

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 specimens
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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 layers 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

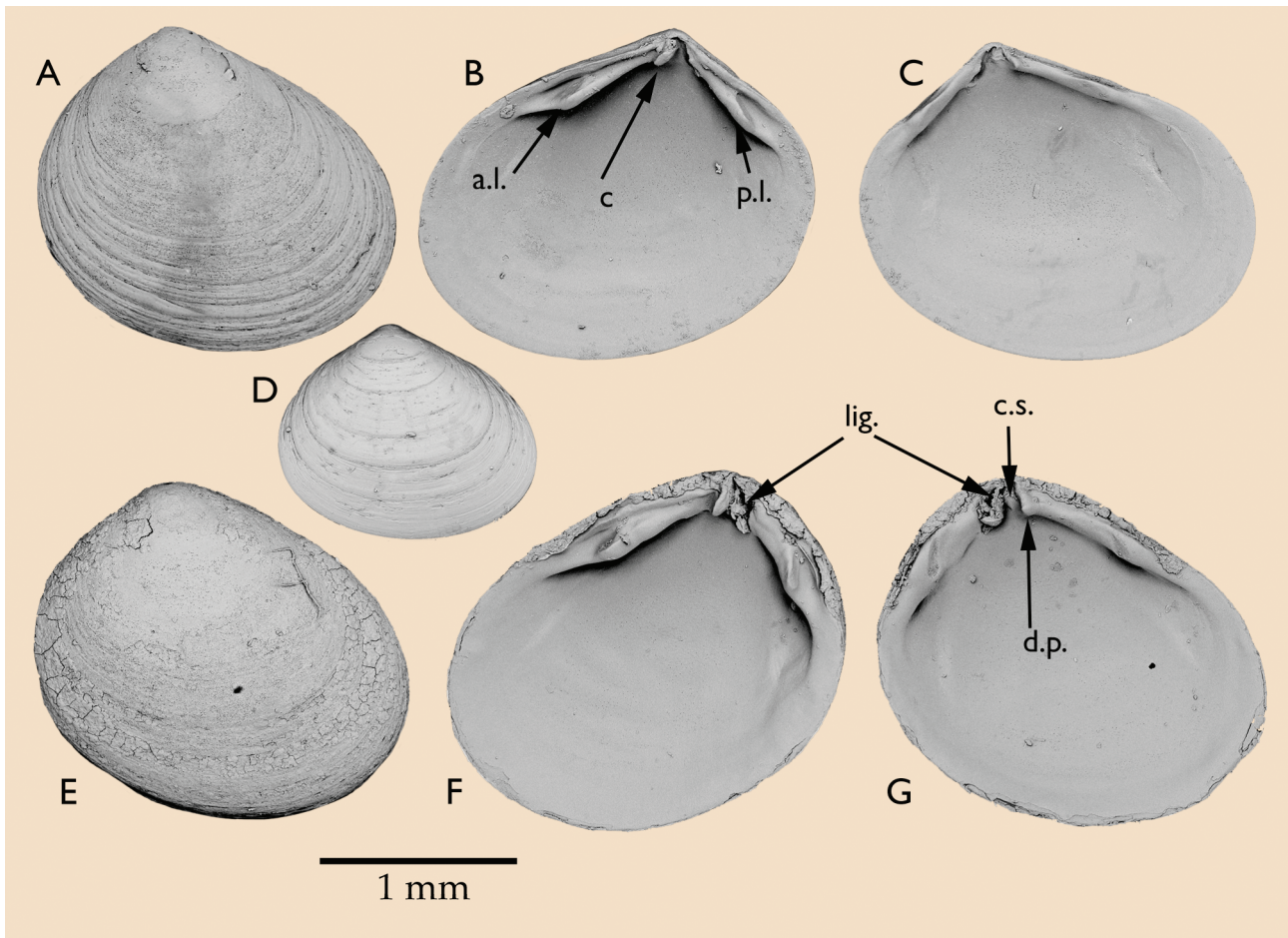


Figure 1 *Epilepton clarkiae*, scanning electron micrographs of shells, all from Donegal, NW Ireland. **A-C** typical adult shell, **A** external; **B** internal of right valve; **C** internal of left valve. **D** juvenile. **E-F** gerontic form, **E** external showing oxide deposits, **F** internal 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 sagittally in 2- μ m 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

