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A REDESCRIPTION OF THE SEA ANEMONE *BUNODOSOMA BISCAYENSIS* (FISCHER, 1874) (ACTINIARIA, ACTINIIDAE)

by

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Key words: Actiniaria, *Bunodosoma biscayensis*, verruca, vesicle, nematocysts, distribution, France, Côte Basque.

Bunodes biscayensis Fischer, 1874, a species of Actiniaria described from Moulleau, Arcachon, south-western coast of France, and never recorded since, was rediscovered in July 1985 and found again in 1986 and 1987 in several localities along the French "Côte Basque" between the mouth of the river Adour and St. Jean-de-Luz. The species is here redescribed and referred to *Bunodosoma* Verrill, 1899, a genus of tropical and subtropical Atlantic and West-American intertidal and shallow water forms, hitherto not recorded from the Mediterranean and/or the Atlantic coast of Europe. Speculations are advanced as to the possible further distribution of *B. biscayensis*. A discussion is added concerning the morphological terms verruca and vesicle. The study is completed with an updated generic diagnosis of *Bunodosoma*.

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INTRODUCTION

In July 1985, spending two weeks on the "Côte Basque" in south-western France, I was struck by the occurrence in some localities, notably at Plage d'Ilbarritz, of a conspicuous intertidal sea anemone, which I had never seen before.

Specimens preserved in formalin-seawater as well as living individuals were taken to Leiden for further study. As a result of this study the species was identified as *Bunodes biscayensis* Fischer, 1874, originally described on the basis of a sample (one, or possibly a few specimens) from Moulleau, at the entrance of the Bay of Arcachon, and, in spite of efforts by Fischer, never found again. Fischer's description appears rather accurate and leaves no doubt about the identity of the anemones presently found. However, it only includes data on morphology and colour, so that a redescription of the species according to current standards, including information on anatomy and cnidom, is desirable. The species, superficially reminiscent of *Bunodactis verrucosa* (Pennant, 1777), is here referred to *Bunodosoma* Verrill, 1899, a genus of predominantly tropical and subtropical sea anemones exclusively known from the Atlantic and from the Pacific coast of America, and so far not reported from the Atlantic coast of Europe and the Mediterranean.

SYSTEMATIC PART

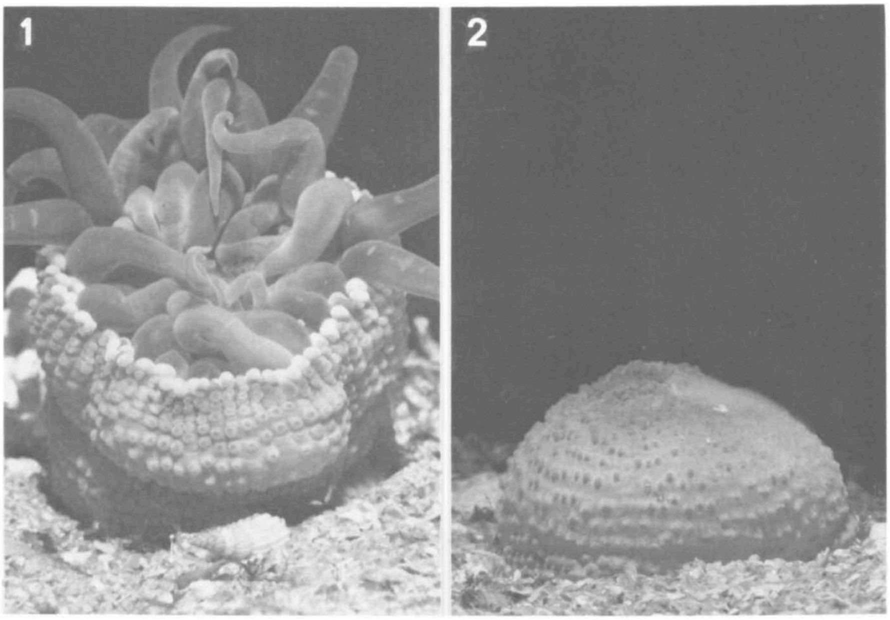
Bunodosoma biscayensis (Fischer, 1874)

Bunodes biscayensis Fischer, 1874: 229-231 [description] 239, 241; 1875: 187 [name]; 1887: 433, 437 [name]; 1889: 271-272 [short redescription; not found again since 1874], 304, 308 [name].
Bunodactis biscayensis, – Carlgren, 1949: 65.
Aulactinia biscayensis, – Dunn et al., 1980: 2078.
not *Bunodactis verrucosa* form III, – Schmidt, 1972: 86.

Material — France, Côte Basque, between the mouth of the Adour (Bayonne) and Saint Jean-de-Luz. RMNH Coel. 17487, between Biarritz and Bidart, south side of Plage d'Ilbarritz, rock formations down a sandy beach with pools and crevices; mostly in sand-filled rock crevices; 18-vii-1985; 13 specimens. In addition five living individuals, collected on 28-vii-1985, were taken for further study. RMNH Coel. 17488, idem, 12/19-vii-1986, 16 specimens. In addition 25 specimens were taken alive on 19/20-vii-1986 for further study. RMNH Coel. 17718, idem, 1-viii-1987, 4 specimens. RMNH Coel. 17489, Bidart, north of Plage du Centre, sandy beach with intertidal limestone formations, pools, etc., 23-vii-1985, 1 specimen. RMNH Coel. 17490, Bayonne, mouth of Adour, north side of northern pier, where rock boulders and sandy beach meet; 13-vii-1986, 3 specimens.

Morphology. — Base more or less circular in outline, firmly adherent (not easily detached without causing damage). Diameter up to c. 5 cm; 4 cm in the largest preserved specimen.

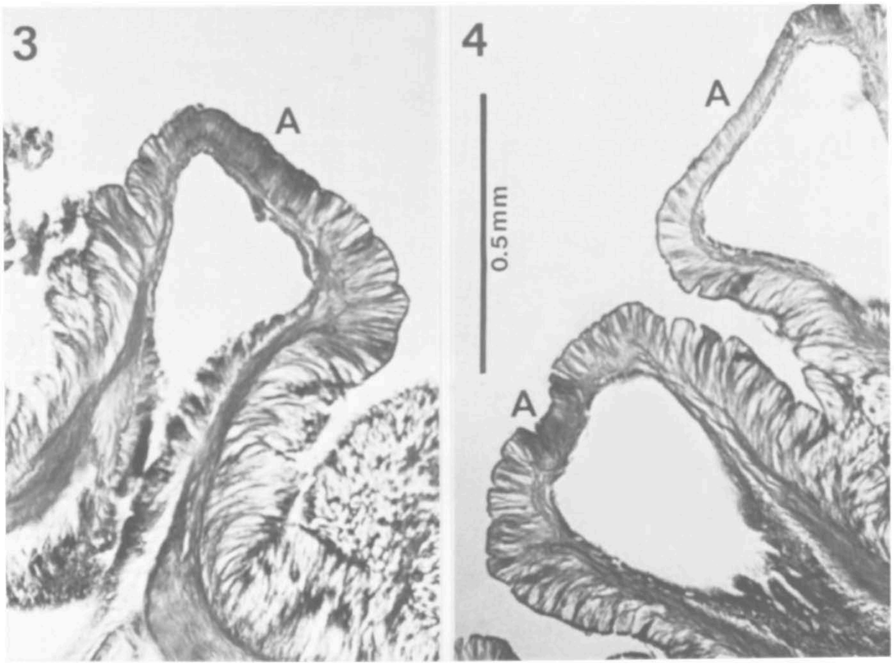
Column usually a cylinder in expansion, somewhat distending towards the oral disc, often exceeding the diameter of the base in length, and able of considerable elongation. Surface completely covered with distinct, vesicular, adhesive verrucae (see figs. 3-4 and the discussion on p. 552) regularly arranged in numerous longitudinal rows corresponding to the endo- and exocoels (fig. 1). Depending, however, on the state of contraction or expansion this arrangement may be quite obscure. In contracted specimens the verrucae are closely set and seemingly arranged at random. Especially in living, elongated individuals, but also in more or less "blown up" contracted anemones a more or less transverse arrangement becomes obvious, though rather irregular



Figs. 1-2. *Bunodosoma biscayensis*. Aquarium photographs (c. natural size) demonstrating the longitudinal and transverse arrangement of the columnar verrucae (cf. p. 536); note the dark spots in the centre of the verrucae, representing areas of differentiated, adhesive ectoderm. (Under aquarium conditions, verrucae generally soon loose their adhesive properties; in addition they tend to reduce gradually in size and to loose their compound character); also note the prosobranch snail *Epitonium clathratulum* in fig. 1 (cf. p. 549).

