

foot and with the anterior ventilator connection to the surface also maintained by the elongate foot. The posterior inhalant aperture lost its function as the main conduit of water into the mantle cavity. The gills became simplified with the loss of the outer demibranch but thickened to accommodate more bacteriocytes in the subfilamental tissue. Loss of the outer demibranch of the gills, the reduced labial palps, the simple gut and the reversion to an anterior-posterior water flow are all likely paedomorphic features (Reid & Brand 1986; Reid 1990).

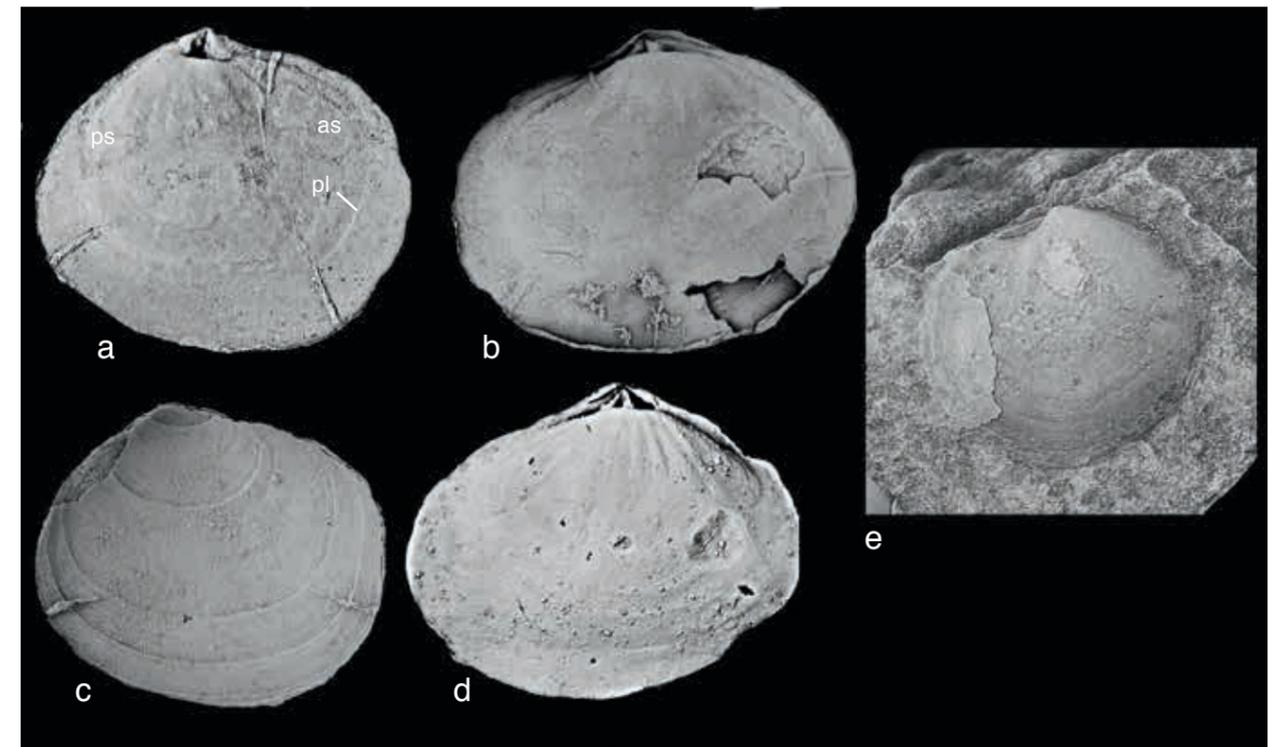
#### Palaeozoic faunas

Only seven genera of lucinids have been described from Palaeozoic rocks (Table 5). The earliest heteroconch bivalves are known from early–mid Ordovician (Cope, 2002, Fang & Cope, 2004, Polechová, 2013, 2016) part of a diversification into burrowing in soft substrates (Fang,

2006) and the earliest lucinids probably date from this radiation. *Babinka prima* Barrande, 1881 was proposed by McAlester (1965, 1966) as the oldest but his claim of an independent origin from other bivalves based on the repeated pedal muscle scars similar to those of monoplacoplorans is now refuted and it is presently classified as a separate superfamily Babinkoidea (Carter *et al.* 2011). Previously, we questioned the lucinoid affinities of *Babinka* (Taylor & Glover, 2000) but study of more and better images (Fig. 133) has caused a reassessment of our position. Lucinoid features of *Babinka* are the anteriorly extended shape, the hinge dentition of two cardinal teeth in each valve and the anterior adductor muscle scar slightly detached ventrally from the pallial line (Fig. 133 a). Another possible early lucinid is a *Paracyclas* sp. (Fig. 133 e) from the late Ordovician (Sandbian) of Girvan Scotland, (Stewart, 2012). This has the shape and appearance of a lucinid but internal details are obscure. Fang & Cope (2004) described an earlier (Floian) but poorly preserved *Paracyclas* from China. Other small *Paracyclas* species are known from the late Ordovician and Silurian but their detailed morphology is unstudied.

