

Muscle scars in euomphaline gastropods from the Ordovician of Baltica

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Abstract. A discrete pair of muscle scars is described for the first time on the umbilical wall of the open-coiled, hyperstrophic ophiletoidean gastropod *Asgardispira*, a close relative of the widely distributed *Lytospira*, from the middle Ordovician of the eastern Baltica. In a unique specimen of the euomphaloidean *Lesueurilla* of similar age and derivation, the muscles have coalesced into a single scar. A pair of pedal retractor muscles is characteristic of several major groups of gastropods both in the Lower Palaeozoic and at the present day, and was likely an ancestral character of the class. The consolidation of muscle attachment to a single site may reflect the tightening of the logarithmic spiral of the shell and is probably related to the increasing development of anisostrophic coiling and shell re-orientation during gastropod evolution.

Key words: gastropods, muscle scars, Ordovician, Baltica.

INTRODUCTION

Snails are attached to their shells by muscles which often leave distinct attachment scars on the shell interior. Muscle scars may be readily visible in limpets and other cap-shaped shells but they are usually difficult to see in coiled shells where the muscle attachment site lies on the adaxial surface at some distance within the aperture, as a columellar scar. Scars may be prominent in thick-shelled forms, but they are often inconspicuous, especially on thinner shells. If preserved, muscle attachment scars in fossil material are usually only discerned on internal moulds but in most cases incomplete exfoliation of specimens, adherent matrix or just their adaxial location in coiled forms prevent their recognition.

Amongst lower Palaeozoic univalve molluscs, muscle scars are well known in cephalopods (Mutvei 1957, 2002; Kröger & Mutvei 2005) and in the rapidly expanding, cap-shaped or slightly coiled shells of monoplacophoran molluscs, such as the tergomyans *Tryblidium* Lindström, 1880 and *Pilina* Koken & Perner, 1925 (Lindström 1884; Peel 1977a) or the cyrtoneillids *Cyrtolites* Conrad, 1838, *Cyrtoneilla* Hall, 1879 and *Yochelsonellis* Horný, 1966 (Horný 1961, 1962, 1963, 1997a, 2002, 2005, 2009; Rollins 1969). Cambrian–Ordovician helcionelloid monoplacophorans can often be compared loosely with tergomyan monoplacophorans in terms of shell shape, but not in their interpreted anatomy (Peel 1991a, 1991b; Parkhaev 2007, 2008, 2017), but soft tissue attachment is often epithelial (Ushatinskaya & Parkhaev 2005).

However, the concentration of attachment sites into distinct muscle sites has been described by Parkhaev (2002, 2014) and in the strongly coiled, anisostrophic, pelagiellids (Runnegar 1981). Attachment scars are also described in morphologically similar Palaeozoic gastropod limpets such as *Archinacella* Ulrich & Scofield, 1897, *Floripatella* Yochelson, 1988, *Guelphinacella* Peel, 1990 and *Barrandicella* Peel & Horný, 1999. Muscle scars are well known in Palaeozoic members of the bilaterally symmetrical (isostrophic) *Bellerophon* group where the gastropod shell is coiled through several whorls and both umbilical shoulders may be well exposed in internal moulds (Knight 1947; Peel 1972, 1976, 1993; Horný 1995a, 1997b, 1997c, 1997d, 1999). Several attachment sites are present in *Sinuities* Koken, 1896 and *Sylvestrosphaera* Peel, 1980 (Horný 1986) but in *Bellerophon* Montfort, 1808 itself, muscle attachment is consolidated to a single pair of scars located one on each shoulder, deep within the shell (Knight 1947; Peel 1972, 1982). A prominent spiral ridge formed by the migrating dorsal margin of each scar is the most frequently observed indication of the muscle attachment sites.

In helically coiled, anisostrophic gastropods, paired muscle attachment scars are reported in adult shells in several Palaeozoic platyceratoideans and rarely in pleurotomarioideans, but at the present day they are also present in some extant vetigastropods, neritomorphans, patellogastropods and a few caengastropods (Fretter & Graham 1994; Ponder & Lindberg 1997). Traditionally,

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the differential development of such muscles in early ontogeny has been considered to be the driving mechanism in torsion, the defining gastropod character (Knight 1952; Crofts 1955; Ghiselin 1966; Lever 1979; Salvini-Plawen 1980; Pennington & Chia 1985; Haszprunar 1988; Page 2006). However, developmental studies of several recent gastropod taxa have clearly indicated that the muscles enabling torsion in the larva are not retained in the adult (Page 1997, 1998, 2002, 2003; Wanninger et al. 1999, 2000). Thus, as somewhat forcibly stated by Wanninger et al. (2000, p. 185), it is evident that fossil material only provides reliable information concerning attachment sites of adult shell muscles and not torsion. However, Page & Ferguson (2013) noted that even the youngest larvae of an extant neritimorph had bilateral larval retractor muscles and pedal retractor muscles and that the latter carried through into the juvenile and adult stages. It is an interesting speculation, therefore, that the rather widespread occurrence of a pair of muscle attachment scars in adult ancestral gastropods half a billion years ago may have had greater developmental significance than the largely biomechanical function of adult muscles at the present day.

