

SPECIES OF *SPIOCHAETOPTERUS* (POLYCHAETA, CHAETOPTERIDAE) IN THE ATLANTIC-MEDITERRANEAN BIOGEOGRAPHIC AREA

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SARSIA



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Five species of the genus *Spiochaetopterus*: *S. typicus* Sars, *S. bergensis* Gitay, *S. costarum* (Claparède), *S. oculus* Webster, and *S. solitarius* (Rioja) have been compared. These species can be divided into two groups: group A, with boreal biogeographic affinity, consisting of *S. typicus* and *S. bergensis*; group B, with temperate biogeographic affinity, consisting of *S. costarum*, *S. solitarius* and *S. oculus*. The two groups differ in the shape of the specialized setae of segment A4, the number of segments in region B, and the structure of the tube. Representatives of group A have a middle region of two segments, modified setae of segment A4 are distally rhomboid and the tubes are without articulations. Representatives of group B have a middle region of many, always more than 2 segments; modified setae of A4 are distally cordate, and the tubes are with articulations. In each geographic unit of the Atlantic-Mediterranean area, the species are divided into two groups of different sizes. The usefulness of such systematic characters as the number of segments in region B, ornamentation of the tubes and relative size of the pro- and peristomium is reexamined. New characters include the detailed morphology of the A4 setae, location of the secretory part of the ventral shield, and the structure of the secretory pores. Two diagnostic keys to species, one based on the tubes and the other on the A4 setae, are included.

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KEYWORDS: Polychaeta; Chaetopteridae; *Spiochaetopterus*; specialized setae; glandular shield; tube structure; Atlantic-Mediterranean area.

INTRODUCTION

The most recent in-depth revision of the genus *Spiochaetopterus* Sars, 1856 is that of Gitay (1969) who synonymized *Telepsavus* Costa, 1861 with it and recognized four species: *S. typicus* Sars, 1856; *S. bergensis* Gitay, 1969; *S. madeirensis* Langerhans, 1880 and *S. costarum* (Claparède, 1870). According to Gitay (1969), *S. costarum* included five subspecies: *S. c. costarum*; *S. c. oculus* Webster, 1879; *S. c. pottsi* (E. Berkeley, 1927); *S. c. monroi* Gitay, 1969; and *S. c. okudai* Gitay, 1969. Three taxa originally described in the genus were considered either indeterminable or members of *Phyllochaetopterus*. Bhaud (1972) reviewed the genus in connection with a redescription of *S. costarum* from the type locality (Naples); a visit to 'terra typica' failed to yield a chaetopterid with the body only divided into two parts; however, he confirmed the generic synonymy, accepted the four species included by Gitay and, *inter alia*, discussed various aspects of variation and biogeography in the species of the genus. He confirmed that use of the genus *Telepsavus* is not

justified. Kudenov (1975) examined the descriptions of type species of the genera of the family and redefined the genera, mainly on the basis of the shape of the modified setae of A4 observed on a macroscopic basis. Based on literature records, Fauchald (1977) stated that the genus *Spiochaetopterus* comprised 12 species; it is not clear whether he recognized any of the taxa treated as synonyms by Gitay (1969) or the species and subspecies described by that author. Bhaud & al. (1994) redescribed *S. solitarius*, originally placed by Rioja (1917) in the genus *Phyllochaetopterus*, from populations at the type locality (Santander Bay, northern Spain) and in the northwest Mediterranean, France. The only comparative studies to date have been based on a limited number of specimens in questionable states of preservation. In this study, representatives of the genus *Spiochaetopterus* are re-described, using a very large number of individuals for the Mediterranean species; taking advantage of the study of live individuals when possible to observe natural colouration and behaviour; and, finally, studying variability of old and new characters used to differentiate the taxa.

MATERIAL AND METHODS

Material examined

S. typicus. a. Zoological Museum of the University of Copenhagen. From Dr J.B. Kirkegaard: 1) 2 specimens Skagerrak 58°02'N, 8°48.5'E (Stn 211; 640 m, 6/4/57); 2) 1 specimen, Lenefjord, Norway (depth not given) 20/6/1926 Hj. Broch col.; 3) 2 specimens, Hurry Fjord, East Greenland off Constable Point 70°30'N, 22°30'W (45 m, 7/7/1933) sediment given as 'tough clay'. From M.E. Petersen: 5 specimens Marmorilik W Greenland (71°07.8'N, 51°20.4'W), stn 13, 202m, 13/9/1980, det. E.S. Petersen.

b. Zoological Museum of the University of Bergen: no. 2260, one specimen from Vadsko, (Gitay revision 1967) leg Dr D.C. Danielsen; no. 58231, 2 specimens within tube, from Straume, 20-30 m, mud (8/11/1960); no. 58231: 2 specimens within tube, Nordstrand, 28-29 m, mud (28/9/1960); no. 58231: 2 specimens within tube, from Straume, 20-30 m, mud (28/9/1960) leg Dr E. Sjøteland; no. 18606: 4 specimens within tube, from Hjeltefjorden.

S. bergensis. a. From Dr. D.C. Danielsen. 6 specimens, numerous tubes: Sorfjorden, E Akre, Hordaland, W Norway, 396-397 m depth, fine sandy bottom; type locality 60°15'35"N, 6°35'00"E.

b. From J.B. Kirkegaard. 3 specimens, numerous tubes: Skagerrak, 640 m depth (Stn 211; 6/4/1954)

c. 10 specimens and numerous tubes from F. Pleijel, Tjärnö Marine Biology Laboratory, collected by Prof. R. Rosenberg; Norwegian trench, deep Skagerrak, Stn OS1: 58°08'.00N, 9°10.99E, 637 m depth, 31 % clay 60 % silt, May 1993.

S. costarum a. Mediterranean Sea: 8 specimens collected in the Bay of Naples, Italy, close to the Marine Biological Station, off Via Caracciolo, at a depth of 3-4 m by M. Bhaud in July 1970 with the use of a long-handled rake equipped with a bag attached at the level of the teeth; the collection area is situated at the offshore boundary of seagrass in black anoxic muddy sediment; 6 specimens from the Etang de Thau, close to Sète, France, collected by Travé-Morlot (TRAVÉ-MORLOT 1987): very abundant species at station 2 (332 m², n = 17, SD: 173) situated close to bivalve culture set-up, 8-9 m depth, organic pollution, species constant throughout the year and generally exclusive occurrence.

b. Atlantic coast. 1. Arcachon, 15 specimens near the Marine biological station on fine sandy bottom slightly muddy at low tide and at supralittoral level; collected by C. Cazaux and M. Bhaud during June 1974. 2. Galicia, Spain: 6 specimens, inner part of Rias Bajas, present in large numbers in anoxic muddy sand sediments; collected during June 1995 by E. Lopez-Jamar. Total of 35 specimens.

S. solitarius. Description is based on material from the northwestern Mediterranean mainly from Banyuls (French Mediterranean coast) where both live and preserved specimens were studied. Specimens have also been collected near the Marine Station of Blanes (Spain, Mediterranean Sea); from Santander (NW Spain, Atlantic coast) and from La Coruña (NW Spain Atlantic coast). 55 specimens were used for numbering setigers in region B. This pool was

formed with specimens collected from several years, several seasons and two places, as follows (number in brackets): Port Vendres 10/1992 (11), 12/1992 (13), 3/1993 (9); Santander 11/1992 (5), 8/1993 (17). Details about the sites and the nature of the bottom are given in BHAUD & al. 1994.

S. oculatus. a. Bogue Sound, North Carolina, USA: Diplanthera bed off Pine Knoll Shores, sandy mud, c. 0.3 m, 23 Oct. 1964, coll. & ident. M.E. Petersen (3 specimens + tubes) in collection of the author.

b. Gloucester Point; Virginia, USA: in front of the Virginia Institute of Marine Science; lower tides; 30 specimens provided by M. Thompson to the author, collected during early spring 1995.

Terminology

To facilitate descriptions and simplify comparisons, organization of the body is standardized. The body of chaetopterids is comprised of three regions: an anterior region with 9 or more segments, a middle region with 2 or more segments, and a posterior region with a variable number of segments. These regions are herein designated A, B, and C, respectively, as earlier suggested by CROSSLAND (1904). A4 thus refers to setiger 4 in region A, B2 refers to setiger 2 in region B, etc. In the same way, the terminology for the different regions of ventral shield or plastron of region A are standardized and I propose to use VS-a, VS-b, VS-c for first, second or third ventral shield region so that the entire plastron can be described accurately. The use of the terms 'thorax' and 'abdomen' (NISHI 1996; MIKKELSEN & VIRSTEIN 1982) should be avoided; they cannot account for the three regions of the body and their use is based on an inappropriate comparison with wholly unrelated higher taxa.

Use of new characters

The small number of species in *Spiochaetopterus* suggests that the relationships among them may be resolved by a relatively limited number of characters. A survey of the literature (BLAKE 1996; DAY 1967; GITAY 1969; FAUVEL 1927) shows that the characters used have included the number of specialized setae in A4, the number of setigerous segments in regions A and B, and the number of setae in notopodia of region C. In addition, the organization of the body according to a very stable ground plan in the whole family has favoured similar descriptions in different geographical areas and has simultaneously hindered the use of new criteria. In this paper, new criteria are suggested and evaluated. For each feature, a minimum of data from literature is given, as well as new method of using it.

a) Number of segments in region B. At the specific level, variation (or lack of such) in number of middle (B) segments is used to differentiate species within *Spiochaetopterus*: Conflicting information on the number

of segments in region B (e.g., for *S. typicus*, 2 to 10 segments according to DAY (1967), but only 2 according to GITAY (1969); and for *S. costarum*, 20 according to GITAY (1969), 30-40 according to BLAKE (1996), California, and up to 67 according to OKUDA (1935), Japan), suggested that the species were being incorrectly interpreted. The need to examine the variability in the number of segments in B requires no further justification. An example will be given in Fig. 1.

b) Specialized setae of A4. The existence of specialized setae on A4 is an important feature for the family and these setae are the only hard structures in this family which can be manipulated easily. These setae have not been the object of a precise morphological study (see for instance GITAY 1969) because observations by compound microscope seem insufficient for discerning differences. Earlier papers (BHAUD 1977, 1979; BHAUD & al. 1988, and KUDENOV 1975) have shown that the morphology of A4 setae may be diagnostic at the genus level. The more detailed analysis presented here suggests that they are also diagnostic at the species level. For a useful comparison of morphology, the definition of several parameters is given (Fig. 2). The A4 seta of *Spiochaetopterus* spp. is in two parts: shaft and inflated tip; the boundary is at the point where the diameter of the cross-section of the shaft begins to increase. The swollen tip is divided into two on each side of the largest diameter: the upper part or head and the lower part or collar which forms the base of the head. The head is obliquely truncated by an upper oblique plane. This plane allows definition of dorsal and ventral side: opposed to or on the same side as the plane of truncation, respectively. In lateral view, the side plane is defined by the dorsal elevation of the head, the lateral oblique edge and the lateral horizontal edge. In ventral view, the upper oblique plane is limited by two lateral oblique edges and the horizontal ventral edge. The two lateral edges may be slightly serrated, giving them the ability to cut. The width of the head may be taken from the lateral view (lateral width) or the ventral view (ventral width). The length of the swollen tip, or head, is given by distance between the sharp point and the boundary to the shaft. Comparisons of A4 setae are based on Scanning Electron Microscopy (SEM). The specialized setae were dissected out of fixed specimens, then plunged into a bath of NaOH at high concentration (0.5 g of anhydrous pellets in 50 ml of distilled water) for one hour with monitoring the digestion of the flesh surrounding the seta every 10 minutes. The setae were then washed in three successive baths of distilled water (15 minutes each) and taken through an alcohol series progressive transfer to 95 % methanol. Before observation the setae were transferred to 100 % methanol, air

