

**Morphology, ecology and juvenile development of
Cossura pygodactylata Jones (Polychaeta, Cossuridae)
in Arcachon Bay, SW France, with a reassessment
of the geographical distribution of *C. pygodactylata*
and *C. soyeri* Laubier**

Guy BACHELET * & Lucien LAUBIER **

* Centre d'Océanographie et de Biologie marine
CNRS & Université de Bordeaux I
2, rue du Professeur Jolyet
33120 Arcachon, France

** Laboratoire de Physiologie des Etres Marins
Institut Océanographique
195, rue Saint-Jacques
75005 Paris, France

ABSTRACT

During a quantitative survey of subtidal infauna in Arcachon Bay (Bay of Biscay, NE Atlantic), more than 1,000 specimens of *Cossura* were collected in two muddy, shallow channels of the bay. Comparison of these specimens with the types of *C. pygodactylata* Jones, 1956 and *C. soyeri* Laubier, 1963 showed that the cossurids from Arcachon were almost identical with the former species. Only the noto- and neurosetal bundles of the first biramous setigers tended to be more spaced in the french specimens than in the holotype of *C. pygodactylata*; this minor divergence does not justify the erection of a new species. Examination of many juveniles, some of them being as small as four setigers, allowed the description of post-settlement juvenile development. During a two-year survey in the Courbey channel, the highest densities (ca. 1,500 ind./m²) were recorded in April-May. As noted by several authors, there are few useful taxonomic characters in the genus *Cossura*. Specimens are often collected as anterior fragments, whereas species identification necessitates an examination of different regions of the body. For example, the two closely related species *C. pygodactylata* and *C. soyeri* differ only by the number of thoracic setigers and the structure of the pygidium. Re-examination of several specimens previously identified as *C. soyeri* showed that some of them were actually *C. pygodactylata*. The geographical distribution of *C. pygodactylata* is extended from the Pacific coast of North America to both sides of northern Atlantic, whereas *C. soyeri* appears to be restricted to the Mediterranean Sea and the northern Gulf of Mexico.

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RÉSUMÉ

Morphologie, écologie et développement juvénile de *Cossura pygodactylata* Jones (Polychaeta, Cossuridae) dans le bassin d'Arcachon, SW France, et mise au point sur la distribution géographique de *C. pygodactylata* et *C. soyeri* Laubier

Lors d'une étude quantitative de l'endofaune subtidale du bassin d'Arcachon (golfe de Gascogne, Atlantique NE), plus d'un millier de spécimens appartenant au genre *Cossura* ont été échantillonnés à faible profondeur (3 à 5 m) dans les fonds vaseux de deux chenaux. La comparaison de ces spécimens avec les types de *C. pygodactylata* Jones, 1956 et de *C. soyeri* Laubier, 1963 a montré que les cossuridés d'Arcachon sont identifiables à la première espèce. Seuls les faisceaux de soies des noto- et neuropodes des premiers sétigères biramés ont tendance à être davantage espacés chez les spécimens arcachonnais que sur l'holotype de *C. pygodactylata*; cette divergence mineure ne justifie pas la création d'une nouvelle espèce. L'examen d'un grand nombre de juvéniles, à partir de stades à quatre sétigères, a permis la description des premières phases du développement benthique. Au cours d'un suivi de deux années dans le chenal du Courbey, les densités les plus élevées (environ 1500 ind./m²) ont été relevées en avril-mai. Ainsi que l'ont noté plusieurs auteurs, peu de critères taxonomiques sont utilisables dans le genre *Cossura*. Les spécimens sont souvent récoltés à l'état de fragments antérieurs, alors que l'identification spécifique nécessite l'examen des différentes parties de l'animal. Ainsi, les espèces voisines *C. pygodactylata* et *C. soyeri* diffèrent seulement par le nombre de sétigères thoraciques et la structure du pygidium. Un réexamen de plusieurs spécimens préalablement identifiés comme *C. soyeri* a montré que certains d'entre eux étaient en réalité des *C. pygodactylata*. La distribution géographique de *C. pygodactylata* est étendue de la côte Pacifique nord-américaine aux deux côtés de l'Atlantique Nord, alors que *C. soyeri* paraît limitée à la Méditerranée et au nord du golfe du Mexique.

INTRODUCTION

Cossurids are small thread-like polychaetes characterized by a single median tentacle inserted on the dorsum of an anterior setiger. Other characters of the family Cossuridae Day, 1963 include a prostomium without appendages, reduced parapodial lobes, parapodia uniramous on one or more anterior segments or entirely biramous, all setae simple, and a pygidium with anal cirri (see EWING, 1987, for a revised diagnosis of the family). The family includes two genera, *Cossura* Webster & Benedict, 1887 with 17 species and *Cossurella* Hartman, 1976 with five species. The genus *Cossurella* is characterized as having a body distinctly divided into two regions and, in addition to simple setae, a single acicular seta in each ramus of the posterior parapodia (GARDINER & WILSON, 1977; EWING, 1987). Although FOURNIER & PETERSEN (1991) distinguished three body regions, there are no clear-cut divisions along the body in *Cossura* species, and all parapodia have only simple capillary setae.

As noted by DAY (1967), there are few useful taxonomic characters which may be used for identifying cossurids. The principal diagnostic features are the number of asetigerous peristomial segments, the segment of insertion of the mid-dorsal tentacle, the number of uniramous setigers, the types of setae, the number of thoracic setigers and the structure of the pygidium (EWING, 1984; FOURNIER & PETERSEN, 1991). Unfortunately, the number of peristomial segments appears to be an artifact of fixation, biramous setigers have been interpreted as uniramous by several authors when the bundles of setae were close together, and the posterior end is often missing (FOURNIER & PETERSEN, 1991; see below). The most important specific character in *Cossura* is the setiger from which the single dorsal appendage arises; although a greater or lesser part of the tentacle tip may be lost during collection and sieving, the entire structure is never broken off (THULIN, 1921; LAUBIER, 1963). FOURNIER & PETERSEN (1991) also found that the number of thoracic setigers might be, in spite of some local variation, species-specific. Taxonomic difficulties are not the unique problem in cossurids. Although occurring from shallow waters to abyssal depths, they are often recorded in low numbers and on a single occasion within a geographical area. Therefore, little is known about their ecology and population dynamics.

During a quantitative survey of macrobenthic assemblages in subtidal areas of Arcachon Bay, SW France, several specimens of *Cossura* sp. were collected in two muddy, shallow channels of the bay (DE MONTAUDOUIN, 1988). Later, while processing a collection of polychaetes collected during a two-year study of bivalve recruitment in one of the above channels (MADANI, 1989), one of us (GB) found more than 900 extra specimens of *Cossura*. These worms were tentatively identified as *C. soyeri* Laubier, 1963, which was the most commonly cited species in European temperate waters. However, comparison of our specimens with the types of *C. soyeri* Laubier and *C. pygodactylata* Jones, 1956 showed that the cossurids from Arcachon should be referred to the latter species. According to FOURNIER & PETERSEN (1991), both species belong to a group of *Cossura* with the dorsal branchial filament arising from the second setiger, but differ by the number of thoracic setigers (17-19 in *C. pygodactylata* vs. 30-31 in *C. soyeri*) and the shape of the pygidium.

