Muscle scars, mode of life and systematics of *Pollicina* (Mollusca) from the Ordovician of Baltica

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Abstract. *Pollicina* is a distinctive, but uncommon, univalved mollusc originally described from the Middle Ordovician (Darriwilian Stage) of the Baltic. The slender, bilaterally symmetrical shell expands slowly and is curved through up to about 90 degrees, but straightens in the latest growth stages. *Pollicina corniculum*, the type species from the St Petersburg region of Russia is redescribed, as is *Pollicina crassitesta*, the most common representative from the Tallinn area of Estonia. Muscle scars in *P. crassitesta* form a continuous circum-apertural band on internal moulds about half way between the apex and the apertural margin. The bilaterally symmetrical shell, orthocline aperture, circum-apertural muscle scar and frequent displacement of the apertural margin, as evidenced by dislocations in growth ornamentation, indicate that *Pollicina* lived as a limpet, clamped against the substrate. Suggestions that it was an open coiled gastropod lying on the sediment surface are rejected. As with most Ordovician limpet-formed shells, assignment of *Pollicina* to Tergomya or Gastropoda is equivocal, even controversial, not least on account of the tall shell and muscle band. Despite similarities with the tergomyan *Cyrtolites*, *Pollicina* is placed tentatively together with the archinacelloidean gastropods.

Key words: Mollusca, Gastropoda, muscle scars, habit, Ordovician, Darriwilian, Baltica.

INTRODUCTION

Univalved molluscs with cap-shaped or limpet-formed shells have existed throughout the Phanerozoic. Vermeij (2017) calculated that this shell morphology has arisen independently more than 50 times in the evolutionary history of gastropods, and to this may be added a morass of monoplacophoran and poorly known bilaterally symmetrical shells in the early–middle Palaeozoic (Runnegar & Jell 1976; Peel 1991a, 1991b; Geyer 1994; Parkhaev 2008, 2017; Bouchet et al. 2017). Most familiar at the present day are the patellids which dominate rocky shores at intermediate latitudes and which can be used to illuminate the dilemma facing malacologists seeking to unravel gastropod evolutionary history. Despite a host of modern phylogenetic and developmental studies (Koufopanou et al. 1999; Wanninger et al. 1999, 2000; Lindberg 2009; Kristof et al. 2016), elucidation of their palaeontological record is frustrated by the morphological simplicity of their bilaterally symmetrical shell and muscle scar, the only characters that are preserved in most fossil scenarios.

Lindberg (1986, 1988) proposed that Patellogastropoda was the sister group of other gastropods, although this hypothesis has since evolved (Zapata et al. 2014). It has

been suggested that the earliest gastropods were limpet-formed (Golikov & Starobogatov 1975; Haszprunar 1988; Parkhaev 2017). However, Lindberg (1988, 2008, 2009) and Ponder & Lindberg (1997) proposed that the ancestor of patellogastropod limpets was likely a coiled gastropod. The oldest confirmed patellogastropod is Triassic in age, based on studies of shell structure (Hedegaard et al. 1997), although numerous claims of Palaeozoic patellids exist in historical and more recent literature, as discussed below. Thus, the early history of undoubted patellogastropods, or their supposed coiled ancestors, has not been established in the Palaeozoic, almost half of their supposed geological range, frustrated by the inadequacy of shell-based information of the almost featureless shells and confusion with morphologically similar shells of co-existing monoplacophoran mollusc groups (Peel 1991a, 1991b; Yochelson & Webers 2006). Fortunately, ongoing studies of protoconchs and new phylogenetic approaches (Frýda et al. 2009; Frýda 2012) offer a potential way forward.

This paper examines a distinctive but poorly known Ordovician univalve which lies in limbo between gastropods and monoplacophoran molluscs. *Pollicina* has proven to be enigmatic ever since the name was introduced by Holzapfel (1895) in a publication which described

Devonian fossils from Germany. However, the designated type species of *Pollicina* is an Ordovician form originally described from the East Baltic. This Ordovician type species, *Pollicina corniculum* (Eichwald, 1860; Fig. 1), has
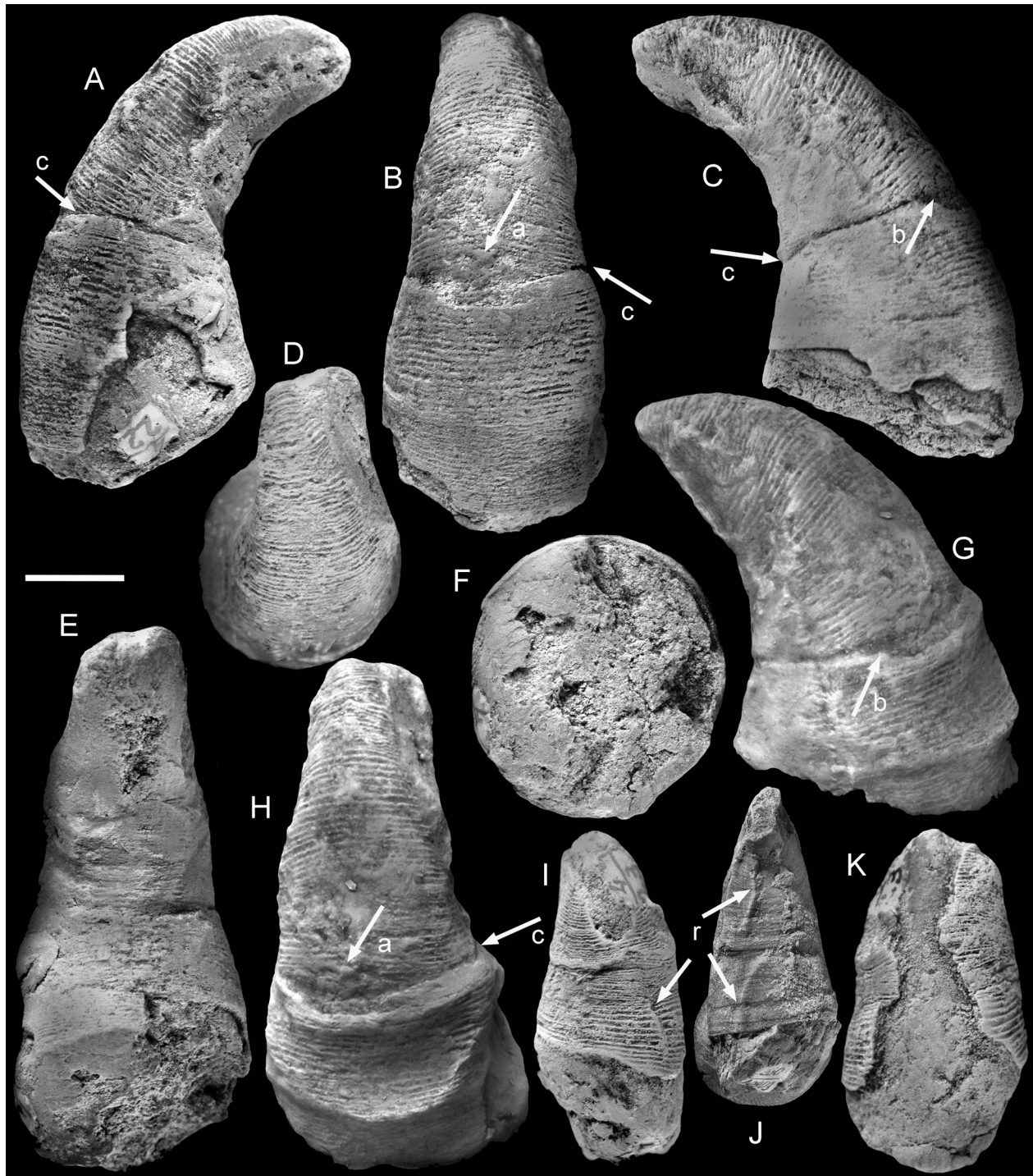

Fig. 1. *Pollicina corniculum* (Eichwald, 1860). Ordovician, Darriwilian, Kunda Stage, Popowka or Pulkowa [=Pulkovo], St Petersburg, Russia. **A–F**, lectotype, PSM 4/22: A, lateral view; B, supra-apical surface; C, lateral view; D, supra-apical surface at apex, with adherent matrix on right side; E, sub-apical surface; F, apertural view. **G**, **H**, replica of lectotype, PSM 4/22, showing prominent comarginal rugae: G, oblique lateral view; H, supra-apical surface. **I**, **K**, replica of paralectotype, PSM 4/23. **J**, CNIGRM 15692 (380/10903), sub-apical surface showing irregular longitudinal ridges. Arrow a locates equivalent points in B and H. Arrow b indicates equivalent points in C and G. Arrow c indicates the prominent transverse growth dislocation in A–C, H. Arrow r indicates ridges perpendicular to margin in I, J. Scale bar = 5 mm.

been evaluated in several studies, (Knight 1941, 1952; Kisselev 1994; Evans & Cope 2003; Yochelson & Webers 2006) but the Devonian species proposed by Holzapfel (1895) has not.

