

Pinnocaris and the origin of scaphopods

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The description of a tiny coiled protoconch in the Ordovician *Pinnocaris lapworthi* Etheridge, 1878 indicates that this ribeirioid rostroconch mollusc cannot be the ancestor of scaphopods, resolving recent debate concerning the role of *Pinnocaris* in scaphopod evolution. The sense of coiling of the scaphopod protoconch is opposite to that of *Pinnocaris*. Scaphopod protoconchs resemble helcionelloid molluscs (Cambrian–Early Ordovician) in terms of their direction of coiling, although the scaphopod shell is strongly modified by the extreme anterior component of growth. Convergence is identified between scaphopods and two helcionelloid lineages (*Eotebenna* and *Yochelcionella*) from the Early–Middle Cambrian. The large stratigraphical gap between helcionelloids and the first undoubted scaphopods (Devonian or Carboniferous) supports the notion that the scaphopods were derived from conocardiid rostroconchs rather than directly from helcionelloids. However, the protoconch of conocardiid rostroconchs closely resembles the helcionelloid shell, suggesting that conocardioids in turn were probably derived from helcionelloids.

Key words: Mollusca, Rostroconchia, Scaphopoda, Helcionelloida, *Pinnocaris*, Ordovician.

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Introduction

The model of molluscan phylogeny proposed by Runnegar and Pojeta (1974) and Pojeta and Runnegar (1976, 1979) considered scaphopods to have been derived from the ribeirioid rostroconch mollusc *Pinnocaris* Etheridge, 1878 in the Ordovician. The description of the supposed scaphopod *Rhytidentalium kentuckyensis* Pojeta and Runnegar, 1979 from the Ordovician of the U.S.A. provides supporting morphological and stratigraphic evidence for this hypothesis (Pojeta and Runnegar 1979). Runnegar (1996) regarded ribeirioids and scaphopods as sister groups. Yochelson (1978, 1979) claimed that the first true scaphopods evolved in the Devonian from a non-shelled ancestor, although he later even rejected these pre-Carboniferous supposed scaphopods (Yochelson 1999, 2002; Yochelson and Goodison 1999; Yochelson and Holland in press).

Engeser and Riedel (1996) dismissed the hypotheses of Runnegar and Pojeta (1974), Pojeta and Runnegar (1976, 1979) and Yochelson (1978, 1979), and proposed that scaphopods evolved in the Devonian as a sister group to the conocardiid rostroconchs, a more advanced group of rostroconchs than the ribeirioids. Engeser and Riedel (1996) reclassified scaphopods as an order of the class Rostroconchia, the revised class thus having a record from the Cambrian to the present day and not being extinct, as originally proposed by Pojeta et al. (1972). In discounting the derivation of the scaphopods from *Pinnocaris*, Engeser and Riedel (1996) particularly emphasised the difference in location of the protoconch between scaphopods (where it is located at the extreme posterior of the tubular shell with all subsequent shell growth towards the anterior) and *Pinnocaris* (where the

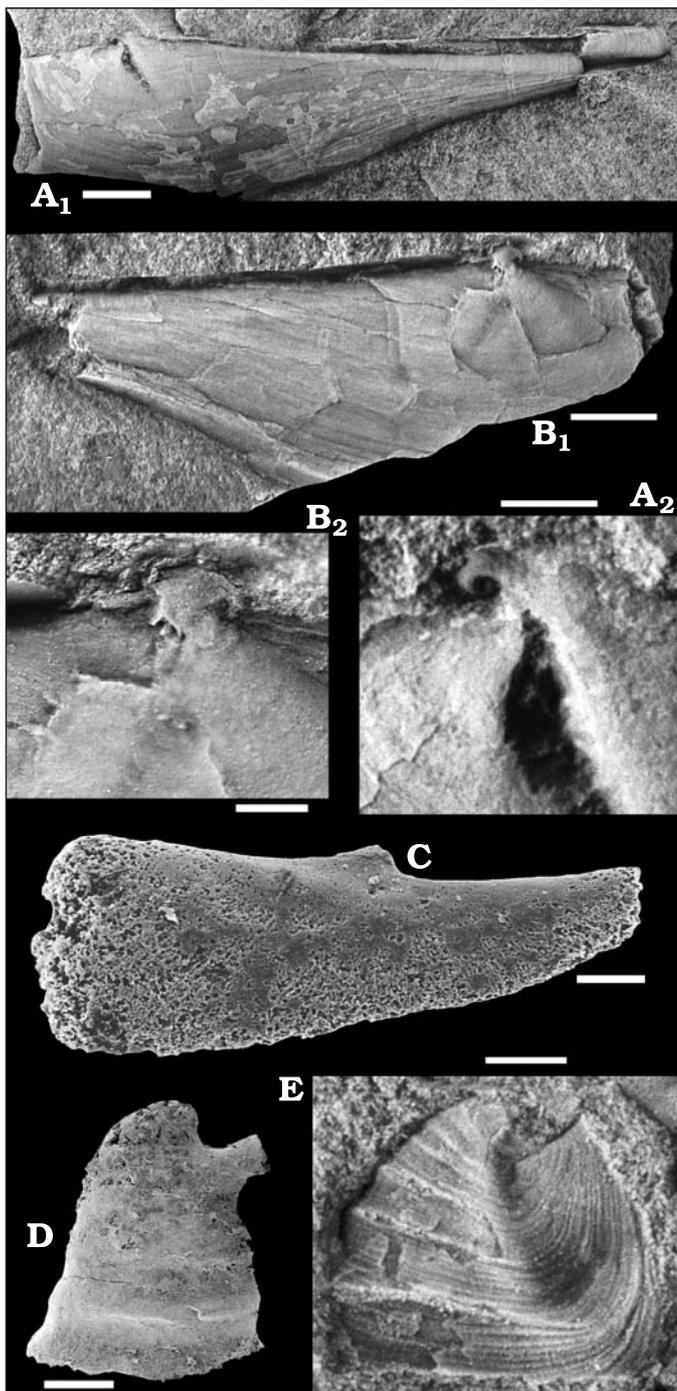
dorsal apex is closer to the supposed anterior and there is a profound posterior component of growth).

