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THE GYMNASOMATA (GASTROPODA : OPISTHOBRANCHIA) IN THE PLANKTON OF THE FRENCH MEDITERRANEAN COAST

Ruth BARNICH¹, Daniela UTHE²

¹ Forschungsinstitut Senckenberg, Senckenberganlage 25, D-60325 Frankfurt, Germany

² Institut f. Spezielle Zoologie u. Vergleichende Embryologie, Westf. Wilhelms-Universität Münster, Hüfferstraße 1, D-48149 Münster, Germany

MEDITERRANEAN GYMNASOMATA
TAXONOMY
IDENTIFICATION
SUCKERS
SCANNING ELECTRON MICROSCOPY

ABSTRACT. – During plankton investigations on the French coast at Banyuls-sur-Mer and Villefranche-sur-Mer in the years 1989-1995 six out of ten species of Gymnosomata (Gastropoda, Opisthobranchia) recorded for the Mediterranean were found, i.e. *Pneumoderma atlanticum*, *Pneumodermaopsis canephora*, *P. ciliata*, *P. paucidens*, *Cliopsis krohnii* and *Paraclione longicaudata*. Specimens in different developmental stages (polytrochous larvae, transitory stages and adults) could be identified by their main identification characters, i.e. protruded prehensile organs such as suckerarms, proboscis or buccal cones. The species found in the samples are presented in an identification key with clear figures and descriptions based on light and scanning electron microscopical investigations are provided. SEM is used for the first time to study pneumodermatid suckers.

GYMNASOMATA MÉDITERRANÉENS
TAXONOMIE
IDENTIFICATION
VENTOUSES
MICROSCOPIE ÉLECTRONIQUE
À BALAYAGE

RÉSUMÉ. – Six espèces de Gymnosomata (Opisthobranchia, Gastropoda) sur dix connues pour la Méditerranée ont été trouvées dans les années 1989-1995 dans le plancton de la côte française, à Banyuls-sur-Mer et à Villefranche-sur-Mer : *Pneumoderma atlanticum*, *Pneumodermaopsis canephora*, *P. ciliata*, *P. paucidens*, *Cliopsis krohnii* et *Paraclione longicaudata*. Des spécimens à différents stades de développement (larves polytroches, stades transitoires et adultes) présentant des caractères d'identification essentiels, les organes buccaux dévaginables, comme les bras à ventouses, la trompe ou les cônes buccaux, ont pu être identifiés. Les espèces présentes dans les échantillons sont présentées dans une clé d'identification avec des figures précises et à l'aide de descriptions basées sur des études au stéréomicroscope et au microscope électronique à balayage. Cette dernière technique est utilisée pour la première fois pour décrire les ventouses des Pneumodermatidae.

INTRODUCTION

During plankton investigations carried out on the French Mediterranean coast, samples were taken at Banyuls-sur-Mer and Villefranche-sur-Mer in spring and autumn of the years 1989-1995. Among many other planktonic gastropods several species of Gymnosomata (Gastropoda, Opisthobranchia) were found. Together with the shell-bearing Thecosomata the shell-less Gymnosomata represent the holoplanktonic pteropods. Pteropods are mainly characterized by their locomotory organs, the wings which are derived parts of the molluscan foot and present an adaptation to their planktonic mode of life. Other adaptations of gymnosomes are the loss of the shell during development, the streamlining of the body and the small body-size. Gymnosomes are predators with specialized evaginable prehensile organs such as

proboscis (with jaws, radula and paired hooksacs) and suckerarms or buccal cones. Unfortunately identification of gymnosomes proves to be very difficult. This is due to the fact that preserved specimens are often highly contracted and the prehensile organs, which are the main identification characters, are often not protruded. Therefore, relaxation before fixation is very important (Lalli & Gilmer 1989).

Major taxonomic works on gymnosomes were carried out by Pelseneer (1887 and 1888), Meisenheim (1905), Tesch (1913), Pruvot-Fol (1926 and 1954) and more recently by van der Spoel (1976). Lalli & Gilmer (1989) published a comprehensive work on the biology of holoplanktonic gastropods. Mediterranean gymnosomes were studied primarily by Kwietniewski (1902, 1903), Steuer (1911), Pruvot-Fol (1954) and Franc (1949). Unfortunately these works generally list and give short descriptions of the Mediterranean

species but provide only few or poor quality illustrations.

