24'E, Selimiye, 62 km E of Antalya, 0-1 m, some discharge of fresh water, sandy bottom with stones and *Posidonia* spec., 4.v.1959; Turkey Exp. 1959, leg. C. Swennen "71"; 3 specimens).

Unfortunately, the specimens from Sivota, Greece, were preserved straight into alcohol 70%. As a result the internal tissues are very badly preserved, so that their structure and organization are impossible to study. In addition, due to massive discharge of tentacular nematocysts, the oral disc and tentacles are covered with a coating of entangled nematocyst tubes prohibiting verification of the tentacular arrangement and of the number of tentacles. However, the general form and size of the specimens, the presence of a well developed investment, the characteristic clavate tentacle tips (see also the photograph by Ates, 1990), the shape of the retractors of the mesenteries and the cnidom (only the external tissues studied) leave no doubt about their identity.

Morphology.— Body in the expanded living specimen from Kreta about 6 cm long and 2 cm in diameter, in the rather contracted preserved condition about 18 mm

long and ca 20 mm in cross-section. Contracted preserved specimens often tumbler shaped, their length \times maximal diameter varying from 18×12 to 22×24 mm. Scapus with a rather thick investment. Scapulus narrow. Tentacles distinctly clavate and entacmaceous, those of the primary and secondary cycles much better developed than the others; tips, especially in preserved specimens, characteristically with distinct longitudinal grooves and ridges radiating from the centre. Number of tentacles ca 70-90, (irregularly) hexamerously arranged in 5 cycles, the two youngest cycles incomplete (arrangement in the specimen from Kreta according to the scheme $6 + 6 + 12 + 20 + 40 = 84$).

Colour.— No data available on the material from Israel and S Turkey. In the Greek specimens, the investment was orange- to greyish brown. Oral disc brownish, variegated with opaque white; tentacles variegated with reddish brown, especially the older ones rather dark at the base with more or less distinct B-marks (cf. Ates, 1990: fig. 5).

Anatomy.— Mesenteries arranged in four cycles. Those of cycle I macrocnemic and fertile, the directives included, united with the stomodaeum over its entire length, with strongly developed circumscrip retractors, crenate to more or less lobulate in cross-section. Cycle II-IV microcnemic, sterile. Members of cycle I and II can be clearly distinguished, but the distinction between the members of cycle III and IV is not always clear; at least cycle IV incomplete in all specimens examined. Acontia profusely present, but their number and distribution cannot be verified due to the state of contraction of the specimens. In Caribbean specimens examined for comparison the mesenteries of cycle I are provided with well developed unilobed filaments, proximally with a single acontium; cycle II and III are provided with discontinuous trilobed filaments only, each separate fragment proximally and/or distally with an acontium, the total number of acontia per mesentery often varying between ca 10 and 20.

Variation.— The number of tentacles and mesenteries may perhaps reach 96. The shape and size of the species are rather variable, but in most of its area of distribution the species does not generally exceed about 10 cm in length, 2-3 cm across the column and less than about 6 cm across the oral disc and tentacles.

In Madeira, the Salvages and the Canary Islands the species often reaches unusual dimensions, up to at least 20 cm across the oral disc in living expanded individuals. Neither have I seen such large specimens in the rest of the distributional range, nor have I positively been informed by divers about their presence there. For a long time, therefore, I have been inclined to regard this giant Madeiran/Canarian form as a separate species, especially as it sometimes shows colours which have not been reported from elsewhere, a striking example being a variety with the oral disc and tentacles uniformly pinkish to deep pink with golden brown discal radii. So far, however, I have not found any convincing morphological, anatomical, or nematocyst characters to support this idea. Nonetheless, this gigantism surely needs further attention.