(fig. 2) (presumably in relation to the arrangement of the circular muscle fibres, between which the verrucae extrude). Over the greater part of the scapus the verrucae are simple to slightly compound (bilobate); immediately near the limbus they tend to be less prominent, while in the marginal region they invariably are more or less stalked and distinctly compound, giving the marginal region a floccose appearance (fig. 6) and obscuring the indented character of the margin, which in fact is divided into numerous, more or less acute, inwardly directed endo- and exocoelic lobes, on the outer aspect of which these compound verrucae are inserted. In regularly hexamerous specimens there are 96 marginal lobes and rows of verrucae. Each lobe bears on its inner aspect a distinct, simple, globular to elliptical acrorhagus (figs. 1, 6), inserted amply above the fossa. The endocoelic acrorhagi as a rule are larger and inserted at a higher level than the exocoelic ones, so that a double crown of alternating, larger and smaller acrorhagi can usually be distinguished.

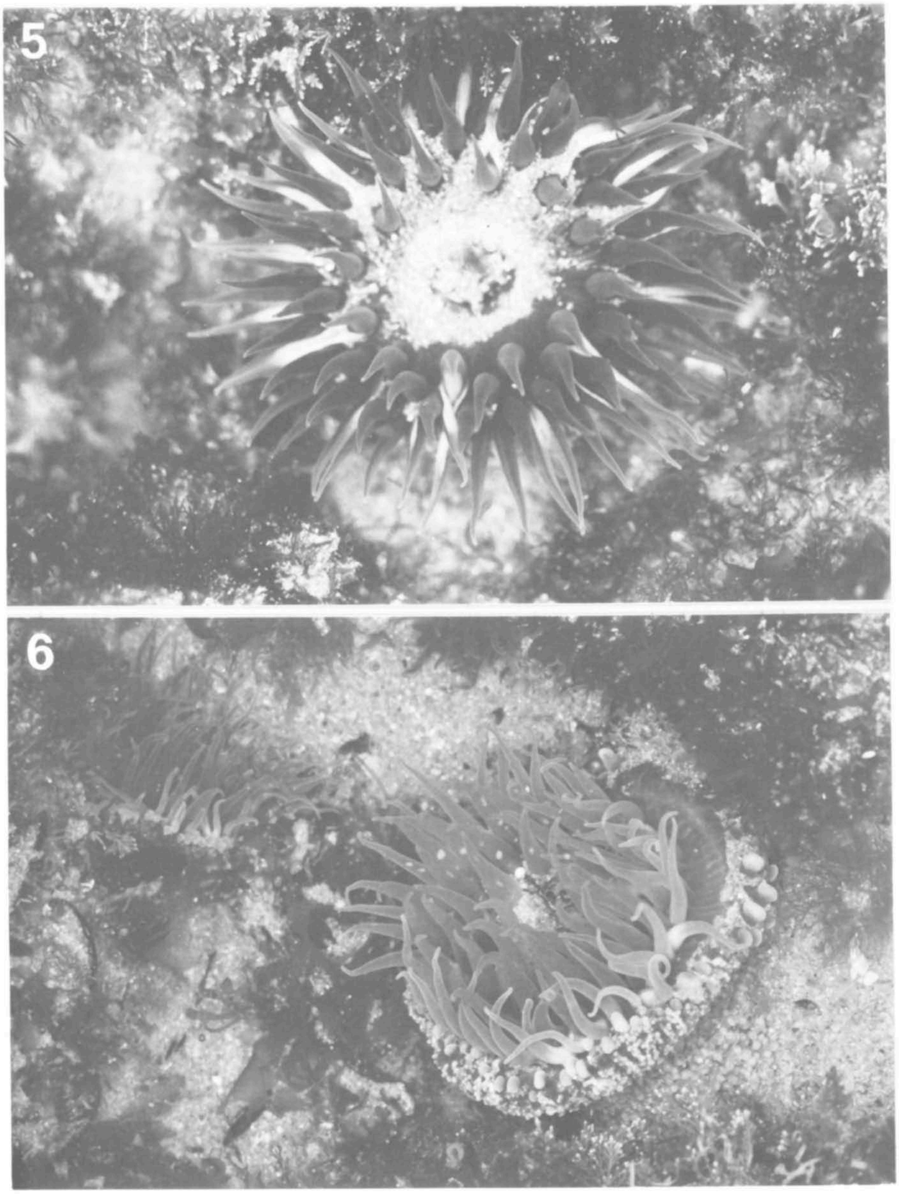
The oral disc is in expansion wider than the base; the central, naked part often with a slightly raised hypostome. Mouth a slit, usually with two si-



Figs. 3-4. *Bunodosoma biscayensis*. Longitudinal sections of verrucae in the upper part of the scapus; A = area of differentiated, adhesive ectoderm.

phonoglyphs. Tentacles of average size, not exceeding the diameter of the disc, entacmaceous, acute and smooth; in preserved condition with numerous longitudinal grooves. In regular specimens they are hexamerously arranged in five cycles: 6 + 6 + 12 + 24 + 48 = 96, but irregularities in number and arrangement are probably of common occurrence (cf. anatomy).

Coloration. — Base and scapus greyish, with orange-ochre longitudinal lines representing the mesenterial insertions. Depending on the state of expansion or contraction these lines may be obscured by the columnar verrucae, which in regulary hexamerous specimens are arranged in 12 whitish longitudinal bands alternating with 12 greyish bands (cf. fig. 7). The white bands are made up of three rows of verrucae each; the central row (corresponding with the primary and secondary endocoels) entirely white, the two adjacent rows bicoloured, i.e. the part facing the white central row also being white, the part facing away being greyish. The alternating grey bands consist of five rows of verrucae each. In large specimens the central row (and sometimes part of the verrucae of the adjacent rows) of each of the grey bands (corresponding with the tertiary endocoels) also tend(s) to be white, especially in the marginal



Figs. 5-6. *Bunodosoma biscayensis*. In situ close-ups (c. natural size) in small tidal pools at Ilbarritz; note the conspicuous, white-streaked tentacles, and the fine, dark, median line on the upper side of the outer tentacles (especially right below) in fig. 5, and the floccose marginal region with well-developed acrorhagi in fig. 6.

Fig. 7. *Bunodosoma biscayensis*. In situ close-up (c. natural size) of individual in moist, sandy, *Mytilus*-fringed depression, showing banded pattern of the column.

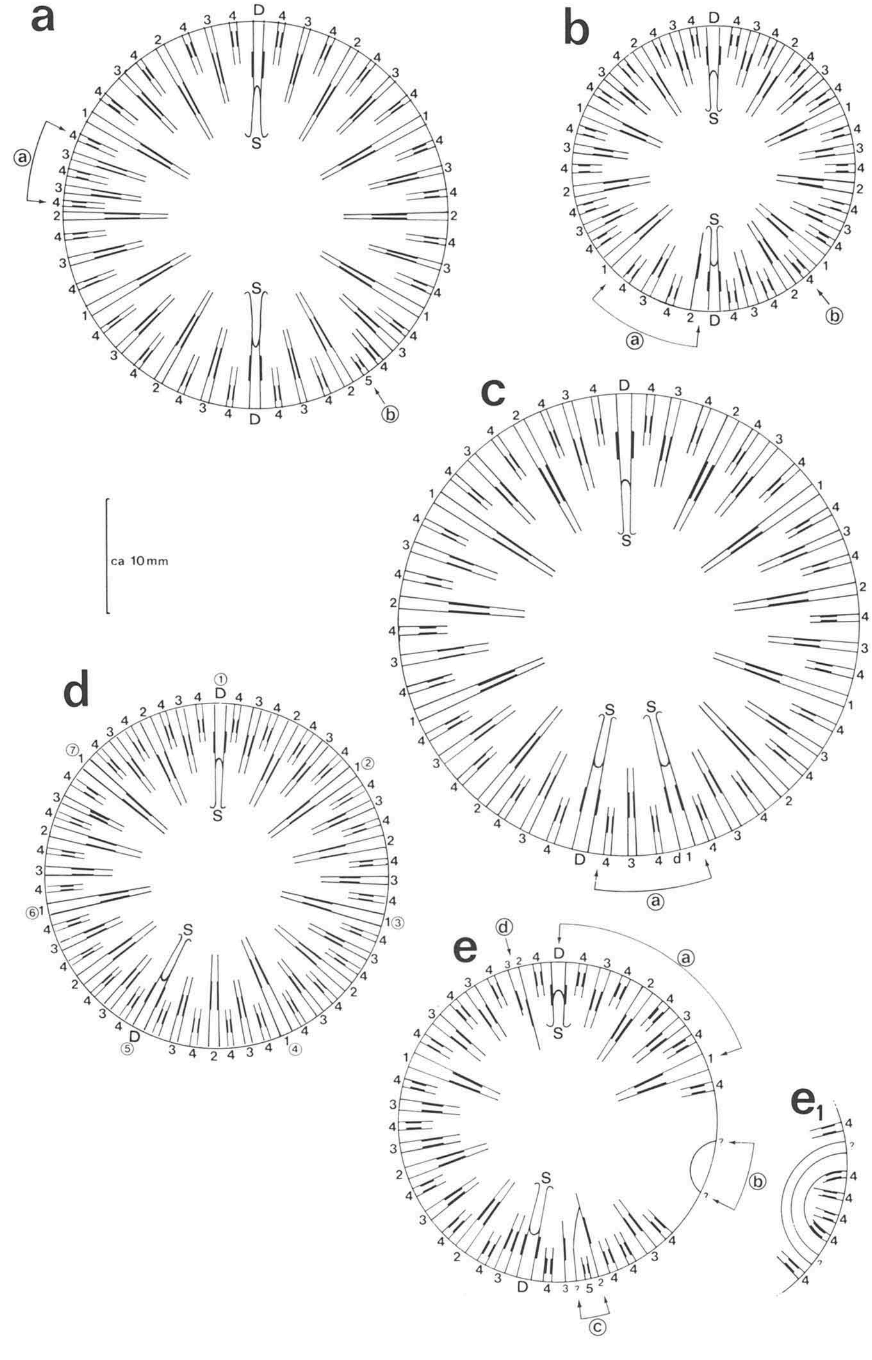
region, so that there is in fact a pattern of 24 pale and 24 dark bands (as described by Fischer, 1874: 229). The banded pattern on the scapus is quite distinct in some individuals, faint in others. The 12 primary white bands are always more conspicuous than the 12 secondaries. Deviations from the regular number of pale and dark longitudinal bands are not uncommon; the number of these bands was found to vary between 10(20) and 14(28), relative to corresponding deviations in the arrangement and development of the mesenteries (cf. anatomy).

