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Report of a cohesive gelatinous egg mass produced by a tropical marine bivalve

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Abstract. Gelatinous egg masses are common in a number of animal phyla. However, they are virtually unknown in marine bivalves, with structures that could be thought of as gelatinous egg masses being reported for only five species. We describe the gelatinous egg mass and intracapsular development in the tropical lucinid *Phacoides pectinatus*. The embryos developed within individual capsules embedded in a large flimsy, spherical mass. Swimming veligers hatch at 198 μm shell length. They did not feed, settled within several days of hatching, and metamorphosis was completed within 2 weeks of hatching. Gelatinous egg masses might be detected in members of more lucinid species if studies of development included field or *in vivo* observations of reproduction in addition to producing embryos by stripping the gonads.

Additional key words: Bivalvia, Lucinidae, development, Caribbean, Heterodonta

Gelatinous egg masses are thought to confer a number of advantages in aquatic environments. They can provide protection either mechanically; via embedded chemical defenses (Ebel et al. 1999), antibacterial compounds (Benkendorff et al. 2001), or sunscreens (Przeslawski et al. 2004); and from desiccation (Pechenik 1979). In addition, the gel and spacing increases oxygen diffusion between embryos in comparison with clusters of eggs that lack gel (Chaffee & Strathmann 1984; Moran & Woods 2007).

The utility of gelatinous egg masses is supported by the fact that they have evolved multiple times among a diversity of animals including arenicolid, nereid, sabellid, and maldanid polychaetes (Strathmann & Strathmann 1989), several families of fishes (Breder & Rosen 1966), and various insects with aquatic development. Gelatinous egg masses are particularly common in molluscs, and are almost ubiquitous among cephalopods and opisthobranch gastropods, in addition to occurring in trochids and members of the caenogastropod littorinid genera *Lacuna* TURTON, 1827, and *Littorina* FÉRUSAC, 1822. In contrast, gelatinous egg masses are rare, if ever, observed in marine bivalves (Miyazaki 1938; Sastry 1979).

In most bivalve species, eggs and sperm are released into the water column for external fertiliza-

tion and embryonic development (Morton et al. 1998), although a number of species brood their developing embryos within the mantle cavity (reviewed in Sastry 1979). In an extensive review of marine bivalve development, Sastry (1979; see also Sellmer 1967) listed eight species that have been shown to produce eggs with gelatinous coverings or external capsules, and a few additional records are available in the literature. These can be broken down into two categories: those that release eggs with individual gelatinous coverings, which may or may not stick together, and those that form more cohesive masses.

Eggs with gelatinous egg coverings are not uncommon among bivalves, and seem to be most common at high latitudes. Ockelmann (1958) listed eight species of marine bivalves from Greenland, whose members produce eggs with a mucous covering and an adhesive membrane. He mentioned the possibility that these bivalves attach the eggs to the substrate, but it is doubtful that they result in the production of any kind of cohesive mass. These species belong to the families Astartidae [*Astarte borealis* (SCHUMACHER, 1817), *Astarte crenata* (GRAY, 1824), *Astarte elliptica* (BROWN, 1827), *Astarte montagui* (DILLWYN, 1817), *Astarte sulcata* (DA COSTA, 1778)] and Tellinidae [*Macoma loveni* (JENSEN, 1905), *Macoma moesta* DESHAYES, 1855, *Macoma torelli* (JENSEN, 1905)]. Egg membranes of some thickness have also been reported for the cardiid species *Ciliatocardium ciliatum* (O. FABRICIUS, 1780) and several anomalodesmatans,

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including the laternulid *Laternula elliptica* (KING & BRODERIP, 1831) (Ansell & Harvey 1997), although these are not thought to attach to the substrate. Likewise, the typical “veneracean” eggs, described by Ockelmann (1964) as possessing a well-developed gelatinous envelope around a vitellus, are not reported to adhere to each other or to the substrate. In two cases, however, *Musculus discors* (LINNAEUS, 1767) and *Musculus niger* (J.E. GRAY, 1824) adults were reported to spawn gelatinous egg strings that attach to the substrate (Ockelmann 1958:238–239; Thorson 1935). Finally, the protobranchs *Solemya velum* SAY, 1822, and *Solemya reidi* BERNARD, 1980, produce individual adhesive capsules that are deposited on the substrate (Gustafson & Reid 1986; Gustafson & Lutz 1992).