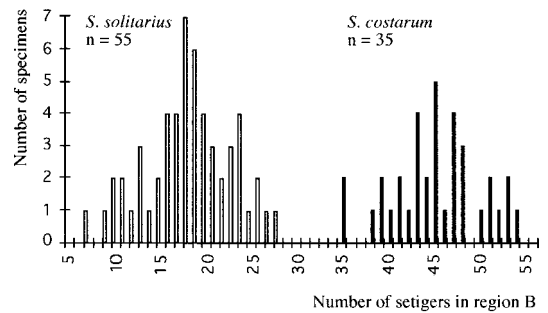


Fig. 1. Comparison of number of segments in part B for two partially sympatric species: *Spiochaetopterus costarum* and *S. solitarius*. Specimens are from several geographical sites and over several seasons. The non-overlapping distributions of the two species is clear. Origin of these specimens is given in section Material examined.

dried, mounted on a grid with double-side sticky tape and shadowed with gold palladium. All observations were made at the University of Perpignan on a SEM Hitachi S. 520. Some pictures were taken from the author's collection prepared at the Pierre and Marie Curie University (Paris VI).

c) Structure of the epidermis. STORCH & WELSCH (1970) described the fine structure of the tegument of *C. variopedatus*. This structure is unique among polychaetes. Inside large cells, the cytoplasm is located at the periphery of the cells and the center is occupied by one huge vacuole. Glycogen is present in all parts of the cytoplasm with several areas of concentration. The distal part of the cell is stretched to form microvilli on which a mucoid and a finely filamentous material are superimposed. Extracellular fibers, frequently observed in many species, are lacking in this species. These authors used small fragments of tegument without giving the origin, ventral or dorsal, of the fragments. The goal of the current study is not to develop in-depth histological information, but to locate ventral secretion areas and secretory pores. For that, epidermis of five species was studied by SEM.

d) Structure of the tube. The tubes are frequently mentioned in the literature, but they are often empty or contain the partially decomposed body as a magma in which it is difficult to discern the different parts of the animal (see BELLAN 1964). Consequently it was not possible to link a character of the structure of the tube with a given species. This is the reason why structure of the tube has not been used at the specific level. However several studies are available. BROWN & MCGEE-RUSSELL (1971) studied the ultrastructural architecture of *Chaetopterus* tubes. The tube wall consists of alternating layers of aligned protein fibres imbedded in an unstructured matrix. The

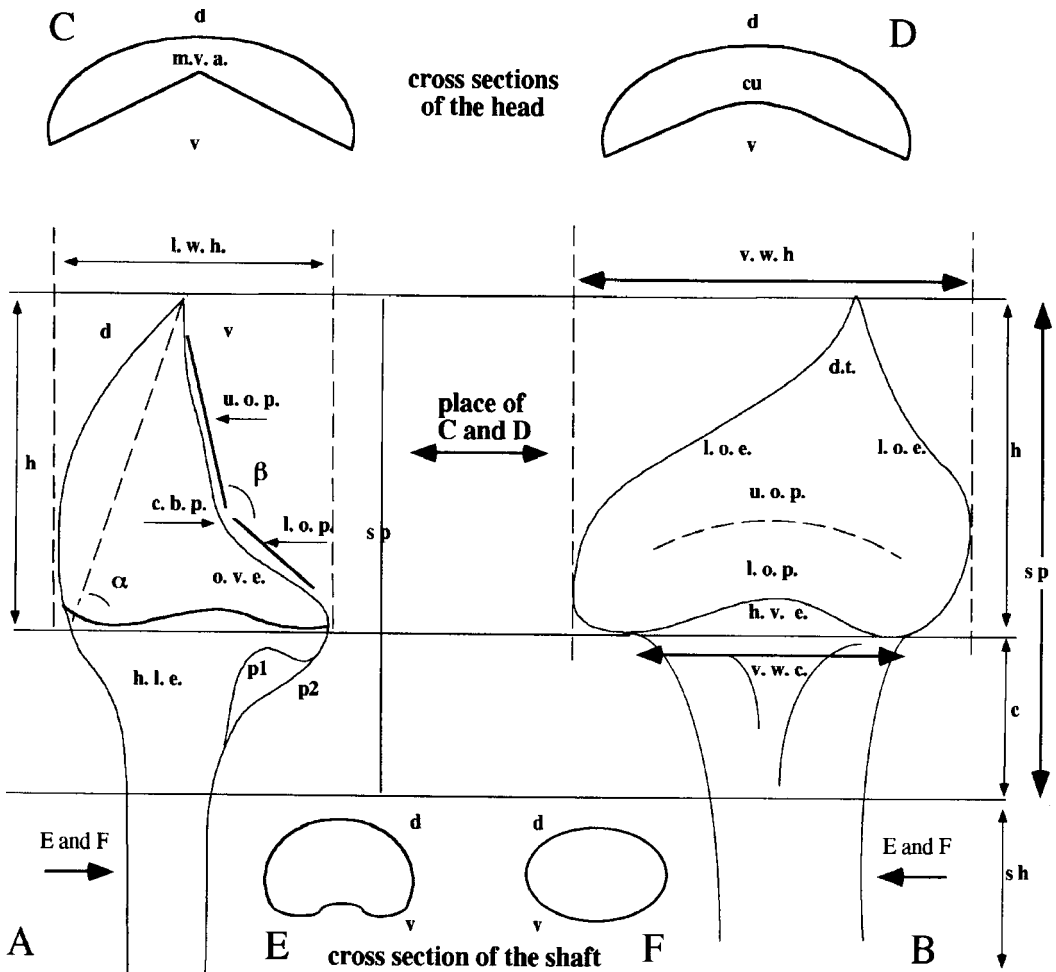


Fig. 2. Diagram of specialized A4 seta of *Spiochaetopterus* spp. in lateral (A) and ventral (B) view. Above the two views A and B cross sections of the head show the junction of two oblique planes as a straight line (C) or a curved surface (D). Between the two views are shown two cross sections of the shaft: with, in E, and without, in F, a groove throughout the length. α : angle formed by vertical dorsal side with horizontal; β : angle between upper and lower oblique planes; c: collar; c.b.p.: curved or broken profile of the oblique plane; cu: curve joining the two lateral parts of oblique plane; d: dorsal side; d.t.: dorsal tip; h: elevation of the head; h.l.e.: horizontal lateral edge; h.v.e.: horizontal ventral edge; l.o.e.: lateral oblique edge of the upper plane; l.o.p.: lower oblique plane; l.w.h.: lateral width of head; m.v.a.: mark of vertical axis; o.v.e.: oblique ventral edge; sh: shaft; s.p.: swollen part (collar + head); u.o.p.: upper oblique plane; v: ventral side; v.w.h.: ventral width of head; v.w.c.: ventral width of collar, immediately under the head. On A are given two profiles of the collar: marked overhang for p1 and reversed cone for p2.

protein fibres range in diameter from 50 to 400 μm . BROWN & MCGEE-RUSSELL (1971) demonstrated a connection between their own work and studies by STORCH & WELSCH (1970) who surveyed the fine structure of the epidermis cuticle complexes in 18 species of polychaetes. This cuticle consisted, in part, of alternating layers of aligned protein fibres, similar in organization to those of the *Chaetopterus* tube wall. *Chaetopterus* lacked the layers of aligned fibres adhering to the epidermis. BROWN & MCGEE-RUSSELL (1971) suggested that *Chaetopterus*

forms a fibrillar meshwork along its surface, but rather than retaining it as an adherent cuticle, sloughs it off, and constructs a tube from the materials. In this study attention is limited to the wall structure using SEM, with an attempt to extend the observations given for *Chaetopterus* to representatives of *Spiochaetopterus*. Two kinds of tube were examined: ones with no articulations and with uniform appearance of the external wall (wrinkled tube) and ones with alternation of articulations and joints (ringed or multiarticulated tube).

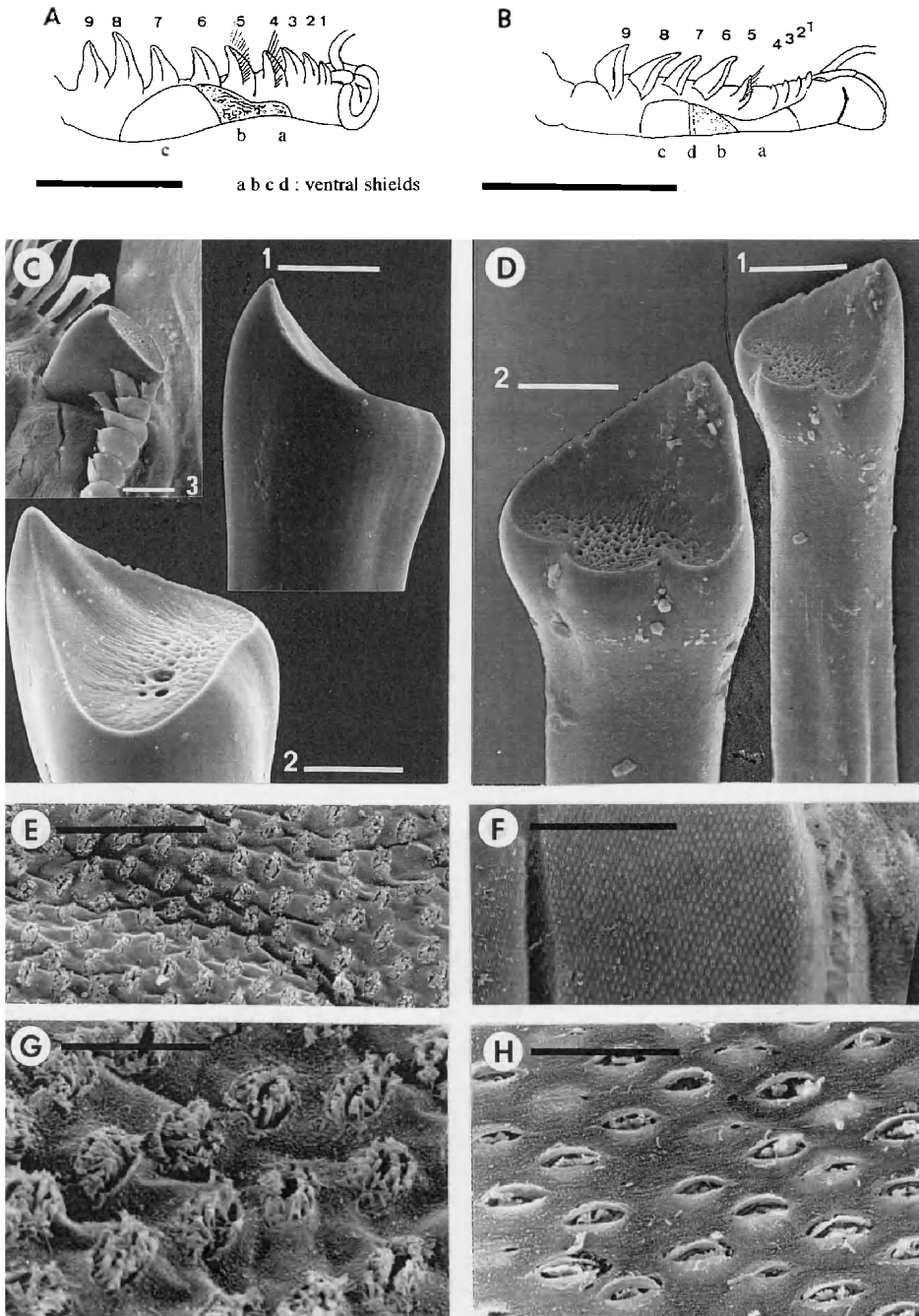


Fig. 3. *Spiochaetopterus*. Morphology of two boreal species. A, C, E and G: *S. typicus*. B, D, F and H: *S. bergensis*. A and B: appearance of region A with boundaries of ventral shields. Notice also the morphology of peristomium. C and D: specialized seta of A4. C3 represents the orientation of the specialized seta in A4 of *S. typicus* as seen in A: the oblique (or ventral) section of the seta faces the fore part with a slight deviation toward the medio-dorsal axis. D1 and D2 show two magnifications of same seta; note in D2 shaft without deep ventral groove. E and F: morphology of the secretory part of the ventral shield, anterior part to the right. G and H: same morphology at a larger magnification. The scale bars have the following values: A: 3 mm; B: 1 mm; for C to H values given in μm . C1:210; C2: 250; C3: 300; D1: 80; D2: 55; E: 37; F:150; G: 10; H: 20.

