# MORPHOLOGY, BIOLOGY AND SYSTEMATIC POSITION OF EPILEPTON CLARKIAE (CLARK, 1852) (GALEOMMATOIDEA: MONTACUTIDAE) A BIVALVE COMMENSAL WITH SIPUNCULANS

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Abstract The shell morphology and anatomy of the micro bivalve Epilepton clarkiae is described from specimens collected in NW Ireland. Anatomical features of a very large subtriangular hypobranchial gland, a pedal protractor bisecting the anterior adductor muscle, a byssus gland divided into symmetrical left and right halves, gills represented by a single demibranch and paired seminal receptacles indicate that the genus Epilepton is most correctly placed in the superfamily Galeommatoidea, and family Montacutidae with closest similarities to the genera Litigiella, Jousseaumiella, and Mioerycina. The genus Potidoma is confirmed to be congeneric with Epilepton. Epilepton clarkiae is a commensal with sipunculans with the specimens examined here associated with Phascolosoma granulatum. The geographic range is from the Mediterranean to southern Scandinavia.

*Key words* Epilepton clarkiae, *morphology*, *commensalism*, *distribution*, *systematics*.

#### **INTRODUCTION**

Epilepton clarkiae (Clark 1852) is a very small bivalve, which is a perhaps obligatory commensal with species of sipunculans. Although distributed from the British Isles to the Mediterranean, most records are of empty shells, and only two studies contain a few observations on the soft anatomy (Pelseneer 1925; Deroux 1961). Consequently, the systematic position of the species is questionable. Originally described as Lepton clarkiae, the species was later transferred to the subgenus Epilepton, established on shell characters and without a diagnosis by Dall (1899) and later upgraded to a genus. Pelseneer (1925), who studied the live animal, referred the species to Montacuta Turton 1822 and Deroux (1961) included it in Potidoma Deroux 1961. As new and ample material of the species has become available, we have restudied the species' morphology and mode of life. This has enabled us to provide a diagnosis of the genus *Epilepton*, to discuss its systematic position, and to give new data on its ecology.

### MATERIAL EXAMINED

20 specimens, live collected, St John's Point, Donegal Bay, NW Ireland, 5 September 1987, coll. PG Oliver, NMW.Z.1987.074.11: 20 speci-

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mens, live collected, Feorinyeo Bay, Blacksod Bay, Co. Mayo, W Ireland, 19 March 1988, coll. PG Oliver, NMW.Z.1988.070.222: 3 specimens, live collected, Oxwich Bay, Gower Peninsula, S. Wales, 23 August 1980, coll. PG Oliver, NMW.Z. 1980.188.1: 1 specimen, live collected, Pwlldu Head, Gower peninsula, S. Wales, 24, October, 1980, coll. PG Oliver, NMW.Z.1980.219.40.

The above specimens from Ireland and Gower were associated with the sipunculan Phascolosoma granulatum Leuckhart [identified by PG Oliver using Gibbs (1977)]. In Ireland, this species was found in narrow but extensive silt-filled crevices in shales at the mid to lower tide levels. In these crevices were many polychaetes (cirratulids) and the bivalve Mysella bidentata (Montagu). On the Gower, the microhabitat was similar but the shale lavers between the limestones were less accessible, the sipunculans were smaller and were often accompanied by the echiurid, Thalassema.

#### **METHODS**

The specimens were fixed in 4% formaldehyde in seawater and subsequently preserved in 70% ethanol. For microanatomical studies, two specimens from Donegal Bay had the shell and mantle removed to display the organization of the mantle cavity. Five other specimens (shell length (SL) 1.5-1.75 mm) from the same locality were decalcified in Bouin's fluid and embedded



**Figure 1** *Epilepton clarkiae*, scanning electron micrographs of shells, all from Donegal, NW Ireland. **A-C** typical adult shell, **A** external; **B** internal of right valve; **C** internal of left valve. **D** juvenile. **E-F** gerontic form, **E** external showing oxide deposits, **F** internal of right valve, **G** internal of left valve. **a.l.** anterior lateral tooth, **c.** cardinal tooth, **c.s.** cardinal socket, **d.p.** dorsal process of anterior lateral tooth **p.l.** posterior lateral tooth

in Araldite. They were sectioned transversally, horizontally or sagitally in 2-µm thick sections that were stained with toluidine blue.