The basic colour of the tentacles is greyish to greyish-green or greyish-brown; on their upper surface they bear a fine, dark median line running from base to tip (fig. 5). This line, however, may be inconspicuous, especially in the older (= primary and secondary) tentacles. Cross-bars or spots, except for the odd one, are absent in most specimens, but the tentacles of some specimens may be marked on the upper surface by a row of 4-10 distinct, white or translucent blotches and specks. The under surface of the tentacles, except in the outer cycle, is invariably marked by a conspicuous, brightly red longitudinal streak, broad near the tentacle base, tapering and becoming faint towards the tip.

The outermost (= exocoelic) cycle of tentacles displays a conspicuous pattern: tentacles immediately flanking the primaries are – on the side facing these – marked proximally by a conspicuous dorso-lateral opaque-white streak which fades away distally and which is sharply bounded by the afore-mentioned dorsal median line (fig. 5). The exocoelic tentacles flanking the secondaries are often marked similarly, though the markings tend to be less pronounced. Thus in regular individuals the outermost cycle of tentacles shows an arrangement of either 6 "pairs" of white-streaked tentacles (w) with 18 non-white-streaked "pairs" (n) (arrangement scheme: w - 3n - w - 3n, etc.), or of 12 white streaked "pairs" flanking both the primaries and the secondaries, alternating with 12 non-white-streaked "pairs" (scheme: w - n - w - n, etc.).

Oral disc without a conspicuous pattern or distinctive marks, generally in dull shades of grey, green or brown with the mesenterial insertions often visible as dark lines. In addition there may be faint, creamy blots or radii, especially near the centre of the disc around the yellow-brown to reddish-brown hypostome.

Anatomy. — Number of mesenteries proximally and distally equal: in regularly hexamerous specimens 48 pairs arranged in four cycles (6 + 6 + 12 + 24 = 48), but deviations are common. Out of ten dissected specimens five were perfectly hexamerous while the other five showed smaller or larger irregularities, the number of mesenteries varying between 39 and 56 pairs (cf. fig. 8). The character of the deviations varied from the presence of a few additional pairs of mesenteries in one or two of the secondary exocoels (fig. 8a), to a truly irregular condition where it is difficult or impossible to make a sharp distinction between subsequent mesenterial cycles (fig. 8e). In such specimens mesenteries which in arrangement seem to belong to a particular cycle, may in development conform to a cycle of lower or higher order. In the centre of the base the mesenteries unite in a more or less regular knot. There are normally two pairs of directives connected with distinct siphonoglyphs. In one specimen (fig. 8c) an additional siphonoglyph proved to be present in connection with the aberrant presence of a single additional directive mesentery. All or nearly all mesenteries, including the directives, are perfect and fertile; in some specimens a minority of the quaternaries proved sterile. The various mesenterial cycles insert at different levels on the stomodaeum-wall, the primaries being united with the stomodaeum over its entire length, the quaternaries just reaching the stomodaeum adorally. The sexes are separate. Filaments and gonads (generally well-developed and exclusively situated within the range of the unilobed region of the filaments) of the various mesenterial cycles, in relation to the range of the free edge of the mesenteries, also insert at different levels, reaching most proximally in the youngest cycle, distalmost in the oldest cycle. Gonads of the directives are small or rudimentary, situated near the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ca 10mm

base, amply below the siphonoglyphal slips. Oral and marginal stomata distinct; marginal stomata ovate, oral stomata more circular and larger. Sphincter restricted to distinctly circumscribed, palmate and tending to a more or less bi- or trilobed condition (fig. 9) (cf. Carlgren 1952; 374, 375, figs. 3-4). Retractors of the mesenteries well-developed, diffuse to restricted-diffuse. Parieto-basilar muscles distinct, in the lower part of the body projecting as free flaps. Basilar muscles distinct, visible as prominent ridges along both sides of the mesenterial insertions. As in other species of *Bunodosoma* the body tissues are devoid of zooxanthellae.

Cnidom. — A detailed survey of the cnidom of three specimens of *Bunodosoma biscayensis* is presented in table 1 (see also fig. 10).

The columnar homotrichs were observed only in undischarged condition. In the upper and central part of the scapus they are more or less ovoid in shape and opaque (fig. 10: 1a, left); a seemingly rather short tube could only be observed in the capsule near the terminal orifice. Towards the base of the anemone they tend to resemble acrorhagial homotrichs, showing a more elongate shape and a long tube (fig. 10: 1a, right). Whereas these cnidae were only found sparsely to sporadically in the greater part of the column, they tend to be common around the limbus. This was also noticed in several other species of *Bunodosoma* and in related genera. Obviously it is of no taxonomic importance. Homotrichs invariably are the predominant nematocysts in the acrorhagi (even in species of *Phymactis* Milne Edwards, 1857, where these structures contain a significant additional component of long spirulae). Ever since Abel's classic study (1954) many publications have appeared about the function of the acrorhagi (e.g. Bonnin, 1964; Francis, 1973; Brace, 1981; Bigger,

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Fig. 8(a-e). *Bunodosoma biscayensis*. Schematic representation of the arrangement of the mesenteries just below the stomodaeum in five individuals (all drawn at the same scale) showing deviations from the normal, hexamerous plan. [Numbers indicate mesentery pairs of subsequent cycles; smaller numbers indicate non-paired mesenteries; D = directive pair; d = non-paired directive mesentery; S = siphonoglyph]. Fig. 8a. One secondary exocoel with five instead of three pairs of mesenteries (a) and one additional pair in one of the quaternary exocoels (b). Fig. 8b. One primary exocoel with only half a set of secondary, tertiary and quaternary mesenteries (a) and a secondary exocoel with one pair of mesenteries instead of the usual three (b). Fig. 8c. Mesenterial arrangement perfectly hexamerous, but with an additional section with four pairs of mesenteries (a), including a "semi"-directive pair (with only one directive, d) connected with an additional siphonoglyph. Fig. 8d. Seven pairs of primary mesenteries (indicated by encircled numbers) and one additional primary exocoel, filled up regularly, resulting in a regular, heptamerous arrangement, though self-evidently with asymmetrically placed siphonoglyphs. Fig. 8e. Mesenterial arrangement very irregular, with only one primary exocoel filled up regularly (a); some mesenteries have fused (b, c); one "pair" consist of members of different order (d); the zone almost devoid of mesenteries represents a distinct scar (mechanical damage?) which at a more distal level (fig. e1) shows a different, though no less irregular, aspect.