In the present paper, we describe adult and juvenile stages of *C. pygodactylata* from Arcachon. To clear up the confusion between *C. pygodactylata* and *C. soyeri*, specimens from different collections are reexamined and the geographical distribution of both species is reassessed.

MATERIAL AND METHODS

A total of 1,100 specimens of *C. pygodactylata* were obtained from mud in two channels, Courbey and Cousse, of Arcachon Bay (44°40'N, 1°10'W), at depths of 3-5 m below mean low water. In the Courbey channel, three stations were sampled monthly from February 1985 to January 1987, using a 225 cm² Ekman grab. Three replicate box-cores (depth of penetration generally 15 cm) were taken at each station, thus covering a total surface of 0.2 m² at each sampling date. Samples were fixed in 4 % buffered formaldehyde solution, then gently sieved through a 0.2 mm screen, transferred to 70 % alcohol and sorted after staining with Rose Bengal.

Samples were also collected in February 1988 in the Cousse channel and in a single station of Courbey channel. At both stations, six samples were taken using an Ekman grab. The content of four grabs was sieved on a 1.0 mm mesh; three 8 cm² cores were taken in each of the two other grabs and washed through sieves of 1.0 and 0.1 mm mesh opening. Samples were processed as above.

Specimens were studied using Wild stereomicroscope and compound microscope. Drawings were made by means of a camera-lucida drawing tube; measurements were made with an ocular reticule.

Specimens for SEM were transferred in glutaraldehyde, critical-point dried in carbon dioxide and individually mounted on aluminium stubs. After coating in gold, the specimens were viewed and photographed with a Jeol JSM-840A scanning electron microscope using an accelerating voltage of 10 kV.

Cossura pygodactylata Jones, 1956

Figs 1-4

Cossura pygodactylata Jones, 1956: 127, fig. 1a-f. — REISH, 1958: 53, fig. 1. — LAUBIER, 1963: 840 (in key), 841 (in table). — HARTMAN, 1969: 273, figs 1-3. — FAUCHALD, 1972: 207 (in key). — ORENSANZ, 1976: 5 (in key). — FOURNIER & PETERSEN, 1991: 66, table 1.

Cossura longocirrata — BERKELEY & BERKELEY, 1956: 544, fig. 6. — ? BANSE, 1963: 204. — GIBBS, 1969: 314, table 1, 319, table 3, 324. — CURTIS, 1977: 31; 1979: 2. — ? RALLO, 1988: 137, 140, fig. 2 (*non* Webster & Benedict, 1887).

Cossura, nr. *longocirrata* — HARTMAN, 1954: 11, 15.

Cossura candida — HARTMAN, 1955: 44, *pro parte*.

Cossura soyeri — GARDINER & WILSON, 1977: 169, fig. 4a-c. — ? DAUVIN & GENTIL, 1980: 8. — BANSE, 1981: 633, *pro parte*. — HOBSON & BANSE, 1981: 55. — ? AGUIRREZABALAGA, 1984: 122 (in table). — ? AGUIRREZABALAGA *et al.*, 1984: 103. — ? SOLA & IBAÑEZ, 1986: 172, 173, 175 (in tables) (*non* Laubier, 1963).

Cossura sp. — DE MONTAUDOUIN, 1988: 18.

MATERIAL EXAMINED. — Eastern North Pacific: San Francisco Bay, off Point Richmond, California, mud, 16 Apr 1955, one complete specimen (Holotype, USNM 27609). — Orcas Island, Harney Pass, Washington, mud, Jul 1967, coll. H.L. Sanders, one complete specimen + 37 anterior ends (USNM 42014, labelled 25 specimens).

Western North Atlantic: Southport, North Carolina, black silt, 3-10 m, Sept 1976, coll. T. Finn, 10 ant. ends + one posterior end + three fragments of abdominal region (USNM 54141).

English Channel: Stonehouse Pool, Sta. 11, Plymouth Sound, silt/clay, 5 m, 25 Jul 1967, coll. P.E. Gibbs, four complete specimens + 16 ant. ends (BMNH ZB 1980. 341-360). — Bay of Morlaix, Brittany, France, muddy sand, 15 m, Apr 1980, four ant. ends, coll. J.C. Dauvin (Reference collection of Station Biologique de Roscoff).

Bay of Biscay: Courbey channel, Arcachon Bay, France, mud, 3-5 m, Mar 1985 - Feb 1988, 59 complete spec. + 723 ant. ends + five post. ends. — Cousse channel, Arcachon Bay, France, mud, 3 m, 15 Feb 1988, 109 complete spec. + 49 ant. ends + 27 post. ends [all specimens from Arcachon, coll. G. Bachelet; part of this material is deposited in the MNHN (UC 351)]. — Bidasoa estuary, Spain, sandy mud, 2.5 m, May 1992, coll. J.C. Sola, seven ant. ends (INSUB). — Basque coast, off San Sebastian, muddy sand, 100 m, Sta. G1, three ant. ends; Sta. G4, two ant. ends; Sta. G6, one ant. end; Sta. G8, five ant. ends. — Basque coast, off Bilbao, muddy sand, 100 m, Sta. B8, one ant. end (all specimens from Basque coast, coll. F. Aguirrezabalaga, INSUB). — Basque coast, off the Ría de Gernika, 100 m, coll. A. Rallo, 1 slide with one ant. end (UPV).

DIAGNOSIS. — A species of *Cossura* with dorsal tentacle arising from posterior margin of setiger 2. Proboscis with 4-8 finger-shaped processes. Setiger 1 uniramous, following setigers biramous. Thorax with 13-21 setigers. Pygidium with three long anal cirri (two dorsolateral and one mid-ventral) and 10-20 intercirral papillae. Juveniles without pygidial processes and with fewer thoracic setigers than adults.

MATERIAL FROM ARCACHON

DESCRIPTION OF ADULTS (Figs 1-2). — Body is slender, threadlike, rounded in section, tapered to both ends. The longest complete specimen is 0.35 mm wide, 5.7 mm long for 43 setigers. The animals are usually colorless in alcohol, however some are uniformly yellow ochre.

The prostomium is bluntly conical, without appendages or eyespots, about twice as long as the peristomium. No nuchal organs have been observed. The peristomium is achaetous and without appendages, as long as the next segment. Some specimens seem to have two peristomial segments. However, when material is abundant within a sample, a complete gradation may be found, with some specimens apparently having two asetigers, others having a single asetiger, and others with only a slight, circular dip in the middle of the prostomium. In specimens with one peristomial segment, the mouth opens ventrally between the prostomium and peristomium. In those with two apparent asetigers, the buccal aperture is situated between these two "segments". Sagittal sectioning of anterior ends of such specimens does not show any septum in line with the prostomial dip. It is thus clear that there is only a single peristomial segment in our specimens, as found by JONES (1956) in *C. pygodactylata* from San Francisco Bay and by THULIN (1921) and FOURNIER & PETERSEN (1991) for *C. longocirrata*. The first apparent asetiger in some specimens is actually the basal portion of the prostomium which looks like a segment as longitudinal muscles contract (THULIN, 1921; JONES, 1956). The proboscis has been seen partially protruded in two worms only; according to JONES (1956), it terminates in 4-8 finger-shaped processes.