This paper describes muscle scars on internal moulds of two Ordovician euomphaline gastropods with loosely coiled, anisostrophic shells from the palaeocontinent of Baltica, contributing new morphological information from one of the major lower Palaeozoic gastropod groups. The specimens were probably derived from the late Middle Ordovician (Darriwilian Stage) of the east Baltic area, although their exact collection localities are not known. They are some of the oldest described anisostrophic undisputed gastropods with preserved muscle scars, although Runnegar (1981) described a single scar in the macluritoidean *Matherella* Walcott, 1912 from the latest Cambrian Theresa Formation of New York. Runnegar (1981) and Parkhaev (2006) have also described muscle scars in the problematic anisostrophic Cambrian fossils *Pelagiella* Matthew, 1895 and *Aldanella* Vostokova, 1962 which they interpreted as gastropods, but this interpretation is controversial, as are some of the alternative suggestions (Dzik & Mazurek 2013). The earliest uncontested gastropods are from the upper Cambrian (Ponder & Lindberg 2008; Frýda 2012).

In the ophiletid *Asgardaspira* Wagner, 2002, the whorls rise in an open coil from or close to the apex to form a dextral hyperstrophic shell (Fig. 1F). The whorls remain barely in contact in the widely phaneromphalous dextral shell of *Lesueurilla* Koken, 1896 in which coiling is essentially planispiral (Fig. 2A, B). In *Asgardaspira* a pair of discrete muscle scars occurs on the baso-umbilical wall, deep within the shell, but in *Lesueurilla*

these scars have coalesced to form a single figure-of-eight muscle attachment area. This fusion into a single scar probably foreshadows the presence of only a single columellar scar in most extant gastropods (Fretter & Graham 1994) as a response to increasing anisostrophism and realignment of the axis of coiling (Linsley 1977; McNair et al. 1981; Peel 1987, fig. 14.31).

SYSTEMATIC PALAEOLOGY

Note on terminology. Wagner (2002, p. 9) clarified the varied usage and ambiguity of sinus, slit and selenizone in connection with the interpreted exhalant zone in Palaeozoic gastropods. He applied the term ‘peripheral band’ to the trace at the acute angulation on the upper whorl surface in *Asgardaspira* (Fig. 1F) and *Lesueurilla* (Fig. 2A). This usage, although clearly defined by Wagner (2002, fig. 2E) and applicable to most anisostrophic gastropods, is not followed here since the structure does not lie near the whorl periphery; it is not a trace of the whorl distal from the axis of coiling. In the present context, the acute angulation is referred to as the dorsal angulation in accordance with its location in a gastropod shell in standard orientation (Figs 1F, 2A).

Class GASTROPODA Cuvier, 1797
Superfamily OPHILETOIDEA Koken, 1897
Family OPHILETIDAE Koken, 1897

Remarks. Morris & Cleevely (1981) and Rohr & Measures (2001) placed *Lytospira* Koken, 1896 within the euomphaloidean Family Ophiletidae Knight, 1956, although Knight et al. (1960) had considered ophiletids to be pleurotomarioids. Knight et al. (1960) placed *Lytospira* within the Family Euomphalidae of the Superfamily Euomphaloidea, the authorship of both of which was attributed to de Koninck (1881) by Knight et al. (1960) and P. J. Wagner (2017, <http://www.fossilworks.org>), but to White (1877) by Bouchet et al. (2017). Wagner (2002) placed *Lytospira* and the closely similar new genus, *Asgardaspira*, within the euomphaline Superfamily Ophiletoidea Knight, 1956 but made no family assignment.

Bouchet et al. (2017, p. 333) listed a Superfamily Ophiletoidea Koken with date 1907, equivalent in rank to Euomphaloidea, and placed these together within ‘Palaeozoic basal taxa that are certainly Gastropoda’. This superfamily was based on the statement of authorship given by Perner (1907, p. 153) of a Subfamily Ophiletidae, within the Family Euomphalidae, to Koken. Perner (1907) made reference to a Family Ophiletidae proposed by Koken (1897, p. 163) but he did not consider this to have been formally introduced. However,

Koken's (1897) proposal and discrimination of the family from true euomphalids in the text (noted by Perner 1907, p. 153) appear to suffice for authorship, and this date is adopted here. *Lytospira* was not included within Ophiletidae, either by Koken (1897) or Perner (1907), the latter placing *Lytospira* within the Subfamily Euomphalinae of Euomphalidae (Perner 1907, p. 164). Koken & Perner (1925) placed it within Euomphalidae.

Genus *Asgardaspira* Wagner, 2002

Type species. *Lytospira yochelsoni* Rohr, 1994 from the Antelope Valley Formation (Ordovician, Whiterockian) of Nevada.

Remarks. Many species of *Lytospira* have been described, notably by Koken & Perner (1925) on the basis of

internal moulds, and the group is in great need of revision. Wagner (2002) separated *Asgardaspira* from *Lytospira* due to the presence in the former of an acute dorsal angulation generating a spiral band (the peripheral band of Wagner 2002, fig. 6E), and suggested that many species assigned to *Lytospira* in the literature belonged in *Asgardaspira*. *Lytospira evolvens* Koken, 1897 is one such species, according to P. J. Wagner (2017, <http://www.fossilworks.org>), although both the specimens illustrated by Koken & Perner (1925) are internal moulds, as is the present specimen. Wagner's (2002) assignment is followed here. However, the significance of the character he used to discriminate the two genera is questioned and a revision of the relationship between the two genera is desirable.