For Scanning Electron Microscopy the shells were cleaned in a mild, bleach solution, washed, dried and mounted for imaging by a CAMSCAN SEM in back-scattered mode.

# DESCRIPTION

# GALEOMMATOIDEA J. E. GRAY, 1840 Montacutidae Clark, 1855

Genus *Epilepton* **Dall**, **1899** *Type species: Lepton clarkiae* Clark, 1852

*Diagnosis*: Shell minute, obliquely oval, single anterior and posterior lateral teeth, large in right valve but smaller in left valve; single small

cardinal in right valve only; ligament internal. Protractor pedis muscles dividing the anterior adductor muscle in two, gills with only inner demibranch, paired pouch-shaped seminal receptacles that open into the suprabranchial cavity.

### Epilepton clarkiae (Clark 1852)

*Lepton clarkiae* Clark 1852a: 191; – Forbes & Hanley 1852, vol. 4: 255; – H. and A. Adams, 1858: 478;– Jeffreys 1863, vol. 2: 202; – Orton 1923: 861; – Winckworth 1923: 86; – 1924: 1.

*Lepton (Epilepton) clarkiae* – Winckworth 1932: 243

*Montacuta clarkiae* – Pelseneer 1925: 172, figs.; – Salisbury 1932: 102, Fig. 2

*Epilepton clarkiae* – Thiele 1934: 860; – Winckworth 1951: 133; – Plymouth Marine Fauna 1957: 325; – Heppell 1964: 311; – Tebble 1966: 87; – Bowden & Heppell 1968: 266; – Warén



**Figure 2** *Epilepton clarkiae,* scanning electron micrographs of umbo of shell showing prodissoconchs I and II, Donegal, NW Ireland.

1983: 163; – van Aartsen *et al.* 1984: 65, fig. 330; – Høisæter 1986: 120; – Borja 1987: 219; – Hayward & Ryland 1990: 756; – Troncoso & Urgorri 1990: 250; – Smith & Heppell 1991: 66; – van Aartsen 1996a: 34, Fig. F; –1996b: 50, fig. 40L, 40R; – Salas 1996: ; – Giribet & Peñas 1997: 48; – Delongueville & Scaillet 1999: 29; – Kallonas *et al.* 1999: 15. *Potidoma clarkiae* – Deroux 1961: 149, fig. 18; – Boss 1965: 185; – Guerin 1971: 407

The shell (Figs. 1 & 2) The shell is minute, with a maximum length of 2.5mm. The outline is obliquely subovate with distinct umbos and expanded anteriorly with the beaks well behind the mid-line (Fig. 1A-C). The dorsal margins are almost straight and slope to equally rounded, anterior and posterior margins. The hinge is strong. The right valve has large single anterior and posterior laterals plus a single small anterior cardinal; the left valve has marginal laterals that fit into sockets in the right valve. There is no cardinal in the left valve, only a gap between the lateral and ligament acting as a socket. The left anterior lateral bears a small projection at its dorsal end (d.p. in Fig.1G) that resembles a cardinal tooth but it is attached to the lateral tooth. The ligament is internal, on a triangular but flat, vertically oriented, subumbonal resilifer situated behind the cardinal tooth/socket. Most

of the shells have some ferrous (rusty or black) deposit on the outer surface. Prodissoconch I is ca. 120  $\mu$ m in diameter, that of prodissoconch II ca. 380  $\mu$ m (Fig. 2).

Larger shells or gerontic shells (Fig. 1E-F) become more oval with indistinct umbos and are relatively more tumid. The hinge teeth become more massive and less well defined; the beaks become worn and the resilifer appears to break through the beaks.

The change in shape may be related to the confined spaces in which the species lives, especially when in crevices.

Anatomy (Figs. 3A, 4 & 5) The posterior adductor muscle is slightly smaller than the anterior one, which is divided into two unequally large parts by the small protractor pedis muscles. The anterior and posterior pedal retractors are equally powerful. There are two pallial openings, anteriorly and ventrally a large combined inhalant and pedal opening, and posteriorly a much shorter exhalant opening. Whether one of them, or both, may protrude beyond the shell in live specimens is not known. The mantle edges are smooth without papillae or tentacles. Numerous radial muscles run from the shell to the inner mantle fold. The raised inner folds of the mantle are non-ciliated except on the part in front of where they fuse, where they become heavily ciliated and glandular. This tract is probably concerned with the rejection of waste matters. A conspicuous hypobranchial gland occupies a large subtriangular area of the left and right inner mantle wall immediately ventral to the posterior adductor muscle.