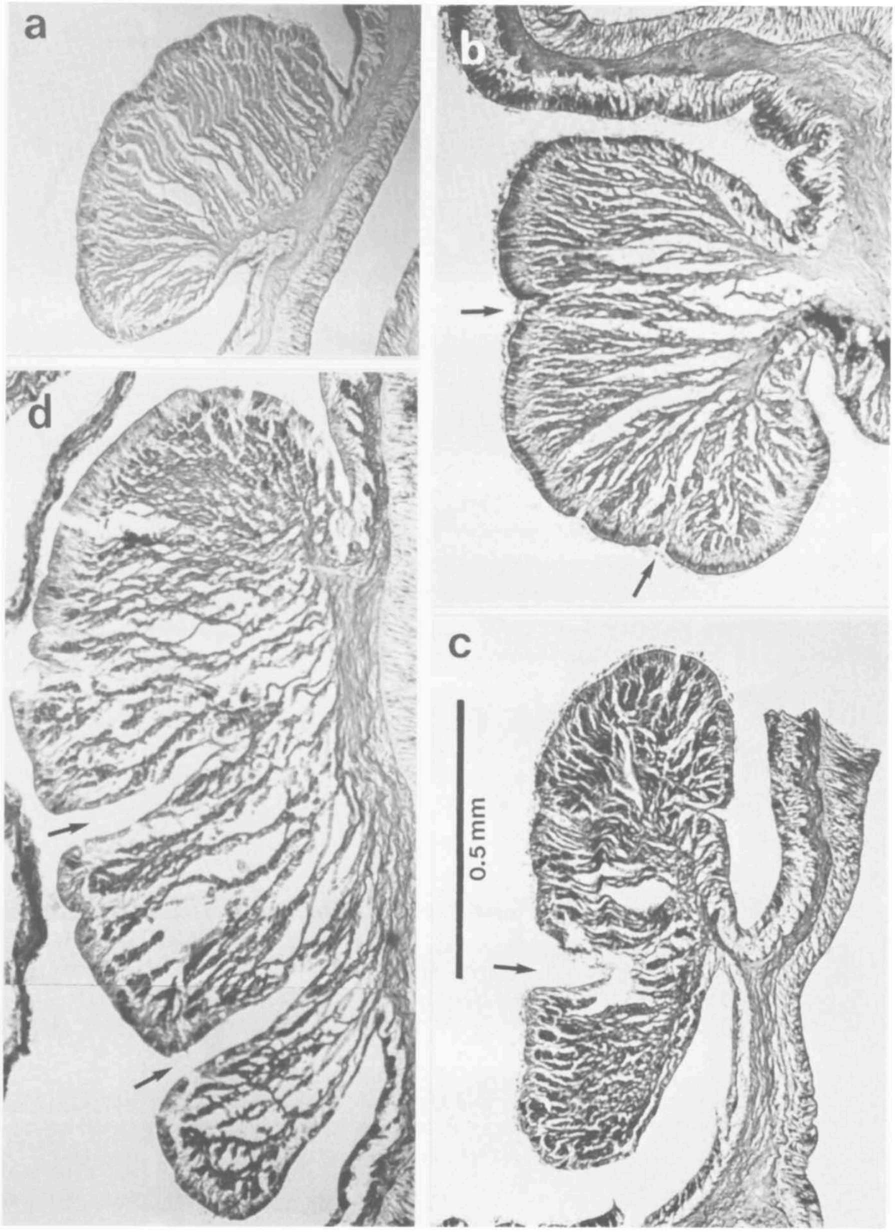

Fig. 9a-d. *Bunodosoma biscayensis*. Variation of the marginal sphincter in four individuals of variable size; note the slightly to distinctly lobed character in figs. b, c and fig. d, respectively (incisions indicated by arrows); all figures at the same scale.

1982), and there is now convincing evidence that they are organs serving aggression and defense, functioning inter- and intraspecifically in the competition for space. Homotrichs contained in the acrorhagi form the functional agent in this process. In an earlier paper (Den Hartog, 1977: 468) I suggested that the scattered presence of homotrichs in the columnar ectoderm of many Actiniidae may serve, though in a lesser degree, the same purpose as the acrorhagial homotrichs. The fact that columnar homotrichs generally are relatively common around the limbus, as in several species of *Bunodosoma*, supports this idea, as the limbal region in particular is a zone of potential contact between crowded individuals. On the other hand, this reasoning seems invalid in the case of *B. biscayensis*, as this species is usually found with the base and the lower part of the column buried in the sand.

Also noticeable in *Bunodosoma biscayensis* is the presence in the filaments of penicilli B_1 (5e) and long, narrow, often slightly curved or faintly S-shaped spirulae (5b). Schmidt (1972: 99) stated penicilli B_1 to occur very rarely in Endomyaria and only assessed the presence of these cnidae in two taxa of Actiniidae: *Actinia equina mediterranea* Schmidt, 1971, and "*Bunodactis*" *rubripunctata* (Grube, 1840) [cf. Schmidt, 1969: 307; 1972: 64-66, 89; as *Anthopleura rubripunctata* (Appendix, note 1)]. However, although sometimes inconspicuous and occurring in small numbers, they are present in the filament of a host of Actiniidae (Appendix, note 2), including most species of *Bunodosoma*.

The above-mentioned spirulae too, occur in various species of Actiniidae (e.g. in species of *Bunodactis* sensu lato, *Anthopleura* sensu lato, *Bunodosoma* and *Urticina* Ehrenberg, 1834), and may be present in the filaments and/or in the scapus. However, they have only rarely been recorded in the literature (cf. e.g. Hand, 1955: figs. 11L, 13N, 15I, 19I). Even a careful worker as Schmidt seems to have overlooked these cnidae in e.g. *Bunodactis verrucosa* and "*B.*" *rubripunctata* (cf. Schmidt, 1972: 84, 89), two species in which, according to my own experience, they are invariably present. In preserved material it may be very difficult to recognize such spirulae as cnidae. I have, however, observed them discharge under the microscope in smears of living tissue of various species. In *Bunodosoma biscayensis* the discharged tube is relatively short, the shaft and the terminal tube reaching c. 3/4 and 1.5-2 times the capsule-length, respectively. The number of these unusual spirulae seems to vary considerably from one specimen to another (at least in some species), and I have as yet no good impression about their distribution in *Bunodosoma*.

Reproduction. — The sexes of *Bunodosoma biscayensis* are separate, and the species may be assumed to be oviparous. I have not found any indication of vivipary (Appendix, note 3). In spite of the regular presence of irregularities in

Organ	Nematocyst type	Specimen	Average and range (in parentheses) of length and width of nematocyst capsules in microns	N	Abundance
1. Scapus	a. Homotrichs	A	20.6(16.9-22.3) x 4.1(3.6-5.3)	10	---
		B	18.8(16.9-21.4) x 4.9(4.5-5.3)	12	-
		C	21.9(20.5-27.6) x 4.2(4.0-4.9)	10	--
	b. Spirulae	A	14.9(13.4-18.2) x 1.9(1.8-2.2)	20	++
		B	15.1(11.6-17.8) x 2.0(1.8-2.2)	25	++
		C	15.3(13.4-19.1) x 2.0(1.8-2.2)	30	++
	c. Spirulae	A	20.7(18.7-23.1) x 2.4(2.2-2.7)	20	-
		B	20.1(17.8-22.3) x 2.8(2.7-3.1)	25	+
		C	21.0(17.8-23.6) x 2.6(2.4-2.9)	30	+
2. Acrorhagi	a. Spirocysts	A	ca. 25-35 x 2.7-3.5	-	+
		B	ca. 30-36 x 3.0-3.5	-	+
		C	ca. 25-35 x 3.0-3.5	-	+
	b. Homotrichs	A	40.5(35.6-46.3) x 4.7(4.5-5.1)	20	+++
		B	43.3(33.8-48.9) x 4.9(4.5-5.3)	20	+++
		C	41.5(38.3-45.4) x 4.7(4.0-5.3)	20	+++
	c. Spirulae	A	ca. 13-15 x 2	2	---
		B	ca. 15 x 2	4	---
		C	ca. 14-16 x 2	4	---
3. Tentacles	a. Spirocysts	A	ca. 12-25 x 2.2-3.2	-	+++
		B	ca. 15-25 x 2.5-3.0	-	+++
		C	ca. 16-27 x 2.4-3.3	-	+++
	b. Spirulae	A	10.1(8.5-11.6) x 1.6(1.4-1.8)	10	--
		B	11.7(10.7-12.5) x 1.7(1.6-1.8)	10	--
		C	13.0(10.7-15.1) x 1.7(1.6-1.8)	10	--
	c. Spirulae	A	20.1(18.7-21.4) x 2.4(2.2-2.7)	20	++
		B	21.6(19.1-24.0) x 2.5(2.4-2.7)	20	+++
		C	21.9(19.6-24.0) x 2.6(2.2-2.7)	20	+++
4. Stomodaeum	a. Spirulae	A	15.8(12.5-20.5) x 2.2(2.0-2.4)	20	+
		B	14.8(13.4-16.9) x 2.2(1.8-2.7)	15	-
		C	16.6(14.2-18.7) x 2.1(1.8-2.7)	20	+
	b. Spirulae	A	24.3(22.3-26.7) x 2.9(2.7-3.1)	20	++
		B	24.5(21.4-18.5) x 3.4(3.1-3.6)	20	++
		C	24.3(21.4-27.6) x 3.2(2.9-3.6)	30	++
	c. Penicilli A	A	ca. 17.5-20.0 x 4.5-5	3	---
		B	ca. 20.0-22.5 x 4	2	---
		C	18.7(17.8-20.5) x 4.5(4.0-4.9)	5	---
5. Filaments	a. Spirulae	A	13.6(12.5-16.9) x 1.7(1.4-1.8)	20	+
		B	14.2(11.6-16.9) x 1.8(1.6-2.0)	20	+
		C	14.4(12.9-16.0) x 1.9(1.8-2.0)	20	+
	b. Spirulae	A	38.9(35.6-41.8) x 1.7(1.6-1.8)	10	-
		B	42.1(36.5-48.9) x 1.8(1.6-2.0)	15	+
		C	39.9(35.6-46.3) x 1.8(1.6-1.8)	20	+
	c. Spirulae	A	33.2(25.8-39.2) x 5.4(4.5-6.2)	25	++
		B	36.9(30.3-40.1) x 5.7(4.5-6.2)	20	++
		C	41.2(36.9-47.2) x 5.5(4.9-5.8)	25	++
	d. Penicilli A	A	19.7(17.8-22.3) x 4.7(4.5-5.3)	20	++
		B	23.1(21.4-24.0) x 4.8(4.2-5.1)	20	++
		C	21.3(19.6-23.1) x 5.1(4.0-5.3)	25	++
	e. Penicilli B_1	A	17.1(15.6-18.3) x 3.1(2.9-3.6)	20	++
		B	18.7(16.0-20.5) x 3.4(3.1-3.6)	20	++
		C	19.4(16.9-21.8) x 3.4(3.1-3.6)	20	++