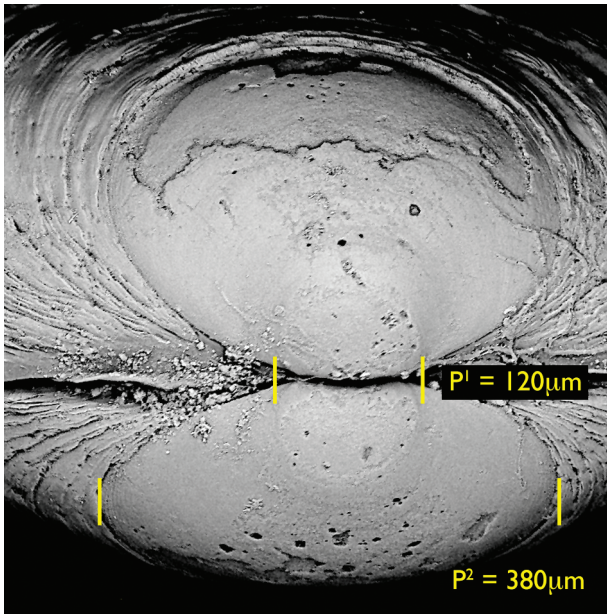


Figure 2 *Epilepton clarkiae*, scanning electron micrographs of umbo of shell showing prodissoconchs I and II, Donegal, NW Ireland.

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 μm in diameter, that of prodissoconch II ca. 380 μm (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 exhalant 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.

