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Musculature of an Ordovician (Darriwilian) patelliform gastropod from Estonia

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ABSTRACT

A unique internal mould of the patelliform mollusc *Eesticonus aariensis* n. gen. n. sp. is described from the Middle Ordovician (Darriwilian Series, Kunda Stage) of northern Estonia. Well-preserved muscle attachment scars are compared to those of *Floripatella* from strata of Middle Ordovician (Dapingian Series) age in Utah, originally considered to be the oldest known patelloidean gastropod but possibly an untorted mollusc. Comparison with the muscle scar pattern in *Archinacellina* from the Ordovician of Bohemia suggests that *Eesticonus* is an archinacelloidean gastropod, but not a patellogastropod.

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Bilaterally symmetrical, limpet-like mollusc shells are known from the Cambrian to the present. Vermeij (2017) noted that the morphology has arisen more than 50 times in gastropod history, indicating that the acquisition of this shell form is not a unifying phylogenetic feature. It has long been suggested that the earliest gastropods had limpet-like shells, based on numerous claims of Palaeozoic patellids in historical and more recent literature (Knight 1952; Golikov & Starobogatov 1975; Haszprunar 1988; Yochelson & Webers 2006; Frýda 2012; Parkhaev 2017). However, the Palaeozoic fossil record of gastropods is overwhelmingly dominated by conispiral morphologies (Koken 1897; Ulrich & Scofield 1897; Koken & Perner 1925; Wenz 1938–44; Knight et al. 1960; Frýda 2012).

Lindberg (1986, 1988) introduced the name Patellogastropoda, corresponding to the Docoglossa of traditional usage, for a concept based on the familiar present-day limpet *Patella* Linnaeus, 1758 and its relatives. Patellogastropoda was later placed within the Subclass Eogastropoda of Ponder & Lindberg (1995) that was recognised as the sister group of essentially all other gastropods, the latter being referred to Orthogastropoda. However, based on studies of shell structure, Lindberg (2008, 2009), Ponder & Lindberg (1997) and Frýda (2012) noted that the oldest confirmed patellogastropod is Triassic in age (Hedegaard et al. 1997).

Lindberg (1988) sensibly proposed that the ancestor of patellogastropod limpets was probably a coiled gastropod (see also discussion by Frýda 2012; Frýda et al. 2008). This viewpoint was formalised by Ponder et al. (2020) in their presentation of two infraclasses within Eogastropoda. The Infra-class Euomphaliformii included characteristically coiled, mainly conispiral Palaeozoic superfamilies such as Euomphaloidea, Macluritoidea, Palaeotrochoidea, Platyceratoidea,

Orthonychoidea and the patelliform Archinacelloidea. Limpets placed within the Infraclass Patellogastropoda included the late Palaeozoic to Recent orders Patellida and Nacellida.

Discussion of the Eogastropoda–Orthogastropoda model has developed through phylogenomic analyses of living taxa, although the methodology obviously excludes members of extinct fossil groups such as the Euomphaliformii of Ponder et al. (2020). Zapata et al. (2014) reviewed models for the internal relationships of the five principal extant gastropod clades (Patellogastropoda, Vetigastropoda, Neritimorpha, Caenogastropoda, Heterobranchia) and rejected the Orthogastropoda hypothesis. Cunha & Giribet (2019) placed Patellogastropoda together with Vetigastropoda, an orthogastropod group (sensu Ponder & Lindberg 1995) with a prominent Palaeozoic record, in a clade Psilogastropoda (new). Neritimorpha, Caenogastropoda and Heterobranchia were referred to the clade Angiogastropoda (new). A close relationship between Patellogastropoda and Vetigastropoda was also one of the possibilities considered by Zapata et al. (2014).

The lack of proven patellid patellogastropods in the Palaeozoic should not imply that patellogastropods or patelliform shells were absent. Rather, the issue of patellogastropod origins is complicated by the occurrence of numerous conical (cap-shaped) or slightly coiled bilaterally symmetrical shells assigned to other molluscan groups, or left unassigned due to a lack of preserved diagnostic features. Yochelson & Webers (2006) summarised the development of scientific thought concerning many of these groups. Foremost amongst these are the untorted, monoplacophorous, molluscs placed within Class Tergomya (alternative names include Monoplacophora and Tryblidia) that are well represented in Late Cambrian–Devonian strata (Horný 1961, 1963, 1965a, 1965b, 2002; Peel

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1990, 1991a, 1991b; Peel & Horný 1999; Yochelson & Webers 2006) but readily compared to extant members of the class (Lemche & Wingstrand 1959; Wingstrand 1985; Lindberg 2009). Classic descriptions of the shells of *Tryblidium* Lindström in Angelin & Lindström, 1880 and *Pilina* Koken & Perner, 1925 from the Ordovician and Silurian of the Baltic region, with a series of paired internal muscle scars along the dorsum, were given by Lindström (1884) and Koken & Perner (1925).

Cambrian and earliest Ordovician strata have yielded numerous univalves referred to the Class Helcionelloida by Peel (1991a, 1991b), which is approximately equivalent in composition to the Order Helcionelliformes (within gastropod Subclass Archaeobranchia) of Parkhaev (2019) and earlier papers cited therein (see discussion by Geyer 1994 and Peel & Kouchinsky 2022). However, the resemblance of their bilaterally symmetrical shells, which are generally coiled through a quarter of a whorl or more, to patellids is superficial and a variety of structures on the shell interior in Helcionelloida are seemingly unique to the group (Peel 1991a, 1991b; Kouchinsky 2000; Parkhaev 2000, 2002, 2006; Vondrasco et al. 2010, 2011; Peel & Kouchinsky 2022). Late Cambrian to early Ordovician Hypseloconida were placed within Class Tergomya by Peel (1991a) and Yochelson & Webers (2006), but a provocative submission by Dzik (2010) argued that similarities in muscle scars patterns with the bivalved *Angarella* Asatkin, 1932 suggested brachiopod affinities.