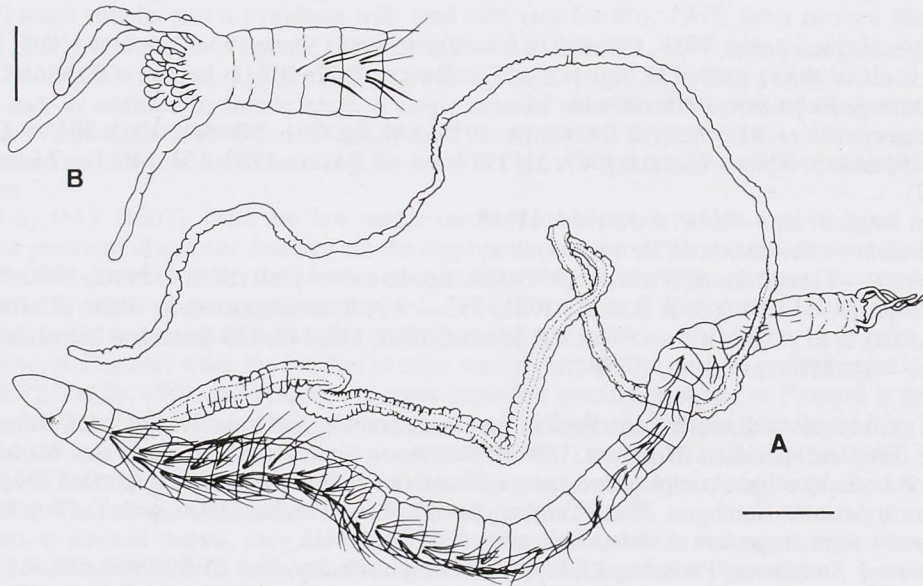


FIG. 1. — *Cossura pygodactylata* Jones, Arcachon Bay. A, entire worm, left lateral view. B, posterior end in lateral view. Scale bars : A = 200 μ m, B = 75 μ m.

The single median tentacle is inserted dorsally on the posterior end of the second setigerous segment. This branchial filament (BERKELEY & BERKELEY, 1956; LAUBIER, 1963; FOURNIER & PETERSEN, 1991) shows circular and irregular wrinkles over its whole length and is constricted near its point of insertion. The tentacle is usually longer than the body (up to 3x) but, due to its high contractility, there is no relationship between body length and tentacle length.

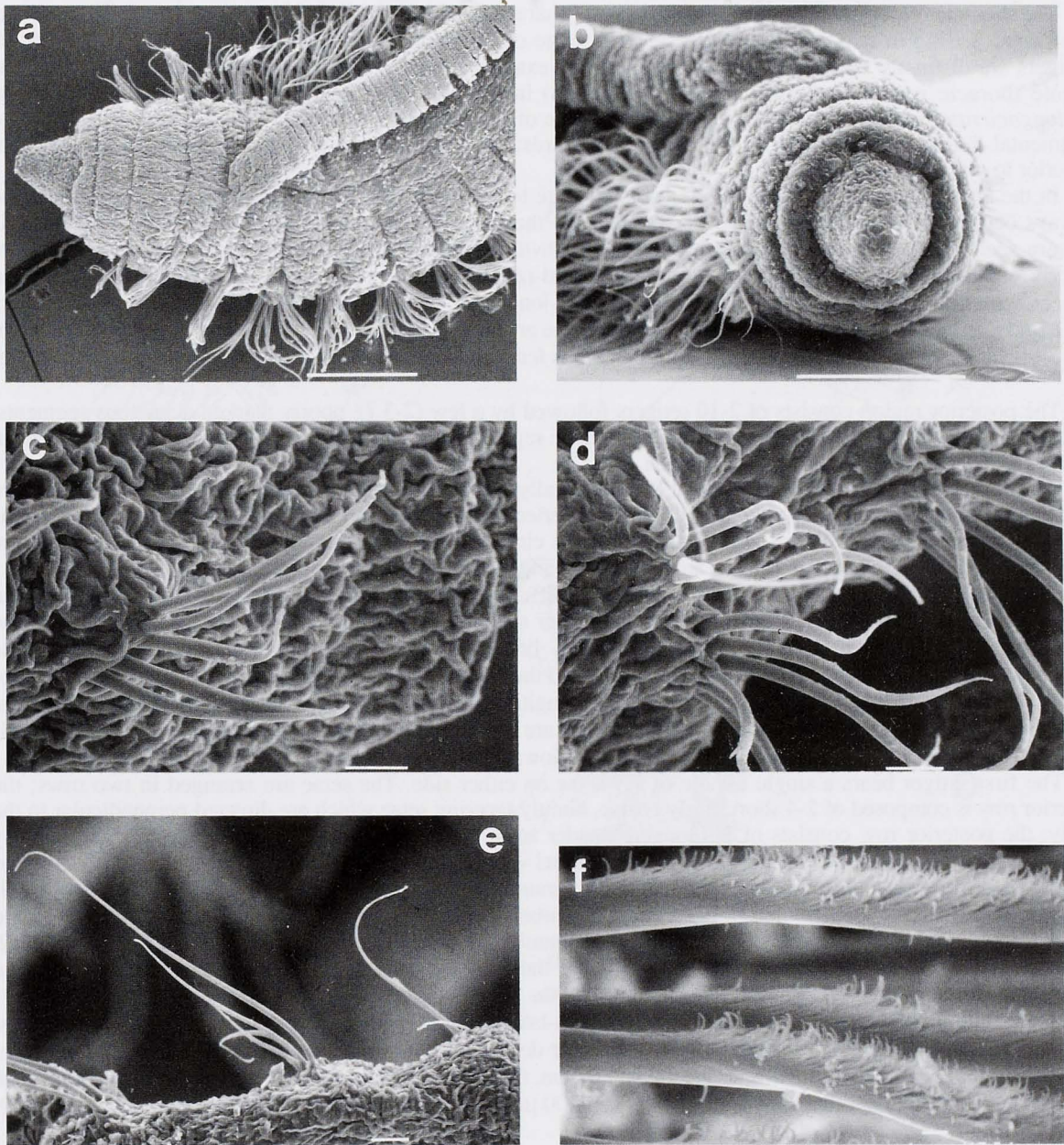


FIG. 2. — *Cossura pygodactylata*, SEM figures of adult specimens from Arcachon Bay. A, anterior end in dorsal view. B, same animal in frontal view. C, single bundle of setae of setiger 1, in posterior view. D, setiger 6 in dorso-lateral view. E, bundles of setae from posterior abdominal region, in lateral view. F, detail of capillary notosetae from setiger 2, in frontal view. Scale bars : A-B = 100 μ m, C-E = 10 μ m, F = 1 μ m.

