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THE DIDEMNID ASCIDIAN FAUNA OF FRANCE

BY

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KEY-WORDS : Fauna of France
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Taxonomy

MOTS-CLÉS : Faune de France
Ascidies Didemnidae
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Abstract

The 27 Didemnid species found on the French coasts are described and illustrated in drawings, according to the probable sequence of the appearance of the genera in the course of evolution. One of these species, *Diplosoma carnosum* Von Drasche, 1883, was only found recently on the French coasts. A new synonymy has been established between *Polysyncraton asterix* Monniot, 1974, and *Polysyncraton canetense* Brément, 1913. We recall the problems of identification characterizing this very homogeneous group of Ascidiens, and give simplified diagnoses of genera and species.

The main evolutionary trend consists of a gradual coiling of the sperm duct seemingly correlated with a lengthening of the alimentary canal, accompanied by a decrease in the number of tentacles around the base of the oral siphon and a general reduction in zooid size.

The Didemnids originate from the family of the Polycitoridae : thus, the present tropical genus *Echinoclinum*, the oldest of the Didemnids, is a descendant of the Polycitorid genus *Cystodytes*. *Echinoclinum* existed in what is now France during the Eocene age (upper Ypresian, Cuisian, of the Paris Basin), but has now disappeared from the French coasts.

Résumé

Faune de France des Ascidies Didemnidae.

Les 27 espèces de Didemnidae des côtes de France sont présentées à l'aide d'illustrations et selon l'ordre probable d'apparition des genres au cours de l'évolution. Parmi ces espèces, une est nouvelle pour les côtes de France, *Diplosoma carnosum* Von Drasche, 1883. Une synonymie nouvelle est établie entre *Polysyncraton asterix* Monniot, 1974, et *P. canetense* Brément, 1913. La direction évolutive principale des espèces françaises est celle de l'enroulement graduel du spermiducte, corrélé à l'allongement du tube digestif, à la perte du quatrième rang de stigmates branchiaux et à la diminution du nombre de tentacules buccaux. Les difficultés d'identification propres à ce groupe très homogène d'Ascidies sont rappelées ainsi que la diagnose simplifiée des genres et des espèces. L'origine des Didemnidae est à rechercher dans la famille des Polycitoridae. Le genre tropical actuel *Echinoclinum*, le plus ancien des Didemnidae, dérive du genre *Cystodytes* qui appartient à la famille des Polycitoridae. Ce genre *Echinoclinum* a existé « en France » à l'Eocène (Yprésien supérieur, Cuisien, du bassin de Paris). Il a maintenant disparu des côtes de France.

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INTRODUCTION

General considerations

This paper is a synthesis of the results obtained during a systematic review of the Didemnid Ascidians of the French coasts; it includes 27 species. The Ascidian fauna of France by HARANT and VERNIÈRES (1933) comprises 24 species. The species of the two faunas are often classified in different ways, due to the revision of the nomenclature.

Only three species have remained unchanged: *Didemnum lahillei*, *D. protectum* and *D. peyrefittense*. Modifications concerning the other species were dealt with in a previous work (LAFARGUE, 1977).

The particular feature of the present revised nomenclature is its redefinition of the morphological species of Didemnid Ascidians by pursuing the enquiry to its very limits, i.e. going back to the sources and conducting a direct comparative investigation of populations collected alive by SCUBA diving at the « type-localities » indicated for each species of the Ascidian fauna by HARANT and VERNIÈRES (1933). This method is not exhaustive because only the chief « type-localities » could be explored to any satisfying extent; it was completed by the indispensable examination of the « type-specimens ». This allowed better interpretation of the data in the literature. Except in a few cases, the use of these data alone does not permit any definite identification of the species. The reasons are numerous; they include the variability of the appearance of the colonies within the same species, the small size of the zooids (1-2 mm), the muscular contraction of the thoraces (when the anaesthesia was not perfect), and the resemblance between different species belonging to the same genus. All these factors made it necessary to introduce the notion of a « morphological species » in relation to the Didemnid Ascidians.

The morphological species in the Didemnid Ascidians

By « morphological species » we mean the taxonomic entities principally defined by morphological characters. In this study, most of the species were established by

comparative examination of several hundred colonies, collected by SCUBA diving at a depth of 0 to 50 m from a variety of habitats (rocks, boulders, seagrass, etc.).

Any systematician familiar with modern conceptions of taxonomy (GENERMONTE, 1980) and with the biological concept of the species (GENERMONTE and LAMOTTE, 1980) will sooner or later come up against the limitations imposed by the use of morphological characters for species separations (BLANDIN, 1980).

Nevertheless, the study of these characters remains the indispensable first stage in the identification of a species. It allows the initial separation of material that may then be submitted to karyological, biochemical or mixiological criteria. Although karyological studies of Ascidians are not yet very advanced, it should be noted that the largest number of chromosomes found in Ascidians ($2n=52$) was discovered in *Polysyncraton lacazei*, a Didemnid species (COLOMBERA and LAZAROTTO-COLOMBERA, 1978).

The conduct of mixiological investigations requires previous elimination of the particular problems relating to these slightly protandric, hermaphrodite species which do not thrive in the aquarium.

Biochemical criteria have not so far been investigated in connection with Ascidians.

Identification of the morphological species comprises two phases: during the first, its definition is established by the identification of a cluster of morphological criteria which are constant but not necessarily present throughout the developmental cycle. This set of characteristics can only be defined by comparing comparable taxonomic units in a large number of colonies, such as zooids at the same degree of extension, maturity and conservation, or larvae in the same phase of development. The second phase of morphological species identification consists in defining the new taxonomic unit's position among existing species.

The polymorphism of Ascidian species makes this definition tricky. The most stable characters are those relating to zooid and larval structure. They can only be visualized by microscope study and are much less conspicuous than colony characters such as size, shape or colour. Unfortunately, however, the latter vary

considerably and therefore constitute an unreliable basis for classification. The factors of variation are numerous and closely imbricated. They include the nature of the substratum, trophic conditions, degree of illumination, hydrodynamics, etc.

Each species exhibits what is termed a typical form when environmental conditions are optimal. In this case, colony size and thickness are at their maximum and the zooids are fully formed and functional. When conditions are unfavourable, colonies survive in a modified habitus. In extreme cases, colonies are thin and resinous in appearance, and their zooids are reduced to an abdomen, the thorax having disappeared. Other differences concern colour, and here the variations found are probably not entirely due to the presence (or absence) of pigments but also to the degree of illumination. Most species have a basic tint described as typical. In some cases, this basic colour varies within one and the same colony to form patterns of different shades, or it may disappear completely, leaving the zooids and tunica colourless. In other cases, colour can vary radically. Thus, as an extreme example, each colony of *Didemnum maculosum* displays a different tint which may be violet, white, black, brown, rosy, etc. However, although colour is the most conspicuous criterion, it is in fact the least reliable and should only be regarded as a preliminary indication. As already mentioned, colour varies within the same species. Conversely however the same shade may be displayed by two different species which can even belong to different genera. This is illustrated by the examples of *Trididemnum cereum*/*Didemnum protectum* (Pl. XI) and *Polysyncraton lacazei*/*Didemnum fulgens* (Pl. IX, C1, C2).

Consequently, the characteristics allowing identification of a species are those not directly subject to environmental variations. This is the case for the zooids and larvae, which are embedded in the common tunica.

The spicules occupy an intermediate position, as their form is typical for each species, but their density varies with age and environment. For example, when *Didemnum fulgens* is present in the infralittoral fringe (the first two metres of depth), it forms small soft colonies with few spicules; but deeper down, the colonies are large, hard and rich in spicules. However, while the structure of the spicules is specific, they are not easy to identify for two reasons: firstly, they are very similar in species of the same genus, and secondly, they vary slightly within the same colony depending on age and position, since spicules are formed in the

spiculogenic organs of the zooids, then migrate into the tunica and grow in size. Spicule size also depends on the « generation rank » of the zooid producing them: thus, the spicules of the first blastozooid are bigger than those of the oozoid.

In short, there are no two strictly identical specimens, and two colonies of the same species will differ according to age, physiological stage, season and environment. Knowledge of the amplitude of intraspecific variability can only be acquired by studying the largest possible number of colonies, collected in different biotopes and in a variety of geographical zones (the description of species which follows is based on the study of some 10,000 colonies).

Two populations will be considered as belonging to two distinct species if at least one constant morphological difference permits their distinction. The finding of forms intermediate between two species proves the non-validity of such a distinction. This method leads to a reliable but approximate division of species. It may be open to criticism for distinguishing too few species, but it certainly does not create too many. *Didemnum maculosum*, for example, covers a whole complex of genetic species which could not be split up on the basis of morphological and anatomical characteristics only, and includes at least two species of parasitic Notodelphyid copepods belonging to the genus *Anoplodelphys* (LAFARGUE and LAUBIER, 1978). In the light of our present knowledge of host-parasite relations in Didemnids, this seems to suggest the existence of chemical means by which these *Anoplodelphys* copepods « recognize », within the *Didemnum maculosum* complex, two different species which, to the systematist, look identical. In the case of the host-parasite relationships between Didemnids and Notodelphyids, they are indeed of three different types:

1) Generally, copepods display a strictly parasitic specificity which means that one copepod species is associated with only one species of Didemnid Ascidian. Thus, two closely related Ascidian species of the same genus are parasited by two closely related copepod species of the same genus. These characteristics suggest a host-parasite coevolution.

2) One Ascidian species may harbour two copepod species, but in that case they will belong to different genera.

3) The same copepod species may associate with different Didemnid species. This is true of *Ooneides amela*, but such cases are few.

The difficulties involved in identifying Didemnid Ascidians explain why all these species, whatever their genus, have been confused in the past. These difficulties are not always the same; thus, for a given genus, they may vary with the degree of species divergence. During evolution, the interspecific/intrageneric distance shrinks, and the most specialized or so-called recent species become the least distinguishable. This category includes species belonging to the genera *Didemnum* and *Trididemnum*, and indeed most of these species rarely exhibit an original criterion permitting their rapid distinction from the other species of the genus.

The exceptions are *Trididemnum cf. savignyi* which has a long thoracic appendix which is tiny in the other three species of the genus, and *Didemnum coriaceum* whose wing-shaped spiculogenic organs are horizontal and not, as in the other species, vertical.

In view of this disconcerting homogeneity of the Didemnid species, it would be illusive to try and identify them in an unfamiliar geographical zone, where only the identification of genera is possible. To distinguish between species it would be necessary to undertake a comparative study of the populations of all the species of this genus in the region concerned. This type of investigation requires the collection by SCUBA diving of intact colonies with their supports, which must then be suitably anaesthetized and preserved.

Consequently, the keys to the identification of the French species described in this paper should be used with caution by non-experts or for work in regions other than the French coasts.

It is no easier to determine the ecological requirements of the Didemnid Ascidians than to define the different species. Their distribution is varied and sometimes general (except for that of *Didemnum pseudofulgens*). Thus, *Lissoclinum perforatum* is found at any depth between the surface and 150 m or more; whereas on the Roches de Toreilles (32 m down, Banyuls area) colonies belonging to 9 species of the genus *Didemnum* live side by side on the same *Cystoseira* thallus or even superimposed in epibioses of the 2nd, 3rd and 4th degree.

Although it is difficult to separate the different species of Didemnidae because of their similarity but this resemblance allows detection of the phyletic bonds. It is interesting to note that the structure of the tentacular crown is a characteristic element both of the genus and of the species intermediate between two genera.

The sequence in which the genera and species are listed in this work corresponds to the gradual coiling of the sperm duct which seems to indicate the evolutionary trend in this family (LAFARGUE, 1983).

For each species, the order of the characters described corresponds to their degree of reliability; consequently the most reliable (zooids and larvae) come first, and the least reliable (colonies), last.

The colour photographs in the different plates were taken by SCUBA divers near Banyuls-sur-mer (Pyrénées-Orientales) using a Nikonos III camera with a 28 mm objective and a ring for 1.1 amplification. The diving mask had a magnifying-glass.

LIST OF SPECIES DESCRIBED

Echinoclinum brachiatus (Buge et Monniot, 1972) :
fossil species

Lissoclinum perforatum (Giard, 1872)

Lissoclinum weigelei Lafargue, 1968

Diplosoma singulare Lafargue, 1968

Diplosoma carnosum Von Drasche, 1883

Diplosoma listerianum (Milne Edwards, 1841)

Diplosoma spongiforme (Giard, 1872)

Polysyncraton haranti Lafargue, 1975

Polysyncraton canetense Brément, 1913

Polysyncraton lacazei (Giard, 1872)

Polysyncraton bilobatum Lafargue, 1968

Didemnum fulgens (Milne Edwards, 1841)

Didemnum drachi Lafargue, 1975

Didemnum pseudofulgens Médioni, 1970

Didemnum peyrefittense Brément, 1913

Didemnum commune (Della Valle, 1877)

Didemnum granulosum (Von Drasche, 1883)

Didemnum coccineum (Von Drasche, 1883)

Didemnum amourouxi Lafargue, 1976

Didemnum coriaceum (Von Drasche, 1883)

Didemnum lahillei (Hartmeyer, 1909)

Didemnum maculosum (Milne Edwards, 1841)

Didemnum protectum (Daumézou, 1908)

Trididemnum cf. savignyi (Herdman, 1886)

Trididemnum cereum (Giard, 1872)

Trididemnum inarmatum (Von Drasche, 1883)

Trididemnum delesseriae Lafargue, 1968

Didemnopsis translucidum Lafargue, 1968

INVENTORY OF SPECIES

Genus **ECHINOCLINUM** Van Name, 1902

Incompletely known genus, adult similar to *Lissoclinum* and gemmiparous larvae.

Echinoclinum brachiatus

(Buge et Monniot, 1972)

(Pl. IV : A)

Synonymy and description :

Cystodytes (?) *brachiatus* Monniot et Buge, 1972 p. 86.

Description concerns the shape of fossil spicules from the Paris Basin, Eocène (Ypresian, Cuisian Period).

Distribution : today the genus *Echinoclinum* has a tropical distribution and is not found on French coasts. In the Philippine Islands there is one species *Echinoclinum philippinense* Tokioka, 1967, quite similar to *E. brachiatus* by the shape of the spicules (Pl. IV : B).

Genus **LISSOCLINUM** Verrill, 1871

Brief diagnosis of the genus : tentacular crown : 20-26 tentacles of 5 orders, orders 4 and 5 incomplete.

Sperm duct straight, middle gut cylindrical and bent.

Spiculogenic wing-shaped organs between the 2nd and 3rd rows of stigmata, spicules present.

Four rows of stigmata.

No thoracic appendix.

Non-gemmiparous larvae with four rows of stigmata; larval test : not transparent.

Lissoclinum perforatum (Giard, 1872)

(fig. 1 : A, B, C; Pl. I : F;

Pl. V : A, C; Pl. VII : D)

Synonymy :

Leptoclinum perforatum Giard, 1872 p. 152.

Diplosoma pseudoleptoclinum Von Drasche, 1883 p. 39.

Lissoclinum argyllense Millar, 1950 p. 389.

pars Lissoclinum pseudoleptoclinum HARANT, 1927 p. 221; HARANT, 1930 p. 287-288; HARANT and VERNIÈRES, 1933, p. 74 and p. 15, fig. 20.

Didemnum perforatum HARANT and VERNIÈRES, 1933, p. 69 and p. 67, fig. 77.

Lissoclinum pseudoleptoclinum PÉRÈS, 1959, p. 303; PÉRÈS, 1948, p. 60; PÉRÈS, 1952, p. 41.

Lissoclinum argyllense LAFARGUE, 1968, p. 422; 1975c, p. 292.

Lissoclinum argyllense MÉDIONI, 1970, p. 45.

Material studied : 150 colonies.

Simplified diagnosis of the species : absence of cloacal languet.

Single-lobe testicle (under right side of thorax) (LAFARGUE and LAUBIER, 1980).

Flabellate spicules, densely distributed.

Larvae with 4 pairs of lateral ampullae and 3 adhesive papillae.

Colonies : flat, smooth; mostly white, grey or pinky-beige, occasionally yellow or sea-green; rims without white borders.

Description : LAFARGUE, 1975c, p. 292.

Ecology : eurybathic; from the infralittoral fringe, fouling of ship hulls in harbours down to the bathyal zone (biocoenosis of rocks in open sea, Canyon de la Cassidaigne, Marseilles region).

Distribution (fig. 8) : English Channel (Roscoff), Atlantic Ocean (Glenan Archipelago, Saint-Jean-de-Luz) and Mediterranean Sea (Banyuls, Marseilles, Port-Cros).

Lissoclinum weigelei Lafargue, 1968

(fig. 1 : D, E, F; Pl. I : C; Pl. V : D;

Pl. VI : A)

Synonymy :

Lissoclinum weigelei Lafargue, 1968 p. 429; 1975c p. 298.

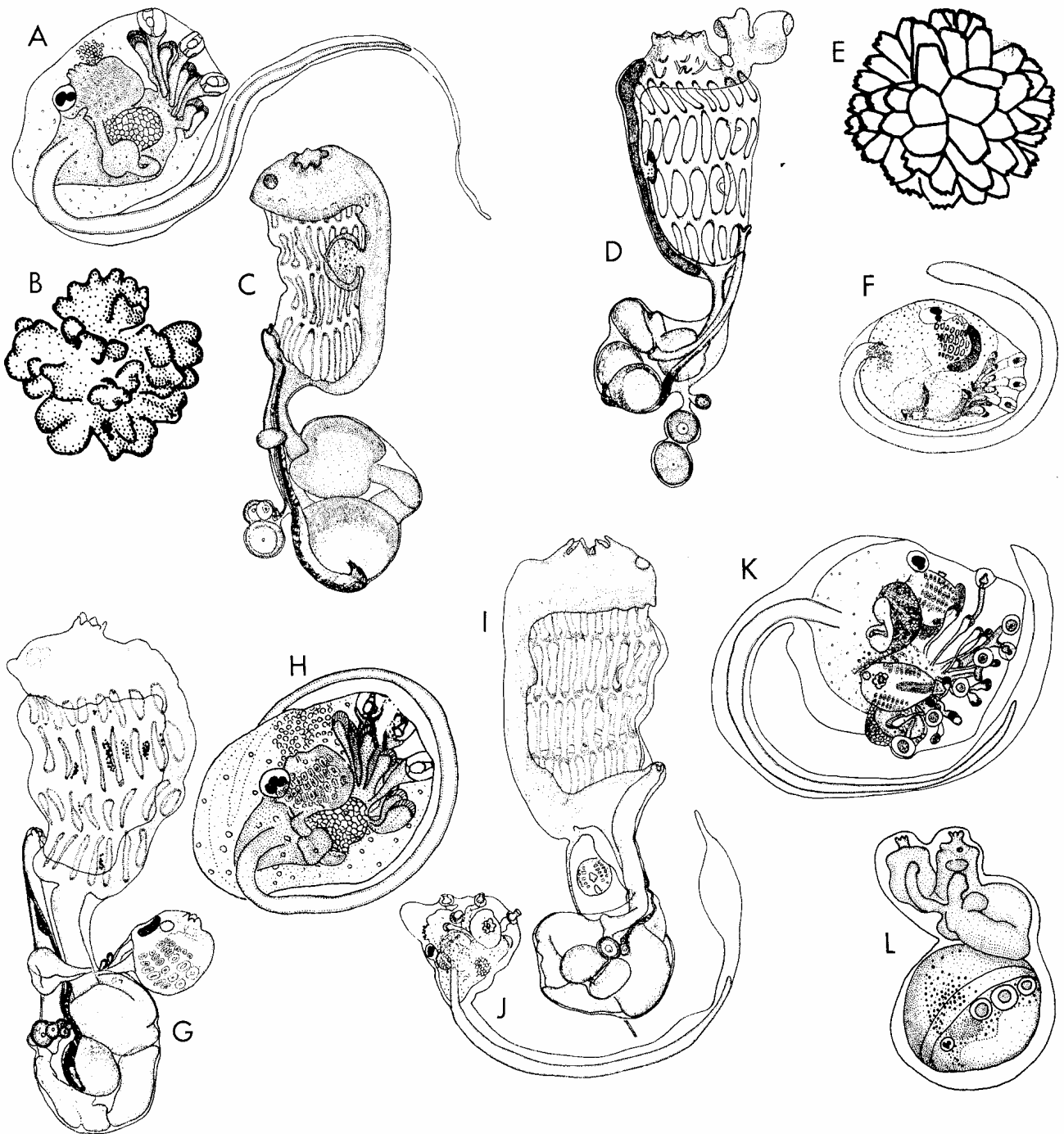


FIG. 1. — *Lissoclinum perforatum* (Giard) : A, larva; B, spicule; C, zooid.
Lissoclinum weigelei Lafargue : D, zooid; E, spicule; F, larva.
Diplosoma singulare Lafargue : G, zooid; H, larva.
Diplosoma listerianum (Milne Edwards) : I, zooid; J, larva.
Diplosoma spongiforme (Giard) ; K, larva; L, zooid.

FIG. 1. — *Lissoclinum perforatum* (Giard) : A, larve; B, spicule; C, zoïde. *Lissoclinum weigelei* Lafargue : D, zoïde; E, spicule; F, larve.
Diplosoma singulare Lafargue : G, zoïde; H, larve. *Diplosoma listerianum* (Milne Edwards) : I, zoïde; J, larve. *Diplosoma spongiforme* (Giard) : K, larve; L, zoïde.