Table 1. *Bunodosoma biscayensis*. Survey of the cnidom of three specimens (RMNH Coel. 17487) (cf. fig. 10).

the anatomy (cf. p. 539) and the occasional presence of external scars, there is also no substantial proof that the species reproduces asexually by longitudinal fission. I ascertained this process neither in the field, nor during two years of aquarium observations. Slight irregularities (cf. fig. 8), therefore, might stand for normal developmental variations. Other irregularities, notably those cor-

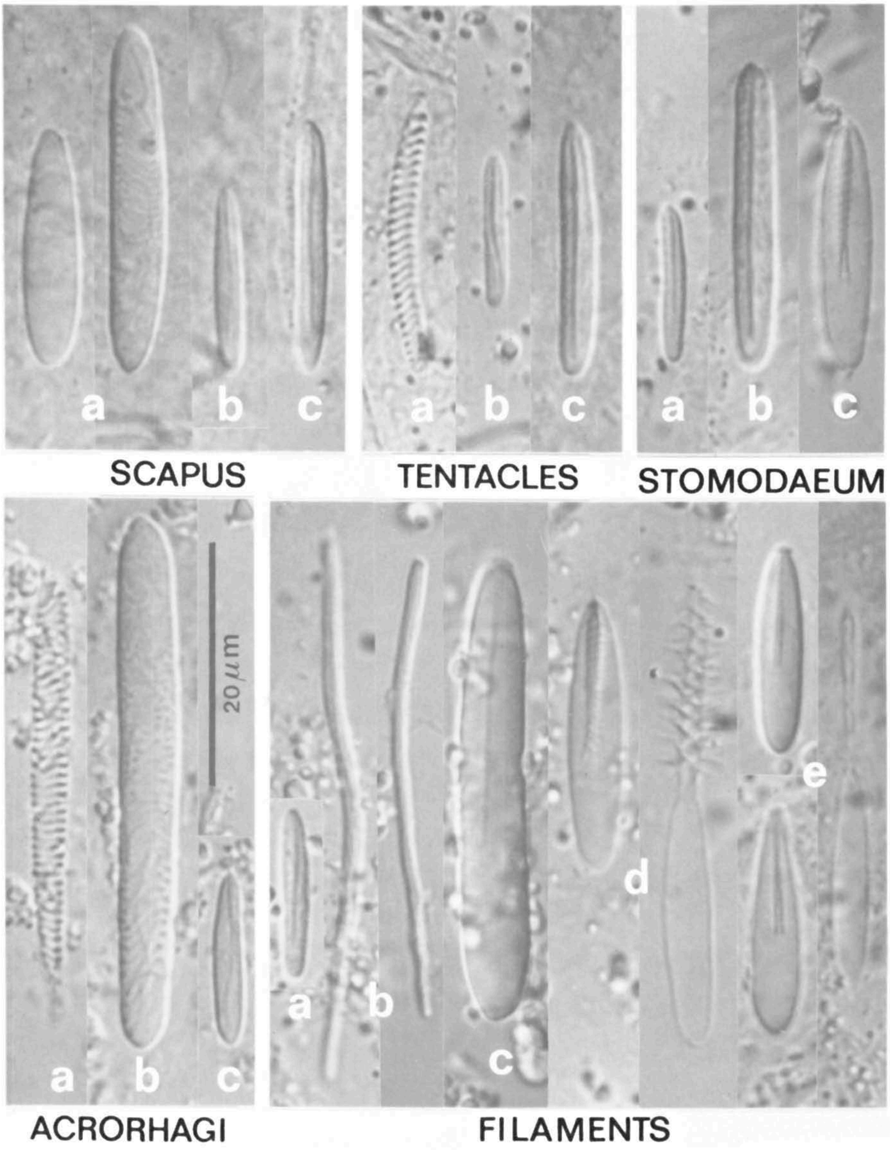

Fig. 10. *Bunodosoma biscayensis*. Pictorial survey of the cnidom (symbols correspond to those used in table 1).

related with external scars, might be the result of damage by inter/intraspecific acrorhagial contacts (cf. p. 551) or mechanical damage (The rocks at Plage d'Ilbarritz, where most individuals were collected, form a favourite site for holiday-makers, searching the area with nets, hooks, etc., for fish bait and edible organisms such as shrimps, crabs and mussels. These activities could be responsible for at least a certain number of mechanically damaged and irregularly regenerated anemones).

Distribution and ecology. — So far *Bunodosoma biscayensis* is exclusively known from a few localities on the south-west coast of France (fig. 11). The

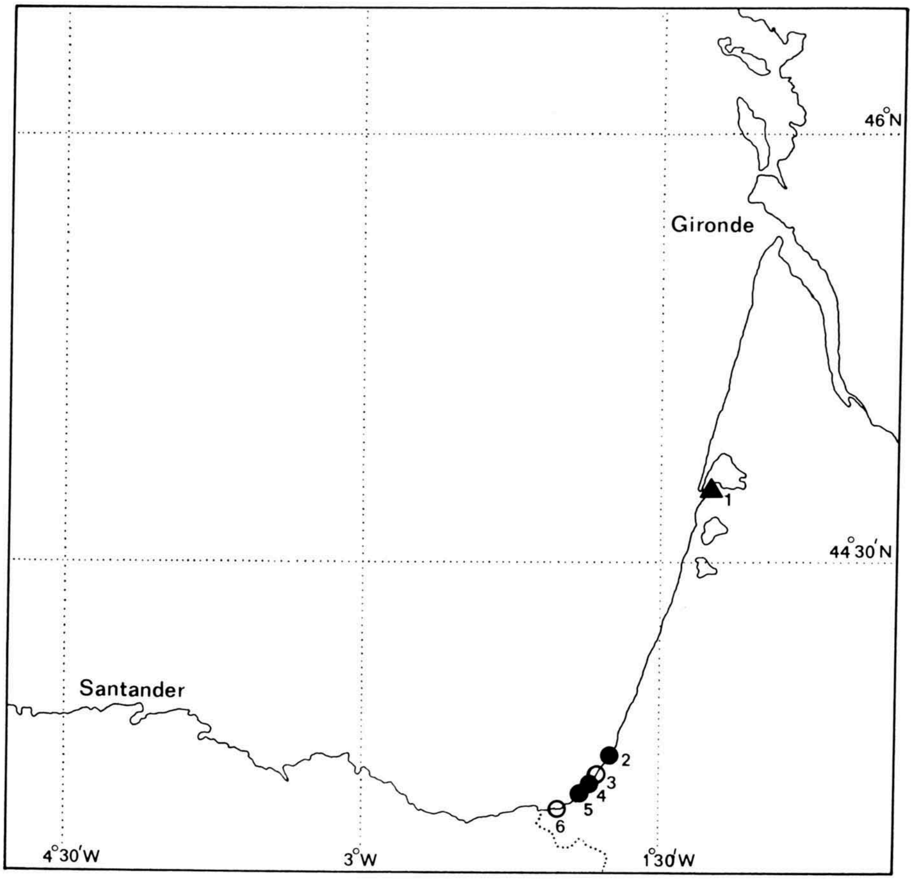

Fig. 11. Localities where *Bunodosoma biscayensis* has been found (all south-west coast of France): 1. Arcachon, Moulleau (Fischer, 1874: type locality); 2. Mouth of Adour, north-side of northern jetty; 3. Biarritz, rocks at sea front near biological station; 4. Rocky area just south of Plage d'Ilbarritz; 5. Bidart, intertidal limestone rocks north of Plage du Centre; 6. St. Jean-de-Luz, north-side of bay, at foot of little pier at sea front. (Open circle = no material collected).