RESULTS

Species studied can be divided into two groups. Group A has boreal biogeographic affinity, and consists of *S. typicus* and *S. bergensis*. Group B has temperate biogeographic affinities, and consists of *S. costarum*, *S. solitarius* and *S. oculatus*.

Comparison between Spiochaetopterus typicus and S. bergensis (Fig. 3)

Among boreal species, GITAY (1969) differentiated *S. typicus* from *S. bergensis* on the following characters: the size of the specimens (*S. typicus* is bigger); the shape of the peristomium (horseshoe-shaped in *S. typicus* and shovel-shaped in *S. bergensis*); the appearance of the parapodia of the middle region (respectively 'fleshy' and foliaceous). However, the main difference was that the ventral surface of A7-A8 has a white shield in *S. typicus*, while in *S. bergensis* the ventral surface of A6-A8 has a brown-to-reddish gland. This difference does not appear clearly. In 4 examined specimens of *S. typicus*, the ventral surface at the medioventral line has a patch of gray that extends on A4 and includes A5, and also extends laterally onto A6 (Fig. 3A); weak intensity of the coloration allows to differentiate the anterior part at the level of A4 (vs a) from the posterior part (vs b); next comes a large white shield (vs c) that begins between A5 and A6, is widest between A6 and A7, and then gradually shrinks as it crosses A7 and A8. Of the 9 specimens of *S. bergensis* examined from Scandinavia, 6 have weak coloration marks on ventral part of A4 to A5 (vs a on Fig. 3B) then a clearly visible light brown ventral arc on A6 (vs b on Fig. 3B); the anterior boundary of this arc is oblique and the more ventral part of this arc is at the level of A5. This shield begins just after setae A5 and continues across all of parapodium A6. Next comes a sharp, narrow boundary line arranged in a half-girdle of even width at the level of the setae of A6 (vs d on Fig. 3B), and then a pearly white shield on A7 (vs c on Fig. 3B), terminating at the level of the setae of A8. On the 3 other specimens, the coloration is more diffuse or absent. The main difference of ventral shields was the presence of an additional ring (vs d) in *S. bergensis*, but it is difficult to know whether this difference is diagnostic.

A more marked difference was related to body size and morphology of A4 specialized seta (Fig. 3C, D). More precisely, in the two species, the overhang of the ventral edge is not clearly marked and this edge is weakly prominent; the oblique plane is rounded-triangular. Difference in size is very marked, size ratio of the A4 modified chaeta of *S. bergensis* to *S. typicus* being 1 : 3. The ventral width of the seta reaches 100-120 µm in *S. typicus* and 35-40 µm in *S. bergensis*. Detailed SEM observations on the secretory area supply final differences. In *S.*

typicus the opening is lined with two rows of microvilli (Fig. 3E, G). In *S. bergensis* the pores are simple slits (Fig. 3F, H)

Tubes of these two species are not articulated and by this character, they are distinct from other species in the Atlantic. SARRS (1856) described tube of *S. typicus* as a pipe 12-16 inches long and 1/8 inch in diameter, 'sillonné transversalement d'anneaux bien fins et serrés', formed by a succession of small and tight rings giving regular undulations to the longitudinal outline of the tube (Fig. 8 A-C). Description of the tube of *S. bergensis* (GITAY 1969) is short: 'tubes twisted, semitransparent, sometimes with an outer layer of fine sand grains; they are about 70 mm long or more and have a diameter of 0.5 - 1 mm'. The wall is not regularly undulated but crumpled and when transversal swellings are formed, they are developed on only a part of the whole circumference (Fig. 8 D, E)

Comparison of Spiochaetopterus costarum, S. solitarius and S. oculatus (Figs 4-7)

The use of the number of segments as a character was evaluated after a comparison between the two partially sympatric species *S. costarum* and *S. solitarius*, (Fig. 1). In spite of the limited number of specimens used, the number of segments in region B appears to be a viable feature. RIOJA (1931) reported 14-28 segments for region B of *S. solitarius*; the maximum number is nearly the same as for specimens collected more recently. This recent complement has been made by BHAUD (1998) based on the study of 335 individuals of *S. solitarius* and 72 of *S. costarum* and results confirm those of Fig. 1. In *S. solitarius*, there is a maximum number of 28 (this paper) or 29 (BHAUD 1998) setigerous segments in region B. This number may be considered as species specific and used as a discriminative feature. If there is a clear gap in the number of B segments of these two species, this difference still requires explanation: it presupposes the absence of specimens formed with a limited number of segments in B region; in other words this gap presupposes, in *S. costarum*, the absence of autotomy. This question is dealt with in BHAUD 1998.

For *S. oculatus*, among 30 specimens collected, 22 had B region intact (B was followed by some segments of the region C). The number of segments in B region varied in the range 14-23 with respective number of specimens as follows (number of B segments given between brackets): 2 (14), 2 (15), 1 (16), 4 (17), 1 (18), 5 (19), 3 (20), 0 (21), 1 (22), 3 (23). WEBSTER (1879) noted that the middle region is composed of 20-23 segments. Number of segments in C region was counted on 4 specimens on which C region was apparently not injured. Number of segments was 27, 33, 38 and 42 with, in each case, several additional segments in growing phase.

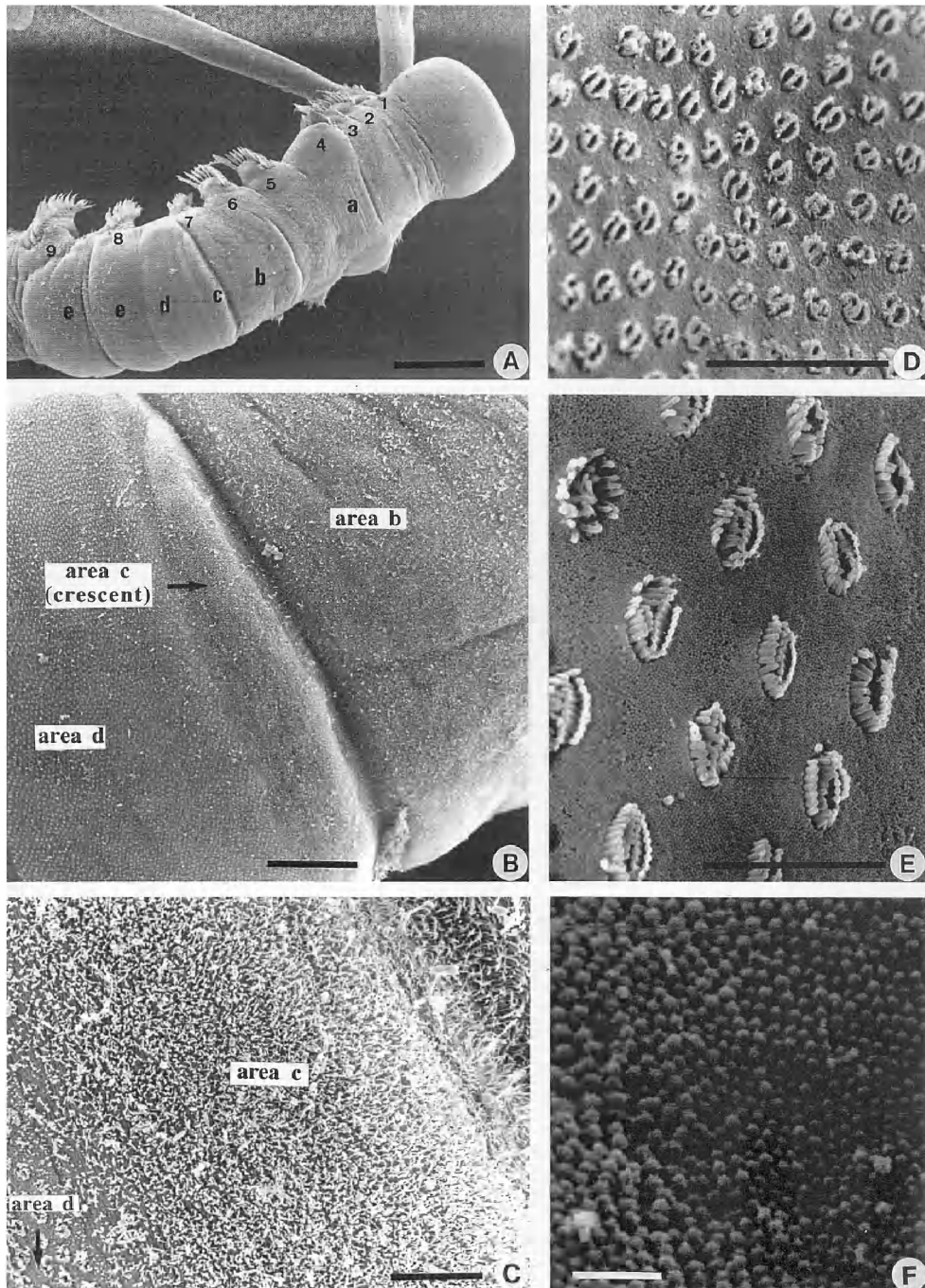


Fig. 4. *Spiochaetopterus solitarius*. (specimen from Port-Vendres harbour). Ventral shield observed by SEM. A: region A in ventral view with setigerous segments numbered and indication from a to e of five areas defined based on their appearance. B: details of the central part of A, at the level of A7 and A8 characterised by the crescent c; this latter is bounded at the front by a deep furrow and, at the rear, by area d. C: details of crescent c covered with a fine ciliation. D and E: the area posterior to the crescent (marked by d on A) displaying an alveolate structure probably corresponding to secretion pores. F: the ventral posterior area (marked by e on A) characterized by a granular surface. Scale bars have following values (μm): A: 320; B: 80; C: 20; D: 13; E: 7 and F: 0.66.

A differentiated ventral shield is characteristic of Chaetopteridae. This shield has been thought to be wholly glandular. However, this shield is differentiated into several areas, which do not all have a secretory function.