The patelliform *Floripatella* Yochelson, 1988, originally described from the Middle Ordovician (Dapingian) of Utah, USA has aroused particular interest on account of the claim by Yochelson (1988) that it was the earliest patelloidean gastropod. As such, *Floripatella* would represent an extension of the known geological range of patelloids back to the Ordovician. While the oldest known patellogastropod based on preserved shell structure is of Triassic age (Hedgegaard et al. 1997), claims of patellid affinity have been made on the basis of muscle scar patterns on rare internal moulds from the Silurian. Thus, *Damilina* Horný, 1961 from the Silurian of Bohemia has been interpreted as a patellogastropod limpet (Horný 1961, 1963; Starobogatov & Mazaev 1999; Mazaev 2015; see also Ponder et al. 2020). Bouchet et al. (2017) placed Family Damilinidae Horny, 1961 in Superfamily Lottioidea Gray, 1840 of Subclass Patellogastropoda, Order Patellida. The holotype of *Floripatella rousseaui* Yochelson, 1988, the type species of *Floripatella*, displays well preserved muscle scars on the internal mould (Fig. 1A,B,G,I). However, Lindberg (2009) and Vermeij (2017) suggested that *Floripatella* was a tergomyan monoplacophoran and not a gastropod.

In the context of Ordovician strata in the Baltic region, cap-shaped shells of the genera *Archinacella* Ulrich & Scofield, 1897 and *Pollicina* Koken in Holzapfel, 1895 (Fig. 2) are conspicuous (Koken 1897; Koken & Perner 1925; Peel 2020a, 2020b); *Archinacella* is widely distributed in the Ordovician (Ulrich & Scofield 1897; Wahlman 1992; Yochelson & Webers 2006). *Archinacella* has been interpreted variously as a gastropod or a tergomyan, as summarised by Peel (1990, 2020a) and Peel & Horný (1999) who considered it to be a gastropod, but

not a patellogastropod, an opinion maintained by Ponder et al. (2020). *Pollicina* was interpreted as a gastropod related to *Archinacella* by Peel (2020a, 2020b), largely on the basis of the muscle scars on the internal moulds in both taxa. However, the distinctive tall and shallowly curved shell form of *Pollicina* (Fig. 2) is not seen in patellids and Evans & Cope (2003) suggested it was a tergomyan.

This paper describes a unique internal mould of a patelliform mollusc from the Middle Ordovician, Darriwilian Series, Kunda Stage of Aari, Haljala, in northern Estonia, as *Eesticonus aariensis* n. gen. n. sp. (Fig. 3). *Eesticonus aariensis* displays a well preserved comarginal muscle attachment scar developed around the shell apex that is similar in general disposition to the muscle scar seen in *Floripatella rousseaui* (Fig. 1) but close comparison is made also with *Pollicina crassitesta* Koken (1897) from eastern Baltic Darriwilian strata (Fig. 2), and with archinacellid species, as a prelude to evaluating its systematic position.

Systematic palaeontology

Abbreviations and repositories. – Repositories of figured specimen are indicated by the following prefixes: CNIGRM, F.N. Chernyshev Central Geological Survey Research Museum, St. Petersburg; ELM, Estonian Museum of Natural History, Tallinn; NM L, National Museum, Prague; TUG, geological collections of the University of Tartu, Natural History Museum; USNM PAL, paleobiological collections of the National Museum of Natural History (Smithsonian Institution), Washington D.C.

PHYLUM MOLLUSCA CUVIER (1797)
Genus *Floripatella* Yochelson (1988)
 1988 *Floripatella* Yochelson, p. 196.
 2009 [*Floripatella*] Lindberg, p. 198.

Type species. – *Floripatella rousseaui* Yochelson (1988), from the Kanosh Shale of Utah, USA; Middle Ordovician, Dapingian Series.

Discussion. – Yochelson (1988, p. 197) commented that initial examination of available material of the type species *Floripatella rousseaui* from Utah prompted him to recognise several genera but he subsequently united the specimens into a single variable species. His illustrations, some of which are reproduced here on the basis of new digital scans of the original negatives (Fig. 1), show substantial variation in the shape of the aperture in dorsal perspective and the lateral profile. The holotype is almost circular in plan view, with a diameter of about 20 mm (Fig. 1B,D). In the lateral profile presented by Yochelson (1988; Fig. 1A), its height is slightly more than one-quarter of its length. The apparent sub-apical surface (left in Fig. 1A) is flat in this view, whereas the apparent supra-apical surface is shallowly convex (right in Fig. 1A); the apex is located slightly closer to the supra-apical margin. According to Yochelson (1988), this illustration represents the right side of a latex cast from the external mould, with the convex supra-apical surface thereby interpreted as anterior. Comparison of the poor photograph (Fig. 1A) with dorsal views of the internal mould (Fig. 1B,D) is