Lissoclinum weigelei Médioni, 1970 p. 45.

but not *Lissoclinum fragile* (Van Name, 1902) which according to its spicule structure comprises several distinct species found on the Island of Guadeloupe (LAFARGUE and LAUBIER, 1980, Pl. VII, 17 and MONNIOT, 1983, Pl. V F).

Material studied : 220 colonies.

Simplified diagnosis of the species : small cloacal languet.

Two-lobed testicle on left side (under left side of thorax). Presence of acicular spicules.

Larvae with 9 lateral ampullae and 3 adhesive papillae.

Colonies : soft and fragile. Spicules give them a powdery appearance; colour : beige, white spotted with black or brown; rims with white borders.

Description : LAFARGUE, 1975c, p. 298.

Ecology : near-surface caves, projecting rocks faces in the infralittoral zone, horizontal rock faces on the Roches de Tavac (Banyuls region).

Distribution (fig. 8) : Atlantic Ocean (Glenan Archipelago, Saint-Jean-de-Luz) and Mediterranean Sea (Banyuls, Port-Cros).

Genus **DIPLOSOMA** Mac Donald, 1859

Brief diagnosis of the genus : tentacular crown comprising 20-26 tentacles of 5 orders, orders 4 and 5 incomplete.

Straight sperm duct; cylindrical bent middle gut.

Absence of spiculogenic organs and spicules.

Four rows of stigmata.

Thoracic appendix present, except for *D. singulare*.

Absence of cloacal languet.

Larvae : gemmiparous with one blastozoid, except for *D. singulare*, and four rows of stigmata.

Diplosoma singulare Lafargue, 1968

(fig. 1 : G, H)

Synonymy :

Diplosoma singulare Lafargue, 1968 p. 409.

Material studied : 7 colonies.

Simplified diagnosis of the species : intermediate species between the genera *Lissoclinum* and *Diplosoma*. All characters are those of *Lissoclinum perforatum* except for the absence of spiculogenic organs and spicules.

Larvae with 4 to 5 pairs of lateral ampullae and 3 adhesive papillae.

Colonies : soft and transparent. Their bright orange colour is due to pigmentation of the zooids.

Description : LAFARGUE, 1968 p. 409.

Ecology : rare. On supple fronds of red algae.

Distribution (fig. 8) : Atlantic Ocean (Glenan Archipelago).

Diplosoma carnosum Von Drasche, 1883

(fig. 2)

Synonymy :

Diplosoma carnosum Von Drasche, 1883 p. 41.

pars Diplosoma gelatinosum var. *spongiforme* sub. var. *carnosum* HARANT and VERNIÈRES, 1933 p. 74.

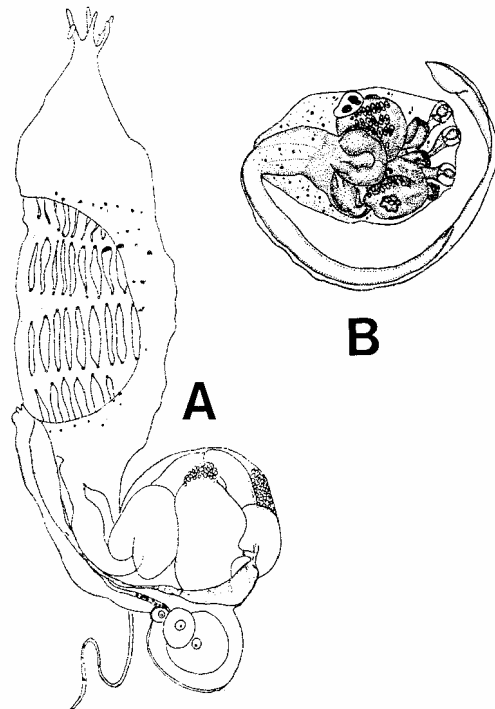


FIG. 2. — *Diplosoma carnosum* Von Drasche : A, zooid; B, larva.

FIG. 2. — *Diplosoma carnosum* Von Drasche : A, zoïde; B, larve.

? *pars Diplosoma listerianum carnosum* form PÉRÈS, 1956a, p. 282.

Diplosoma carnosum LAFARGUE and VALENTICIC, 1973 p. 139.

Material studied : 40 colonies.

Simplified diagnosis of the species : has the characteristics of the genus.

Long subendostylar thoracic appendix.

Testicle divided into 2-5 follicles, topped by a « supra-testicular » gland.

Larvae with 2-4 pairs of lateral ampullae on either side of 3 adhesive papillae.

Colonies : slightly translucent, white, grey, pinky-beige or light brown. Enveloping and thick (layer up to 8 cm thick).

Description : LAFARGUE and VALENTICIC, 1973 p. 139.

Ecology : various substrata on detrital sediments. On August 27, 1984, this species was collected by trawlings, at depths of 27 to 70 m. The colonies were attached to agglomerations of the serpulid *Protula tubularia* Montagu.

Distribution (fig. 8) : Banyuls (Mediterranean Sea). This is the first reference to this species outside its « type-locality » in the Northern Adriatic Sea (Rovinj, Yugoslavia).

Diplosoma listerianum (Milne Edwards, 1841)

(fig. 1 : I, J; Pl. VI : D)

Synonymy :

Diplosoma listerianum LAFARGUE, 1968 p. 406; LAFARGUE, 1975c p. 301.

pars Diplosoma listerianum PÉRÈS, 1956a p. 282.

pars Lissoclinum pseudoleptoclinum PÉRÈS, 1956b p. 7.

Material studied : 180 colonies.

Simplified diagnosis of the species : has the characteristics of the genus.

Long, subendostylar thoracic appendix.

Two-lobed testicle on left side.

Ovaries with several eggs; segmentation of eggs in the common tunica at the base of the colony.

Larvae with 2 pairs of lateral ampullae and 3 adhesive papillae.

Colonies : transparent, with or without white pigmented granulations.

Description : LAFARGUE, 1975c p. 301.

Ecology : Infralittoral fringe, on rigid substrata such as hulls of ships in harbours, or deeper, on flexible substrata and, very occasionally, on rigid substrata.

Distribution (fig. 8) : English Channel (Roscoff), Atlantic Ocean (Glenan Archipelago, Arcachon) and Mediterranean Sea (Banyuls, Port-Cros).

Diplosoma spongiforme (Giard, 1872)

(fig. 1 : K, L; Pl. V : B2;

Pl. VI : B, C)

Synonymy :

Astellium spongiforme Giard, 1872 p. 157.

Diplosoma spongiforme LAHILLE, 1890 p. 123.

Diplosoma chamaeleon Von Drasche, 1883 p. 40.

Lissoclinum cupuliferum Kott, 1952 p. 79.

Diplosoma cupuliferum LAFARGUE, 1968 p. 413.

Diplosoma cupuliferum MÉDIONI, 1970 p. 46.

pars Diplosoma listerianum PÉRÈS, 1956a p. 282.

Diplosoma spongiforme LAFARGUE, 1975c p. 304.

Material studied : 350 colonies.

Simplified diagnosis of the species : long subendostylar thoracic appendix.

Two-lobed testicle on left side.

Ovary with one fertilized egg; intra-ovarian segmentation and development.

Larvae with 2 to 7 pairs of lateral ampullae and 3 to 8 adhesive papillae.

Colonies : translucent, grey, black, beige or white.

Description : LAFARGUE, 1975c p. 304.

Ecology : infralittoral and circalittoral zones; substrata : all kinds but usually rigid.

Distribution : English Channel (Roscoff); Atlantic Ocean (Glenan Archipelago) and Mediterranean Sea (Banyuls, Port-Cros).

Genus **POLYSYNCRATON** Nott, 1891

Brief diagnosis of the genus : tentacle crown : 20-26 tentacles (except for *P. bilobatum* : 12).

Coiled sperm duct (4-5 coils, loose except for those of *P. bilobatum*). Spherical middle gut.

Divided testicle.

Spiculogenic organs and spicules present. Spiculogenic organs are circular, except for *P. bilobatum* in which they are wing-shaped.

Four rows of stigmata.

Presence or absence of appendix, depending on the species.

Presence of cloacal languet.

Gemmiparous larvae with 2 blastozoids. Four rows of stigmata. Numerous lateral ampullae arranged in a crown.

Polysyncraton haranti Lafargue, 1975

(fig. 3 : A, B, C; Pl. I : E)

Synonymy :

Polysyncraton haranti Lafargue 1975b p. 154.

pars Lissoclinum batailloni Harant, 1927 p. 221 (paratype).

pars Lissoclinum batailloni PÉRÈS, 1959 p. 302.

Material studied : 20 colonies.

Simplified diagnosis of the species : intermediate species between the genera *Lissoclinum* and *Polysyncraton*.

3 to 6 testicular follicles on right side, arranged in a rosette.

Presence of circular spiculogenic organs at the level of the second row of stigmata.

Flabellate spicules with wide tops, like a molar.

Absence of thoracic appendix.

Larvae with 9 to 10 pairs of lateral ampullae and 3 adhesive papillae.

Colonies : rigid, large, voluminous with leafy lobes, brick-red, uniformly coloured.

Description : LAFARGUE, 1975b p. 154.

Ecology : rare; below a depth of 35 metres; found at the off-shore circalittoral level in the Mediterranean Sea (only one colony was collected at a depth of 20 m).

Distribution (fig. 8) : Mediterranean Sea (Banyuls).

Polysyncraton canetense Brément, 1913

(fig. 3 : D, E, F; Pl. I : D)

Synonymy :

Diplosomoides canetensis Brément, 1913 p. 4.

Polysyncraton canetensis MÉDIONI, 1970 p. 41.

pars Lissoclinum batailloni Harant, 1927 p. 221 (holotype).

Polysyncraton lacazei var. *canetense* HARANT and VERNIÈRES, 1933 p. 73.

pars Lissoclinum batailloni PÉRÈS, 1959 p. 302.

Polysyncraton asterix Monniot, 1974 p. 1314.

An examination of the types preserved at the Museum d'Histoire Naturelle (Paris) and kindly lent by Mme Monniot, permitted the establishment of this new synonymy. The male gonads are in the process of involution and the zooids are contracted and poorly preserved.

Specimens were obtained by dredging off the Azores at a depth of 350-400 m.

Polysyncraton canetense LAFARGUE, 1975b p. 149.

Material studied : 200 colonies.

Simplified diagnosis of the species : 3 to 5 testicular lobes arranged in a rosette on the right side.

Presence of circular spiculogenic organs between the first and second rows of stigmata.

Spicules with thin dentate tops.

Absence of thoracic appendix.

Larvae with 12 pairs of lateral ampullae and 3 adhesive papillae.

Colonies : small (2 to 3 cm large), dark pink spotted with white and yellow.

Description : LAFARGUE, 1975b p. 149.

Ecology : infralittoral zone and coastal open-sea circalittoral zone (200 m deep, Canyon de la Cassidaigne, Marseilles region), bathyal zone (350-400 m, Azores Archipelago).

Distribution (fig. 8) : Mediterranean Sea (Banyuls, Port-Cros, Marseilles). This species has not been found in the French Atlantic littoral zone, but exists at Dakar (Senegal) and around the Azores Archipelago.

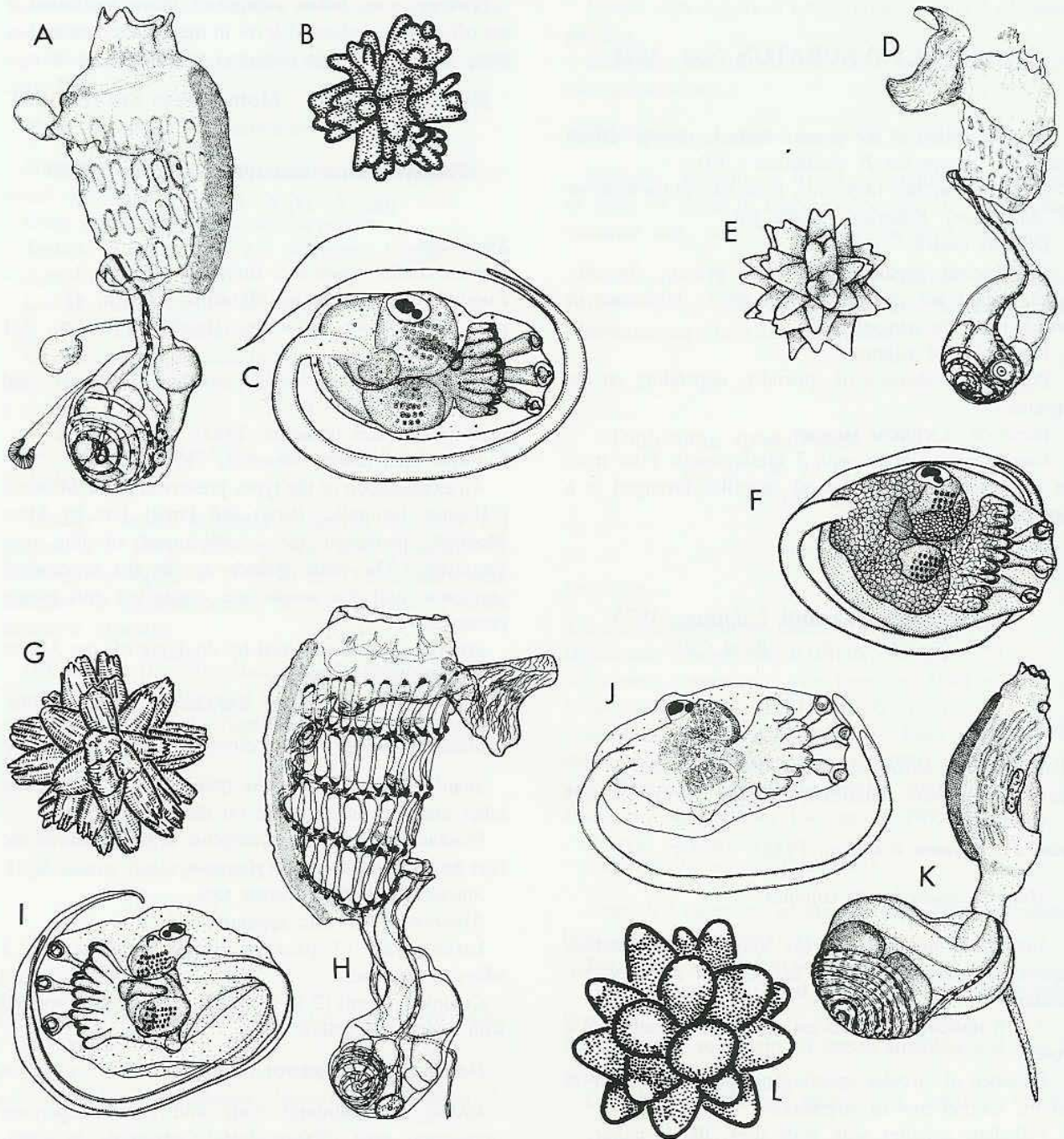


FIG. 3. — *Polysyncraton haranti* Lafargue : A, zooid; B, spicule; C, larva.

Polysyncraton canetense Brément : D, zooid; E, spicule; F, larva.

Polysyncraton lacazei (Giard) : G, spicule; H, zooid; I, larva.

Polysyncraton bilobatum Lafargue : J, larva; K, zooid; L, spicule.

FIG. 3. — *Polysyncraton haranti* Lafargue : A, zoïde; B, spicule; C, larve. *Polysyncraton canetense* Brément : D, zoïde; E, spicule; F, larve. *Polysyncraton lacazei* (Giard) : G, spicule; H, zoïde; I, larve. *Polysyncraton bilobatum* Lafargue : J, larve; K, zoïde; L, spicule.

Polysyncraton lacazei (Giard, 1872)

(fig. 3 : G, H, I; Pl. I : B;

Pl. VII : A, B, C; Pl. IX : B1, C2)

Synonymy :

Leptoclinum lacazei Giard, 1872 p. 153.*Didemnoïdes macrophorum* Von Drasche, 1883 p. 37.*Diplosomoides lacazei* LAHILLE, 1890 p. 129.*Didemnoïdes resinaceum* (Von Drasche, 1883) HARANT, 1929 p. 47.pars *Polysyncraton lacazei* HARANT, 1927 p. 220; HARANT and VERNIÈRES, 1933 p. 73; HARANT, 1930 p. 283-284.? *Didemnoïdes massiliense* DAUMÉZON, 1908a p. 179.*Polysyncraton lacazei* LAFARGUE, 1968 p. 398; 1975b p. 138; MÉDIONI, 1970 p. 40.

Material studied : 800 colonies.

Simplified diagnosis of the species : 5 to 6 testicular lobes arranged in a rosette on the left side.

Presence of circular spiculogenic organs in the upper part of the second row of stigmata. Star-shaped spicules with more than 20 branches. Larvae with 13 pairs of lateral ampullae and 3 adhesive papillae.

Colonies : spread out in varying degrees, depending on the available surface of substratum; thicker than 5 mm; yellow, orange, red, bluish mauve, violet and black, variously spotted with white; velvety appearance.

Description : LAFARGUE, 1975b p. 138.

Ecology : frequent in the infralittoral zone in the sea-grass beds (rhizomes of *Posidonia*), on horizontal shady vertical rock-faces, and in the circalittoral zone (coralligenous biocoenosis and rocky floors).

Distribution (fig. 8) : English Channel (Roscoff), Atlantic Ocean (Glenan Archipelago) and Mediterranean Sea (Banyuls, Port-Cros, Marseilles).

Polysyncraton bilobatum Lafargue, 1968

(fig. 3 : J, K, L; Pl. I : A;

Pl. XII : Above)

Synonymy :

Polysyncraton bilobatum Lafargue, 1968 p. 398.pars *Leptoclinum fulgens* VON DRASCHE, 1883 p. 33.pars *Leptoclinum fulgidum* LAHILLE, 1890 p. 94.pars *Didemnum fulgens* PÉRÈS, 1956a p. 280; PÉRÈS, 1957 p. 183; PÉRÈS and PICARD, 1958 p. 273.pars *Polysyncraton bilobatum* MÉDIONI, 1970 p. 38.*Polysyncraton bilobatum* LAFARGUE, 1975b p. 134.

Material studied : 300 colonies.

Simplified diagnosis of the species : intermediate species between the genera *Didemnum* and *Polysyncraton*.

2 testicular lobes (like 2 half-spheres with their flat sides tightly joined). Sperm duct with 6-8 tight coils. Wing-shaped vertical spiculogenic organs between the second and the third rows of stigmata.

Star-shaped spicules with about 15 rounded tops. Presence of a thoracic appendix at the peduncular insertion.

Larvae with 6 to 8 pairs of lateral ampullae and 3 adhesive papillae.

Colonies : fairly hard, thin (1 to 2 mm thick), with sizes varying from a few centimetres to a few decimetres, white, pale yellow, orangy beige, pale orange or bright orange.

Description : LAFARGUE, 1968 p. 398 and 1975b p. 134.

Ecology : with *Didemnum coriaceum*, *Polysyncraton bilobatum* is the most common species in the area of Banyuls-sur-Mer. It abounds in the infralittoral zone on rhizomes of *Posidonia*, on vertical overhanging rock faces, and in the circalittoral zone on hard substrata and on microcosms of trawlable sea beds. *P. bilobatum* resembles *Didemnum fulgens*, but is more eurybathic than the latter species, which is restricted to the infralittoral zone.

Distribution (fig. 8) : English Channel (Roscoff), Atlantic Ocean (Glenan Archipelago) and Mediterranean Sea (Banyuls, Port-Cros).

Genus **DIDEMNUM** Savigny, 1816

Brief diagnosis of the genus : tentacle crown comprising 16 tentacles of 3 complete orders.

Sperm duct with 8 to 9 tight coils and spherical middle gut. Single testicle, on the left side.

Presence of wing-shaped spiculogenic organs and spicules. Star-shaped spicules with rhombohedral rays, except for *D. lahillei*.

Four rows of stigmata in the adult but only three in the larvae at the time of hatching (the 4th is formed after metamorphosis). Presence of a long thoracic appendix with a peduncular insertion. Simple cloacal aperture.

Non-gemmiparous larvae with 2 or 3 adhesive ampullae, depending on the species.

Didemnum fulgens (Milne Edwards, 1841)

(fig. 4 : A, B, C; Pl. II : C;
Pl. VIII : A, B; Pl. IX : C1, D)

Synonymy :

Leptoclinum fulgens Milne Edwards, 1841 p. 299; VON DRASCHE, 1883 p. 33.

Didemnum maculosum f. *fulgens* HARANT, 1927 p. 219.

Didemnum fulgens HARANT and VERNIÈRES, 1933 p. 71.

Leptoclinum fulgidum GIARD, 1872 p. 652; LAHILLE, 1890 p. 94.

pars Didemnum maculosum BERRILL, 1950 p. 125.

Didemnum fulgens LAFARGUE, 1968 p. 395; 1976 p. 277; MÉDIONI, 1970 p. 31.

Material studied : 500 colonies.

Simplified diagnosis of the species : presence of star-shaped spicules with a variable number of rays. Dense regular spicule distribution.

Wing-shaped vertical spiculogenic organs at the level of the fourth row of stigmata.

Larvae with 4 to 8 pairs of lateral ampullae and 2 adhesive papillae.

Colonies : flat, large (18 cm × 18 cm), orange coloured; smooth surface, firm texture.