In *S. solitarius* most of the ventral side is ciliated; the ciliation is interrupted by a secretory area, marked d in Fig. 4 A-C, and located between the level of setal bundles of A7 and A8. This area is easily identified by the presence of regularly arranged oval pores. They are up to 3.2 μm long and the opening is divided into two parts. Posterior to this area, and also between pores of area d, the epidermis observed by SEM appears to be formed by a very dense cover of spherical structures which may represent the distal parts of microvilli, already observed by STORCH & WELSCH (1970) in *Chaetopterus variopedatus*.

In *S. oculatus*, BARNES (1964) indicated that secretions for tube construction are produced by epidermal glands that open onto the surface of the anterior region of the body. This secretory surface is supposed to extend from the anterior margin of the head through all of region A to the level of setiger A9 and to cover the entire convex ventral side of the body. By light microscopy on a preserved specimen, it is easy to observe the secretory area which is smaller than indicated by Barnes. A major part of the ventral area is ciliated. The smaller area dedicated to secretion does not reduce its importance for tube construction, the mucus being spread out and transported by the dense cover of cilia. The following areas of the ventral side were identified from SEM (Fig. 5A, B). Area a is the most anterior area, marked with a fine net of brown spots; a more marked transverse brown line divides this area into two equal parts. The whole area is covered with papillae of which the more marked are near the median line. Area b is a ciliated area separated from area a by a very marked furrow seen at lower magnification (12.5x - 25x); the coloration is the same as in area a. Area c is a dark brown crescent, larger and darker along the anterior edge; the external boundary appears to be formed by the juxtaposition of elongated ampullae. Area d forms a second crescent characterized by an epidermis with regularly arranged openings. This crescent is smooth and bright when observed through a compound microscope. Area e is the posteriormost part of region A, occurring on setigers A7, A8 and A9 and often divided into three parts without obvious connection with the segments. The integument is sharply delimited, smooth, pearly, without papillae, microvilli, or cilia; it may be rich in large vacuoles. In spite of their similarity when observed through a compound microscope, areas d and e differ in structure.

In *S. costarum*, the secretory area and its pores have also been found; the secretory area is located immediately posterior to the coloured crescent. By comparing

the position and density of the secretory pores it is possible to differentiate the three temperate species. In *S. solitarius* (Fig. 6A-B) the pores are regularly spaced. The angle between the lines of pores is closer to 60° than 90°. This means that they form a hexagon with a supplementary pore in the center. The distance between the centres of two neighbouring pores is 5 to 6 μm . In *S. costarum* (Fig. 6C-D) the pores are arranged in two orthogonal lines, at least in the posteriormost part of the crescent. The distance between two pores is 6.0-8.5 μm . In *S. oculatus* (Fig. 6E-F) the pores are not regularly spaced and the distance between the centres of two neighbouring pores is 4.2-4.8 μm . The structure of the pores is apparently the same in the three species. The overall shape is oval. The opening is circumscribed by independent vertical elements arranged in four longitudinal series. Each series has 10-12 elements which can shut the gland if the series approach one another. In this case the two external series are the only ones to remain visible. Although it is too soon to attribute specific characteristics to the secretory area, it calls for further study. The size of the secretory crescent, the distribution of the pores, their density and structure are all potentially useful characteristics for classification.

The morphology of specialized setae in *S. solitarius* has been described by BHAUD & al. (1994, fig. 3A-C). This is a modified chaeta with a single, distally swollen, asymmetrical and obliquely cordate head. The cross section of the shaft is oval and a groove is present throughout the length. This description applies to other species as well and therefore needs to be completed. Observed in its entirety, the overall shape is slightly curved which can serve as a differentiating characteristic. Seen from the oblique angle the lateral edge is a smooth, unbroken curve.

In the A4 seta of *S. oculatus* the shape of the upper oblique plane is clearly cordate (Fig. 5C); the cross section of the shaft is oval; a deep groove runs the whole length of the shaft; a clear angle is formed by the sketching of the ventral edge of the lateral plane (Fig. 9E1-3) and constitutes a useful characteristic for differentiation from other species. The elevation of the head (h on Fig. 2) is considerable and more clearly marked than in the other two species.

In *S. costarum* (as in *S. solitarius*) the oblique ventral edge of the seta seen from the side (o.v.e. in Fig. 2) is not broken but curved. The lower part of the ventral balcony (cf area c in Fig. 2) is readily visible in *S. oculatus* and *S. solitarius*; the collar is conical, the horizontal ventral edge (h.v.e. in Fig. 2) in a raised position and the ventral part of the upper plan in a nearly horizontal position (Fig. 5C). This lower part of the ventral balcony is not visible in *S. costarum* due to the low position of

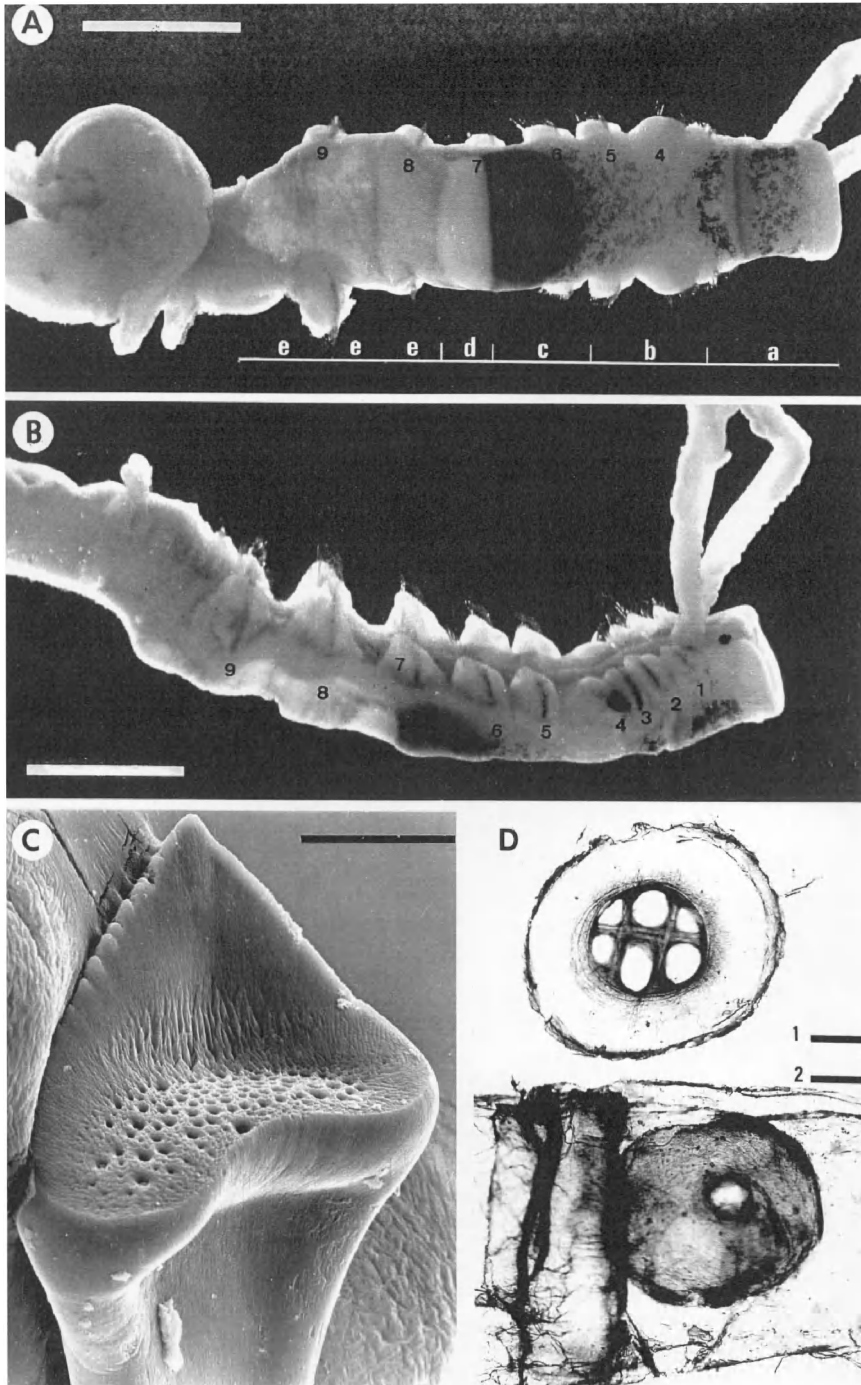


Fig. 5. *Spiochaetopterus oculatus* from Virginian coast. Two photographs of ventral (A) and lateral (B) view. Parts a to e, on A, show ventral shields without defining their secretory role or lack of it. Photo by J. Lecomte, Marine Station of Banyuls. C: morphology of A4 setae seen in 3/4 view: the upper surface of the head is formed with two planes of which the intersection is clear; corresponding references in Fig. 2 are upper oblique plane, lower oblique plane and curve or fold of ventral oblique plane. D: two types of septa; 1: complex septum withdrawn from the tube; 2: septum with one central opening photographed still in the tube; in two cases diameter of septa is 850 μm . The scale bars have the following values (μm) A and B: 1200; C: 50; D 1: 210 and 2: 300.