Rohr (1994, fig. 6.1) noted a deep sinus in *Lytospira yochelsoni*, the type species of *Asgardaspira*, culminating

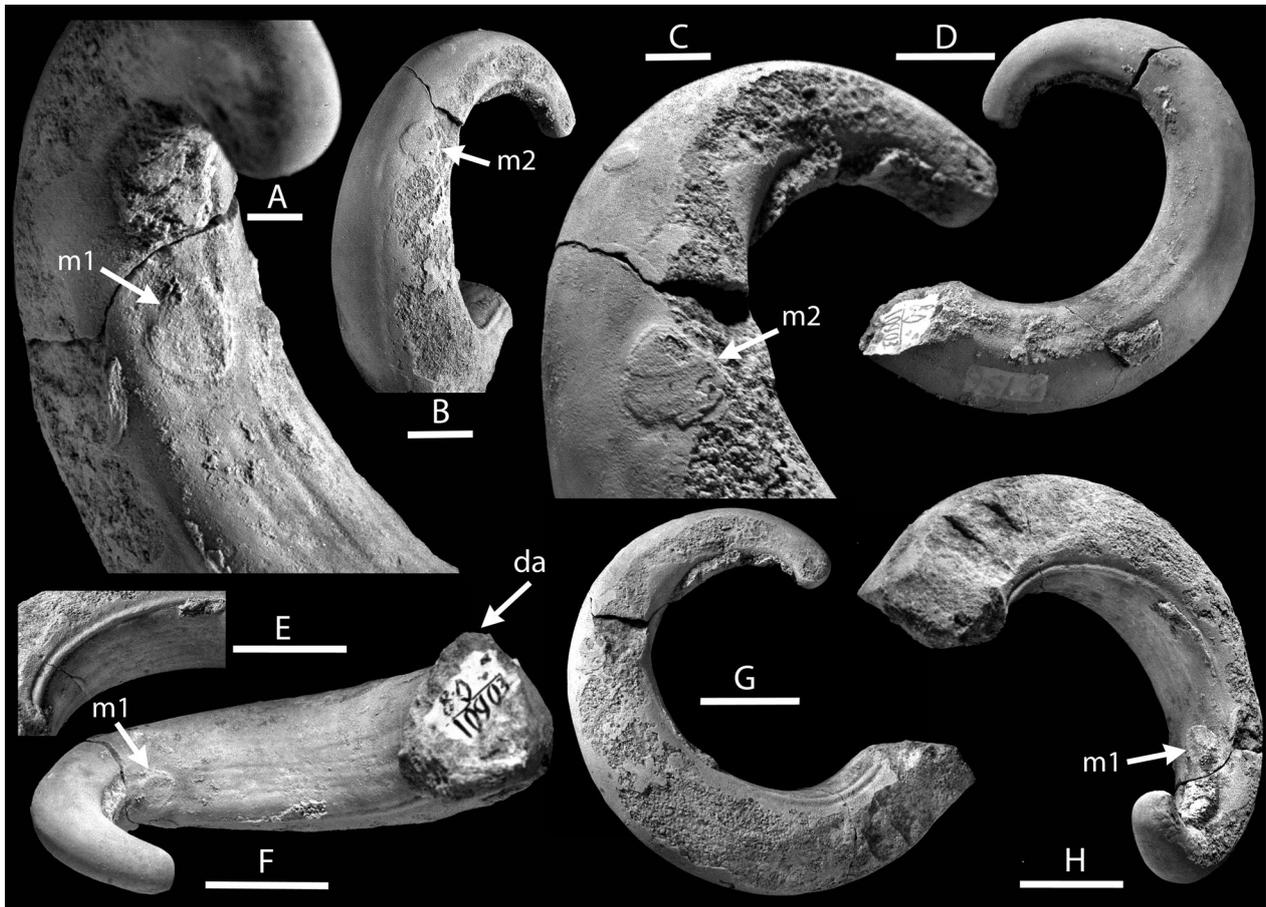


Fig. 1. *Asgardaspira evolvens* (Koken, 1897), CNIGRM 5756 (80/10903), internal mould; **A**, detail of umbilical wall showing muscle attachment scar (m1); **B**, oblique basal view showing spiral trace on outer whorl surface and muscle attachment scar m2; **C**, detail of muscle attachment scar m2; **D**, upper surface showing broad dorsal ridge; **E**, detail of circumbilical ridge and groove complex; **F**, standard orientation of dextral hyperstrophic shell, showing location of muscle attachment scar m1 and the dorsal angulation (da); **G**, basal surface; **H**, oblique umbilical view showing circumbilical ridge and groove complex and muscle attachment scar m1 (arrow). Scale bars: 2 mm (A, C); 4 mm (B); 10 mm (D–H).

at an acute crest which is visible as a spiral band in his illustration. There is no indication of a slit. The holotype of *Lytospira angelini* Lindström, 1884, the type species of *Lytospira*, also shows a deep sinus (but no slit) at the dorsal angulation and a spiral band is visible on the internal mould (Lindström 1884, pl. 13, fig. 36; Knight 1941, pl. 71, fig. 1). A pronounced peripheral flange is present at the junction between the basal surface and the outer whorl surface in the holotype of *Lytospira yochelsoni* (Rohr 1994, fig. 6.3) but this is not expressed on the uniformly curved shell interior. The flange (basal carina and stubby frill of Wagner 2002, p. 71) probably reflects shell thickening due to stacking of the flared apertural margin associated with a peripheral notch. A flange of this type is not known in *Lytospira angelini* where the junction between the base and the outer wall is uniformly convex on both the internal mould and the shell exterior (Lindström 1884, pl. 13, fig. 37).

Thus, internal moulds cannot be referred to *Lytospira* or *Asgardaspira* with certainty. However, a spiral trace on the internal mould, located at the junction between the weathered base and the outer whorl surface (Fig. 1B), promotes assignment of the present material to *Asgardaspira* at this time.