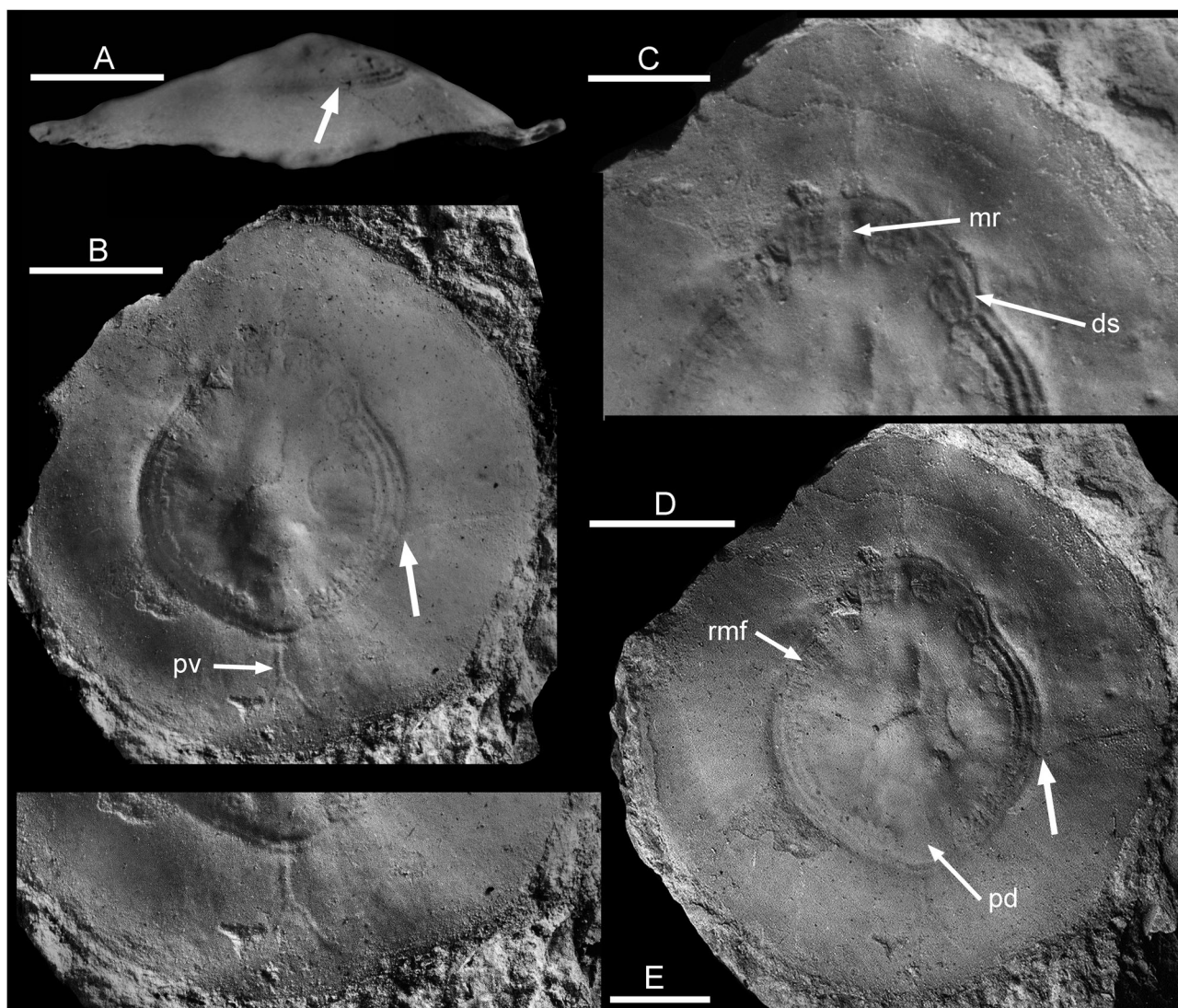


Figure 1. *Floripatella rousseaui* Yochelson, 1988, USNM PAL 410165, holotype, internal mould, Middle Ordovician, Darriwilian, Kanosh Shale, Millard County, Utah. **A.** lateral view oblique to the plane of symmetry **B** where large arrows locates intersection of a radial crack with the muscle scar in **B** and **D**. **B.** dorsal view with arrow **pv** locating the putative pallial vessel impression discussed by Lindberg (2009, fig. 6). **C.** detail of muscle scar showing median ridge (**mr**) and one discrete scar (**ds**). **D.** dorsal view, as **B** but with alternative lighting, showing radial muscle fibres (**rmf**) and pericardium depression (**pd**). **E.** detail of margin with pallial vessel. Scale bars: 3 mm, **C,E**; 5 mm, **A,B,D**. Photographs prepared from negatives supplied by E.L. Yochelson.

difficult, but a faint radial crack (large arrows in Fig. 1A,B,D) seems to provide a linkage. If so, the illustrated lateral profile (Fig. 1A) lies at about 45 degrees (clockwise rotation relative to Fig. 1B) oblique to the plane of symmetry, and represents a view from the lower right in Fig. 1B,D. This would place the shallowly convex supra-apical surface (right in Fig. 1A) on the upper right in Fig. 1B,D, antero-lateral in the interpretation of Yochelson (1988). The specimen is composite, with impression of the muscle scar from the internal mould onto the mould of the exterior.

Yochelson (1988) figured two paratypes with an oval dorsal profile that he interpreted as a laterally compressed specimen, although no evidence of distortion was seen. The apex is located much closer to the margin (Yochelson 1988, fig. 2.1, 2.5, 2.8) than in the holotype (Fig. 1A) and their lateral profiles are therefore dissimilar. Based on the published illustrations, the assignment of these two specimens to *Floripatella rousseaui* is considered to be tenuous.

Genus *Eesticonus* new genus

Type species. – *Eesticonus aariensis* n. gen. n. sp. from the Middle Ordovician, Darriwilian Series, Kunda Stage of northern Estonia.

Derivation of name. – From Eesti Vabariik, the official name of the Republic of Estonia.

Diagnosis. – Univalve, with oval aperture and height about two-thirds of length; early growth stage laterally compressed. Apex located at about one-quarter of length measured from sub-apical margin. Sub-apical surface shallowly concave, supra-apical surface very shallowly convex. Shell thin, with fine comarginal growth lines crossed by closely spaced, sharp radial ridges. Semi-continuous muscle attachment scar located on internal mould at about one-third of distance from apex to aperture.

