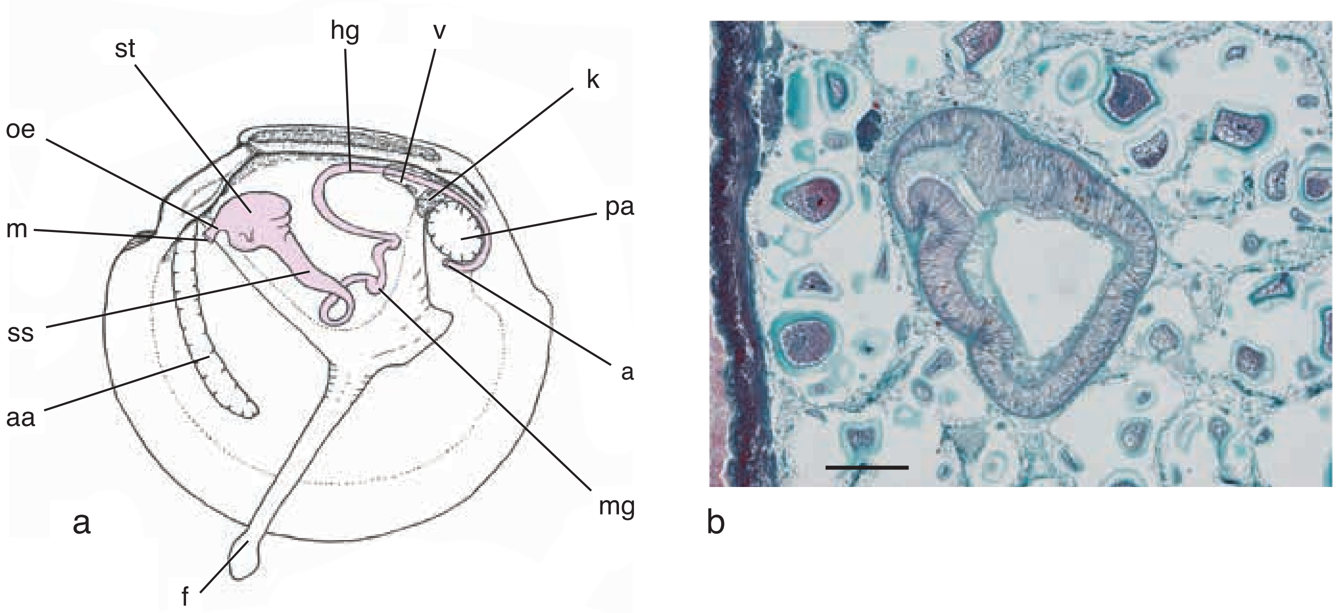

Figure 16. Digestive system and stomach.
a. *Phacoides pectinatus* digestive system viewed from left side (modified from Narchi & Farini Assis 1980).
Abbreviations: a – anus, aa – anterior adductor muscle, f – foot, hg – hind-gut, k – kidney, lc –m – mouth, mg – mid-gut, oe – oesophagus, pa – posterior adductor muscle, ss – style sac, st – stomach, v – ventricle.
b. *Rasta thiophila* cross section of stomach surrounded by ovary. Scale bar = 200 µm

and 'mining' of sulphide concentrations in the sediment. In most lucinids the main part of foot is vermiform, long and cylindrical and can be extended for at least four to six times the length of the animal. *Fimbria fimbriata* has a broader, less extensible foot (Morton, 1979). Many lucinid species have a stubby, flattened posterior component – the heel (Allen, 1958) but this is absent in others (e.g. *Rasta* Taylor & Glover, 1997). The long, cylindrical part of the foot has layers of circular and longitudinal muscle (Allen, 1958; Taylor & Glover, 1997b) surrounding a central blood space (Fig. 14 c). The distal tip is bluntly pointed but can become bulbous. The outer epithelium consists of columnar cells which become highly ciliated near the tip. Also at the tip, there are two types of sub-epithelial gland cells with different staining properties and Allen (1958) thought that these gland cells were responsible for producing the mucus which lines the anterior incurrent duct.

Visceral mass

Although usually laterally compressed and smooth the body wall in some lucinids is extended as dome-shaped swellings in *Cardiolucina* species (Fig. 17) as originally observed by Pelseneer (1911), lateral pouches in *Parvilucina crenella* and into rams-horn shaped extensions (Fig. 9 d) in *Bathaustriella*, *Ferrocina* and *Troendleina suluensis* (Glover *et al.* 2004; Taylor *et al.* 2013). These lateral pouches and extensions are occupied by gonadal and digestive gland tissue (Fig. 17). In molecular analyses *Bathyustriella*, *Ferrocina*, *Troendleina* and *Parvilucina* form part of the same subclade of Lucininae and the visceral extensions may be an apomorphy of the group.

Stomach and intestine

Details of the digestive tract have been investigated in relatively few lucinids (Purchon, 1958; Allen, 1958; Morton, 1979; Narchi & Farani Assis, 1980; Johnson *et al.* 1996; Simone *et al.* 2015). The oesophagus is usually short (Allen, 1958) but longer in *Fimbria* (Morton, 1973). The stomach in all examined lucinids is simple with 2–3 duct openings to digestive diverticula, the style sac and mid-gut are conjoined and the latter runs posteriorly without major loops, passes through the ventricle as the hind gut and over the posterior adductor muscle terminating at the anus near the posterior aperture (Fig. 16).