Asgardaspira evolvens (Koken, 1897)

Figure 1

Figured material. Specimen CNIGRM 5756 (80/10903) in the collection of the F. N. Chernyshev Central Geological Survey Research Museum, St Petersburg, Russia. The specimen is labelled '*Lytospira evolvens* Kok., Pl. XIII, fig. 1, Ordovician (C₁,a) Kandel', but this is a reference to the illustration in Koken & Perner (1925) rather than the origin of the specimen itself. The specimen is clearly not one of the two illustrated by Koken & Perner (1925, pl. 12, fig. 3; pl. 13, fig. 1), both of which are stated to have been deposited in the Museum of Reval (= Tallinn). According to Koken & Perner (1925), the first of these is from B₃ (Kunda Stage) at Karrol (now called Karula) and the second is from C₁, α (Aseri Stage) at Kandel (now called Kandle). Koken (1897) gave the stratigraphic derivation of these Estonian specimens as Obere Linsenschicht (= Kandle Formation, Aseri Stage of local usage; Middle Ordovician, Darriwilian Stage).

Remarks. Rohr (1994) delimited *Lytospira yochelsoni* (now *Asgardaspira yochelsoni*) from all other species of *Lytospira* in possessing a circumbilical spiral ridge on the shell exterior at the junction between the umbilical and basal walls. Rohr (1994) noted that Koken & Perner (1925) considered a spiral groove on the interior of the whorl (equivalent to a ridge on the internal mould) to be a diagnostic feature of *Lytospira*, but commented that

this feature was absent in the two specimens of *Lytospira yochelsoni* available to Rohr (1994). Neither is it known from the type species of *Lytospira*, *Lytospira angelini* Lindström, 1884. Such an internal spiral groove complex is present in material here assigned to *Asgardaspira evolvens* (Fig. 1) but it is not equated with the external spiral ridge described by Rohr (1994).

The specimen described here is an internal mould coiled through about three quarters of a whorl, with a maximum preserved length of 43.5 mm; fragments of shell are retained on the concave adaxial surface near the apex (Fig. 1C). When viewed in standard orientation, with the aperture facing the viewer, the aperture lies to the right and above the apex (Fig. 1F). The whorls are not in contact but the separation is uniform and does not show appreciable uncoiling. Thus, the shell can be described as open coiled and dextral hyperstrophic (Fig. 1F). The specimen has been broken about a quarter of a whorl from the apical termination and subsequently glued together. The dorsal and lateral surfaces are smooth (Fig. 1D) but the basal surface is irregular, probably as a result of differential weathering (Fig. 1C), and has been eroded in the latest quarter of a whorl (Fig. 1H).

The adapical termination of the mould is smoothly rounded, indicating closure of the earliest whorls by a transverse septum, probably one of several such septa of the type illustrated by Lindström (1884, pl. 13, fig. 36) and Knight (1941, pl. 71, fig. 1) in the holotype of *Lytospira angelini*, from the Middle Ordovician of Utby, Lindgården in Dalarna, central Sweden. Thus, the earliest portion of the original shell, probably a whorl or more in extent and lying adapical to this septum, is not preserved. The aperture of the internal mould is also broken away and there are no traces on the internal mould of the prominent comarginal growth ornamentation illustrated by Lindström (1884) and Koken & Perner (1925). The aperture at the latest preserved stage is tear-shaped, sub-triangular in cross section, with its long axis parallel to the axis of coiling and its greatest width close to the flattened base (Fig. 1F). The shallowly convex umbilical surface and the more strongly convex outer whorl surface converge to form the arched dorsum (Fig. 1F) which carries a raised, shallowly convex, spiral band on the internal mould bounded by weak depressions (Fig. 1D), representing a shallow excavation on the shell interior. This band corresponds to the culmination of the dorsal sinus seen in *Lytospira angelini* (Lindström 1884, pl. 13, fig. 36). In the earliest third of the specimen, as preserved, the profile is more elliptical with the adaxial lateral surface ('umbilical wall') flattened and passing angularly onto the uniformly convex outer whorl surface which lacks the spiral band on the dorsum.

A prominent spiral ridge and groove complex is gradually developed on the internal mould during the last half whorl at the junction between the base and the umbilical wall (Fig. 1H). This consists of a strong, convex, central ridge, representing a broad groove on the shell interior (Fig. 1E–H). It is bounded by grooves, representing smoothly rounded, spiral ridges on the shell interior. During the same growth interval, about seven somewhat discontinuous shallow, rounded grooves and ridges are developed on the umbilical wall (Fig. 1A, F).

Muscle scars. Two distinct muscle scars are preserved as slightly raised areas on the internal mould about half a whorl back from the latest preserved growth stage, just adapertural of the transverse repaired break. The first of these (labelled m1 in Fig. 1) is located on the umbilical wall just prior to the zone of spiral grooves and ridges (Fig. 1A, F). It has a length of about 4.8 mm and width of about 3 mm, and is marked with concentric striations. The second muscle scar (m2 in Fig. 1) is located on the transition from the base to the outer whorl surface (Fig. 1B) and is subtriangular in shape, widening towards the aperture; length about 3.7 mm, width 3.4 mm. Trans-

verse striations on the scar parallel the adapertural margin (Fig. 1C). In axial view, muscle scar m2 lies on a radius that is closer to the aperture than scar m1, but m1 has a shorter distance to the aperture in terms of spiral distance around the surface of the mould.

In addition to the muscle scars on the shell interior, some specimens of the *Lytospira/Asgardaspira* morphological group carry prominent scars on the shell exterior. These scars, however, result from cementation of shells and other extraneous materials to the outer surface of the shell as a form of camouflage (Linsley & Yochelson 1973; Boucot 1990; Rohr 1993), without affecting the inner surface. No traces of such attachments have been discerned in the present material.