The slowly expanding, slightly curved, bilaterally symmetrical shell of *Pollicina* (Fig. 1) is universally accepted as molluscan in origin but the position of the genus within Mollusca is controversial. Several of the various earlier interpretations as cephalopod, 'hyolithid' pteropod, capulid gastropod, euomphaloidean gastropod, monoplacophoran or the problematic xenoconchs and toxeumorphorids were reviewed by Evans & Cope (2003) who placed *Pollicina* within the monoplacophoran Class Tergomya Horný, 1965a *sensu* Peel 1991a. However, Yochelson & Webers (2006) maintained that *Pollicina* was a gastropod. Bouchet et al. (2017, p. 194) noted that usually *Pollicina* has been treated as a gastropod but that this view had been rejected by Evans & Cope (2003).

The late Ellis L. Yochelson (1929–2006) nurtured an interest in *Pollicina* that extended over four decades and resulted in several unpublished manuscripts, aspects of which were cited by Peel & Yochelson (1984), Evans & Cope (2003) and Yochelson & Webers (2006). Yochelson & Webers (2006, p. 25) summarized Yochelson's theory that *Pollicina* was an uncoiled or open coiled mollusc related to euomphaloidean gastropods, an opinion that is not supported herein. However, Yochelson's interest has materially advanced the present study since he passed on to me photographs and replicas of the type material of *Pollicina corniculum* (Eichwald, 1860), the lectotype and paralectotype of which are illustrated herein (Fig. 1). Yochelson's photographs of the original specimens and the replicas of these specimens were produced in Washington D.C. during the late 1980s and their identity is confirmed by comparison with subsequent illustrations of the types by Kisselev (1994). It is evident, however, that Yochelson's photographs and the replicas were prepared prior to the preparation of Kisselev's (1994, fig. 1A–D) illustrations of the designated lectotype since that illustration figures a specimen which has been sectioned apically, along the plane of symmetry, presumably to investigate the possible presence of septa. The replica of the lectotype also demonstrates the presence of prominent transverse rugae (Fig. 1G, H) not clearly seen in the illustrations of Kisselev (1994) or the Yochelson photographs (Fig. 1A–C herein).

Comparison between *Pollicina corniculum* and most other material assigned to *Pollicina* is hindered by differences in preservation. Available specimens of *Pollicina corniculum* usually preserve the shell and display the external ornamentation of sharp comarginal lamellae (Fig. 1). Most of the other available specimens assigned to the genus by Koken (1897) and Koken & Perner (1925) are internal moulds where details of

ornamentation are lacking (Figs 2D–J, 3C–O), although a rare exception is provided by the lectotype of *Pollicina crassitesta* Koken, 1897 (Fig. 2A–C). This general lack of information concerning ornamentation urges caution in comparisons of internal moulds both with *Pollicina corniculum* and with internal moulds from other localities and horizons. The internal moulds are valuable, however, in showing details of shell musculature that are not known in *Pollicina corniculum*.

Pollicina is re-described on the basis of its two most common species: *Pollicina corniculum* from the St Petersburg region of Russia and *Pollicina crassitesta* from Estonia. The latter material preserves muscle scars which promote a discussion of the systematic position of *Pollicina*. The distribution of shell attachment muscles, together with the nature of growth ornamentation in *Pollicina corniculum*, indicate that at least some specimens of *Pollicina* lived as limpets clamped against hard substrates.

Repositories of figured specimens are indicated by the following prefixes: CNIGRM, F. N. Chernyshev Central Geological Survey Research Museum, St Petersburg; ELM, Estonian Museum of Natural History, Tallinn; PSM, Museum of the Department of Historical Geology, St Petersburg State University.

AUTHORSHIP OF *POLLICINA*

Holzapfel (1895, pp. 182–183) attributed authorship of *Pollicina* to 'Koken (in Litt.)' quoting a written communication from Ernst Koken in which the type was designated as *Cyrtolites laevis* Eichwald from the Ordovician of Baltica. In this letter, Koken noted that he had used the name *Pollicina* in a manuscript, and it is reasonable to assume that this was the manuscript of Koken (1897). Eichwald (1842, p. 71) had assigned *Cyrtolites laeve* to *Cyrtoceras laeve* [Sowerby in] Murchison, 1839 which he considered to be a cephalopod. However, Eichwald (1860, p. 1048) recognized that his species was distinct from *Cyrtoceras laeve* Sowerby in Murchison, 1839 (which he referred to as *Cyrtolithes laevis*) and delimited a new species as *Cyrtolithes corniculum*. His description lacked illustrations, referring to Eichwald (1842, pl. 3, figs 5, 6), and he reinterpreted his species as a pteropod related to hyolithids (Eichwald 1860). *Cyrtolithes* is an emendation of *Cyrtolites* Conrad, 1838 common in literature from the late 19th century.

Koken (1897, p. 197) clearly claimed authorship of *Pollicina*, referring to *Pollicina* Koken (in Holzapfel 1895) in his description of the genus. This description was reproduced unchanged in the 1925 monograph *Die Gastropoden des baltischen Untersilurs*. However, the authorship of this work is tainted by uncertainty reflecting
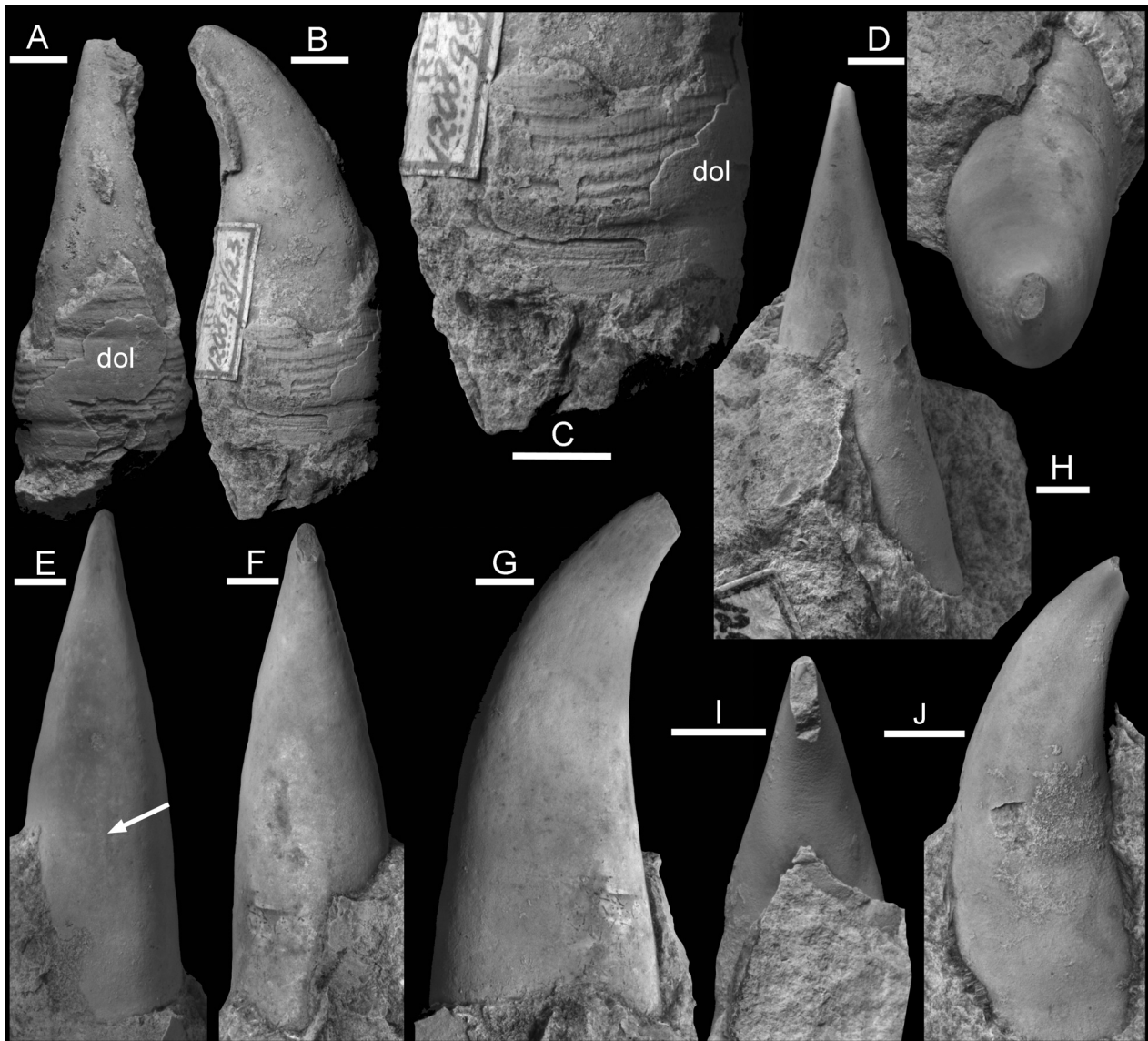
Fig. 2. *Pollicina crassitesta* Koken, 1897. Ordovician, Darriwilian, Kunda Stage, Tallinn, Estonia. **A–C**, ELM g8:23 [1208g8/23], lectotype, internal mould with adherent ornamented shell patches and diagenetic outer layer (dol), Domberg (=Toompea): A, supra-apical surface; B, lateral view; C, detail of lateral surface to show ornamentation. **D–G**, ELM g8:7 [1208g8/7], internal mould lacking apex, Springthal (=Tondi): D, apical view showing elliptical scar after the broken apex; E, supra-apical surface with median spiral trace arrowed; F, sub-apical surface; G, lateral view. **H–J**, ELM g8:22 [1208g8/22], internal mould with broken apex, Springthal (=Tondi): H, supra-apical surface; I, sub-apical surface with elliptical scar after broken apex; J, lateral view. Scale bars = 5 mm.