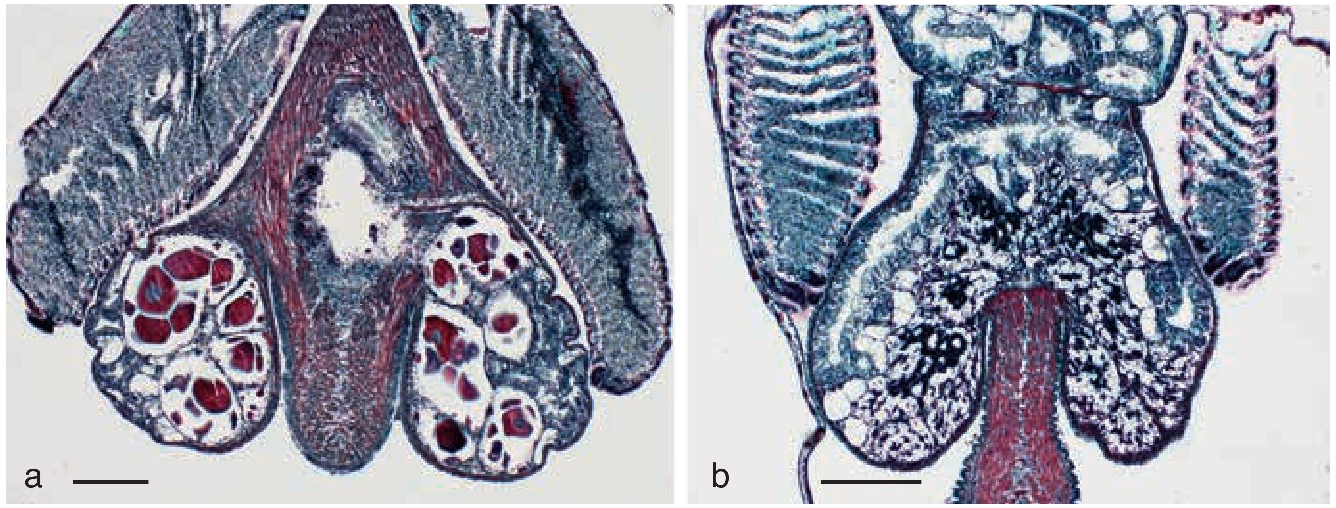

Figure 17. Visceral pouches of *Cardiolucina pisiformis* Dampier, Western Australia.
a. Vertical section of a female showing subspherical visceral pouches containing ovary and digestive gland. Scale bar = 200 µm. **b.** Section of a male with visceral pouches occupied by testis and digestive gland. Scale bar =200 µm.

Reproductive features

Oocyte development was studied in *Phacoides pectinatus* from Guadeloupe by Frenkiel *et al.* (1997) who showed that females were in a permanent state of reproductive maturity, with fully grown oocytes possessing a thick jelly coat. A similar result was also found by Christo *et al.* (2016) in southern Brazil. Studies of the gametogenic cycle of *Loripes orbiculatus* from Brittany (Johnson & Le Pennec, 1994) demonstrated a major spawning event in May and a minor event in November, while in Mauritania Geest *et al.* (2014) showed two major spawning events in January–February and July–August. Spawning of *Codakia orbicularis* from Florida took place between May and October (Alatalo *et al.* 1984).

Although information is available for only a few species it seems that developing lucinid oocytes have a thick jelly coat that expands after fertilization and released into a gelatinous capsule (500 µm in diameter in *Lucinoma aequizonata* and 350 µm in *Codakia orbicularis*) in which larval development takes place (Alatalo *et al.* 1984; Gros *et al.* 1997, 1999; Bigatti *et al.* 2004). There is some evidence of the release of aggregates of capsules; from a Panama seagrass habitat Collin & Giribet (2010) recorded a gelatinous mass containing capsules with developing embryos of *Phacoides pectinatus*. Benthic gelatinous bodies containing developing embryos have also been recorded in *Loripes orbiculatus* (Pelseneer, 1926). It is possible that benthic gelatinous egg masses are more common in lucinids for Bigatti *et al.* (2004) observed released oocytes grouped within a gelatinous mass held in the mantle cavities of *Ctena orbiculata*, *Codakia orbicularis* and *Lucina pensylvanica*.

Embryonic and larval development

This has been studied in detail for only two species. In the shallow water *Codakia orbicularis* hatching of swimming veligers from large eggs takes place 48 hours after fertilization and after about 16 days the velum is lost and the larvae reach the crawling plantigrade stage. After the initial hatching there is little growth of the larval shell recorded with protoconch 2 as a narrow rim (Gros *et al.* 1997). For the deep water *Lucinoma aequizonata* development was followed from release of egg capsules to the emergence of D shaped veliger larvae 12 days after fertilization (Gros *et al.* 1999).