Discussion. – The holotype of *Floripatella rousseaui* differs from *Eesticonus* in being almost circular in plan view (Fig.

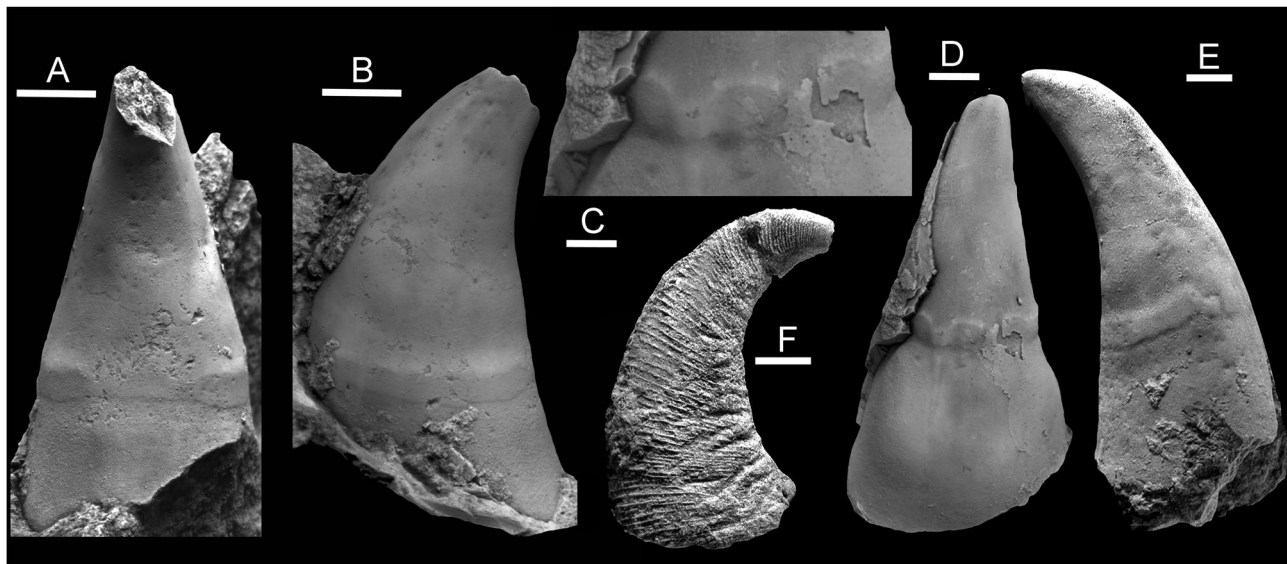


Figure 2. *Pollicina* Koken in Holzappel, 1895, Ordovician, Darriwilian, Kunda Stage. **A–E.** *Pollicina crassitesta* Koken, 1897, internal moulds. **A,B.** ELM G1:2919, sub-apical and lateral views with muscle attachment scar, Tallinn. **C,D.** ELM g1:2323, oblique views of supra-apical surface with muscle attachment scar, Tallinn. **E.** CNIGRM 15600, lateral view with muscle attachment scar, Laaksberg (=Lasnamägi), Estonia. **F.** *Pollicina corniculum* (Eichwald, 1860), CNIGRM 15702, lateral view showing comarginal ornamentation on shell exterior, Pulkowa (=Pulkovo), St. Petersburg, Russia. Scale bars: 2 mm, C; 4 mm, A,B,D,E; 5 mm, F.

1B,D) compared to the oval form of *Eesticonus*. *Floripatella* is much lower in lateral perspective than *Eesticonus* (Fig. 3A), with height only about one-quarter of the length (Fig. 1A). Additionally, the apex in *Eesticonus* lies closer to the sub-apical margin (Fig. 3A). The muscle attachment scar in *Eesticonus* (Fig. 3A,D) is located at less than one-third of the distance from the apex to the apertural margin but at half of the distance from the apex to the apertural margin in *Floripatella* (Fig. 1B,D).

When viewed in lateral perspective, the shell in *Pollicina* is much more slowly expanding than that in *Eesticonus*, such that its height is more than twice the length of the aperture (Fig. 2F) compared to two-thirds in *Eesticonus* (Fig. 3A). Additionally, in contrast to *Eesticonus*, the apex in *Pollicina* overhangs the sub-apical margin.

The well-preserved muscle attachment scar of *Eesticonus aariensis* invites comparison with *Damilina* Horný (1961) from the Silurian of Bohemia, but the shell of *Damilina* is distinguished from *Eesticonus* by its low conical form and sub-central apex (Horný 1963). *Calloconus* Perner (1903) from the lower Devonian of Bohemia, as re-described by Horný (1963), has a similar shell form to *Eesticonus* but is ornamented by prominent comarginal lamellae in contrast to the fine radial ridges of *Eesticonus* (Fig. 3E, arrow). Its musculature is not known.

Numerous limpet-like shells from the Ordovician have been referred to *Archinacella* Ulrich & Scofield, 1897, which is widely distributed and varied in form, but often poorly known (Koken 1897; Koken & Perner 1925; Wahlman 1992; Peel & Horný 1999; Yochelson & Webers 2006). The holotype of the type species, *Archinacella powersi* Ulrich & Scofield (1897), was re-described by Peel & Horný (1999) who noted that the apex in the low, oval shell was located above the short, concave sub-apical surface almost above the apertural margin. The apex in the morphologically similar

Archinacellina Horný, 1961 overhangs the sub-apical apertural margin. *Eesticonus* is readily distinguished from both by its taller shell and proportionately longer sub-apical surface.