Many gymnosome species are oceanic and rarely to be found in coastal waters (Lalli & Gilmer 1989), nevertheless, among the 10 species known to occur in the Mediterranean Sea, different developmental stages of 6 species were present in the investigated samples from the French coast: *Pneumoderma atlanticum*, *Pneumodermopsis canephora*, *P. ciliata*, *P. paucidens*, *Cliopsis krohnii* and *Paraclione longicaudata*. Since the complete development is only known for a few species, age determination is very difficult in gymnosomes. Current information is mainly based on the investigations of Lebour (1931) and Morton (1958) concerning *Clione limacina* and of Lalli & Conover (1973) concerning *Paedoclione doliiformis*. In *C. limacina*, veligers hatch within a few days with a bilobed velum and a thin shell. The following stage, the polytrochous larva, shows 3 locomotory ciliary bands and small wings while velum and shell are lost. The prehensile organs, being the most important identification characters, are already present in this stage. Throughout a gradual metamorphosis the wings grow in the neck region between head and trunk, the ciliary bands are reduced, the body begins to elongate and gills begin to show. The adult stage is characterized by large muscular swimming wings but remainders of the median and posterior ciliary band may still be present. Some species like *P. doliiformis* show neoteny: sexual maturity and spawning occur at a small size, before all larval characters are lost. This paper does not deal with veligers as their identification is almost impossible. However, polytrochous larvae with protruded prehensile organs as well as transitory stages and adults can be identified.

The aim of this paper is to provide a comprehensive review of the species encountered in the plankton of the French Mediterranean coast. The species are presented in a simple key with clear figures facilitating identification. The following systematic section gives a brief account of works of taxonomic interest for the Mediterranean species and descriptions based on light and scanning electron microscopy. SEM is used here for the first time to compare and describe the different pneumodermatid suckers. Similarities to cephalopod suckers are briefly discussed.

MATERIAL AND METHODS

The investigated gymnosomes were sorted from plankton samples taken off the coast of Villefranche-sur-Mer and Banyuls-sur-Mer (France) in spring and autumn 1989-1995. Different oblique hauls covering a depth range from 0 to 70 m were made using nets of

300 µm ("Super-Homogène"-net) and 500 µm ("Régent"-net) mesh-size. Specimens were relaxed using 7% MgCl₂ in distilled water until the prehensile organs were protruded. This method required several hours, but proved very successful, preventing dissection of the animals. Specimens were then fixed in 3% glutaraldehyde added to 90% seawater and transferred to 70% ethanol. Altogether 60 specimens were found in the samples and identified by light microscopy. To get more detailed information some specimens were investigated using scanning electron microscopy. These specimens were critical-point-dried using CO₂, coated with gold and examined with a Hitachi SEM H-530. Due to the variable evagination of the feeding apparatus, the body length of gymnosomes was measured from the base of the anterior tentacles to the posterior end of the body. Buccal parts (radula, jaws and hooksacs) are useful features in the identification of adult molluscs. But, as most of the investigated specimens were polytrochous larvae or in a transitory stage, buccal parts were not completely developed and therefore not studied (see Pruvot-Fol 1924).

MEDITERRANEAN SPECIES OF GYMNOSOMATA DE BLAINVILLE, 1824

Sources: Tesch 1913; Pruvot-Fol 1954; van der Spoel 1976; Lalli & Gilmer 1989.

Classification according to van der Spoel 1976.

Pneumodermatidae Pelseneer, 1887:

Pneumoderma atlanticum (Oken, 1815)*

Pneumoderma mediterraneum (van Beneden, 1838)

Pneumodermopsis canephora Pruvot-Fol, 1924*

Pneumodermopsis ciliata (Gegenbaur, 1855)*

Pneumodermopsis paucidens (Boas, 1886)*

Cliopsidae Costa, 1873:

Cliopsis krohnii Troschel, 1854*

Clionidae Gray, 1840:

Clioninae Pruvot-Fol, 1926:

Paraclione flavescens (Gegenbaur, 1855)

Paraclione longicaudata (Souleyet, 1852)*

Thalassopterus zancleus Kwietniewsky, 1910

Thliptodontinae Pruvot-Fol, 1926:

Thliptodon gegenbauri Boas, 1886

(* = species found in the samples).

Identification key for gymnosomes found in the plankton of the French Mediterranean coast

Identification is possible for polytrochous larvae as well as any other older stage with protruded prehensile organs. Gills are only present in transitory stages and adults. To obtain animals with

evaginated feeding apparatus, relaxation before fixation is required (see Material and methods).

1. a) no evaginable proboscis; 2 pairs of buccal cones (arms without suckers, but with papillose surface); no gills; body elongated, posterior end pointed; median footlobe very small

Paraclione longicaudata (Fig. 1A)

b) evaginable proboscis present; no buccal cones, with or without suckerarms; gills present; body short or elongated

2. a) no suckerarms; only long proboscis present; body short, cylindrical, posterior end rounded; no median footlobe, but small median tubercle present, posterior gill present

Cliopsis krohnii (Fig. 1 B)

b) 2 or 3 arms with stalked suckers; body elongated; median footlobe well developed ..