Superfamily EUOMPHALOIDEA White, 1877
Family LESUEURILLIDAE Wagner, 2002

Remarks. Knight et al. (1960) placed *Lesueurilla* Koken, 1896 within the Family Euomphalidae, together with *Lytospira*. Wagner (2002) erected Lesueurillidae within Euomphaloidea, a classification followed by Bouchet et al. (2017).

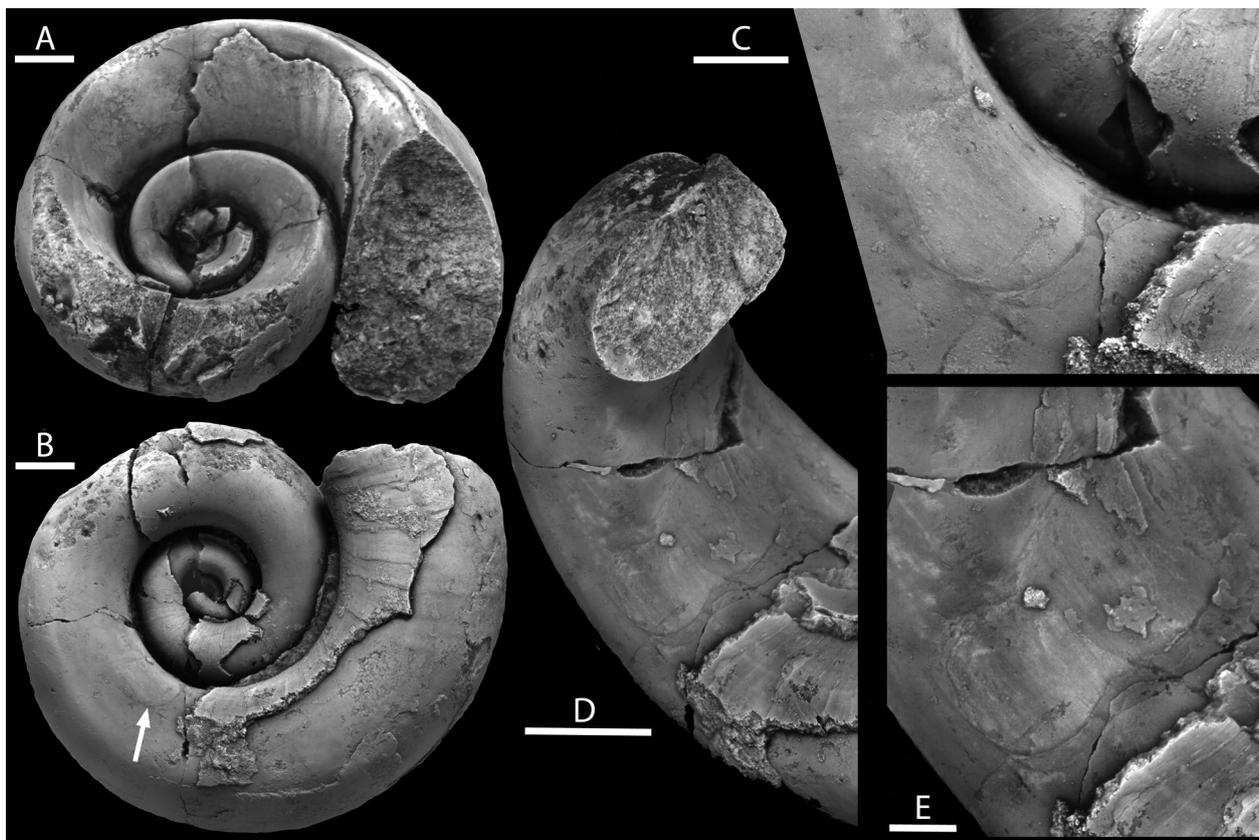


Fig. 2. *Lesueurilla* cf. *helix* (Eichwald, 1856), SMNH Mo 70510, internal mould with adherent shell patches; **A**, oblique apical view; **B**, **C**, basal view showing muscle attachment scar (arrow), enlarged in **C**; **D**, **E**, early whorls removed to show figure-of-eight muscle attachment scar. Scale bars: 5 mm (**A**, **B**, **D**); 2 mm (**C**, **E**).

Genus *Lesueurilla*, Koken 1896

Type species. Maclurea infundibulum Koken, 1896 from the Middle Ordovician of Öland, Sweden.

Lesueurilla cf. helix (Eichwald, 1856)
Figure 2

Figured material. Specimen SMNH Mo 70510, labelled from the 'Ordovician of Estland', in the palaeozoological collections of the Swedish Natural History Museum (Naturhistoriska Riksmuseet), Stockholm, Sweden.

Remarks. This Estonian specimen is an internal mould with adherent patches of shell preserving at least two and a half whorls (Fig. 2A, B); the apex is missing. The specimen has been broken historically and glued back together again, although the earliest preserved whorl is misaligned; the aperture is not preserved (Fig. 2A). To enable closer study, the glued inner portion was removed along a prominent fracture about three quarters of a whorl back from the latest growth stage (Fig. 2D) after initial examination and photography.

The shell is essentially planispiral but the tear-shaped whorl profile (Fig. 2A), with the long axis parallel to the axis of coiling, results in the apical surface being more deeply excavated than the base. Sutures are deep, with consecutive whorls barely in contact. The acute dorsum is the locus of a broad sinus that is marked by a raised ridge on the internal mould (Fig. 2A). Ornamentation consists of fine transverse growth lines with regularly spaced stronger transverse elements in the latest preserved growth stage (Fig. 2B).