External egg masses have only been reported for five species of marine bivalves. The special egg sac in the protobranch *Nucula delphinodonta* MIGHELS & C.B. ADAMS, 1842 is composed of a mucus-like material, probably secreted by the hypobranchial gland, mixed with foreign bodies, and attached to the posterior ends of the valves of the shell (Drew 1901). So far, no other protobranchiate bivalves have been reported to reproduce in this manner (Zardus 2002).

In *Turtonia minuta* (FABRICIUS, 1780), the mantle margin secretes an egg capsule attached to the byssus, containing ten to 20 eggs (Oldfield 1955; Jeffreys 1863; Ockelmann 1964). Other authors have reported the same species producing two to six eggs in each capsule, which is then attached to stones and algae (Matveeva 1953). In addition, Ockelmann (1964) observed 13 females that each had one to four egg capsules attached to the byssus, and each capsule contained one to 16 embryos. Lovén (1848) reported the spawning in the cardiid *Parvicardium exiguum* (GMELIN, 1791) in the summer months near the coast of Bohuslän (Sweden). The eggs are laid enclosed in a “thick gelatinous mantle,” within which the development progresses until the shell-bearing veliger has attained a length of 90 µm (Jørgensen 1946). An egg capsule has also been reported for the lucinid *Loripes lacteus* (LINNAEUS, 1758) (Pelseneer 1926; Lebour 1938). Pelseneer (1926) reports that this species deposits stalked egg capsules on the sand and these are figured to contain numerous eggs. However, Miyazaki (1938) claims that Guiart¹ suggests, contrary to Pelseneer’s report, that the egg mass is cast freely into the water column and not deposited onto a substratum. Finally, the semelid *Abra tenuis* (MONTAGU, 1803) produces eggs enclosed in sticky

gelatinous envelopes, which are laid in a gelatinous mass within the sediment (Gibbs 1984: fig. 4C). It seems that in this case, fertilization may occur in the mantle cavity of the female, followed by extrusion of the eggs in an external mass.

The few accounts of egg masses in marine bivalves suggest that this is a rare form of reproduction in the group. The details of the reported cases remain vague as most reports were incidental and only one report of a gelatinous mass from a bivalve has been published since the 1960s. Here, we provide details on the first known cohesive gelatinous egg mass, produced by a tropical lucinid.

Methods

During a field expedition to Bahía Almirante, Bocas del Toro, Panama, in March 2009, G.W. Rouse collected an egg case similar to those of arenicolid polychaetes. The flimsy, spherical mass was collected from the soft bottom in a *Thalassia* bed and did not appear to be connected directly to the substrate.

The mass (Fig. 1A–D) was maintained somewhat below ambient temperature in the laboratory (20°–23°C) in a small dish with seawater until the embryos hatched naturally after 6 d. Larvae (Fig. 1E,F) were placed in clean dishes and fed with the microalgae (*Isochrysis galbana* PARKE 1949). Some portions of the egg mass were maintained in an aquarium and others were fixed in 96% EtOH for subsequent molecular and scanning electron microscopy (SEM) examination.

Prodissoconchs of embryos were prepared, dehydrated in 96% EtOH, and separated from their egg envelope using an eyelash. The prodissoconchs were then left to air dry and mounted with a humid eyelash onto a carbon biadhesive tape on a metal stub. Samples were then coated in platinum/palladium and examined in a Carl Zeiss EVO[®] 50 SEM under 20 kV and × 800–1000 magnification.

Molecular sequence data and identity of the mass

DNA was extracted from (a) a single veliger and (b) from a fragment of the egg mass containing ten veliger larvae using Qiagen’s DNeasy blood & tissue kit (Valencia, CA, USA). Amplification of 18S rRNA (primers 1F–9R) (Giribet et al. 1996), 28S rRNA (28Sa–28S rd5b) (Whiting et al. 1997; Schwendinger & Giribet 2005), 16S rRNA (16Sa–16Sb) (Edgecombe et al. 2002), and histone H3 (H3aF–H3aR) (Colgan et al. 1998) was carried out using standard PCR amplification under normal conditions for 35 amplification cycles. Sequences from the two DNA extractions were identical for the four

¹From a translation of Miyazaki; Guiart’s citation or date not provided in Miyazaki.