3. a) 2 arms with more than 10 suckers; lateral and posterior gill present; lateral footlobes horseshoe-shaped

Pneumoderma atlanticum (Fig. 1C);

Pneumoderma sp. (Fig. 1 D, E)

b) 3 suckerarms: the 2 lateral may be fused, wreath-like, encircling the median arm; only lateral gill present: genus *Pneumodermopsis*

4. a) 2 lateral arms each with 1 small terminal sucker, the median one with 1 enormous urn-shaped terminal sucker, 2 superior and 2 inferior smaller suckers

Pneumodermopsis canephora (Fig. 2 A)

b) 2 lateral arms forming a wreath around the median arm, wreath with several suckers on the margin

5. a) 2 lateral arms fused dorsally; median arm with 1 terminal cup-shaped sucker, 2 superior and 2 inferior flattened suckers (suckers with indented edges)

Pneumodermopsis paucidens (Fig. 2 B)

b) 2 lateral arms not fused dorsally; median arm with 1 mid-size terminal sucker (cup-shaped), 2 large superior cup-shaped and 2 minute inferior flattened suckers

Pneumodermopsis ciliata (Fig. 2 C)

SYSTEMATIC SECTION

Pneumodermatidae Pelseneer, 1887

Pneumoderma Dumeril, 1806

Pneumoderma atlanticum (Oken, 1815);
Fig. 1 C; Pl. I B-D

Pneumodermis atlantica Oken, 1815: p. 327.

Pneumoderma violaceum - Kwietniewski 1902:
p. 45; - Kwietniewski 1903: p. 307, pl. 14 fig. 13,

pl. 15 figs. 23, 25, 26, 30-35, 37, 38, 41-43; - Steuer 1911: p. 20; - Tesch 1913: p. 112.

Pneumoderma atlanticum - Pruvot-Fol 1924:
p. 385, pl. 15 figs. 1-9; figs. XXVI-XXX; - Pruvot-Fol 1954: p. 134, fig. 41a-c; - van der Spoel 1976: p. 80, fig. 79.

— Material: transitory stages (13 spms.; length: 1.5-3.5 mm).

Identification characters: body elongated, head smaller than trunk; median footlobe about as long as or shorter than the horseshoe-shaped lateral lobes; evaginable proboscis with long ventral papilla present; 2 suckerarms with more than 10 suckers; stalked flattened suckers (consisting of a suction-disk surrounded by a distinct rim; width of rim about 1/4 of disk); lateral and posterior gills present (only transitory stages and adults); maximum body length: 13 mm.

— Geographical distribution: Atlantic, Mediterranean (present material: Banyuls, Villefranche), Indian Ocean, Pacific.

— Remarks: Specimens of *Pneumoderma mediterraneum* (van Beneden, 1838) were missing from the samples. The main identification character of this species is the presence of suckerarms with less than 10 suckers per arm, even in adults (van der Spoel 1976). According to Pruvot-Fol (1954) this species occurs in the same oceans but is less frequent than *P. atlanticum*.

Pneumoderma sp. Fig. 1 D-E; Pl. I A

— Material: polytrochous larvae (6 spms.; length: 1-1.5 mm); transitory stages (9 spms.; length: 1.5-3.5 mm); adults (2 damaged spms.; length: 5.6-8.0 mm).

Identification characters: body elongated, head smaller than trunk; median footlobe about as long as or shorter than the horseshoe-shaped lateral lobes; lateral and posterior gills present (only older stages).

— Geographical distribution: present material: Banyuls, Villefranche.

— Remarks: As the genus *Pneumoderma* is represented by two different species in the Mediterranean identification to species level was impossible for some specimens in bad shape or with invaginated suckerarms. The main identification character of the genus are the size and shape of the median and lateral footlobes.

Pneumodermopsis Keferstein, 1862

Pneumodermopsis canephora Pruvot-Fol, 1924; Fig. 2 A; Pl. II D-F

Pneumodermopsis canephora Pruvot-Fol 1924:
p. 370, pl. 15 figs. 18-20, pl. 16 figs. 1-10, figs. XVIII-XXV; - Pruvot-Fol 1954: p. 139, figs. 43f, 45c-f; - van der Spoel 1976: p. 69, fig. 66.