Amongst the several species assigned to *Lesueurilla* by Koken & Perner (1925), the present specimen most closely resembles *Lesueurilla helix* (Eichwald, 1856) in terms of the shape of the whorl.

Muscle scars. A subcircular muscle scar was observed at the junction between the basal and umbilical surfaces almost half a whorl back from the preserved aperture (Fig. 2B, C). Removal of the inner whorls demonstrated that this scar was part of a larger scar with a figure-of-eight shape (Fig. 2D, E), the long axis of which lies transverse to the whorl. The scar is slightly raised above the surface of the internal mould and is delimited by a sharp groove. It is ornamented with numerous longitudinal striations parallel to the spiral of the shell, but traces of concentric striations are present near the margin. If viewed as two intersecting circles (although there is no suggestion in the ornamentation that two separate scars are present), the larger circle lies almost centrally on the umbilical wall, whereas the smaller one crosses the umbilical shoulder onto the base.

COMPARISON OF MUSCLE SCAR PATTERNS

The main difference in shell morphology between the described specimens of *Asgardaspira* and *Lesueurilla* is not the basic shape of the whorl in cross section (it is elongated approximately parallel to the axis of coiling in both forms), or its rate of expansion, but in the rate of expansion of the logarithmic spiral of the shell. Thus, consecutive whorls remain just in contact in *Lesueurilla* (Fig. 2B) but are widely separated in the open coiled *Asgardaspira* on account of its more rapidly expanding spiral (Fig. 1D), the effect being enhanced by the pronounced hyperstrophic coiling of the latter (Fig. 1F). More complete illustrations of this open coiling were given by Koken & Perner (1925, pl. 13, fig. 3), Knight et al. (1960, fig. 107), Yochelson (1971, pl. 1, fig. 5) and Rohr (1993, fig. 1.4). The aperture is broken away in both of the described specimens but in each case the muscle attachment sites lie almost half a whorl back from the latest preserved growth stage. The muscle scars in *Asgardaspira* lie one on each side of the circum-bilical angulation separating the basal and umbilical walls. The two halves of the single figure-of-eight scar in *Lesueurilla* are similarly placed.

Hypomphalocirrus Linsley, 1973 from the Devonian of North America was considered to be a paragastropod, not a gastropod, by Linsley & Kier (1984) but was placed within Euomphaloidea by Bouchet et al. (2017). The open coiled shell is similar in coiling pattern to *Asgardaspira* but it was considered to be sinistral by Linsley & Kier (1984) and Schopf & Morris (1994). A single large muscle scar described by Schopf & Morris (1994) in *Hypomphalocirrus* is located about three quarters of a whorl back from the aperture, somewhat deeper in the shell than the paired muscles of *Asgardaspira* and *Lesueurilla*. However, the single muscle scar is located on the outer whorl surface in contrast to the baso-umbilical position of the scars in *Asgardaspira* and *Lesueurilla*. While deeply placed muscle scars are known in many anisostrophic gastropods, the location of the muscle scar on the outer whorl surface is highly unusual. Dorsally placed muscle scars are seen in some platyceratids (Horný 1964; Peel 1977b; Mazaev 1996), and even in the isostrophic cyrtoneform molluscs (Horný 1965; Rollins 1969), but these have shell forms and modes of life quite unlike *Hypomphalocirrus*.

Horný (1995b) described a large muscle attachment scar in *Oriostoma* Munier-Chalmas, 1876 from the Silurian of Bohemia which was located on the baso-umbilical wall close to the aperture; the possible presence of a second scar on the umbilical wall was also discussed. *Oriostoma* has a tightly coiled shell with globose whorls unlike the open coiled *Asgardaspira* or the widely

phaneromphalous *Lesueurilla*. The shallow placing of the muscle scar in *Oriostoma* may reflect this more globose shell or the well-known occurrence of a heavily calcified operculum (Lindström 1884; Peel 2015). The varied systematic placing of oriostomatids in the literature was noted by Bouchet et al. (2017, p. 370, footnote 22).

The relationship and systematic affinities of macluritoideans and euomphaloideans have been widely discussed (Linsley & Kier 1984; Yochelson 1984; Wagner 2002; Frýda et al. 2008; Frýda 2012) but Bouchet et al. (2017, p. 333) recognized both as superfamilies of ‘Palaeozoic basal taxa that are certainly Gastropoda’. The widely phaneromphalous form of many macluritoideans is similar to that of *Lesueurilla* but paired muscle scars are only known from the operculum of some species of *Maclurites* Le Sueur, 1818 (Knight 1952; Rohr & Gubanov 1997; Rohr & Yochelson 1999). It is not known if these opercular muscles equate with a pair of separate muscle scars on the inner surface of the conch, as supposed by Knight (1952), or originated within a single attachment scar. While muscles in most extant anisostrophic gastropods undoubtedly perform a similar range of functions to those in their Palaeozoic predecessors, reorientation of the shell and modifications to shell form and mantle cavity function (Linsley 1977; McNair et al. 1981; Peel 1987, fig. 14.31) have usually resulted in the consolidation of these muscles to a single attachment site, the familiar columellar muscle.

Muscle scars are often preserved in Palaeozoic platyceratoidean gastropods. The scars are commonly paired, but unequal in size and irregular; they may be band-like, close to the periphery of the irregular cap-shaped late growth stage, or large sub-circular scars, commonly associated with a second small scar (Yochelson 1956; Horný 1964, 2004; Mazaev 1996; Frýda et al. 2008). Platyceratoidean shell form varies from turbiniform to cap-shaped and is therefore notably unlike the widely phaneromphalous *Lesueurilla* and open coiled *Asgardaspira*. Platyceratid shells are often highly irregular on account of their frequent symbiotic relationship with echinoderms, although not all platyceratoideans share this mode of life (Bowsher 1955; Rollins & Brezinski 1988; Horný 2000a, 2000b; Baumiller 2002, 2003; Frýda et al. 2009).