Although consisting of numerous similar segments, the body may be divided into three weakly separable regions according to the number and position of the setae in each segment and the respective length of setigerous segments. As in other cossurids there are no defined parapodial lobes and the setae arise directly from the lateral body wall.

The thoracic region extends to setiger 16-21; it is characterized by short (50-85 μm long), crowded segments with setae arising in bundles close to the anterior edge of each setiger. Setiger 1 is uniramous; thereafter all setigers are distinctly biramous. A mid-dorsal groove extends from the base of the unpaired tentacle over the whole thoracic region. As noted by LAUBIER (1963) in *C. soyeri* and FOURNIER & PETERSEN (1991) in *C. longocirrata*, some specimens have a transition zone of 1-2 setigers between the thorax and abdomen, where segmental length increases and setae migrate backwards; other specimens show more abrupt transition from anterior to mid-region.

In the abdominal region (7-20 setigers) segments are longer (70-160 μm) than in the thorax. Fragmentation always occurs within a few segments posterior to the thorax-abdomen transition, i.e. after setiger 17-30; this pattern seems to be characteristic (JONES, 1956; FOURNIER & PETERSEN, 1991). In some specimens there are poorly marked intersegmental constrictions in the mid-region; in others the abdomen takes on a moniliform aspect, with, for example, abdominal segments 160 μm long x 240 μm wide vs. thoracic segments 70 μm long x 170 μm wide measured on an entire specimen. The setae are similar to those of thoracic region and emerge from, or just behind, the middle of each segment. In ovigerous females, oocytes are present from setiger 19-20 to setiger 26.

The posterior region consists of 2-10 setigers followed by a few (2-3 ?), poorly marked achaetous segments. The segments are short and crowded, as in the thoracic region. The setae emerge mid-laterally of each segment and are smaller and fewer than in the abdomen.

The pygidium of adult specimens is cleft mid-dorsally and bears three long, thin anal cirri, 130-250 μm in length and 8-10 μm in diameter; one pair of cirri is inserted dorsolaterally on the edge of the anal lobes, whereas the third cirrus arises mid-ventrally. In addition to these cirri, 5-10 short (ca. 30 μm long) finger-like papillae are arranged laterally on the margin of each anal lobe. Cirri and papillae do not seem to be retractile.

The setae are all simple capillaries of two, slightly different kinds: shorter and thicker (4-5 μm wide) setae in the anterior row of thoracic setigers (see below), longer and thinner (2-3 μm wide) setae in the posterior row. Under transmitted light the setae appear to be slightly limbate and minutely spinulose along one margin; the ultrastructural arrangement of longitudinal filaments and the occurrence of very thin channels in the outer layer of the setae (SPECHT, 1988) also give the impression of longitudinally-striated shafts. SEM reveals that the setae are roughly cylindrical, have a smooth proximal shaft and are covered with dense, minute hairs along most of their length. This pilosity is directed upwards in neurosetae, downwards in notosetae.

The first setiger bears a single bundle of 5-7 setae on either side. The setae are arranged in two rows; the anterior row is composed of 2-4 short, fairly coarse, bluntly tapering setae which are directed perpendicular to the body; the posterior row consists of 2-4 longer, slender setae, tapering gradually towards the tips and slightly curved posteriorly. This setal arrangement in two parallel vertical series, i.e. an anterior row of setae thicker and shorter than those of a posterior row, persists in the biramous thoracic setigers; in these segments, there are 9-15 setae on either side, distributed in nearly equal numbers between the noto- and neuropodia (4-8 setae) and between the anterior and posterior rows. The highest number of setae (7-8 per ramus) is found in setigers 2-12. The setae of the anterior row project laterally, while those of the posterior row are directed posteriorly and dorsally in the notopodium, posteriorly and ventrally in the neuropodium.

In the abdominal region the setae are positioned mid-laterally in each segment, but without indication of rows. All setae become long, slender capillaries; their number decreases to 4-9 on either side. Progressively the tips of all setae tend to be directed forward. In the preanal region, the number of setae is gradually reduced to 1-4 on each side; all setae are thin capillaries, some are long (90-100 μm), whereas others (developing setae ?) are short (20-40 μm).

DESCRIPTION OF BENTHIC JUVENILES (Fig. 3). — Several morphological characters are common to both adults and juveniles: the shape of prostomium and peristomium, the mid-dorsal tentacle inserted on posterior margin of setiger 2, the lack of parapodial lobes, the first setiger uniramous, and the following setigers biramous. The most conspicuous differences between juveniles and adults lie in the body regions and the anal segment.

Segmentation is barely visible in young specimens. Therefore, the segmental length and the position of setal bundles on each segment cannot be used to distinguish body regions. However, with the exception of the very