The gill axis is nearly vertical. Each gill is triangular and consists of an inner demibranch only, with about 20 gill filaments. An outer demibranch is absent. The left and right demibranchs are fused behind the foot, and immediately anterior to the exhalent opening, the gills are fused to the mantle's edge.

The foot was not observed in live specimens and in all preserved ones it was heavily contracted. It has a ciliated sole, on to which open many subepithelial mucous glands. The byssus gland is fairly large and opens along a relatively long byssus groove that extends halfway to the tip of the foot. The gland is divided in equal left and right parts and produces a single thin byssus thread.



**Figure 3** *Epilepton clarkiae.* **A**, the organs of the visceral mass as seen from the left side after removal of the left shell valve, mantle and gill. **B**, sperm cell (light microscopy). a, acrosome: aa, anterior adductor muscle; apr, anterior pedal retractor; bg, byssus gland cg, cerebral ganglion; dg, digestive gland; foot; hy, hypobranchial gland; k, kidney; li, ligament; lp, labial palp; mp, midpiece; n, nucleus; ov, ovary; pa, posterior adductor muscle; pe, pericardium; pp, protractor pedis muscle; ppr, posterior pedal retractor; rd, right demibranch; rs, left receptaculum seminis; ss, style sac; te, testis; vg, visceral ganglion. Arrows indicate extent of inhalant/pedal and exhalant openings. Scales represent 500µm (A) and 1 µm (B).

The labial palps are of average size, but details in its structure were not studied. The stomach is entirely wrapped into the digestive gland. The style sac emerges from the stomach's posterior left and occupies left side of the visceral mass and its blind-ending part lies immediately beyond the surface of the visceral mass. The intestine leaves the stomach posteriorly on the right side and after a single loop ascends dorsally before continuing into the rectum.

The kidney is of ordinary structure, but very voluminous. Many of its cells contain a few and small heavily stained inclusions.

Sexual organ All sectioned specimens (SL 1.5-1.75 mm) were hermaphroditic and the gonad an ovotestis. Its posterior most part forms an undivided space placed immediately ventral to the ligament and occupied solely by the testis. Spermatogenesis occurs all along the walls while the numerous closely packed sperm cells are orientated more or less with their heads turned towards the wall of the testis and their flagella facing the lumen. Branching forwardly from the testes occur a few ovarian tubules. They are far better developed on the right than on the left side where they have to make room for the style sac. The basal part of the gonadal branches is a transitional area that contains both female and male parts. The oocytes in two specimens (1.7 and 1.75 mm) were numerous, 35-40 being represented in a single section, with a diameter of 25-30  $\mu$ m and ca. 40  $\mu$ m. Sexual openings were never found and may be temporary structures.

Only one type of sperm occurs (Fig. 3B). The sperm cells are 5.0-5.5  $\mu$ m long, elongate oval, with the largest diameter, 1.0  $\mu$ m, occurring in the posterior fourth of the nucleus. Anteriorly the nucleus is capped by a ca. 1.5  $\mu$ m long and elongate conical and pointed acrosome. The midpiece is relatively short.

*Seminal receptacles* Two pouch-shaped vesicles lie superficially in the visceral mass squeezed in between the posterior adductor muscle, the kidney and the posterior part of the mantle cav-



**Figure 4** *Epilepton clarkiae.* A sagittal section; **B** sagtittal section through anterior part of body; **C** horizontal section through posterior part of visceral mass and gills; **D** transverse section through foot and byssus gland. aa, anterior adductor muscle; apr, anterior pedal retractor; bg, byssus gland cg, cerebral ganglion; dg, digestive gland; in, opening of intestine into stomach; f, foot; k, kidney; li, ligament; lp, labial palp; ov, ovary; pa, posterior adductor muscle; pp, protractor pedis muscle; ppr, posterior pedal retractor; re, rectum; sb, suprabranchial chamber; ss, style sac; st, stomach; te, testis; vg, visceral ganglion. Arrowhead denotes opening of byssus gland. Toluidine stained 2-µm thick Araldite sections. Scale bars: A and B: 200 µm, C: 100 µm, and D: 50 µm.