the degree of editing and collation of several texts carried out by Jaroslav Perner which had been prepared (and in some cases printed) years before by Ernst Koken (1860–1912). Perner also authored supplementary material prepared after Koken's death. New taxa in the monograph are attributed individually both to Koken and Perner but delimitation of their individual contributions is often uncertain. The work has been cited as by Koken alone (Yochelson 1963; Wahlman 1992; Bouchet et al. 2017), as Koken edited by Perner (Knight 1941; Knight et al. 1960) or Koken & Perner together (Wenz 1938; Ebbestad

1999; Isakar & Ebbestad 2000; Evans & Cope 2003; Peel 2019). The last option, as Koken & Perner (1925), is followed here, although acts which are clearly referable to a specific author are noted.

Knight (1941, p. 264, footnote) considered the assignment of authorship of *Pollicina* to Koken by Holzapfel (1895) to be just a matter of courtesy and he regarded therefore Holzapfel (1895) as the author of *Pollicina*. Knight (1941, pl. 5, fig. 2; see also Knight & Yochelson 1960) reproduced Eichwald's (1842) illustration since he was unable to locate the type material of *Pollicina*. Knight's (1941) practice
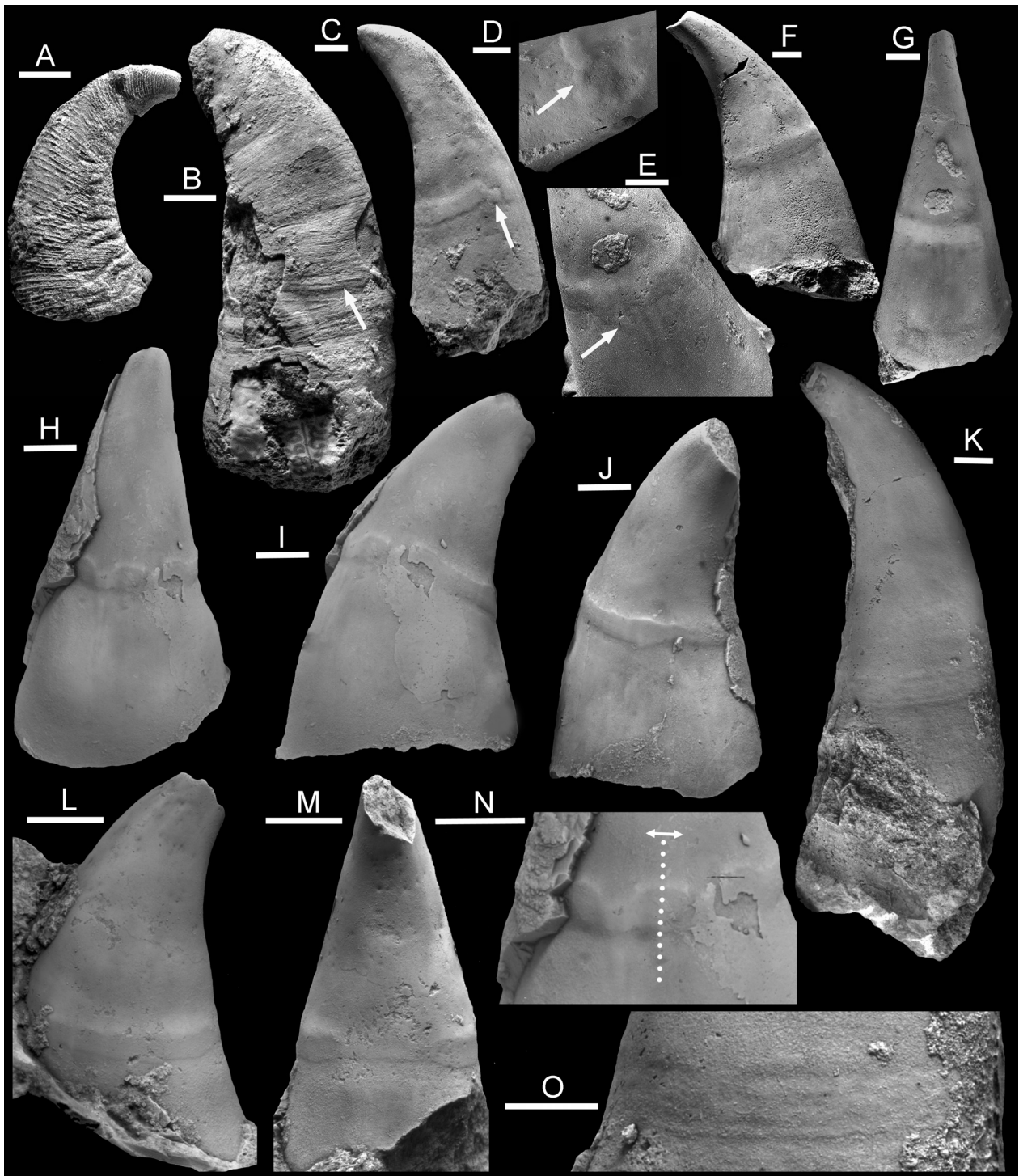
Fig. 3. *Pollicina* Koken in Holzapfel, 1895. Ordovician, Darriwilian, Kunda Stage. **A**, **B**, *Pollicina corniculum* (Eichwald, 1860), Pulkowa (=Pulkovo), St Petersburg, Russia: A, CNIGRM 15702 (200/10903), lateral view with deep scratches resulting from preparation on right side; B, CNIGRM 15703 (201/10903), lateral view showing dislocation of growth lines, arrow. **C–N**, *Pollicina crassitesta* Koken, 1897, internal moulds. **C–D**, CNIGRM 15600 (394/10903), lateral view with small scars arrowed, Laaksberg (=Lasnamägi), Tallinn. **E–G**, CNIGRM 15597 (392/10903), Laaksberg (=Lasnamägi), Tallinn: E, sub-apical surface with median ridge–furrow complex arrowed; F, lateral view; G, supra-apical surface. **H–J**, **N**, ELM g1:2323, Tallinn: H, oblique view of supra-apical surface (see detail in N); I, lateral view; J, oblique view of sub-apical surface; N, detail of muscle band on supra-apical surface with median plane of symmetry indicated. **L**, **M**, ELM G1:2919, Tallinn: L, lateral view; M, sub-apical view. **K**, **O**, *Pollicina* sp., ELM G1:353, internal mould, Estonia, precise locality unknown: K, lateral view; O, detail of muscle band. Scale bars = 5 mm (E–G), otherwise 4 mm.

concerning authorship has been followed by most later authors (Knight & Yochelson 1960; Kisselev 1994; Evans & Cope 2003; Yochelson & Webers 2006). However, Bouchet et al. (2005, 2017) followed Wenz (1938, p. 87) in considering 'Koken (in Holzapfel), 1895' to be the author. This action is followed here, rephrased as *Pollicina* Koken in Holzapfel, 1895.

