



The polystyelid ascidian *Distomus hupferi* (Michaelson, 1904) in northern France, and comments on its European congenetics

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Abstract: The polystyelid ascidian *Distomus hupferi*, known mainly from northwest Africa, inhabits rocky shores in northern Brittany, along with *D. variolosus*, more common on laminarian stipes. Specimens show both species around Roscoff in the 1960's; comments by earlier researchers suggest they both were there 80 years ago. Shape and arrangement of the testes differ markedly between these species, and other traits reinforce the distinction made on that basis. The Mediterranean species *D. fuscus* has testes shaped like those of *D. hupferi* but arranged like those of *D. variolosus*, and it has many more longitudinal branchial vessels and more stomach grooves. Hartmeyer's opinion remains convincing that *D. fuscus*, customarily taken to be a southern form of *D. variolosus*, is a valid species. The possibility that all three species are actually ecotypes of *D. variolosus* remains to be explored but currently is unsupported by clear evidence.

Résumé : L'ascidie polystyélide *Distomus hupferi*, connue principalement de l'Afrique du nord-ouest, habite la côte rocheuse Nord de Bretagne, avec *D. variolosus*, celle-ci plus abondante sur les stipes de laminaires. Des échantillons récoltés dans les années 1960 montrent que ces deux espèces coexistaient alors dans cette région et les travaux d'auteurs plus anciens suggèrent même leur présence dans la région il y a 80 ans. Les deux espèces diffèrent par la forme et la disposition des testicules et d'autres caractères confirment cette distinction. L'espèce méditerranéenne *D. fuscus* a des testicules qui ressemblent par leur forme à ceux de *D. hupferi*, et par leur disposition à ceux de *D. variolosus*. *D. fuscus* a par ailleurs beaucoup plus de sinus branchiaux longitudinaux et plus de plis stomacaux que les autres espèces. L'opinion de Hartmeyer selon laquelle *D. fuscus* est une espèce valide demeure vraisemblable, bien qu'elle soit habituellement considérée comme une forme méridionale de *D. variolosus*. Une dernière éventualité subsiste, les trois espèces pouvant être des formes écologiques de *D. variolosus* ; mais cette hypothèse n'est pas actuellement étayée par des preuves suffisamment nettes.

Keywords: tunicate, ascidian, Styelidae, *Distomus*, Europe, systematics

Introduction

Colonies of the styelid ascidian genus *Distomus* form patches that encrust very low intertidal and subtidal rocky surfaces and living surfaces, especially laminarian stipes but also occasionally mussel shells and even pyurid ascidians along European shores. European representatives of the

genus have striking traits - - intensely blood-red color; a thin but tough, opaque tunic clothing densely crowded zooids that project separately from each other for about half their 1 cm height above the colony's basal sheet of common tunic, cloacal siphons that open directly to the sea from each zooid rather than indirectly (like *Botryllus*) via common cloacal cavities. These appearances serve to identify this animal to genus virtually unmistakably in the field.

Sure identification of ascidians to species, however, usually involves careful dissection that is often impossible