Cnidom.— For a survey of the cnidom of two specimens from Kreta and Israel, respectively, see table 3. Scapus, tentacle tips (of primaries) and acontia of the largest specimen from Sivota were also examined; the nematocyst sizes of this specimen were found to be slightly larger than those presented in the table, the large spirulae

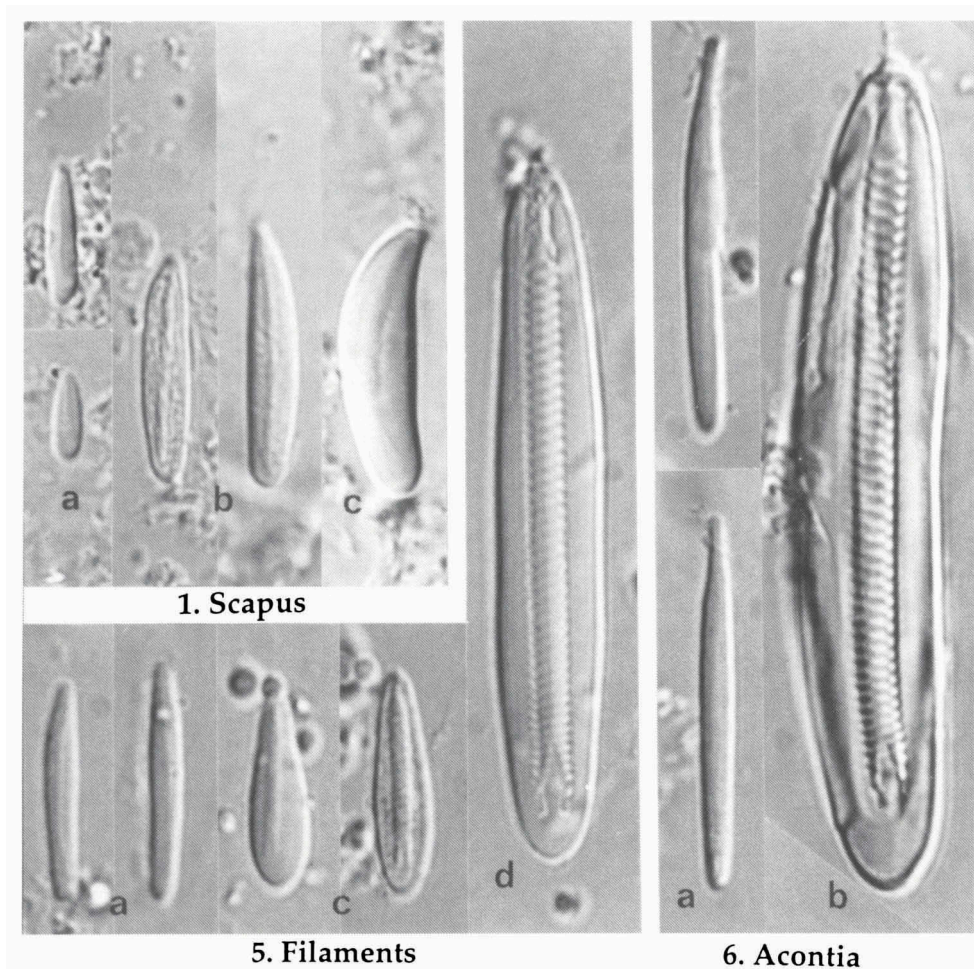
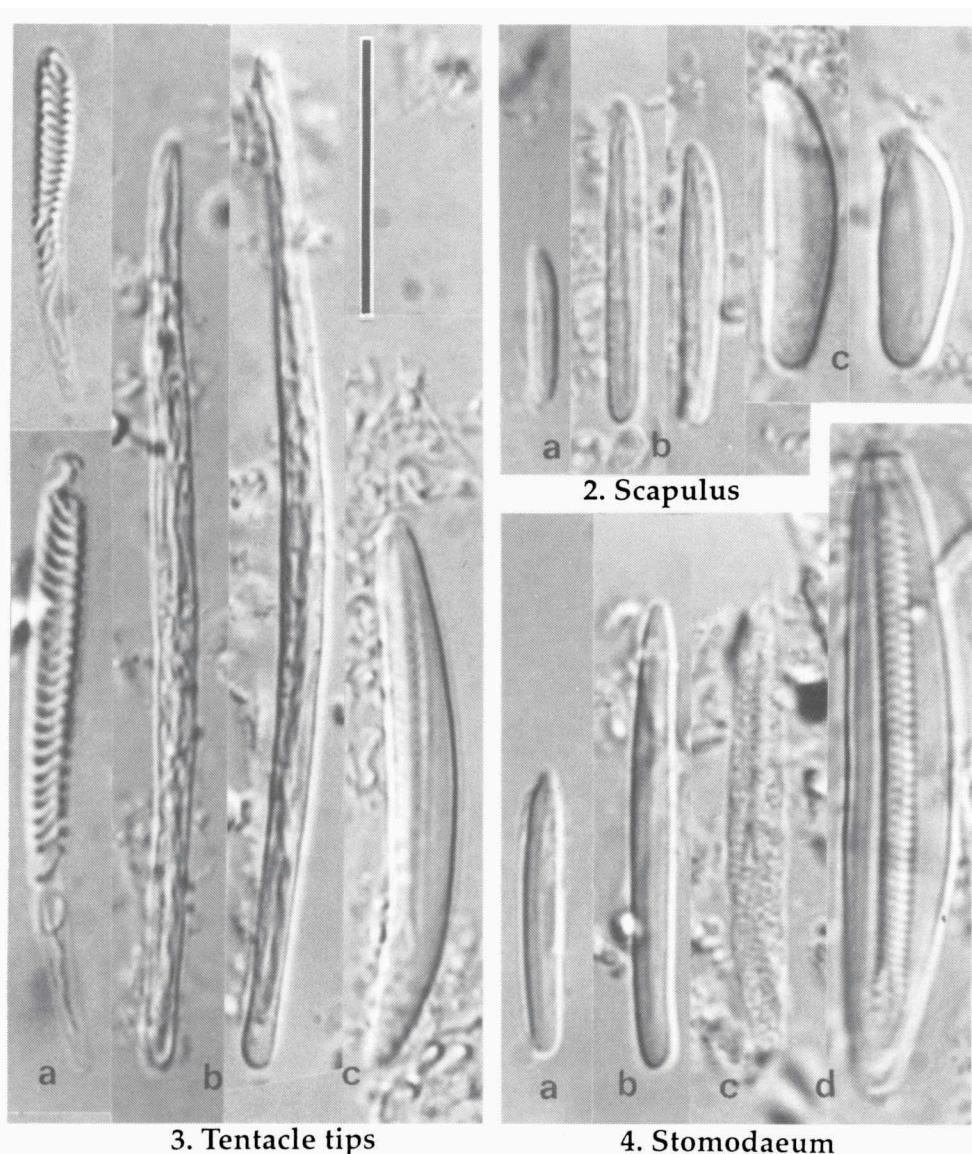