Perner (in Koken & Perner 1925) repeatedly employed the spelling *Policina*. Yochelson & Webers (2006, p. 25) inadvertently referred to *Pollicinia*.

In the main text of Koken & Perner (1925, p. 325), *Pollicina* is referred to the gastropod 'Family Capulidae', but a footnote authored by Perner (Koken & Perner 1925, p. 227) proposed a new capuliform family, the Family Pollicinidae. In his study of scaphopod-like molluscs, Starobogatov (1974) independently proposed Pollicinidae as a new family within the Order Toxeumorphorida Shimansky, 1962 of the molluscan Class Xenoconchia Shimansky, 1963, although he regarded the xenoconchs as a subclass within the Class Solenoconchia Lacaze-Duthiers, 1857, a little used appellation largely equivalent to Scaphopoda Bronn, 1862 (Peel & Yochelson 1984; Steiner & Kabat 2001). Kisselev (1994) recognized Perner as the author of Pollicinidae but he retained the assignment to Xenoconchia, Toxeumorphorida. Peel & Yochelson (1984) abandoned the Class Xenoconchia and relocated Toxeumorphorida as a third order within the Class Hyolitha Marek, 1963, alongside Hyolithida Syssoiev, 1957 and Orthothecida Marek, 1966, but excluded *Pollicina*. Evans & Cope (2003, p. 145) regarded Starobogatov (1974) as the author of Pollicinidae which they regarded as tergomyan monoplacophoran. Bouchet et al. (2017, p. 194) affirmed 'Perner, 1925 (in Koken)' as the author of the family, rephrased herein as Pollicinidae Perner in Koken & Perner, 1925.

SYSTEMATIC PALAEONTOLOGY

Family POLLICINIDAE Perner in Koken & Perner, 1925
Genus *Pollicina* Koken in Holzapfel, 1895

Type species. Cyrtolithes corniculum Eichwald, 1860 (= *Cyrtoceras laeve* Eichwald, 1842 *non* Sowerby in Murchison, 1839) from the Ordovician (Darriwilian Stage) of the East Baltic. Eichwald's (1860) species *Cyrtolithes corniculum* was formally fixed as type species of *Pollicina* by Bouchet et al. (2017) under the name *Cyrtolites corniculum* Eichwald, 1860, with reference to Article 70.3 of the International Code of Zoological Nomenclature (ICZN 2012), in accordance with earlier usage by Koken (1897), Koken & Perner (1925), Knight

(1941), Knight & Yochelson (1960), Kisselev (1994) and Evans & Cope (2003).

Other species. Koken (1897) and Koken & Perner (1925) described several Ordovician species of *Pollicina*, most of which are based on internal moulds in limestone from Estonia, northwest Russia and Sweden, and from glacial erratics in northern Germany. A revision of the status of all these is not attempted herein, but *Pollicina ampliata* Koken in Koken & Perner, 1925 from the Sandbian at Raasiku (= Rasik), Estonia, is much younger and more rapidly expanding than other species and should be excluded from the genus. *Pollicina conoidea* Koken in Koken & Perner, 1925 was transferred to *Hypseloconus*? *conoidea* by Yochelson (1963) and to *Pygmaeoconus conoideus* by Yochelson (1977). Two other new species, *Pollicina acuta* and *Pollicina brevis*, lack illustrations and Perner in Koken & Perner (1925) commented that he could not locate the original specimens.

Evans & Cope (2003) assigned flattened specimens from the middle Ordovician of the United Kingdom to *Pollicina corniculum*. Tentative identifications of *Pollicina* from the lower Cambrian of Denmark and southern Sweden by Poulsen (1967) and from the middle Cambrian of Australia by Runnegar & Jell (1976) are discounted.

This redescription of *Pollicina* is based on type and additional material of *Pollicina corniculum* from Russia and *Pollicina crassitesta* Koken, 1897 from Estonia.

Diagnosis. Bilaterally symmetrical, slowly expanding cyrtoconic shell which is slightly curved or coiled through up to about 90 degrees; apex blunt, overhanging the sub-apical surface. Aperture orthocline or nearly so, oval to circular in cross section, with its maximum dimension less than half the total height of the shell. Ornamentation of comarginal growth lines that vary from slightly lamellose to fine and even, but may be rugose and with frequent transverse irregularities. Muscle scar is a circum-apertural band located at about half the distance from the apertural margin to the apex.

Discussion. Specimens of *Pollicina corniculum* from Russia and crushed material figured by Evans & Cope (2003) have a bluntly rounded apex but details of the protoconch are not well known, as is the case with most Ordovician limpet-formed shells. Internal moulds of *Pollicina* may be rounded at the apex as a result of apical shell thickening or development of an apical plug. Septation of the most apical part was clearly illustrated by Evans & Cope (2003, text-fig. 4).

In terms of its cyrtoconic shell form, *Pollicina* is similar to several Cambrian (Miaolingian and Furongian) molluscs (Webers et al. 1992; Stinchcomb & Angeli 2002; Yochelson & Webers 2006) often interpreted as

hypseloconidan tergomyans (Peel 1991a, 1991b), but the relationships of many of these univalved shells from the late Cambrian–Ordovician and their classification are equivocal (Yochelson & Webers 2006; Bouchet et al. 2017). Characteristically, the apex in tall, slowly expanding hypseloconidan shells does not overhang the sub-apical margin (Yochelson & Webers 2006, p. 22, fig. 8), as it does in *Pollicina*.

Knightoconus Yochelson, Flower & Webers, 1973, in lateral perspective, has convex and concave surfaces which are superficially similar to the supra-apical and sub-apical surfaces of *Pollicina* but illustrations by Webers & Yochelson (1989) and Webers et al. (1992) indicate that coiling in *Knightoconus* is sigmoidal during ontogeny. Thus, the initially convex supra-apical surface of the juvenile *Knightoconus* becomes concave in later growth stages and is therefore not equivalent in terms of coiling direction to the sub-apical surface of *Pollicina*. The convex surface of the adult *Knightoconus* is derived from the sub-apical surface of the juvenile and not equivalent to the supra-apical surface of *Pollicina*. Juvenile shells are not known from most hypseloconids but their form can be interpreted as in *Knightoconus*. In many, the aperture narrows beneath the convex surface while it is sub-circular in *Pollicina*.

Some specimens originally assigned to *Shelbyoceras* Ulrich & Foerste in Bridge, 1930, especially *Shelbyoceras bessemerense* Ulrich, Foerste & Miller, 1943 from the Cambrian (Furongian Series) of Alabama, which was relocated to *Hypseloconus bessemerense* by Stinchcomb & Echols (1966) and later partly to *Gayneconus* Stinchcomb & Angeli, 2002, also have a cyrtoconic shell. *Shelbyoceras* was first described as a cephalopod but reinterpreted as a septate monoplacophoran mollusc by Stinchcomb (1980). However, most *Shelbyoceras* are more rapidly expanding with prominent comarginal costae on lateral surfaces. The plane of the aperture is orthocline in *Pollicina* such that the apex overhangs the subapical margin. It is oblique in specimens of *Gayneconus bessemerense* (Stinchcomb & Echols 1966; Stinchcomb & Angeli 2002) and in the type species of *Shelbyoceras* illustrated by Stinchcomb (1980), such that the apex does not overhang the subapical margin. In *Shelbyoceras bigpineyensis* Stinchcomb, 1986, from the upper Gasconade Formation of Missouri, the aperture is elliptical, width about two thirds of length, compared to slightly oval or sub-circular in *Pollicina*. Unlike other species of *Shelbyoceras*, septation is restricted to the tip, as in *Pollicina*.

The apertural margin is almost orthocline in *Ulrichoconus* Stinchcomb & Angeli, 2002, a robust, septate shell from the Cambrian (late Miaolingian Series) of Missouri, USA (Stinchcomb & Angeli 2002, figs 2.1–2.3). *Orthoconus* Stinchcomb, 1986, originally described

from the Eminence Formation (Cambrian, Furongian Series) of Missouri, has an elliptical aperture and prominent longitudinal ribs not seen in *Pollicina*. Similar specimens were described from the Cambrian (Furongian Series) of Minnesota by Yochelson & Webers (2006).

In terms of gross form of the tall, slowly expanding shell, *Pollicina* superficially resembles some specimens assigned to the Silurian–Devonian platyceratoidean *Orthonychia* Hall, 1843, not least the type species *Orthonychia subrecta* Hall, 1843 as illustrated by Knight (1941, pl. 88, fig. 5). However, the great majority of the numerous Devonian specimens assigned to *Orthonychia* lack bilateral symmetry and are often irregular and twisted in their later growth (Perner 1903; Frýda et al. 2008, 2009).