Fig. 12. Locality just south of Plage d'Ilbarritz, where *Bunodosoma biscayensis* occurs abundantly.

species was found intertidally in wet rock crevices or in tidal pools, especially fixed to sand-covered, rocky substrate, a habitat also frequented by *Bunodactis verrucosa*, and proved to be especially common south of Plage d'Ilbarritz, among intertidal rock formations down the beach (figs. 12-14). Remarkably, not a single specimen was found at e.g. Plage de Mayarco, a locality seemingly offering comparable life conditions. At ebb-tide I observed that many individuals of *B. biscayensis* extruded remains of prey, mainly small *Mytilus edulis* L., and in addition remains of small crabs and barnacles. It was noticeable that anemones in water-filled crevices and pools were on the average considerably larger than their congeners in moist crevices and depressions on the often *Mytilus*-covered plateaus. This might be explained by the fact that these anemones may expand during a longer period per day, increasing their catching potential, and also because these more sheltered spots may attract other organisms including potential prey. Moreover, detached organisms such as young *Mytilus*, gastropods, etc., are more likely to precipitate in such spots than on the wave exposed rock surfaces. The observation that small *Mytilus*, up to c. 2 cm long, apparently form the main food of *B. biscayensis* at Ilbarritz is somewhat enigmatic as this bivalve usually lives firmly attached to the rocks

Figs. 13-14. Habitat of *Bunodosoma biscayensis* at Ilbarritz; note *Mytilus edulis* carpets in fig. 14.

or to its congeners with its byssus threads. A small wentletrap, *Epitonium clathratulum* (Kanmacher, 1797) (see fig. 1), also occurs at Plage d'Ilbarritz, in the same habitat as *B. biscayensis*, and turns out to be a parasite/micropredator of the anemone (Den Hartog, 1987).

Four living individuals of *Bunodosoma* taken to Leiden in 1985, and kept in an unheated aquarium with water of supposedly good quality, declined in the course of the winter when the water temperature dropped below 8°C. Although subsequently transferred to a tank with warmer water three specimens died, whereas a single specimen recovered and is still alive (information Mr. R. M. L. Ates, Zaandam, The Netherlands, to whom I entrusted these specimens). A fifth anemone, kept by myself in a small tank with water of poor quality, but at a constant temperature of 22°C, did not show the least signs of decline.

In this context it seems appropriate to consider the general temperature conditions of the Bay of Biscay: The average monthly temperature for January/February varies between 8 and 12°C. The coastal waters of the south-eastern part between the estuary of the River Gironde and Santander on the north coast of Spain are encompassed by the mean February isotherms of 9° and 10°C, (cf. Crisp & Fischer Piette, 1959: 279-281, fig. 1). To the north temperatures become lower, whereas increasing to c. 12° towards the north-western tip of Spain, to c. 14-15°C in southern Portugal, and up to c. 17°C in southern Morocco. In August/September, the warmest period of the year, mean monthly temperatures along the Basque coast of France and especially Spain may amply exceed 19°C, reaching up to 22°C (cf. Crisp & Fischer-Piette, l.c.). In western and southern directions Spanish and Portuguese coastal waters remain significantly cooler, and high summer temperatures as occur in the south-eastern corner of the Bay of Biscay are not found until as far south as Lisbon, the coast of subtropical north-west Africa and the Mediterranean.

I may here recall that *Bunodosoma* is a genus of predominantly tropical and subtropical sea anemones. Some species, however, in the periphery of their range, penetrate into more temperate waters, where winter temperatures of surface waters in the coldest month may drop to an average minimum of c. 8-13°C, but where summer temperatures generally reach a monthly maximum of at least 17-20°C. Thus, the South-African *B. capensis* (Lesson, 1830) (possibly, however, referable to another genus, cf p. 556), according to Carlgren (1949 : 51), ranges from Durban on the tropical Indian Ocean coast (warmest month c. 25°C, coldest month c. 20°C; these and following temperature data derived from Gorshov, 1978, unless stated otherwise) to Lüderitz Bay on the Atlantic coast of Namibia (warmest month c. 17°C) coldest month c. 13°C). In the eastern Atlantic *B. pustulata* (Drayton, 1849) (= *B. cavernata* sensu Verrill, 1864 – non Bosc, 1802) ranges from Cape Hatteras (warmest month c. 24°C; coldest month c. 13°C) southward along the subtropical and tropical coast of the United States, the larger Antilles and the continental coast of Central and South America, to at least Mar del Plata, Argentina (warmest month c. 19°C; coldest month c. 11°C). The West American *B. californica* Carlgren, 1951 (of which the southern range is unknown, but may well extend all along the Central American coast and even further south) occurs throughout the Gulf of California. In the northernmost part of the Gulf (almost 32°N) water temperatures in the summer may reach 30°-32°C, whereas in the winter they may drop to 10°-12°C and in exceptionally cold winters locally to 8°-9°C (Brusca, 1980: 14).

Various other examples of predominantly tropical or subtropical Actiniaria penetrating in temperate waters could be listed. Although additional factors may be involved, it seems obvious that relatively high summer temperatures in the periphery of the range of such species will generally be a prerequisite for successful sexual reproduction, whereas the mere limits of existence are governed by winter minima.

Therefore, although the possibility cannot be excluded that *B. biscayensis* represents an endemic taxon of the south-eastern Bay of Biscay (which, however, would be a solitary case among Actiniaria), it is, considering the above data, more likely that this region forms its northern distribution limits [as in *"Bunodactis" rubripunctata* and *Telmatactis forskali* (Ehrenberg, 1834)]. Taking into account the relatively low summer temperatures in north-western Spain and Portugal, the Biscayan *Bunodosoma's* might even represent an isolated population of a discontinuously distributed subtropical species, or of a species which only in "favourable" years succeeds in spreading northward (settlement of larvae) and in maintaining itself along the "Côte Basque" of France (and presumably Spain), where the relatively high summer temperatures would favour sexual reproduction. In unusually cold winters such a population might again be reduced or even wiped out, which would explain why Fischer (1889: 271-272) never rediscovered the species (Appendix, note 4).

Bunodosoma biscayensis seems to be absent in Madeira, the Azores, the Canary and Cape Verde Islands, and on the Cape Verde Peninsula (Senegal). Since 1976 I have made extensive littoral collections in these areas without ever finding this conspicuous species. It has also not been reported from the better known parts of the Mediterranean. Thus, if not an endemic of the south-eastern Bay of Biscay, the further area of distribution is likely to include the poorly investigated Atlantic coasts of Portugal, south-western Spain, Morocco and Mauritania, and possibly the south-western Mediterranean.

Notes on behaviour. — Under aquarium conditions it was observed that the species is able to dig itself slowly but steadily into the sand by means of the pedal disc and to attach itself to underlying solid substrates. Incidentally, it was also observed that the species may show a very strong intraspecific acrorhagial response, especially after feeding. This response involves strong elongation of the body, shrinking and partial withdrawal of the tentacles, smoothing away of the fosse and inflation of the acrorhagi, in extreme cases up to about half the length of the tentacles. In this condition the body is more or less curved downwards and may swing around, as if making "searching" movements for and towards nearby individuals. Application of acrorhagial ectoderm was also observed, as well as the actual withdrawal of victims/combattants, ploughing their way through the bottom sand – sometimes over a distance of some 15 cm – out of reach of their aggressors. Although victims/combattants – easily recognized by adherent acrorhagial tissue and/or necrotic spots – sometimes seem seriously damaged, they tend to recover within a few days and so far no fatalities have occurred in the aquarium. As a matter of fact the majority of the 25 individuals taken to the Netherlands in 1986, kept for almost a week in a small container, had badly suffered from mutual attacks, but they all survived. Acrorhagial response in *B. biscayensis* was only once observed in the field, in a small tidal pool containing several individuals. These preliminary observations, however incomplete, seem to indicate that the species is a promising object for further studies on intra- and possibly interspecific competition in Actiniidae.