The biological affinities of the Cambro-Ordovician genus *Pinnocaris* (Figs. 1, 2) have been debated since its original description by Etheridge (1878) from the Ordovician of the Girvan district of southern Scotland. Nicholson and Etheridge (1880) concluded that the elongate, supposedly bivalved invertebrate was a crustacean (Arthropoda) rather than a bivalve (Mollusca). Their predicament seems to be embodied in their description (Nicholson and Etheridge 1880: 207) of *Pinnocaris* as “bivalve, bent along the middle line” which casts doubt on whether or not two separate valves are present; it is evident from the present material that *Pinnocaris* is univalved. Jones and Woodward (1895) also suggested that *Pinnocaris* was bivalved, although they thought that an intermediary plate may have been present dorsally between the valves in the elongate, narrow, portion of the shell. They considered the shell to be chitinous in composition, in accordance with their interpretation as a phyllopod crustacean.

Kobayashi (1933) reviewed the systematic position of a variety of ribeirioids (but not *Pinnocaris*), concluding that they were arthropods. Some of the genera comprising Kobayashi’s (1933) new family Ribeiridae were considered to be bivalves in the *Treatise on Invertebrate Paleontology* but *Pinnocaris* is stated to be of uncertain systematic position, and excluded from both the bivalvian and arthropodian schemes of classification (Moore 1969a, b).

Pojeta and Runnegar (1976) interpreted *Pinnocaris* as a mollusc with a calcareous shell and assigned it to the class Rostroconchia Pojeta, Runnegar, Morris, and Newell, 1972. Rostroconchs are conchiferan molluscs with “an uncoiled and untorted univalved shell which straddles the dorsal

midline, and a bivalved adult shell... [with] dorsal commissure lacking" (Pojeta and Runnegar 1976: 48). They assigned *Pinnocaris* to the most primitive order (Ribeirioida Kobayashi, 1933) of the rostroconchs in which a transverse internal support, or pegma, joining the two lateral areas is located beneath (anterior in their orientation) the apex and all shell layers cross the dorsum, i.e., the shell is a single entity at all growth stages. In the reconstruction of Pojeta and Runnegar (1976), *Pinnocaris* is exogastrically coiled, with shell coiling expanding from the anterior apex towards the posterior (clockwise when viewed with the anterior to the left;



Figs. 1A₂, 2), although the highly modified morphology of the elongate shell results in extreme narrowing and extension of the posterior shell relative to the more equidimensional anterior.

Peel (1991a) accepted the notion of anterior and posterior in *Pinnocaris* suggested by Pojeta and Runnegar (1976) but he believed that the shell was endogastrically coiled, i.e., with the shell coil expanding anteriorly (anticlockwise when viewed from the left). This interpretation followed Peel's (1991b) description of the Middle Cambrian helcionelloid *Eotebenna viviannae* Peel, 1991 (Fig. 1C). The latter is elongate and strongly attenuated posteriorly, in similar fashion to *Pinnocaris lapworthi* and its coiling direction is clearly endogastric (Peel 1991b: fig. 19; Fig. 1C, E). Peel (1991a, b) suggested that helcionelloid molluscs, including *Eotebenna* Runnegar and Jell, 1976, formed a class Helcionelloida characterised by endogastric coiling (see also Geyer 1994), whereas Runnegar and Pojeta (1974) and Pojeta and Runnegar (1976), and in various papers summarised by Runnegar (1996), considered helcionelloids to be exogastric monoplacophorans.