Pollicina corniculum (Eichwald, 1860)
Figures 1A–K, 3A, B

1842 *Cyrtoceras laeve* Eichwald, p. 71, pl. 3, figs 5, 6 (non Sowerby in Murchison 1839).
1860 *Cyrtolithes corniculum* Eichwald, p. 1048.
1897 *Pollicina corniculum*, Koken, p. 197.
1925 *Pollicina corniculum*, Koken & Perner, p. 228, pl. 38, figs 8, 12, 13.
1994 *Pollicina corniculum*, Kisselev, p. 36, fig. 1A–F.
2003 *Pollicina corniculum*, Evans & Cope, p. 145, text-fig. 4.

Type material. PSM 4/22 (lectotype; Fig. 1A–H) and PSM 4/23 (paralectotype; Fig. 1I, K) designated by Kisselev (1994). Ordovician, Darriwilian, Kunda Stage. Eichwald (1842) gave the locality as Popowka [Popovka River] but subsequent authors and specimen labels refer to the locality as Pulkowa (Koken 1897; Koken & Perner 1925) or Pulkova, St Petersburg, Russia. Kisselev (1994) and Evans & Cope (2003) refer to Polkovo, the current Russian spelling.

Additional figured material. CNIGRM 15702 (200/10903; Fig. 3A) and CNIGRM 15703 (201/10903; Fig. 3B), specimens illustrated by Koken & Perner (1925). CNIGRM 15692 (380/10903; Fig. 1J). Ordovician, Darriwilian, Kunda Stage, Pulkowa [Pulkovo], St Petersburg.

Other material. More than 10 specimens from Pulkovo, labelled Pulkowa, in the collection of the F. N. Chernyshev Central Geological Survey Research Museum (CNIGRM), St Petersburg, Russia.

Diagnosis. Type species of *Pollicina* in which the slowly expanding cyrtoconic shell is often uniformly curved through 90 degrees (Figs 1A, 3A). Shell thin, but thickening near the aperture; ornamentation of thin comarginal lamellae that are slightly flared and irregular.

Description. The slowly expanding cyrtoconic shell is curved usually through about 90 degrees such that the apex overhangs the sub-apical margin (Fig. 1C). The greatest dimension of the slightly oval aperture in the lectotype (Fig. 1F), lying within the plane of symmetry of the shell, is almost half the total height (Fig. 1A). The shell coil straightens and reduces its rate of expansion in larger specimens, as the aperture is approached, such that the maximum apertural dimension is only about one third of the total height (Fig. 3B). In cross section, the shell is oval even at the earliest preserved stages (Fig. 1D, F, H). The apertural margin is orthocline and may be slightly flared to form irregular rugae in the latest growth stages (Fig. 1G–I). Ornamentation consists of closely spaced, acute, comarginal growth lines which are usually slightly lamellose and irregular (Fig. 3A, B), and may be interrupted by discontinuities (Fig. 1A–C, H, arrow c). In most specimens the shell is thin but the lectotype shows thickening near the aperture (Fig. 1A).

Discussion. The fact that Eichwald (1842) gave the locality as Popowka, and not Pulkowa, as used by Koken (1897) and Koken & Perner (1925), or Pulkovo, as used by Kisselev (1994) and Evans & Cope (2003), casts a measure of doubt on the designation by Kisselev (1994) of the lectotype. Popowka lies a few kilometres to the southeast of Pulkovo, to the south of St Petersburg. However, that specimen (illustrated here as Fig. 1G) agrees closely with the engraving given by Eichwald (1842, pl. 3, fig. 5), so the identification is maintained despite the confusion.

Illustrations of the lectotype and paralectotype of *Pollicina corniculum* given by Kisselev (1994, fig. 1) are accompanied by incorrect scale information in the figure caption. This error was inadvertently perpetuated by Evans & Cope (2003, p. 143). Kisselev (1994) stated that the magnification of the lateral view of the lectotype and paralectotype is × 5, indicating a specimen height of only 9 mm for the lectotype. Measurements of the replicas and scales on photographs supplied by E. L. Yochelson indicate that these specimens are more than twice this size (Fig. 1).

Perception of the form of the shell in illustrations of the lectotype of *Pollicina corniculum* (Fig. 1A–H) is susceptible to differences in orientation and lighting. Thus, the prominent transverse rugae visible near the aperture in recently prepared illustrations of the replica (Fig. 1G, H) are only poorly visible in corresponding illustrations of the lectotype itself prepared by Yochelson (Fig. 1B, C) and Kisselev (1994). Lighting of the supra-apical surface in Fig. 1H is strongly oblique to emphasize the rugae. These appear less marked when the specimen has been rotated slightly and lighting is uniform (Fig. 1B). Corresponding points are indicated by arrows (Fig. 1B, H, arrow a). Figure 1G is illuminated with oblique lighting, and the specimen is oriented oblique to the lateral

surface, with the apex tilted towards the viewer when compared to Fig. 1C; this orientation causes the shell to appear less strongly coiled and more rapidly expanding than in a true lateral view (Fig. 1C). Corresponding points are indicated by arrows (Fig. 1C, G, arrow b). Equivalent rugae are visible in the paralectotype (Kisselev 1994, fig. 1E; Fig. 1I, K).

Prominent comarginal discontinuities in growth are present in the lectotype (Fig. 1A–C, H, arrow c) and specimens in the CNIGRM collection in St Petersburg (Fig. 3B, arrow). Several specimens also show short ridges perpendicular to the growth ornamentation (Fig. 1I, J, arrow r). Minor irregularities in the spacing of the growth lines are numerous but evidence of breakage and repair of the apertural margins has not been observed.

Evans & Cope (2003) attributed several specimens from Darriwilian strata in the United Kingdom to *Pollicina corniculum*. The specimens are crushed in mudrocks, which hinders their precise identification to species, but internal closure of the apex by a transverse septum is seen in some illustrated examples. Evans & Cope (2003) considered the small conical portion of the shell lying adapical of this septum to be a protoconch but details of its morphology are not well known. Septation has not been demonstrated in available specimens of *Pollicina corniculum* from the East Baltic which usually preserve the outer shell, although the apex is often not well preserved. The apex is broken away in most available internal moulds in limestone of *Pollicina* but, unsurprisingly in such a narrow shell, septation, the presence of apical thickening or an apical plug has been widely observed. Koken & Perner (1925, p. 228) recorded but did not illustrate septation in *Pollicina acuta* Koken, 1897 from the Darriwilian of Dalarna, Sweden.

Pollicina crassitesta Koken, 1897
Figures 2A–J, 3C–J, L–N

1897 *Pollicina crassitesta* Koken, p. 198.
1925 *Pollicina crassitesta*; Koken & Perner, p. 229, pl. 38, figs 1–3, 9–10, 11?.

Type material. ELM g8:23 [1208g8/23], here designated lectotype, original of Koken (1897, p. 198), the same specimen illustrated by Koken & Perner (1925, pl. 38, fig. 9; Fig. 2A–C), Domberg (=Toompea), Tallinn. Ordovician, Darriwilian, Kunda Stage, Estonia.

Other figured material. ELM g8:22 [1208g8/22], original of Koken & Perner (1925, pl. 38, fig. 10; Fig. 2H–J), Springthal (=Tondi), Tallinn. ELM g8:7 [1208g8/7], Springthal (=Tondi), Tallinn, original of Koken & Perner (1925, pl. 38, figs 1, 2; Fig. 2D–G). The specimen illustrated as Koken & Perner (1925, pl. 38, fig. 11) has not been identified.

CNIGRM 15597 (392/10903), Laaksberg (=Lasna-mägi), Tallinn. CNIGRM 15600 (394/10903), Laaksberg (=Lasnamägi), Tallinn. ELM g1:2323, Tallinn. ELM g1:2919, Tallinn. Ordovician, Darriwilian, Kunda Stage, Estonia.

Diagnosis. Species of *Pollicina* in which the laterally compressed apex of the internal mould is elongate elliptical in cross section with its long axis on the plane of symmetry. Shell thick; ornamentation of prominent comarginal lamellae and fine growth lines crossed by spiral cords separated by fine grooves.