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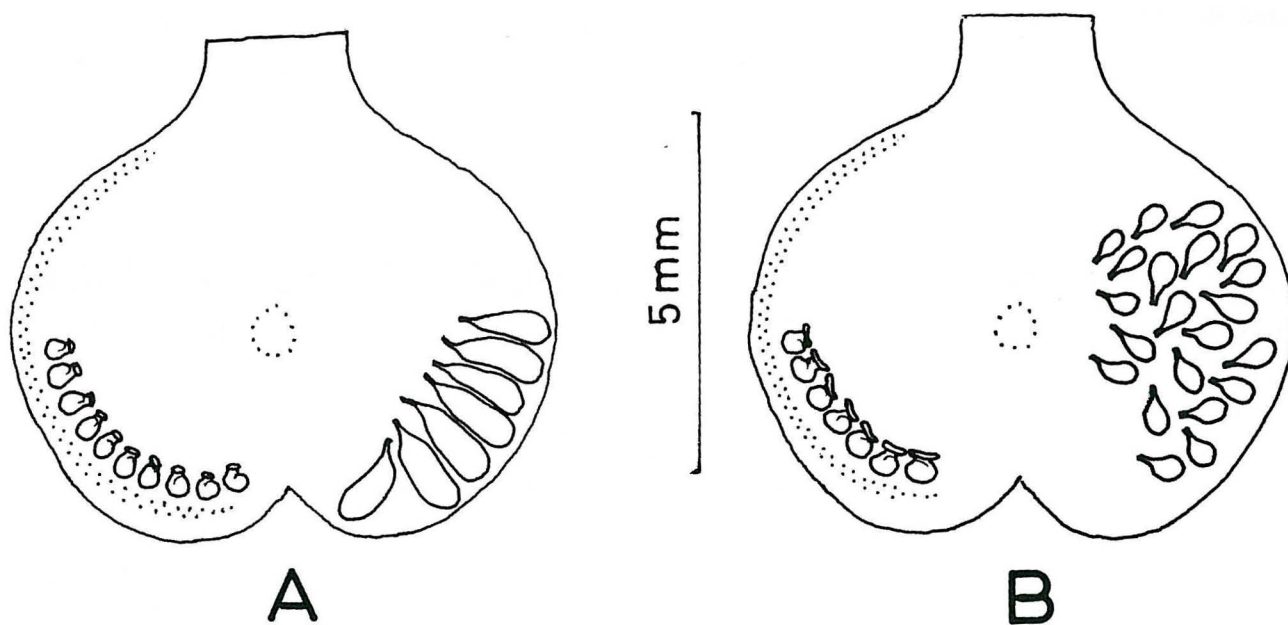


Figure 1. Schematic depictions to compare (A) *Distomus hupferi* and (B) *D. variolosus* from Roscoff. Zooid opened ventrally and pharynx and gut-loop removed to show shape and arrangement of ovaries (in right ventral wall of zooid, next to dotted endostyle) and of testes (in left ventral or lateral wall of zooid). Circlet of dots in center of zooid represents cloacal aperture.

Figure 1. Représentation schématique comparant les espèces *Distomus hupferi* (A) et *D. variolosus* (B) de Roscoff. Zoïdes ouverts ventralement, pharynx et anse digestive retirés pour montrer la forme et la disposition des ovaires (dans la paroi ventrale droite du zoïde, près de l'endostyle en pointillé) et des testicules (dans la paroi ventrale ou latérale gauche du zoïde). Au centre du zoïde, le cercle en pointillé représente l'ouverture cloacale.

except on fixed specimens and sometimes difficult even then. The preparatory effort involved, the delicacy of surgical exploration, and the obscurity of some crucial internal traits (e.g., number and arrangement of internal longitudinal pharyngeal vessels, number of ridges on the stomach) can be discouraging when external traits have carried the identification to genus so easily. For convenience, custom more than scrutiny may then guide or even decide matters. As a result, some ascidian species can be overlooked or misidentified, even in genera as conspicuous and apparently as distinctive in the field as *Distomus*.

During the summers of 1964-65, for a study of its gonadogenesis, I collected *Distomus variolosus* Gaertner, 1774 from Roscoff and the nearby Ile de Callot. R. Borojevic took colonies subtidally by SCUBA from the stipes of laminarian algae, and I collected intertidally mostly from granitic surfaces. Examination of these specimens revealed two distinct forms, which I designated "Type A" and "Type B" to denote differences in the pharynx and gonads, field characters (coloration, prominence of buds around a colony's margin), and habitat (Newberry, 1968). In 1994, in Drs. C. and F. Monniot's laboratory, MNHN Paris, I re-examined this material and at their suggestion compared *Distomus variolosus* with *D. hupferi* (Michaelsen, 1904), using specimens of both species identified from various European sites by J.-M. Pérès and by C. Monniot. This re-examination has

established that "*D. variolosus* Type B" is indeed that species, while "*D. variolosus* Type A" is actually *Distomus hupferi*. This paper describes differences between these two species and compares them with a third, *Distomus fuscus* Della Chiaje, 1841, whose status has fallen into confusion.