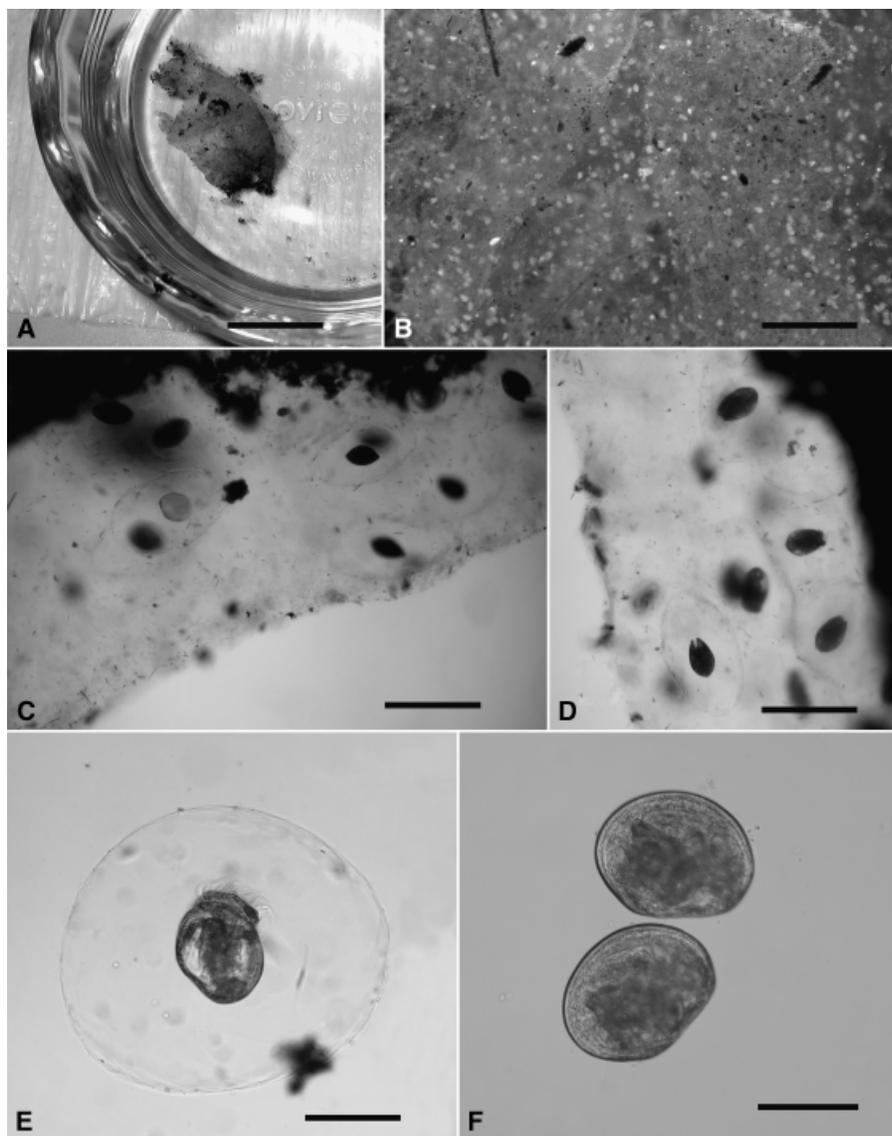


Fig. 1. Egg mass, embryos, and hatchlings of *Phacoides pectinatus*. **A.** Portion of the gelatinous egg mass 6 d after collection. The gel is torn on the left side of the mass. Scale bar = 25 mm. **B.** A close view of the egg mass showing the uniform distribution of embryos within the gel mass. Scale bar = 2 mm. **C.** Each lens-shaped capsule contains a single embryo. Opaque embryos are alive, and the transparent shell of a dead embryo can be seen towards the upper left. Scale bar = 400 μm . **D.** Embryos open and close the shell, and extend the velum within the mass. Scale bar = 350 μm . **E.** A single embryo showing the extended velum and long compound cilia. Scale bar = 180 μm . **F.** Hatchlings. Scale bar = 100 μm .

markers. We used the BLASTn algorithm to compare our sequences with those deposited in NCBI's GenBank. DNA sequences have been deposited in GenBank under accession numbers GQ980261–GQ980264.

Results

Developmental observations

The flimsy, spherical mass was not superficially distinct from a polychaete egg mass and was therefore not observed closely until its identity as a bivalve egg mass became apparent. The mass was fairly transparent and had a yellowish-brown color due to numerous diatoms embedded in the outer layer of the

gel (Fig. 1). The outer layer of 2–3 mm seemed somewhat tougher than the rest of the gel. Inside the gel, each embryo was individually surrounded by a transparent lens-shaped capsule 570 μm (SD = 84; $n = 5$) in diameter. The capsules did not appear to be connected by chalazae or other membranes or tubes, and the capsules appeared to be organized haphazardly but with a more or less uniform density (Fig. 1A–D).