Description : LAFARGUE, 1976 p. 277.

Ecology : this species is clearly sciaphilic and is extremely common on all kinds of substrata (mineral, plant or animal) in the infralittoral and circalittoral zones. Colonies are well developed along the lower border between the precoralligenous or coralligenous layer and sand (depth : 22 to 25 m; Cap Oullestreil, Cap de l'Abeille).

Distribution (fig. 8) : English Channel (Roscoff), Atlantic Ocean (Glenan Archipelago) and Mediterranean Sea (Banyuls, Port-Cros).

Didemnum drachi Lafargue, 1975

(fig. 4 : D, E, F; Pl. II : H)

Synonymy :

Didemnum drachi Lafargue, 1975a p. 179.

Material studied : 250 colonies.

Simplified diagnosis of the species : dense regular distribution of spicules.

Presence of small wing-shaped vertical spiculogenic organs between the third and fourth rows of stigmata.

Larvae with 5 to 7 pairs of lateral ampullae and 3 adhesive papillae.

Colonies : poorly calcified on the surface; either uniformly orange or mottled with white; generally large (20 cm), extremely enveloping but poorly adherent.

Description : LAFARGUE, 1975a p. 179.

Ecology : common species but scattered throughout the circalittoral zone at depths of 20 metres or more. Colonies often envelop the Gorgonians *Eunicella stricta*, and spread to neighbouring coralligenous formations.

Distribution (fig. 8) : Mediterranean Sea (Banyuls, Port-Cros).

Didemnum pseudofulgens Médioni, 1970

(fig. 4 : G, H, I; Pl. II : E;
Pl. XII : Below)

Synonymy :

Didemnum pseudofulgens Médioni, 1970 p. 35; LAFARGUE, 1975a p. 174.

Material studied : 300 colonies.

Simplified diagnosis of the species : dense regular distribution of spicules.

Colonies are very calcified on the surface, and bright red or bright orange in colour.

A few asymmetrical spicules, with 5 or 6 rays (Pl. II : E). Presence of large wing-shaped vertical spiculogenic organs between the third and fourth rows of stigmata.

Larvae with 8 to 10 pairs of lateral ampullae and 3 adhesive papillae.

Colonies : thin (1 to 3 mm thick), leathery and bright red.

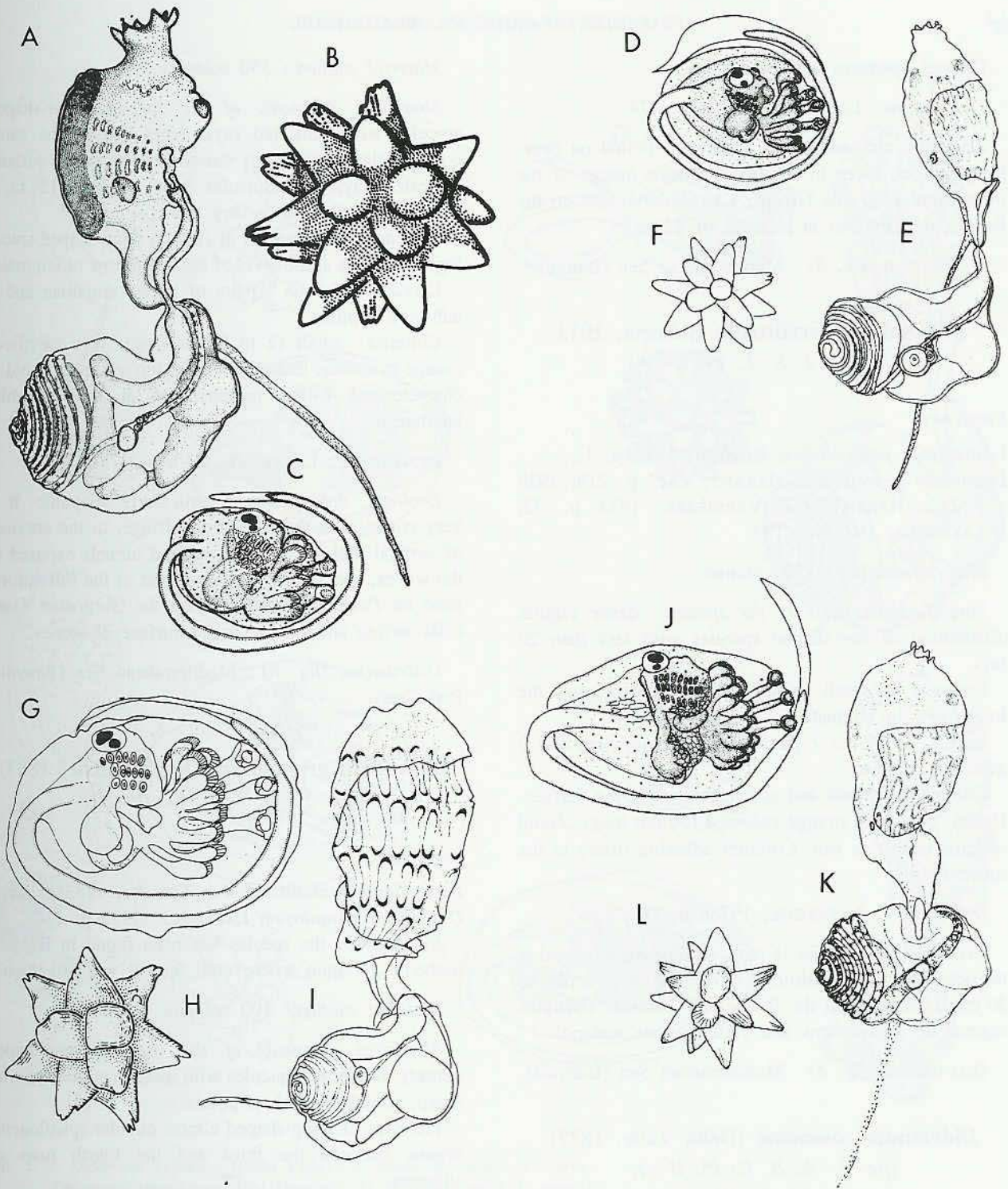


FIG. 4. — *Didemnum fulgens* (Milne Edwards) : A, zoïde; B, spicule; C, larve.

Didemnum drachi Lafargue : D, larve; E, zoïde; F, spicule.

Didemnum pseudofulgens Médioni : G, larve; H, spicule; I, zoïde.

Didemnum peyrefittense Brément : J, larve; K, zoïde; L, spicule.

FIG. 4. — *Didemnum fulgens* (Milne Edwards) : A, zoïde; B, spicule; C, larve. *Didemnum drachi* Lafargue : D, larve; E, zoïde; F, spicule.

Didemnum pseudofulgens Médioni : G, larve; H, spicule; I, zoïde. *Didemnum peyrefittense* Brément : J, larve; K, zoïde; L, spicule.

Cloacal apertures with white rim.

Description : LAFARGUE, 1975a p. 174.

Ecology : rare and highly localized. Found on overhanging rock faces in the upper fifteen metres of the infralittoral zone (Ile Grosse, Cap Rédéris) and on the Roches de Toreilles at a depth of 32 m.

Distribution (fig. 8) : Mediterranean Sea (Banyuls).

Didemnum peyrefittense Brément, 1913

(fig. 4 : J, K, L; Pl. II : F)

Synonymy :

Leptoclinum peyrefittense Brément, 1913 p. 1.

Didemnum peyrefittense HARANT, 1927 p. 218; 1930 p. 282; HARANT and VERNIÈRES, 1933 p. 72; LAFARGUE, 1975a p. 183.

Material studied : 150 colonies.

Simplified diagnosis of the species : dense regular distribution of star-shaped spicules with less than 20 rays.

Presence of small spiculogenic organs beneath the fourth row of stigmata.

Larvae with 5 to 7 pairs of lateral ampullae and 3 adhesive papillae.

Colonies : smooth and mucilagenous on the surface. Honey, beige and orange coloured (20 cm long). Zooid systems visible *in situ*. Colonies adhering firmly to the substratum.

Description : LAFARGUE, 1975a p. 183.

Ecology : this species is particularly sciaphilic and is restricted to the circalittoral level below a depth of 20 m. It abounds on the Roches de Toreilles (Banyuls region) on microcosms and coralligenous material.

Distribution (fig. 8) : Mediterranean Sea (Banyuls).

Didemnum commune (Della Valle, 1877)

(fig. 5 : A, B, C; Pl. II : I;
Pl. X : C)

Synonymy :

Leptoclinum commune Della Valle, 1877 p. 46; VON DRASCHE, 1883 p. 34.

Didemnum commune LAFARGUE, 1976 p. 275.

Material studied : 350 colonies.

Simplified diagnosis of the species : star-shaped spicules with truncated rays. Note that in the same colony, there are also star-shaped spicules without truncated rays. All spicules have at least 15 rays. Spicules distribution is very dense.

Presence of rectangular or circular wing-shaped spiculogenic organs at the level of the fourth row of stigmata.

Larvae with 5 to 7 pairs of lateral ampullae and 2 adhesive papillae.

Colonies : small (2 to 3 cm long), very calcified, orange in colour; leathery, warted surface (each zooid is characterized by a protuberance at the branchial aperture).

Description : LAFARGUE, 1976 p. 275.

Ecology : this species is particularly sciaphilic. It is very common in the infralittoral fringe, in the crevices of vertical rock faces, in caves and tunnels exposed to the waves, and also in the lower part of the infralittoral zone on *Posidonia* rhizomes, on the Gorgonian *Eunicella stricta* and on the lower surface of stones.

Distribution (fig. 8) : Mediterranean Sea (Banyuls, Port-Croq).

Didemnum granulosum (Von Drasche, 1883)

(fig. 5 : D, E, F; Pl. III : D)

Synonymy :

Leptoclinum granulosum Von Drasche, 1883 p. 35.

Didemnum granulosum LAFARGUE, 1972 p. 134.

Since 1975, the species has been found in Banyuls harbour, a region where until then it was unknown.

Material studied : 100 colonies.

Simplified diagnosis of the species : star-shaped densely distributed spicules with more than 20 rays with sharp, rounded or blunt points.

Presence of wing-shaped almost circular spiculogenic organs between the third and the fourth rows of stigmata.

Larvae with 5 to 7 pairs of lateral ampullae and 3 adhesive papillae.

Colonies : of various sizes (5 to 15 cm), extremely calcified. Granular or smooth surface, white (Banyuls harbour), grey, beige-veined, brown or violet (Port-Croq).

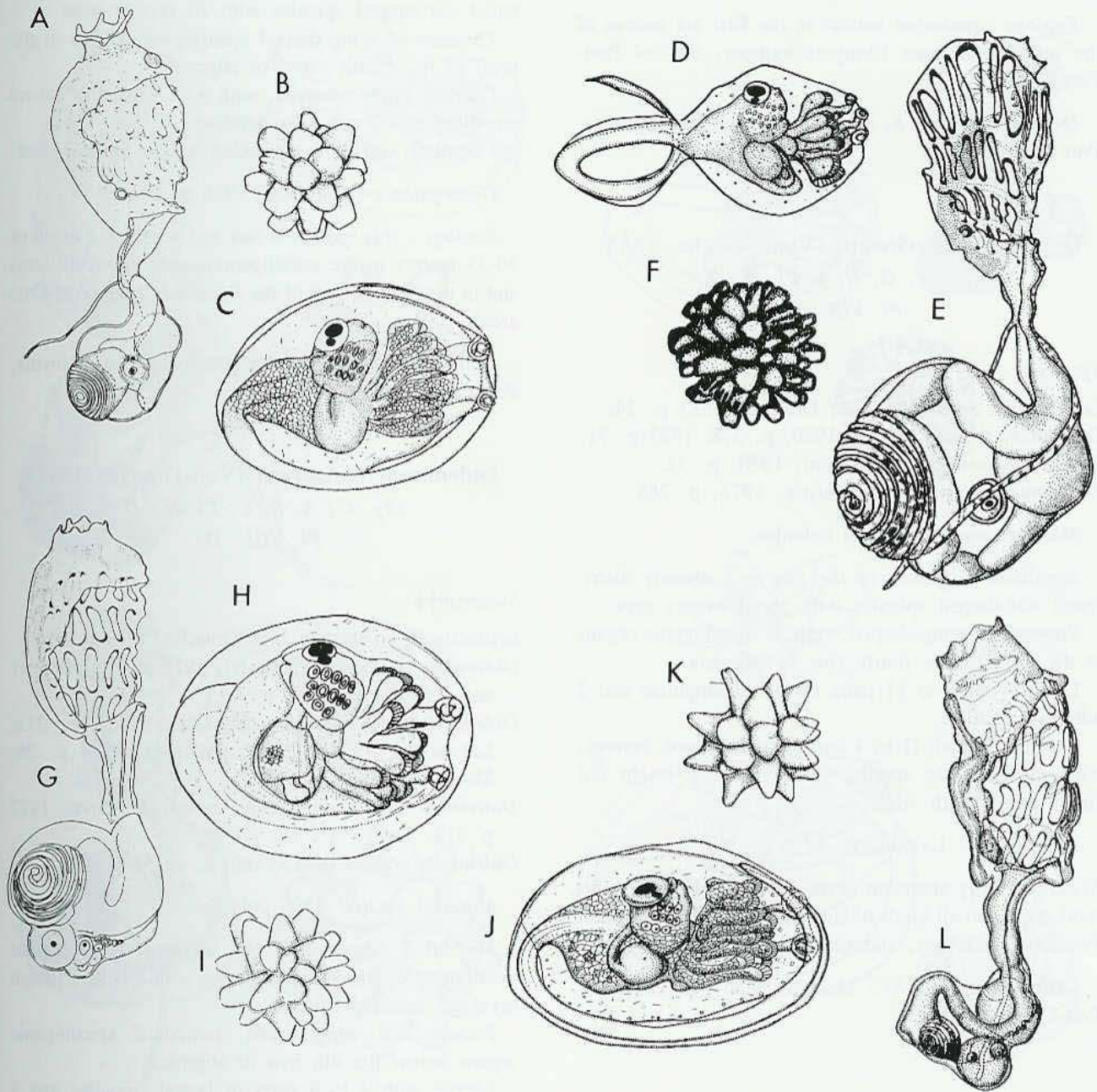


FIG. 5. — *Didemnum commune* (Della Valle) : A, zoïde; B, spicule; C, larve.
Didemnum granulosum (Von Drasche) : D, larve; E, zoïde; F, spicule.
Didemnum coccineum (Von Drasche) : G, zoïde; H, larve; I, spicule.
Didemnum amourouxi Lafargue : J, larve; K, spicule; L, zoïde.

FIG. 5. — *Didemnum commune* (Della Valle) : A, zoïde; B, spicule; C, larve. *Didemnum granulosum* (Von Drasche) : D, larve; E, zoïde; F, spicule. *Didemnum coccineum* (Von Drasche) : G, zoïde; H, larve; I, spicule. *Didemnum amourouxi* Lafargue : J, larve; K, spicule; L, zoïde.

Description : LAFARGUE, 1972 p. 134.

Ecology : protected habitat in the first six metres of the infralittoral zone (Banyuls harbour, Bay of Port-Cros).

Distribution (fig. 8) : Mediterranean Sea (Banyuls, Port-Cros).

Didemnum coccineum (Von Drasche, 1883)

(fig. 5 : G, H, I; Pl. II : A;

Pl. VIII : C)

Synonymy :

Leptoclinum coccineum Von Drasche, 1883 p. 34.

Didemnum grassei Harant, 1930, p. 278; 1933 p. 71.

Didemnum posidoniae Médioni, 1970, p. 32.

Didemnum coccineum LAFARGUE, 1976, p. 268.

Material studied : 1,200 colonies.

Simplified diagnosis of the species : densely distributed star-shaped spicules with about twenty rays.

Presence of wing-shaped, vertical spiculogenic organs at the level of the fourth row of stigmata.

Larvae with 8 to 11 pairs of lateral ampullae and 2 adhesive papillae.

Colonies : small (1 to 3 cm) of firm texture, convex, wine-red variously spotted with white, or bright red finely dotted with white.

Description : LAFARGUE, 1976 p. 268.

Ecology : fairly abundant in the infralittoral and circalittoral zones, on all kinds of substrata (vertical rock faces, *Posidonia* rhizomes, sponges, etc.).

Distribution (fig. 8) : Mediterranean Sea (Banyuls, Port-Cros).

Didemnum amourouxi Lafargue, 1976

(fig. 5 : J, K, L; Pl. II : G)

Synonymy :

Didemnum amourouxi Lafargue, 1976 p. 268.

Material studied : about 10 colonies. Since this species was first described, in the region of Banyuls, it has also been found at Port-Cros.

Simplified diagnosis of the species : densely distributed star-shaped spicules with 20 rays at most.

Presence of wing-shaped spiculogenic organs at the level of the fourth : row of stigmata.

Larvae : wine coloured, with 8 to 9 pairs of lateral ampullae and 2 adhesive papillae.

Colonies : soft, with a crinkled surface, and wine-red.

Description : LAFARGUE, 1976 p. 268.

Ecology : this species is rare and occurs at a depth of 30-35 metres in the coralligenous zone (Banyuls area) and in the deepest part of the *Posidonia* zone (Port-Cros area).

Distribution (fig. 8) : Mediterranean Sea (Banyuls, Port-Cros).

Didemnum coriaceum (Von Drasche, 1883)

(fig. 6 : A, B, C; Pl. II : D;

Pl. VIII : D)

Synonymy :

Leptoclinum coriaceum Von Drasche, 1883 p. 35.

Didemnum maculosum HARANT, 1927 p. 218; HARANT and VERNIÈRES, 1933 p. 71.

Didemnum helgolandicum CARLISLE, 1954 p. 313; LAFARGUE, 1968 p. 387; MÉDIONI, 1970 p. 28; MONNIOT, 1969 p. 453.

Didemnum candidum subsp. *canum* HARANT, 1927 p. 218.

Didemnum coriaceum LAFARGUE, 1975a p. 188.

Material studied : 500 colonies.

Simplified diagnosis of the species : dense regular distribution of star-shaped spicules with less than fifteen rays and rounded tips.

Presence of wing-shaped, horizontal spiculogenic organs below the 4th row of stigmata.

Larvae with 4 to 9 pairs of lateral ampullae and 3 adhesive papillae.

Colonies : white, grey or violet, uniformly coloured or spotted with yellow, orange, violet or brown. Surface is smooth or displays asperities. Leathery texture.

Description : LAFARGUE, 1975a p. 188.

Ecology : ubiquitous cosmopolitan species. Very abundant on rocky floors and in seagrass beds; found in the infralittoral and circalittoral zones, on all kinds of

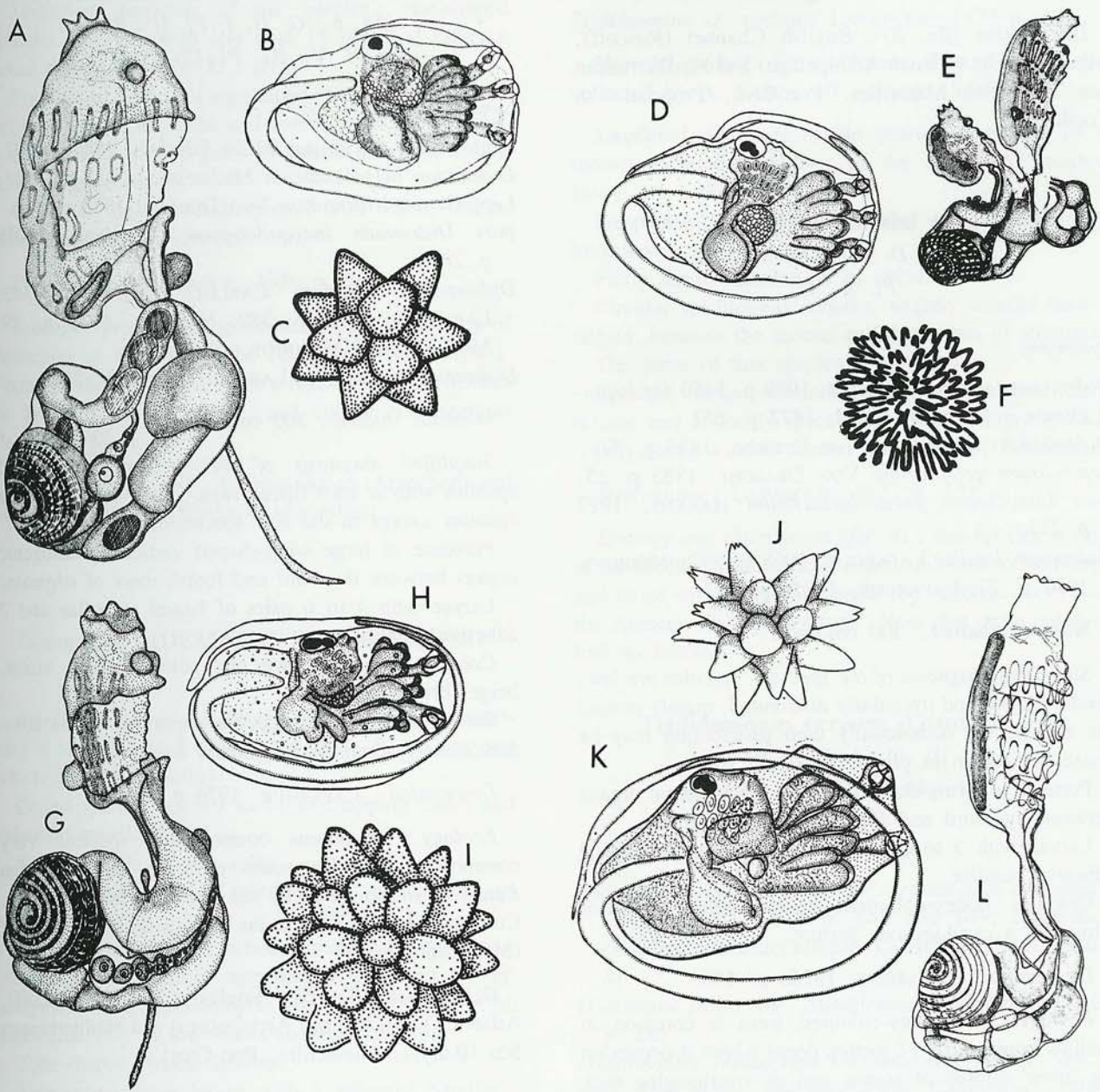


FIG. 6. — *Didemnum coriaceum* (Von Drasche) : A, zoïde; B, larve; C, spicule.
Didemnum lahillei Hartmeyer : D, larve; E, zoïde; F, spicule.
Didemnum maculosum (Milne Edwards) : G, zoïde; H, larve; I, spicule.
Didemnum protectum (Daumézou) : J, spicule; K, larve; L, zoïde.