This paper describes the protoconch of *Pinnocaris lapworthi*, making comparisons with Cambrian helcionelloid molluscs and with the protoconch of living scaphopods. It demonstrates that the derivation of scaphopods from *Pinnocaris* suggested by Runnegar and Pojeta (1974) and Pojeta and Runnegar (1976, 1979) cannot be maintained, confirming the suggestion of Engeser and Riedel (1996). However, the present conclusion is based upon fundamental differences in the coiling direction and ontogeny of the protoconchs of *Pinnocaris* and scaphopods, rather than the analysis of shell growth vectors and the position of the protoconch relative to the adult shell presented by Engeser and Riedel (1996).

Institutional abbreviations.—NHM, palaeontological collections of the Natural History Museum, London; MGUH, Geological Museum of Copenhagen University. GGU indicates collections made by the Geological Survey of Greenland, Copenhagen, now a part of the Geological Survey of Denmark and Greenland.

Fig. 1. *Pinnocaris* and *Eotebenna*. **A**, **B**. *Pinnocaris lapworthi* Etheridge, 1878, Ordovician, Girvan, southern Scotland; A₁, A₂, lateral view of internal mould of partially crushed specimen with adherent shell patches showing the pegma and the coiled protoconch, NHM In 20372, scale bars: A₁ 3 mm, A₂ 1 mm; B₁, B₂, lateral view of partially crushed specimen showing the coiled protoconch, NHM In 20400; scale bars: B₁ 3 mm, B₂ 1 mm. **C**. *Eotebenna viviannae* Peel, 1991, Middle Cambrian, Andrarrum Limestone, Bornholm, Denmark, right side of phosphatic internal mould showing the protoconch, MGUH 19.565, scale bar 100 μ m. **D**. *Yochelcionella greenlandica* Atkins and Peel, 2004, Lower Cambrian, Aftenstjernesø Formation, Peary Land, North Greenland, lateral view of right side showing the prominent snorkel, MGUH 27.018 from GGU sample 271470, scale bar 200 μ m. **E**. *Eotebenna arctica* Peel, 1989, Lower Cambrian, Henson Gletscher Formation, Freuchen Land, North Greenland, lateral view which has been horizontally mirrored to enhance comparison, MGUH 18.701 from GGU collection 315109, scale bar 1 mm.

Protoconch of *Pinnocaris*

The protoconch of *Pinnocaris lapworthi* is a minute, isostrophic shell that is coiled through a full whorl and has open umbilici (Figs. 1A, B, 2); it is not cup-shaped as assumed by Engeser and Riedel (1996). The height of the protoconch measured perpendicular to the dorsum of the adult is about 0.5 mm and its length is between 1 and 2 mm. Shell coiling expands towards the attenuated termination of the adult shell, such that the sub-apical surface in lateral perspective corresponds to the relatively short distance to the broadly rounded termination of the adult shell. The supra-apical surface is long, forming the dorsal surface towards the attenuated termination.

Two specimens with well-preserved protoconchs have been observed in a collection of more than 50 specimens preserved in the Natural History Museum, London. Both specimens form part of the Mrs Robert Gray collection and were collected from the Ardmillan Group at Balclatchie, Girvan, southern Scotland. Specimen NHM In 20372 was figured by Jones and Woodward (1895: pl. 15: 8, 9) and by Pojeta and Runnegar (1976: pl. 9: 13, 14), but accompanying descriptions make no reference to the well-preserved coiled protoconch. The external mould and the corresponding internal mould figured by Jones and Woodward (1895: pl. 15: 8, 9, respectively) represent the supposed left valve, with the protoconch thus lying close to the interpreted anterior margin. Pojeta and Runnegar (1976, fig. 13) figured the same external mould and a latex replica of this specimen (their fig. 14), which they also interpreted as a left valve. While the illustrations of Jones and Woodward (1895) indicate that the specimen is preserved in a small slab, those of Pojeta and Runnegar (1976) have been trimmed artificially free from matrix. The specimen is 29 mm long and wedge-shaped, and broadly rounded at one termination which was considered anterior by Jones and Woodward (1895) and Pojeta and Runnegar (1976); the shell narrows uniformly to the opposite, extended and attenuated, termination (Fig. 1A₁). The protoconch of NHM In 20372 is visible on both the external and internal moulds although only the latter, with adherent patches of thin shell (Fig. 2), is figured here. The height of the protoconch is about 0.5 mm and it has a length of between 1 and 2 mm, the precise dimension being uncertain on account of the gradual supra-apical transition towards the attenuated termination of the adult. The sub-apical transition from the protoconch to the adult shell is abrupt. The internal mould of NHM In 20372 shows a prominent radial channel representing the plate-like pegma which united the opposing lateral areas in the apical region. The pegma approaches the dorsal surface at the junction between the protoconch and the sub-apical surface and does not affect the protoconch (Figs. 1A₂, 2). The groove it generates on the internal mould does not cross the dorsum.