Results

Distomus zooids are gynandromorphic hermaphrodites (Fig. 1). Their ovaries are aligned along the right side of the mid-ventral line; the testes in some species (such as *D. hupferi*) are mostly aligned side by side along the left side of the mid-ventral line, but in other species (such as *D. variolosus*) they are scattered rather broadly on the left atrial wall. The arrangement of testes in *D. variolosus* and *D. hupferi* is depicted schematically in Fig. 1, as are slight but consistent differences in the appearance of the two species' ovaries.

Table 1 summarizes traits that, taken as a suite, permit the two species *Distomus hupferi* and *D. variolosus* to be distinguished from each other, even allowing for considerable intraspecific variation. Most but not all of Table 1's distinctions between *D. hupferi* and *D. variolosus* are discussed in Newberry (1968) as distinctions between "Type A" and "Type B" of what I then thought was all *D. variolosus*. In Table 1 counts of internal longitudinal branchial vessels (ILVs) are from mid-pharynx and consider the most ventral,

Table 1. Traits that distinguish *Distomus hupferi* from *D. variolosus*, based on specimens collected at Roscoff and environs, 1964-65. For other traits that do not differ between these two species, see text.

Tableau 1. Caractères qui distinguent *Distomus hupferi* de *D. variolosus*, d'après des spécimens récoltés à Roscoff et ses environs en 1964-65. En ce qui concerne les autres caractères qui ne diffèrent pas entre ces deux espèces, voir le texte.

	<i>Distomus hupferi</i>	<i>Distomus variolosus</i>
in Newberry, 1968:	<i>D. variolosus</i> "Type A"	<i>D. variolosus</i> "Type B"
appearance of colony:	encrusting, with tightly packed zooids buried only basally in the common tunic	encrusting, with tightly packed zooids buried to about a third their height in the common tunic
color in life:	blood red with slight white axial striping through both siphons and extending posteriorly	uniformly blood red, no stripes
buds on colony margin:	many extend finger-like beyond the broad margin of common tunic	extend only within a broad front of spreading common tunic
height of living zooid with tunic:	ca. 7 mm	ca. 9 mm
tunic surface:	usually with smooth patches even if whole zooid is wrinkled by contraction	rough, coriaceous, even pebbly surface, especially when zooid contracts
consistency of formalin-fixed tunic:	firm, but tears easily with forceps	firm and very tough, resists tearing with forceps
oral tentacles (1st order):	ca. 10	ca. 12
formula for internal longitudinal branchial vessels --		
LEFT:	DL O (3) 1 (4) 2 E	DL O (3) 2 (4) 5 E
RIGHT:	DL 1 (4) 1 (3) 2 E	DL 1 (4) 2 (4) 5 E
ovaries -- shape:	small, globular, with stout oviduct; narrow flange around ovipore	small, globular, with stout oviduct; wide, flaring flange around ovipore
arrangement:	10-13 on right side, aligned alongside endostylar axis in the posterior half of the zooid	6-12 on right side, aligned alongside endostylar axis in the posterior half of the zooid
testes -- shape:	large, sausage-shaped sacs, each with a fili-form spermiduct	small, tapering ovoid or bean-shaped sacs, each with a fili-form spermiduct
arrangement:	6-10 on left side, mostly aligned alongside endostylar axis, one or a few displaced out of alignment posteriorly	15-35 scattered on left side, often in clumps, not uniformly aligned alongside endostylar axis
habitat:	not on laminarian stipes, occasionally on furoid algae and on pyrid ascidians, usually on naked rock surfaces	especially on laminarian stipes, also on other living surfaces (e.g. mussels), rarely if ever on naked rock surfaces

rudimentary "fold" on each side to be merely a close apposition of vessels; vessel-counts are representative of each species, but specimens differ somewhat in their particular ILV formulas. I have not included the third European species of the genus, *D. fuscus*, in Table I; but I discuss its key diagnostic traits (form and arrangement of testes, number of internal longitudinal branchial vessels and of stomach grooves) in this paper's Discussion.

While Table 1 summarizes their differences, *Distomus hupferi* and *D. variolosus* resemble each other not only in

their external appearance but also in many internal, anatomic ways. In both species, for example, the dorsal tubercle has a straight or slightly incurled transverse slit, the peripharyngeal band makes a shallow V as it passes behind the dorsal tubercle, the stomach has a dozen ridges and carries a caecum, the anus is smooth and may be cut either squarely or at a slight angle to the rectum, and endocarps are prominent. In each species there is considerable variation in the gut-loop, especially in the length of the intestine and the development of its lining.