**Figure 5** *Epilepton clarkiae*. **A** horizontal section through hind body; **B** transverse section through mid body; **C** oblique section through posterior part of the visceral mass; **D** section through receptaculum seminis showing arrangement of sperm. bg, byssus gland; by, byssus; dg, digestive gland; ex, exhalant aperture; in, intestine; hy, hypobranchial gland; id, inner demibranch; k, kidney; mc, mantle cavity; ov, ovary; pa, posterior adductor muscle; pe, periostracum; ppr, posterior pedal retractor; re, rectum; rs, receptaculum seminis; ss, style sac; st, stomach; vg, visceral ganglion. Toluidine stained 2 μm thick Araldite sections. Scale bars: A-C: 100 μm, D: 20 μm.

ity. They are widely separated by the visceral ganglia and the posterior retractor muscles. In transparent light, they appear as well defined dark bodies in specimens in which the shell has been removed. The receptacles are lined by a non-ciliated cuboidal to squamous epithelium and each opens into the posterior part of the suprabranchial cavity by means of a short and narrow duct. They were filled with mature sperm in four of the sectioned specimens, only partly so in a fifth one. When distended with sperm the maximum diameter of the receptacles in three specimens were 80, 90 and 120 µm, the dorso-ventral length 95-110 µm. Within the receptacles the sperm are arranged differently as in the testis, namely in many clusters with the acrosomes facing towards the centre of each group and the flagella occupying what spaces are left in between the clusters.

# DISCUSSION

# Systematics

The shell of one of three syntypes (USNM 199440) was illustrated by Warén 1983, pl. 8, figs. 1-2. Other illustrations of the shell are those by Tebble (1966), Hayward & Ryland (1990), van Aartsen (1996b) and Delongueville & Scaillet (1999).

Deroux's statement (1961) that the *Montacuta clarkiae* studied by Pérès (1937) is identical with *Mysella bidentata* is correct, since the so-called vesicula seminalis of Pérès' specimens is clearly similar in structure and location to the unpaired seminal receptacle described by Jespersen & Lützen (2001) in the latter species.

The suggestion by Deroux (1961: 150) that *E. clarkiae* is congeneric with *Potidoma subtrigonum* (Jeffreys in de Folin & Periér, 1873)<sup>1</sup> is substantiated by the present study. Deroux (1961) studied *P. subtrigonum* collected from Morgat, Finistère on the Atlantic coast of France and noted it to be commensal with the tubiculous aphroditid polychaete, *Polyodontes maxillosus* Ranzani. Giunchi, Rinaldi, Tabanelli & Tisselli (2006) describe the shell from material collected in the Adriatic. The hinges of both species are similar (compare Giunchi *et al.*, 2006 fig. 2 and Deroux, 1961 fig. 4, P.s. with Fig. 1) but it is noted that the "spike-like umbonal projections" observed in the juvenile shell of P. subtrigonum (Giunchi et al., 2006) are not seen in E. clarkiae. Both species have a very large subtriangular hypobranchial gland, a pedal protractor bisecting the anterior adductor muscle, a byssus gland divided into symmetrical left and right halves, and gills represented by a single demibranch. As in E. clarkiae the ovotestis of P. subtrigonum consists of a posteriorly placed unpaired testis and an ovary branching forwardly from it. Most significantly, P. subtrigonum possesses paired pouch-shaped, cylindrical or pyriform vesicles (Deroux 1961, fig.11, P.s.: "ampoules spermatiques" or "annexe spermatique") containing ripe sperm, but never exhibiting spermatogenesis, and located at exactly at the same place as the seminal receptacles of E. clarkiae. The sperm were not studied in P. subtrigonum.

As pointed out by Heppell (1964), since *Epilepton* has priority over *Potidoma*, *P. subtrigonum* should be transferred to that genus.

Besides *E. clarkiae* and *E. subtrigonum*, a third European species, *E. parrussetensis*, was described from empty shells taken off Vallcarca, Stiges, Barcelona by Giribet & Peñas (1998). The genus *Epilepton* appeared to be confined to the Eastern Atlantic and Mediterranean but an undescribed species can now be confirmed from Rottnest Island Western Australia (Oliver & Lützen, in prep). This species was associated with the sipunculan *Phascolosoma rottnesti* Edmunds, 1956. This observation suggests that *Epilepton* probably has a global distribution.