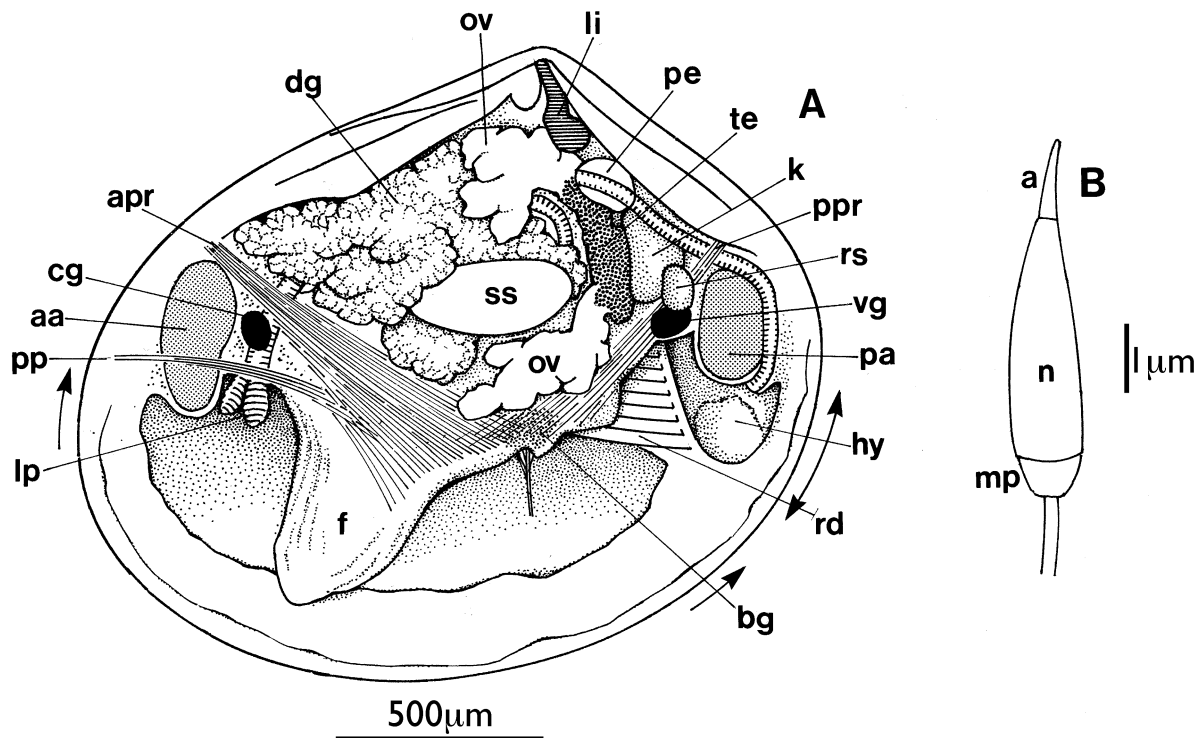


Figure 3 *Epilepton clarkiae*. **A**, the organs of the visceral mass as seen from the left side after removal of the left shell valve, mantle and gill. **B**, sperm cell (light microscopy). a, acrosome; aa, anterior adductor muscle; apr, anterior pedal retractor; bg, byssus gland; cg, cerebral ganglion; 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 500 μm (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 μm and ca. 40 μm . 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 μm long, elongate oval, with the largest diameter, 1.0 μm , occurring in the posterior fourth of the nucleus. Anteriorly the nucleus is capped by a ca. 1.5 μm 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-