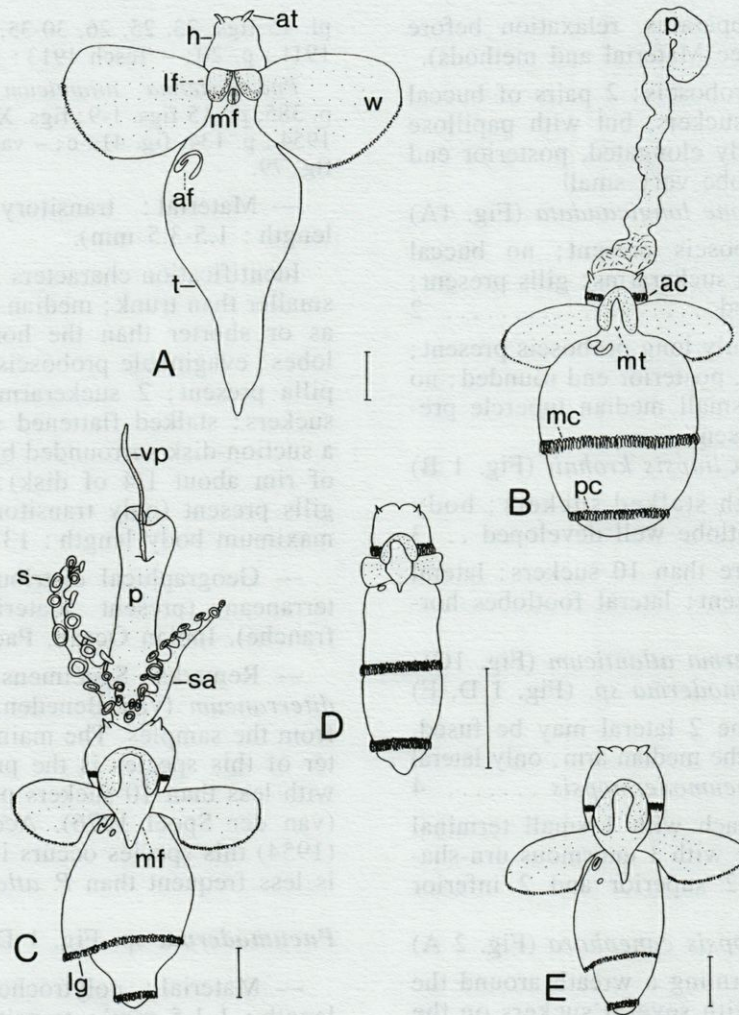


Fig. 1. A, *Paraclione longicaudata*, adult; B, *Cliopsis krohnii*, transitory stage; C, *Pneumoderma atlanticum*, transitory stage; D, E, *Pneumoderma* sp., prehensile organs withdrawn; D, polytrochous larva; E, transitory stage. All specimens presented in ventral view. Bar scales = 500 µm.

Material: polytrochous larvae (6 spms.; length: 0.7-1.5 mm); transitory stages (8 spms.; length: 1.5-3.2 mm).

Identification characters: body elongated, head smaller than trunk; median footlobe as long as or slightly longer than lateral lobes; evaginable proboscis present; 3 arms with stalked suckers, the 2 lateral arms each with a small terminal sucker (flattened, suction-disk surrounded by rim); median arm with 1 enormous urn-shaped terminal sucker, 2 superior and 2 inferior smaller suckers (urn-shaped sucker with a distinct rim covered by papillae, the smaller ones flattened with rim and some tufts of cilia); lateral gill long, reaching sometimes posterior end of body (only in adults), no posterior gill; maximum body length: 12 mm.

Geographical distribution: Atlantic, Mediterranean (present material: Villefranche).

Remarks: One of the investigated specimens, a polytrochous larva, showed a long ventral

papilla on the proboscis. According to Kwietniewski (1902) this feature is present in larvae of the genus *Pneumodermopsis* (resp. *Dexiobranchaea*) but missing in adults. In contrast to the ventral papilla found in all stages of *Pneumoderma* this feature seems to be reduced in adults of *Pneumodermopsis*. Older specimens of *P. canephora* and polytrochous larvae as well as transitory stages of *P. paucidens* and *P. ciliata* from the present material did not show this ventral papilla. Therefore, we suppose that this character is specific for larvae of *P. canephora*, but not for other *Pneumodermopsis* larvae.

Pneumodermopsis ciliata (Gegenbaur, 1855);
Fig. 2 C; Pl. I E-F

Pneumodermon ciliatum Gegenbaur 1855: p. 74, 213.

Dexiobranchaea ciliata - Kwietniewski 1902: p. 45; Kwietniewski 1903: p. 293, pl. 14 figs. 1-5.

Pneumodermopsis ciliata Steuer 1911: p. 19; Tesch 1913: p. 105; Pruvot-Fol 1954: p. 138, figs. 41d-i, 43a, 44; van der Spoel 1976: p. 68, fig. 64.