In both *D. variolosus* and *D. hupferi* at Roscoff the two branchial folds per side vary in prominence along the length of the pharynx as the internal longitudinal vessels (ILVs) often spread apart posteriorly. Most of the Breton specimens I have examined have low folds marked not only by closely apposed ILVs within the branchial sac but also by inflated transverse vascular bridges on the outer wall of the pharynx. Some smaller zooids apparently lack folds, but closely spaced ILVs trace their phantom course (Newberry, 1968, Fig. 2). Branchial structure also varies somewhat among African populations of *D. hupferi* (cp. Sluiter, 1919, 1927, 1928, and Monniot, 1969).

Discussion

Distomus in northwestern Europe

In his comparison of polystyelids from Roscoff, Selys-Longchamps (1917) studied *D. variolosus*, which has stout little testes about the size of endocarps. But he also reported (pp. 189-190) that at different times he encountered *Heterocarpa* [= *Distomus*] from Roscoff with large, sausage-shaped testes, and he remarked that these testes resembled those Michaelsen (1904) described for *Alloeocarpa fusca* (Delle Chiaje, 1841) (= *D. fuscus* in Hartmeyer's 1912 revision of Adriatic ascidians). The testes Selys-Longchamps depicts (1917: Fig. D) are as much like those of *D. hupferi* as they are like those of *D. fuscus*. He also often found colonies whose zooids had small, "incompletely developed," pyriform testes of unpredictable mature form. He found no pattern of intermediates between these "extreme" sizes and shapes. Unfortunately without specifying which colonies came from which substrates, Selys-Longchamps collected both from algal stipes, where in 1964-65 I found entirely *D. variolosus*, and from rock surfaces, where I found predominantly *D. hupferi*.

Selys-Longchamps (1917) concluded that we know too little about their formation and variability to use gonadal structure and proportions as reliable traits to identify species of *Distomus* (or, he said, to identify any other species of a polystyelid genus). But he did not enumerate other traits, such as somewhat more stomach grooves or a much more richly vascularized pharynx, that would indicate that he had collected *D. fuscus*. At that time *D. fuscus* was recognized as a Mediterranean species; the branchial and pyloric distinctions between it and *D. variolosus* had been established. Selys-Longchamps' lack of comment may indicate that his specimens' branchial and pyloric traits were like those of *D. variolosus*, even though their testes were dramatically larger -- as they are in *D. hupferi*.

Hartmeyer (1912) also discounted testis-shape as a reliable criterion by which to separate *D. variolosus* and *D. fuscus*. He reported sausage-shaped testes in *D. fuscus*, "but in *D. variolosus*, besides finding the round testes, I found alongside them the long sausage-shaped ones, even

ones that reached the stately length of 3 mm including the sperm duct. Maybe the testes only take on the long shape during sexual maturity" (pg. 203). In contrast, I found (as apparently did Selys-Longchamps) that testes of a Roscoff colony's zooids were either all short and stout or, except for obviously rudimentary or structurally stunted ones (see below), all much longer than wide even if not yet fully mature (Newberry, 1968). Hartmeyer did not comment on the arrangement of testes in *D. fuscus*. In fact, their non-linear arrangement in the two species, *D. variolosus* and *D. fuscus*, is roughly the same, allowing for the effects of fewer, bigger testes in the latter species and more, smaller ones in the former.

In describing the biology of *Distomus variolosus*, Berrill (1948) rather schematically depicted isolated testes (Fig. 4G) that, lacking a scale-bar, by their form could be those either of *D. variolosus* or of *D. hupferi*. But in another drawing (Fig. 4C) he showed testes aligned side by side, and he described their distribution (pg. 642) as "a series of six or seven arranged in the lower mantle wall parallel to... the endostyle") an arrangement of testes, whatever their individual shape, that is much more like *D. hupferi*'s alignment than like the broad field in *D. variolosus*.