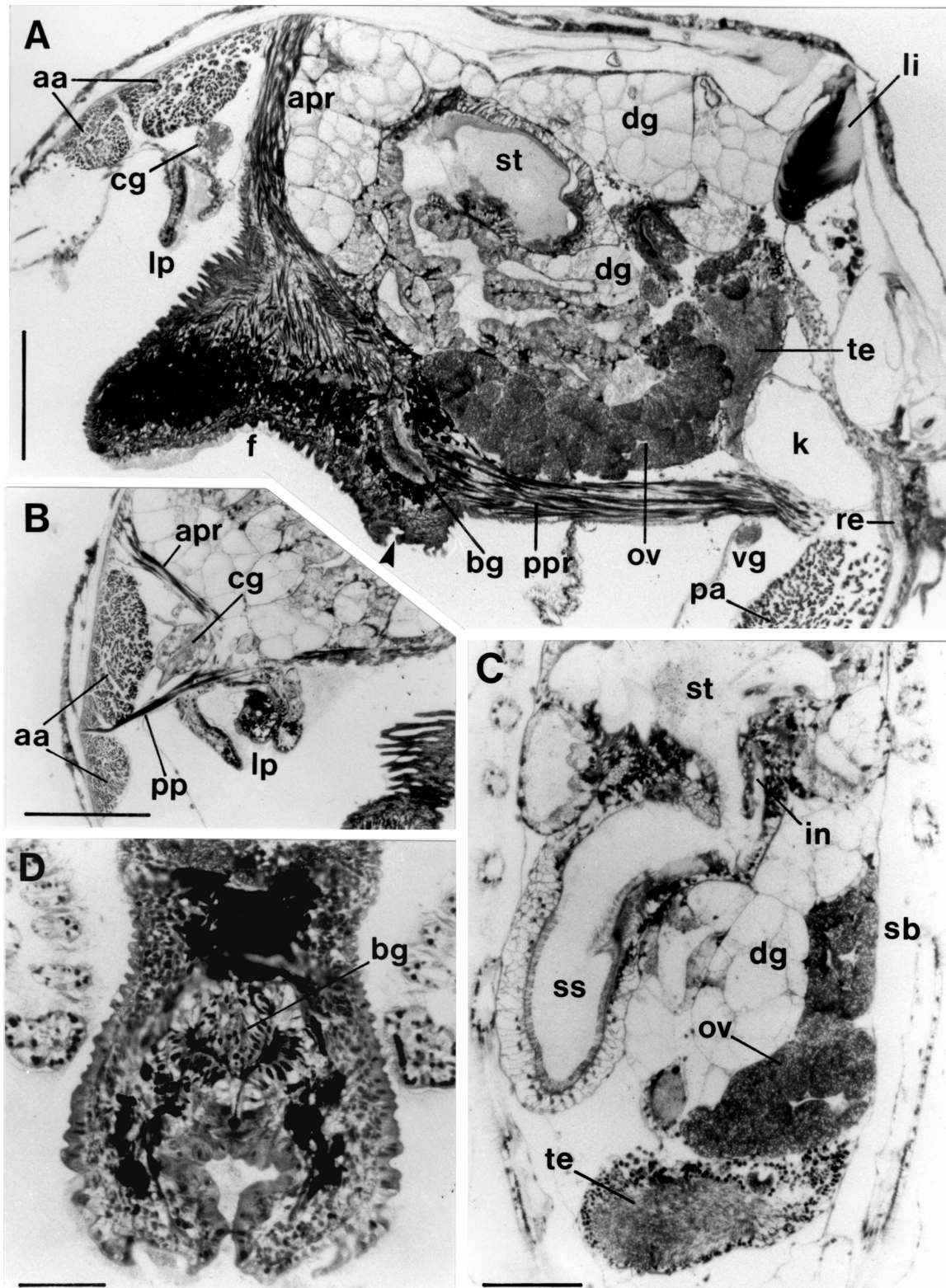


Figure 4 *Epilepton clarkiae*. **A** sagittal section; **B** sagittal section through anterior part of body; **C** horizontal section through posterior part of visceral mass and gills; **D** transverse section through foot and byssus gland. aa, anterior adductor muscle; apr, anterior pedal retractor; 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- μ m thick Araldite sections. Scale bars: A and B: 200 μ m, C: 100 μ m, and D: 50 μ m.