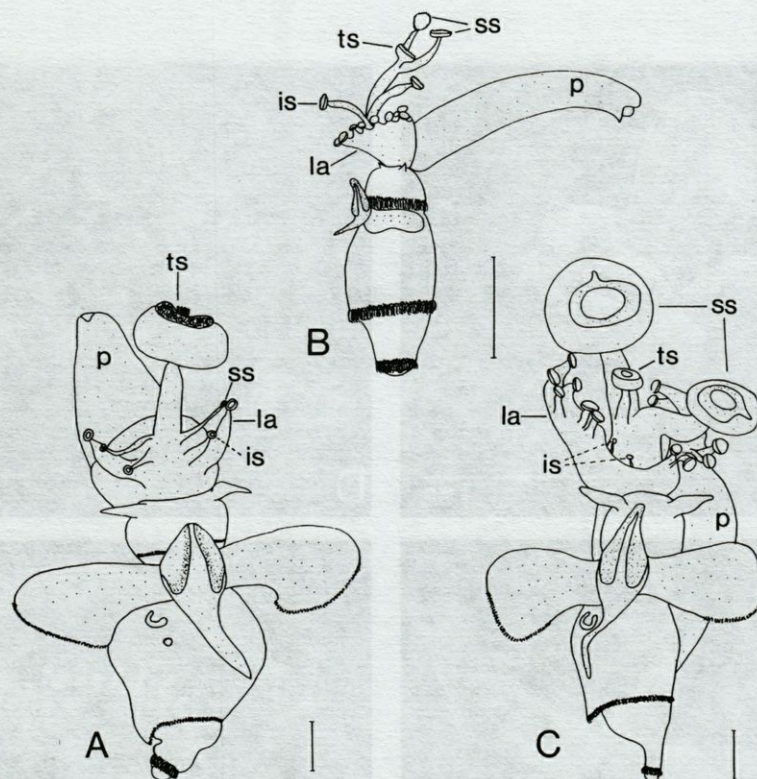


Fig. 2. A, *Pneumodermopsis canephora*, transitory stage; B, *Pneumodermopsis paucidens*, polytrochous larva; C, *Pneumodermopsis ciliata*, transitory stage. All specimens presented in ventral view. Bar scales = 500 μ m.

Material: transitory stages (2 spms.; length: 1.5-2.9 mm).

Identification characters: body elongated, head smaller than trunk; median footlobe much longer than lateral lobes; evaginable proboscis present; 3 arms with stalked suckers, the 2 lateral arms not fused dorsally forming a wreath around the median arm with 6-9 small suckers on its margin (suckers flattened, rimless); median arm with 1 mid-size terminal sucker, 2 large superior and 2 minute inferior suckers (terminal mid-size and large superior suckers cup-shaped with down-turned margin; margin of large suckers characteristically pointed; minute inferior suckers flattened, rimless); lateral gill long, free end reaching almost posterior end of trunk (only in adults), no posterior gill; maximum body length: about 15 mm.

Geographical distribution: Atlantic, Mediterranean (present material: Villefranche), Indian Ocean, Pacific.

Pneumodermopsis paucidens (Boas, 1886)
(Figs. 2 B; Pl. II A-C)

Dexiobranchaea paucidens Boas 1886: p. 160, 223, pl. 7 figs. 105-106; Kwietniewski 1902: p. 46; Kwietniewski 1903: p. 299, pl. 14 figs. 6-9, pl. 15 figs. 22, 46-48.

Pneumodermopsis paucidens Tesch 1913: p. 107; Pruvot-Fol 1954: p. 138, figs. 43c, 45b; van der Spoel 1976: p. 69, fig. 67.

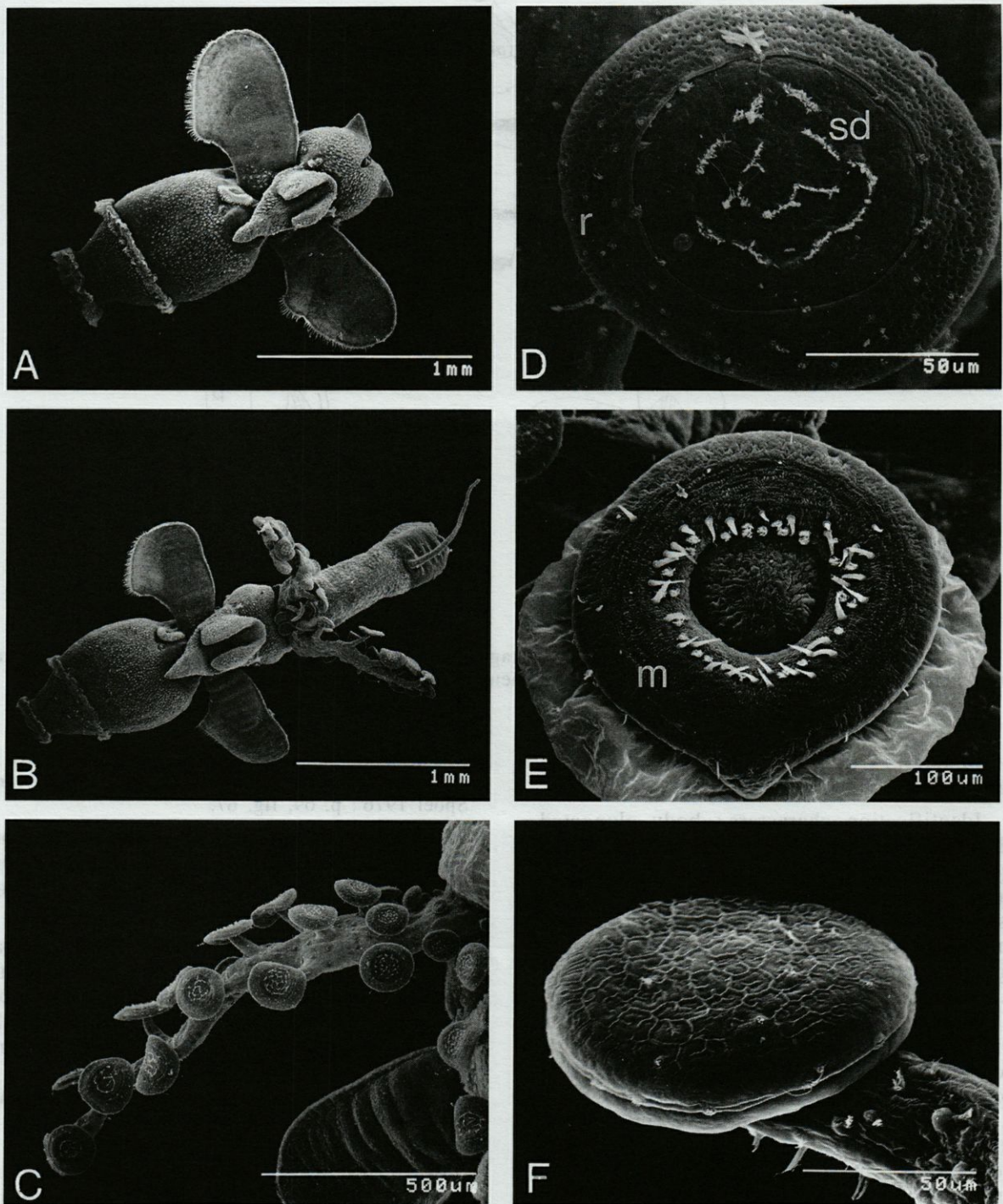
Material: polytrochous larvae (5 spms.; length: 0.7-1.2 mm); transitory stages (5 spms.; length: 2.7-2.8 mm); adults (1 spm.; length: 5.6 mm).