Fig. 7. *Telmatactis cricoides*. Pictorial survey of the cnidom of the specimen from Kreta (RMNH Coel. 19961). Numerals and letters correspond to table 3.

1. Scapus: a. Spirulae; b. Spirulae; c. Penicilli B2c. **2. Scapulus:** a. Spirula; b. Spirulae; c. Penicilli B2c. **3. Tentacle tips:** a. Spirocysts, b. Spirulae; c. Penicillus B2c. **4. Stomodaeum:** a. Spirula; b. Spirula; c. Penicillus A; d. Penicillus B2c. **5. Filaments:** a. Spirulae; c. Penicilli B1; d. Penicillus B2c. **6. Acontia:** a. Spirulae (bottle-shaped); b. Penicillus B2c. Scale bar = 20 µm.

of the tentacle tips reaching up to at least 85 µm in length. This difference reflects the different size of the specimens. Provided insignificant variations, the survey of the cnidom presented in table 3 also agree with that of specimens from the Caribbean, Bermuda and the Cape Verde and Canary Islands (unpublished data). The sporadic presence of penicilli B2c in the (older) tentacles of the specimen from Kreta (tab. 3/fig. 7.3c) is noticeable. Only very few examples of this nematocyst type were found in spite of intensive search, and in most tentacles they seemed absent. In other specimens examined for comparison (from the eastern Mediterranean as well as from the Atlantic) these capsules were generally slightly more common.