The best documented species of the Palaeozoic is *Ilionia prisca* (Hisinger, 1837) known from the Silurian (Ludlovian) of Gotland, Sweden (Figs 134 a–c). This has an elongate and laterally compressed shell with a long, narrow, anterior adductor scar detached from the pallial line and resembling in shape and musculature the early Paleocene *Eomiltha* or the Eocene to Recent *Retromiltha* (Taylor & Glover, 2018). *In situ* fossils in Gotland (Liljedahl, 1991, 1992) lived in fine calcareous muds and are orientated with dorsal margins upwards as in living lucinids. The internal morphology suggests that *Ilionia* held chemosymbionts in the ctenidia with a typical lucinid anterior-posterior water flow. The other common bivalve in the habitat was *Janeia silurica* (Solemyidae) that possibly shared a chemosymbiotic life habit.

From the Devonian species of *Paracyclas* are best known from Europe and North America, although fossils from the Silurian and Ordovician have also



**Figure 133.** Ordovician lucinoideans.

**a–d** *Babinka prima* Barrande, 1881. Images courtesy of Dr Marika Polechová. **a–c** from Lower Ordovician Fezouata Formation, Morocco (Polechová, 2016) **a**. Internal mould of right valve (FSL 711652 University of Lyon, France), L 15 mm. as – anterior adductor scar, pl – pallial line, ps – posterior adductor scar **b**. Internal mould of the left valve (AA.TMT.OI.136a, Cadi Ayyad University, Marrakech), L 18 mm. **c**. External mould of the right valve with sculpture of commarginal lamellae (AA. JBZ. OI. 94, Cadi Ayyad University, Marrakech), L 14 mm. **d**. Lectotype of *Babinka prima* (National Museum, Prague L27086) internal mould of left valve, Middle Ordovician (Darriwilian), Šárka Formation Bohemia, Prague Basin, L 20.5 mm. (Polechová 2013) **e**. *Paracyclas* sp. Late Ordovician (Sandbian), Balclatchie, Girvan, Scotland (NHMUK Pal. L 50060), L 7.3 mm.

been assigned to the genus. The Devonian *Paracyclas* are inflated, subspherical, smooth or with low commarginal lamellae and edentulous hinges and resemble living *Pegophysema* species (Figs 134 c, d). Johnston (1993) introduced the family Paracyclidae claiming that the anterior adductor muscle scar of *P. proavia* was not ventrally detached from the pallial line as in Lucinidae and more closely resembled unguinid morphology. However, our observations of *P. proavia* and *P. elliptica* from Europe and North America clearly show a detached lucinid-like anterior adductor muscle scar (Taylor & Glover 2005, and Fig. 134 e) suggesting that the Australian species figured by Johnston and identified as *P. proavia* is not congeneric. An unusual morphology is shown by *Phenacocyclas pohli* La Rocque, 1950 from the mid-Devonian of Michigan. This is sub-circular with commarginal lamellae, a distinct posterior

sulcus, and a long, detached anterior adductor scar (Figs 134 f, g). Lying between the muscle scar and pallial line is a series of folds that may be impressions of mantle gills situated in a position similar to such structures present in living *Phacoides pectinatus*. Two other genera from the Devonian, *Auriparacyclas* and *Semiparacyclas*, of Novaya Zemlya, Russia, are poorly documented (Navilkin 1968) and difficult to assess.

Lucinidae are particularly rare during the Carboniferous and Permian. A single possible lucinid, *Palaeolucina* Chao, 1927, is reported from the Carboniferous of China (Chen, 1976) but few details of morphology are available (Fig. 134 i). From the Permian, *Gigantocyclus zidensis* Termier & Termier, 1977 from Tunisia and figured by Boyd & Newell (1979), has features resembling living *Pegophyseminae* (Fig. 134 h).

<b>Ordovician</b> 485–444 mya <i>Babinka</i> Barrande, 1881. Type species <i>Babinka prima</i> Barrande, 1881. Ordovician Darriwilian, Bohemia, Prague Basin.
<b>Silurian</b> 444–419 mya <i>Ilionia</i> Billings, 1875. Type species <i>Ilionia canadensis</i> Billings, 1875. Silurian, Canada.
<b>Devonian</b> 419–399 mya <i>Auriparacyclas</i> Nalivkin, 1968. Type species <i>Paracyclas (Auriparacyclas) auriculata</i> Nalivkin, 1968. Devonian, Russia. <i>Paracyclas</i> Hall, 1843. Type species <i>Paracyclas elliptica</i> Hall, 1843. Devonian, USA. <i>Phenacocyclas</i> LaRoque, 1950. Type species <i>Phenacocyclas pohli</i> LaRoque, 1950. Devonian, USA. <i>Semiparacyclas</i> Nalivkin, 1968. Type species <i>Paracyclas (Semiparacyclas) semilunarie</i> Nalivkin, 1968. Devonian, Russia.
<b>Carboniferous</b> 359–299 mya <i>Palaeolucina</i> Chao, 1927. Type species <i>Palaeolucina carbonaria</i> Chao, 1927. Carboniferous, China.
<b>Permian</b> 299–252 mya <i>Gigantocyclus</i> Termier & Termier, 1977. Type species <i>Gigantocyclus zidensis</i> Termier & Termier, 1977. Permian, Tunisia.

**Table 5.** Palaeozoic genera Lucinidae