Identification characters: body elongated, slender, head smaller than trunk; median footlobe about as long as lateral lobes; evaginable proboscis present; 3 arms with stalked suckers, the 2 lateral arms fused dorsally forming a wreath around the median arm with 11-13 small flattened suckers on the margin (suckers without rim or indented edge, but showing some cilia); median arm with 1 terminal cup-shaped sucker with down-turned margin as well as 2 superior and 2 inferior flattened suckers, median arm suckers all with indented edge and tufts of cilia; lateral gill very short (present only in older stages), no posterior gill; maximum body length: about 6 mm.

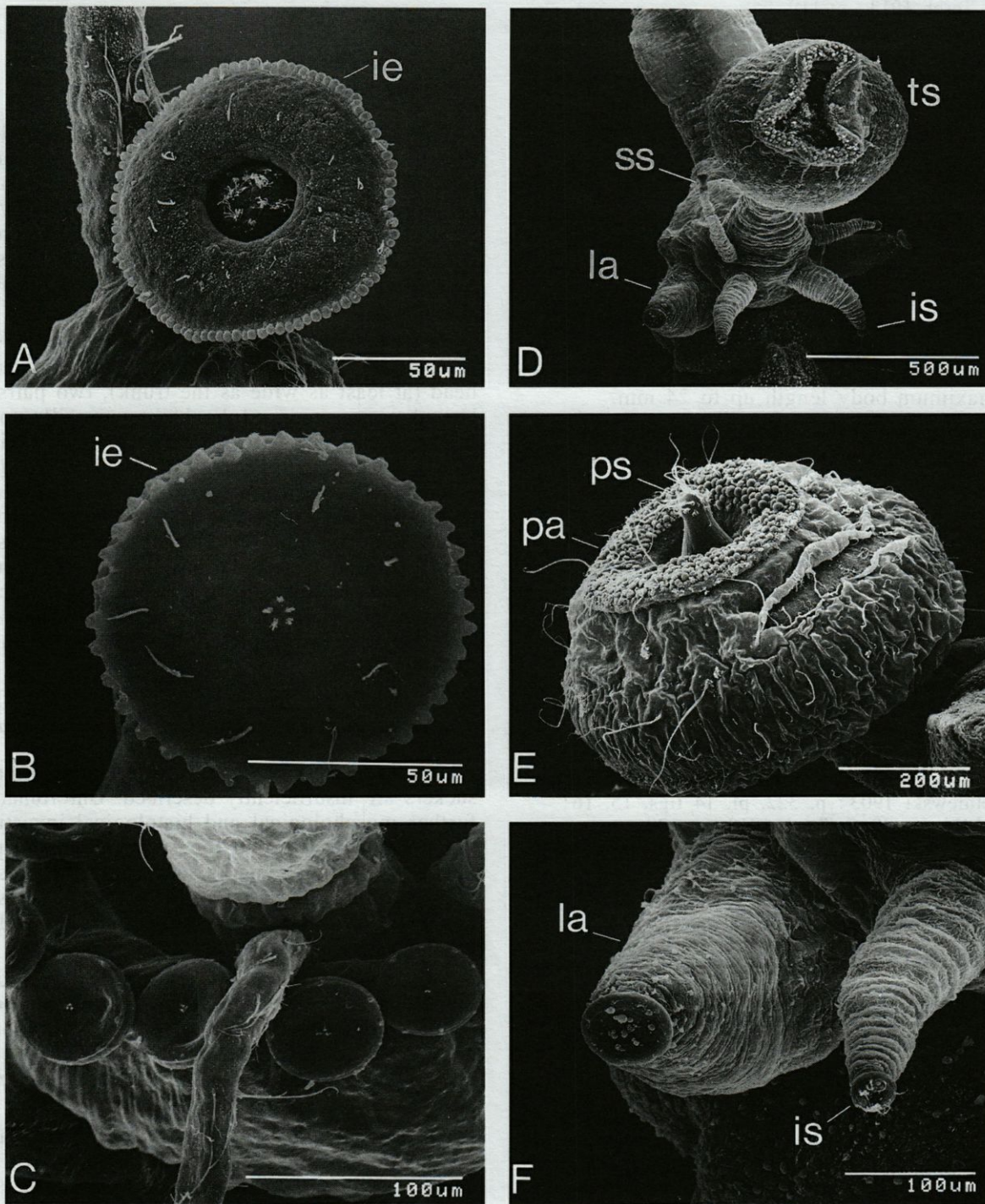
Geographical distribution: Atlantic, Mediterranean (present material: Banyuls, Villefranche), Indian Ocean.