Discussion.— The full synonymy/references and a further discussion of the species will be presented in a revision of the genus *Telmatactis* (Ocaña & den Hartog, in prep.). The present species is closely related to the Indo-Pacific *T. decora* (Ehrenberg, 1834), from which it differs by the character of the retractors of the macro-mesenteries, in cross-section crenate to more or less lobulate in outline in *T. cricoides*, entire in *T. decora*.

Habitat.— The Greek and Turkish specimens were all found in shallow water, 1-4 m deep, attached to the lower side of large stones. Mr R.M.L. Ates (personal communication) found about 30 individuals in an area not exceeding about 20 × 20 m at Sivota, NW Greece, and recorded up to 3 specimens together under a single stone. Details on the habitat of specimens from Israel are not available.

Table 3 (cf. fig. 7). *Telmatactis cricoides*, survey of the cnidom of a specimen from Kreta (K) (RMNH Coel. 19661), and one from Israel (I) (RMNH Coel. 17704).

| Body part | Nematocyst type | Specimen | Mean and range (in parentheses) of length and width of nematocyst capsules in μm | N | Frequency |
|------------------|------------------|----------|---------------------------------------------------------------------------------------------|----|-----------|
| 1. Scapus | a. Spirulae | K | 8.0(6.2 - 8.9) \times 1.9(1.8 - 2.2) | 10 | -- (inc.) |
| | | I | 8.3(7.6 - 8.9) \times 1.8(1.8 - 2.0) | 10 | -- (inc.) |
| | b. Spirulae | K | 17.0(14.7 - 18.7) \times 2.9(2.5 - 3.3) | 40 | + |
| | | I | 15.8(14.2 - 16.9) \times 2.8(2.7 - 2.9) | 20 | + |
| | c. Penicilli B2c | K | 18.8(14.2 - 22.3) \times 5.0(4.5 - 5.8) | 40 | -/+ |
| | | I | 19.8(17.8 - 22.3) \times 5.0(4.2 - 5.3) | 20 | - |
| 2. Scapulus | a. Spirulae | K | 11.3(8.9 - 13.4) \times 1.9(1.8 - 2.0) | 10 | - |
| | | I | ca 9.8 - 12.5 \times 1.6 - 1.8 | 5 | -- (inc.) |
| | b. Spirulae | K | 20.0(16.9 - 23.1) \times 2.8(2.5 - 2.9) | 30 | -/+ |
| | | I | 17.8(16.0 - 19.8) \times 2.7(2.4 - 2.9) | 20 | + |
| | c. Penicilli B2c | K | 19.4(17.8 - 22.3) \times 4.5(4.0 - 4.9) | 20 | --/- |
| | | I | 19.7(18.7 - 20.9) \times 4.7(4.5 - 5.1) | 20 | + |
| 3. Tentacle tips | a. Spirocysts | K | ca 20 - 42 \times 2.2 - 3.3 | — | ++ |
| | | I | ca 20 - 37.5 \times 2.2 - 3.3 | — | ++ |
| | b. Spirulae | K | 68.9(60.5 - 77.4) \times 2.9(2.7 - 3.1) | 20 | +++ |
| | | I | 58.9(53.4 - 62.3) \times 2.7(2.7 - 2.9) | 20 | +++ |
| | c. Penicilli B2c | K | 36.6(32.0 - 45.4) \times 4.7(4.5 - 4.9) | 10 | ---/a |
| | | I | 39.6(35.6 - 42.7) \times 4.9(4.5 - 5.3) | 8 | -- |
| 4. Stomodaeum | a. Spirulae | K | 19.8(16.0 - 24.0) \times 2.1(2.0 - 2.2) | 20 | -/+ |
| | | I | 16.6(14.2 - 18.7) \times 2.0(1.8 - 2.0) | 20 | ++ |
| | b. Spirulae | K | 30.8(27.6 - 35.2) \times 3.0(2.7 - 3.1) | 30 | + / ++ |
| | | I | 26.1(24.0 - 28.5) \times 2.6(2.4 - 2.9) | 10 | -(inc.) |
| | c. Penicilli A | K | ca 27.0 - 30.0 \times 4.5 | 6 | ?(inc.) |
| | | I | 25.3(22.3 - 27.6) \times 4.7(4.2 - 5.3) | 10 | - |
| | d. Penicilli B2c | K | 46.8(42.7 - 49.8) \times 8.1(7.1 - 8.9) | 20 | --/+ |
| | | I | 42.7(40.0 - 47.2) \times 7.8(7.1 - 8.9) | 20 | + |
| 5. Filaments | a. Spirulae | K | 16.1(14.2 - 18.7) \times 2.0(1.8 - 2.0) | 20 | + |
| | | I | 14.9(13.4 - 16.5) \times 1.8(1.8 - 2.0) | 20 | + |
| | b. Penicilli A | K | ca 27.5 - 33.0 \times ca 4 | 2 | ?(inc.) |
| | | I | 27.6 \times 4.9 | 1 | --- ? |
| | c. Penicilli B1 | K | 14.3(13.4 - 15.6) \times 4.4(4.0 - 4.7) | 20 | ++ |
| | | I | 15.7(14.2 - 17.8) \times 3.9(3.6 - 4.5) | 20 | + |
| | d. Penicilli B2c | K | 49.0(45.4 - 55.2) \times 8.6(8.0 - 9.3) | 20 | - |
| | | I | 46.9(39.2 - 51.6) \times 8.6(8.0 - 9.8) | 8 | -- |
| 6. Acontia | a. Spirulae | K | 27.0(24.9 - 28.5) \times 2.0(1.8 - 2.2) | 20 | +++ |
| | | I | 26.0(23.5 - 28.5) \times 2.1(2.0 - 2.2) | 20 | +++ |
| | b. Penicilli B2c | K | 57.4(52.5 - 60.5) \times 10.2(8.9 - 11.6) | 20 | ++ |
| | | I | 48.3(44.5 \times 57.0) \times 9.3(8.5 - 10.7) | 20 | + |