***Eesticonus aariensis* new species**

Fig. 3.

Holotype. – TUG 1787-21 from Aari Quarry, Noonu Parish, Haljala, northern Estonia (59.514111°N; 26.205069°E); Ordovician, Darriwilian Series, Kunda Stage.

Derivation of name. – From its occurrence in Aari Quarry.

Diagnosis. – As for genus, by monotypy.

Description. – In this unique internal mould, the width of the oval aperture is about three-quarters of its length. Its height is about two-thirds of length. The sub-apical surface is shallowly concave. The supra-apical surface is flattened, initially shallowly concave but becoming very shallowly convex in the main portion of the shell (Fig. 3A). The convexity is retained until the apertural margins in lateral areas (Fig. 3B,C) but the shell becomes slightly concave due to minor flaring of the aperture medially (Fig. 3A,H). The apex is located at about one-quarter of the length measured from the sub-apical margin (Fig. 3A). The early growth stage, although largely broken away in the available specimen, is narrower than the mature shell, with shallowly concave lateral areas evident on the adapical side of the muscle scar (Fig. 3D,G); it is slightly raised on the internal mould but the protoconch not known. The shell is thin (Fig. 3E, arrow), slightly reflexed at the apertural margin (Fig. 3A,G), with fine comarginal growth lines crossed by closely spaced, sharp radial ridges spaced at four ridges per mm. A semi-continuous muscle attachment scar on internal mould is located at about one-third of the distance from the apex to the aperture. The scar is raised slightly above the internal mould surface, although a narrow, shallow,

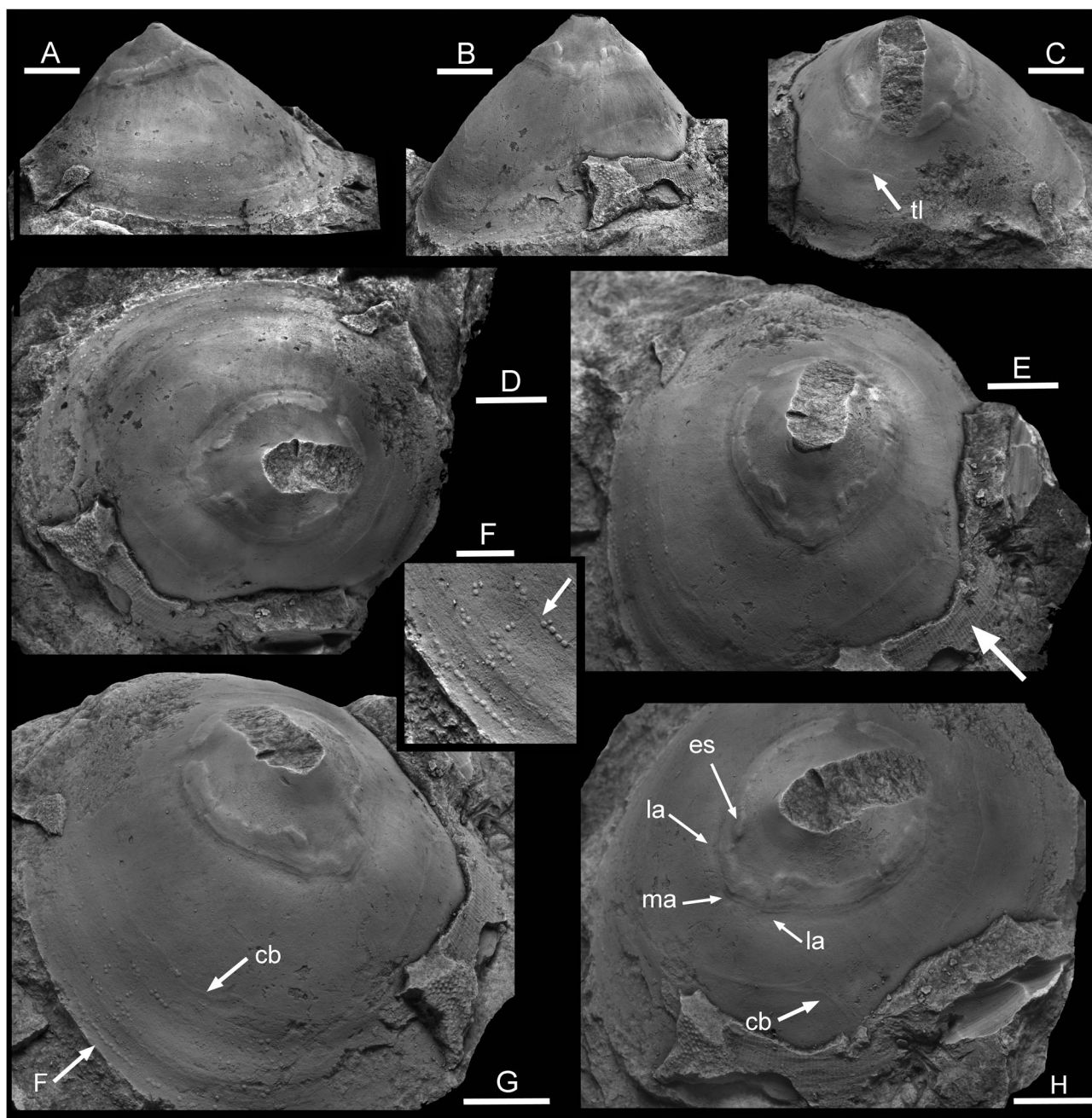


Figure 3. *Eesticonus aariensis* n. gen. n. sp., TUG 1787-21, holotype, internal mould with broken apex showing muscle attachment scars. Ordovician, Darrivilian Series, Kunda Stage, Aari Quarry Noonu Parish, Haljala, northern Estonia. **A.** lateral view. **B.** supra-apical surface. **C.** oblique view of sub-apical surface showing trace of shell laminae (tl). **D.** dorsal view, supra-apical surface to left. **E.** oblique view of supra-apical surface, with radially ornamented shell fragment (arrow). **F.** tubercles on the internal mould representing pits in the dissolved shell, located by arrow F in G. **G.** oblique view of supra-apical surface with raised comarginal band (arrow cb) that may represent an endolith burrow; position of Fig. F indicated by arrow. **H.** oblique view of supra-apical surface showing medial (ma) and lateral (la) angulations; es indicates the extension of the muscle scar band towards the median plane. Scale bars: 2 mm, F; 6 mm, A-E,G,H.