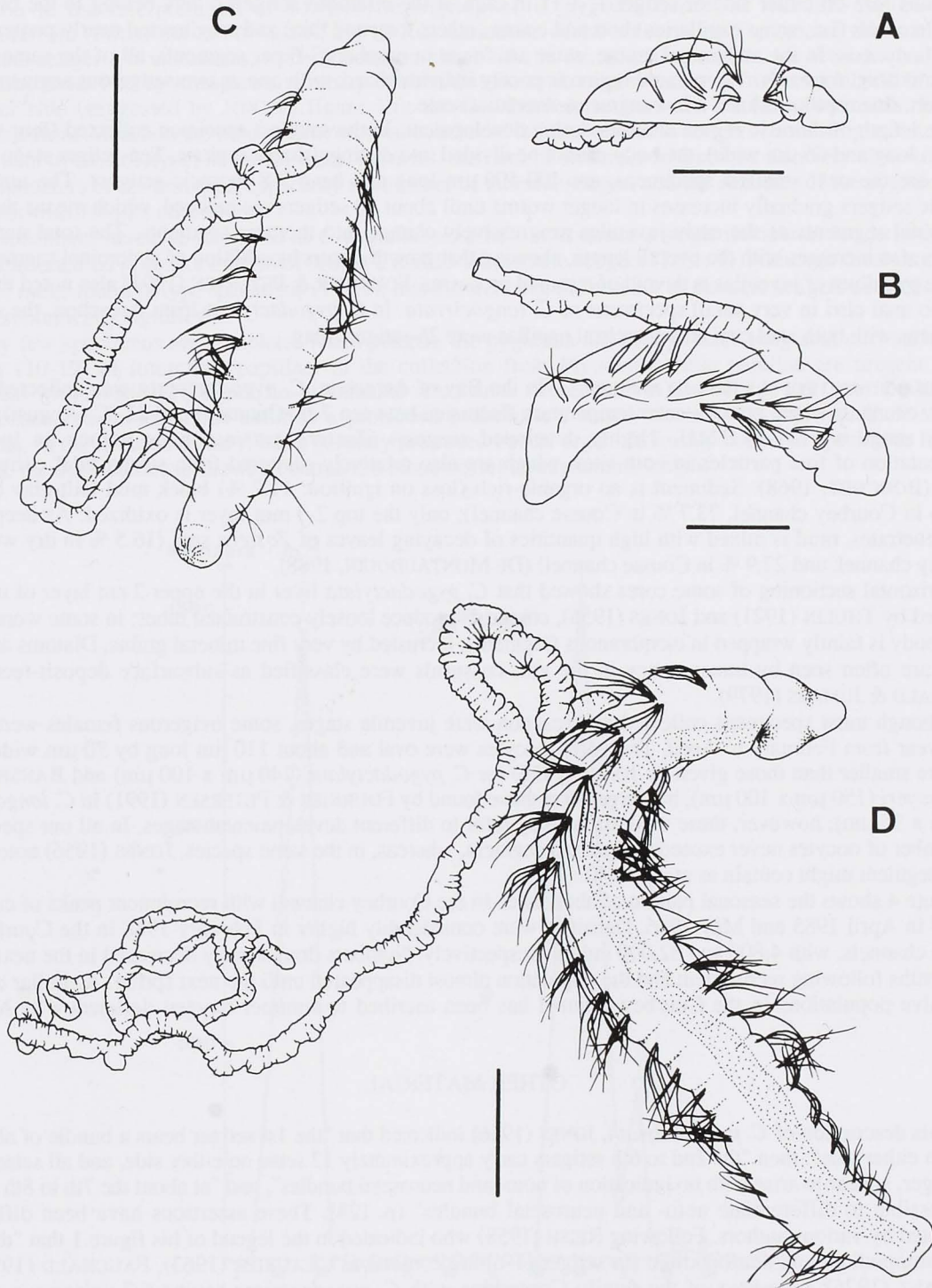


FIG. 3. — *Cossura pygodactylata*, benthic juveniles from Arcachon Bay. A, 4-setiger stage, lateral view. B, 11-setiger stage, lateral view. C, 14-setiger stage, dorsal view. D, 24-setiger stage, ventral view. Scale bars : A-B = 100 μ m, C-D = 200 μ m.

small worms, thorax and abdomen may be separated by observation of the setae. In the thoracic region, setae are numerous (4-5 on either side of setiger 1, 4-11 in each of the biramous setigers); they belong to the two types found in adults (i.e., some capillaries short and coarse, others long and thin) and are directed nearly perpendicular to the body axis. In the abdominal region, setae are fewer in number (2-6 per segment), all of the same slender type, and tilted forwards. The preanal region is poorly individualized, with one or two setigerous segments (with 1-2 short, fine capillaries) and a few segments devoid of setae.

The length of thoracic region changes during development. In the smallest specimen collected (four setigers, 245 μm long and 65 μm wide), the body cannot be divided into distinguishable regions. Ten-setiger stage worms, which are the next smallest specimens, are 400-500 μm long and have 7-8 thoracic setigers. The number of thoracic setigers gradually increases in longer worms until about 20 setigers are reached, which means that some abdominal segments of the early juveniles progressively change into thoracic segments. The total number of setigers also increases with the overall length, showing that growth occurs by addition of abdominal segments.

The pygidium of juveniles is devoid of terminal processes. FOURNIER & PETERSEN (1991) also noted that there were no anal cirri in very small specimens of *C. longocirrata*. In *C. pygodactylata* from Arcachon, the smallest specimens with both anal cirri and intercirral papillae were 26-setigers long.

ECOLOGY AND POPULATION DYNAMICS. — In the Bay of Arcachon, *C. pygodactylata* was collected in two shallow channels where bottom water temperature fluctuated between 7 °C (January) and 21 °C (August); annual salinity range was 27-34 P.S.U.. Highly developed seagrass (*Zostera marina*) beds induce an increased sedimentation of fine particles in both sites, which are also relatively sheltered from strong tidal currents and waves (BOUCHET, 1968). Sediment is an organic-rich (loss on ignition: 11.2 %) black mud (silt-clay content: 60.1 % in Courbey channel, 73.7 % in Cousse channel); only the top 2-3 mm layer is oxidized. As deep as the grab penetrates, mud is mixed with high quantities of decaying leaves of *Zostera* spp. (16.5 % in dry weight in Courbey channel, and 27.9 % in Cousse channel) (DE MONTAUDOUIN, 1988).

Horizontal sectioning of some cores showed that *C. pygodactylata* lives in the upper 2 cm layer of mud. As observed by THULIN (1921) and JONES (1956), cossurids produce loosely constructed tubes: in some worms, part of the body is faintly wrapped in membranous fragments, incrustated by very fine mineral grains. Diatoms and sand grains are often seen by transparency in the gut; cossurids were classified as subsurface deposit-feeders by FAUCHALD & JUMARS (1979).

Although most specimens collected at Arcachon were juvenile stages, some ovigerous females were found every year from February to April. The yolky oocytes were oval and about 110 μm long by 70 μm wide; these sizes are smaller than those given by JONES (1956) for *C. pygodactylata* (140 μm x 100 μm) and BANSE (1981) for *C. soyeri* (150 μm x 100 μm), but larger than those found by FOURNIER & PETERSEN (1991) in *C. longocirrata* (75 μm x 35 μm); however, these dimensions may refer to different developmental stages. In all our specimens, the number of oocytes never exceeded eight per segment, whereas, in the same species, JONES (1956) noted that a single segment might contain as many as 40.

Figure 4 shows the seasonal pattern of abundance in the Courbey channel with recruitment peaks of ca. 1,500 ind./m² in April 1985 and May 1986. Densities were considerably higher in February 1988 in the Courbey and Cousse channels, with 4,800 and 32,000 ind./m² respectively. Numbers dramatically decreased in the next one or two months following recruitment and the population almost disappeared until the next spring. A similar collapse of bivalve populations in the Courbey channel has been ascribed to summer oxygen deficiency by MADANI (1989).

OTHER MATERIAL

In his description of *C. pygodactylata*, JONES (1956) indicated that "the 1st setiger bears a bundle of about six setae on either side"; then "the 2nd to 6th setigers carry approximately 12 setae on either side, and all setae, to the 6th setiger, appear to arise with no indication of noto- and neurosetal bundles", and "at about the 7th to 8th setiger, it is possible to differentiate noto- and neurosetal bundles" (p. 128). These assertions have been differently interpreted by various authors. Following REISH (1958) who indicated in the legend of his figure 1 that "the setae of the notopodium and neuropodium [in setigers 1-6] are continuous", LAUBIER (1963), FAUCHALD (1972) and ORENSANZ (1976) gave keys of the family Cossuridae with *C. pygodactylata* having 6-7 uniramous anterior setigers; however, REISH used the same symbol (the single letter S in his figure 1) for the 1st setiger of *C. delta* in which "the first setigerous segment is biramous with the setae forming a continuous lateral series" (REISH, 1958: 54). On the other hand, HARTMAN (1969: 273) noted in her diagnosis of *C. pygodactylata*: "third segment the first

setigerous, its setae in *biramous* fascicles, as are those farther back". Therefore, it seems that there has been some confusion in the interpretation of JONES's description of *C. pygodactylata*, as was also the case with *C. longocirrata* (FOURNIER & PETERSEN, 1991). Reexamination of the holotype of *C. pygodactylata* definitely shows that setiger 1 is uniramous, with six setae on either side; in the next five setigers, the setae form almost a continuous series but, by transparency, it may be seen that the setae originate clearly from two muscular sheaths on either side (suggested by JONES's figure 1b); the last thoracic setigers are distinctly biramous. In most specimens from Arcachon the noto- and neurosetal bundles of the first biramous setigers (from setiger 2) are more spaced than in the holotype; in few of them, however, the rami of biramous setigers are also very close together. Other characters of the holotype, especially the number of thoracic setigers and the structure of the pygidium, are consistent with JONES's description.