NHM In 20400 is a partially crushed specimen with the tip of the attenuated termination and much of the margin be-

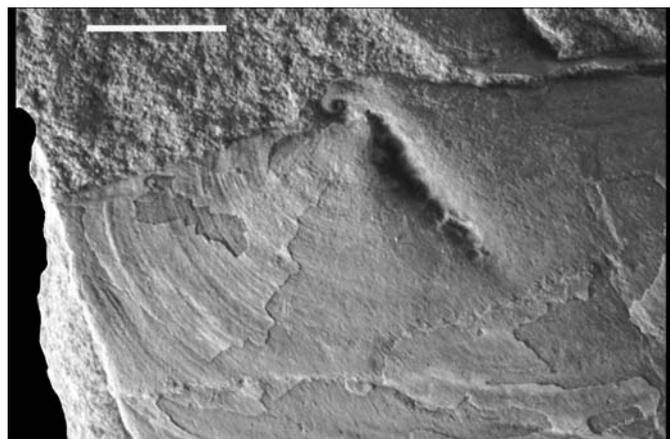


Fig. 2. *Pinnocaris lapworthi* Etheridge, 1878, Ordovician, Girvan, southern Scotland, lateral view of internal mould, showing fine comarginal ornamentation on adherent patches of thin shell on the sub-apical surface, NHM In 20372, scale bar 2 mm.

low the apex broken away (Fig. 1B₁). The protoconch is seen from the opposite side to NHM In 20372 and its external surface is apparently preserved. The supra-apical junction with the adult shell is a line of fracture with the adult shell depressed relative to the protoconch (Fig. 1B₂). The protoconch is of similar size and shape to that in NHM In 20372 but less well-preserved. While the pegma is developed on the shell interior, its location on the external surface of NHM In 20400 is indicated by a dark, shallow depression in Fig. 1B₁.

In general style of coiling, the isostrophically coiled protoconch of *Pinnocaris lapworthi* resembles the adult shells of a variety of helcionelloids, cyrtoneid Tergomya and bellerophonoid gastropods, although these are variously considered to be exogastrically or endogastrically coiled (see discussion in Peel 1991a and Runnegar 1996).

The scaphopod protoconch

An exhaustive recent review of scaphopod biology is given by Reynolds (2002) and the principal morphological features are illustrated in Fig. 3G. Scaphopod protoconchs have been described by Engeser et al. (1993), Steiner (1995), Engeser and Riedel (1996) and Wanninger and Haszprunar (2001), who also summarised earlier literature. The scaphopod protoconch is located at the extreme attenuated termination of the tubular scaphopod shell (Fig. 3D). It is resorbed with growth of the adult shell as the respiratory opening at this termination widens. Wanninger and Haszprunar (2001) presented an excellent series of scanning electron micrographs of the development of *Antalis entalis* (Linnaeus, 1758) which form the basis of Fig. 3A–D. Excellent photographs of juvenile scaphopod shells are also presented by Steiner (1995). At 62 hours after fertilisation (Fig. 3A) the larval shell field extends in humped, saddle-shaped,