FIG. 6. — *Didemnum coriaceum* (Von Drasche) : A, zoïde; B, larve; C, spicule. *Didemnum lahillei* Hartmeyer : D, larve; E, zoïde; F, spicule. *Didemnum maculosum* (Milne Edwards) : G, zoïde; H, larve; I, spicule. *Didemnum protectum* (Daumézou) : J, spicule; K, larve; L, zoïde.

substrata (e.g. *Cystoseira*, leaves and rhizomes of *Posidonia*, *Microcosmus*, Gorgonians, etc.).

Distribution (fig. 8) : English Channel (Roscoff), Atlantic Ocean (Glenan Archipelago) and Mediterranean Sea (Banyuls, Marseilles, Port-Cros, Propriano in Corsica).

***Didemnum lahillei* (Hartmeyer, 1909)**

(fig. 6 : D, E, F; Pl. III : C;
Pl. X : D)

Synonymy :

Didemnum lahillei Hartmeyer, 1909 p. 1450 for *Leptoclinium gelatinosum* Giard, 1872 p. 653.

Didemnooides resinaceum Von Drasche, 1883 p. 37.

Leptoclinium gelatinosum VON DRASCHE, 1883 p. 35.
pars Lissoclinium pseudoleptoclinium HARANT, 1927 p. 221.

Didemnum lahillei LAFARGUE, 1968 p. 382; MÉDIONI, 1970 p. 27; LAFARGUE, 1975a p. 187.

Material studied : 300 colonies.

Simplified diagnosis of the species : spicules are few, needle-shaped and irregularly distributed, mainly around the zooids, but occasionally their distribution may be dense, as shown in photo D, Pl. X.

Presence of wing-shaped vertical spiculogenic organs between the third and fourth rows of stigmata.

Larvae with 5 to 6 pairs of lateral ampullae and 3 adhesive papillae.

Colonies : honey-coloured, chocolate brown, violet or white, of a cartilagenous texture.

Description : LAFARGUE, 1975a p. 186.

Ecology : the honey-coloured form is common in shallow zones (2 to 12 metres deep) where it occurs on the lower surface of stones and on overhanging rock faces.

Chocolate brown colonies are found in caves on vertical surfaces and in dark biotopes between 15 and 40 metres deep in the lower part of the infralittoral zone and upper part of the circalittoral zone.

Distribution (fig. 8) : North Sea (Wimereux), English Channel (Roscoff), Atlantic Ocean (Glenan Archipelago) and Mediterranean Sea (Banyuls, Marseilles, Port-Cros).

***Didemnum maculosum* (Milne Edwards, 1841)**

(fig. 6 : G, H, I; Pl. II : B;
Pl. V : B1; Pl. IX : A)

Synonymy :

Leptoclinium maculosum Milne Edwards, 1841 p. 297.

Didemnum helgolandicum Michaelsen, 1921 p. 118.

Leptoclinium tridentatum Von Drasche, 1883 p. 36.

pars Didemnum inaequilobatum Daumézou, 1908b p. 285.

Didemnum candidum CARLISLE, 1954 p. 313;
LAFARGUE, 1968 p. 389; MÉDIONI, 1970 p. 29;
MONNIOT and MONNIOT, 1967 p. 4.

Didemnum maculosum LAFARGUE, 1976 p. 260.

Material studied : 300 colonies.

Simplified diagnosis of the species : star-shaped spicules with at least fifteen rays. Dense distribution of spicules except in the soft specimens.

Presence of large wing-shaped vertical spiculogenic organs between the third and fourth rows of stigmata.

Larvae with 4 to 6 pairs of lateral ampullae and 2 adhesive papillae.

Colonies : vary in size and colour; white, violet, beige, brown or black.

Surface is smooth or exhibits asperities. Some colonies closely resemble *Didemnum coriaceum*.

Description : LAFARGUE, 1976 p. 260.

Ecology : ubiquitous cosmopolitan species. Very common on old Bryozoans covering the Gorgonian *Eunicella stricta* on rocky sea floors 10 to 28 m deep. Collected at 120-150 m in the Canyon de la Cassidaigne (Marseilles area).

Distribution (fig. 8) : English Channel (Roscoff), Atlantic Ocean (Glenan Archipelago) and Mediterranean Sea (Banyuls, Marseilles, Port-Cros).

***Didemnum protectum* (Daumézou, 1908)**

(fig. 6 : J, K, L; Pl. III : B;
Pl. XI : B)

Synonymy :

Leptoclinium protectum Daumézou, 1908b p. 286.

Didemnum protectum HARANT, 1927 p. 218; 1930 p. 282; HARANT and VERNIÈRES, 1933 p. 72;
LAFARGUE, 1976 p. 263.

Material studied : about 50 colonies.

Simplified diagnosis of the species : star-shaped spicules generally with less than 15 rays and rather a dense distribution (*Pl. XI : B*).

Presence of vertical wing-shaped circular spiculogenic organs between the third and fourth rows of stigmata.

Larvae with 4 to 6 pairs of lateral ampullae and 2 adhesive papillae.

Colonies : fleshy, black spotted with white, resembling *Trididemnum cereum*.

Description : LAFARGUE, 1976 p. 263.

Ecology : present on the wooden stakes in the Bay of Arcachon at shallow depths (the upper two metres). Found on the *Cystoseira* in the circalittoral zone (Roches de Toreilles, near Banyuls), and on the coralligenous floor near Marseilles.

Distribution (fig. 8) : Atlantic Ocean (Arcachon) and Mediterranean Sea (Banyuls, Marseilles).

Genus **TRIDIDEMNUM** Della Valle, 1881

Brief diagnosis of the genus : tentacle crown comprising 8 tentacles of 2 orders (except in *T. cf. savignyi* which has 10 tentacles).

Coiled sperm duct (10 to 11 overlapping coils) and spherical middle gut.

Single testicle on left side.

Presence of cupular spiculogenic organs and of spicules.

Four rows of stigmata in both the adult and the larva.

Very small thoracic appendix (except in *T. cf. savignyi*) with a subendostylar insertion. Presence of an abdominal ring at the thorax-abdomen junction.

Tube-shaped cloacal aperture.

Non-gemmiparous larvae with 3 adhesive papillae.

Trididemnum cf. savignyi (Herdman, 1886)

(*fig. 7 : A, B; Pl. III : A*)

Synonymy :

? *Didemnum savignyi* Herdman, 1886 p. 261.

Has a doubtful « type-locality » : st 142 (?) « Challenger », Cape of Good Hope, at a depth of 175 m. A

little known species. Its zooids are characterized by the presence of a long thoracic appendix.

Trididemnum cf. savignyi LAFARGUE, 1972 p. 121.

Material studied : three colonies. Two of these were collected by A. RAMOS off Alicante (Spain).

Simplified diagnosis of the species : presence of a thoracic appendix as long as the abdomen, inserted below the endostyle.

Presence of star-shaped spicules with about twenty branches.

Fairly dense distribution of spicules.

Circular spiculogenic organs, slightly smaller than a stigma, between the second and third rows of stigmata.

The larva of this species is not known.

Colonies : beige coloured, smooth surface with a firm texture and a poorly spiculated superficial layer; each colony forms a muff around a rhizome of *Posidoniae*.

Description : LAFARGUE, 1972 p. 121.

Ecology and distribution (fig. 8) : this species is rare in the Mediterranean Sea; it was found once in Port-Cros and twice on the Spanish coast (by Alfonso RAMOS of the Alicante Fishing Institute). Note that these colonies had no larvae.

Trididemnum cereum (Giard, 1872)

(*fig. 7 : C, D, E; Pl. III : E;*

Pl. X : A, B; Pl. XI : A)

Synonymy :

Didemnum cereum, *Didemnum sargassicola*, *Didemnum niveum* Giard, 1872 p. 648 and 649; *Didemnum cereum*, *Didemnum niveum*, LAHILLE, 1890 p. 73 and 81.

Didemnum fallax var. *osculiferum* DAUMÉZON, 1908b p. 285.

Didemnoïdes resinaceum DAUMÉZON, 1907 p. 589.

pars Didemnum inaequilobatum Daumézon, 1908b p. 285.

Trididemnum tenerum PÉRÈS, 1956a p. 578; 1957 p. 182.

Trididemnum cereum LAFARGUE, 1968 p. 369; MÉDIONI, 1970 p. 27; LAFARGUE, 1974 p. 176.

Material studied : 800 colonies.

Simplified diagnosis of the species : tiny subendostylar thoracic appendix.

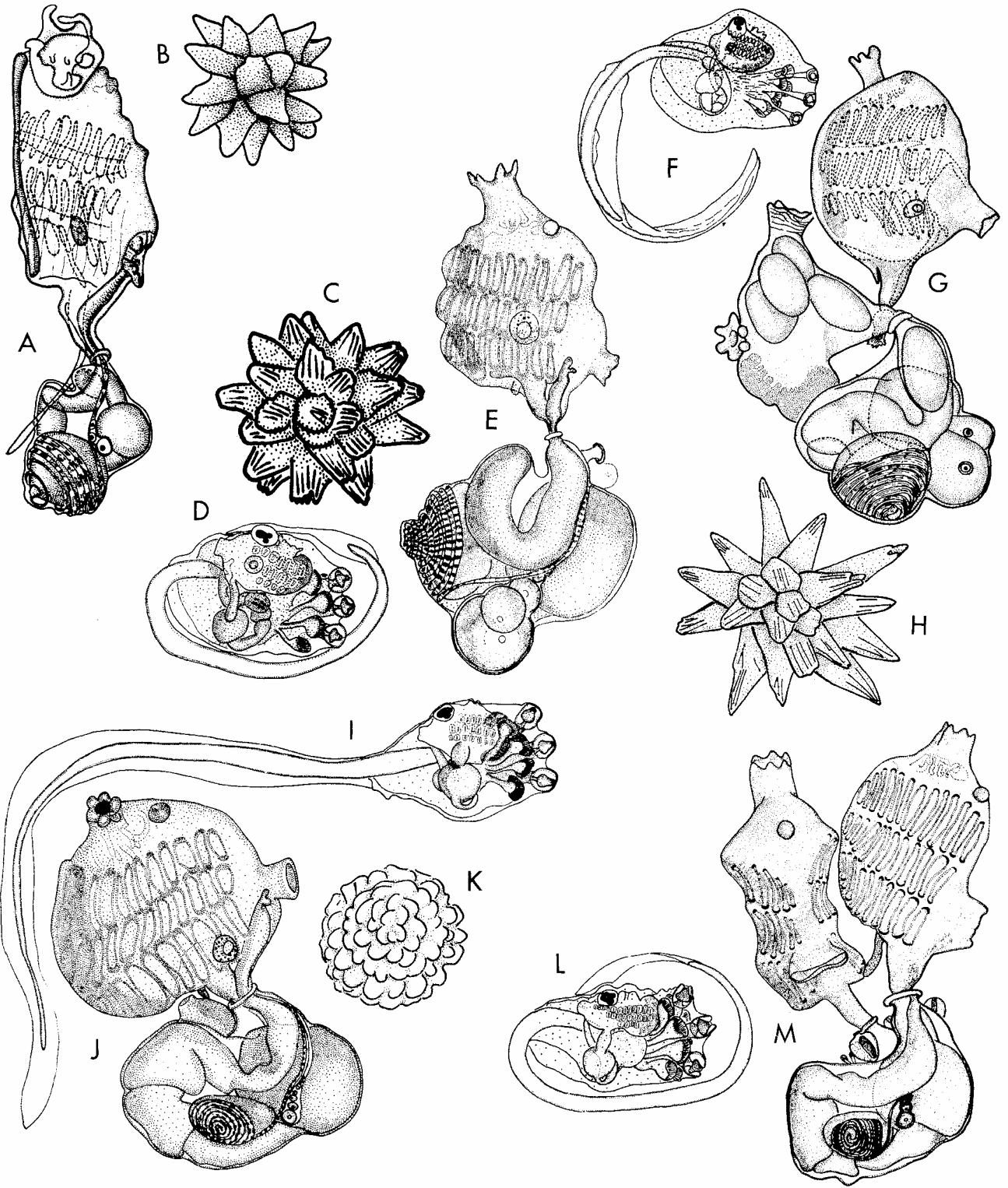


FIG. 7. — *Trididemnum cf. savignyi* (Herdman) : A, zooid; B, spicule.
Trididemnum cereum (Giard) : C, spicule; D, larva; E, zooid.
Trididemnum inarmatum (Von Drasche) : F, larva; G, zooid; H, spicule.
Trididemnum delesseriae Lafargue : I, larva; J, zooid; K, spicule.
Trididemnum translucidum Lafargue : L, larva; M, zooid.

FIG. 7. — *Trididemnum cf. savignyi* (Herdman) : A, zoïde; B, spicule. *Trididemnum cereum* (Giard) : C, spicule; D, larve; E, zoïde.
Trididemnum inarmatum (Von Drasche) : F, larve; G, zoïde; H, spicule. *Trididemnum delesseriae* Lafargue : I, larve; J, zoïde; K, spicule.
Didemnopis translucidum Lafargue : L, larve; M, zoïde.

Dense distribution of spicules which are star-shaped, slightly asymmetrical and have 15 fibrous rays with dentate tips.

The spiculogenic organs are large (the same size as the stigmata) and are located between the second and third rows of stigmata, in the middle of the thorax.

Larvae have 4 pairs of lateral ampullae with very dilated extremities, and 3 adhesive papillae; spiculogenic organs are already visible.

Colonies : fleshy, of various colours (transparent and colourless, grey, beige, orange or black) either uniformly coloured, or striped or spotted with white and black; strong tunica.

Description : LAFARGUE, 1974 p. 176.

Ecology : colonies are small in the infralittoral fringe, but larger in the infralittoral zone. Substrata are varied (rocks, algae or animals).

Distribution (fig. 8) : English Channel (Roscoff), Atlantic Ocean (Brest, Glenan Archipelago) and Mediterranean Sea (Banyuls, Marseilles, Port-Cros).

Trididemnum inarmatum (Von Drasche, 1883)

(fig. 7 : F, G, H; Pl. III : F)

Synonymy :

Didemnum inarmatum Von Drasche, 1883 p. 33.
not *Didemnoides inarmata* DAUMÉZON, 1908b p. 287.
not *Didemnopsis inarmata* PÉRÈS, 1956a p. 277.
Trididemnum inarmatum LAFARGUE, 1974 p. 178.

Material studied : about 40 colonies.

Simplified diagnosis of the species : very small subendostylar thoracic appendix (smaller than one stigma). Presence of star-shaped slightly eccentric spicules, generally with less than 20 rays. Some spicules are completely or partly formed by needles or plates (Pl. III : F).

Spiculogenic organs are small (smaller than one stigma), and are situated above the third row of stigmata.

Larvae have 2 to 4 pairs of lateral ampullae with well dilated extremities, and 3 adhesive papillae; spiculogenic organs are already visible.

Colonies : large, thick, fleshy, brown in colour (generally coloured uniformly) with a fairly fragile tunica.

Description : LAFARGUE, 1974 p. 178.

Ecology and distribution (fig. 8) : this rare species was found in the Mediterranean Sea below a depth of 20 m in the lower part of the infralittoral zone and in the circalittoral zone (Banyuls and Port-Cros region).

Trididemnum delesseriae Lafargue, 1968

(fig. 7 : I, J, K)

Synonymy :

Trididemnum delesseriae Lafargue, 1968 p. 374.

Material studied : 500 colonies.

Simplified diagnosis of the species : tiny subendostylar thoracic appendix.

Few spicules, of two main types : the largest are rosette-shaped (fig. 7 : K) and the smallest are formed by needles.

Spiculogenic organs (smaller than one stigma) are situated below the third row of stigmata.

Larvae have 4 pairs of lateral ampullae with very dilated extremities, and 3 adhesive papillae. **Spiculogenic organs are not visible.**

Colonies : thin (1 mm thick), small (1 cm in diameter) and translucent, spotted with white.

Description : LAFARGUE, 1968 p. 374.

Ecology and distribution (fig. 8) : this species was found in the Glenan Archipelago (Atlantic Ocean) in the infralittoral zone, on the fronds of supple algae such as *Delesseria sanguinea*.

Genus **DIDEMNOPSIS**

Brief diagnosis of the genus : tentacle crown : 8 tentacles of 2 complete orders.

Sperm duct with 10 to 11 overlapping coils and spherical middle gut.

Single testicle on left side.

Absence of spiculogenic organs and of spicules

Three rows of stigmata in both the adult and larva.

Tiny thoracic appendix with subendostylar insertion.

Presence of abdominal ring at the thorax-abdomen junction.

Tubular cloacal aperture.

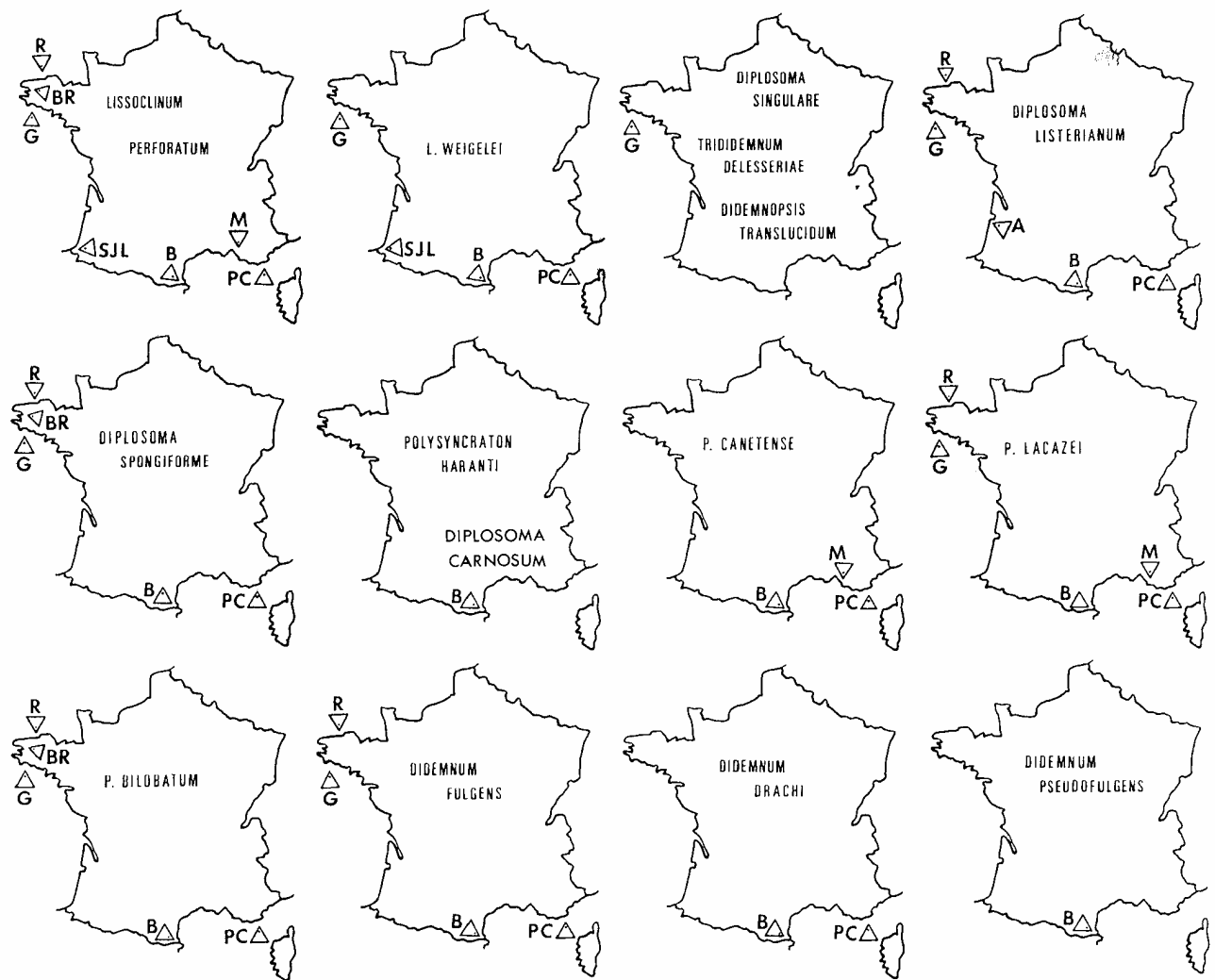


FIG. 8. — Distribution of Didemnid Ascidians on the French coasts. A : Arcachon; B : Banyuls; Br : Brest; G : Glénan; M : Marseilles; PC : Port-Cros; P : Propriano; R : Roscoff; SJL : Saint-Jean-de-Luz; W : Wimereux.