Description. The slowly expanding, bilaterally symmetrical, cyrtoconic shell is curved usually through about 60 degrees, producing a tall shell in which the apex overhangs the sub-apical margin, although the earliest growth stage is not known. In lateral view (Figs 2G, 3C) the maximum dimension of the aperture, measured in the plane of symmetry, is usually less than half the total height. The cross section of the internal mould is strongly elliptical at the earliest preserved growth stage, its maximum dimension lying within the plane of symmetry of the shell and being twice the width (Fig. 2D, F, I); it becomes proportionately wider, oval, in later growth stages. The apertural margin is orthocline and periodically the outer shell surface may be slightly constricted near the aperture (Fig. 2A–C). Near the aperture, ornamentation of the thick shell consists of relatively broad, flat-topped, comarginal growth lamellae that are separated by narrower U-shaped grooves, both marked with fine growth lines (Fig. 2C); they are crossed by numerous fine spiral cords. Internal moulds are generally smooth, without indications of transverse rugae, although a circum-apertural raised band of muscle scars may be prominent at about half the distance from the apex to the aperture (Fig. 3C, E–I).

Discussion. *Pollicina crassitesta* was illustrated by Koken (1897, p. 198) with a schematic drawing based on the specimen here designated as lectotype (Koken & Perner 1925, pl. 38, fig. 9; Fig. 2A–C). Siegfried (1935, p. 145) listed the figured specimens of Koken & Perner (1925, pl. 38, figs 1–3, 9–11) as paratypes, commenting that one of these specimens should be selected as lectotype. The location of the specimen in figure 11 was not known to Siegfried (1935) and it was not available in the present study. These specimens are not paratypes, since the author of *Pollicina crassitesta* was Koken (1897) and not Koken & Perner (1925). Of the specimens mentioned by Siegfried (1935), only that illustrated by Koken & Perner (1925, pl. 38, fig. 9; Fig. 2A–C) can be demonstrated conclusively to have been part of Koken's (1897) original lot. Koken (1897) did refer, however, to other specimens in his original lot, so the sole illustrated specimen cannot be assumed to be the holotype by monotypy.

Koken (1897) and Koken & Perner (1925) described a thin outer shell layer overlying a strongly ornamented and thicker inner layer as characteristic of *Pollicina crassitesta* and this layer is emphasized in the original sketch (Koken 1897, p. 198). The thin outer layer is clearly visible in the lectotype (Fig. 2A–C, dol) where it covers prominent growth ornamentation and is evidently diagenetic in origin.

Pollicina crassitesta is delimited from most specimens of *Pollicina corniculum* in the F. N. Chernyshev Central Geological Survey Research Museum, St Petersburg, by its uniformly thick shell, although the shell of the lectotype of *Pollicina corniculum* is also relatively thick in its latest growth stages (Fig. 1A). The lateral surfaces are flattened in the earliest preserved growth stages in *Pollicina crassitesta* such that the length of the whorl cross section is about twice the width (Fig. 2D, I) whereas the cross section is almost circular in *Pollicina corniculum*. Spiral cords cross the prominent growth ornamentation in the lectotype of *Pollicina crassitesta* (Fig. 2A–C) but are absent in *Pollicina corniculum*.

MUSCLE SCARS IN *POLLICINA*

Internal moulds of *Pollicina corniculum* with muscle scars have not been identified. The following description is based on internal moulds of *Pollicina crassitesta* collected in Estonia. When preserved, the muscle attachment area forms a raised, rather broad, comarginal band that is most conspicuous on the lateral surfaces but usually can be traced around the sub-apical and supra-apical surfaces (Fig. 3C–J, L–N). In lateral view, the band usually occurs at just below half the height of the internal mould, but variation in the placement of the band in part reflects breakage of the aperture and probably differences in the rate of expansion of the shell cone (compare Fig. 3C, K, L). The band is most weakly expressed near the median plane of the supra-apical surface where it may intersect one or more obscure spiral ridges, the ridge–furrow complex (Fig. 3E, arrow). In lateral view, the band is inclined towards the sub-apical surface (Fig. 3F), corresponding to the inclination of the apertural margin in its current location, and not parallel with the apertural plane of the latest growth stage.

The muscle band in CNIGRM 15597 (392/10903) from Lasnamägi (Fig. 3E–G) is continuous but takes a slight step towards the aperture on the median portion of the supra-apical surface, adjacent to the ridge–furrow complex (arrow in Fig. 3E). The same deflection is apparent in CNIGRM 15600 (394/10903), also from Lasnamägi, where the previously broad band appears to give way to several small scars as the median plane is approached (Fig. 3C, D). Similar displacement is also

evident in ELM g1:2323 from Tallinn (Fig. 3H–J, N) where a slight notch and raised section of the band are visible in the adapical margin of the muscle on each side of the plane of symmetry (Fig. 3N). The muscle attachment scar is also narrower below the apex (Fig. 3J), as in a second specimen from the same locality (Fig. 3M).

The shell in ELM g1:353 (Fig. 3K) is more slowly expanding than other illustrated internal moulds, in which respect it is similar to a figured specimen of *Pollicina corniculum* (Fig. 3B). In contrast to other illustrated muscle scars, the band here is slightly depressed into the surface of the internal mould and its surface is marked with several comarginal grooves and ridges (Fig. 3O). The precise collection locality of this specimen in Estonia is not known, but it is labelled *Pollicina cyathina* Koken, 1897, a species that was originally described from Rättvik, in Dalarna, Sweden. It is here referred to as *Pollicina* sp.

MODE OF LIFE OF *POLLICINA*

The circum-apertural distribution of muscle scars in *Pollicina crassistesta* indicates that it clamped the shell aperture against the substrate when disturbed, invalidating the suggestion by Yochelson & Webers (2006) that it was an open coiled gastropod which would have lain on the sediment surface on its lateral area, with the axis of coiling and plane of the aperture vertical. Peel (2019) described muscle scars in the Ordovician euomphaline gastropods *Asgardaspira* Wagner, 2002 and *Lesuerilla* Koken, 1896 from Baltica which undoubtedly lived with their base on or in the sediment surface and with a vertical axis of coiling in the manner envisaged for *Pollicina* by Yochelson & Webers (2006). In each of these genera, the muscle attachment area is reduced and restricted to the umbilical shoulder of the whorl (Peel 2019), quite unlike the circum-apertural distribution of muscle scars seen in *Pollicina*. Placement of the scars in *Asgardaspira* and *Lesuerilla* more than half a whorl back from the aperture indicates deep withdrawal of the soft parts into the narrow shells. The aperture in *Asgardaspira* and *Lesuerilla* was most probably closed by an operculum but if developed during ontogeny this would have been superfluous in adult *Pollicina*, as in present-day limpets (Vermeij 2017).

Yochelson (in Peel & Yochelson 1984, p. 218) supported interpretation of *Pollicina* as an open coiled gastropod, claiming that coiling in *Pollicina corniculum* deviated slightly from bilateral symmetry. Yochelson (in Yochelson & Webers 2006, p. 25) emphasized this supposed anisostrophy with reference to material from Estonia, exactly the same specimens that are reviewed herein. However, these specimens and material from Estonia in the F. N. Chernyshev Central Geological Survey Research Museum

(CNIGRM), St Petersburg, do not show the asymmetry that Yochelson & Webers (2006) cited.

The interpreted limpet-formed mode of life of *Pollicina* is supported by the frequent displacement of the apertural margin witnessed by disturbances in growth lines and the periodic development of transverse rugae in specimens of *Pollicina corniculum* (Fig. 1A, H–K, 3B). Similar displacements appear to be present in crushed specimens assigned to *Pollicina corniculum* from the Ordovician of the United Kingdom by Evans & Cope (2003) but specimens of other species described by Koken (1897) and Koken & Perner (1925) are mainly internal moulds lacking information concerning the outer surface of the shell. Apart from infrequent minor chipping, the displacements in *Pollicina corniculum* from Pulkovo do not show penetrative scars and repaired injuries which could be attributed to physical breakage or failed predatory attacks (Ebbestad & Peel 1997; Alexander & Dietl 2003; Lindström & Peel 2005; Ebbestad et al. 2009). They reflect re-positioning of the shell aperture against a hard substrate, as is common in many platyceratid gastropods (Perner 1903; Bowsher 1955; Rollins & Brezinski 1988; Boucot 1990; Horný 2000; Gahn & Baumiller 2003; Frýda et al. 2008). Many of these platyceratids also show longitudinal ridges or folds as a result of their accomodation of irregularities in the surface to which they attach. Ridges of this kind are present also in some specimens of *Pollicina corniculum* (arrows in Fig. 1I, J). Clearly, this is not to imply that the isostrophic *Pollicina* is related to anisostrophic platyceratid gastropods (Frýda et al. 2009), although its placement together with platyceratids by Koken (1897) and Koken (in Koken & Perner 1925) is possibly indicative of his views concerning its mode of life. Not least, the muscle scar patterns of the two groups are usually quite different (Horný 1964; Mazaev 1996; Frýda et al. 2008), although U-shaped muscle scars have been described in tall, slowly expanding, specimens of *Orthonychia* by Rollins & Brezinski (1988). Neither is there any supporting evidence that *Pollicina corniculum* enjoyed a symbiotic relationship with echinoderms, as is the case with many platyceratids from the Ordovician to Permian (Bowsher 1955; Rollins & Brezinski 1988; Boucot 1990; Gahn & Baumiller 2003), although platyceratids may be associated with hard substrates other than echinoderms (Horný 2000).