Distribution (fig. 8).— Only recently recorded for the first time from the (Central) Mediterranean (Ates, 1990). This occurrence is here fully confirmed by four additional records, both for the Central and the eastern Mediterranean: Kreta, S Turkey, and Israel (2×). Furthermore, Mr Ates (in litt. 5.viii.1994) sent me evidence in the form of a postcard that this same species also occurs in Malta (this postcard, "Underwater scenes in Malta/photo by Derek Chirchop", unmistakably shows two expanded specimens of the present species with the characteristic clavate tentacle tips).

Apparently absent from the western Mediterranean (with the restriction that the North African coast is almost unknown, perhaps with the exception of the surroundings of the Strait of Gibraltar) and the Atlantic coast of SW Europe, the species occurs throughout the tropical Atlantic Ocean: Caribbean, Bermuda, Brazil, St Paul Rocks, Fernando do Noronha, São Thomé (Gulf of Guinea), Cape Verde Islands, Cap Vert Peninsula (Senegal), Ascension and St Helena. Additionally, the species is common in the subtropical Canary Islands and Madeira, but is apparently absent in the Azores (where it was not found during 11-weeks of intensive collecting in 1979 and 1981 in the framework of the CANCAP-project; for information on this project and for a list of collecting stations, see Den Hartog, 1984, and Van der Land, 1987).