Didemnopsis translucidum Lafargue, 1968
(fig. 7 : L, M)

Synonymy :

Didemnopsis translucidum Lafargue, 1968 p. 364.

Material studied : about 10 colonies.

Simplified diagnosis of the species : the thoracic appendix is the size of a stigma. The tunica, perfectly translucent because of the absence of spicules, reveals

systems of steel-blue zooids (when alive); it is cartilaginous, and firm but not resistant.

Larvae have 4 pairs of lateral ampullae with very dilated extremities, and 3 adhesive papillae.

Colonies : similar in appearance to *Botryllus*, but colourless; thickness : 4 to 5 mm; diameter : 10 cm.

Description : LAFARGUE, 1968 p. 364.

Ecology and distribution (fig. 8) : this species is very localized. It was found in the Glénan Archipelago (Atlantic Ocean) in the infralittoral fringe, at the Gluet Marine Station. It adheres to rocks close to the water surface in places washed by the waves.

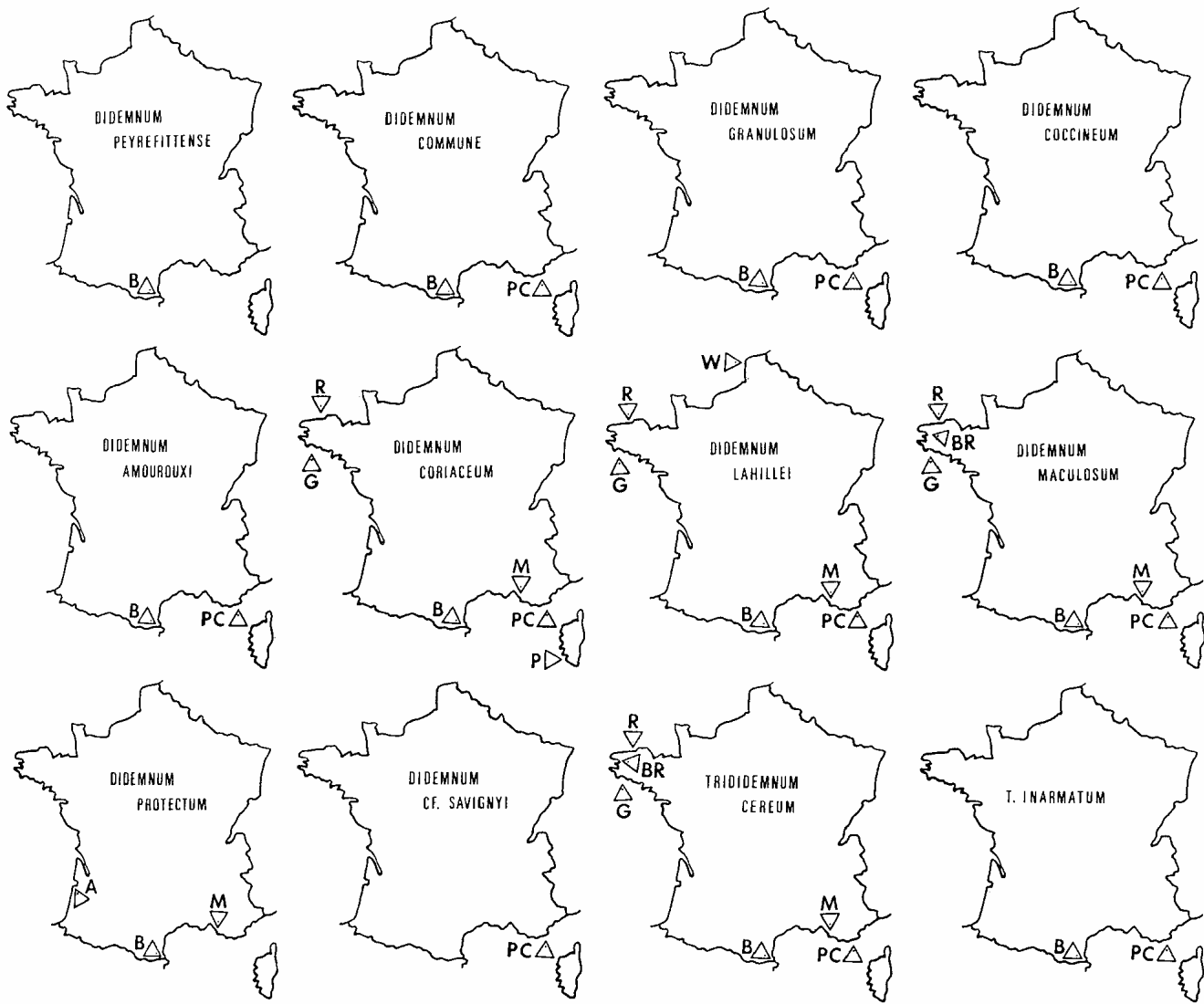


FIG. 8. — Cartes de répartition des Ascidies Didemnidae sur les côtes de France. A : Arcachon; B : Banyuls; Br : Brest; G : Gléan; M : Marseille; PC : Port-Cros; P : Propriano; R : Roscoff; SJJ : Saint-Jean-de-Luz; W : Wimereux.

KEYS TO IDENTIFICATION

Techniques of investigation

The following precautions should be taken when identifying species belonging to this family, as this identification is especially difficult :

1) MATERIAL :

Due to high intra-species variability, identification should always be based on the investigation of several

colonies rather than of a single specimen. Reliable identification requires work on a series of colonies comprising all stages of the reproductive cycle, including male gonads at the peak of maturity and larvae close to hatching. However, these hermaphrodite species are protandrous, so that these two conditions are never found in the same colony. As it may sometimes be difficult to obtain both larvae and mature adults for identification, we have established a second somewhat

less precise key which should only be used when larvae or mature male gonads are not available.

2) PREPARATION :

a) *Note the texture and colour of the living colony.*

b) *Anaesthesia and fixation :*

We describe below the fixation method practiced by X. TURON of Barcelona University (Spain) with good results : place the colonies, still attached to their substratum, in a suitable glass container and immerse it in a tank of running sea-water until perfect extension of the zooids is obtained. Then gently take the container and the Ascidians out of the tank and add about 10 menthol crystals per litre of sea water. About two hours later, when the colonies cease to react to a slight mechanical stimulus, put the container in a freezer until ice begins to form on the surface. Add 10% (v/v) of commercial grade formaldehyde and leave for 24 hours at room temperature. Then transfer the colonies into 7% buffered formaldehyde. Wait several weeks before extracting the zooids.

c) *Staining :*

Rinse the specimens in distilled water to eliminate the formalin. Add the staining agent, Masson's acid hemalum (3 drops per 10 ml) and observe the staining process with a binocular lens for 2-5 min. When the desired degree of colouration is obtained after 2-3 min, rinse thoroughly.

Composition of Masson's acid hemalum :

Hematoxylin (Geigy, Basel)	0.2 g
Potassium alum	5 g
Distilled water	100 ml

Preparation :

Add 0.2 g hematoxylin to 100 ml of a saturated boiling solution of potassium alum. Boil for a few minutes, cool and filter. Add about 2% acetic acid until the colour changes to red. The stain remains stable for one month if kept protected from light.

Key A : Species identification

(WHEN MATURE COLONIES AND LARVAE ARE AVAILABLE.
OTHERWISE REFER TO KEY B)

Abbreviations : p.l.a. = pairs of lateral ampullae; s.o. = spiculogenic organs.

Note : The number of spicule rays indicated is that counted on the visible part of the spicule as seen under a microscope.

The « back » of the thorax is defined as the shortest line between the oral and atrial siphons. The endostyle is on the « ventral » face. (The main morphological features of a mature zooid are shown in *figure 9*.)

TABLE OF GENERA

A) *Straight sperm duct :*

— Presence of spicules and wing-shaped s.o. between the 2nd and 3rd rows of stigmata. Larvae with a non-transparent test. *Lissoclinum*

— Absence of spicules and s.o. The texture of the colonies is soft but resistant (except for *Diplosoma singulare*, intermediate between the two genera, the genus *Diplosoma* being further characterized by the presence of a thoracic appendix, not present in the genus *Lissoclinum*) *Diplosoma*

B) *Coiled sperm duct*

1. Four rows of stigmata. Wide atrial aperture with or without languet 2

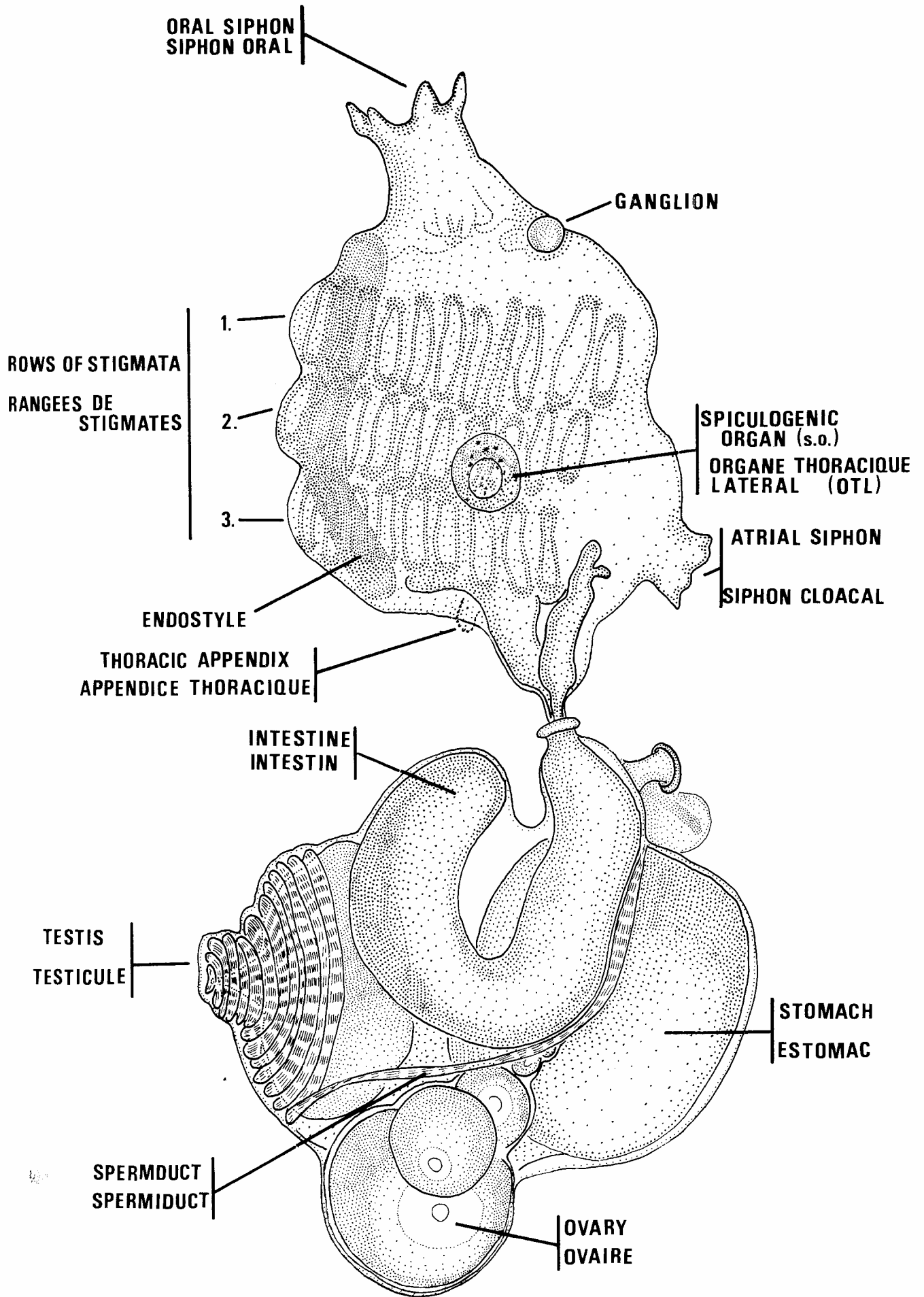
— Three rows of stigmata. Tubular atrial aperture ... 3

2. Several male follicles. Larvae with four rows of stigmata *Polysyncraton*

— One male follicle. Thoracic appendix present. Atrial aperture without languet. Larvae with three rows of stigmata *Didemnum*

FIG. 9. — Main morphological features of a mature zooid (*Tridemnum cereum*, left side).

FIG. 9. — Éléments morphologiques principaux d'un zoïde mûr (*Tridemnum cereum*, face latérale gauche).



- 3. Circular s.o. and spicules present *Trididemnum*
- S.o. and spicules absent *Didemnopsis*

TABLE OF SPECIES

Lissoclinum : 2 species

- Absence of cloacal languet. Colony : leathery, white, orangy-yellow, pinky-beige or grey. Flabellate spicules densely distributed. One male follicle on the right side. Larvae with 4 p.l.a. *L. perforatum*
- Presence of cloacal languet. Colony : soft texture, white with brown dots. Two male follicles on the left side. Larvae with 4 p.l.a. *L. weigelei*

Diplosoma : 4 species

- 1. — Gonads on the left side 3
- Gonads on the right side 2
- 2. — Transparent colonies, yellow zooids. One male follicle. Thoracic appendix absent. Larvae with 4-5 p.l.a. *D. singulare*
- Translucent colonies, thicker than 5 mm. 2-5 male follicles. Supratergular glands. Larvae with 2-4 p.l.a. *D. carnosum*
- 3. — Transparent colonies. 2 male follicles. Embryos develop in the common test. Larvae with 2 p.l.a. *D. listerianum*
- Translucent colonies, grey, black, beige or white. 2 male follicles. Embryos develop inside the parent zooid. Larvae with a variable number of p.l.a. ... *D. spongiforme*

Polysyncraton : 4 species

- 1. — Thoracic appendix absent 3
- Thoracic appendix present 2
- 2. — Testicle comprising two tightly joined hemispheres. Leathery orange colonies, not subdivided into two sheets, otherwise strongly resembling *Didemnum fulgens*. Wing-shaped s.o. between the 2nd and 3rd rows of stigmata. High spicule density; some spicules with typically rounded tops of rays. No cloacal languet *P. bilobatum*
- Testicle made up of 5-6 follicles. Fleshy red colonies of velvety appearance. Regularly distributed spicules with >20 rays, circular s.o. level with 2nd row of

stigmata. Thoracic appendix present. Cloacal languet present *P. lacazei*

3. — Generally small colonies (diam. : 2-3 cm), rough texture, deep pink spotted with white and yellow. Large circular s.o. between the 1st and 2nd rows of stigmata. Densely packed spicules, with slender rays split into 2 or 3 sharp peaks *P. canetense*

— Large massive brick-red colonies. Large spicules with rays generally divided into at least 3 blunt peaks, s.o. of various sizes level with the 2nd row of stigmata *P. haranti*

Didemnum : 12 species

- 1. — Larvae with three adhesive papillae (6 species) 2
- Larvae with two adhesive papillae (6 species) 5
- 2. — Spicule distribution : dense and regular 3
- Spicules : few and clustered around the zooids. This is the only species possessing spicules with acicular rays. Colonies with a cartilaginous texture, honey-coloured or chocolate-brown. S.o. : vertical, between the 3rd and 4th rows of stigmata *D. lahillei*
- 3. — S.o. vertical 4
- S.o. horizontal, below the 4th row of stigmata, spicules with less than 15 rays, regularly and densely distributed. Colonies with visible zooid systems; white or grey speckled with orange, violet or brown; leathery texture. Larvae with 4-9 p.l.a. *D. coriaceum*
- 4. — Colonies with a smooth and mucilaginous surface, honey-coloured. Spicules with less than 20 rays, densely and regularly distributed; small s.o. below the 4th row of stigmata. Larvae with 5-7 p.l.a. *D. peyrefittense*
- Colonies with a slightly calcified surface, orange veined with white. Rare spicules with less than 20 rays; small s.o. between the 3rd and 4th rows of stigmata. Larvae with 5-7 p.l.a. *D. drachi*
- Colonies with an extremely calcified surface, red or bright orange. Spicules with less than 15 rays, a few of them asymmetrical in shape with 5-6 rays only; large s.o. between the 3rd and 4th rows of stigmata. Larvae with 8-10 p.l.a. *D. pseudofulgens*
- Colonies with an extremely calcified surface, granular, grey or beige veined with brown. Spicules with more than 20 rays; s.o. between the 3rd and 4th rows of stigmata. Larvae with 5-7 p.l.a. *D. granulosum*

TABLE II. — Species determination table for the genus *Didemnum* when there are no gonads.TABLEAU II. — Table de détermination spécifique pour le genre *Didemnum* si il y a absence de gonades.

Colony		Spiculogenic organs			Spicules		Larvae			Species
Appearance, Texture	Colour	Shape	Position	Density	Distribution	Nbr of rays	Nbr of adh. pap.	Pairs of lat. amp.		
thin, leathery	r/w	ws	3-4, v	++	regular	≤15	3	8-10	<i>D. pseudofulgens</i>	
large, surface with few spicules	or	ws, > stigma	3-4 or 4, v	++	irregular : concent. in basal layer	≤15	3	5-7	<i>D. drachi</i>	
muclilaginous surface	y	ws, tiny	4, v	++	irregular : concent. in basal layer	≤15	3	5-10	<i>D. peyrefitense</i>	
cartilaginous	(var.)	ws, > stigma	3-4, v	+	irregular : concent. around zooids	≥40	3	5-6	<i>D. lahillei</i>	
leathery	(var.)	ws	below 4, h	++	irregular : concent. in basal layer	<15 (blunt)	3	4-9	<i>D. coriaceum</i>	
hard, granular surface	(var.)	ws	3-4, v	+++	regular	>20	3	5-7	<i>D. granulolum</i>	
leathery	(var.)	ws	3-4, v	++	regular	>15	2	4-6	<i>D. maculosum</i>	
fleshy	bk	ws	3-4, v	++	irregular : forming trails	<15 (°)	2	4-6	<i>D. protectum</i>	
soft, crinkled surface	vt	ws	4, v	+	irregular : concent. in basal layer	~20	2	8-9	<i>D. amourouxi</i>	
tiny, convex, smooth surface	r, r/w	ws	4, v	++	regular	<20	2	8-11	<i>D. coccineum</i>	
leathery	y-or	ws	4, v	+++	irregular : watted surface	>15	2	5-7	<i>D. commune</i>	
thin, firm, smooth surface	y-or	ws	4, v	+++	regular or irregular	(var.)	2	4-8	<i>D. fulgens</i>	

Abbreviations :

- 1) Spicule distribution : +++ very dense distribution, ++ abundant, + rare
 - 2) Position of spic. org. : 3-4 : « between the 3rd and 4th rows of stigmata », 4 : « level with the 4th row of stigmata »
 - 3) Colour : r : red, w : white, or : orange, y : yellow, bk : black, vt : violet, r/w : red with white spots, or trails...
 - 4) Spiculogenic organs : ws : wing-shaped, v : vertical, h : horizontal
 - 5) Other : (var.) : various, adh. pap. : adhesive papillae, lat. amp. : lateral ampullae.
- (°) Specimens from Arcachon : ≥15.

5. — Spicules with non-blunt peaks 6
 — A few spicules with blunt peaks and more than 15 rays, densely distributed. Generally small colonies (diam. : 2-3 cm) with a warted surface and tough texture. S.o. at the level of the 4th row of stigmata. Larvae with 5-7 p.l.a. *D. commune*
6. — Colonies with a leathery texture 7
 — Colonies with a fleshy texture, thick, black with white dots (resembling *Trididemnum cereum*). Most spicules have less than 15 rays, densely distributed; small s.o. between the 3rd and 4th rows of stigmata. Larvae with 4-6 p.l.a. *D. protectum*
 — Colonies : soft with high spicule density, dark red. Spicules with less than 20 rays; s.o. level with 4th row of stigmata. Larvae with 8-9 p.l.a. *D. amourouxi*
7. — Colonies : convex, generally small (diam. : 1-3 cm), wine red or bright red with white dots. Densely packed spicules with about 20 rays; s.o. level with 4th row of stigmata. Larvae with 8-11 p.l.a. *D. coccineum*
 — Flat colonies with a firm texture and a smooth surface, large (18×18 cm). Densely distributed spicules with a variable number of rays; s.o. at the level of the 4th row of stigmata. Larvae with 4-8 p.l.a. *D. fulgens*
 — Colonies of various colours, including white, violet, beige, brown and black, and of firm texture. Spicules usually numerous with more than 15 rays; large s.o. between the 3rd and 4th rows of stigmata. Larvae with 4-6 p.l.a. *D. maculosum*

Trididemnum : 4 species

1. — Tiny (imperceptible) thoracic appendix 2
 — Thoracic appendix as long as the abdomen. Firm colonies, beige in colour. Spicules with about 20 rays, few in the uppermost layer but numerous elsewhere *T. cf. savignyi*
2. — Spicules are few; s.o. smaller than a stigma 3
 — Spicules numerous with 15 rays; large s.o. (the size of a stigma), between the 2nd and 3rd rows of stigmata in the middle of the thorax. Colonies : fleshy, of various colours *T. cereum*
3. — Colonies : small, thin, translucent, attached to flexible algae. Rare spicules of various shapes; s.o. below the 3rd row of stigmata. Larvae without visible s.o., and with 4 p.l.a. *T. delesseriae*
 — Large, massive, fleshy colonies, dark brown. Spicules with less than 20 rays, very rare; s.o. in the upper part of the 3rd row of stigmata. Larvae with visible s.o. and 2-4 p.l.a. *T. inarmatum*

Didemnopsis : 1 species

Didemnopsis translucidum : Translucent colonies of cartilaginous texture with visible zooid systems. Larvae with 4 p.l.a.