All specimens herein re-identified as *C. pygodactylata* have in common a single uniramous setiger, the dorsal tentacle inserted on posterior margin of setiger 2 and 13-21 thoracic setigers (Table 1). Although diverging a little from the range found in type specimens (17-19), this difference in the number of thoracic setigers does not appear to be taxonomically significant.

Very few specimens are complete. When present, the pygidium has always three long anal cirri and a large number (10-19) of intercirral papillae. In the collection from Plymouth, these papillae are present in two specimens with 20 and 22 setigers, i.e. at a smaller size than at Arcachon. It is also notable that, over the hundreds of specimens examined, none exhibits a protruded proboscis; a single worm, collected by J.C. SOLA, San Sebastian, in the Bidasoa estuary, has a partially protruded buccal organ. In freshly collected specimens from the Bidasoa, the dorsal tentacle shows a central, red blood vessel throughout its length.

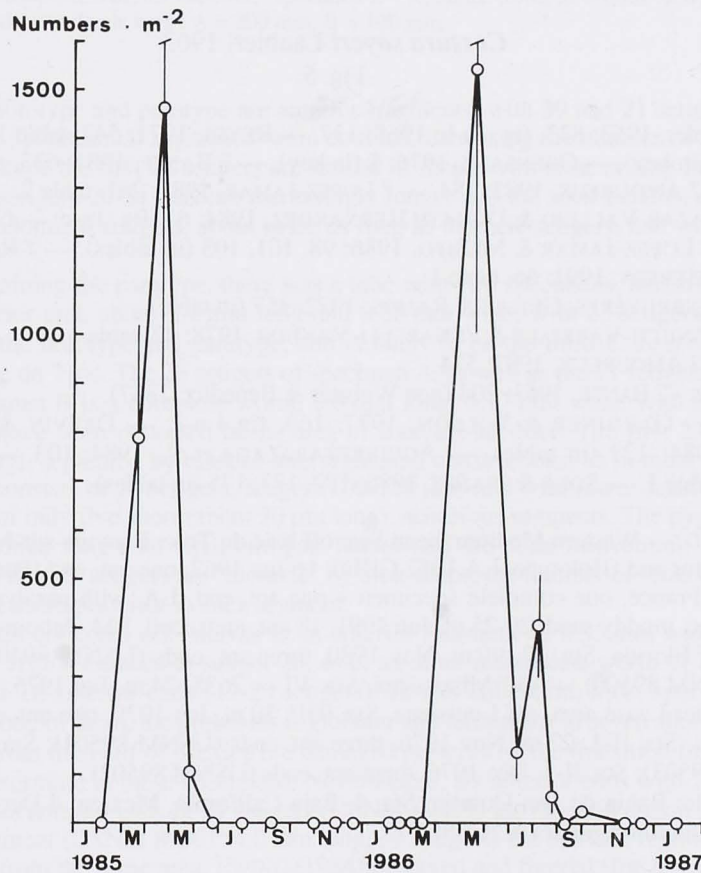


FIG. 4. — Seasonal mean abundance (± 1 S.D.) of *Cossura pygodactylata* in the Courbey channel, Arcachon Bay, from February 1985 to January 1987.

The number and size of oocytes vary between locations. In an anterior fragment collected in September in North Carolina, there are about 30 oocytes (70 μm x 35 μm) per segment, i.e. a similar number of oocytes, but smaller by half in size, than those found in April in California (JONES, 1956). Other specimens have considerably fewer oocytes in each segment, as those from Arcachon: eight oocytes (100 μm x 80 μm) in the Bidasoa estuary (May), six oocytes (80 μm x 60 μm) in Plymouth Sound (July), or even four oocytes (80 μm x 40 μm) in the worm collected by RALLO (1988).

There remains some doubt about the identity of specimens from the Bay of Morlaix and the Spanish Atlantic coast where complete worms have never been collected (Table 1). The number of thoracic setigers recorded in these worms is characteristic both of *C. pygodactylata* and *C. longocirrata*; only the structure of the pygidium, with numerous intercirral processes in the former species and none in the latter, differs between both species (FOURNIER & PETERSEN, 1991). However, due to the arctic-boreal distribution of *C. longocirrata* (FOURNIER & PETERSEN, 1991) and the neighbouring occurrence of *C. pygodactylata* at Plymouth and Arcachon, the specimens of *Cossura* from Morlaix and the Basque coast are likely to be referable to *C. pygodactylata*.

REMARKS. — BANSE (1981) examined specimens from several sites in Washington, that he referred to as *C. soyeri*. It may be inferred from his description that the abdominal region begins after the first 30 setigers (p. 633). However, he reported further (p. 634) that some animals had segments from about setiger 17 packed with oocytes. Some of these specimens have been reexamined by us and identified as *C. pygodactylata*; in this lot (USNM 42014) there was also an anterior fragment of 19 setigers and 2.2 mm long, with the dorsal tentacle inserted on the posterior margin of setiger 3 (probably "*Cossura* sp." in BANSE's paper, p. 634). Specimens of *Cossura* from this area may belong to two or three species.

Cossura soyeri Laubier, 1963

Fig. 5

Cossura soyeri Laubier, 1963: 833, fig. 1a-h; 1965: 137. — REYSS, 1971: 542, table 1, 552, 609, table 21. — FAUCHALD, 1972: 207 (in key). — ORENSANZ, 1976: 5 (in key). — ? BANSE, 1981: 633, *pro parte*. — ? HOBSON & BANSE, 1981: 55. — ? AMOUREUX, 1982: 184. — ? LOPEZ-JAMAR, 1982: 261, table 2. — EWING, 1984: 4-4, 4-6, fig. 4-4a-d. — ? SALAZAR VALLEJO & DONATH HERNANDEZ, 1984: 61, fig. 1a-c. — GAMBI & GIANGRANDE, 1986: 852, table 1. — ? LOPEZ-JAMAR & MEJUTO, 1986: 98, 101, 103 (in tables). — ? ROSENFELDT, 1989: 214, 234. — FOURNIER & PETERSEN, 1991: 66, table 1.

Cossura soyerii - DESBRUYÈRES, GUILLE & RAMOS, 1972: 357 (in table).

Cossura soyeri - COGNETTI-VARRIALE & ZUNARELLI-VANDINI, 1978: 42, table 1.

Cossura cf. *soyeri* - ? AMOUREUX, 1987: 574.

Cossura longocirrata - ? BANSE, 1963: 204 (*non* Webster & Benedict, 1887).