depression corresponding to a ridge on the shell interior delimits its abapical margin.

Discussion. – The description is based on a single internal mould about 42 mm long, the holotype (Fig. 3), with small adherent small patches of thin shell (Fig. 3E, arrow); the apex is broken away.

The holotype of *Floripatella rousseaui*, the type species of *Floripatella*, differs in having an almost circular aperture (Fig. 1B,D) when compared to the oval aperture of *Eesticonus aariensis*, and is about half its overall length. Its height is about

one quarter of the length (Fig. 1A), much lower than *Eesticonus aariensis* (Fig. 3A). The apex in *Floripatella rousseaui* lies more centrally than in *Eesticonus aariensis* where it is noticeably closer to the sub-apical margin (Fig. 3A). The muscle attachment scar is located at about half of the distance from the apex to the apertural margin in the holotype of *Floripatella rousseaui* (Fig. 1B) but at less than one-third of the distance from the apex to the apertural margin in *Eesticonus aariensis* (Fig. 3A,D). On account of the greater curvature of the shell, the muscle band is inclined to the apertural plane in *Eesticonus*

aariensis (Fig. 3A) whereas it is parallel to the aperture in *Floripatella rousseaui* (Fig. 1A).

The supposed laterally compressed paratype internal mould of *Floripatella rousseaui* (Yochelson 1988, fig. 2.1, 2.5) is about 50% longer than the holotype of that species, narrower in plan view and apparently taller. It also shows a different lateral profile, with both the supra-apical and sub-apical slopes being shallowly convex. Additionally, the muscle scar band is located closer to the apex than in the holotype, in a position similar to that seen in *Eesticonus* (Fig. 3).

In lateral profile, *Micropileus ordovicinus* (Horný, 1963) from the Middle Ordovician of Bohemia shows similar inclination of the sub-apical surface, but the supra-apical surface is more strongly convex, parallel to the aperture near the apex (Horný 1963, 2002). Its muscle scar is poorly known.

Muscle scar in *Eesticonus*

Description. – The muscle attachment scar in the holotype of *Eesticonus aariensis* is raised above the surface of the internal mould and is thus equivalent to a depression formed by muscle insertion on the shell interior. The relief of the scar in the following description refers to the internal mould. The muscle scar is dominated by a raised U-shaped band that extends around the supra-apical surface across one lateral area, over the dorsum, and across the other lateral area. Narrow gaps at the two prongs of the U-shape separate a crescentic scar beneath the apex from the principal scar. This crescentic scar is damaged on its apical margin as a result of breakage of the apex of the internal mould, and may be divided medially. However, a fine trace on its adapertural side is continuous. This trace also continues in weakened form across the gaps between the crescentic scar and the principal U-shaped scar. The two narrow gaps and the crescentic scar are not perfectly symmetrical about the median dorsal plane (Fig. 3C,D), although the apparent asymmetry is exaggerated by the breakage of the apex of the internal mould.

The adapertural margin of the U-shaped scar on each lateral surface is a relatively smooth curve marked by two narrow ridges and, outside of these, a broad shallow depression. As this adapertural margin approaches the mid-dorsal line of the supra-apical surface, slight changes in curvature produce a pair of slightly protruding angulations (Fig. 3H, arrows la) lying one on each side of a pointed median angulation (Fig. 3H, arrow ma). The adapical margin of the U-shaped scar is irregular but symmetrical from one lateral surface to the other (Fig. 3D,E). Each lateral branch of the scar is approximately uniform in width but the band doubles its width (along a radial line) as the median dorsal plane of the supra-apical surface is approached to produce a small, but prominent, elongate, extension to the scar on each dorso-lateral shoulder (Fig. 3H, arrow es). Indentations in the adapical margin of the U-shaped scar on the mid-dorsum correspond to the angulations (Fig. 3H, la, ma) on the adapertural scar margin. Thus, the median dorsal area of the U-shaped attachment scar appears to be composed of two pairs of smaller scars (Fig. 3E), although these are conjoined and with their adapertural margin delimited by the unbroken pair of marginal ridges. The lateral areas of the internal mould are shallowly

convex, steepening towards the apertural margin (Fig. 3B). Fine radial striations are developed on their surface close to the muscle scar, while weak comarginal undulations develop near to the margin (Fig. 3A).

Remarks. – The slight asymmetry of the sub-apical scar may suggest that the bilateral symmetry of the single specimen of *Eesticonus aariensis* is derived from a trochiform gastropod ancestor, but slight asymmetry is not uncommon in the muscle scar patterns of other Palaeozoic univalve specimens, such as the tryblidiid tergomyan *Pilina cheyennica* Peel, 1977.