Distinctive characters of the species. — Another Atlantic species of *Bunodosoma* with the column marked by alternating, dark and light longitudinal bands of verrucae is the Caribbean *B. granuliferum* (Lesueur, 1817). This species also frequently displays the conspicuous pattern of white-streaked exocoelic tentacles flanking the primaries (and not rarely the secondaries too). But there are also differences: in *B. granuliferum* the tentacles tend to be marked by more, and more significant, cross-bars, while in *B. biscayensis* a fine dark, median line is usually present on the oral face of the tentacles and a conspicuous, red streak on the aboral face; a condition I have never observed in the former. The column of *B. granuliferum* tends to be shorter and wider distally than in *B. biscayensis*. The scapular verrucae in the former also tend to be more profuse, especially near the margin, and are, unlike in the latter, absolutely incapable of adhering to sand, shell fragments, etc.

In *B. granuliferum* the directive mesenteries are sterile, in *B. biscayensis* as a rule fertile.

The cnidom of the two species differs in several respects. In the column of *B. biscayensis* occur homotrichs, especially near the base, which are absent in *B.*

granuliferum. Both species share the possession of two size-classes of spirulae in the scapus, but the largest size-class in *B. biscayensis* is significantly smaller than in *B. granuliferum* (c. 20-21 × 2.4-2.8 µm versus c. 24-29 × 3.1-3.8 µm) and the same holds for the largest size-class of spirulae in the tentacles (c. 20-22 × 2.4-2.6 µm versus c. 22-30 × 2.4-2.9 µm). Lastly, penicilli B_1 occur in significant numbers in the filaments of *B. biscayensis*, whereas I never found these in *B. granuliferum*.

Bunodosoma biscayensis cannot be confused with any other European sea anemone. As mentioned in the introduction the species shows some superficial resemblance to *Bunodactis verrucosa*, notably to the large form described by Schmidt (1972: 82-87) as *B. verrucosa* form III. However, upon close examination, there are many differences, the most important being that *B. biscayensis* bears acrorhagi, absent in *B. verrucosa*. In addition the verrucae of *B. biscayensis*, unlike those of *B. verrucosa*, tend to be compound (especially in the marginal region), more closely set and adhesive. Furthermore there are considerable differences in coloration of oral disc and tentacles (cf. Stephenson, 1935: 156-159, pl. 9, figs. 1-2; Schmidt, 1972: 82-83, 86-87, 142 fig. 32; Manuel, 1981: 112-113, fig. 39). Very characteristic of *B. verrucosa* is the invariable presence of a vivid lilac to crimson spot in each of the corners of the mouth slit. Such spots are absent in *B. biscayensis*. The cnidom of the two species also shows differences: in the scapus of *B. verrucosa* occur cnidae of one type only, viz., small spirulae (ca. 14-17 × 2-2.5 µm), whereas the cnidom of the scapus of *B. biscayensis* includes homotrichs and two size-classes of spirulae. The cnidom of tentacles, stomodaeum and filaments does not significantly differ.

DISCUSSION ON THE MORPHOLOGICAL TERMS VESICLE AND VERRUCA

The columnar outgrowths of *Bunodosoma* are generally referred to as vesicles (cf. e.g. Carlgren, 1949: 51), but their adhesive nature in *B. biscayensis* [and also in Gulf of Mexico specimens of the wide-spread *B. pustulata* (cf. p 549), which possibly therefore represent a separate species or subspecies] demonstrates that there is no fundamental difference between these "vesicles" and verrucae.

Although the term wart or verruca originally covered both adhesive and non-adhesive structures [cf. Gosse, 1860: xiii ("sucking warts"), 190, 197 (warts never seen used as suckers in *Bunodactis gemmacea* Ellis & Solander, 1786) (= *B. verrucosa*); Stephenson, 1918: 8 ("thickwalled . . . . outgrowths of the body wall which often(!) have the power of attaching themselves to foreign bodies"], it is in practice almost exclusively applied to adhesive structures. Stephenson (1928: 15) later on excluded the non-adhesive structures from the definition (purposively?), but curiously kept using the term with regard to the non-adhesive columnar structures of *Bunodactis verrucosa* (cf. Stephenson, 1935: 156ff). Carlgren (1938: 8) defined verrucae as wart- or blister-like evaginations (in some species compound) with a differentiated area of ectoderm, frequently(!) adherent and without special development of nematocysts. He defined vesicles as non-adhesive evaginations with special ectodermal nematocyst concentrations. In his widely used "Survey of the Ptychodactiaria, Corallimorpharia and Actiniaria" (1949: 10) he unfortunately again restricted the term verrucae to adhesive evaginations only, and defined vesicles more loosely as: "ampullaceous, non-adhesive evaginations of the column, simple or compound; with more or less numerous nematocysts of various categories", a definition which also applies to the vesicular evaginations (of most species) of *Bunodosoma*. Schmidt (1972: 3) again distinguished between adhesive and non-adhesive verrucae, but, somewhat confusing, used the German term "Saugwarz" (which implicates adhesive properties) as an overall term [nonetheless, he often employed the more indifferent term "Warz", also in the generic diagnosis of *Bunodactis* (1.c.: 82)]. Manuel (1981: 98) only mentions that verrucae apparently are non-adhesive in some species (1.c.: 109, 112, 114). Doumenc & Foubert (1984: 47) again restricted the term to structures of adhesive nature, but employed the term freely to non-adhesive vesicular structures on the column of such widely different genera as *Bunodosoma* (1.c.: 64) (and several other genera of Actiniidae) on the one hand, and *Bunodeopsis* Andres, 1881 (Boloceroidaria) on the other hand (1.c.: 66). If anything, the structures found in *Bunodeopsis* are vesicles in the sense of Stephenson (1938: 8) and Carlgren (1949: 10), characterized by thickened ectoderm and special nematocyst batteries, and no verrucae. Curiously, Doumenc & Foubert disregarded the general term vesicle, whereas introducing the specific term "vesicule pedonculée" to include more or less stalked, columnar evaginations as occur in e.g. *Alicia* Johnson, 1861, ignoring the fact that the simple vesicular outgrowths in *Bunodeopsis* (to which they applied the term verrucae) are fully homologous.

In conclusion, it is the often inaccurate and inconsistent use of the terms verruca and vesicle which has created the confusion. In practice one often leaves the existing definitions for what they are, applying the term verruca to more or less button or cup-shaped, adhesive columnar specializations, also if reduced and non-adhesive [as e.g. in *Anthopleura ballii* (Cocks, 1850) and *Urticina eques* (Gosse, 1860)]. However, when columnar evaginations are more or less vesicular and non-adhesive one is apt to refer to them rather uncritically as vesicles (though, for obscure reasons not in the case of *Bunodactis verrucosa*), regardless of the question whether they form special nematocyst batteries (as according to the definition they should) or not, as e.g. in *Bunodosoma* (cf. Carlgren, 1949: 51).

I am aware that this is not the last word in this matter and that we can only have meaningful definitions on the basis of comparative histological studies of the various forms of specialized, columnar structures. In anticipation of such a study the term verruca should in my view be retained in its original sense, so as to include a variety of both adhesive and non-adhesive columnar evaginations. Consequently I present the following definition/description: "Verrucae" are hollow, cup- to button-shaped or vesicular, sometimes compound, columnar evaginations, small or of moderate size, involving all three bodylayers and without special nematocyst batteries. The central or apical part of these structures generally shows a layer, often relatively thin, of modified ectoderm, consisting of supporting cells and special gland cells, and (always?) devoid of nematocysts. Depending on the degree of ectodermal modification these structures may be weakly to strongly adherent, rarely non-adherent.

Verrucae in this sense are nearly always arranged in regular longitudinal rows; endocoelic, or both endo- and exocoelic. They are mainly if not entirely restricted to the Endomyaria, and particularly common in the family Actiniidae.

The term "vesicle" is best restricted to the evaginations of the column-wall of Boloceroidaria. These outgrowths, like verrucae, affect all three body layers. They vary from small, simple, vesicular structures, to large, compound, cauliflower-like bladders (as in *Alicia*) or simple to strongly branched, expandable "pseudo-tentacles" (as in the Caribbean genus *Lebrunia* Duchassaing & Michelotti, 1860, and the Indo-Pacific genus *Phyllodiscus* Kwietniewski, 1898). Unlike verrucae they are irregularly arranged and form or bear special ectodermal nematocyst batteries with thickened ectoderm.

Further notes. — On the basis of the present study I do not hesitate to include the rediscovered species in *Bunodosoma* Verrill, 1899. The species conforms in all principal characters to other representatives of this genus, including the type species, *B. granuliferum* (Lesueur, 1817), even though the adhesive nature of the columnar verrucae is unusual and not a general trait of the genus.