The well-developed anisostrophic coiling of most pleurotomarioidean and murchisonioidean gastropods generally hinders recognition of muscle scars since adaxial portions of the whorl are covered, but a single scar was described by Fortey & Peel (1990, fig. 12) in *Plethospira(?) floweri* Fortey & Peel, 1990 from the Early Ordovician Poulsen Cliff Formation of Washington Land, North Greenland. The scar is spirally elongate

in contrast to the equidimensional scars described in *Asgardaspira* (Fig. 1A, C). The unusual location of the scar at the upper suture of the whorl in the high spired shell, rather than at the baso-umbilical shoulder, may suggest that a pair of muscle attachment scars was present. Traces of scars on the baso-umbilical shoulder are often observed on internal moulds but rarely described (Peel 1977b, fig. 8).

Paired muscle attachment scars in Palaeozoic pleurotomarioideans are known from pseudo-isostrophic specimens described by Peel (1986, 2001, 2004) from the Carboniferous of the United Kingdom. The scars are located on the umbilical shoulders, half a whorl or more back from the aperture, as in contemporaneous bellerophontoideans (Knight 1947; Peel 1972, 1982). Their visibility on internal moulds reflects the almost bilateral symmetry of adults, with the open umbilici developed on each side equivalent to the basal and apical umbilici in *Lesueurilla*. As with the bellerophontoideans, the muscle scars usually show spiral elongation and a pronounced spiral trace associated with the abaxial margin of the scars, features not seen in the specimens of *Asgardaspira* and *Lesueurilla*.

A pair of muscle scars was described by Horný (2000b) in the craspedostomatid *Spirina* Kayser, 1889 from the Silurian of Bohemia. As with material described by Peel (1986, 2001, 2004), the symmetry of the scar on the umbilico-lateral shoulders likely reflects the pseudo-isostrophic coiling of the shell.

The morphology and systematic position of bellerophontiform molluscs (Peel 1991b) has been the subject of intense debate in the literature and need not be repeated here; they encompass a spectrum of isostrophic molluscs ranging from untorted monoplacophorous molluscs to torted gastropods. Recent summaries are given by Frýda et al. (2008), Frýda (2012) and Bouchet et al. (2017). A gastropod Superfamily Bellerophontoidea McCoy, 1852 (in Sedgwick & McCoy 1851–1855) was recognized by Bouchet et al. (2017). As first described by Knight (1947), muscle attachment sites in *Bellerophon* consist of a pair of muscle scars located one on each umbilico-lateral shoulder of the isostrophically coiled shells (Peel 1972, 1982). The scars are relatively well known on account of the ease of visibility of these locations on coiled internal moulds (Peel 1972, 1976, 1980, 1993; Wahlman 1992; Horný 1995a, 1997a, 1997b, 1997c, 1999). Symmetry in size and location of the muscle scars reflects the bilateral symmetry of the shells, with the axis of coiling parallel to the substrate in the living animal. Development of anisostrophic coiling would likely disrupt symmetry in both these characters, just as secondary acquisition of isostrophic coiling in adult shells would enhance it

(Peel 2001, 2004). Thus, muscle scars in *Asgardaspira* (Fig. 1) and *Lesueurilla* (Fig. 2) are located close to the baso-umbilical shoulder rather than symmetrical about the mid-dorsal plane as in bellerophontoideans.

THE RIDGE AND GROOVE COMPLEX IN *ASGARDASPIRA*

Several species assigned in the literature to *Lytospira* (but not the type species *Lytospira angelini*) or *Asgardaspira* display a prominent circumbilical ridge and groove complex at the junction between the umbilical (adaxial) wall and the base (Koken 1897; Ulrich & Scofield 1897; Koken & Perner 1925; Rohr 1993). This complex is seemingly unconnected with the circumbilical ridge developed only on the outside of the shell in *Asgardaspira yochelsoni* (Rohr 1994). On the internal mould the complex consists of a central rounded ridge bounded by grooves (Fig. 1E, G, H), corresponding to a median channel with bounding ridges on the interior of the shell wall (Rohr 1993, fig. 3.2). The complex is most prominent near the aperture and gradually decreases in expression over a distance of about one third of a whorl back from the latest preserved growth stage, terminating adaperturally of the muscle scars (Fig. 1H). The median rounded ridge on the internal mould terminates as a small notch within the thickness of the shell at the apertural margin but without the development of a sinus or band visible in the growth lines on the shell exterior.

Rohr (1993) discussed the possibility that the complex might represent a muscle track and its position on the baso-umbilical wall is not inconsistent with the position of the columellar muscle in many living gastropods. However, columellar muscles are usually located some distance back from the aperture to facilitate withdrawal of the soft parts into the protective shell, unlike the location of the complex in *Asgardaspira*. True muscle attachment scars are also deeply placed in *Asgardaspira*, adapical of the spiral ridge and groove complex. Columellar muscles in present-day gastropods may be associated with folds on the columella itself which have been considered to facilitate the mechanical action of the muscle (Signor & Kat 1984), but see Price (2003). It is possible that the ridge and groove complex could help constrain the action of a muscle bundle extending adaperturally beyond the aperture from the preserved muscle attachment scars but the function of such a muscle bundle is not known; convincing analogues have not been discovered amongst living gastropods. The complex might reflect the attachment site of an operculum, but muscle attachment just on the periphery

of an operculum is not conducive to effective function. Although certainly present, opercula are not known in *Asgardaspira*, *Lytospira* or *Lesueurilla* (or in most fossil gastropods) but several euomphalines have a prominent calcified operculum (Yochelson & Linsley 1972; Yochelson 1979; Peel 2015).