The muscle attachment scar in the tall, slowly expanding *Pollicina* (Fig. 2) is located much closer to the aperture than in the more rapidly expanding shell of *Eesticonus aariensis* (Fig. 3A,B). However, the adapertural deflection of the muscle scar in the median dorsal area of both taxa is similar, but more strongly expressed than that developed in *Eesticonus aariensis* (compare Fig. 2C–E and Fig. 3E). The adapertural margin of the scar on the lateral areas is also clearly marked in both, but the muscle band in *Pollicina* displays abrupt terminations to the attachment area below the apex, with a continuous adapertural margin trace but without the crescentic scar crossing the median plane of the sub-apical surface (Fig. 2A).

The muscle scar in the low, cone-shaped shell of *Damilina* Horný (1961), from the Silurian of Bohemia, is developed as a prominent U-shaped band in which the slightly wider prongs are joined by a thin but distinct pallial line (Horný 1963). The scar is crossed by radial grooves on the internal mould, equivalent to ridges on the shell interior, which caused Horný (1963) to suggest that it was composed of numerous juxtaposed scars, rather than a continuous single muscle scar. Apparent segmentation of the comarginal scar is often seen in patellids due to the passage of blood vessels to the circum-apertural gills (Ponder et al. 2020). *Damilina* was interpreted as a typical patellid (Horný 1963, Starobogatov & Mazaev 1999), see also Mazaev (2015), Bouchet et al. (2017) and Ponder et al. (2020), although information concerning its shell structure is lacking. *Damilina* lacks the extension of the U-shaped scar on the mid-dorsum of *Eesticonus* and the small scars placed between the prongs of the principal scar.

The narrow muscle scar on the internal mould of the holotype of *Archinacella powersi* was re-evaluated by Peel & Horný

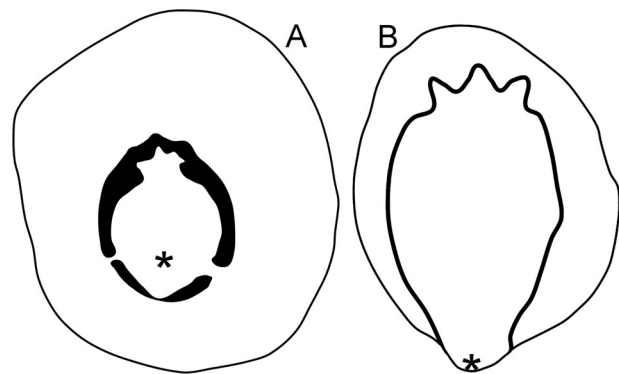


Figure 4. Drawings of the muscle attachment scars on internal moulds of the holotype of *Eesticonus aariensis* (A) and a paratype (NM L 5903) of *Archinacella modesta* (B), the latter based on Peel & Horný (1999, fig. 10A). Specimens are oriented as gastropods, with the anterior uppermost. Asterisks locate position of shell apex.

(1999). It is continuous across the median line of the sub-apical surface, in contrast to *Eesticonus*, but it fades as it passes along the lateral areas towards the supra-apical apertural margin. In *Eesticonus* the scar is continuous across the median dorsal area of the supra-apical surface (Fig. 3G,H). *Archinacella* from the Upper Ordovician of Bohemia (Horný 1961) is similar in shape to *Archinacella powersi* but with a slightly more prominent overhanging apex. A paralectotype illustrated by Peel & Horný (1999, fig.10) shows the thin muscle scar crossing the median dorsal in similar fashion to the taller *Eesticonus*, although the scar in the latter is located much closer to the apex (Fig. 3A,D). The scars in the two taxa are similar, however, in developing angulations where the muscle scar crosses the dorsum of the supra-apical surface, although this feature is much more strongly developed in *Archinacella* (Fig. 4B).

While generally similar, with an oval, circum-apical pattern, the muscle attachment scar of *Floripatella* differs in detail from that of *Eesticonus*. It should be recalled, however, that comparison is made on the basis of just a single specimen of each taxon. The surface of the internal mould in *Floripatella* shows several swellings that may reflect the position of internal organs, a feature in patellids discussed by Lindberg (2009). The absence of similar structures in *Eesticonus* probably reflects the greater height of the shell (Fig. 3). While the median extension of the U-shaped scar across the dorsum on the supra-apical surface of *Eesticonus* preserves three small angulations, the extension in *Floripatella* is diffuse and apparently made up of two pairs of discrete scars (Fig. 1C, D, arrow ds), the pairs being separated medially by a ridge on the internal mould (Fig. 1C, arrow mr). However, the angulations in *Eesticonus* may represent incipient separation of the paired muscle seen in *Floripatella*.

In *Floripatella*, a distinct radially striated, comarginal scar on each lateral surface terminates at a smooth, raised area located on the mid-dorsum, termed the pericardium depression of the inner shell surface by Lindberg (2009, fig. 6; Fig. 1D, arrow pd). This depression is not recognised in *Eesticonus* where narrow gaps at the two prongs of the U-shaped scar separate a crescentic scar beneath the apex from the principal scar that dominates the lateral areas. As in *Eesticonus*, a continuous, distinct, pallial line delimiting the adapertural side of the muscle scars, crosses the dorsum from one lateral area to the other in *Floripatella*. Comarginal ridges are prominent in the U-shaped scar of *Floripatella* (Fig. 1B–D) but restricted to the adapertural margin of the scar in *Eesticonus* (Fig. 3G,H). The radial striations seen within the lateral scars in *Floripatella* (Fig. 1D, arrow rmf) are not observed in *Eesticonus*.

Other structures. – The internal mould of *Eesticonus aariensis* shows a fine comarginal trace on the sub-apical surface reflecting the edge of an inner shell laminae (Fig. 3C, arrow tl). The division of an irregular comarginal band on the supra-apical surface (Fig. 3G,H, arrow cb) may represent an endolith burrow on the shell interior. Repeated comarginal series of small tubercles (Fig. 3F, arrow F in 3G) represent small oval pits associated with the growing edge of the innermost shell layer, in some cases seemingly joined by a faint trace (Fig 3F, arrow). In their shape, they resemble cell strands of the

present-day cyanobacterium *Hyella* Bornet & Flahault (1888), as illustrated by Radtke & Golubic (2011).