After initial development in the field and 24–48 h in the laboratory, the egg mass was examined and found to contain developing trochophores that were not superficially distinct from polychaete embryos. After 4 d, bivalve veligers were clearly visible in the mass (Fig. 1C–E), and after 7 d, they hatched as swimming veligers (Fig. 1F). Hatchlings had a traditional shell

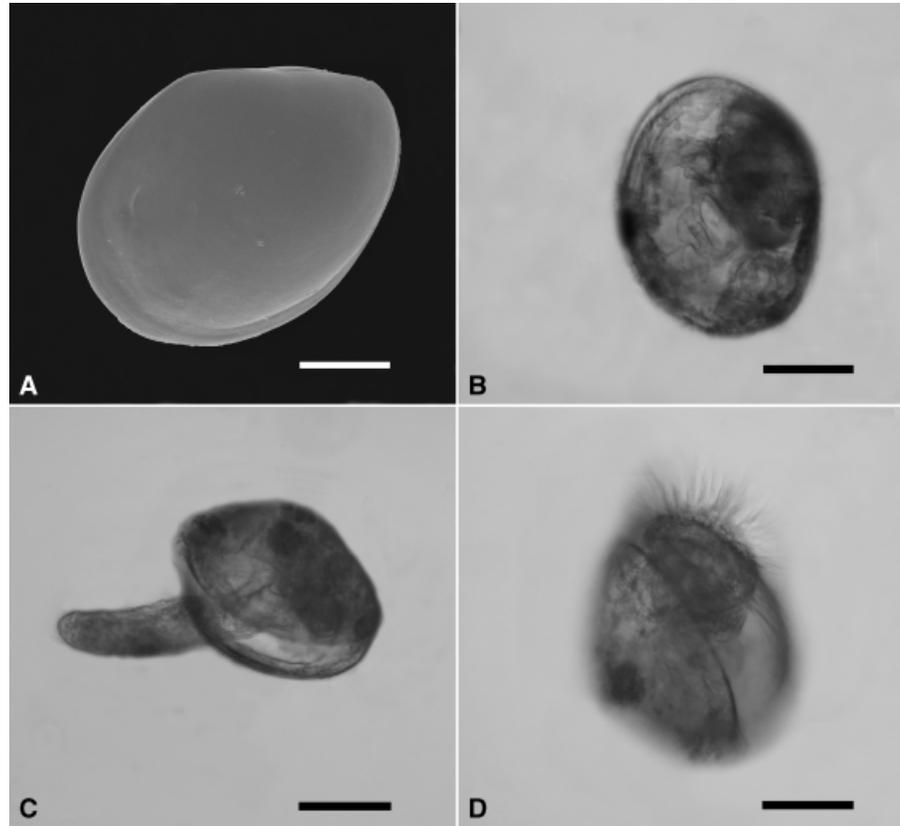


Fig. 2. *Phacoides pectinatus*. **A.** Scanning electron micrograph of the shell of an excapsulated embryo 2 d before hatching, showing the shape and absence of sculpture on prodissoconch I. Scale bar = 50 μm . **B.** Juvenile with a closed shell, showing internal structures. Scale bar = 70 μm . **C.** Light micrograph showing the well-developed foot, which moves actively. Scale bar = 90 μm . **D.** Two-week-old veliger, which seems to have settled on the bottom of the dish, but has not yet metamorphosed. Scale bar = 75 μm .

length (longest length parallel to the hinge) of 198 μm (SD = 3.6; range = 190–206 μm ; $n = 28$), a major axis (maximum diameter) of 204 μm (SD = 3.7; range = 197–211 μm ; $n = 28$), and a minor axis (width) of 163 μm (SD = 2.9; range = 155–169 μm ; $n = 28$).

After hatching, veligers had a smooth shell (Fig. 2A) and swam actively for 1–2 d, after which they were seen to lie on the bottom of the culture dish, actively extending the foot. Metamorphosis did not require the addition of any substrate, although a visible biofilm developed naturally on the bottom of the dish after a few days. Despite being provided with microalgae in suspension, the veligers did not appear to feed: the stomach did not turn brownish-yellow as is typical of feeding veligers. Four of the juveniles survived for 2 weeks; they were active at this time (Fig. 2B,C), but had not grown significantly (mean = 199 μm ; $n = 4$). One additional veliger had not yet metamorphosed at that time (Fig. 2D).

Molecular analyses

DNA sequence data unambiguously identified this material as a lucinid with very strong support for its identity as *Phacoides pectinatus* (GMELIN, 1791). This identification was based primarily on the 18S and 28S

rRNA sequence data from recently published phylogenies of Lucinoidea (see also Williams et al. 2004; Taylor et al. 2007). Members of *P. pectinatus* are common in the Bocas del Toro region, where they live burrowed in the black sulfide-rich mud around mangroves and seagrass, and the observed larval morphology is similar to that of other lucinids.