Berrill (1948) did not describe *Distomus*'s branchial or pyloric traits, just its gonads, larvae, and budding. His comments about the pharynx and stomach in his monographic account (1950) of *D. variolosus* rule out *D. fuscus*, but they seem to depend largely on Lacaze-Duthiers and Delage (1892), not on his own 1948 work. In addition, his Fig. 68H of 1950, attributed to Lacaze-Duthiers and Delage, in fact is not from that source; it appears to be modified from Selys-Longchamps (1917, Fig. D). This is a significant confusion, since, as I note above, Selys-Longchamps included that drawing to show what in his opinion were not the typical testes of *D. variolosus*.

The double-row arrangement of Roscoff *Heterocarpa glomerata* (= *Distomus variolosus*) testes in Lacaze-Duthiers and Delage (1892, Pl. XX, Fig. 11), copied by Berrill (1950, Fig. 68E), is a highly stylized arrangement, but the testes themselves, rather stiffly depicted, at least suggest the proportions and arrangement of *Distomus variolosus*'s testes, or at least not of *D. hupferi*'s. What Selys-Longchamps was surprised to find "at different times" must have been specimens that differed in their testes from those depicted by Lacaze-Duthiers and Delage.

Both Selys-Longchamps (1917) and Berrill (1948) noted that one or a few tiny, pyriform testes may lie among the big, sausage-shaped ones, sometimes as ripe as their neighbors, either seemingly crowded out but still aligned with the others (Selys-Longchamps) or at the anterior end of the row (Berrill). The latter pattern -- one or two tiny testes at the anterior end of a row of a half-dozen big ones -- is particularly frequent in the Roscoff specimens of *Distomus hupferi* I have examined.

Distomus fuscus in southern Europe

Distomus variolosus occurs widely in Great Britain (Berrill, 1950) and northern France. Harant and Vernières (1933) called this "forme typica" and compared it with a Mediterranean "forme fusca", which they called "abundant" in beds of the pyurid ascidian *Microcosmus* in southeast France and Spain. Their synopsis notes that zooids of "forme fusca", though smaller than "forme typica" (7 mm vs. 10 mm) have twice as many (28 vs. 14) ILVs per side in the branchial sac and half again as many (18 vs. 12) stomach grooves as does "forme typica". Their "forme fusca" of *D. variolosus* is *D. fuscus* Della Chiaje, 1841 (see Michaelsen, 1904, and Hartmeyer, 1912). Harant and Vernières noted the mutual "penetration" of the ranges of the two "formes", particularly the spread of "forme fusca" around the Mediterranean into Portugal, southwestern France, and even southern Brittany. This intermingling suggests to me that these "formes" really are two species retaining their separate identities in each other's company.

The Harant and Vernières (1933) account of *Distomus variolosus* "forme fusca" is puzzling and troubling. They seem to have missed, misread, or dismissed Hartmeyer's case for retaining *D. fuscus* as a distinct species (Hartmeyer, 1912). While their Fig. 44 is labelled "*Distomus fuscus*", their text declares it merely a form of *D. variolosus*. Their sketch (Fig. 44) is an odd mix. They depict little testes like those of "northern" *D. variolosus* but draw them aligned in a single row, while in fact *D. fuscus* has large, sausage-shaped testes spread over the whole left atrial wall. And they show ovaries variously oriented over a broad field of the right atrial wall rather than aligned, as they really are in all European species of *Distomus*, in a row close to the endostyle. Their Fig. 44 merely suggests a few of the stomach's 16-18 grooves, and (an unfortunate but accepted practice in drawing all but aplousobranch ascidians) it does not depict the pharynx at all.

Since Harant and Vernières' monograph, their synonymy of *Distomus variolosus* and *D. fuscus* has prevailed essentially by custom; at least, I cannot find any argued case for it either in their own monograph or since. Add to this the external similarity of *D. variolosus* and *D. hupferi*, and the question arises whether Mediterranean and Iberian Atlantic ascidians regularly reported as *D. variolosus* (e.g., by Tursi, 1980; Turon, 1990; Vázquez Otero, 1993) are indeed that species or are sometimes *D. fuscus* or *D. hupferi*. For sheer efficiency, ecological surveys understandably identify *Distomus* from the outside by its conspicuous generic appearance, not by time-consuming attention to details like ILVs or stomach grooves. But the result may be that a widespread member of the inshore European fauna confronts us with a potential confusion of two or even three species both within and between such studies.