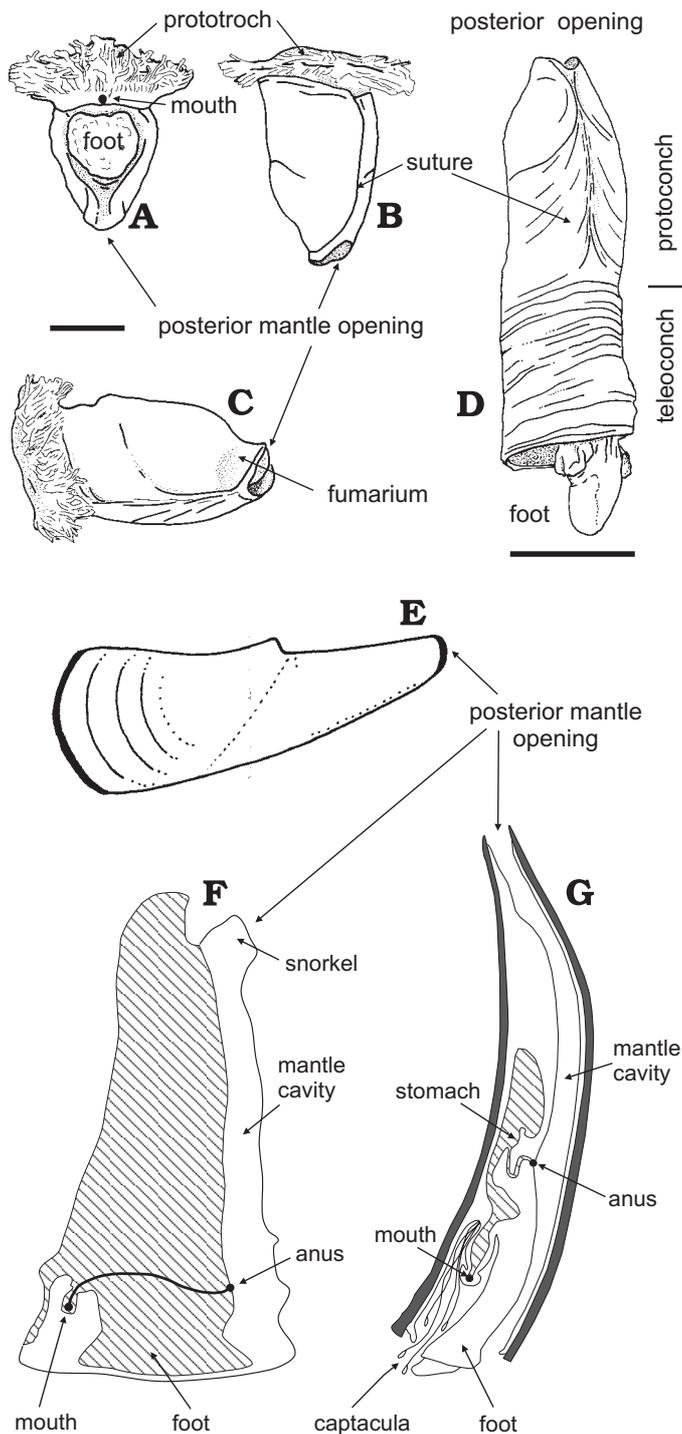


Fig. 3. **A–D**, larval development of the scaphopod *Antalis entalis* (Linnaeus, 1758); drawings based on SEM illustrations by Wanninger and Haszprunar (2001). **A**. Larva 62 hours post fertilisation (hpf) in ventral aspect. **B**. Larva at 74.5 hpf in latero-ventral view. **C**. Larva at metamorphic competence in latero-ventral view, 95 hpf, oriented for comparison with *Pinnocaris*, *Eotebenna*, and *Yochelcionella*. **D**. Post-metamorphic juvenile showing the sutured protoconch and teleoconch with complete comarginal growth lines. Scale bars 100 μ m (**A–C**), 250 μ m (**D**). **E**. *Eotebenna vivianae* Peel, 1991 in lateral view, the thickened lines indicate gapes. **F**. Reconstruction of *Yochelcionella* based on *Yochelcionella gracile* Atkins and Peel, 2004. **G**. Scaphopod anatomy, simplified and redrawn from Reynolds (2002). **E–G**, not to scale.

form around the dorsal area from one lateral surface to the other, flanking the ventral foot. Posteriorly, the shell margin is excavated and extended to form a fold (appearing as a trough in the ventral view). A few hours later, the growing lateral areas of the shell (the genae of Engeser et al. 1993 and Steiner 1995) have encased the foot and joined at a ventral suture (Fig. 3B, C); there is a well-developed sub-apical surface passing posteriorly into the protruding fumarium which is now developed around the posterior mantle opening (Fig. 3C). Subsequent shell growth is largely anterior, with comarginal annulations and without any trace of the suture on the ventral surface of the shell (Fig. 3D). Wanninger and Haszprunar (2001) informally referred all the annulated shell growth stage to the teleoconch (Fig. 3D), but Engeser et al. (1993) and Engeser and Riedel (1996) recognised an annulated stage within the protoconch prior to teleoconch formation.

In lateral perspective, the sense of coiling of the protoconch of *Antalis entalis* is clearly endogastric, an observation also made by Waller (1998). This endogastric form, however, is strongly modified by the extreme anterior growth which characterises the adult. Indeed, most adult shells are exogastrically coiled (Fig. 3G). Notwithstanding the dominant growth towards the anterior, the sense of expansion is anti-clockwise when the protoconch is viewed in lateral perspective (Fig. 3C), as confirmed by the location of the foot and the mouth in the developing individual (Fig. 3A). Prior to encasement of the foot and formation of the ventral suture, the tiny protoconch scaphopod shell is helcionelloid in form (compare Fig. 3C, E). Furthermore, by reversing the comparison, the disposition of the mouth and foot in *Antalis entalis* supports the restoration of helcionelloids as endogastric (Fig. 3F), as proposed by Peel (1991a, b) and Geyer (1994).