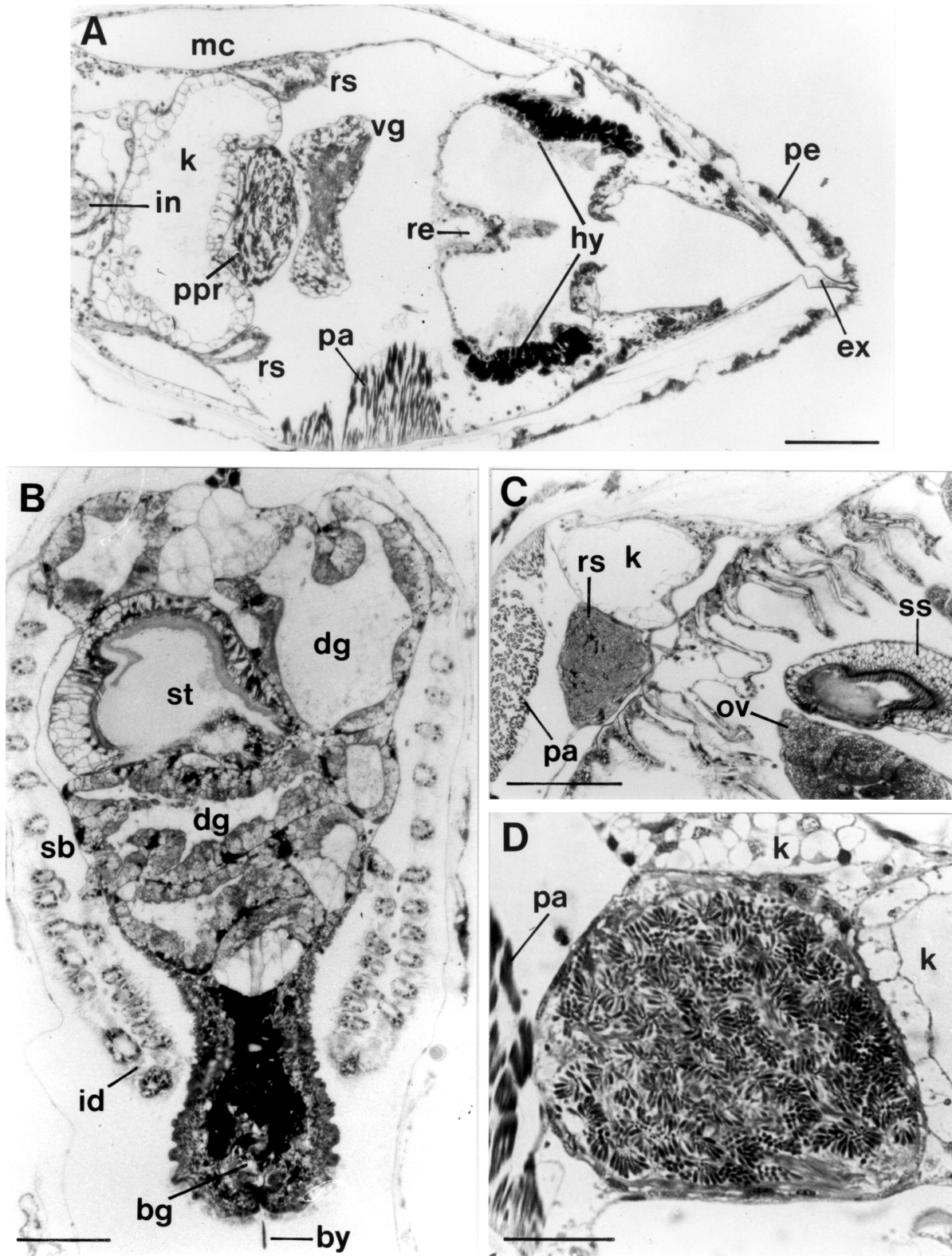


Figure 5 *Epilepton clarkiae*. **A** horizontal section through hind body; **B** transverse section through mid body; **C** oblique section through posterior part of the visceral mass; **D** section through receptaculum seminis showing arrangement of sperm. bg, byssus gland; by, byssus; dg, digestive 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)¹ 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 Rottneest Island Western Australia (Oliver & Lützen, in prep). This species was associated with the sipunculan *Phascolosoma rotnnesti* 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 neoleptonids (Ponder 1969).

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

¹ Deroux (1961) regarded *Lepton subtrigonum* Jeffreys, 1873 as a nomen nudum. This is not accepted here and we follow the nomenclature 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).

HABITAT

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).

REPRODUCTION

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 µm). 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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REFERENCES

- ADAMS H & ADAMS A 1858 *The Genera of Recent Mollusca*. Volume II. Van Voorst, London. 661pp.
 BORJA AY 1987 Catélogo de los moluscos marinos de la costa vasca. *Iberus* 7: 211-223.
 BOSS KJ 1965 Symbiotic Erycinacean Bivalves. *Malacologia* 3: 183-195.
 BOURNE GC 1906 On *Jousseaumia*. A new genus of eulamellibranchs commensal with the corals *Heterocyathus* and *Heteropsammia*. *Reports of the Pearl Oyster Fisheries of the Gulf of Manaar* 37. Suppl. Report, Part 5: 243-266, pls 1-3.
 BOWDEN J & HEPPELL D 1968 Revised list of British Mollusca. 2. Unionacea - Cardiacea. *Journal of*