Key B : Species identification

(WHEN MATURE COLONIES AND LARVAE
 ARE NOT AVAILABLE)

TABLE I : *Diplosoma*, *Lissoclinum*, *Polysyncraton*,
Trididemnum.

TABLE II : *Didemnum*.

BIOGEOGRAPHY

The preceding classification shows that there are twice as many species of Didemnid Ascidiarians in the Mediterranean as in the Atlantic (22 in the Banyuls region versus 14 in the Glenan Archipelago). The geographical distribution of the Didemnidae is still unknown because of the difficulty of identifying species belonging to this family of Ascidiacea. Their distribution is probably rather wide, as established for instance for *Didemnum coriaceum*, a species present in the English Channel, the

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Atlantic Ocean, the Mediterranean Sea and the Red Sea (Gulf of Eilat).

During a recent diving expedition in the region around Dakar (Senegal), we collected the following nine species of Didemnid Ascidiarians, which are also part of French fauna : *Lissoclinum weigelei*, *Diplosoma listerianum*, *D. spongiforme*, *Polysyncraton canetense*, *P. lacazei*, *P. bilobatum*, *Didemnum maculosum*, *D. coriaceum* and *Trididemnum cereum*. Four of these species were

reported for the first time in the Dakar area by MONNIOT, 1969 : they include *Diplosoma listerianum*, *Didemnum coriaceum* (which MONNIOT called *D. helgolandicum*), *Polysyncraton lacazei* and *Trididemnum savignyi* (Herdman, 1886). This latter, described by MONNIOT on p. 451, might be the same as the one found off French coasts, but this cannot be established

with certainty because there were no larvae among the Mediterranean specimens. On the other hand, examination of the *Polysyncraton canetense* specimens from the Azores and Dakar allowed the inclusion of these Atlantic areas in the distributional range of this Mediterranean species.

CLASSIFICATION AND EVOLUTION

The classification of the 27 species of Didemnidae from the French coasts reflects their evolution. The 5 species lacking calcareous spicules seem to derive from those which have spicules. For instance, the genus *Diplosoma* is derived from the genus *Lissoclinum* and the genus *Didemnopsis* from the genus *Trididemnum*. The 22 species with calcareous spicules can be arranged in a linear succession of four genera, representing the probable order in which they appeared in the course of evolution, as follows : *Lissoclinum*, *Polysyncraton*, *Didemnum* and *Trididemnum*. This sequence is characterized by the emergence of evolutionary attainments that are difficult to discern because they concern gradual rather than spectacular morphological transformations of the male gonad (coiling of the sperm duct), of the alimentary canal (lengthening of the terminal gut) and of the respiratory system (disappearance of the fourth row of branchial stigmata).

These transformations are not isolated but inter-related. Their correlating factor might be the concomitant diminution observed in zooid size that can be seen along the same axis (from *Lissoclinum* to *Trididemnum*) : as structures such as the gut or the sperm duct cannot be shortened indefinitely without impairing their respective functions of digestion and sperm maturation, they have to curve and form loops, in the case of the gut (giving the impression of a lengthening that in reality is only relative) or, in the case of the sperm duct, they coil up inside a shrinking abdomen. The same process may account for the disappearance of the fourth row of stigmata (compensated by an increase in the

number of stigmata in each remaining row) and a reduction in the number of buccal tentacles. Consequently, in the case of the Didemnidae, the simultaneous presence of, for example, a straight sperm duct and three rows of stigmata has never been observed and is highly improbable.

The family Didemnidae is probably derived from the family Polycitoridae through the intermediate stages represented by the genera *Cystodytes* (Polycitoridae) and *Echinoclinum* (Didemnidae). Today, the genus *Echinoclinum* is tropical and is not found on French coasts. Long ago, during the Eocene Age (Ypresian, Cuisian period) this genus existed in the Paris Basin. The fossilized spicules belonging to this species of *Echinoclinum* were tentatively attributed to the genus *Cystodytes* by BUGE and MONNIOT (1972). Their flat, radial shape makes them unusual for both the Ascidian families Didemnidae and Polycitoridae. Plate IV shows that these fossilized spicules (A) are closer to the spicules of the present tropical species *Echinoclinum philippinense* Tokioka, 1967 (B) than to those of any other species of Ascidian. Therefore, in this revised nomenclature, this fossil species from the Paris Basin is named *Echinoclinum brachiatus* (Buge and Monniot, 1972).

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PLATES I-XII

PLANCHES I-XII

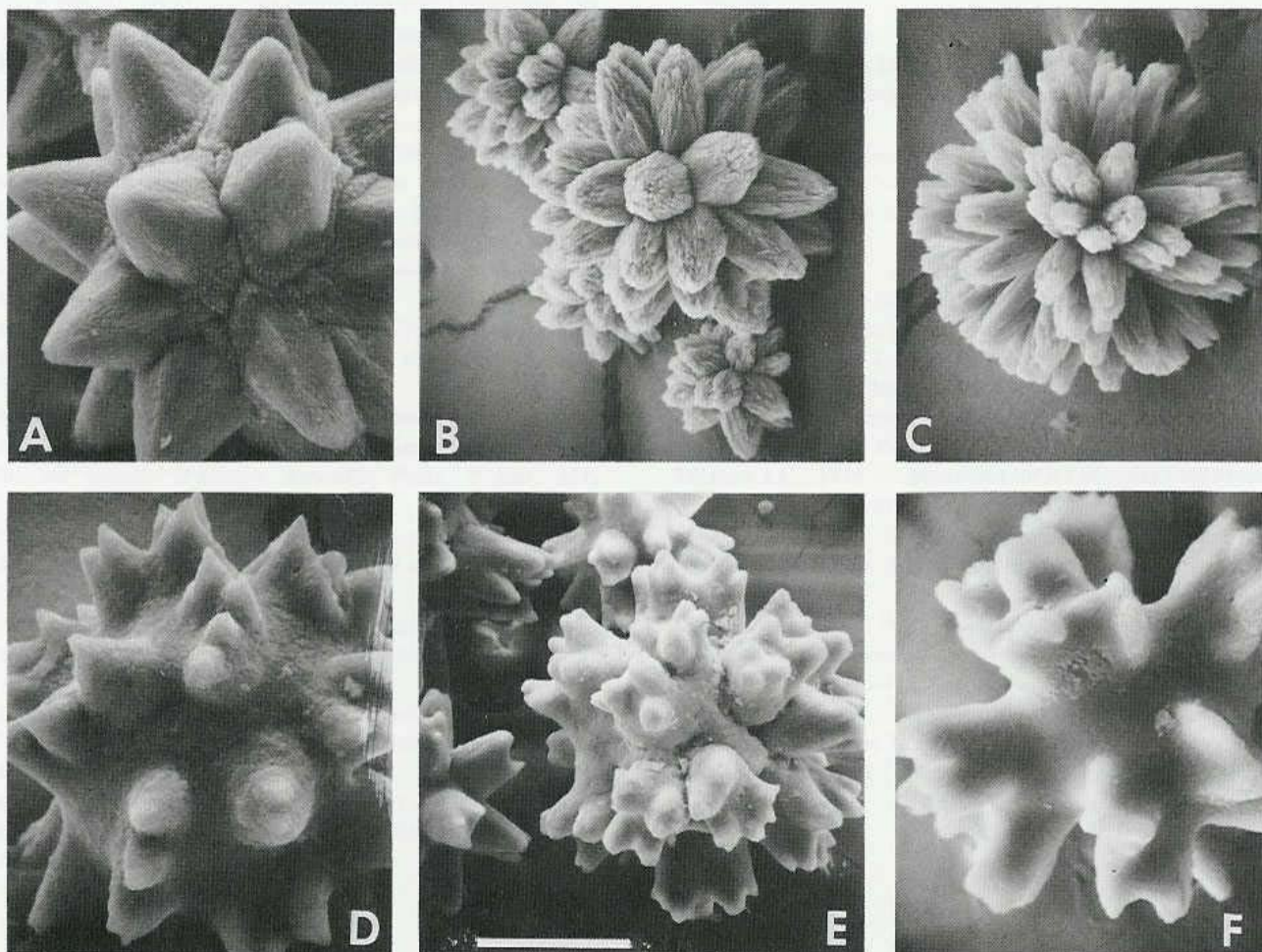


PLATE I

Spicules of Didemnidae, viewed by scanning electron microscopy. A, *Polysyncraton bilobatum* Lafargue; B, *P. lacazei* (Giard); C, *Lissoclinum weigelei* Lafargue; D, *Polysyncraton canetense* Brément; E, *P. haranti* Lafargue; F, *Lissoclinum perforatum* (Giard). Scale bars : A, C, D, F : 12 μm ; B, E : 25 μm .

PLANCHE I

Spicules de Didemnidae, vus au microscope électronique à balayage : A, *Polysyncraton bilobatum* Lafargue; B, *P. lacazei* (Giard); C, *Lissoclinum weigelei* Lafargue; D, *Polysyncraton canetense* Brément; E, *P. haranti* Lafargue; F, *Lissoclinum perforatum* (Giard). Le trait d'échelle mesure 12 μm : A, C, D, F; 25 μm : B, E.

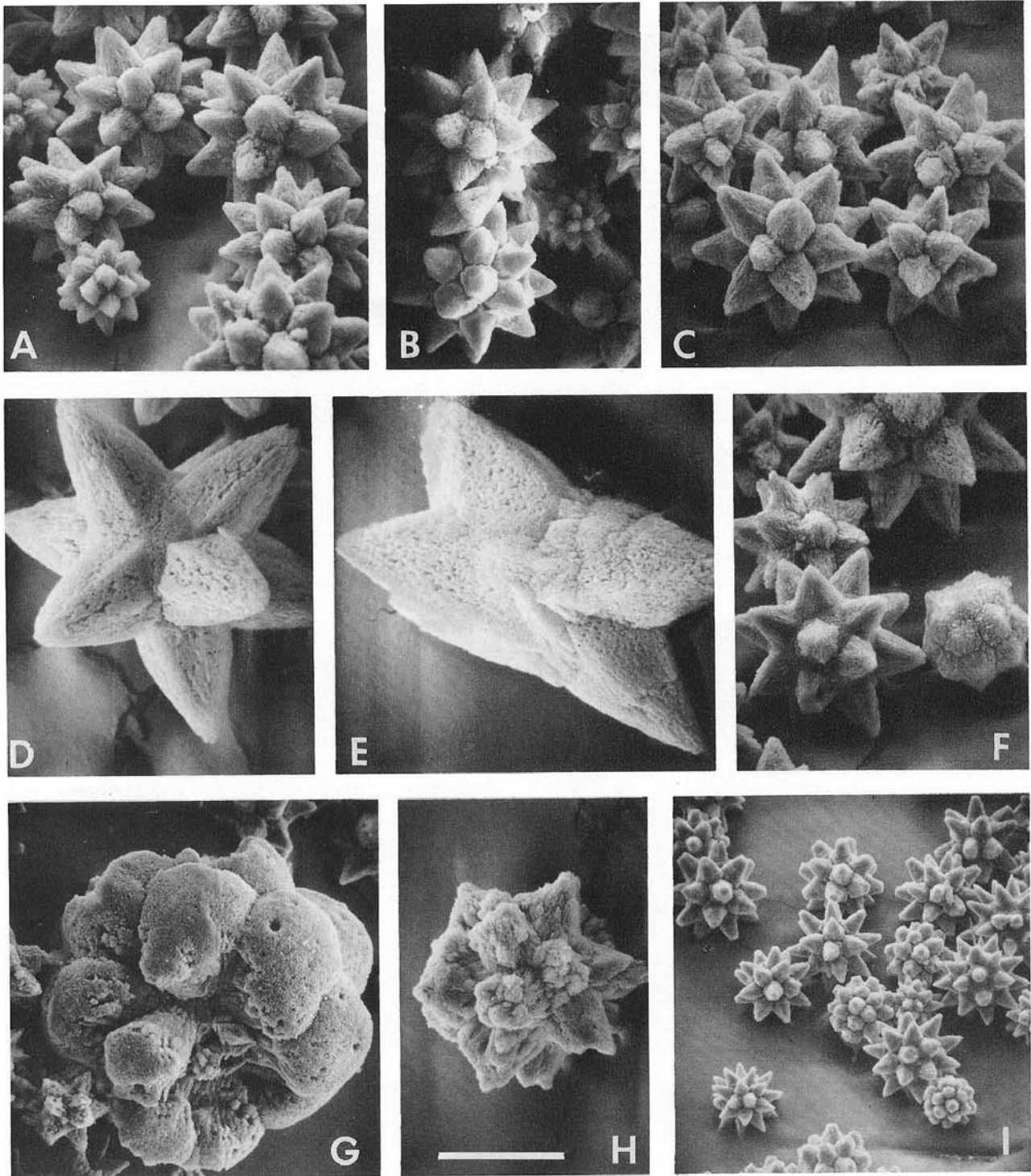
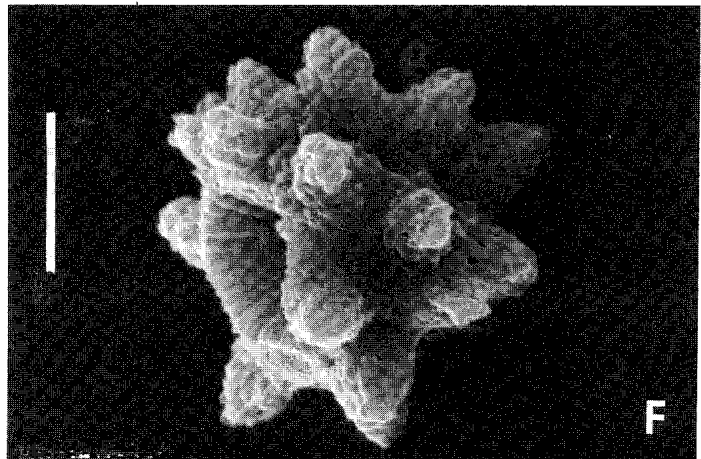
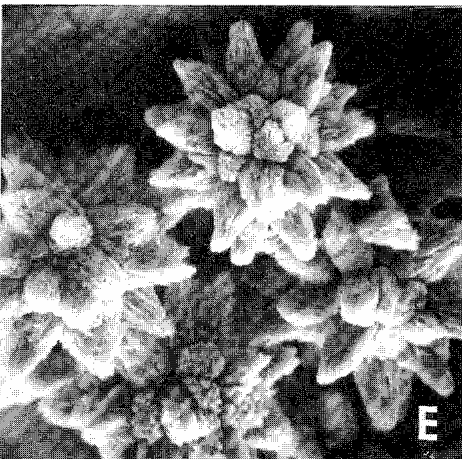
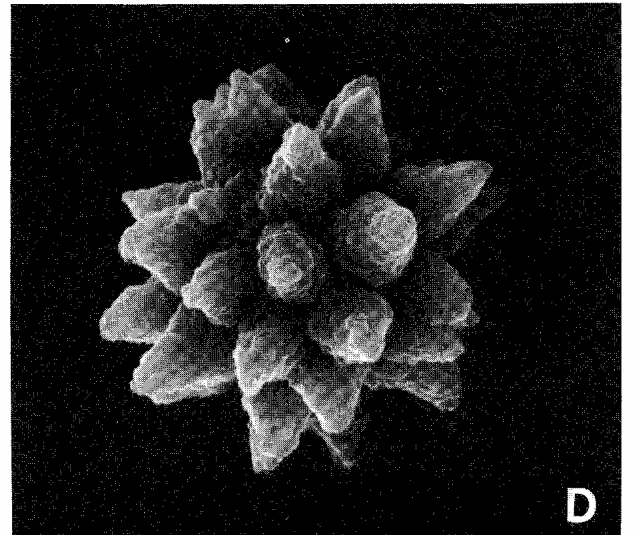
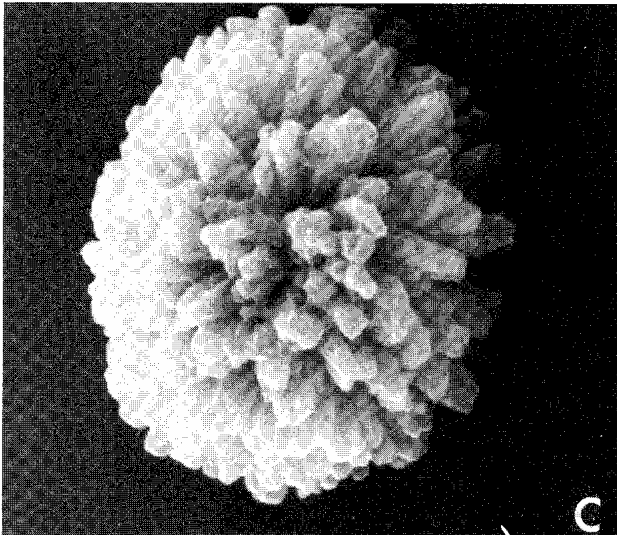
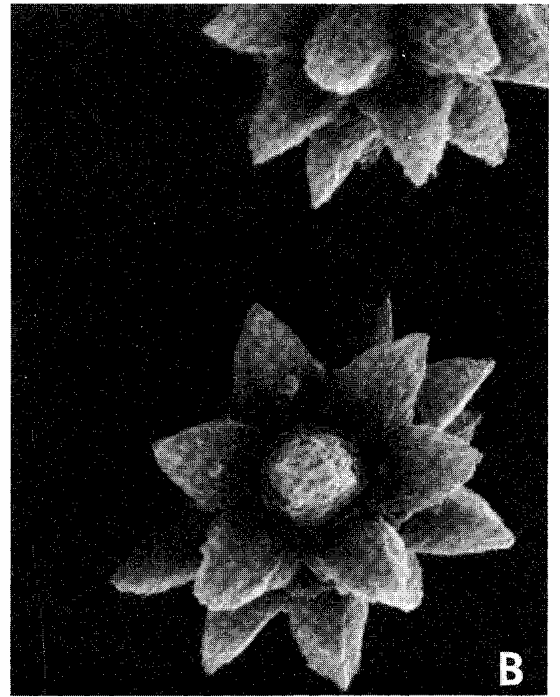
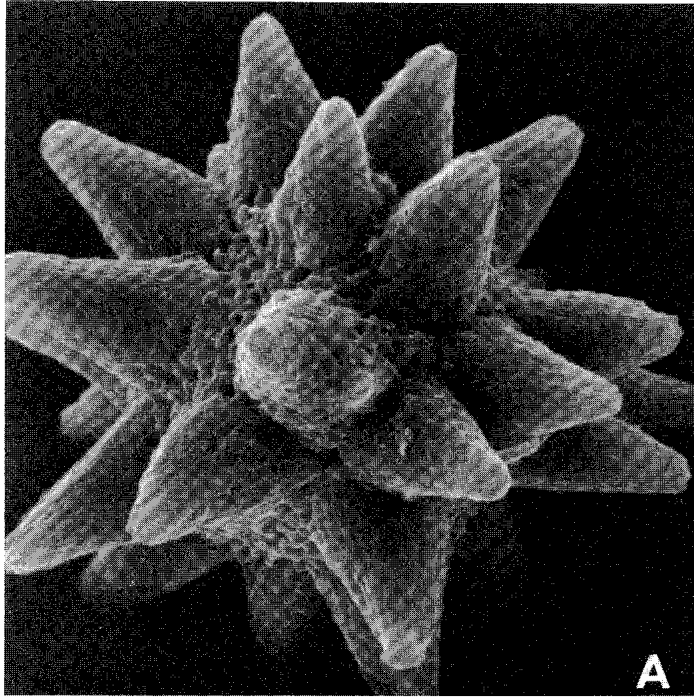


PLATE II

Spicules of Didemnidae, viewed by scanning electron microscopy. A, *Didemnum coccineum* (Von Drasche); B, *D. maculosum* (Milne Edwards) soft, atypical form; C, *D. fulgens* (Milne Edwards); D, *D. coriaceum* (Von Drasche); E, *D. pseudofulgens* Médioni; F, *D. peyrefittense* Brément; G, *D. amourouxi* Lafargue; H, *D. drachi* Lafargue; I, *D. commune* (Della Valle). Scale bars : A, B, C, F, H : 25 μm ; D, E : 12 μm ; G, I : 50 μm .