Pinnocaris and scaphopods

As oriented in the model of scaphopod origins proposed by Runnegar and Pojeta (1974) and Pojeta and Runnegar (1976, 1979), it is evident from the present comparison of ontogenies that the larval shells of *Pinnocaris* and *Antalis entalis* have opposite coiling directions (Fig. 4). *Pinnocaris* is clearly exogastric while the sense of coiling in *A. entalis* is endogastric, although the tubular adult subsequently becomes exogastric. Thus, the arguments of Morris (1979, 1990) and Engeser and Riedel (1996) concerning the unsuitability of *Pinnocaris* as an ancestor to scaphopods are supported, but from the more fundamental perspective of shell coiling in the earliest growth stage rather than their analyses of post-larval shell growth vectors.

Morris (1979, 1990) and Engeser and Riedel (1996) sought the origin of scaphopods within the conocardioid rostroconchs (Middle Ordovician to Permian) rather than amongst the Ribeirioidea (Pojeta and Runnegar 1976). Morris (1990) pointed out similarity in shell form between elon-

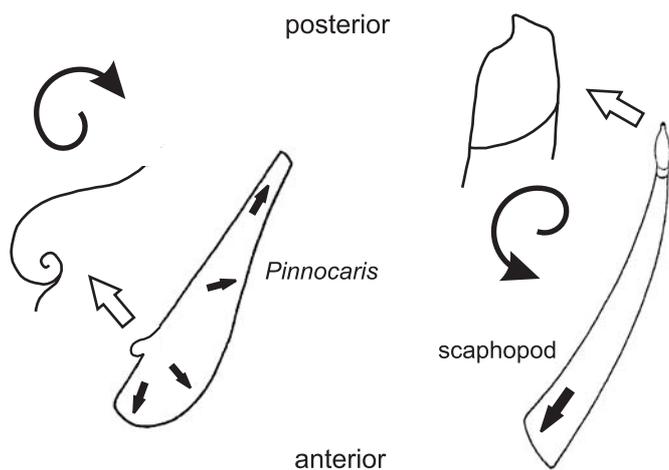


Fig. 4. Comparison of the location and coiling direction of protoconchs in *Pinnocaris* (clockwise expansion of the shell) and scaphopods (anti-clockwise expansion). Straight black arrows indicate growth vectors. Note that the overall coiling pattern of the adult scaphopod is exogastric.

gate Carboniferous conocardioids and scaphopods, but noted that this must reflect convergence since the appearance of scaphopods predates these unusually elongate conocardioids. Engeser and Riedel (1996) argued for a close relationship of scaphopods with the conocardiid genera *Conocardium* Bronn, 1835 (Devonian–Carboniferous) or *Arceodomus* Pojeta and Runnegar, 1976 (Carboniferous–Permian). They concluded that scaphopods probably arose during the Devonian since suitable ancestral conocardiids are not described from earlier strata, although Yochelson (2002) and Yochelson and Holland (in press) rejected the Devonian record of scaphopods. Thus, Engeser and Riedel (1996) discounted the Ordovician *Rhytidentalium kentuckyensis* as a scaphopod on the grounds that they were unable to identify a suitable ancestor within the confines of their hypothesis. *Rhytidentalium* was described by Pojeta and Runnegar (1979) from silica replicas from the Lexington Limestone of Kentucky, U.S.A. While the nature of the elongate, slightly curved and slowly expanding tube is obscure, Pojeta and Runnegar (1979) have demonstrated that *Rhytidentalium* has both the form and size of many scaphopods.

Engeser and Riedel (1996) assumed that the rostroconchian protoconch was cup-shaped, although this is clearly not the case in *Pinnocaris*. Neither is it the case in the conocardioid *Hippocardia?* of Pojeta and Runnegar (1976: pl. 47: 13–15; see also Runnegar 1978: pl. 1: 2, 3 and Pojeta 1987: fig. 14.70K). The endogastrically coiled protoconch in this Carboniferous specimen overhangs the tubular rostrum which Engeser and Riedel (1996) consider to be homologous to the fumarium in scaphopods. Similar protoconchs are discernible in other Carboniferous conocardioids and have been illustrated most recently by Rogalla and Amler (2003: pl. 4: 7, 8, 13, 14), contrasting with the exogastrically coiled protoconch of *Pinnocaris*. When considered in connection with the developmental studies of *Antalis entalis* presented by

Wanninger and Haszprunar (2001), it is this underlying coiling pattern of the conocardioid protoconch which provides the strongest support for their thesis that the “Scaphopoda evolved by ontogenetic predisplacement of a conocardiid adult shell into the larval ontogeny” (Engeser and Riedel 1996: 125).