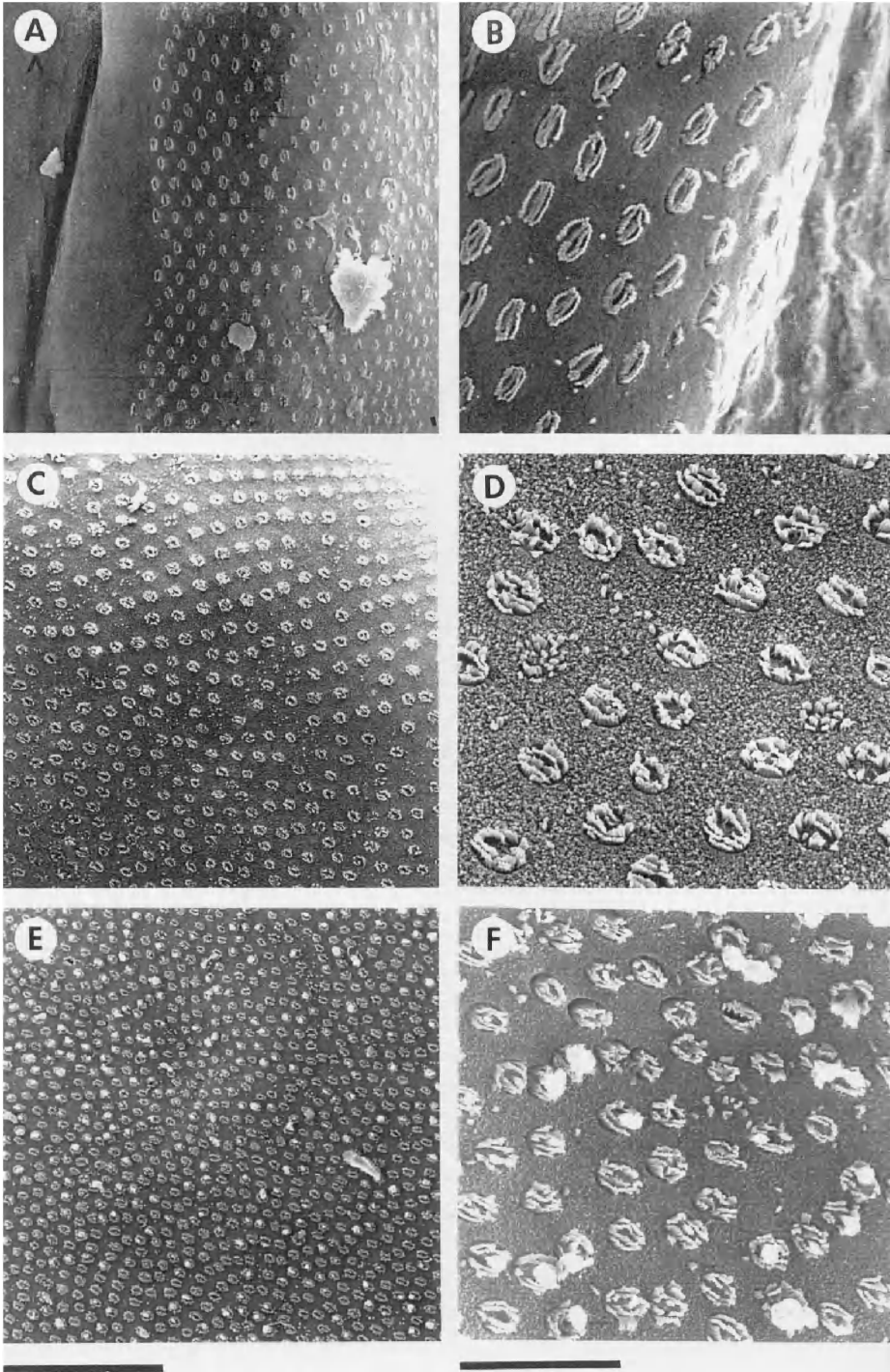


Fig. 6. *Spiochaetopterus*. Morphology of secretory pores of three temperate species. A and B: *S. solitarius*; (from Port-Vendres harbour): anterior (A) and posterior (B) boundary of the crescent. C and D: *S. costarum* (from Galicia) displaying the most regular pattern of pore distribution. E and F: *S. oculatus* (from Virginia) with the most disordered pattern of pore distribution. The scale bars have the following values (μm): A, C and E: 48; B, D and F: 12.

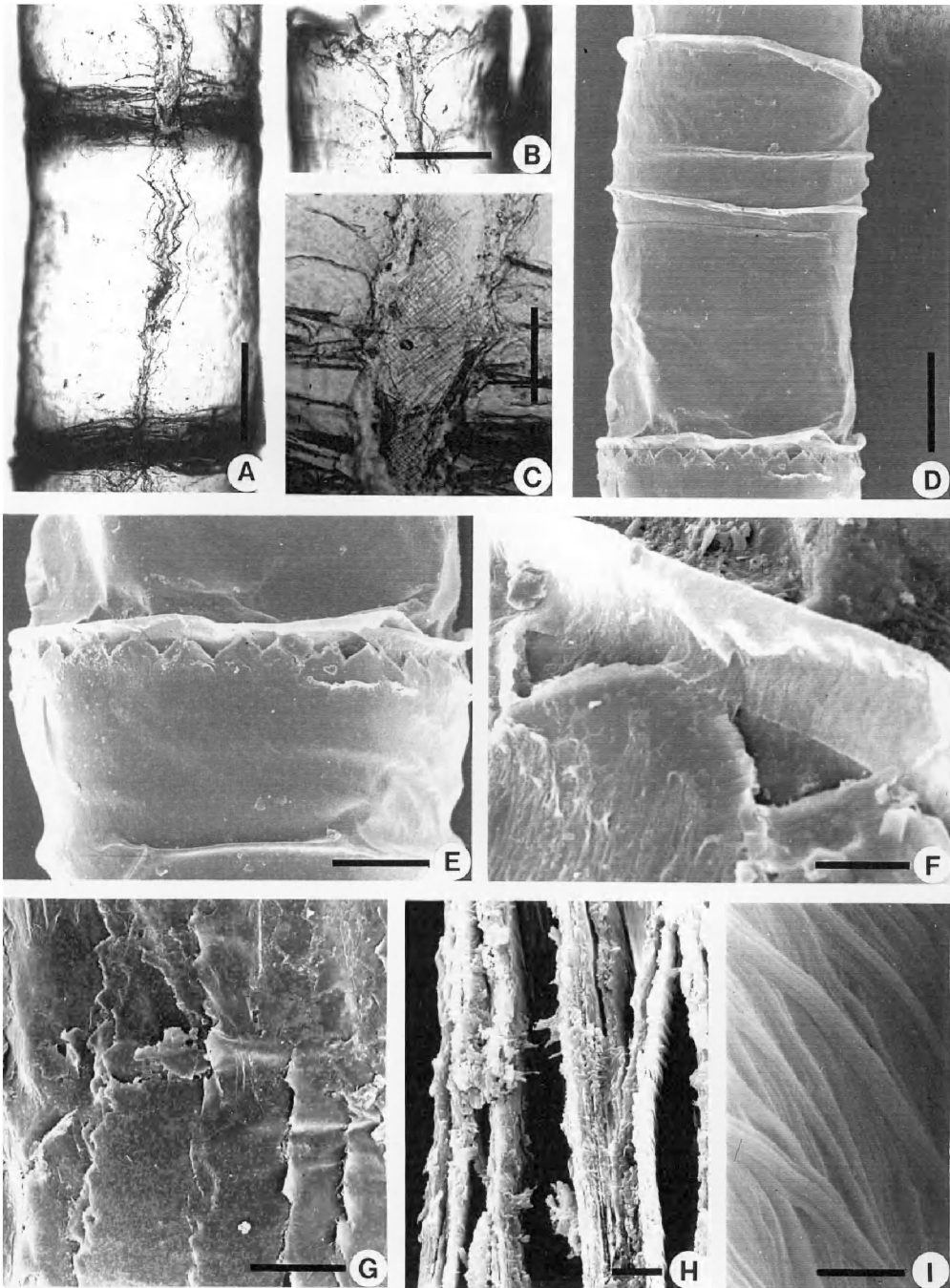


Fig. 7. *Spiochaetopterus costarum*: structure of the tube (specimens from Galicia). A: part of a tube between two consecutive constrictions showing a lengthwise serrated tear. B: cross- and lengthwise serrated tears. C: focus on the first layer secreted after rupture of tube wall. This layer is formed with two groups of fibers, each group with specific direction and an angle close to 90° between the two directions. D: part of the tube built after the circular tear marked by the series of teeth. E and F: detail of the preceding at the level of the discontinuity. G: line of lengthwise tears. H: cross section of tube wall with several partly separated layers. I: oblique fibers of an elementary layer. The scale bars have the following values (μm): A: 480, B:480, C:240, D:480, E: 240, F:48, G: 200, H: 8, I: 2.5

the horizontal ventral edge (h.v.e. in Fig. 2). Consequently, the ventral part of the upper plane is oblique in this species.

Detailed examination of the morphology of the specialized setae on A4 has made possible identification of characteristics which I consider useful as specific determiners. These characters are based on the relative size of several parts and also on the asymmetry of the head. They are used in the key of species based on A4 morphology (subsequent section).

The position of the A4 setae in the parapodium is perfectly determined. Observed on *S. costarum* and controlled on other species, the specialized seta is in a precise position: it is in an external position inside the bundle, and is therefore the most lateral; the classic lanceolated setae being close to the median dorsal axis, or, if present on the ventral side of A4 seta, are not so numerous as on median dorsal axis. The dorsal side of the specialized seta faces the ventral and posterior side of the body. The ventral side of the seta faces the ciliated furrow on the dorsal axis of the body and the fore part. Accordingly, the direction of the ventral face is not exactly perpendicular with the longitudinal axis of the body (angle varying from 90 to 60°). This seta is asymmetric and the most marked lobe with the serrated upper ridge is in an outer position. From only one seta, it is possible to determine its position on the right or left of A4 segment. These features, observed also on *S. solitarius* and *S. oculatus*, seem common to the genus and relate to the behaviour of the animal in its tube (BARNES 1964, 1965).

The tubes of Chaetopteridae are structures that reflect the behavior of the animals (BARNES 1965) and probably their anatomy as well. For instance, the length of the joints between articulations may be related to the length of the ventral shield, or to the distance animals are able to throw out the opening for building a new section. The directions of deposited layers may also be related to the movement of the animal when secreting the tube (see for instance BARNES 1965: 224 fig. 4F).

On *S. solitarius*, BHAUD & al. (1994) described the transverse serration at the tube opening and also transverse serrations further down the tube, representing previous tube openings. This pattern of serrations is also observed on tubes of *S. costarum* (Fig. 7D-F). In this species there is another clearly visible longitudinal rupture which runs lengthwise following approximately the same meridian (Fig. 7A-C). It is formed by one or several series of parallel indentations which always occur in pairs because they are the result of the rupture of some or all of the wall layers. This rupture pattern is related to the body growth in the width of the tube and not the result of the action of A4 specialized setae because the rupture line is external, and the specialized seta cannot act

externally. The edge of the lips is serrated as in the first type but the depth of the serration is small. The serration appears smaller than first type and the angle between the two directions of the lines of ridges is constant. These directions are close to the ones formed by fibers of two successive layers (Fig. 7G-I) and rupture lines are probably the mechanical result of deposition of successive layers by oblique movement of the animal. Another feature of the tube of *S. costarum* is related to the independence of different secreted layers. A tangential view close to a cross section illustrates this well (Fig. 7G-I). Four successive layers are visible. The innermost layer which is also the most recently secreted, has just been cut across: the teeth are regularly formed. An older edge of tube curling outwards, has imperfect serration.

The morphology of the tube of *S. oculatus* ($d = 0.80-0.85 \mu\text{m}$) indicates multiarticulation with alternation of homogeneous zones and joints (or rings); the circular rings are slightly inflated, separated by a zone with an approximately constant diameter; the length between two successive joints may be equal to or smaller than the width of the tube; clear marks of layers broken lengthwise have been observed. Septa are present; they possess 1 to 4 simple perforations (BARNES 1964: fig. 2C) and also a compound perforation: a large perforation (diameter half of the one of the tube) appearing closed as by a grill of 3 bars, two in one direction and the third perpendicular to the others, giving six irregular perforations.