Bunodosoma, including *B. biscayensis* and the Gulf of Mexico population of *B. pustulata*, represents a uniform species-group and it would therefore be ill-founded to remove these two species merely on the basis of the adhesive properties of their verrucae. The alternative would be either the erection of a new genus or to transfer them to *Anthopleura* Duchassaing & Michelotti, 1860, which, in contrast, in its present sense (cf. Carlgren, 1949: 53-54) is a heterogeneous assemblage of species. A comparison of the type species of *Anthopleura, A. krebsi* Duchassaing & Michelotti, 1860, with *Bunodosoma biscayensis*, reveals the illogicality of including these two species in the same genus. In *Anthopleura krebsi* there are well-spaced, strongly adhesive, button- to cup-shaped verrucae, arranged in endocoelic longitudinal rows only, which near the margin tend to be confluent. Apart from *A. krebsi*, such species as *A. thallia* (Gosse, 1854) (cf. Stephenson, 1935; Manuel, 1981: 116), *A. carneola* (Verrill, 1907), and *A. stellula* (Ehrenberg, 1834) (cf. Schmidt, 1970) may be included in *Anthopleura* sensu stricto (cf. also Schmidt, 1972: 92-93). Not, however, a species like *A. xanthogrammica* (Brandt, 1935) which has the entire column covered with strongly adhesive verrucae. This last-named species in several respects comes closer to *Bunodosoma*.

As to the adhesive character of verrucae as a taxonomic character I may further bring to notice the genus *Urticina* Ehrenberg, 1834 (= *Tealia* Gosse, 1858). This genus includes forms like *Urticina felina* (L. 1767), with distinct, strongly adhesive verrucae, but also forms with reduced, non-adhesive verrucae such as *U. crassicornis* (Müller, 1776) and *U. eques* (Gosse, 1858) (= *T. lofotensis* (Danielssen, 1890)) (cf. e.g. Carlgren, 1921; Stephenson, 1935; Manuel, 1981). All the same, the homology of these organs and the congeneric status of these taxa is universally accepted.

DIAGNOSIS OF *BUNODOSOMA* VERRILL, 1899

In anticipation of a revision of the genus *Bunodosoma* (in preparation) I conclude this paper with an emended generic diagnosis:

Actiniidae with a well-developed pedal disc. Column densely covered with numerous simple to compound, vesicular, non-adhesive, rarely adhesive, verrucae, arranged in endo- and exocoelic rows (this arrangement often obscured in contracted or preserved specimens), running from the limbus (or almost so) to the margin, each row ending proximally on the outer face of a short marginal lobe. Verrucae may be more or less reduced and less prominent near the base, whereas in the marginal region they tend to be relatively compound. Both endo- and exocoelic marginal lobes (may) bear distinct acrorhagi on their inner aspect.

Organization of the body generally regularly hexamerous, with two pairs of directives connected with siphonoglyphs; number of mesentery pairs, respectively tentacles (in parentheses), usually 48(96) or 96(192) arranged in 4(5) or 5(6) cycles, occasionally with a partial or complete additional cycle; individual irregularities may occur in at least some species. Number of mesenteries in full-grown individuals proximally and distally equal. All mesenteries, the youngest cycle sometimes excepted, are perfect and fertile; directives sterile or fertile.

The sexes are separate (always?) and ovipary probably is the usual mode of sexual reproduction; vivipary occurs in some species. Asexual reproduction by longitudinal or transverse fission has not been reported.

Oral and marginal stomata distinct. Sphincter circumscribed and well-developed; retractors diffuse; parieto-basilar and basilar muscles distinct. Tissues invariably without zooxanthellae.

Cnidom. — Scapus: one or two size-classes of spirulae; additional homotrichs present in most species, especially near the limbus.

[One species, viz., *Bunodomosa capensis* (Lesson, 1830), in addition has atrichs (cf. Schmidt, 1972: 7 figs. d-e) and penicilli A in the columnar ectoderm and possibly should be transferred to another genus. (K. W. England, in litt., 14-V-1986)].

Acrorhagi: spirocysts, predominant homotrichs, and dispersed small spirulae.

Stomodaeum: spirulae, and few penicilli A_1.

Filaments: spirulae and penicilli A_1; additional penicilli B_1 present in most species; long, slender spirulae at least occasionally present in some species.

APPENDIX

Note 1. Columnar homotrichs seem to occur especially, though not invariably, in species possessing acrorhagi. On the other hand, they are present in at least some species which never develop acrorhagi, e.g. in *"Bunodactis" rubripunctata* (Grube, 1840). Schmidt (1972: 91), referring to the definition by Carlgren (1949: 8) claimed the short verrucate marginal lobes of this species to represent true acrorhagi and adapted Carlgren's definition to include these structures (Schmidt, 1972: 3). He subsequently transferred this species, generally accommodated in *Bunodactis* Verrill, 1899, to *Anthopleura* Duchassaing & Michelotti, 1860. Although Carlgren's definition admittedly is somewhat inaccurately worded, the structures referred to by Schmidt have little if nothing in common with acrorhagi. The undesirability and incorrectness to extend the definition in the sense of Schmidt becomes obvious if we consider the type-species of *Anthopleura krebsi* Duchassaing & Michelotti, 1860, with marginal structures comparable to those in *"B." rubripunctata*, but in addition with true acrorhagi, situated on the inner aspect of these. It is true that the marginal lobes of *"B." rubripunctata* in analogy with acrorhagi contain (or at least may contain) numerous homotrichs; the same, however, applies to the region around the limbus. In conclusion, Schmidt's arguments to transfer *"B." rubripunctata* to *Anthopleura* are invalid, but even so he touched an important matter, viz., the present status of the genera *Bunodactis* and *Anthopleura*, and there are certainly arguments – though of a different nature – to remove *"B." rubripunctata* from its present genus.

Note 2. Hand (1955) in his paper on Central Californian Actiniaria did not formally differentiate between various types of penicilli, but in several species he distinguished and figured more than one size-class of these cnidae. From his figures it is obvious that he observed penicilli B_1 in the following species of Actiniidae: *Epiactis prolifera* Verrill, 1869 (Hand, l.c.: 44 fig. 9H), *Anthopleura xanthogrammica* (Brandt, 1835) (: 51 fig. 11N), *A. elegantissima* (Brandt, 1835) (: 57 fig. 13 O), *A. artimisia* (Pickering, 1848) (: 67 fig. 15 O), *Tealia crassicornis* (Müller, 1776) (: 74 fig. 17H), and *T. lofotensis* (Danielssen, 1890) (: 85 fig. 21H) (For a remark on the identity of this last-named species, see Den Hartog, 1986: 87 footnote). I have established the presence of penicilli B_1 in the filaments of various species of the following genera: *Actinia* L. sensu lato, *Bunodactis* sensu lato, *Anthopleura* sensu lato (including two of the three species studied by Hand), *Pseudactinia* (Carlgren, 1928), *Urticina* Ehrenberg, 1834 (= *Tealia* Gosse, 1858), *Phymactis* Milne-Edwards, 1857, and *Bunodosoma* (all Actiniidae). In addition I have found these cnidae in *Mesacmaea* Gosse, 1853 (Haloclavidae), and *Halcampoides* Danielssen, 1890 (Halcampoididae).

Note 3. Both in the older and contemporary literature (e.g. Stephenson, 1928; 1929; 1935; Manuel, 1981: 17) vivipary is often considered a mode of sexual reproduction (i.e. following internal fertilization). Recent investigations, however, indicate that internally brooded juveniles are not necessarily – and possibly never – produced sexually, but rather asexually by apomictic parthenogenesis (e.g. Gashout & Ormond, 1979; Carter & Thorpe, 1979; Schäfer, 1981).

Note 4. As large numbers of anemones survived the cold winter of 1984-1985 (the coldest in the region since 1956), water temperature data of this winter would give an impression of low temperature tolerance of the species under natural conditions. My efforts, however, to obtain such data so far were in vain. Therefore, to illustrate the climatic conditions I have to restrict myself to air temperature data for Biarritz and Cap Ferret (near Arcachon) (received via the Netherlands Centrum voor Oceanografische Gegevens, NCOG). The table below gives temperature data (in °C) for January and February in 1956, 1985 and for the period 1956-1986.

		BIARRITZ			CAP FERRET		
		1956	1985	'56-'86	1956	1985	'56-'86
Mean Temp. $\frac{(Tn + Tx)}{2}$	Jan.	8.6	4.1	8.0	7.7	2.7	7.2
	Feb.	0.1	8.2	11.5	–0.3	9.5	7.9
Mean Min. Temp. (Tn)	Jan.	5.4	0.6	4.5	5.1	–0.4	4.4
	Feb.	–3.7	7.0	5.3	–4.2	5.9	5.3
Mean Max. Temp. (Tx)	Jan.	11.8	7.7	11.5	10.3	5.7	10.0
	Feb.	4.0	15.4	12.9	3.6	13.1	11.5

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