Helcionelloids and scaphopods

Many helcionelloids develop a prominent fold in the sub-apical apertural margin (Peel 1991a, b; Parkhaev in Gravestock et al. 2001). Described species of *Eotebenna* Runnegar and Jell, 1976 show an evolution in shell form (Fig. 5) from the Early Cambrian *Eotebenna arctica* Peel, 1989, with a tightly coiled logarithmic spiral (Fig. 1E), to the Middle Cambrian *Eotebenna viviannae* Peel, 1991 which has an elongate, strongly allometric, sigmoidal growth form (Figs. 1C, 3E). Shell form in *Eotebenna arctica* can be compared with that in the scaphopod protoconch prior to encasement of the foot (Fig. 3C), although the former is much more tightly coiled and laterally compressed when compared with the essentially tubular

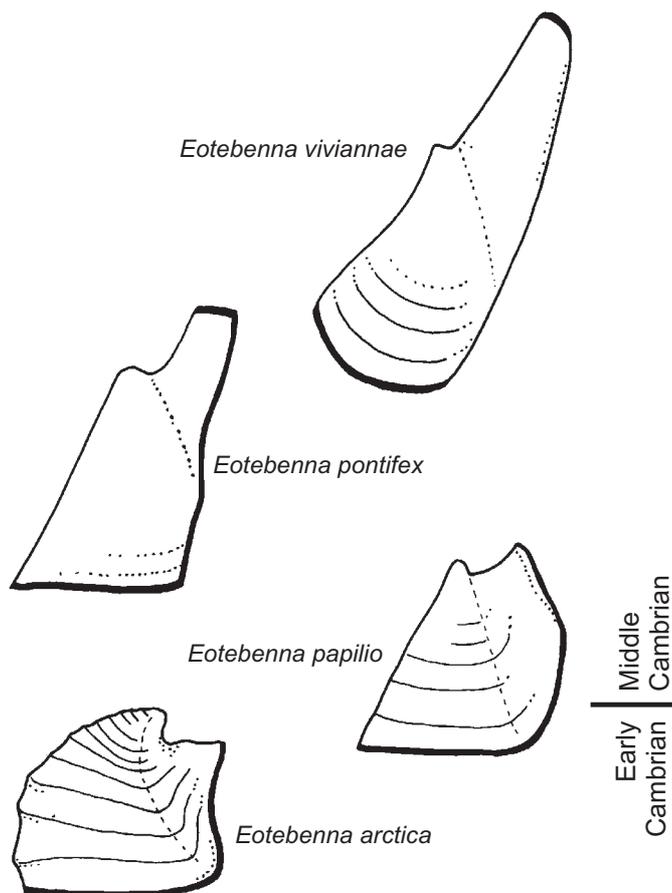


Fig. 5. Evolution of shell form in the helcionelloid *Eotebenna*, showing convergence on the scaphopod morphology in response to penetration of the substratum. Thickened lines indicate open shell margins (after Peel 1991a, b). Not to scale.

scaphopod. *Eotebenna viviannae* has adopted a shell form similar in function to the post-metamorphic juvenile *Antalis entalis*, with the large supra-apical opening and narrow sub-apical opening reflecting its infaunal mode of life (Peel 1991a: fig. 32; Figs. 3A, 5). Unlike *A. entalis*, however, the ventral margin of *E. viviannae* apparently remains sutured throughout life, although opposing lateral shell margins are closely juxtaposed at least in late growth stages. Shell growth in *E. viviannae* takes place at both terminations and along the ventral margin until the lateral margins meet, after which growth at the terminations prevails. Growth in post-larval scaphopods is confined to the anterior with resorption at the posterior termination, but concentration of growth anteriorly in *E. viviannae* would quickly produce a scaphopod-like shell form. Note the tendency for the dorsal margin of *E. viviannae* to be addorsally concave in lateral perspective (Fig. 3C), in similar fashion to scaphopods (Fig. 3G).

In *Yochelcionella* Runnegar and Pojeta 1974, the protoconch overhangs the tubular snorkel (Figs. 1D, 3F), interpreted as anterior by Pojeta and Runnegar (1976) but posterior by Peel (1991a, b). Comparison with *Antalis entalis* supports Peel's (1991a, b) restoration, with the yochelcionellid snorkel being equivalent to the fumarium and the principal growth component being tubular extension towards the sediment interface (Fig. 3F, G). In tall, slender species of *Yochelcionella*, such as *Yochelcionella ostentata* Runnegar and Jell, 1976 and *Yochelcionella gracile* Atkins and Peel, 2004 (Fig. 3F), the resemblance to the scaphopod protoconch is striking, although yochelcionellids show considerable variety in the degree of coiling and lateral compression of the shell. The under surface of the snorkel often carries a suture closely similar to that seen along the under surface of the scaphopod fumarium. Unlike scaphopods, the snorkel in *Yochelcionella* is not known to be resorbed during life and the shell often has prominent comarginal ornamentation.