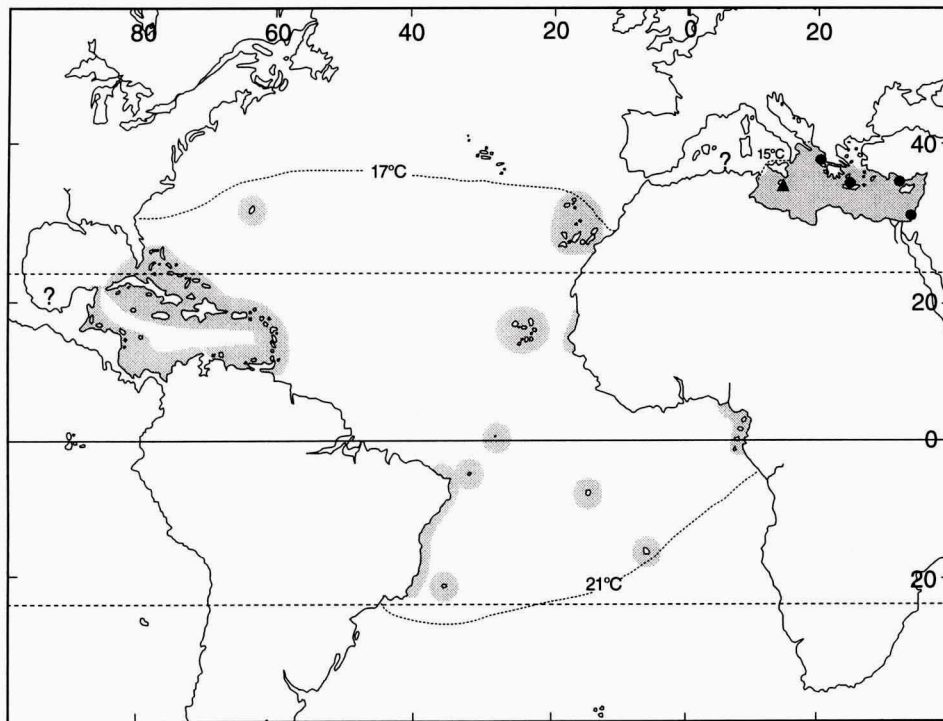


Fig. 8. *Telmatactis cricoides*. Distribution (shaded), based on the literature and RMNH collections. Dots indicate the known eastern Mediterranean records; the triangle indicates the record from Malta based on circumstantial evidence. The dotted lines represent the isotherms of the mean temperature of the coldest months (15°C in the Mediterranean, 17°C in the N Atlantic, and 21°C in the S Atlantic) as related to the limits of the known distributional range. Temperature data after Gorshkov, 1978 and Thiede, 1980.

Zoogeographical remarks

The distributional range of *Telmatactis forskalii* stamps this species as a basically subtropical East Atlantic/Mediterranean element (fig. 4). Southwards the species penetrates into the tropical Cape Verde Islands where the mean temperature of the warmest month may exceed 26°C, and in northward direction its range extends to the coast of SW France, where summer temperatures may reach subtropical values (22-23°C), but where mean temperatures of the coldest month vary between 9 and 10°C (Crisp & Fischer-Piette, 1959: 280). Its rarity in the Cape Verde Islands and its possible absence from the Cap Vert Peninsula might be correlated with high summer temperatures, the mean temperature of the warmest month at Cap Vert exceeding 27°C. Summer temperatures in its easternmost Mediterranean range reach similar high maxima, but no data are available on the frequency of the species in this region.

Telmatactis cricoides and *T. solidago* form part of the amphi-Atlantic warm water fauna. So far, these species have only been found in waters where the mean temperature of the coldest month does not drop below about 17°C (figs 6, 8). They have not been reported from the Azores, the Atlantic coasts of SW Europe and the western Mediterranean. It seems especially unlikely that their presence in the relatively well investigated western Mediterranean has been overlooked so far (with the restriction that information from the North African coast is wanting). Admittedly *T. solidago* has a rather cryptic way of life, but *T. cricoides* actually is a more conspicuous species than the well-known *T. forskalii*.

The discontinuous distribution of *Telmatactis cricoides* and *T. solidago* can be most plausibly explained by low winter temperatures, notably during the past Pleistocene glaciations, which presumably caused these species to disappear from the western Mediterranean and SW Europe. Temperatures in the western Mediterranean during the peak of the last glacial period (ca 18,000 years B.P.) are generally assumed to have been considerably lower than at present (with an anomaly of 4-6°C in winter and 7-9°C in summer), whereas shallow water temperatures in the easternmost part of the Mediterranean were only slightly lower (ca 1-2°C) (Thiede, 1980: figs 1, 5; Por, 1989: 25). Hence, relic populations of both *Telmatactis cricoides* and *T. solidago* are likely to have survived in this part of the Mediterranean to re-extend their range in westward direction under the influence of increasing water temperatures after the peak of the last glacial period.