Not *Cossura soyeri* - GARDINER & WILSON, 1977: 169, fig. 4 a-c. — DAUVIN & GENTIL, 1980: 8. — AGUIRREZABALAGA, 1984: 122 (in table). — AGUIRREZABALAGA *et al.*, 1984: 103. — AGUIRREZABALAGA, IBANEZ & ROS, 1986: table 1. — SOLA & IBAÑEZ, 1986: 172, 173, 175 (in tables).

MATERIAL EXAMINED. — Western Mediterranean Sea: off baie du Troc, Banyuls-sur-Mer, France, mud, 35 m, 27 June 1962, one anterior end (Holotype, LA 1052 GIIa); 16 Jun 1962, one ant. end (Paratype, LA 1051 GIIa). — ? Banyuls-sur-Mer, France, one complete specimen + one ant. end (LA, with paratype). — off Palavas-les-Flots, Languedoc, France, muddy sand, 20-25 m, Jun 1991, 18 ant. ends, coll. J.M. Amouroux (LA).

Gulf of Mexico: off Florida, Sta. 12, 90 m, Nov 1980, three ant. ends (USNM 89499); Sta. 33, 145 m, Jul 1981, one ant. end (USNM 89500). — Off Mississippi, Sta. VI — 2638, 24 m, Jun 1975, three ant. ends (USNM 75148). — South Timbalier Lease area, off Louisiana, Sta. 03P, 30 m, Jan 1979, one ant. end (USNM 89504). — Off Port Aransas, Texas, Sta. II-1, 22 m, Nov 1976, three ant. ends (USNM 89501); Sta. II-4, 36 m, Nov 1976, two ant. ends (USNM 89503); Sta. II-1, Dec 1976, three ant. ends (USNM 89502).

Eastern North Pacific: Bahia de San Quintin, Sta. 4, Baja California, Mexico, 4 Dec 1981, numerous dried specimens, coll. L.E. Calderon Aguilera (CICESE).

DIAGNOSIS. — A species of *Cossura* with dorsal tentacle arising from posterior margin of setiger 2. Proboscis with about seven short processes. Setiger 1 uniramous, following setigers biramous. Thorax with 20-31 setigers. Pygidium with three long anal cirri (two dorsolateral and one mid-ventral), without intercirral processes.

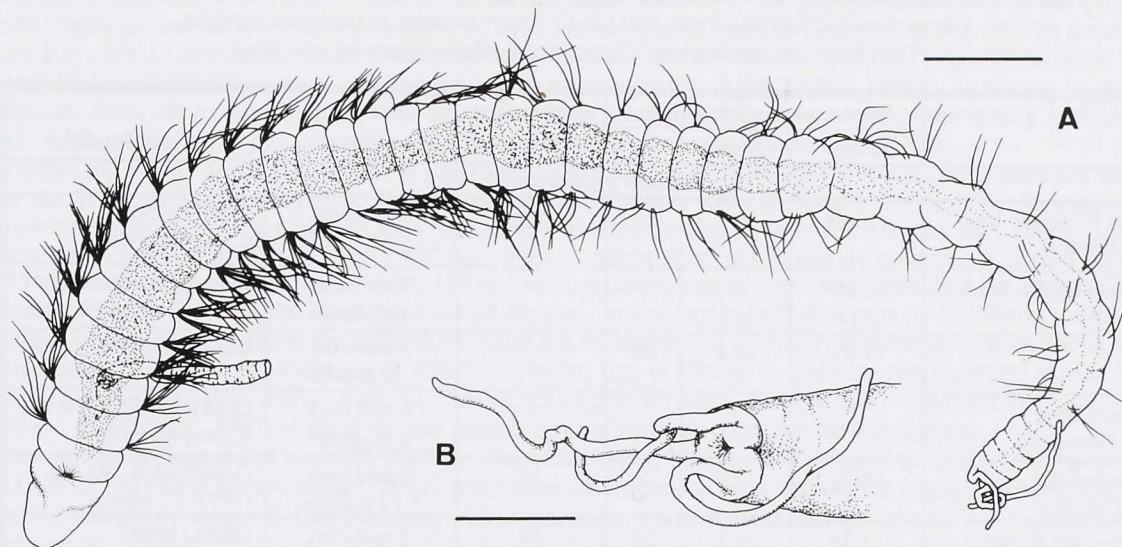


FIG. 5. — *Cossura soyeri* Laubier, Banyuls-sur-Mer, "specimen B". A, entire worm in ventral view, dorsal tentacle broken. B, posterior end in ventral view. Scale bars : A = 200 μ m, B = 100 μ m.

REMARKS. — The holotype and paratype are anterior fragments, with 39 and 21 setigers respectively; in the original description two "peristomial segments" were counted, increasing the number of segments to 41 and 23, respectively. In the holotype the first 28 setigers are similar in shape, with setae arising in bundles at the anterior edge of each segment; setigers 29-31 become increasingly longer and the setal bundles migrate posteriorly; the last eight setigers are abdominal setigers, about twice as long as thoracic setigers, and with setae emerging from the middle of segments.

Within the vial containing the paratype, there was a tube with two specimens, hereafter designated A and B. Specimen A is an anterior end, about 2.1 mm long and 0.36 mm wide, with 23 setigers; this specimen is dark brown in color, as are the holotype and paratype, and is likely to be the third *C. soyeri* collected by LAUBIER (1963, 1965) off the baie du Troc. The 23 setigers of specimen A, as well as the 21 setigers of the paratype, are all thoracic setigers. Specimen B is a complete worm, 2.6 mm long, 0.17 mm wide, with 33 setigers; its origin is unknown but it might have been collected in the area of Banyuls-sur-Mer. The first 23 setigers are similar in shape (about 55 μ m long), separated by marked intersegmental constrictions, as in most specimens reexamined. The abdominal region consists of 10 setigers, longer (100-110 μ m) and with fewer setae than in the thorax. The preanal region consists of only five short (about 20 μ m long), achaetous segments. The pygidium has a slight mid-dorsal cleft and bears three long anal cirri, one pair lateral and the other midventral; there are no intercirral processes. Although the first 23 setigers are "thoracic" by their shape, the number of setae decreases by setiger 19-20 and the setae become more posterior in each segment.

The longest specimen collected off Palavas is an anterior fragment of 0.35 mm wide and 6.7 mm long for 45 setigers; the anterior region extends to setiger 26, as in an other incomplete worm of 28 setigers. Setigers are all thoracic in the other 16 anterior ends (17-29 setigers). In this collection, most specimens show a partially protruded proboscis; in one of them, the proboscis is globular and terminates in seven short processes.

Several specimens from the Gulf of Mexico are damaged posteriorly; the transition from thorax to abdominal regions is difficult to determine in these specimens. Nevertheless, six anterior ends with 20-30 setigers have only thoracic segments. In two anterior ends of 21 setigers (USNM 89499) the thoracic region extends to setiger 20. In the longest anterior fragment (USNM 89501: 4.0 mm long, 33 setigers) the thoracic region consists of 29 setigers. In complete specimens from the same area, EWING (1984) observed and figured (fig. 4-4d) a pygidium with three filamentous caudal cirri, similar to the pygidium of specimen B.

The principal morphological characters of all reexamined specimens of *C. soyeri* are summarized in Table 1.