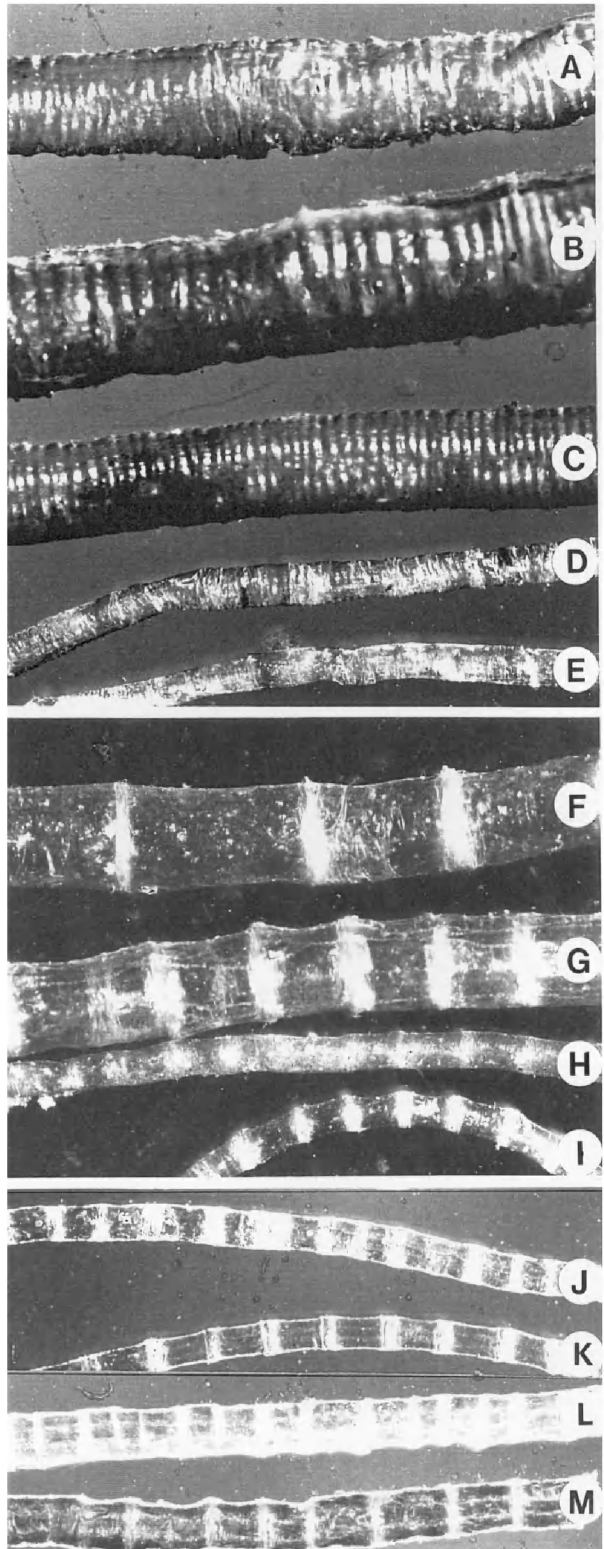
Other criteria for differentiation inside the group B were used. Examination of preserved specimens of *S. oculatus* (in formaline) revealed conspicuous ocular spots on lateral parts of the prostomium; they were clearly observed when the tentacles were directed dorsally (Fig. 5B). The relative length of segments in region A is not constant: sections between setal bundles of A7 and A8, and of A8 and A9 are longer than more anterior sections of region A (see also BARNES 1964: 399, fig. 1A). The coloration of the body shows neither violet spots (as in *S. costarum*) nor violet line (as in *S. solitarius*) laterally. The ventral side is characterized by a conspicuous blackish brown crescent at the level of A6-A7. From A1 to A6, the ventral side is marked with brown spots arranged as a net. The original description by WEBSTER (1879) may be quoted: 'the anterior region is white above; the first six segments are white below, with numerous brown specks, which often run together, forming blotches which may occupy more space than the white'. This species has been compared with *S. costarum* and *S. solitarius*. For BARNES (1964) the main difference between *S. costarum* and *S. costarum oculatus* is that the first uses only one mucus bag to collect food particles while the second uses eight or more. For GITAY (1969), *S. c. oculatus*

differs from *S. c. costarum* by only two features: feeding mechanisms and the appearance of the parapodia, and consequently is considered as a subspecies of *S. costarum* (see Discussion).

Though these three species inhabit different geographic areas (partial allopatric situation), they share distinct features in the A4 setae, the ornamentation and size of the tube. However, a detailed examination reveals significant differences.

1) The coloured double stripe on both sides of region A is missing on *S. oculatus*. These four longitudinal stripes are clearly visible on both live and alcohol-preserved specimens of *S. solitarius*. On each lateral part of A region the notopodia are limited by two undulating stripes, one dorsal and one ventral. In dorsal view, the two upper stripes approach one another at the forepart of A1, leaving the two tentacles outside. 2) The eye-spots are black, large and well defined in *S. oculatus*, but they are brown and not so well defined in *S. solitarius*. 3) The prostomium extends as far as the peristomium or is very slightly shorter in *S. oculatus* whereas in *S. solitarius* the difference between the two is more distinct. 4) The tube diameter is different (0.9 mm for *S. oculatus* and 0.5-0.6 mm for *S. solitarius*). 5) A last difference, perhaps the most marked, concerns the detailed morphology of the A4 modified setae. The oblique plane is markedly discontinuous on A4 setae of *S. oculatus* and is in a continuous curve on *S. solitarius* and *S. costarum*. In lateral view, angle ' β ' is close to 90-100° in *S. oculatus* and 140° in *S. solitarius*. In conclusion: *S. oculatus* appears to be a distinct species; its closest relative, among European fauna is *S. solitarius*.

Fig. 8. Tubes of the 5 studied species of *Spiochaetopterus*; actual width of the tubes is given in mm. A to E: two species from boreal biogeographic affinity. A-C: *S. typicus* (1.9, 2.6 and 1.6 mm, respectively) from Straume. D-E: *S. bergensis* (both 0.6 mm) from type locality. Middle part (F—>I) with the two temperate species; F-G: *S. costarum* from Sète (F), and Napoli (G) (both 1.6 mm); H-I: *S. solitarius* from Banyuls (both 0.6 mm). Lower part (J—>M) with two species morphologically close but occupying different distribution areas; J-K: *S. solitarius* from Santander (0.6 and 0.55 mm); L-M: *S. oculatus* from Virginia coast (0.9 mm). Note difference between undulated wall of *S. typicus* and *S. bergensis* and the annulated tube of other species. Tubes were grouped in three lots for photographs as follows: A to E, F to I and J to M. From one lot to the others scale is approximately the same.



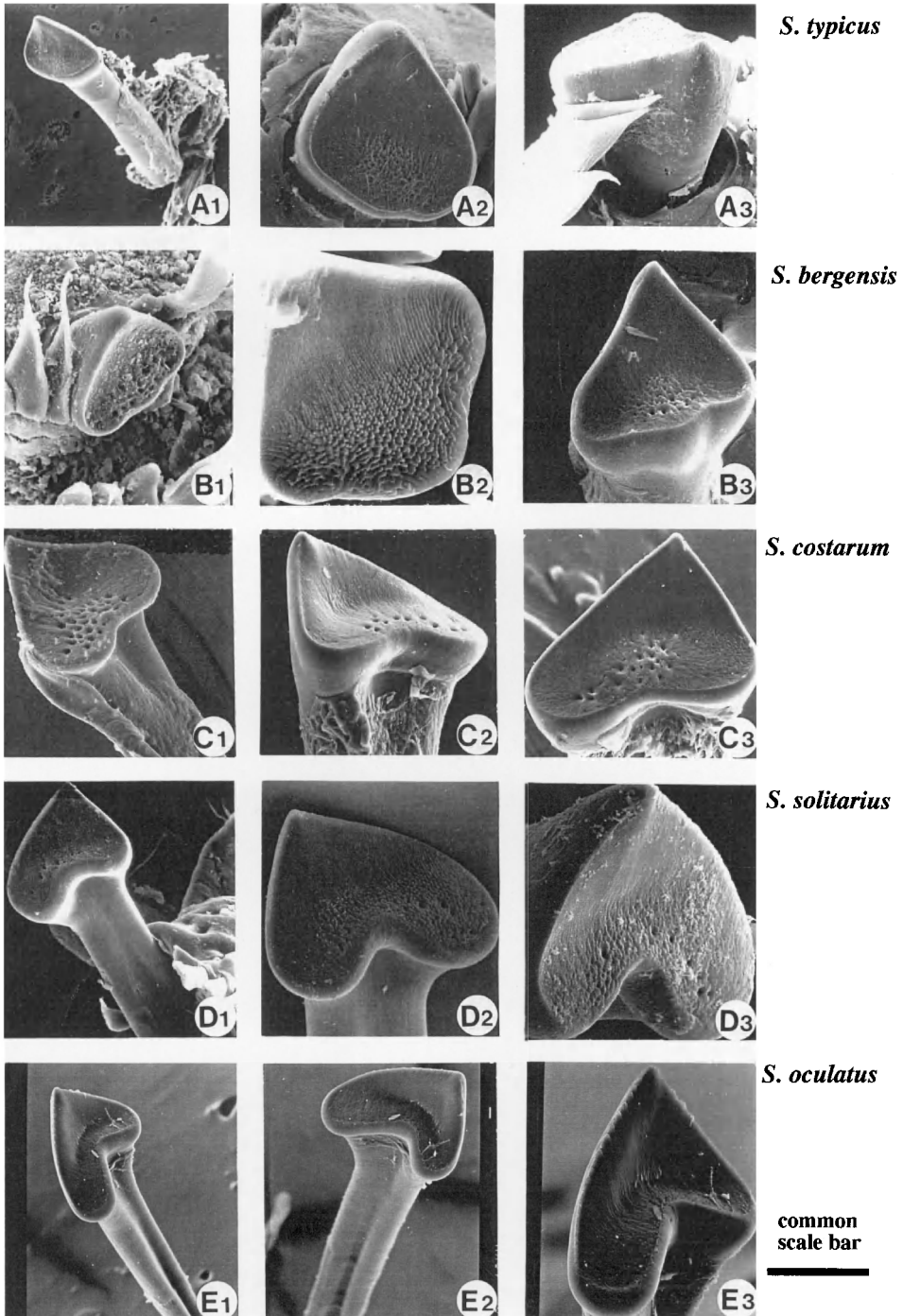


Fig. 9. SEM photographs of specialized setae of A4 in the 5 studied species of *Spirochaetopterus*. A: *S. typicus* from Leneffjord ; B: *S. bergensis* from type locality; C: *S. costarum* from Sète; D: *S. solitarius* from Port-Vendres Harbour; E: *S. oculatus* from Virginia coast. A-B: northern species; C-E: southern species. For *S. oculatus* note difference between this SEM observation and original drawing in WEBSTER (1879, plate VIII, fig. 102). The common scale bar has the following values (μm): A1: 140, A2 and A3: 70; B1: 40, B2: 20 and B3: 30; C1: 80, C2 and C3: 70; D1: 20, D2 and D3: 10; E1 and E2: 100, E3: 60. The three figures for each species are in the most cases of the same chaeta, allowing to link aspect change to orientation of the seta.

DISCUSSION

Link between TEM and SEM

After observation of the ventral shield of these five species, I attempt to understand how the pictures of external surface obtained by SEM may be included in the context of results of cross sections of integument through TEM observations. The integument of polychaetes is usually a simple or pseudostratified layer of squamous, cuboidal, or columnar cells overlain by a cuticle. This cuticle is frequently penetrated by microvilli from the epidermal cells. These cells rest on an extracellular matrix (GARDINER 1992 and RICHARDS 1984 for Polychaeta in general; WELSCH & al. 1984, STORCH & WELSCH 1970 and STORCH 1988 for Chaetopteridae). Available observations were based on examination by TEM of cross sections of the outer body wall. The locations of the sections were not given and, accordingly, doubt remains about the accuracy of the correspondence SEM-TEM given here. The following comments concern pictures of the ventral shield devoted to secretion. In the five species studied, this area appears more or less regularly pierced with pores. In four species (*S. typicus*, *S. solitarius*, *S. costarum*, *S. oculatus*), all pores are fully developed. The opening is lined with two rows of elongated elements which are classed as microvilli (Fig. 3E-H; Fig. 4D, E; Fig. 6A-F). For *S. bergensis*, several steps are detected in the formation of openings. The future location of some pores is indicated by a bright surface (high electronic load); other pores are simple slits; and in a third stage pores are clearly open but not surmounted by microvilli; they are very elongated, resembling button-holes. For all species, pores suggest the presence of cells located, in the majority of polychaetes, under the surface cuticle but in chaetopterids, cells are exposed directly to the exterior since a cuticle is absent (BROWN & MCGEE-RUSSELL 1971). These cells should be the large epidermal cells with one central huge vacuole and numerous microvilli on the upper part (STORCH & WELSCH 1970). This general structure is modified in the secretory area, with differentiation of two kinds of microvilli differing in size. Microvilli of the central part of the epidermal cells are better developed and line the tear of the cell through which the vacuole empties. Each pore corresponds to one epidermal cell. In *S. bergensis*, the cuticle seems more important and microvilli surrounding the pores either do not extend beyond the upper level of the pores, or are absent. A last question concerns cell renewal. The cells may be replaced *in situ* or there may be a shift of secretory cells from the deep furrow observed in the anterior part of the secretory shield of several species. The latter would imply a differentiation in development of the pores along the shield. However, the homogeneous appearance of openings on the entire surface of the secretory shield,

without antero-posterior differentiation, suggests a replacement of epidermal cells *in situ*. The pore edge, formed by several rows of microvilli, is probably continuous.