- Conchology* **26**: 237-372, tabs.
- CHAVAN A 1960 Remarques sur la charnière des Erycinacea and Cyamiacea. *Bulletin de la Société géologique de la France* (7) **1**: 712-718.
- CLARK W 1852a On a new British species of *Lepton*. *Annals and Magazine of Natural History*, London 2. Ser. **IX**: 191-192.
- CLARK W 1852b Further observations on *Lepton Clarkiae*. *Annals and Magazine of Natural History*, London 2. Ser. **IX**: 293-294.
- COAN EV, SCOTT PV & BERNARD FR 2000 Bivalve sea shells of Western North America. *Santa Barbara Museum of Natural History Monographs no. 2, Studies of Biodiversity* **2**. 764 pp.
- FORBES E & HANLEY S. 1852 (1852-1853) *History of British Mollusca and their shells*. Volume IV. Van Voorst, London. 301pp.
- DALL WH 1899 Synopsis of the recent and tertiary Leptonacea of North America and the West Indies. *Proceedings of the United States National Museum, Washington* **21**: 873-897, pls.
- DELONGUEVILLE C & SCAILLET R 1999 Relevé de l'association de *Epilepton clarkiae* (W. Clark, 1852) et de *Mioerycina coarctata* (S. V. Wood, 1851) avec *Phascolion strombi* (Montagu, 1804) en Méditerranée. *Apex* **14**: 29-32.
- DEROUX G 1961 Rapports taxonomiques d'un Leptonacé not décrit "*Lepton subtrigonum*" Jeffreys (nomen nudum - 1873). *Cahiers de Biologie marine* **2**: 99-153.
- DE FOLIN L & PERIÉR L 1873 (1872-1976) *Les Fonds de la Mer*. Volume 2 (pp65-112). Savy. Paris. 365pp.
- FOX T JESPERSEN Å & LÜTZEN J in press (2007) Sperm transfer and reproductive biology in species of hermaphroditic Bivalves (Galeommatoidea: Montacutidae). *Journal of Morphology*.
- GIBBS PE 1977 *British Sipunculans*. Synopsis of the British Fauna (New Series) no.12. Linnean Society of London and Academic Press, London. 35 pp.
- GIRIBET G & PEÑAS A 1997 Fauna Malacológica del litoral del Garraf (NE de la Peninsula Ibérica). *Iberus* **15**: 41-93.
- GIRIBET G & PEÑAS A 1998 A new *Epilepton* species (Bivalvia, Montacutidae) from the Western Mediterranean. *Iberus* **16**: 117-121.
- GIUNCHI L, RINALDI E, TABANELLI C & TISELLI M 2006 Considerazioni su *Lepton subtrigonum* Fischer, de Folin & Périer ex Jeffreys ms., 1873 e *Lepton lacerum* Fischer, de Folin & Périer ex Jeffreys ms., 1873 (Bivalvia: Leptonidae). *Bollettino Malacologico* **42**: 85-96.
- GUERIN J-P 1971 Reproduction et développement au laboratoire de *Potidoma clarkiae* (Mollusque lamellibranche). *Rapport et procès-verbaux des réunions. Commission internationale pour l'exploration scientifique de la Mer Méditerranée* **20**: 407-409.
- HAYWARD PJ & RYLAND JS 1990 *The marine fauna of the British Isles and north west Europe 2, Molluscs to chordates*. Clarendon Press, Oxford, i-xvi, 628-996, illustr.
- HEPPELL D 1964 Recorder's Report: marine Mollusca. *Journal of Conchology* **25**: 308-313.
- HOEKSEMA DF, VAN AARTSEN JJ, KEUKALAAR-VAN DER BERGE T, VAN NIEULANDE FAD & SIMONS GF 1995 On the identity and distribution of *Litigiella glabra* (P. Fischer. 1873). *La Conchiglia* **275**: 17-22
- HØISÆTER T. 1986 An annotated checklist of marine mollusks of the Norwegian coast and adjacent waters. *Sarsia* **71**: 73-145.ter
- JEFFREYS JG 1863 *British Conchology, or an Account of the Mollusca which now inhabit the British Isles and Surrounding Seas*. **2**: 1-465 pp. London.
- JESPERSEN J & LÜTZEN J 2001 Ultrastructure of the seminal receptacle and the dimorphic sperm in the commensal bivalve *Mysella bidentata* (Veneroidea; Galeommatoidea; Montacutidae). *Acta Zoologica* **82**: 107-115.
- KALLONAS M ZENETOS A & GOFAS S 1999 Notes on the ecology and distribution of Microbivalvia in Greek waters. *Conchiglia* **31** (291): 11-20.
- LÜTZEN J TAKAHASHI T & YAMAGUCHI T 2001 Morphology and reproduction of *Nipponomysella subtruncata* (Yokoyama), a galeommatoidean bivalve commensal with the sipunculan *Siphonosoma cumense* (Keferstein) in Japan. *Journal of Zoology, London* **254**: 429-440.
- LÜTZEN J & KOSUGE T 2006 Description of the bivalve *Litigiella pacifica* n.sp. (Heterodonta: Galeommatoidea: Lasaeidae), commensal with the sipunculan *Sipunculus nudus* from the Ryukyu Islands, Japan. *Venus* **65**: 193-103.
- LÜTZEN J & TAKAHASHI T 2003 *Athritica japonica*, sp. nov. (Bivalvia: Galeommatoidea: Leptonidae), a commensal with the pinnotherid crab *Xenophthalmus pinnotheroides* White, 1846. *The Yuriyagai* **9**: 11-19.
- OLDFIELD E 1961 The functional morphology of *Kellia suborbicularis* (Montagu), *Montacuta ferruginosa* (Montagu) and *M. substriata* (Montagu), (Mollusca, Lamellibranchiata). *Proceedings of the Malacological Society of London* **34**: 255 -295.
- ORTON JH 1923 Some New Commensals in the Plymouth District. *Nature* **112**: 861.
- PELSENEER P 1911 Les Lamellibranches de l'Expédition du Siboga. Partie anatomique. *Siboga Expeditie, Monograph* **53a**: 1-125.
- PELSENEER P 1925 Un lamellibranche commensal de lamellibranche et quelques autres lamellibranches commensaux. *Travaux de la Station zoologique de Wimereux* **9**: 164-182.
- PÉRÈS JM 1937 Sur trois especes du genre *Montacuta* (Kellyidae). *Travaux de la Station biologie de Roscoff* **15**: 5-28.
- PLYMOUTH MARINE FAUNA. 1957. *Marine Biological Association of the United Kingdom*, 3rd Edition, 457 pp.
- PONDER WF 1968 Three commensal bivalves from New Zealand. *Record of the Dominion Museum, Wellington* **6**:125-131.
- PONDER WF 1969 Notes on two neoleptonid bivalve molluscs. *New Zealand Journal of marine and Freshwater Research* **3**: 262-272.
- SALAS C 1996 Marine bivalves from off the Southern