Conclusions

Tursi (1980) includes *Distomus variolosus* in a survey of Italian ascidians. Turon (1990) and Vázquez Otero (1993) describe its ecological habits in Mediterranean and Atlantic Spain; understandably, given the confusing situation described above, neither investigator reports *D. fuscus* or *D. hupferi* in these southern European waters. Southern European *D. variolosus* should be examined anew (a) to check colonies growing on or amidst subtidal *Microcosmus* for zooids that have an especially complex pharynx and numerous stomach grooves, suggesting *D. fuscus*, and (b) to check even dense colonies growing on non-laminarian substrates for *D. hupferi* masquerading as *D. variolosus*.

Distomus hupferi was once considered rare along the European Mediterranean coast (Harant and Vernières, 1933; Monniot, 1969), but has been found increasingly often in recent decades along the Iberian Atlantic coast (C. Monniot, pers. comm.). It is widely distributed in West Africa (Sluiter, 1919, 1927, 1928; Monniot, 1969). My collections indicate that this species evidently was common around Roscoff in the 1960's. MNHN-Paris collections have specimens of *D. hupferi* collected, for example, at Dinard in the 1980's but until now not identified to species. Selys-Longchamps (1917) may have collected the species "from time to time" around Roscoff, and Berrill (1948) appears to have found it around Plymouth. Their tantalizing accounts suggest that *D. hupferi* should be sought not only on French shores but also to the north, where again, without the dissection that is needed for certain identification, all little red polystyelids customarily have been called *D. variolosus*.

The following brief key permits identification of these three species of *Distomus* using formalin-fixed, dissected specimens and even restricting use of the testes as criteria of identification to those situations where they most certainly differ in shape and, especially, arrangement:

1. pharynx with about 24 ILVs per side, 16-18 external grooves on the stomach; long, sausage-shaped testes scattered about the left atrial wall..... *D. fuscus*
- pharynx with about 10-12 ILVs per side, 10-12 external grooves on the stomach..... 2
2. 15-35 testes: stout, stubby sacs the size of endocarps, scattered about the left atrial wall..... *D. variolosus*
- 6-10 testes: long, sausage-shaped sacs, aligned side by side along mid-ventral line except for a few out of alignment posteriorly *D. hupferi*

If, despite Selys-Longchamps' and Hartmeyer's caveats, one were to let the form and arrangement of testes guide one's specific identification of European *Distomus*, the following rules of thumb would apply:

D. variolosus: mature testes rather small (size of endocarps) and stout, scattered widely on the left atrial wall.

D. fuscus: mature testes large and sausage-shaped, scattered on the left atrial wall.

D. hupferi: mature testes large and sausage-shaped, almost all aligned side by side next to the endostyle.

The resemblances among *Distomus variolosus*, *D. fuscus*, and *D. hupferi* do raise the possibility that some or all of these names refer merely to ecological variants of one species (which by priority would be *D. variolosus*). In effect, this is what Harant and Vernières concluded about *D. variolosus* and *D. fuscus*, although they accepted *D. hupferi* as a distinct species. Geographic or habitat-induced variations in ascidian morphology can be dramatic, as the solitary and clumped forms of the simple styelid *Dendrodoa grossularia* show (cf. Lacaze-Duthiers and Delage, 1892; Harant and Vernières, 1933; Berrill, 1950). For example, biotic substrates like laminarian stipes might influence resident *Distomus variolosus* in ways that rocky substrates do not. But it remains an untested speculation whether such an influence could affect the quantity, form, and arrangement of testes, the elaborateness of the flange around each ovipore, and branchial vascularization and stomach-wall structure in such thorough ways as differentiate these three kinds of *Distomus*. In lieu of evidence for substrate-induced ecological variation within *D. variolosus*, the usual assessment of relevant distinguishing traits (ILVs, stomach grooves, shapes and arrangement of gonads) indicates that *D. hupferi* inhabits Brittany's northern coast and probably has for a very long time.

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