Cliopsidae Costa, 1873

Cliopsis Troschel, 1854; (Fig. 1B)



Pl. I. A, *Pneumoderma* sp., transitory stage; specimen with prehensile organs withdrawn (ventral view). B-D, *Pneumoderma atlanticum*, transitory stage; B, specimen with protruded suckerarms and proboscis (ventral view); C, suckerarm with stalked flattened suckers; D, sucker consisting of suction-disk and rim. E, F, *Pneumodermopsis ciliata*, transitory stage; E, large superior cup-shaped sucker of median arm with down-turned margin; F, flattened, rimless sucker of lateral arm.



Pl. II. A-C, *Pneumodermopsis paucidens*, polytrochous larva; A, terminal cup-shaped sucker of median arm with indented edge; B, superior flattened sucker of median arm with indented edge; C, small flattened, rimless suckers of fused lateral arms. D-F, *Pneumodermopsis canephora*, transitory stage; D, enormous urn-shaped terminal sucker of median arm in contrast to the superior and inferior median arm suckers and the lateral arm suckers; E, urn-shaped sucker of another specimen showing piston and rim covered by papillae; F, flattened terminal sucker of lateral arm and inferior sucker of median arm showing small rim and cilia.

Cliopsis krohnii – Troschel 1854 : 222, pl. 10 figs. 1-12; – Tesch 1913 : p. 119.

Clionopsis krohni – Kwietniewski 1902 : p. 45; – Kwietniewski 1903 : p. 314.

Cliopsis krohni – Pruvot-Fol 1924 : p. 353, pl. 15 fig. 12, figs. II-IX; – Pruvot-Fol 1954 : p. 145, figs. 48, 49a; – van der Spoel 1976 : p. 93, fig. 100.

— Material : transitory stage (1 spm.; length : 1.3 mm).

— Identification characters : body short cylindrical, posterior end rounded, head smaller than trunk; no median footlobe, but median tubercle present, lateral lobes horseshoe-shaped; very long evaginable proboscis present (about twice as long as body); no buccal cones or suckerarms; posterior gill present (only in older stages), no lateral gill; maximum body length up to 24 mm.

— Geographical distribution : Atlantic, Mediterranean (present material : Villefranche), Indian Ocean, Pacific.

Clionidae Gray, 1840

Clioninae Pruvot-Fol, 1926

Paraclione Tesch, 1903

Paraclione longicaudata (Souleyet, 1852)
(Fig. 1A)

Clione longicaudatus Souleyet, 1852 : p. 286.

Clione longicaudata – Kwietniewski 1902 : p. 46; – Kwietniewski 1903 : p. 322, pl. 14 figs. 15, 16; – Steuer 1911 : p. 20; – Tesch 1913 : p. 129.

Clionina longicaudata – Pruvot-Fol 1924 : p. 364, pl. 15 figs. 15-17, figs. XIV-XVII.

Paraclione longicaudata – Pruvot-Fol 1954 : p. 150, figs. 52d-e; – van der Spoel 1976 : p. 106, fig. 117.

— Material : adults (2 spms.; length : 2.0-4.0 mm).

— Identification characters : body long and slender, posterior end pointed; head smaller than trunk; median footlobe very small, median tubercle present; no evaginable proboscis; 2 pairs of buccal cones (arms without suckers, but with papillose surface); no gills; body covered by black chromatophores; maximum body length : up to 10 mm.

— Geographical distribution : Atlantic, Mediterranean (present material : Villefranche), Indian Ocean.

— Remarks : Specimens of *Paraclione flavescens* (Gegenbaur, 1855) were missing in the samples. Due to their distinct median footlobe and larger body size (maximum body length : 22 mm) they can easily be separated from those of *P. longicaudata* (see Tesch 1913). According to Pruvot-Fol (1954) *P. flavescens* is rare in the Mediterranean.

GENERAL REMARKS

1. Further clionid species missing in the samples

Thliptodon gegenbauri Boas, 1886 (Thliptodontinae) : main identification characters : large head (at least as wide as the trunk), no buccal cones or suckerarms, large hooksacs, no gills; bathypelagic, only found near Messina where numerous bathypelagic animals were captured near the surface (Kwietniewski 1902, 1903; Tesch 1913; Pruvot-Fol 1924, 1954).