- Iberian Peninsula collected by the Balgim and Fauna 1 expeditions. *Haliotis* **25**: 33-100.
- SALAS C & GOFAS S 1998 Description of four new species of *Neolepton* Monterosato, 1875 (Mollusca: Bivalvia: Neoleptonidae), with comments on the genus and on its affinity with the Veneracea. *Ophelia* **48**(1): 35-70.
- SALISBURY AE 1932 On *Lepton squamosum* (Montagu) and *Montacuta ferruginosa* (Montagu) and some other mollusks observed in the Salcombe estuary, Devon. *Proceedings of the Malacological Society, London* **20**: 100-103.
- SEAWARD DR 1982 *Sea Area Atlas of the Marine Molluscs of Britain and Ireland*. Nature Conservancy Council, Peterborough. 114pp.
- SMITH SM & HEPPPELL D 1991 *Checklist of British Marine Mollusca*. National Museums of Scotland Information Series no. 11, 114 pp.
- STEPHEN AC & EDMONDS SJ 1972 The phyla Sipuncula and Echiura. *Trustees of the British Museum (Natural History), London*. 528 pp.
- Tebble N 1966 *British Bivalve Seashells*. Trustees of the British Museum (Natural History), London, 213 pp, pls.
- THIELE J 1934 *Handbuch der systematischen Weichtierkunde* **2** (3). Jena
- TRONCOSO JS & URGORRI V 1990 New data about the distribution of six species of mollusks in Galician coasts. *Iberus* **9**: 247-252.
- VAN AARTSEN JJ MENKHORST HPMG & GITTENBERGER E 1984 The marine Mollusca of the Bay of Algeciras, Spain with general notes on *Mitrella*, Marginellidae and Turridae. *Basteria* Suppl. **2**: 1-135.
- VAN AARTSEN JJ 1996a Galeommatacea and Cyamiacea. *La Conchiglia* **279**:31-36.
- VAN AARTSEN JJ 1996b Galeommatacea and Cyamiacea.II. *La Conchiglia* **281**: 27-53, 61
- WARÉN A 1983 Marine Mollusca described by W. Turton and W. Clark. *Journal of Conchology* **31**: 161-171.
- WINCKWORTH R 1923 *Montacuta bidentata* (Montagu). *Journal of Conchology* **17**: 86.
- WINCKWORTH R 1924 Specimens of molluscs and other animals associated with them found in a day's digging at Salcombe. *Proceedings of the Malacological Society of London* **16**: 1.
- WINCKWORTH R 1932 The British marine Mollusca. *Journal of Conchology* **19**: 211-252.
- WINCKWORTH R 1951 A list of the marine Mollusca of the British Isles: additions and corrections. *Journal of Conchology* **23**: 131-134.