PLANCHE II

Spicules de Didemnidae, vus au microscope électronique à balayage : A, *Didemnum coccineum* (Von Drasche); B, *D. maculosum* (Milne Edwards) forme molle atypique; C, *D. fulgens* (Milne Edwards); D, *D. coriaceum* (Von Drasche); E, *D. pseudofulgens* Médioni; F, *D. peyrefittense* Brément; G, *D. amourouxi* Lafargue; H, *D. drachi* Lafargue; I, *D. commune* (Della Valle). Le trait d'échelle mesure 25 μm : A, B, C, F, H; 12 μm : D, E; 50 μm : G, I.



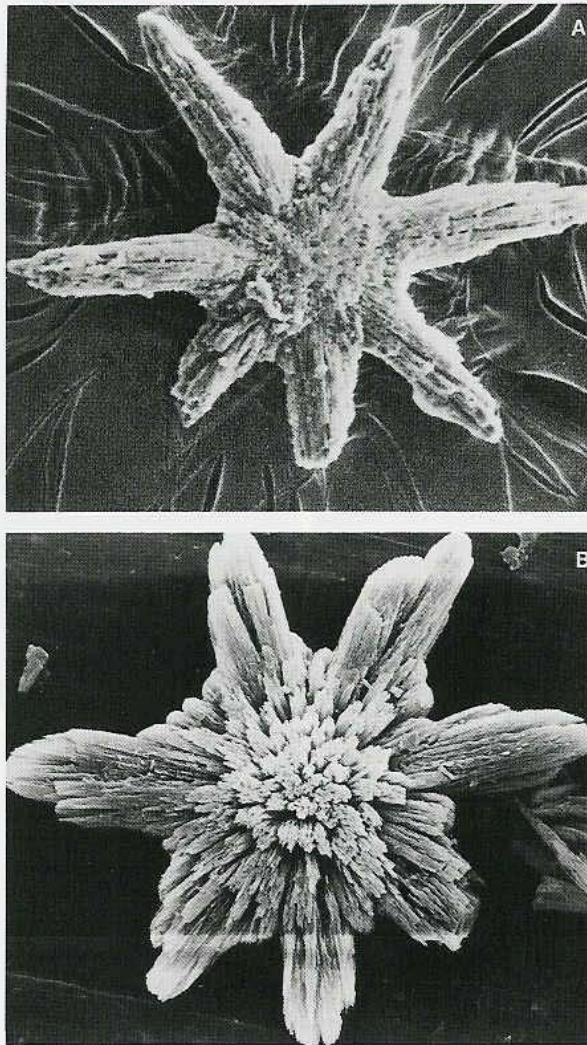


PLATE III

Spicules of Didemnidae, viewed by scanning electron microscopy : the shape of the spicules has not changed for 38-58 million years. A, fossilized spicule of *Echinoclinum (Cystodytes ?) brachiatus* Buge and Monniot, from the Paris Basin, Eocene, Ypresian (from BUGE and MONNIOT, 1972). Size : about 250 μm ; B, spicule of *Echinoclinum philippinense* Tokioka, recent tropical species. Size : about 150 μm .

PLANCHE III

Spicules de Didemnidae vus au microscope électronique à balayage : la forme des spicules n'a pas varié en 38-58 millions d'années. A, spicule fossile de *Echinoclinum (Cystodytes ?) brachiatus* Buge et Monniot, du bassin de Paris, Eocène, Yprésien (d'après BUGE et MONNIOT, 1972). Taille : 250 μm environ. B, spicule de *Echinoclinum philippinense* Tokioka, espèce tropicale actuelle. Taille : 150 μm environ.

PLATE IV

Spicules of Didemnidae, viewed by scanning electron microscopy. A, *Trididemnum cf. savignyi* (Herdman); B, *Didemnum protectum* (Daumézon); C, *D. lahillei* Hartmeyer; D, *D. granulosum* (Von Drasche); E, *Trididemnum cereum* (Giard); F, *T. inarmatum* (Von Drasche). Scale bars : A : 8 μm ; C : 10 μm ; B, D : 16 μm ; F : 12 μm ; E : 25 μm .

PLANCHE IV

Spicules de Didemnidae, vus au microscope électronique à balayage : A, *Trididemnum cf. savignyi* (Herdman); B, *Didemnum protectum* (Daumézon); C, *D. lahillei* Hartmeyer; D, *D. granulosum* (Von Drasche); E, *Trididemnum cereum* (Giard); F, *T. inarmatum* (Von Drasche). Le trait d'échelle mesure 8 μm : A; 10 μm : C; 16 μm : B, D; 12 μm : F; 25 μm : E.

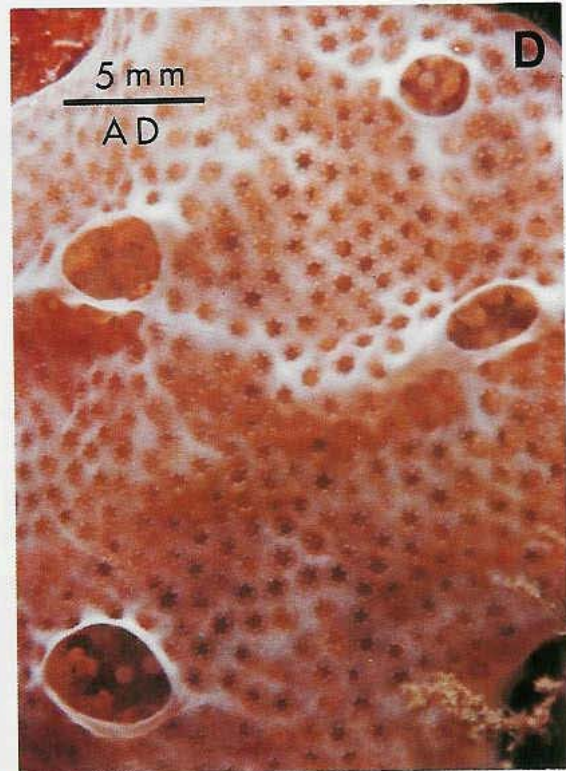
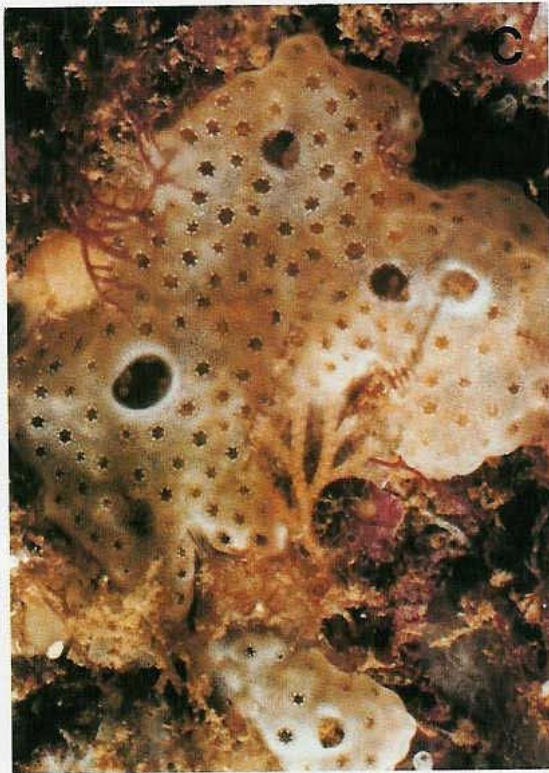
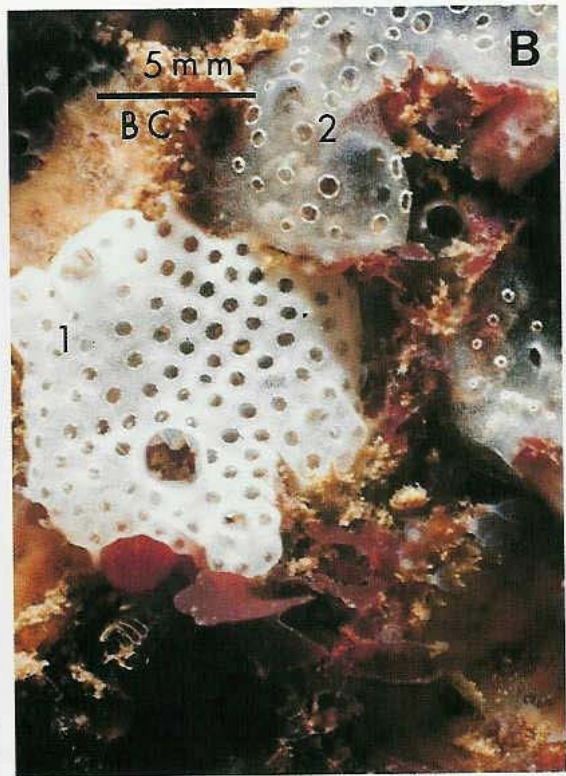
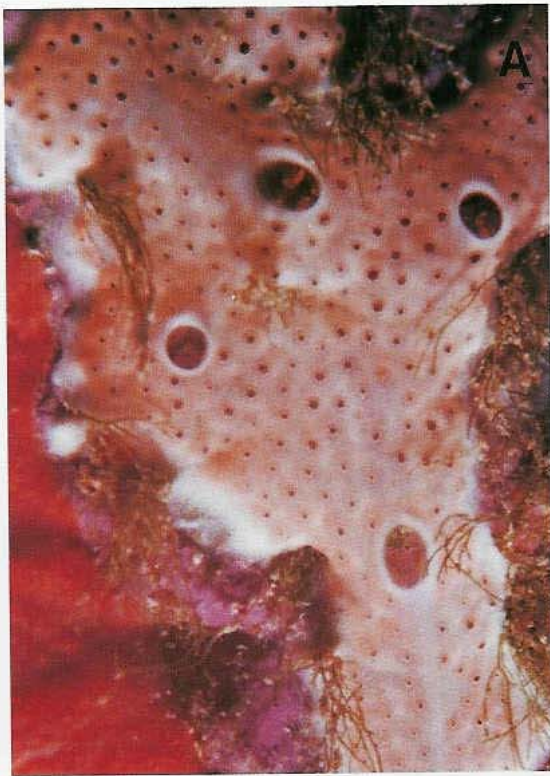


PLATE V

Underwater photographs of colonies by F. LAFARGUE (m = metres deep). A : *Lissoclinum perforatum* (Giard) beige-pink form, Grotte du Cap Béar, 3 m. B : 1. *Didemnum maculosum* (Milne Edwards), white form; 2. *Diplosoma spongiforme* (Giard), grey form, Grotte du Troc, vertical face, 2 m. C : *Lissoclinum perforatum* (Giard), beige form, Grotte du Troc, vertical face, 2 m; D : *Lissoclinum weigelei* Lafargue, beige-pink form, Grotte du Cap Béar, vertical face, 3 m.

PLANCHE V

Photographies sous-marines de colonies réalisées par F. LAFARGUE (m = mètres de profondeur). A : *Lissoclinum perforatum* (Giard) forme beige rosé, grotte du Cap Béar, 3 m. B : 1. *Didemnum maculosum* (Milne Edwards) forme blanche; 2. *Diplosoma spongiforme* (Giard) forme grise, Grotte du Troc paroi verticale 2 m. C : *Lissoclinum perforatum* (Giard) forme beige, Grotte du Troc, paroi verticale, 2 m. D : *Lissoclinum weigelei* Lafargue, forme beige rosé, Grotte du Cap Béar, parois verticale, 3 m.

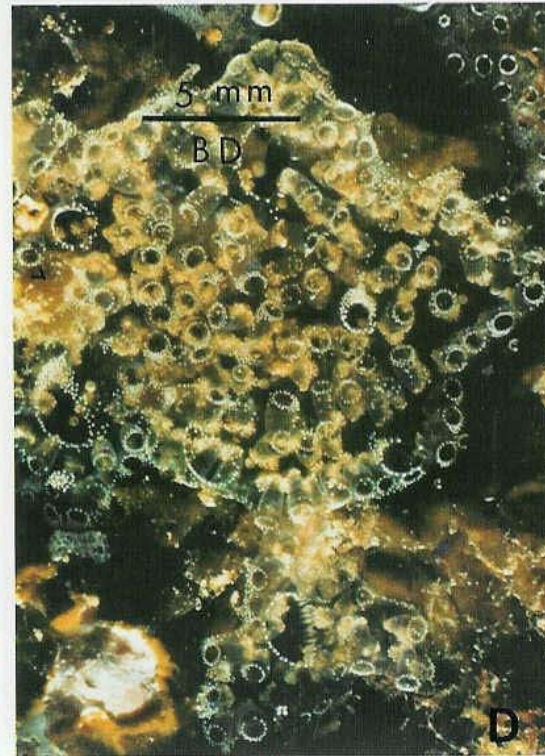
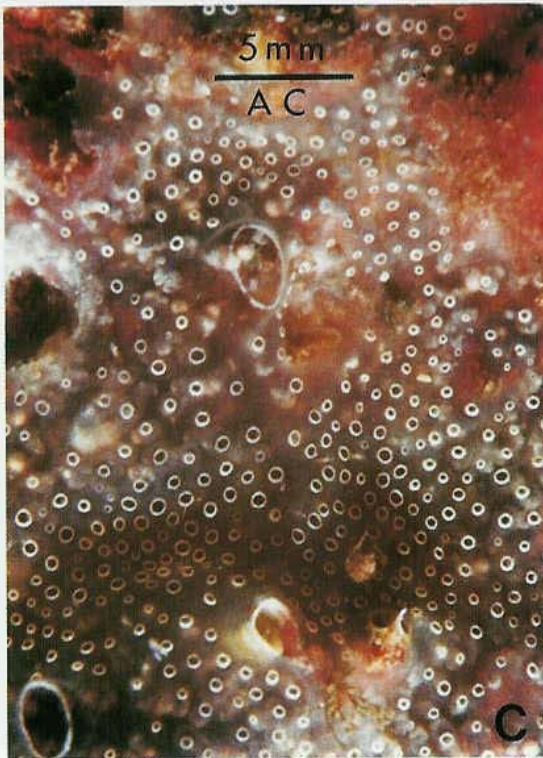
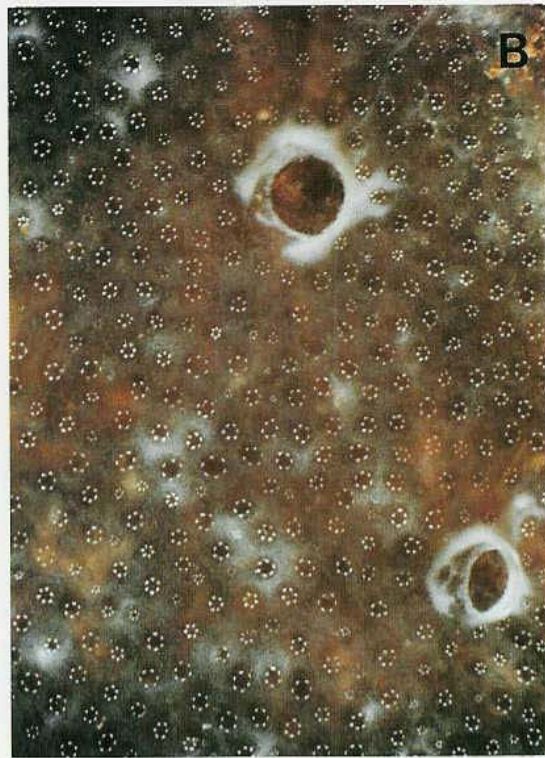


PLATE VI

Underwater photographs of colonies by F. LAFARGUE (m = metres deep). A : *Lissoclinum weigelei* Lafargue, beige form, Grotte du Cap Béar, vertical face, 2 m. B : *Diplosoma spongiforme* (Giard), punctuated form, Cap Peyrefitte, vertical face, 15 m. C : *D. spongiforme* annulated form, île Grosse, vertical face, 12 m. D : *D. listerianum* (Milne Edwards) typical form, vertical face, infralittoral « fringe » $\frac{1}{2}$ depth : 50 cm.

PLANCHE VI

Photographies sous-marines de colonies réalisées par F. LAFARGUE (m = mètres de profondeur). A : *Lissoclinum weigelei* Lafargue, forme beige, grotte du Cap Béar, paroi verticale, 2 m. B : *Diplosoma spongiforme* (Giard) forme ponctuée, Cap Peyrefitte, paroi verticale, 15 m. C : *D. spongiforme* forme annelée, île Grosse, paroi verticale, 12 m. D : *Diplosoma listerianum* (Milne Edwards) forme typique, paroi verticale, frange infralittorale, 50 cm de profondeur.

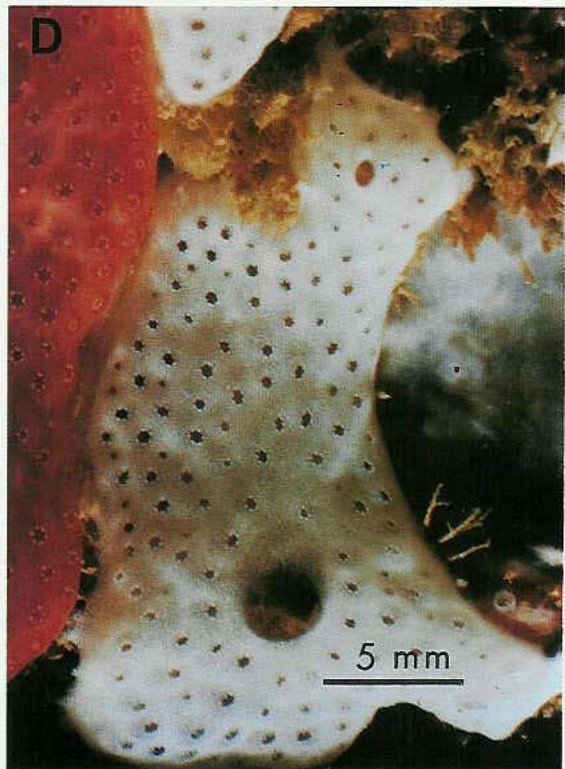
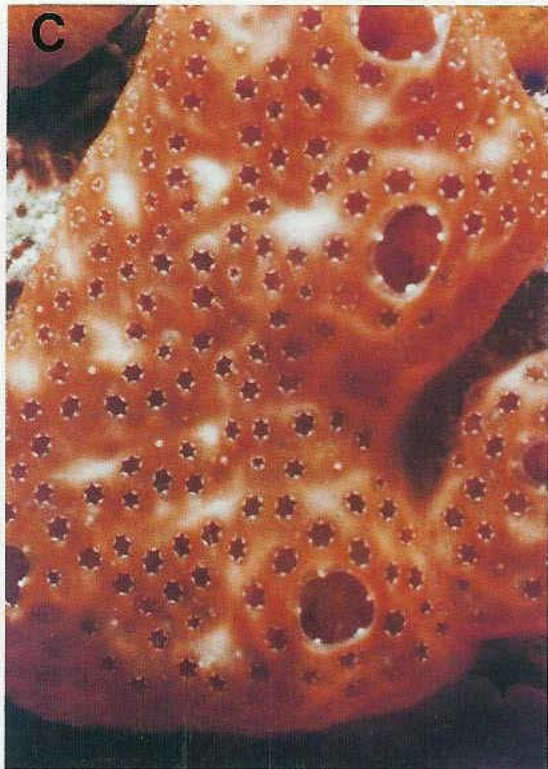
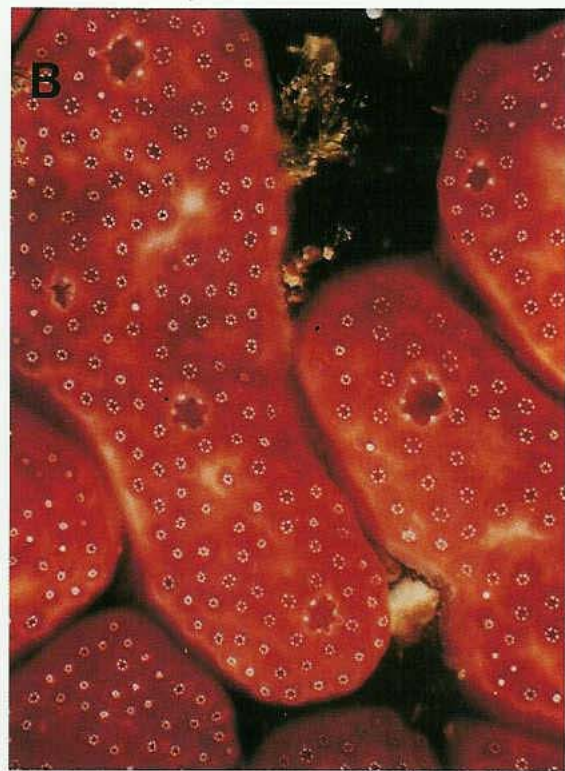
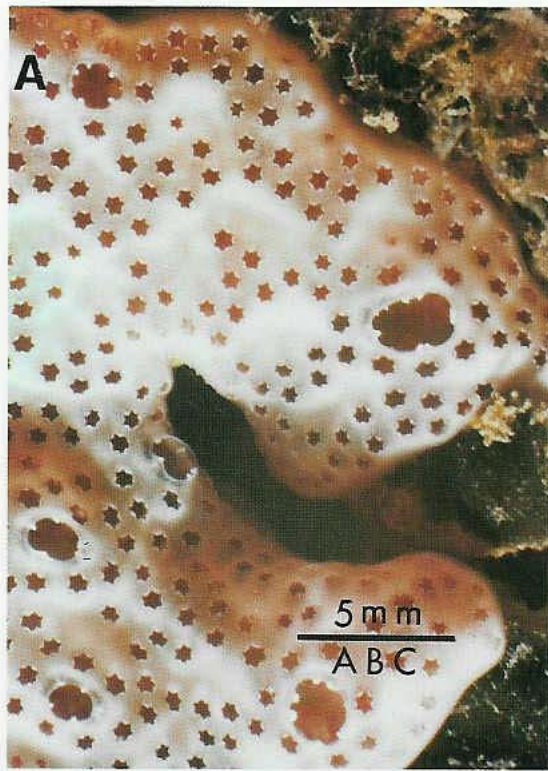


PLATE VII

Underwater photographs of colonies by F. LAFARGUE (m = metres deep). A : *Polysyncraton lacazei* (Giard) amethyst form, Cap Oullestreil, vertical face, 10 m. B : *P. lacazei* typical red form, Grotte du Cap Béar, vertical face, 2 m. C : *P. lacazei* a different colony, Grotte du Cap Béar, vertical face, 4 m. D : *Lissoclinum perforatum* (Giard), typical white form, Grotte du Cap Béar, vertical face, 2 m.