TABLE 1. — Comparison of the main morphological characteristics of specimens referred to as (1) *Cossura pygodactylata* Jones and (2) *C. soyeri* Laubier in the present paper. Data from reexamination of specimens unless otherwise specified.

	Number of thoracic setigers			First setiger with oocytes	Structure of pygidium	Record reference
	Range	Average	n			
(1) <i>Cossura pygodactylata</i> Jones						
San Francisco Bay, California	17-19 ^a	-	-	18-20 ? ^a	3 anal cirri + 12-20 papillae ^a	JONES (1956: <i>C. pygodactylata</i>)
Orcas Island, Wash.	16-17 ^b	-	-	-	3 anal cirri + papillae ^c	BERKELEY & BERKELEY (1956: <i>C. longocirrata</i>)
"	17-21	18.8	20	-	3 anal cirri + 12 papillae	BANSE (1981: <i>C. soyeri</i>)
Disco Bay, W Greenland	?	-	-	-	3 anal cirri + papillae ^b	CURTIS (1977, 1979: <i>C. longocirrata</i>)
Southport, N Carolina	14-16	15.0	5	16	3 anal cirri + 12 papillae	GARDINER & WILSON (1977: <i>C. soyeri</i>)
Plymouth Sound, England	14-18	16.1	20	18	3 anal cirri + 10-12 papillae	GIBBS (1969: <i>C. longocirrata</i>)
Bay of Morlaix, France	14-17	16.0	3	-	(missing)	DAUVIN & GENTIL (1980: <i>C. soyeri</i>)
Arcachon Bay, France	16-21	17.5	37	19-20	3 anal cirri + 10-19 papillae	this study
Bidasoa estuary, Spain	14-17	16.4	7	19	(missing)	SOLA & IBÁÑEZ (1986: <i>C. soyeri</i>)
Basque coast, Spain	21 ^d	-	1	-	(missing)	AGUIRREZABALAGA (1984: <i>C. soyeri</i>)
"	13-20	16.7	10	21	(missing)	AGUIRREZABALAGA, IBÁÑEZ & ROS (1986: <i>C. soyeri</i>)
"	18	-	1	19	(missing)	RALLO (1988: <i>C. longocirrata</i>)
(2) <i>Cossura soyeri</i> Laubier						
Banyuls-sur-Mer, French Mediterranean	28 or 31	-	1	32?	(missing)	LAUBIER (1963: <i>C. soyeri</i>)
"	23	-	1	-	3 anal cirri	this study
Languedoc, French Mediterranean	≥ 26	26.0	2	-	(missing)	this study
Gulf of Mexico	20-≥30	23.0	3	-	3 anal cirri ^e	EWING (1984: <i>C. soyeri</i>)

^a JONES (1956). ^b FOURNIER & PETERSEN (1991). ^c Three lobes between each pair of cirri, according to BERKELEY & BERKELEY (1956), but at least five lobes and several stubby intercirral processes, according to FOURNIER & PETERSEN (1991). ^d A.H. ARIÑO, Pamplona (pers. comm.). ^e EWING (1984).

GEOGRAPHICAL DISTRIBUTION

Records of *C. pygodactylata* have been infrequently listed in the literature, perhaps because of the non-occurrence of the characteristic pygidium in most collected specimens and also the possible confusion with both *C. longocirrata* (FOURNIER & PETERSEN, 1991) and *C. soyeri*. Originally recorded from central – San Francisco Bay (HARTMAN, 1954, 1955; JONES, 1956) – and southern California – Hueneme canyon, off Los Angeles (HARTMAN, 1969) –, *C. pygodactylata* is also present more northerly in the Eastern North Pacific, i.e. in British

Columbia (FOURNIER & PETERSEN, 1991). The present study extends its geographic distribution to the Western (North Carolina) and Eastern North Atlantic (English Channel, Bay of Biscay). The species may also be present in Disko Bay, West Greenland, where specimens referred to *C. longocirrata* by CURTIS (1977, 1979) have been reexamined and identified as *C. cf. pygodactylata* by FOURNIER & PETERSEN (1991). It occurs in muddy sediments, from silt to muddy sand; with the exception of the Spanish Basque coast, where it may be found at depths of about 100 m, *C. pygodactylata* usually inhabits shallow waters between 1 and 30 m.

Unlike the former species, *C. soyeri* is sometimes considered as a cosmopolitan species. It is basically known from the Western Mediterranean — French and Spanish Catalan coast (LAUBIER, 1963, 1965; REYSS, 1971; DESBRUYÈRES *et al.*, 1972), Gulf of Lions (this study), Tyrrhenian Sea (GAMBI & GIANGRANDE, 1986), Adriatic (COGNETTI-VARRIALE & ZUNARELLI-VANDINI, 1978) — where it occurs in muddy bottoms, at depths between 12-35 m, but also up to 1,000 m (REYSS, 1971). The re-examination of specimens collected by EWING (1984) confirms its occurrence in the Northern Gulf of Mexico, in fine sediments at depths of 21-189 m. Additional records (not examined because the collections could not be located) of *C. soyeri* include several locations in the Celtic Sea — 610-1,400 m (AMOUREUX, 1982) —, in the Bay of Biscay — Galician rias (LOPEZ-JAMAR, 1982; LOPEZ-JAMAR & MEJUTO, 1986); Banc Le Danois, 450-1,500 m (AMOUREUX, 1987) —, and off Portugal — 320-1,040 m (AMOUREUX, 1987) —; these records need to be confirmed by collecting new specimens.

Specimens collected in Ensenada Harbour, Baja California, Mexico and referred to *C. soyeri* by SALAZAR VALLEJO & DONATH HERNANDEZ (1984) were anterior fragments with the dorsal tentacle arising from the posterior margin of setiger 2. Unfortunately, these specimens became dried during storage. We examined some dried worms, labelled "*C. soyeri*", from a neighbouring location; the worms were impossible to determine but, in one of them, the tentacle was clearly inserted on the anterior margin of setiger 3 as in *C. candida* Hartman collected from the same area and also re-examined. It is hypothesized that cossurids from the Mexican Pacific coast with the dorsal tentacle on setiger 2 might be *C. pygodactylata* rather than *C. soyeri*.

Another disconcerting record of *C. soyeri* is that of ROSENFELDT (1989) in the central Red Sea at 601 m depth. The single specimen was an anterior end of 41 setigers, 1.5 mm [sic] long. No detail is given about the dorsal tentacle or the number of thoracic setigers, so this record is doubtful.

In conclusion, the geographical distribution of *C. pygodactylata* is extended to the entire Pacific coast of North America and to both sides of the northern Atlantic, whereas *C. soyeri* appears to be restricted to the Mediterranean Sea and the northern Gulf of Mexico. Such a latitudinal distribution of these two species in the Atlantic seems ecologically justified, whereas the extended distribution of *C. pygodactylata* on the Pacific coast from California to Washington is more difficult to explain. It is also clear that the very few morphological characters available to distinguish these two species do not strengthen this conclusion. From this point of view, it would be desirable to confirm the morphological results using genetical methods of species identification.

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