Variation of tube size in time and space

In this family, the tubes are frequently mentioned in the literature, but they are often empty or contain a poorly fixed mass of tissue in which it is difficult to discern the different parts of the animal and thus to identify the specimen with certainty. The size, ornamentation and structure of the tube wall have never been used in identification. First one must know what confidence to place in measures of the size of the tubes; this leads to a study of the modalities of variation in tube size both in time and space. If it is possible to show that definitive size for each species is reached early, this size could be used as a characteristic of the species. My own observations suggest that this is possible.

1) *S. solitarius* collected at several different seasons of the year in the Banyuls area show no variation in tube size. This is also true for tubes of other species as *S. costarum* from all year round observations by LOPEZ-JAMAR (1982, 1985) and REY & MORA (1984).

2) Direct observations also indicate that the definitive tube size is reached early. In August 1971 *S. costarum* larvae with metamorphosis in progress were obtained, enabling measurements of the diameter of the first tube built. This tube is very clear and transparent; it was 5.5 mm long for the body of 4.5 mm long. The tube diameter reached 900-940 µm. Remembering that the adult tube size ranges from 1 to 1.7 mm, the tube diameter of the youngest individuals approaches the lower limit of the range given for adult tubes. Moreover, this size is already larger than that of the tube of *S. solitarius*, which is close to 0.6 mm. Observations are rare for boreal species possessing the largest tubes. It is likely they need more time to reach definitive size. However, the following argument casts doubt on this.

3) There is a positive relation between size of larva and size of adult tube. To the tube of the most common species: *S. typicus* (3 mm width SARS 1856, 2 to 5 mm width GITAY 1969), *S. costarum* (1 to 1.5 mm width GITAY 1969, 1-1.7 mm width REY & MORA 1984) and *S. solitarius* (0.6 mm width BHAUD & al. 1994) correspond planktonic larvae of different widths: 1200 µm for *S. typicus* (MILEIKOVSKY 1967), 500 µm for *S. costarum* (BHAUD 1966) and 400 µm for *S. solitarius* (BHAUD, unpublished). Remark: from references in GITAY 1969, one cannot formally conclude that figures concern body or tube; however this author gives for *S. bergensis* same size for body and tube; this is probably the same for other species which is rational from observations on preserved specimens in tubes.

4) Notwithstanding the above observations, it is possible to collect tubes of different sizes. These might be the tubes of the same species at different stages of development. This is a pertinent question especially when considering boreal species, which may have large tubes, given that the construction of the tubes must take a considerable amount of time. *S. typicus* could give rise to this situation although it has yet to be observed. For temperate species a mixed collection implies the presence of two partially sympatric and syntopic species. Two examples show that the difference in size is species-specific and not linked to ontogenesis. Among the large number of *S. solitarius* collected in the Port-Vendres Harbour, I found a very small number of larger filled tubes. Animals of these larger sized tubes have been carefully checked; they belong to *S. costarum*. The same thing occurred in a sample kindly provided by E. Lopez-Jamar from the Bay of La Coruña (Atlantic coast). Most of the worms (500 tubes or more with animal inside) belong to *S. solitarius* (tube diameter close to 0.6 mm). However, 24 tubes had a larger diameter (1.4 mm), and examination indicated that these belonged to *S. costarum*, recognizable by violet spots on A and the absence of coloured stripes. In conclusion, size is a good criterion for use in relation to small chaetopterids.

5) As a last test, the size of different tubes from geographically different sites belonging undisputably to the same species was compared: *S. solitarius* from Santander harbour (N Spain, Atlantic coast) and the Bay of La Coruña (NW Spain, Atlantic coast), Blanes (Spain, Mediterranean Sea) and Banyuls (French Mediterranean coast) and ones of *S. costarum* from Arcachon beach (Atlantic Ocean), Galician Rias Bajas (Spain, Atlantic coast), Banyuls and Naples (Mediterranean Sea). The size of the tubes does not appear to differ between populations of the same species.

6) Observation of sexual maturity may help to decide on the definitive characteristics of observed tube diameter and width body size. Sars (1856) noted in several specimens, from 18th - 19th segments a lateral bag with an irregularly rounded shape and with a red-cinnabar color. Each bag is full with a large quantity of eggs which appear immediately under the tegument. I observed also signs of sexual maturity in *S. costarum* (reproduction in summer), *S. solitarius* (reproduction in winter) and *S. oculatus* (reproduction in spring). On specimens from Virginia, gonads are disposed in B region, on dorsal face of segments, in two bags elongated in a cross position on each side of the median axis.

Finally, these heterogeneous observations converge and suggest that the definitive tube size, in each species, is fastly reached.

Species or subspecies?

In his overview of the genus *Spiochaetopterus*, GITAY (1969), used 11 features to differentiate species. A species distinguished by at least three of the first seven features was considered as a separate species. These features were: morphology of prostomium, presence or absence of eyes, morphology of peristomium, size of grown specimens (if difference exceeds 100 %) number of middle part segments (if difference exceeds 100 %), morphology of neuropodia in B and in C parts). Three comments may be made. 1) The number of discriminatory features does not affect the validity of an identification. One character alone can be enough to retain or describe a species. It is therefore important to examine each separate character. 2) The 100 % difference in the number of segments in part B; it may be seen from Fig. 1 that this number varies from 7 to 28 (or 7 to 29 in BHAUD 1998) with a ratio 1 : 4. Following Gitay's criterion, a difference in number of B segments, of, for instance, 10 to 25 segments (variation higher than 100 %) forms a valuable character despite the fact they are placed at each end of the range of *S. solitarius*. 3) The basis for defining subspecies is not convincing. *S. oculatus* illustrates this. It was originally described by WEBSTER 1879:47, pl. 8 fig. 98-102, redescribed by HARTMAN (1945:35), and later by GITAY (1969:15). For this author a specimen distinguished by at least three of the seven most important features listed, is considered as a separate species, and specimens distinguished by any two of the same list inhabiting a part of the range of a closely related species are considered to be of subspecific rank. However, *S. oculatus* does not inhabit a part of *S. costarum* area and the rank of species is justified by the morphology of A4 seta (head, shaft and ratio t l / w s: total length/width shaft); the structure of the tube (width size, integrity of successive layers of the wall tube, organisation of septa) and by the particularly marked eyespots (Fig. 5B). Also, in contrast to the opinion of Gitay, *S. madeirensis* LANGERHANS, 1880 is herein considered as a synonym of *S. solitarius*. LANGERHANS (1880) based the separation on the latter having a cleft and bilobed prostomium. This difference has been observed several times on living *S. solitarius*, and seems to be related to muscular contraction and conditions of fixation. In addition, the number of 9-10 segments in the B region is in agreement with the range of B segments given for *S. solitarius* (Fig. 1).

CONCLUSIONS

1) *S. oculatus* is a valid species found in the western Atlantic, from Massachusetts to the Gulf of Mexico (DAY 1973). It is clearly separated from the two eastern temperate species. Currently, no single species has been

KEY TO SPECIES BASED ON THE TUBE (FIG. 8)

Results of previous observations led to create two keys for identification based on the structure of the tube and on the morphology of the specialized setae of A4. The characteristics used in the tube-based key are the ones most commonly observed, but they may not be present all along the tube length. Some tubes, more often the articulated ones (as those of *S. oculus*), may lack articulations and display a homogeneous structure on a length similar to 6 to 8 articles. In the same way, in *S. solitarius* a large portion of the tube (2.5 cm on 8.5 of the whole length) may also lack articulations. The tube of *S. bergensis* shows all transitions between a very localized, high density of pleats giving the aspect of a joint, and a smaller density of homogeneously spaced pleats. What is characteristic is the presence, in variable density, of short pleats as lengthened lens. The width measures furnished in the literature are given in Table 1. Figures are also based on my own observations. This key is based on a reduced number of characteristics: presence or absence of articulations, outline of the tube: undulating or approximately a straight line, desquamated or not, related to the possibility of recognising each layer forming the tube.

- 1A Tube not articulated 2
 1B Tube multiarticulated with alternation of homogeneous zones and joints; bamboo-like appearance: circular articulations slightly inflated, separated by region with constant diameter 3
 2A Longitudinal outline of tube with regular undulations; circular swelling continuous and developed on the whole circumference, $d = 1.6-2.6$ mm *S. typicus*
 2B Longitudinal outline of tube with external wall crumpled, irregularly pleated; with a slight roughness and marks of longitudinal tears, $d = 0.6-0.8$ mm *S. bergensis*
 3A Successive layers visible, clear desquamation at articulations; clear marks of broken layers lengthwise, $d = 1.1-1.3$ mm *S. costarum*
 3B Successive layers indistinct, numerous marks of cross incisions of the tube; $d < 1$ mm 4
 4A Length between two successive joints longer than width of tube, tube clear amber without marks of longitudinal incision; septa with 1-3 simple perforations, $d = 0.6$ mm *S. solitarius*
 4B Length between two successive joints equal or smaller than width of tube, clear marks of broken layers lengthwise, septa with 1-4 simple perforations (BARNES 1965: fig. 3E) and also a composite perforation (defined in the text), $d = 0.8-0.85$ mm *S. oculus*

KEY TO SPECIES BASED ON A4 SPECIALIZED SETAE (FIG. 9)

- 1A Upper oblique plane rhomboid; horizontal ventral edge with protuberance; cross section of shaft approximately oval or with flattened ventral face; ventral limit of upper oblique plane as simple ledge; overhang not clearly marked, horizontal ventral edge weakly protruding; oblique plane rounded-triangular (*S. typicus* + *S. bergensis*) 2
 1B Upper oblique plane clearly cordate; horizontal ventral edge incised or excavated, without protuberance; shafts grooved throughout length; ventral limit of upper oblique plane as balcony with clear overhang 3
 2A Seta large, length: 1200 μm , ventral width of head: 100-120 μm ; horizontal ventral edge evenly rounded, close to the part of a circle *S. typicus*
 2B Seta small, length: 430 μm (Gitay: 370 μm), ventral width of head: 35-40 μm ; horizontal ventral edge in three juxtaposed equal rounded protuberances *S. bergensis*
 3A Dorsal elevation of head clearly longer than side width; ventral edge of lateral side plane broken, with a distinct angle; angle β (Fig. 2) close to 90°; cross section of the head gives two planes on each side of central vertical axis; head relatively flattened (in dorso-ventral axis) *S. oculus*
 3B Dorsal elevation of head of the same size as side width; ventral edge of lateral side plane as unbroken curved line; angle β (Fig. 2) close to 120°; oblique section gives two planes on each side of large curve; head relatively thick (in dorso-ventral axis) (*S. solitarius* + *S. costarum*) 4
 4A Seta relatively short and compact, ratio t/l / ws close to 5; shape slightly curved; maximal length: 300-350 μm *S. solitarius*
 4B Seta slender and straight, ratio t/l / ws close to 8; maximal length: 650-700 μm *S. costarum*

NB. t/l : total length; ws : width of shaft

found to be common to the two sides of the Atlantic and thus none can be considered as pan-Atlantic. *S. solitarius* also appears as a valid species found in the eastern part of the Atlantic Ocean (northern coast of Spain) and in the Mediterranean Sea in a relatively restricted area (French and Spanish Catalan coasts), the specific location being unusually limited. A new population of *Spiochaetopterus sp* was sampled in the mouth of St Lawrence River, E Canada, by P. Brunel from Montreal, GIROQ (Groupe Interuniversitaire de recherche océanographique du Québec). I isolated specimens from this collection. These specimens deserve a special study because a short observation of tubes (with rings and articulations) does not permit these specimens to be assigned with any boreal species dealt with in the present work (study in progress).