Thiele (1943), Winckworth (1951), Chavan (1960), and Troncoso & Urgorri (1990) argued that *Epilepton* should be included in the family Neoleptonidae of the superfamily Cyamioidea. This view was based entirely on similarities in shell characters and was refuted by Salas & Gofas (1998). It is invalidated by the present findings of a byssus gland, a ventral furrow in the foot, and a protractor pedis muscle, structures that are absent in the Neoleptonidae. In addition, *E. clarkiae* has neither two posterior siphons nor a pallial sinus, as may occur in some neoleptonidas (Ponder 1969).

The proper place of *Epilepton* is in the superfamily Galeonmatoidea, but except for the Galeonmatidae, the other families of that super-

<sup>&</sup>lt;sup>1</sup> Deroux (1961) regarded *Lepton subtrigonum* Jeffreys, 1873 as a nomen nudum. This is not accepted here and we follow the nomencature of CLEMAM.

family are ill defined. Thus, Coan et al. (2000) could find no consistent characters with which to separate the families Lasaeidae, Erycinidae (=Leptonidae), Kellidae and Montacutidae. Most authors have included Epilepton in the Leptonidae on similarities in shell structure, but the only anatomically examined leptonids, species of Arthritica Finlay differ remarkably in gonad and, especially, sperm structure (Lützen & Takahashi 2003; Jespersen & Lützen, in prep.). Pelseneer (1925) transferred E. clarkiae to Montacuta of the Montacutidae, but the species does not fit any of the major characteristics of that genus. In Montacuta, as defined by its type species, M. substriata (Montagu), each valve has a long, anterior laminar (lateral?) tooth but no cardinals, a very narrow internal ligament extending obliquely posteriorly from the umbo, no seminal receptacles, and small and short, ovoid sperm cells which, many together, associate with spherical spermatocytes to form spermatozeugma (Fox et al. 2007).

That the gills in *Epilepton* are represented by a single demibranch is of little value as a diagnostic character, since gill reduction has taken place in most montacutids plus in several species of the other families. More significantly, the protractor pedis muscles divide the anterior adductor into a larger dorsal and a smaller ventral sector and are not

inserted either dorsal or ventral to the adductor as in almost all other galeommatoids. A similar course occurs in a small number of other bivalves traditionally included in the Montacutidae (Montacuta substriata, M. semiradiata Tate, Curvemysella paula (A. Adams), Tellimya ferruginosa (Montagu), Benthoquethia integra (Hedley), Litigiella cuenoti (Lamy), Nipponomysella subtruncata (Yokoyama), species of Jousseaumiella Bourne, and Mioerycina coarctata (S.V.Wood) (Bourne 1906; Pelseneer 1911; Deroux 1961; Oldfield 1961; Ponder 1968; author's unpublished observations). Some of these species (E. clarkiae, E. subtrigonum, Litigiella cuenoti, Jousseaumiella heterocyathi Bourne, J. heteropsammiae Bourne, and M. coarctata) further have in common that they have paired pouch-shaped seminal receptacles and, except for *E. subtrigonum*, that they are commensal with sipunculans. For these reasons, we consider *Epilepton* to be most closely related to the genera Litigiella, Jousseaumiella, and Mioerycina.

There are, however, differences in shell and sperm structures that suggest that these genera should not be synonymised. Molecular data may perhaps be more informative and better indicate the relationships of these taxa. The shell of *Mioerycina* is fragile, elongate and has a weak hinge of a single cardinal peg in each valve (van Aartsen 1996b). The shell of *Jousseaumiella* is minute; not exceeding 1.5mm, roughly triangular with a hinge composed of anterior and posterior laterals, a single cardinal in the right valve and paired cardinals in the left valve (Bourne 1906). In Litigiella, the shell is more oblique than in Epilepton and the ligament is set on a relatively long oblique resilifer (Hoeksema et al. 1995; Lützen & Kosuge, 2006). The sperm cells of *E. clarkiae* are of an ordinary and simple structure, but still similar in size and dimensions to the sperm of M. coarctata, N. subtruncata, and species of Jousseaumiella. (Bourne 1906; Jespersen & Lützen 2000; Lützen et al. 2001). The sperm cells in Litigiella are more elongate which is probably correlated with their being orderly arranged perpendicular to the epithelium of the receptacle (Lützen & Kosuge, 2006) in contrast to the more haphazard way of orientation displayed by the four other genera.