Stinchcomb (1975) and Stinchcomb & Angeli (2002) noted the correlation of hypseloconids with digitate stromatolites in shallow water carbonates of Cambrian–Ordovician boundary strata in Missouri, although the septate *Shelbyoceras* was not associated with stromatolites. Taking into account the tallness of the shells relative to the small size of the foot, it seems that the stromatolite buildups may have offered sheltered living sites, at least in comparison to the high energy patellid-dominated rocky

shore environments of the present day. However, Vermeij (2017) has pointed out that these familiar patellid communities of middle latitudes represent an adaptation to resist predation and that many limpets occur in less dynamic settings. Yochelson & Webers (2006) cast doubt on the stability of the limpet interpretation of the slender *Pollicina* shell in their striving to find evidence of anisostrophism.

It is clear that the slender shell form of *Pollicina* is not characteristic of limpets at the present day or through geological time, although numerous univalves in just the late Cambrian–early Ordovician approach such a form (Stinchcomb & Echols 1966; Stinchcomb 1980; Webers & Yochelson 1989; Webers et al. 1992; Stinchcomb & Angeli 2002; Yochelson & Webers 2006). A loose parallel can be drawn with the widespread development of irregular, tall, clamping shells of *Orthonychia* amongst the platyceratoidean gastropods in certain mainly Devonian environments (Perner 1903; Frýda et al. 2008, 2009).

SYSTEMATIC POSITION OF *POLLICINA*

Opinions that *Pollicina* was a cephalopod (Eichwald 1842), hyolith or toxeumorphorid xenoconch (Eichwald 1860; Starobogatov 1974; Kisselev 1994) are readily rejected, as discussed in part by Evans & Cope (2003). In reviewing Yochelson's suggestion (in Peel & Yochelson 1984) that *Pollicina* was an open coiled gastropod, Evans & Cope (2003) inferred a lack of the characteristic gastropod anisostrophic coiling in the crushed material that they assigned to *Pollicina*. Furthermore, they considered that the blunt apex indicated a protoconch much larger than that of gastropods, without any suggestion of torsion (Evans & Cope 2003). Yochelson & Webers (2006) did not respond to the comments of Evans & Cope (2003) but restated the open coiled gastropod hypothesis. Evidence concerning the nature of the protoconch of *Pollicina* is currently inconclusive. However, the present paper discounts the shell anisostrophism claimed by Yochelson & Webers (2006) and describes muscle scar patterns indicative of a limpet-formed mode of life. Thus, their interpretation of *Pollicina* as an open coiled gastropod, lying on its side in the manner of euomphaloideans, is rejected.

The issue of preserved muscle scars in hypseloconid tergomyans is controversial and most relevant material is poorly preserved. Yochelson & Webers (2006) reviewed various studies but were generally negative to claims of serially arranged scars, although such were described by Stinchcomb (1980). Dzik (2010) presented a provocative analysis of Ordovician shells with serially arranged muscle scars, but none resemble *Pollicina*.

Evans & Cope (2003) did not make close comparison with limpet-formed lower Palaeozoic supposed gastropods, such as *Archinacella* Ulrich & Scofield 1897 or *Floripatella* Yochelson, 1988. They presented a detailed comparison of *Pollicina* with hypseloconid tergomyans (Peel 1991a, 1991b), but preferred assignment to the cyrtonellid tergomyans on the basis of general shell form. It is relevant to note here that Parkhaev (in Bouchet et al. 2017) distributed cyrtonellids *sensu* Peel (1991a, 1991b) between three subclasses of untorted molluscs. The arguments presented by Evans & Cope (2003) are well founded, although it should be remembered that many of the molluscs described by Stinchcomb (1980), Stinchcomb & Echols (1966), Stinchcomb & Angeli (2002) and Yochelson & Webers (2006) are poorly known with regard to their ontogeny and muscle scars.

Cyrtolites, as described by Horný (1965a, 1965b) from the Middle Ordovician of Canada, is regularly coiled through several whorls, unlike the cyrtoconic *Pollicina*, and its shell has a greater rate of whorl expansion. Discrete paired muscle scars are distributed in a broad belt across the supra-apical surface and continue as a ribbon-like band beneath the apex on the sub-apical surface (Horný 1965a; Fig. 4A). The pattern is diffuse when
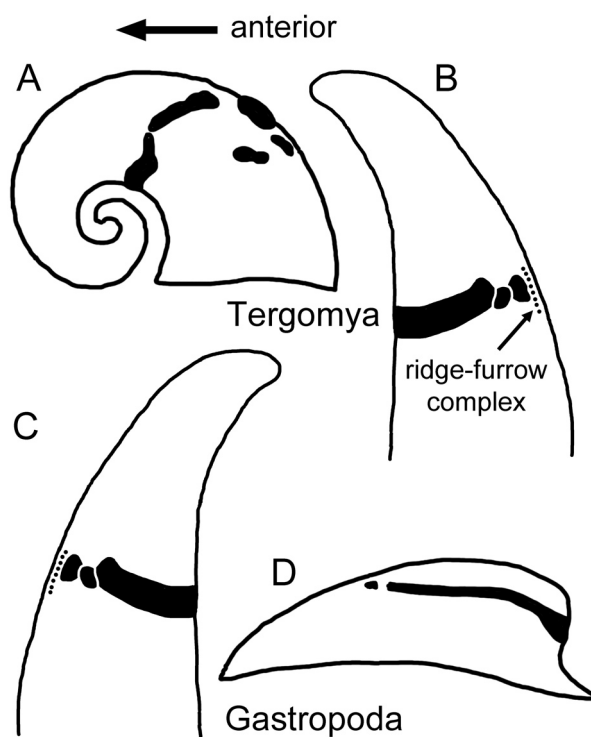

Fig. 4. Muscle scar patterns in Ordovician univalve molluscs. *Cyrtolites* (**A**) and *Pollicina* (**B**) intepreted as Tergomya. *Pollicina* (**C**) and *Archinacella* (**D**) interpreted as Gastropoda.

compared to the circum-apertural muscle band in *Pollicina crassitesta* (Fig. 3C, H, L). However, as noted by Bandel (1982), Harper & Rollins (1982, 2000), Peel (1991a, 1991b) and others, the distribution of muscle scars in cap-shaped molluscs is largely a reflection of their function. Thus, the compact circum-apertural muscle scar of *Pollicina* may result from consolidation of more widely dispersed muscle attachment sites such as those seen in *Cyrtolites*, reflecting the specific mechanical requirements of clamping the tall, narrow shell perpendicularly against its substrate. Points of similarity include the differentiation of scars on the supra-apical surface, immediately to either side of the median ridge–furrow complex in *Pollicina* (Fig. 3C, E) and in cyrtonellids (Horný 1965b, figs 2, 5).

The muscle scar pattern in *Sinuitopsis acutilira* Hall, 1861 from the Devonian of New York State, USA (Rollins & Batten 1968, text-fig. 1) is more consolidated than the widespread pattern in *Cyrtolites*. Thus, it more closely resembles the pattern seen in *Pollicina* in that elongate lateral and latero-ventral scars form a more or less continuous U-shaped band passing beneath the overhanging apex. A pair of dorsal scars and the median ridge–furrow complex lie between the prongs of the U-shape, reminiscent of *Pollicina crassistesta* (Fig. 3C–E), although the dorsal scars in the latter are smaller and less strongly delimited.

Horný (1965a) introduced the Subclass Cyclomya for untorted univalves in which the muscle scars formed a more or less continuous belt around the apex, including the cyrtonellids and a group of spoon-shaped shells based on *Archinacella* Ulrich & Scofield, 1897. A variety of arguments have been proposed by Harper & Rollins (1982, 2000), Peel (1990, 1991a, 1991b) and Haszprunar (2008) for abandoning the Cyclomya as a formal group but *Pollicina* may be compared meaningfully in terms of its muscle scar passing beneath the overhanging apex with archinacelloids (Fig. 4C, D).