2) This study demonstrates that the morphology of specialized setae on A4, already used as an element of diagnosis at the genus level for a local fauna (KUDENOV 1975), provides a precise set of characters at the specific level. These setae are not taken into account in the Glossary of Polychaete terms (MIKKELSEN & VIRNSTEIN 1982) in which only one term: 'cultriform' refers to the family Chaetopteridae. I propose for A4 seta 'acicular seta with obliquely truncated distal end' to describe a very stout, projecting seta in a fascicle of delicate setae, and frequently with an enlarged diameter at the distal end. For a precise description of these setae, observations by compound microscope are insufficient; SEM must be used.

3) The relatively well-known species of the genus *Spiochaetopterus* in the Atlantic-Mediterranean area are five in number. Two distinct groups appear; their difference is reflected geographically: boreal on the one hand and Mediterranean-Atlantic temperate on the other; and also morphologically in the appearance of the specialized setae of segment 4. Within each group the main difference is in the size at maturity. Differences between two partly sympatric temperate species (*S. solitarius* and *S. costarum*) were established based on differences observed in sexually mature specimens of both species.

4) SEM observations confirm the structure of the integument as described without cuticle at least in four species; some doubts remain for *S. bergensis*. The secretory function is located in a relatively small part of the ventral shield easily recognizable by macroscopic observation. Distance between pores, shape and size of the pores and disposition of villousities may be valuable species-specific features.

5) Finally, biogeographic distribution of several species may be corrected. Distribution of *Spiochaetopterus costarum* is not so spread as generally said: Pacific: W Canada to S California, Japan; Indian Ocean: Madagascar; Atlantic-Mediterranean area: E to W N Atlantic, Mediterranean (BLAKE 1996; DAY 1967); in fact, this

species seems limited to the east part of Atlantic Ocean; in addition to this paper, personal observations of Pacific species did not furnish the least argument on the presence of this species in the Pacific Ocean. In his 'Monograph on the Polychaeta of Southern Africa' DAY (1967) questionably noted the presence of *Spiochaetopterus typicus*. The presence of this species (only doubtfully put forward) is unlikely from a morphological point of view: the region B with a number of segments higher than 2 ('two to ten segments') is not characteristic of *S. typicus*. In the same way, *S. typicus* has been reported in Madeira with synonymy of *S. madeirensis* (NÚÑEZ & TALAVERA 1995); but as said previously, 10 segments in region B seems to be a characteristic of *S. solitarius* rather than of *S. typicus*. Last, BELLAN (1960) reported *S. typicus* from Portuguese coasts; however justifications are not given. Consequently, the evidence of the presence of *S. typicus* in temperate waters is not secured and the biogeographical area of this species is presently reduced to northern areas. ELIASON (1962) described a 'forma minor' of *Spiochaetopterus typicus* from Skagerrak (300-680 m depth) with a tube diameter of 0.5-1 mm. This is without doubt *S. bergensis*.

Table 1 which compares Atlantic-Mediterranean species in the genus *Spiochaetopterus*, displays several constant characteristics. The number of segments in region A is 9 or exceptionally 10 in *S. solitarius* and *S. typicus*. These figures deserve further consideration. In *S. solitarius* I on occasion found 10 segments in region A. This figure is unusual and has only been observed twice among 90 specimens in one study and 4 times among a supplementary 68 specimens. For *S. typicus*, SARS (1856) specified that 'la partie antérieure du corps se compose de 10 segments dont le premier est formé par le lobe capital (la tête rudimentaire) avec la proéminence labiale; et 9 autres segments qui ont des tubercules pédals...' [the front part of the body is made up from 10 segments, of which the first is formed by the capital lobe (the rudimentary head) with labial protuberance; and nine other segments with setigerous parapodia]. It is clear that in this species the number of segments in region A is 9 as it is for most of the species in the *Spiochaetopterus* genus. The number of neuropodia in segments B1, B2 and C is respectively: B1: only one ramus (with sometimes 2 in *S. typicus*), B2: 2 rami (with only one in *S. bergensis*), C: always 2 rami. In A4 the specialized setae have an enlarged head, obliquely truncated in a triangular plane of which the tip is the upper tip of the seta. There is only one specialized seta per parapodium; they are however decaying and when the shedding of the old seta is delayed for some reason, it is possible to see two different sized modified setae. Size and number of uncini are not included in this table. Uncini, present on median and posterior region,

Characters Species --->	<i>S. typicus</i>	<i>S. bergensis</i>	<i>S. costarum</i>	<i>S. solitarius</i>	<i>S. oculatus</i>
Worm width (mm) (outside the tube and in live)	this feature is not viable because of deformation of the body; if available material is given after dissection of preserved body from tube, width tube may be used directly (see text in § Discussion: variation of tube size).				
Worm length (mm)	175-200 ⁴ 100-300 ¹	>30 ¹	50-60 ⁵ c: 80 ¹	20 mm	30-60 ⁸
Size ratio pro/peri	pro = peri	pro < peri	pro = peri	pro < peri	pro = peri
Eyespots color	-	-	+ black	+ black	+ black very marked
No. set. A	9 (10) ⁴	9 ¹	9 ¹¹¹	9 (10) ¹¹	9 ³
No. set. B	2 ⁴³	2 ¹³	>30:35-54(N=35) ³ >30:34-54(N=72) ¹¹	>2 <30:7-28 (N-55) ³ >2 <30:6-31 (N-335)11	21-74 (18-37) ⁸ 20-73 ⁷ 14-23 ³
No. set. C.	130-140 ⁴	17 or more ¹	variable ¹ >60 ⁵ >18 ³	9-26 ³	large number, variable ⁸ >38
Dorsal cupules	B1 - B2 ⁴	?	B2 ⁷	B2 ⁹	B2-B14, varies ⁸
Modified setae A4 (Fig 3) Shape of upper oblique plan Number Color	not cordate ³ rounded-triangular with slightly raised edge on broadest side 1(2) dark amber		broadly cordate ³ ; sinus of the ventral curve not deep; upper plane oblique 1 ¹ 1 ³ yellow to amber	clearly cordate ³ ; ventral curve very marked; upper plane oblique 1(2) ³ yellow to amber	clearly cordate ³ ; ventral curve very marked; upper plane vertical 1 (2) ³⁸⁹ yellow to amber
No. rami: Notopodia B Neuropodia B1 B2 Notopodia C Neuropodia C	2 - 3 1 - 2 2 1 2	3 1 1 1 2	3 1 B2 to last: 2 1 2	3 1 B2 to last: 2 1 2	3 1 B2 to last:2 1 2
Color in life peristomium dorsum A VS-6 B - C eggs	rust - brown yellow - white light. brown black-brown red ⁴	? brown reddish ? ?	brown violet violet spots rose / white greenish ⁵ ?	pale pinkish? violet stripes pinkish: lt. grey ? pale (immature)	? white/br. specks brownish purple yellow-white:lt br
Tube width (mm)	2 - 5 ¹ 1.6-2.6 ³ 2.5 ⁴	0.5 - 1 ¹ 0.6 ³	1-1.5 ¹ 1-1.7 ² 1.6-1.7 ³ 1.2 - 1.4 ⁹	0.6 ³ 0.6-0.8 ¹⁰	0.5-0.6 ⁷ 0.7-1.2 ⁸ 0.9 ³
Tube length	750-330 ⁴	= or > 70 ¹	= or > 250 ⁹	75-110 ¹⁰	80-120 (500) ⁸
Tube outline	regularly wavy, without 'rings'; elementary undulation shorter than width of tube		ringed or 'jointed', not wavy; rings at interval = or > width of tube		
Tube septa	?	?	+ ⁹	+ ¹⁰	+ ⁸³
Type locality	Helle, W Norway	Sörfjorden, W Norway	Naples, Italy	Santander, N Spain Atlantic	Northampton Co., Virginia, USA
Depth range	40-50 fms ⁴	400 m ¹ 640 m ⁶	4-5 m ⁹	2-7 m ¹⁰	Low water ⁷ Shallow Subtidal ⁸
Substratum	fine mud ⁴	fine sand ¹	fine sand and silt ⁹	fine sand slightly muddy and dead Posidonia ⁵	sand ⁷ and mud ⁸
Distribution	boreal Atlantic	boreal Atlantic	temperate + sub-tropical; Atl+ Med.	temperate: NW Mediterranean (France+Spain) and Atl (NW Spain)	temperate: USA East Coast, from Massachusetts to the Gulf of Mexico (DAY 1973)

Table 1. Summary of the main features observed on five species in the genus *Spiochaetopterus* from the Atlantic Mediterranean area. This table refers to Fig. 2 and Fig. 8 for the morphology of A4 specialized setae, and to Fig.9 for the features of the tube. References: ¹ GITAY 1969; ² REY & MORA 1984; ³ Present paper; ⁴ SARS 1856; ⁵ CLAPARÈDE 1868; ⁶ KIRKEGAARD 1961, as *S. typicus*; ⁷ WEBSTER 1879; ⁸ BARNES 1964; ⁹ BARNES 1965; ¹⁰ BHAUD & al. 1994; ¹¹BHAUD 1998. A, B, C = anterior, middle and posterior regions of body; A4, B1, B2, etc. = 4th, 1st, 2nd, etc. setiger of named regions. Atl, Medit = Atlantic and Mediterranean; Pro = prostomium; Pe, Peri = peristomium; VS = ventral shield of A.

belong to two morphological types in this family: rectangular and triangular; (type I and II, respectively); they may bear distinct relatively few teeth (close to 10-15, type I) or the teeth may be small and numerous (> 25, type II). These plates, in all examined species of *Spiochaetopterus* belong to the triangular pattern with a high number (often higher than 25) of very small teeth. Like for other setae, uncinal plates are regularly decayed and replaced; their size and number of teeth vary in one individual in terms of the location of the observed segment and probably also within each torus, in terms of the position of the plate. It is too early to use these plates for differentiation of species. I did not include the morphology of setae in C region which is given, in the genus *Spiochaetopterus*, as lanceolated (FAUVEL 1927), or hastate setae (DAY 1967); however, BERKELEY (1927), BERKELEY & BERKELEY (1952) noted that *Leptochaetopterus pottsi* (= *Telepsavus* sp) carried delicate capillary setae. Fuller information is needed. Last, body size (measured outside the tube) and on live specimens is not a viable feature because the body is easily deformed; size of tube must be preferred.

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