The way the sperm are arranged in the receptacle of *E. clarkiae* may perhaps illustrate the original state in which they were transferred. Thus, Fox *et al.* (2007) observed that recently released sperm of *M. percompressa* Dall formed aggregates attaching to each other at the acrosomes.

# DISTRIBUTION

*Epilepton clarkiae* has a wide but sporadic distribution in the northeast Atlantic and Mediterranean (van Aartsen 1996b). In British waters *E. clarkiae* has a recorded but patchy distribution along the western coasts north to Shetland, along the English Channel and north to the Wash (Clark 1852a; Orton 1923; Winckworth 1923, 1924; Salisbury 1932; Tebble 1966; Seaward 1982; Hayward & Ryland 1990). It has been recorded as far north as southern Sweden (Høisæter 1986). On the French side of the Channel it occurs at Wimereux and Morlaix, (Pelseneer 1925; Deroux 1961: 114), while a record by Pérès (1937) from Morgat, Bretagne, as related above rests on misidentification with *Mysella bidentata* (Deroux 1961). The species is further reported from Ria de Arosa, and the Ares and Betanzos estuary, both Galicia, NW Spain (Cadee 1968; Troncoso & Urgorri 1990). It is also known from the Basque coast (Borja 1987) and Atlantic coast of southern Spain (Salas, 1996) and from two localities on the Spanish Mediterranean coast, namely at Garraf, Costa Brava and Benicarlo, Costa del Azahar, Spanish Mediterranean coast (Giribet & Peñas 1997; Delongueville & Scaillet 1999). There are further records from Marseille, France (Guerin 1971) and from Evvoikos Gulf, Aegean Sea, Greece (Kallonas *et al.* 1999).

### Навітат

The species is found from the lower shore into the sublittoral typically in crevices in hard substrates. Clark (1852a) however, stated that his specimens were found free in the Coralline zone (Devon) and nearly all records from the Iberian Peninsula and the Mediterranean are of dislocated, empty shells. Many observations, including our own, show that in life E. clarkiae is associated with various sipunculans, to the skin of which they attach by means of the byssus filaments. In Ireland, England and France the host sipunculans belong to Golfingia elongata (Keferstein), G. vulgaris (de Blainville), Nephasoma rimicola (Gibbs), and Phascolosoma granulatum. Although recorded with Phascolion strombi (Montagu 1804) in the Mediterranean (Delongueville & Scaillet 1999) this association is rare, probably because the space inhabited by this host is insufficient for E. clarkiae to grow. The smaller and more compressed Mioerycina coarctata (= Montacuta phascolionis Dautzenberg & Fischer) typically lives in the apex of Aporrhais shells inhabited by Phascolion. A host identified by Orton (1923) and Winckworth (1924) as Phascolosoma pellucidum (= Golfingia (G.) pellucida (Keferstein)) must be incorrectly identified since this species does not occur in Europe (Stephen & Edmonds 1972). E. clarkiae occurs a few (up to seven) together on the same host (Orton 1923; Pelseneer 1925). Other bivalves such as Mysella bidentata or Mioerycina coarctata may co-occur with E. clarkiae in the sipunculan burrow (Winckworth 1923, 1924; Salisbury 1932; Troncoso & Urgorri 1990)

#### **R**EPRODUCTION

Guerin (1971) raised larvae of E. clarkiae in the laboratory from bivalves that had settled 9 months earlier and were 1380-1620 µm in shell length. The shells of D-larvae were 150 x 110 µm when released, corresponding to a shell length of 120 µm in one of our shells. They reached a size of 390 x 350 µm before they settled. This size tallies with the prodissoconch II illustrated by Tebble (1966, Fig. 41A) and of our material (380 um). It is difficult to explain why newly released larvae illustrated by Pelseneer (1925) are much bigger, unless the magnification given is incorrect. Guerin (1971) caught planktonic larvae in March in the Mediterranean. We examined six of the larger individual in our samples collected in March and September but found no larvae in the brood chamber and no well-developed ovaries. That none of our bivalves collected in March and September were brooding might indicate that the species reproduces only in part of the summer half year in NW Europe. Thus, Tellimya ferruginosa at the same latitudes has a breeding season that is apparently limited to the period between May and August (Fox *et al.* 2007).

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