The musculature and systematic position of *Archinacella* as a gastropod were discussed by Golikov & Starobogatov (1975), Peel (1990, 1991a, 1991b) and Peel & Horný (1999), although it was considered as a monoplacophoran mollusc by others (Knight 1952; Knight & Yochelson 1960; Runnegar & Jell 1976; Wahlman 1992) and to be a mollusc of uncertain position by Bouchet et al. (2017). As in *Pollicina*, the muscle band passes beneath the apex and across the lateral area, but it often fades as it crosses the supra-apical surface. Archinacelloids differ in having low, spoon-shaped, shells rather than the tall, cyrtoconic shell of *Pollicina*. In this respect they are similar in shape to the Carboniferous gastropod *Lepetopsis* Whitfield, 1882 but also to tergomyans such as *Tryblidium* and *Pilina* (Lindström 1880, 1884; Knight 1941). The cyrtoconic shell form of

Pollicina is not seen in other putative gastropod limpets from the Palaeozoic to the present day, although it was present in some late Cambrian–middle Ordovician tergomyan groups (Stinchcomb & Echols 1966; Stinchcomb 1980; Webers & Yochelson 1989; Webers et al. 1992; Stinchcomb & Angeli 2002).

Archinacella and its near relatives are not the only Ordovician cap-shaped fossils that have been interpreted as gastropods (Ulrich & Scofield 1897; Koken & Perner 1925; Horný 1963, 1997; Yochelson 1988, 1994). In older literature (e.g. Billings 1861–1865, see Bassler 1915), many were referred to *Metoptoma* Phillips, 1836, which was originally described from the Carboniferous and interpreted as a gastropod by Knight et al. (1960), while *Archinacella* was interpreted in the same volume as a monoplacophoran mollusc (Knight & Yochelson 1960). Starobogatov & Mazaev (1999) transferred *Metoptoma* to the archinacelloids. Bouchet et al. (2017) regarded metoptomatids and archinacelloideans as Palaeozoic molluscs of uncertain position within Mollusca (Gastropoda or Monoplacophora).

Yochelson (1988) described *Floripatella* from the Kanosh Shale (Ordovician, Dapingian–Darriwilian) of Utah as the oldest known patelloidean gastropod, although Lindberg (2008, 2009) and Vermeij (2017) considered it to be a monoplacophoran mollusc. The holotype within a highly variable sample described by Yochelson (1988) displays a well-preserved muscle scar (Yochelson 1988, fig. 1.4; Peel & Horný 1999, fig. 14; Lindberg 2009, fig. 6) that forms a strongly defined U-shape on the lateral and supra-apical surfaces and a more weakly differentiated band with subsidiary scars across the sub-apical surface. The form of the muscle scar is not unlike that known in *Pollicina crassitesta* (Fig. 3C–J, L–N) or some archinacelloids but the height of the shell in the latter is almost three times its length compared to about one quarter in *Floripatella* (Yochelson 1988, fig. 4.3). Additionally, the apex lies slightly closer to the supra-apical margin in *Floripatella*, in similar fashion to many patellids, whereas it overhangs the sub-apical margin in *Pollicina*.

Peel & Horný (1999) and Starobogatov & Mazaev (1999) transferred *Floripatella* to the Family Damilinidae Horný, 1961. Damilinids were considered to be typical patellids by Horný (1963, 2002) and were classified as lottioiden patellogastropods by Bouchet et al. (2017). In *Damilina* Horný, 1961, as described by Horný (1963), the apex is displaced anteriorly from its posterior marginal position in *Archinacella* and *Lepetopsis*. Unusually, the U-shaped muscle band in *Damilina* is broken into numerous segments by radial blood vessels, a feature of some extant patellids noted already by Lindström (1884, pl. 1, fig. 32) in his description of the tergomyan *Tryblidium* from the Silurian of Gotland, Sweden. This

repeated bundling of muscle fibres has not been seen in *Pollicina crassitexta*, although some separation within the scar may occur on the supra-apical surface (Fig. 3C–E). Variation in the degree of bundling in extant patellids was a major argument proposed by Harper & Rollins (2000) for discriminating between tergomyan and cyclomyan muscle patterns in Palaeozoic univalves, but many scars in Palaeozoic material are sharply defined and evidence of bundling is wanting.

CONCLUSIONS

The combination of a bilaterally symmetrical shell with circum-apertural musculature, comarginal rugae and evidence of frequent repositioning of the apertural margin indicates that at least some species of *Pollicina* lived as limpets clamping against a hard substrate. The slender shell and relatively small size of the foot suggest a low energy habitat and available specimens with preserved growth lines lack substantial evidence of physical or biological breakage of the apertural margin. Suggestions that *Pollicina* lived as an open coiled gastropod (Yochelson & Webers 2006), lying on its lateral area, are rejected.

Placement of *Pollicina* within molluscan classification is equivocal. Acquisition of the unusually tall and slowly expanding shell, and the interpreted limpet mode of life would have modified the muscle attachment field from the dispersed patterns widely (but no doubt simplistically) considered to be characteristic of tergomyans (Peel 1991b). On the other hand, a muscle scar pattern of archinacelloid type would remain largely unchanged despite the changes in shell morphology. The substantial change in shell shape from the elongate, spoon-shape of *Archinacella* to the tall, narrow cone of *Pollicina* is commensurate with a transition from a mobile habit in *Archinacella* to the limpet life style of *Pollicina*. Parallels can be drawn to the development of uncoiled sedentary *Orthonychia* within the usually tightly coiled and often mobile platyceratoideans.

While the apex in *Pollicina* is blunt, there is a lack of conclusive evidence concerning the protoconch and earliest growth stages, but this is bilaterally symmetrical even in modern patellogastropod limpets considered to have been derived from anisotrophic ancestors. The protoconch issue is further complicated in *Pollicina* by septation (Evans & Cope 2003) and internal thickening of the shell at the apex.

The frequent development of tall, slender, shells in the inner cratonic late Cambrian–Ordovician carbonate successions of Laurentia supports assignment of *Pollicina* to the Class Tergomya, with the curvature of the shell indicating similarity to cyrtonellids rather than hypseloconids in the usage of Peel (1991a, 1991b). This is the interpretation

favoured by Evans & Cope (2003). However, these morphologies are exotic in the context of Baltica, which together with the nature of the muscle bands favours a relationship to *Archinacella*. Ironically, as noted above, the placement of *Archinacella* within Mollusca is also controversial, but opinions expressed by Peel (1990, 1991a, 1991b) and Peel & Horný (1999) that it is a superfamily of gastropods (but not patellogastropods) are maintained. The Family Pollinicidae Perner in Koken & Perner, 1925 is therefore placed within the Superfamily Archinacelloidea, established on the basis of the Family Archinacellidae Knight, 1952.

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Baltika Ordoviitsiumi molluski *Pollicina* lihaste kinnitusjäljed, eluviis ja süstemaatika

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Pollicina on iseloomuliku ühepoolmelise kojaga, kuid harva esinev molluskite perekond, mida esmakordselt kirjeldati Balti regiooni Kesk-Ordoviitsiumist (Darriwili lade). Tema sihvakas, bilateraal-sümmeetriline koda laieneb aeglaselt ja on kõverdatud kuni 90-kraadise nurga all, kuid sirgeneb viimastes kasvufaasides. Artiklis on uuesti kirjeldatud Peterburi regioonist pärit perekonna tüüpliiki *Pollicina corniculum* ja Põhja-Eestis Tallinna piirkonnas levinud liiki *Pollicina crassitesta*. *P. crassitesta* lihaste kinnitusjäljed moodustavad valatisena säilinud kivististel pideva ümmarguse rea koja tipu ja ava vahel. Koja sümmeetria, ortokliiniline ava, lihaste kinnitusjäljed ja ava serva sagedane nihkumine, mida tõendavad kasvujoonte dislokatsioonid, näitavad, et *Pollicina* elas substraadi vastu klammerdunult nagu mereliud. Artiklis on ümber lükatud varasem arvamus, et tegemist oli settel lebava vähe keerdunud gastropoodiga. Nagu enamiku Ordoviitsiumi mereliualaadsete fossiilide puhul, ei ole ka *Pollicina* süstemaatiline kuuluvus klassi Tergomya või klassi Gastropoda ühemõtteline. Vaatamata sarnasustele perekonnaga *Cyrtolites*, paigutatakse antud töös *Pollicina* siiski gastropoodide hulka koos sugukonna Archinacellidae esindajatega.