Ridges associated with migrating muscles have been described on internal moulds of a number of bellerophontoidean gastropods (Knight 1947; Peel 1972, 1976, 1982, 1991b, 1993; Horný 1995a, 1997a, 1997b, 1997c) and pleurotomarioideans (Peel 1986), but these ridges frequently have an acute abaxial margin reflecting insertion of the muscle fibres into the shell. Additionally, they are located at some distance back from the aperture with the muscle attachment area placed at their adaxial termination. The situation in *Asgardaspira* is dissimilar. The muscle attachment scars are located deep in the shell interior, beyond the adapical termination of the ridges (Fig. 1H). As such, the ridge and groove complex is clearly not directly connected with the attachment of the pedal retractor shell muscles. The muscle scars are disposed one to each side of the ridge and groove complex whereas a spiral ridge in bellerophontoideans lies dorsally of each of the two muscle scars (Peel 1972, 1982).

Ridge and groove complexes are present between the muscle scars, but dorsally, on the internal moulds of other Palaeozoic gastropods and bellerophontiform molluscs in association with the selenizone. Thus, some bellerophontoideans display a median dorsal ridge and groove complex on the internal mould corresponding to the selenizone (Koken & Perner 1925, pl. 24, fig. 7; Peel 1976, fig. 2; Peel 1991c, figs 26d, 30c). The selenizone indicates the position of the exhalant current from the mantle cavity and in *Asgardaspira* this current was located at the sinus-bearing dorsal angulation, far from the location of the ridge and groove complex.

R. S. Houbrick (in Rohr 1993) suggested that the ridge and groove complex might reflect mantle folds used to channel water into the mantle cavity. Many caenogastropods develop notches or even siphonal canals in this position of the whorl indicating the position of the inhalant stream. Houbrick's suggestion is in accordance with the general opinion concerning the flow of water streams through the mantle cavity (Knight 1952; Linsley 1977, 1978; McNair et al. 1981) and is followed here. However, the illustration of *Asgardaspira yochelsoni* presented by Rohr (1994, fig. 6.4) shows a notch in the angular periphery at the junction between the base and the outer whorl surface which probably also serves as the locus of an inhalant stream. This notch on the abaxial surface does not generate structures comparable to the ridge and groove complex preserved

on the adaxial surface, the latter showing an unusually prominent and persistent morphology. Separate inhalant streams are interpreted in pleurotomarioideans and bellerophontoideans (Knight 1952) and a pair of spiral traces, one on each dorso-lateral area, in some bellerophontoideans (e.g. Peel 1974, pl. 1, figs 2, 11) has been interpreted as a reflection of the location of the gills (Ebbestad 1999). The presence of two inhalant streams in *Asgardaspira* suggests two gills in the mantle cavity, but the issue of a single or pair of gills in euomphalines is contentious (Knight et al. 1960; Morris & Cleavelly 1981; Linsley & Kier 1984; Yochelson 1984).

MODE OF LIFE

Deep location of the muscle scars in strongly coiled gastropods reflects withdrawal of the cephalopedal mass into the shell as a response to environmental stress or predation, in conjunction with the development of an operculum. In contrast, the muscle scars in the various limpet groups are arranged around the periphery, close to the apertural margin, since their defensive strategy involves clamping against the substratum rather than withdrawal into the shell; an operculum is not retained in the adult. The hyperstrophic open coiling of *Asgardaspira* and widely phaneromphalous coiling of *Lesueurilla* indicate that they were probably sessile filter feeding molluscs (Yochelson 1971; Peel 1975; Morris & Cleavelly 1981; Linsley & Kier 1984). Thus, deep placement of the muscle scars probably reflects enlargement of the gills in the mantle cavity in association with this life style, although the slow rate of expansion of the whorl probably requires a relatively longer mantle cavity than in more rapidly expanding shell morphologies. Susceptibility to predation was probably enhanced by the sessile mode of life which in turn may be reflected in the development of a massive operculum in many similarly coiled forms (Yochelson & Linsley 1972; Yochelson 1979; Rohr & Yochelson 1999; Vermeij & Williams 2007; Peel 2015, 2018).

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Lihaste kinnitusjäljed euomphaliinsetel tigudel Baltika Ordoviitsiumis

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Esmakordselt on kirjeldatud lihaste kinnitusjälgede paari ophiletoitse gastropoodi *Asgardispira* avatud keermestiku nabavaheseinal. See tigude perekond on lähedane sugulane Ida-Baltikumi Kesk-Ordoviitsiumis ulatuslikult levinud perekonnale *Lytospira*. Ühel unikaalsel samavanuselisel euomphaloidisel *Lesueurilla* eksemplaril on lihaste kinnitusjäljed liitunud üheks jäljeks. Teo jala taandlihaste ehk retraktorite paarikaupa esinemine on iseloomulik mitmele suurele Vara-Paleosoikumi ja ka retsentsete gastropoodide rühmale, mistõttu peetakse seda nende klassi pärilikuks tunnuseks. Lihaste koondumine ühele kinnituskohale võib olla põhjustatud logaritmiliselt keerduvad teojoja tihene-misest, mida omakorda võis põhjustada ebahütluse kasv keerdumisel, ja selle suunamuutustest tigude evolutsioonis.