The complete 18S rRNA gene (1803 bp) unambiguously identified the sequence of *P. pectinatus* deposited in GenBank (AM774503; 95% query coverage; maximum identity of 99%), the only difference being an indel in the 3' region of the marker, most probably due to an error reading the end of the sequence. Likewise, the 595-bp fragment of 28S rRNA matched the two sequences of *P. pectinatus* deposited in GenBank (AM779677 and AJ581897; query coverage of 100% and 98%, respectively; maximum identity of 99% with both sequences).

The sequences for histone H3 and 16S rRNA were less useful in verifying the identity of the egg mass, as few similar sequences were available in GenBank. The histone H3 sequence had 90% maximum identity (query coverage between 97% and 99%) with *Myrtea spinifera* (MONTAGU, 1803), the only lucinid histone H3 sequence available in GenBank. The 470 bp fragment of the mitochondrial 16S rRNA had no signifi-

cant match (query coverage below 38%; maximum identity ~80%). No lucinid 16S rRNA sequence has been deposited as yet in GenBank.

Phylogenetic analysis of the sequences produced here with those available in GenBank unambiguously placed them with *P. pectinatus*.

Discussion

This is the second report of a lucinid, and the sixth for any kind of bivalve, producing a well-developed gelatinous egg mass containing encapsulated veligers. Although early embryogenesis and development have been studied in a few lucinid species (Alatalo et al. 1984; Frenkiel et al. 1997; Gros et al. 1997, 1999; Bigatti et al. 2004), including *Phacoides pectinata*, the papers by Pelseneer (1926) and Lebour (1938) are the only ones that mention the formation of egg masses. In general, these studies and many others on bivalve development strip the gonads to obtain gametes for study. This means that the natural spawning and deposition of eggs is seldom observed, and it is likely that any kind of accessory gland secretion or packaging of eggs with adhesive coverings would not be reported. However, Gros et al. (1997) induced spawning in individuals of *Codakia orbicularis* (LINNEAUS, 1758) by injection of serotonin, and observed subsequent spawning of individual oocytes that were surrounded by a gelatinous coat but did not form a mass. Development in this species appears to be very similar to that of *P. pectinata*. It is interesting to note that historical studies, which were more likely to include greater effort at natural history observations, are more likely to report egg strings or benthic encapsulated development (Sastry 1979).

Several hypotheses have been put forward as to the reasons why gelatinous egg masses have not evolved in certain groups of marine invertebrates. These include physiological constraints on packing embryos too tightly together, limits on available safe deposition sites, and difficulties transferring sperm to eggs. By forming artificial egg masses with normally free-living embryos, Strathmann & Strathmann (1989) demonstrated that special embryological adaptations are not necessary for development within a gelatinous egg mass. In addition, physiological factors appear to constrain the shape and size of egg masses, as well as the distribution inside the mass (Strathmann & Strathmann 1989; Moran & Woods 2007), but constraints appear to be fairly permissive as many different forms of egg masses occur in nature.

In the case of bivalves, it is not immediately clear why gelatinous egg masses are so uncommon. Constraints on bringing eggs and sperm together inside

the female are overcome in a fairly diverse array of brooding bivalves. However, it has been pointed out that capsules and gelatinous coverings may form an insurmountable barrier for sperm penetration and that, if gel is added after fertilization, then accessory structures may be necessary to form the mass (Strathmann & Strathmann 1989). It would therefore be interesting to examine the anatomy of adults of *P. pectinatus* to search for potential accessory structures.

The pattern of increased maternal care and larger eggs with increasing latitude was observed for bivalves by Ockelmann (1958). This pattern is equivocal for the six species with gelatinous egg masses and those with encapsulated eggs. It is interesting, however, to note that two of the six species known to have gelatinous egg masses host sulfur-oxidizing bacteria, and that members of two of the species with sticky encapsulated eggs, *Solemya velum* and *Solemya reidi*, also host such bacteria. The symbiotic bacteria in individuals of *S. velum* are vertically transmitted, while those in *C. orbicularis* are environmentally transmitted (Gros et al. 1997). The mode of transmission is unknown in *P. pectinatus*. Further observations of lucinid development will be necessary to determine whether gelatinous egg masses are unusually common in this family or whether lucinids are over represented due to artifacts of small sample sizes. It would also be interesting to examine the possible link between chemosymbiotic bacteria and protected development.

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