Discussion

Floripatella rousseaui was interpreted as a patelloidean gastropod by Yochelson (1988) but Lindberg (2009) suggested that it was as an untorted monoplacophorous mollusc. His opinion was based on the presence of an inverted Y-shaped ridge on the internal mould of the holotype that he interpreted as the trace of the efferent pallial vessel located at the posterior margin of the shell (Fig. 1B,E, arrow pv). Circum-pallial vessels also occur in various gastropods, including patellogastropods where they are located antero-laterally, by the side of the head (Ponder et al. 2020, fig. 18.12). The presence of such pallial vessels is not established in *Eesticonus*, nor described in other similar Lower Palaeozoic patelliform taxa. While Lindberg (2009) considered *Floripatella* to be untorted, he recognised that it was not a member of the lineage with multiple dorsal muscle scars leading through *Tryblidium* and *Pilina* to the present-day tergomyans.

Bandel (1982), Harper & Rollins (1982, 2000), Peel (1991a, 1991b; 2020a, 2020b), Peel & Horný (1999) and others have noted that the distribution of muscle scars in cap-shaped molluscs reflects mechanical function as well as systematic position. The series of paired muscle scars located on the supra-apical surface of fossil *Pilina*, *Tryblidium* and numerous other genera convincingly support their interpretation as Tergomya, by comparison to living forms. However, even this conservative pattern (Cambrian–Recent) is modified in the Silurian *Archaeopruga pinnaeformis* (Perner, 1903), where a large elongate muscle is developed on each lateral area between the dorsal series of paired muscles and the apertural margin (Horný 2005).

In Tergomya, the shell apex lies outside (anterior) of the muscle scar ring, but in numerous other cap-shaped shells the apex lies within the muscle scar ring, the cyclomyan condition of Horný (1965a, 1965b). Peel (1991b) sought to explain the formation of many muscle scar patterns in terms of changes in shell morphology associated with diversifying modes of life. He abandoned the Subclass Cyclomya Horný, 1965b in a formal sense, assigning the constituent orders recognised by Horný (1965b) to the gastropods (archinacellids) and Tergomya (cyrtoneilids). Patellids are also cyclomyan in a morphological sense, but it does not follow that all cyclomyan muscle patterns indicate patellid, or even gastropod affinity.

The orientation of the protoconch relative to the adult shell suggests that patellogastropods were derived from a sinistral or hyperstrophic coiled ancestor (Ponder et al. 2020). Peel (2019) described a pair of muscle scars on internal moulds of the open coiled, sinistral/hyperstrophic euomphaline gastropod *Asgardaspira evolvens* (Koken, 1897) from the Middle Ordovician of eastern Baltica, a member of the Infraclass Euomphaliformii, the sister group of Patellogastropoda within Eogastropoda (Ponder et al. 2020) and a possible indicator of the form of the ancestors of patellogastropods. The muscle scars are located one on each side of the angular junction between the umbilical wall and basal surfaces of the whorl, in a position appropriate

to their function in retracting soft parts into the narrow shell. Similar paired muscle scars occur in many gastropod groups and, disposed symmetrically, fulfil the same function in Ordovician–Carboniferous isometric bellerophontoideans as in *Asgardospira* (Peel 1976, 1982, 1993). They are also described in secondarily symmetrical Carboniferous pleurotomarioidean vetigastropods (Peel 1986, 2001, 2004).

Development of a rapidly expanding patelliform shell, adapted to clamping against the substratum, from a slowly expanding trochiform ancestor such as *Asgardospira evolvens* would promote relocation of the pair of muscles to the lateral areas of the shell, with eventual comarginal extension or coalescence to form a muscle attachment band around the apertural margin. Muscle scar patterns in *Pollicina* (Peel 2020a, 2020b) may represent an intermediate stage. The dominance of the lateral muscle attachment areas is seen in both *Eesticonus* and *Floripatella*, but the acquisition of large muscles in *Archaeopruga* indicates that adoption of this location is an adaptive feature not just in gastropods, but also in some tergomyans. Thus, considered in isolation, the overall similarity in the muscle scar patterns described herein provides little reason for suggesting that *Floripatella* and *Eesticonus* were representatives of two different molluscan classes, or overwhelming evidence that they were not.

Peel (2020a) acknowledged the suggestion by Evans & Cope (2003) that the tall, slowly expanding *Pollicina* was a cyrtoneid tergomyan, but chose to interpret this genus typical of the Baltic Middle Ordovician as an archinacelloidean gastropod on the basis of comparison of muscle scars. *Archinacella* has been interpreted as both a monoplacophorous mollusc and a gastropod, but together with the closely related *Archinacellina* it was referred to the gastropods by Peel & Horný (1999). Ponder et al. (2020) considered *Archinacella* to be a patelliform euomphaliformean eogastropod but not a patellogastropod. Close similarity between the muscle scars of *Eesticonus* and *Archinacellina* with respect to the three angulations developed in the scar astride the dorsal area of the supra-apical surface (Fig. 4) motivates assignment of *Eesticonus* to the Archinacelloidea Knight (1956). The status of *Floripatella* is not satisfactorily resolved, but the interpretation of Lindberg (2009) that it represents a monoplacophorous mollusc unrelated to the tergomyan lineage of present-day seas is tentatively accepted. The status of many other Palaeozoic cap-shaped or patelliform molluscs remains arbitrary.

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