Despite these similarities, at this time it is not possible to propose confidently that scaphopods are the direct descendants of helcionelloids, although Waller (1998) regarded helcionelloids as the stem group of the sister groups Scaphopoda and Cephalopoda. Moreover, recent analysis of 18S rDNA sequences by Steiner and Dreyer (2003) support this scaphopod-cephalopod clade and Waller's (1998) proposal. Helcionelloids are now known from the Early Ordovician (Gubanov and Peel 2000, 2001; Peel and Horný in press), but a considerable stratigraphic gap still separates them from the first widely accepted scaphopods in the Devonian or Carboniferous. This gap, however, is partially breached by the controversial Ordovician *Rhytidentalium*. In contrast to the scaphopods, cephalopods are known from Late Cambrian and younger strata and theories concerning their origin have been reviewed by Peel (1991a). The helcionelloids *Eotebenna* and *Yochelcionella* occur in Early–Middle Cambrian strata but similar snorkel-bearing forms, representing early adaptive forays into the scaphopod environment, are not known from younger strata.

Rostroconch evolution

Pojeta (1987: fig. 14.70) figured a number of rostroconch protoconchs but most of these are tubercles on the internal mould which lack information about the direction of coiling. Some may even be scars reflecting detachment of the protoconch in the adult stage, as seems to be the case in a number of the specimens of *Pinnocaris* in the collections of the Natural History Museum. A well-preserved protoconch, however, is present in a specimen of *Ribeiria junior* Runnegar, 1996 from the Middle Cambrian of Australia; the 1–2 mm long internal mould shows a tall cyrtiform protoconch overhanging the pegma (Runnegar 1996: 85, fig. 6.2K). In many of the ribeirioids figured by Pojeta and Runnegar (1976) and Pojeta (1987), there is a clear sense of coiling implied in the form of the internal mould which suggests that the apex overhangs the pegma as in *Ribeiria junior*, and this is the interpretation placed on the class as a whole by Pojeta and Runnegar (1976) and Pojeta (1987). This interpretation is confirmed here by the description of the protoconch of *Pinnocaris* (Figs. 1A, B, 2). The direction of coiling of these ribeirioid protoconchs is thus apparently opposite to that in *Hippocardia?*, suggesting inconsistency in coiling direction in the Pojeta-Runnegar model of rostroconch evolution (Peel and Horný in press).

Peel (1991a, b) considered rostroconchs to be endogastric, and therefore coiled in a similar direction to helcionelloids as he and Geyer (1994) interpreted them. The interpretation is supported by the endogastrically coiled protoconch of *Hippocardia?* (and other forms illustrated by Rogalla and Amler 2003: pl. 4: 7, 8, 13, 14) in which the rostrum would be equivalent to the posterior snorkel of *Yochelcionella* (Figs. 1D, 3F). It is opposed, however, by the current description of the protoconch in *Pinnocaris* (Figs. 1A, B, 2). Peel's (1991a, b) interpretation of the coiling direction in *Pinnocaris* and other ribeirioids is evidently incorrect but recantation does not provide a simple solution. When considered collectively, the described protoconchs of the ribeirioids *Ribeiria junior* and *Pinnocaris lapworthi*, and the conocardioid *Hippocardia?* seem to rule out a common derivation of ribeirioids and conocardioids from a helcionelliform ancestor, be it exogastric (Pojeta and Runnegar 1976, 1979) or endogastric (Peel 1991a, b). The problem was briefly noted by Hinz-Schallreuter (2000: 239) who referred to unpublished work by M. Amler in commenting that the ribeirioids were probably unrelated to later taxa, such as conocardiids. Waller (1998) considered that the relevant endogastric conocardioids show a "secondary opisthogyrate coiling" which gives the shell an endogastric appearance (Waller 1998: 10). Waller (1998) went on to derive the scaphopods from a helcionelloid, rejecting derivation from *Pinnocaris* and finding derivation from conocardioids to be unsupported.

Comparison of the protoconch in the ribeirioid *Pinnocaris* with those described in conocardioids underlines a weakness in the model of rostroconch evolution advanced

by Pojeta and Runnegar (1976). A satisfactory explanation is lacking as to why the protoconch in *Hippocardia*? is endogastric when the model requires a general exogastric form. The difficulty is increased by the clear similarity in shell coiling between helcionelloids (as interpreted by Peel 1991a, b, and Geyer 1994), the protoconch in concardioids such as *Hippocardia*?, as illustrated by Pojeta and Runnegar (1976) and Rogalla and Amler (2003), and the protoconch of scaphopods (Wanninger and Haszprunar 2001). The likely phylogenetic consequences of this similarity are apparent and have been partly realised by Engeser and Riedel (1996) in their relocation of the former class Scaphopoda as an order within the Rostroconchia; it is natural to extend this sequence to include the endogastric helcionelloids. Notwithstanding this helcionelloid-concardioid-scaphopod endogastric linkage, the morphological similarity between helcionelloids and the supposedly exogastric ribeiriods such as *Pinnocaris* is striking, demonstrating that the relation between stem and crown groups in the univalved Mollusca remains unresolved.

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