Thalassopterus zancleus Kwietniewski, 1910 (Clioninae) : main identification characters : large head (at least as wide as the trunk), two pairs of buccal cones, reduced hooksacs, no gills (only larvae found near Messina by Kwietniewski in 1910). According to Pruvot-Fol (1954) *T. zancleus* could be a young form of *Thliptodon gegenbauri* as their radula formula is similar. The described cones could be other developing larval organs or may be these cones are only present in young specimens but reduced in older ones. Unfortunately the development and anatomy of *Thliptodon* have never been completely investigated to check this hypothesis.

2. The suckers of pneumodermatid gymnosomes

The structure and function of pneumodermatid suckers are insufficiently described. Unfortunately, further morphological and histological investigations would be beyond the scope of this paper, but the following remarks summarize the present knowledge mainly based on the works of Meisenheimer (1905) and Pruvot-Fol (1924) as well as our own SEM-studies.

All pneumodermatid suckers are stalked, some with long stalks (e.g. terminal suckers of *Pneumodermopsis* (Figs. 2 A-C)), others with shorter ones (e.g. suckers of *Pneumoderma* (Fig. 1 C, Pl. I C) or lateral arm suckers of *Pneumodermopsis ciliata* (Pl. I F) or *P. paucidens* (Pl. II C)).

Suckers of *Pneumoderma atlanticum* are flattened suction-disks surrounded by a rim (Pl. I D). Tufts of cilia are found on the whole sucker surface; they are not mentioned in Meisenheimer (1905). According to this author the rim consists of an epithelium, secretory cells and bundles of ring musculature, while the disk is formed only by radial musculature covered by a thin epithelium. Meisenheimer described the function of the suckers as follows : Beneath the radial musculature of the disk another layer of muscles is found whose contraction forces the sucker against the surface of the prey. The ring muscles of the rim prevent the lateral extension of the disk. Under the pressure of contraction forces the disk be-

comes arched forming a suction chamber, while the rim covered by secretions of the secretory cells remains in tight contact with the prey.

Pneumodermopsis canephora is characterized by an enormous urn-shaped terminal sucker on the median arm (Pl. II D-E). This sucker shows a distinct rim covered by papillae. According to Pruvot-Fol (1924) the rim is containing large secretory cells, but no ring musculature is mentioned as described for suckers of *Pneumoderma* by Meisenheimer (1905). A very unique feature of the urn-shaped sucker is a piston fastened to the base of the sucker cavity. The tip of the piston and the outer surface of the sucker show some long cilia. In contrast to this enormous sucker the remaining ones (i.e. the superior and inferior median arm suckers and the terminal lateral arm suckers) appear reduced as well in size as in shape (Pl. II D, F). They are flattened showing a rim and some tufts of cilia.

In contrast to the suckers of *Pneumoderma atlanticum* those of *Pneumodermopsis ciliata* are more simply structured. According to Meisenheimer (1905) the small flattened (Pl. I F) as well as the larger cup-shaped suckers (Pl. I E) consist only of radial musculature covered by a thin epithelium. No secretory cells were found by this author. The down-turned margin of the cup-shaped suckers shows tufts of cilia which have not been mentioned before.

The suckers of *Pneumodermopsis paucidens* have never been investigated histologically. Our SEM-studies show that the median arm suckers of *P. paucidens*, i.e. the cup-shaped terminal (Pl. II A) and the flattened superior and inferior suckers (Pl. II B), form a characteristically indented edge which has not been described before, whereas, the flattened lateral arm suckers show a smooth edge (Pl. II C). All suckers of this species are covered by tufts of cilia.

Pneumodermatid suckers are unique in shape and structure and are not to be considered homologous to the suckers of cephalopods. Together with the chromatophores found in the Clionidae these features represent anatomical similarities to cephalopods. They are the results of convergent evolution and do not point to a closer phylogenetic relationship between gymnosomes and cephalopods (Lalli & Gilmer 1989). As in decapod cephalopods suckers of pneumodermatids are stalked, but the latter do not show an acetabulum lined by a thick inner ring nor an infundibulum covered by cuticular polygonal processes. The large cup- or urn-shaped *Pneumodermopsis* suckers resemble those of the vampyromorph cephalopods which are simple unstalked cups with radial musculature forming an acetabulum covered by a thin epithelium (the structure of cephalopod suckers has been investigated by e.g. Nixon & Dilly 1977 and Kier & Smith 1990).

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Abbreviations

ac : anterior ciliary band; af : anal field; at : anterior tentacle; h : head; ie : indented edge; is : inferior sucker; la : lateral arm; lf : lateral foot-lobe; lg : lateral gill; m : margin; mc : median ciliary band; mf : median footlobe; mt : median tubercle; p : proboscis; pa : papillae; pc : posterior ciliary band; ps : piston; r : rim; s : sucker; sa : suckerarm; sd : suction-disk; ss : superior sucker; t : trunk; ts : terminal sucker; vp : ventral papilla; w : wing.

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