In western Mediterranean surface waters, present-day mean temperatures of the coldest month range from less than 13°C in SE France to about 15°C in the Sicilian Channel and the northern Ionian Sea. In the Adriatic these values vary from ca 14-15°C in the south to about 8°C in the northernmost part, and in the Aegean Sea from about 16-17°C in the south to about 11°C in the north (Thiede, 1980: 214 fig. 1). In the eastern Mediterranean these values reach 17-18°C. Mean temperatures of the warmest month in the western Mediterranean and SW European waters also remain relatively low (generally less than 24°C) compared to the situation in the eastern Mediterranean (24-28°C), but are not colder than in the northernmost range of the two species in the south-eastern North Atlantic (Madeira and the Canary Islands).

From the above information it may be obvious that *T. cricoides* and *T. solidago* are definitely absent from at least northern Adriatic and the northern Aegean. The present records of *Telmatactis cricoides* (see fig. 6) would suggest that this species

occurs throughout the Central and eastern Mediterranean, roughly bounded in western direction by the Sicilian Channel and to the north by the southern Adriatic and the southern Aegean island chain (Kreta, Kárpáthos, and Rhodos). Data from the North African coast of the eastern Mediterranean are totally wanting, but provided the presence of suitable substrata there seems no reason to assume that the species would be absent from this coast.

The presence of *Telmatactis cricoides* in the Central Mediterranean implies that it faces minimal temperature values at least 2°C lower than in any locality in its Atlantic range, whereas these values in the eastern Mediterranean are about equal to the lowest values found within the Atlantic range.

The distributional range of *Telmatactis solidago* (fig. 6) might be more restricted to the easternmost part of the Mediterranean. The records from Rhodos are within the range of the isotherm of 17°C of the mean temperature of the coldest month, i.e. in accordance with the situation in the northernmost range of the species in the North Atlantic.

The discontinuous Atlantic/eastern Mediterranean distribution of these two species of *Telmatactis* does not stand alone. Similar examples, which might at least in part be explained by glacial cooling, are known from e.g. molluscs (cf. Barash & Danin, 1992: *Charonia variegata* (Lamarck, 1816); *Cochliolepis costulatus* (De Folin, 1870)) and decapod crustaceans (Holthuis & Gottlieb, 1958, Lewinsohn & Holthuis, 1986): *Athanas amazone* Holthuis, 1951; *Salmonesus ? jarli* (Holthuis, 1951); *Munida curvimana* A. Milne Edwards & Bouvier, 1874; *Micropanope rufopunctata* (A. Milne Edwards, 1869) *Ocypode cursor* (Linnaeus, 1758); *Pachygrapsus transversus* (Gibbes, 1850); *Microcassiope minor* (Dana, 1852).

It is interesting to note that both *Telmatactis cricoides* and *T. solidago* are apparently absent in the mid-Atlantic Azores, as present-day temperatures in these islands would not seem prohibitive for their occurrence (mean monthly temperature of the coldest and warmest month being ca 15°C and 23°C, respectively). Therefore, provided that these species ever occurred in the Azores, glacial cooling may have caused their extinction there too, and if so, they may not have succeeded to recolonize these remote islands ever since. In this connection it is noticeable that several other Actinaria occurring widely spread in the East Atlantic/Mediterranean region, and to which water temperatures in the Azores definitely pose no problem, seem to have failed to (re)colonize the islands, the most striking example being *Anemonia sulcata* (Pennant, 1777), a species hard to overlook. Other apparent absentees are *Bunodactis verrucosa* (Pennant, 1777), "*Bunodactis*" *rubripunctata* (Grube, 1840), and *Calliactis parasitica* (Couch, 1842). As a consequence, the actinian shore fauna of the Azores is poor in species, comprising perhaps no more than some 15 species. During the CANCAP expeditions of 1979 and 1981, only 11, possibly 12 species were obtained, mostly intertidally. All of these are shared with the East Atlantic/Mediterranean region, including 2 species which occur on both sides of the Atlantic (*Alicia mirabilis* Johnson, 1861, and "*Anemonia*" *melanaster* (Verrill, 1907)), and one that is considered cosmopolitan (*Diadumene luciae* (Verrill, 1898)). Not a single species occurring in the Azores is exclusively shared with the western Atlantic. For an elucidating discussion on factors governing the faunal colonization of the Azores, although with emphasis on Hydroidea, I refer to Cornelius (1992).

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