PLANCHE VII

Photographies sous-marines de colonies réalisées par F. LAFARGUE (m = mètres de profondeur). A. *Polysyncraton lacazei* (Giard) forme améthyste, Cap Oullestreil, paroi verticale, 10 m. B : *P. lacazei* forme typique rouge, grotte du Cap Béar, paroi verticale, 2 m. C : *P. lacazei* autre colonie, grotte du Cap Béar, paroi verticale, 4 m. D : *Lissoclinum perforatum* (Giard) forme typique blanche, grotte du Cap Béar, paroi verticale, 2 m.

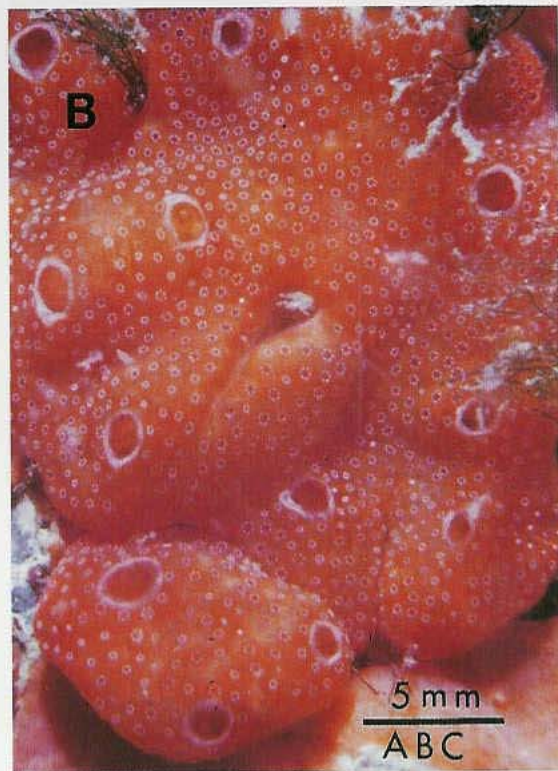
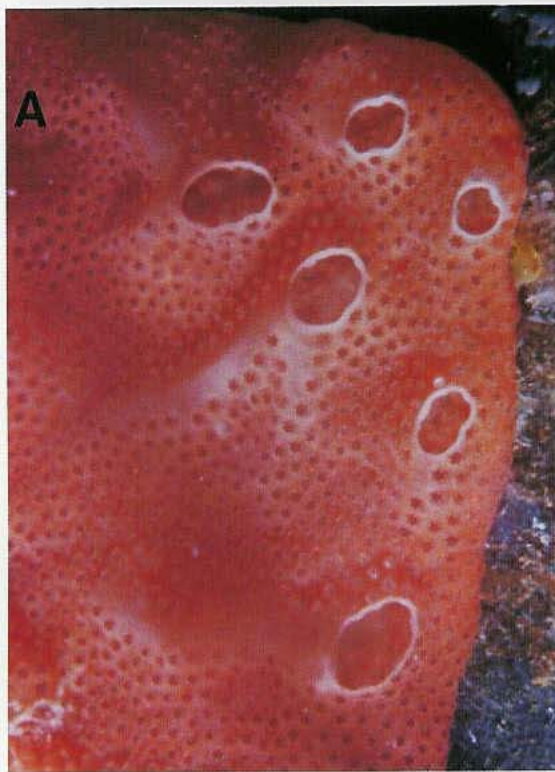


PLATE VIII

Underwater photographs of colonies by F. LAFARGUE (m = metres deep). A : *Didemnum fulgens* (Milne Edwards), typical form, Grotte du Cap Béar, vertical overhanging face, 2 m. B : *D. fulgens* atypical form, with white-punctuated buccal apertures of zooids, Ile Grosse, vertical face, 2 m. C : *Didemnum coccineum* (Von Drasche) typical form, Grotte du Cap Béar, vertical face, 2 m. D : *Didemnum coriaceum* (Von Drasche) mauve form, overhanging face, Cap Rédéris, 25 m.

PLANCHE VIII

Photographies sous-marines de colonies réalisées par F. LAFARGUE (m = mètres de profondeur). A : *Didemnum fulgens* (Milne Edwards) forme typique, grotte du Cap Béar, paroi verticale surplombante, 2 m. B : *D. fulgens* forme atypique avec ouvertures buccales des zoïdes ponctuées de blanc, île Grosse, paroi verticale, 2 m. C : *Didemnum coccineum* (Von Drasche) forme typique, grotte du Cap Béar, paroi verticale, 2 m. D : *Didemnum coriaceum* (Von Drasche) forme violacée, paroi surplombante, Cap Rédéris : 25 m.

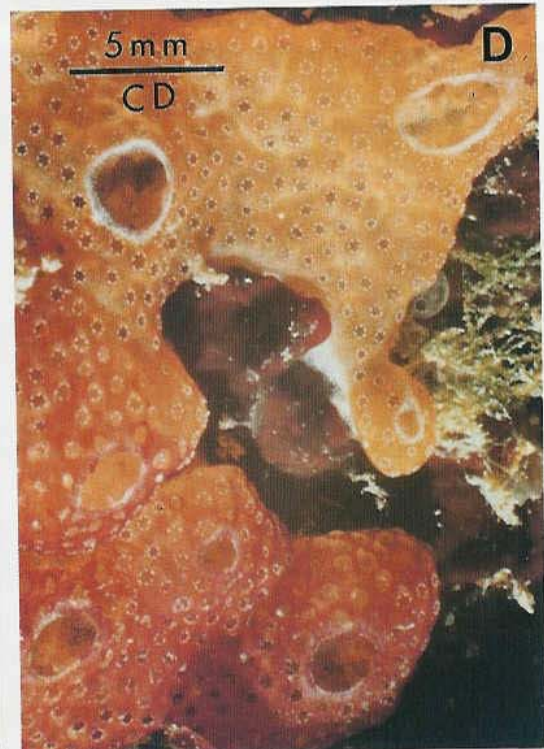
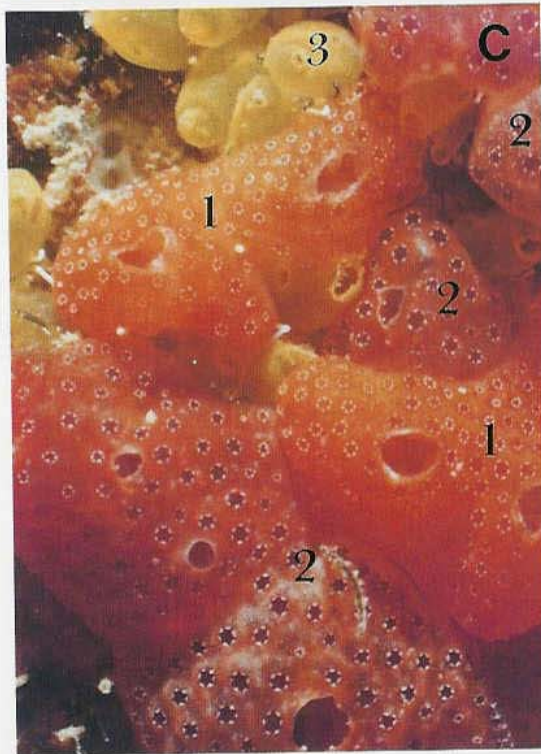
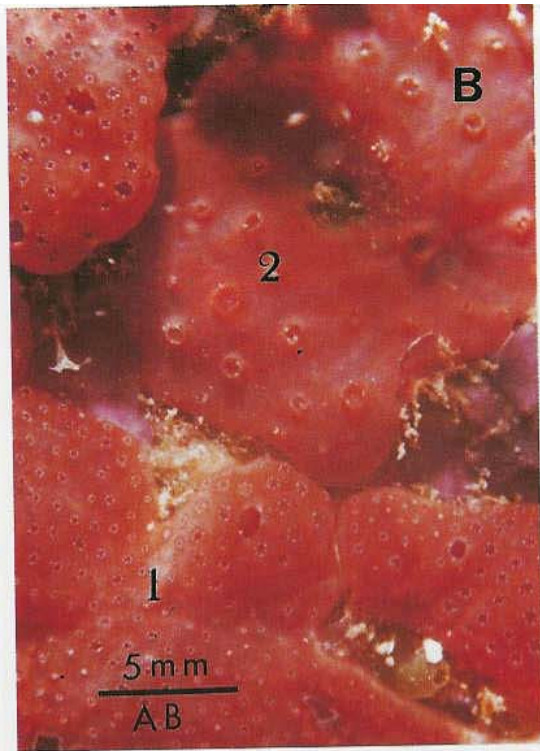
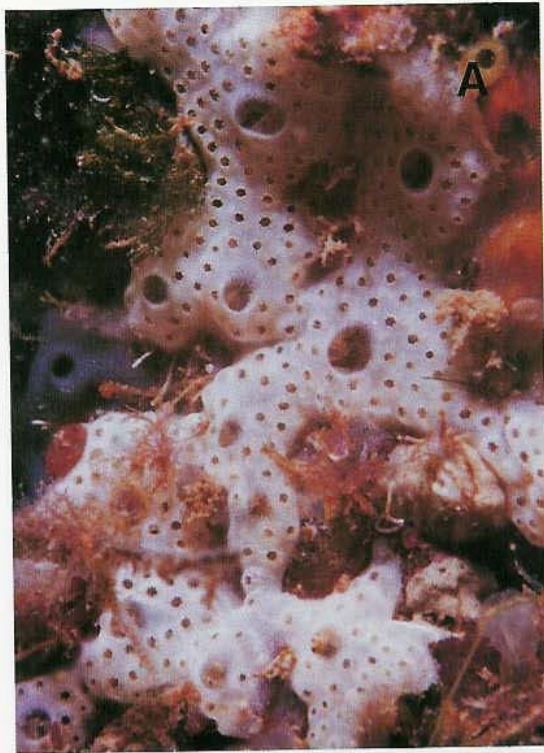


PLATE IX

Underwater photographs of colonies by F. LAFARGUE (m = metres deep). A : *Didemnum maculosum* (Milne Edwards) white form, Ile Grosse, vertical face, 9 m. B : 1. *Polysyncraton lacazei* (Giard) typical form, colour identical to that of the sponge *Hamigera hamigera* (Schmidt), 2. C : strong resemblance between young colonies of (2) *P. lacazei* and (1) *Didemnum fulgens* (Milne Edwards); *Ecteinascidia herdman* (Lahille), 3, Perophoridae, Grotte du Cap Béar, overhanging face, 3 m. D : *D. fulgens* atypical form with low spicule density; pink colour is due to the presence of fibrous algae on the tunic, Grotte du Cap Béar, overhanging face, 3 m.

PLANCHE IX

Photographies sous-marines de colonies réalisées par F. LAFARGUE (m = mètres de profondeur). A : *Didemnum maculosum* (Milne Edwards) forme blanche, île Grosse, paroi verticale, 9 m. B : 1. *Polysyncraton lacazei* (Giard) forme typique de teinte identique à celle du spongiaire 2. *Hamigera hamigera* (Schmidt). C : grande ressemblance entre les jeunes colonies de (2) *P. lacazei* et (1) *Didemnum fulgens* (Milne Edwards); 3. *Ecteinascidia herdmani* (Lahille), Perophoridae, grotte du Cap Béar, paroi verticale surplombante 3 m. D : *D. fulgens* forme atypique à spicules peu denses; la couleur rosée est due à la présence d'algues filamenteuses sur la tunique, grotte du Cap Béar, paroi verticale surplombante, 3 m.

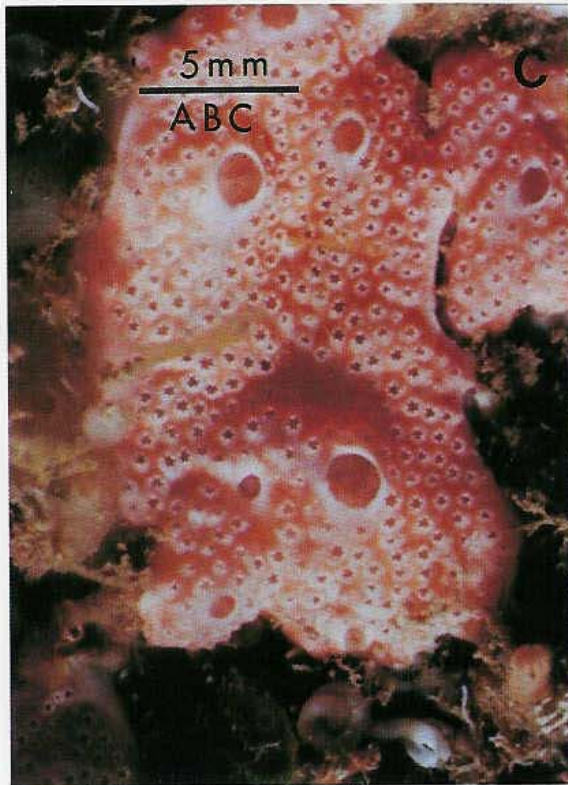
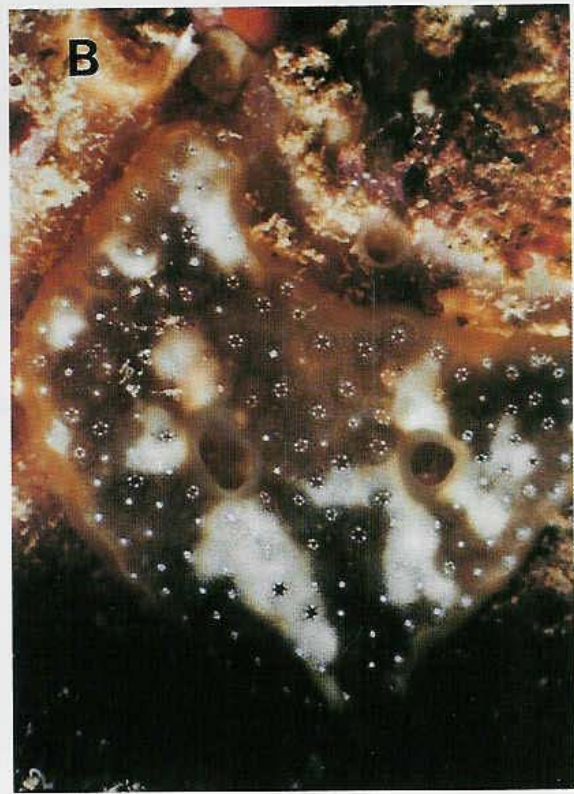


PLATE X

Underwater photographs of colonies by F. LAFARGUE (m = metres deep). A : *Trididemnum cereum* (Giard) striped form, Ile Grosse, overhanging face, 1 m. B : *T. cereum*, young colony, vertical face, blocks on the external face of pier, 4 m. C : *Didemnum commune* (Della Valle) orange form, tunnel of Cap R  d  ris, 2 m. D : *D. lahillei* Hartmeyer, white form, vertical face, 11 m.

PLANCHE X

Photographies sous-marines de colonies r  alis  es par F. LAFARGUE (m = m  tres de profondeur). A : *Trididemnum cereum* (Giard) forme tigr  e,   le Grosse, paroi verticale surplombante, 1 m. B : *T. cereum* jeune colonie, paroi verticale, blocs rocheux de la face ext  rieure de la jet  e du port, 4 m. C : *Didemnum commune* (Della Valle) forme orang  e, tunnel du Cap R  d  ris, 2 m. D : *D. lahillei* Hartmeyer, forme blanche, paroi verticale, 11 m.



PLATE XI

An example of a strong external resemblance (cryptic species) between two species belonging to different genera. A : *Trididemnum cereum* (Giard), B : *Didemnum protectum* (Daumézon). Note the variously pronounced contraction of the zooids inhaling siphons, measuring 0.25 mm when completely expanded. The part of the colony represented in A measures 1 cm, 6 mm in B (Photo by J. LECOMTE, CNRS technician, Laboratoire Arago).

PLANCHE XI

Un exemple de fausse ressemblance (espèces cryptiques) entre deux espèces de genres différents : A, *Trididemnum cereum* (Giard), B, *Didemnum protectum* (Daumézon). Noter la contraction plus ou moins grande des ouvertures buccales des zoïdes qui mesurent, en pleine extension, un quart de millimètre. La portion de colonie photographiée mesure 1 cm pour A et 6 mm pour B. Photographie faite au Laboratoire par J. LECOMTE, technicien CNRS.

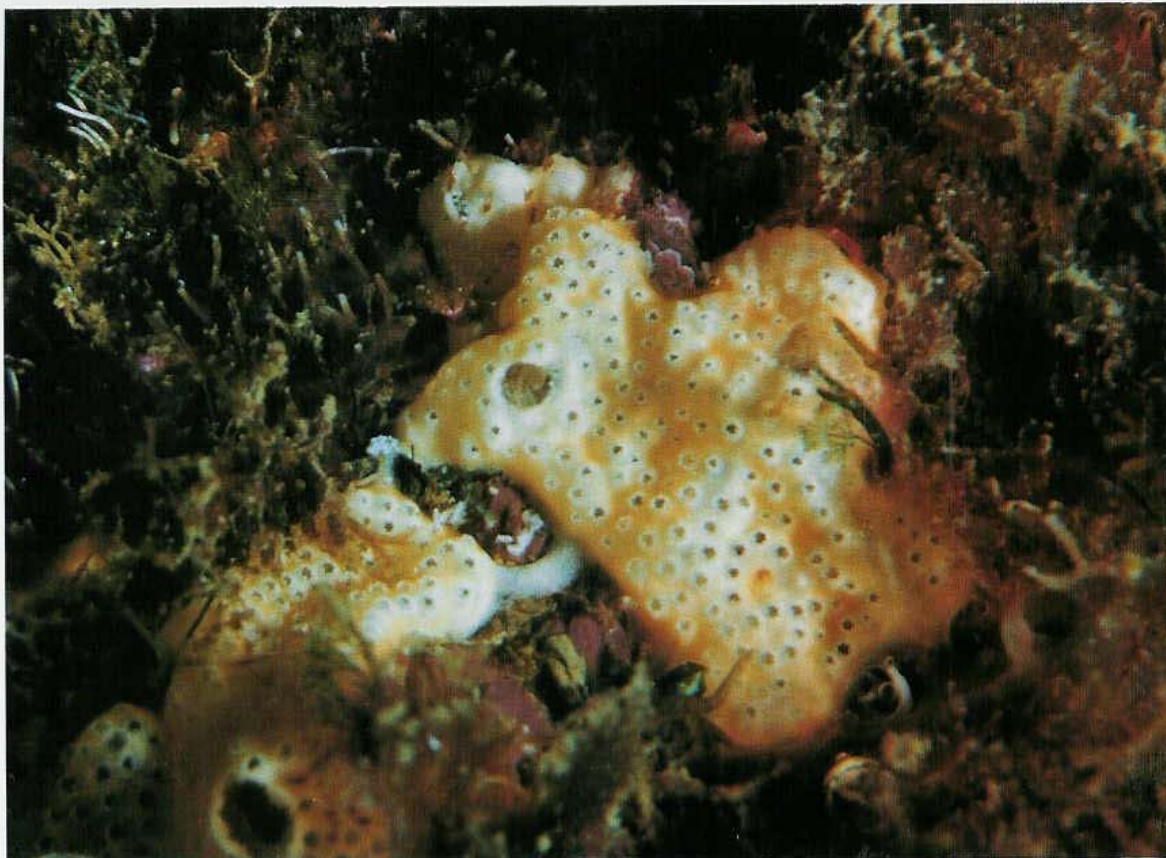


PLATE XII

Above, *Polysyncraton bilobatum* Lafargue : Ile Grosse (Banyuls/Mer), on a vertical face at -8 m. Colony diameter is 2 cm. Photo by F. LAFARGUE. Below, *Didemnum pseudofulgens* Médioni : île Grosse (Banyuls-sur-Mer), on a vertical face at -4 m. Colony diameter is 2 cm. Photo by M. WAHL.

PLANCHE XII

Haut, *Polysyncraton bilobatum* Lafargue. Ile Grosse, sur une paroi verticale à 8 m de profondeur. La colonie mesure 2 cm. Photographie F. LAFARGUE. Bas, *Didemnum pseudofulgens* Médioni : île Grosse (Banyuls-sur-Mer), sur une paroi verticale à 4 m de profondeur. La colonie mesure 2 cm. Photographie M. WAHL.